THE PROBLEM OF LAND CONNECTIONS ACROSS THE SOUTH ATLANTIC, WITH SPECIAL REFERENCE TO THE MESOZOIC

ERNST MAYR (EDITOR), MAURICE EWING, WALTER H. BUCHER, KENNETH E. CASTER, CARL O. DUNBAR, MARSHALL KAY, GEORGE GAYLORD SIMPSON, DANIEL I. AXELROD, THEODOR JUST, WENDELL H. CAMP, P. J. DARLINGTON, JR., ALFRED E. EMERSON, BOBB SCHAEFFER, DAVID H. DUNKLE, EDWIN H. COLBERT, AND ALFRED S. ROMER

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PROCEEDINGS OF THE SYMPOSIUM ON "THE ROLE OF THE SOUTH ATLANTIC BASIN IN BIOGEOGRAPHY AND EVOLUTION," HELD AT THE FOURTH ANNUAL MEETING OF THE SOCIETY FOR THE STUDY OF EVOLUTION, NEW YORK CITY, DECEMBER 28 AND 29, 1949

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INTRODUCTION

ERNST MAYR

Chairman of the Symposium
The American Museum of Natural History

THE EVOLUTION OF FAUNAS and floras is one of the great problems in the field of evolution. It is not a problem that the biologist alone can solve; he needs the assistance of the geologist, because the history of faunas is intimately connected with the history of the continents. The geologist in turn uses the distributional evidence as one of his major sources for clues when reconstructing the face of the earth in past ages.

The outstanding unsolved problem in historical biogeography is whether the southern continents have received all their faunistic and floristic elements from the north or have been at times in direct contact with each other; furthermore, in case such a contact existed, whether it was effected by land bridges or by continuity, subsequently broken by continental drift.

The problem is an old one, but so many new facts have come to light within recent years that a fresh attack seems overdue. The Society for the Study of Evolution seems an ideal organization to undertake such an attack, because it has in its ranks representatives of all the sciences interested in this problem. It was, therefore, a happy thought of Dr. Newell to organize a symposium on the general subject of the biotas of the southern continents. However, it seemed advisable to provide an even more concrete foundation of the discussion and to restrict this broad subject in space and time. This is the reason why it was agreed to concentrate in this Symposium on the history of South America during the Mesozoic and on the possibility of trans-Atlantic connections with Africa. The reason for emphasis on the Mesozoic is that the biogeographic evidence against Tertiary trans-Atlantic connections is sufficiently overwhelming to make it seem unprofitable to pursue the subject further. For the Mesozoic, however, the evidence is ambiguous, and the time seems opportune for a more thorough analysis.

In the field of biology there are essentially two types of problems. One deals with functional phenomena and is open to experiment. The other deals with phenomena that are, in the broadest meaning of this term, historical. This type of problem, although no less interesting or important, can be solved only through the proper interpretation of observed data, and in such cases it is impossible to avoid subjectivity. This is fully borne out by the history of the problem that is the subject of this Symposium.

To evaluate the history of the South Atlantic basin in terms of biogeography and evolution requires a well-balanced integration of data from various subdivisions of geology and of biology. However, such a well-balanced treatment has been conspicuously lacking in the past. Biogeographers have too often constructed land bridges or pushed continents all over the map to explain the puzzling distribution of merely a few species. Geologists, in turn, have been too eager sometimes to accept such uncritical biogeographical evidence. Often, there has been a strange neglect of chronology. A biologist recently used post-Pleistocene and Mesozoic distributions as mutually reënforcing proof for continental drift in the North Atlantic area. It is our endeavor to avoid such methodological errors. This Symposium was not organized to prove a certain theory or to disprove another. Rather it was organized to permit the presentation of the full evidence on certain phases of an important scientific problem to be followed by an open-minded discussion of these data.

I wish to express our thanks to Dr. Norman D. Newell for organizing this Symposium. He began the preparations in 1948 and spared no labor to insure a carefully organized and well-balanced program. The success of the Symposium is owing to his efforts.

THE ATLANTIC OCEAN BASIN

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A CURSORY READING of the literature prior to 1950 makes one immediately aware of the wide divergence of opinion with regard to the interpretation of the geophysical facts concerning the ocean basins. Even so fundamental a question as the existence of sialic layers under the oceans, for example, was in doubt.

Fortunately recent geophysical investigations have provided evidence sufficient to allow us to construct a picture of crustal structure beneath the ocean basins, and to explain the reasons for the earlier lack of agreement.

For the first time, direct measurement of the velocity of elastic waves in basement rocks beneath the Atlantic Ocean basin were made (Ewing *et al.*, 1950), using seismic refraction methods. Elastic waves generated by explosive charges near the water surface were transmitted through the water, sediments, and hard rock layers. The travel time of these waves was obtained by recording the times of arrival with sensitive hydrophones also placed near the surface at a series of distances from the shot point.

The travel times depend on the paths followed by the waves and the speed of the waves through the various layers. Analysis of travel time curves enables one to obtain the thickness of the layers and to infer something of the elastic properties of the material traversed. With the use of these techniques, a "seismic section" of the ocean floor at a point 120 miles northwest of Bermuda was found to consist of a layer of unconsolidated sediments 1.37 kilometers thick underlain by simatic rock. The remarkable feature of this measurement was the absence of sialic material and the close proximity to the ocean floor of rocks known to occur at depths of several ten's of kilometers beneath the continents. If this refraction measurement is representative of ocean-wide conditions, it conflicts with the concept of crustal layering beneath oceans inferred from previous studies of surface waves of earthquakes.

The largest motions appearing on the seismograms of distant earthquakes are associated with the two types of surface waves: Rayleigh waves and Love waves. The passage of a Rayleigh wave is accompanied by retrograde motion of a rock particle in a vertical elliptical orbit, the plane of the ellipse lying in the direction of propagation and the amplitude of particle motion decreasing rapidly with depth. Rayleigh waves are somewhat modified by propagation through a layered crust. The longer waves penetrate to greater depths in the crust and therefore propagate with a velocity determined by the average rate in the entire disturbed zone. A shorter wave therefore propagates at the lower velocity appropriate to the upper crustal layers. Love waves (or surface shear waves) are characterized by particle motion in the horizontal direction at right angles to the direction of propagation. These waves are dispersed in a manner similar to Rayleigh waves in that the longer waves penetrate more deeply and propagate with higher velocity. Since the dispersion of surface waves depends on the thickness and elastic wave velocities of crustal layers, analysis of dispersion on seismograms becomes a powerful tool for determining the nature of these layers between the epicenter and the seismograph station.

Conclusions of seismologists vary concerning the thickness of continental layers using surface wave dispersion as well as compressional and shear wave travel time curves from near earthquakes. It is generally believed, however, that the continental sequence from the surface to the bottom of the crust consists of about 10 to 20 kilometers of granite underlain by an intermediate layer 10 to 20 kilometers thick, below which lies the heavy simatic material of the earth's rock mantle.

Crustal structure under the oceans poses a

more difficult problem. Until recently, most determinations were made by studies of surface wave dispersion.

From studies of the dispersion of Love waves and Rayleigh waves, Gutenberg and Richter (1936) concluded that the Atlantic and Indian oceans are underlain by sialic rocks in marked contrast to the "simatic" Pacific Ocean. Bullen (1939) and De Lisle (1941) discussed the propagation of Rayleigh waves across the Pacific and concluded that a sialic layer with thickness ranging from 6 to 20 kilometers was indicated. Wilson (1940) observed almost negligible dispersion of Love waves crossing Atlantic and Pacific paths and concluded that sialic layers of significant thickness cannot be continuous under the oceans.

Confronted with these divergent views and with the results of the direct refraction measurement in mind, Ewing and Press (1950) reexamined the question of Rayleigh wave dispersion. They found that none of the earlier investigations had taken proper account of the effect upon suboceanic Rayleigh waves of a layer of water and sediments having a combined thickness of about 5.5 kilometers. Some investigators studied surface wave dispersion from "oceanic" earthquakes for which sizable portions of the propagation paths traversed shallow water and land.

It was demonstrated that observed dispersion of Rayleigh waves across the Atlantic and Pacific oceans could be accounted for by considering the propagation of such waves through a system consisting of water and unconsolidated sediments overlying simatic rocks. No significant differences in the nature of the sub-oceanic basement of the Atlantic and Pacific were found.

Moreover, since the water cannot transmit shear waves, the propagation of Love waves (i.e., surface shear waves) across oceanic paths should introduce far less dispersion than that for Rayleigh waves, if the Rayleigh wave dispersion is due to the influence of the ocean and not to crustal layering. This is in agreement with Wilson's observations.

Thus the oceanic crustal structure deduced from the single refraction measurement is compatible with results obtained from the new interpretation of surface waves of earthquakes. Crustal structure beneath the oceans is shown to be remarkably simple, in marked contrast to the layered crust of the continents.[1] The major ocean basins are essentially devoid of the rocks which form the first 40 kilometers of the continents.

One of the major difficulties in the concept of "permanence of ocean basins" has been the supposed existence of "sialic" and "simatic" ocean basins (Umbgrove, 1947). This obstacle is now removed. The fundamental contrast between the complex crust of the continents and the simple crust underlying the major ocean basins, along with the inconsistencies inherent in theories of continental drift (discussed in the section by Bucher), strongly favors permanent ocean basins as primitive features of the crust dating back to the early history of the earth.

Now let us consider the picture presented by the gravity data.

The International Formula for Gravity is the formula adopted internationally for the acceleration of gravity on a spheroid of the mean dimensions of the earth, which has the same mass and moment of inertia as the earth. This earth model has the mass of each spheroidal shell distributed uniformly throughout the shell.

A calculated gravity value for a given station is found by taking the gravity value found for the latitude of the station from the international formula, correcting for the elevation of that station above sea level (the increased distance from the attracting spheroid), and adding the attraction of the known masses of the true earth which extend above sea level and subtracting for the known masses of the true earth which are lacking below sea level (these are usually the known differences of mass between sea water and normal crust). A normal crustal density of 2.67 is usually used for these masses. The difference between the observed value of gravity for the station and the value calculated by the above method is called a Bouguer gravity anomaly. There is a small discrepancy between sea level and the spheroid of reference, which is considered in the calculation, but for the present purposes this effect need not be discussed. The Bouguer gravity

[1] It is probable that some layering exists in the simatic rocks beneath the ocean, with only slight elastic contrasts between the layers.

anomaly then shows the excesses and deficiencies of density within the crust.

The Bouguer anomalies in the oceanic areas are strongly positive, on land areas with elevations close to sea level are almost zero, and in mountainous regions are strongly negative. This then means that the crust is more dense under the oceans and less dense under mountains than a crust of sea level elevation. This leads to the first important conclusion, that the crust underlying the oceans is more dense than the crust under continents.

As a result of this conclusion the concept of isostasy has been developed. This concept is that the crust is in floating equilibrium, or, stated another way, that the mass of each column of the earth's crust of the same area, including the topography of that area, is a constant. There has been considerable argument among geodesists about the distribution of the "compensating masses" within the crust, and there appears to be no conclusion to this argument in the near future. It is sufficient for our present purposes to state that the isostatic anomalies are the difference between the observed gravity value and the value calculated according to a particular theory of isostasy. If the isostatic theory were absolutely correct, the isostatic anomalies would be zero at all points over the earth's surface. The observed isostatic anomalies are very much smaller than the Bouguer anomalies, and the areas of large isostatic anomalies are very restricted in size and number. In the areas of large isostatic anomalies, all of the theories of isostasy show almost the same size anomalies, so that a choice of theories cannot eliminate the major anomalies. This then leads to the second fundamental conclusion, that the earth's crust, with the exception of a few small areas, is almost in perfect isostatic equilibrium.

There are two types of isostatic equilibrium usually discussed, local and regional. Local isostatic equilibrium means that the crust has no strength and that isostatic equilibrium exists for any size area, no matter how small. Regional isostatic equilibrium means that the crust has some strength and that an excess (or deficiency) of mass above (or below) sea level is supported regionally, i.e., by an area surrounding this excess (or deficiency) of mass. Local isostatic equilibrium appears to predominate in some localities and regional isostatic equilibrium in others.

Major summaries of world-wide gravity data are given by Heiskanen (1939), F. A. Vening Meinesz (1948), R. A. Daly (1940), and G. P. Woollard (1949). The data are as yet scanty, particularly in the oceanic areas. The ensuing discussion summarizes the existing data.

1. With the omission of all local detail, the over-all distribution of gravity can be outlined as follows:

There is one profile across the Pacific Ocean from San Francisco to the Philippines. This profile shows very slight deviation from a zero isostatic anomaly, except from Guam to the Philippines where there is a small positive isostatic anomaly.

Over the North American continent there is almost a zero isostatic anomaly.

There are six profiles across, or almost across, the Atlantic Ocean. The North Atlantic profiles show small positive isostatic anomalies, the South Atlantic profiles show slight negative isostatic anomalies, and the equatorial Atlantic profiles show almost zero isostatic anomalies. There are no appreciable differences between the east and west sides of the Atlantic.

In central and eastern Europe the mean isostatic anomalies are slightly positive.

In east Africa the isostatic anomalies are almost zero.

In Siberia the isostatic anomalies are almost zero.

In India the isostatic anomalies are slightly negative.

In the Indian Ocean there are two profiles. The northerly one, crossing almost at the latitude of the southern tip of India, shows small negative isostatic anomalies, while the southerly fragmentary profile, crossing approximately at the latitude of Madagascar, shows slightly positive isostatic anomalies. There are no appreciable differences between the east and west ends of these profiles.

2. Of significant major deviations from the general gravity distribution the following deserve mention:

There are large positive and negative isostatic anomalies in narrow bands associated with the island arcs of the East Indies in

the Pacific and the West Indies in the Atlantic.

The 18 crossings of the continental margins show local isostatic compensation with two exceptions, the Virginia coast and the coast of Brazil near Rio de Janeiro. These coasts show regional compensation with a great radius of regionality.

Concerning volcanic islands, Vening Meinesz comes to the conclusion that "for the Hawaiian Archipelago, for Madeira, for St. Vincent (Cape Verde Islands), for the Bermudas, for the Canary Islands and for Mauritius the gravity data point to regional isostatic compensation distributed over a large area, viz., up to a radius of 170–240 kms. This makes it probable that a rigid crust is present in those areas of a thickness of 25–45 km. For the Azores, and perhaps for Tristan da Cunha local isostatic compensation seems to prevail: for the Azores this may perhaps be explained by the presence of fault-planes in the crust" (Vening Meinesz, 1948, p. 107).

The conclusions that one must draw from these facts are that the gravity data show no discernible difference between the Atlantic, Indian, or Pacific oceans, that there is no discernible difference between the east side and the west side of the Atlantic Ocean and the Indian Ocean, and that there is no discernible difference between the west coast and the east coast of the United States. The isostatic balance of the crust in the various oceans appears to be about equally well adjusted, and the crustal strength and reaction to volcanic island loads appears to be quite similar. Island arc structures and associated gravity anomaly strips are found in almost identical relationships in the Western Pacific and the Western Atlantic.

Insofar as present gravity data are concerned, then, continental drift would have had to be completed at such a remote period that isostatic equilibrium could have been reëstablished by now, or a more rapid recovery of the isostatic equilibrium of the crust must be postulated than seems reasonable.

There is no evidence in the existing gravity data of foundered land bridges in the deep ocean basins unless these parts of the dense oceanic crusts were held up out of isostatic equilibrium and foundered to establish isostatic equilibrium. There is no present evidence that the crust can be maintained more than 2 or 3 kilometers from a position of equilibrium, as such a hypothesis would require.

The conceivable hypothesis that land bridges of continental crustal densities in isostatic equilibrium are converted to oceanic crustal densities in isostatic equilibrium has no support in geologic processes or even in hypothetical geologic processes. If land bridges existed, then, they must be sought in the oceanic areas whose depth is less than 2 to 3 kilometers, unless further data discover areas of greater isostatic unbalance than any presently known.

Any theory of earth structure and processes must explain the high degree of isostatic equilibrium, the great similarity of crustal densities of all the oceans, and the dissimilarity of continental and oceanic crustal densities. The concept of the permanence of continents and ocean basins, therefore, appears the most reasonable from our present gravitational data.

SUMMARY

Both the seismic data and the gravity data show the great similarity of the crustal structure of the Atlantic and the Pacific oceans and their great dissimilarity to the continental crust.

While neither the seismic nor the gravity data coverage is yet sufficient for us to come to a final conclusion, the hypothesis of the permanence of continents and ocean basins fits the existing data best. There are strong indications against the hypotheses of continental drift and foundered land bridges in the deep ocean basins.

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CONTINENTAL DRIFT VERSUS LAND BRIDGES

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THE TITLE OF THIS PAPER suggests the single question to which the following brief discussion attempts to give an answer: Are enough geological and geophysical facts available to make it possible to decide whether or not the concept of continental drift can be used by the student of animal and plant distribution as a working hypothesis with reasonable confidence?

It is natural for a biogeographer to be favorably inclined towards continental drift, if the distribution of the genus or family he is studying can be explained by it. But he knows, of course, that that does not prove the reality of continental drift. Nor does the opposite disprove it, as, for example, the remarkable similarities in fauna and flora of such fundamentally separated regions as the eastern United States and eastern China which share a number of relatively closely related reptiles (alligator, certain skinks, pit vipers), giant salamanders, toothed sturgeons, and an astonishing number of plants. (For references, see Bucher, 1933, p. 110.) There is a perplexing multitude of factors other than the hypothetical drift of continents that influences the dispersal and resulting distribution of organisms, among which land bridges are by no means the most important. As used in the title, land bridges stand for all these demonstrably real factors in opposition to the hypothesis of drift. Their own nature is only briefly touched upon in the closing paragraphs.

When complex problems are discussed, it is important to distinguish between suggestive and decisive evidence. To a detective who must determine whether suicide or murder led to the body crumpled on the floor clutching a pistol, such facts as powder marks on the skin and a typed suicide note are merely suggestive; whether or not the bullet that brought death could have been fired from that pistol is of crucial importance. Facts that follow by necessity from a hypothesis constitute decisive evidence. The vast geological literature on continental drift deals largely with suggestive evidence (Bucher, 1933, pp. 73–76, 86–87, 102–111, 225–230, 457–460, 461–464). This discussion is limited to observations that appear to be decisive.

In order to determine what constitutes decisive evidence, it is essential to perceive clearly what is basic to the concept of continental drift: it is the purely hypothetical assumption that the heavier "simatic" rock materials of which the outer part of the earth's crust consists are so much weaker than the lighter "sialic" rock materials of the continents that, under the action of diminutive stresses applied through geologically long intervals of time, they yield readily, allowing sialic blocks, such as islands and continents, to float in them and move horizontally through them like blocks of wood in molasses. Wegener compared the physical behavior of the two materials to the difference between wax and sealing wax. "A wax figure can exist for a century without collapsing, if only the temperature does not attain the melting point, while the same figure worked in sealing wax would gradually flow away" (Wegener, A., 1924, p. 133).

Truly decisive criteria are, therefore, those that depend on the relative resistance to deformation of the two types of crustal materials. Four such criteria are discussed here.

If the main ocean floor is the surface of simatic material so weak as to permit the stronger sialic bodies to drift through it, then (1) its topography must differ characteristically from that of continental sialic masses; (2) it must be incapable of maintaining depressions that lie significantly below the level of quasi-hydrostatic equilibrium; (3) it must be incapable of supporting mountain chains, i.e., gigantic wrinkles comparable in geometry, dimensions, and geophysical properties to the mountain ranges of the continents; and (4) finally, where simatic and sialic rocks are found side by side in intensely deformed regions, the structural

relations must show that the simatic materials yielded more readily and more nearly like viscous substances than the sialic ones.

The first of these criteria is more powerful than it may appear at first sight. The magnitude of the forces that might produce a drift of continents and islands seems to be of the order of one to several millionths of that of gravity (Wegener, A., 1924, pp. 197–199). If the simatic material of the ocean floor is so weak as to permit it to flow horizontally around an island of sialic material that plows through it under the action of such diminutive forces, gravity itself must cause its surface to be unmistakably level in contrast to the varied surfaces of the blocks and plates of lighter material that float in it. The topographic contrast on the ocean floor should be like that of the flat surface of sea ice compared to that of icebergs frozen in it.

As the ocean floor becomes better known through the use of modern fathometers, it is becoming evident that its topography does not present any such contrast. The recent detailed studies of the floor of the North American basin (in the North Atlantic), for example, by Maurice Ewing and his collaborators, reveal a highly varied topography (Tolstoy and Ewing, 1949, pp. 1532–1535). Even where there is little relief, the surface of the deep-sea floor slopes gently and steadily from the foot of the "continental slope" down to within a few hundred fathoms of the deepest part. Only the relatively small central part, which lies below 5300 to 5500 meters (2950–3000 fathoms), is really flat and nearly horizontal. This surface is, however, level only because it is the top of thick, fine-grained, unconsolidated deep-sea sediments, estimated as 1000 to 2000 meters thick (Ewing, personal communication), which abut against the bordering gentle rise like a liquid against the sloping sides of a flat dish. It is impossible to tell, at present, how much relief there is on the rock surface below. There are knobs ("sea mounts") on it that project above the level sediments, and beyond its borders the sea floor slopes at the rate of 50 to 200 feet per mile, rising more than 10,000 feet over distances measured in many hundreds of miles to the base of the continental slope.

The existence of vast, gentle slopes on the deep-sea floor is the exact opposite of what should be, if the simatic rock materials had the low strength attributed to them by the hypothesis of continental drift. Recognizing the existence of such systematic slope topography is like finding, in the crude but telling illustration of the suspected suicide mentioned above, that the caliber of the death-dealing bullet is different from that of the pistol in the dead man's hand.

That the rock materials of the ocean floor possess no less strength than those of the continents is suggested also by the topography of the submarine elevations, especially the Mid-Atlantic Ridge. The map pattern of the parts for which detailed information has recently been made available is similar to that of the region around the Azores, where elongated ridges and long and narrow, closed depressions alternate, bordered by abrupt slopes. Similar abrupt slopes on the islands are due to faulting. (For discussion and references, see Cloos, 1939, pp. 506–510.) From the foot of submarine cliffs, Ewing has dredged big angular blocks of basalt and related rocks with fresh surfaces, such as would accumulate at the foot of a fault scarp on land (Shand, 1949, pp. 89–92).

In the North Atlantic, between Iceland and the Equator, the Mid-Atlantic Ridge rises in places more than 4000 meters above the surrounding deep-sea floor. In Iceland, the Azores, and a few small islands such as St. Paul (on the Equator) parts of it rise even above sea level. The rocks there exposed and specimens secured by dredging all consist of the same simatic materials (basalt and related rocks) that must underlie the ocean floor. The very existence of such an upland system on the ocean floor is contrary to the concept of great weakness under long-continued stress implied in the "drift" of the islands and continents, provided, of course, that it is built of the same materials. Being well aware of this, Wegener assumed that the Mid-Atlantic Ridge "is the former floor of the rift-valley which was in existence during the period when the Atlantic Ocean was composed of a relatively narrow fracture, which was subsequently filled with sunken margins, shore deposits, and also partly with molten

sial" (Wegener, A., 1924, p. 61). If we are willing to grant the possibility that the Mid-Atlantic Ridge might consist of these materials, though this was postulated by Wegener purely *ad hoc*, a modern map of the submarine topography of the Atlantic (Stocks and Wüst, 1935) confronts us with independent evidence that Wegener's interpretation is not tenable. The ocean floor, especially in the South Atlantic, shows large and conspicuous transverse welts that connect the longitudinal Mid-Atlantic Ridge with Africa and South America, such as the Rio Grande swell which separates the south Brazil basin from the Argentine basin, and the Guinea, Walfisch, and Cape swells which enclose the Angola and Cape basins (Maurer and Stocks, 1933; Wüst, 1938). The presence of such transverse welts is certainly incompatible with Wegener's naive, though clever, attempt to explain away what is inconvenient. They show the ocean floor warped into basins framed by swells such as would be expected on an elastic or plastic sheet, but not on the surface of a very weak material showing quasi-hydrostatic behavior.

The lack of evidence for any approach to a quasi-hydrostatic equilibrium surface on top of the sima of the ocean floor is brought out sharply by the frequency of distribution of elevations on the earth. Wegener used H. Wagner's figures, which give the following distribution, expressed in percentages of the earth's surface:

Depth below sea level (kilometers)	
Below 6	1.0%
6–5	16.5
5–4	23.3
4–3	13.9
3–2	4.7
2–1	2.9
1–0	8.5
Elevation above sea level (kilometers)	
0–1	21.3
1–2	4.7
2–3	2.0
Above 3	1.2

The presence of two maxima in these figures has become one of the cornerstones of the house of thought that Wegener built. "In the whole of geophysics," he wrote, "there is scarcely another law of such clearness and certainty as this one, which states that there are two favored levels on the Earth, which occur alternately side by side and which are represented by the continents and the floors of the oceans . . . If . . . only a single equilibrium level existed, disturbances thereof . . . could then only give rise to two differing frequency-maxima, if physical causes existed for the preference of just these elevations. Since this is not the case . . . " he concludes, the two maxima represent "two undisturbed levels" like those of water "between great sheets of ice" (Wegener, A., 1924, pp. 28–31).

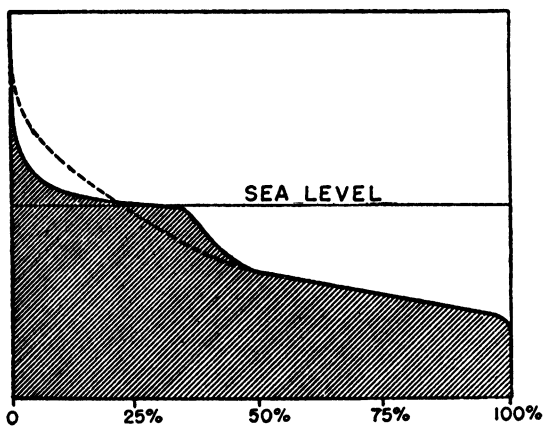

FIG. 1. Solid line: Hypsometric curve, showing distribution of elevations on the earth's surface in per cent of the total area. Dashed line: Inferred shape of the hypsometric curve on a hypothetical earth devoid of weathering and erosion and without the oceans and the singular control exerted by their roughly constant level.

The words "since this is not the case . . . " are an instructive example of abstract reasoning without regard to geological reality. The topography and structure of the continents convinced geologists more than a century ago that much of the land surface is relatively flat and low solely because former mountain ranges and highlands were destroyed by erosion and former troughs and basins with floors now far below sea level were filled up to and above sea level. There can be no doubt that without this incessant destruction wrought by erosion and the presence of a relatively fixed sea level there would be no frequency maximum between 0 and 1 kilometer in elevation. Instead of the present dis-

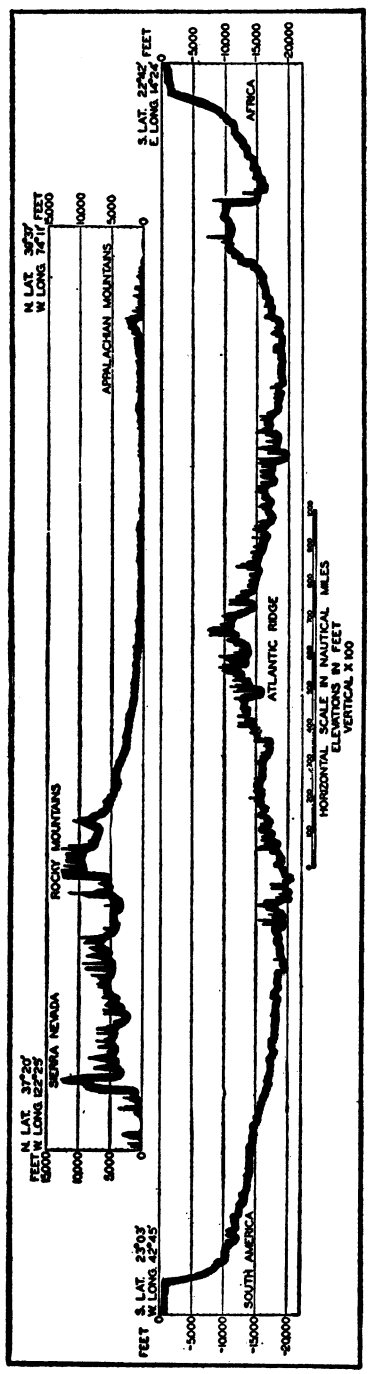

FIG. 2. "Comparison between profiles across the United States and across the South Atlantic using a similar spacing of reference points" (Shepard, 1948, fig. 94, p. 282).

tribution of elevations, shown graphically by the solid line in the cumulative curve of figure 1, the elevation frequency would have to be something like that indicated by the dashed lines in figure 1 (Bucher, 1933, fig. 13a, p. 58). In other words, if there had been no erosion and no controlling sea level, the whole idea of two distinct, primary levels would not have arisen in men's minds. Shepard's "comparison between profiles across the United States and across the South Atlantic using a similar spacing of reference points" (Shepard, 1948, fig. 94, p. 282), reproduced in figure 2, shows that the sea level controlled land surface comes actually much nearer to being level than a typical part of the Atlantic Ocean floor.[1]

Instead of being convincing evidence for the hypothesis, the elevation frequency appears to be an all but fatal argument against it (Bucher, 1933, pp. 51–58).

This becomes most evident when we look at the areas that lie below the lower maximum which was thought to represent the equilibrium surface of the very weak sima. Almost one-sixth (17.5 per cent) of the earth's surface lies below 5000 meters, the lower boundary of the 1000-meter deep zone, which is supposed to represent the mythical equilibrium level. Of this, 1 per cent (or over 5 million square kilometers) extends downward still lower to the greatest depths of the deep-sea trenches, more than 10,000 meters below sea level. This means that the second criterion for the reality of the physical conditions on which continental drift depends is negative also.

To see just how decisive this criterion is, turn to the deep-sea trenches that border the island arc of the Dutch East Indies, from Sumatra to the Banda Sea, and from Celebes to Mindanao. The long, narrow belts of abnormal depth below sea level are aligned on the convex side of a great island arc. They are part of the surface expression of a zone of instability which finds its strongest expression in a continuous and well-defined belt of high negative gravity anomalies, i.e., abnormally low values of the acceleration of

[1] As in railroad profiles, the vertical dimension is enormously exaggerated in these cross sections so that very gentle slopes of one to a few degrees appear like cliffs.

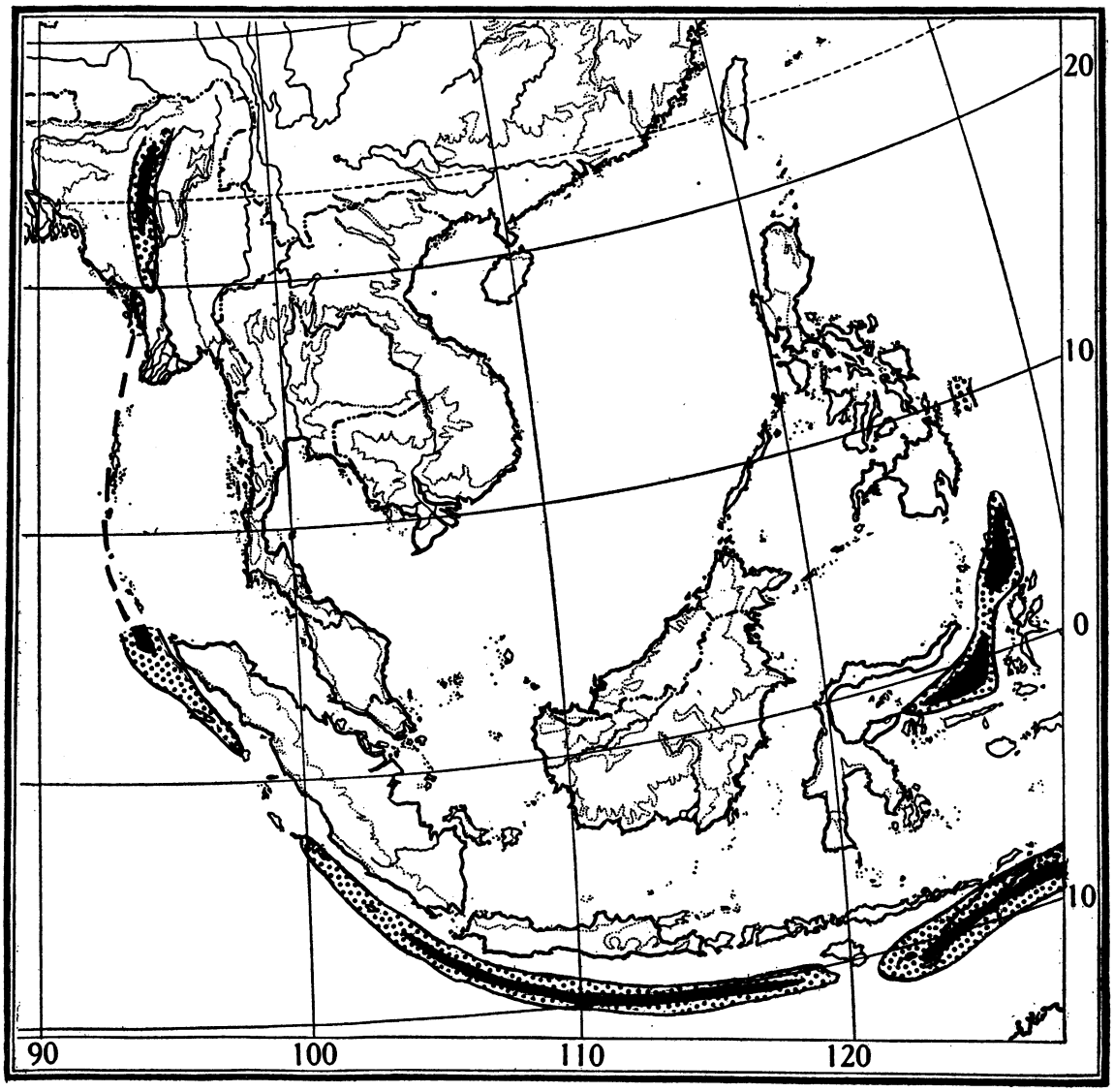

FIG. 3. The belt of large negative gravity anomalies between Burma and the Philippine Islands. Stippling: −50 to −100 milligals; black: −100 to −250 milligals. After Vening Meinesz (1934) and Evans and Crompton (1947).

gravity (fig. 3; Vening Meinesz, 1934, pl. 4). This belt lies between the island chain and the deep-sea trenches and parallel with both. It must be a major zone of crustal deformation, since volcanic and earthquake activity is associated with it in a specific and spectacular manner, together (Umbgrove, 1934, pp. 140–160; 1947, pp. 144–208) with abundant evidence of intense structural deformation of the rocks where they lie exposed on land as, for example, on the island of Timor (Brouwer, 1925, pp. 53–55; Simons, 1940, pp. 188–202) and in Burma (Sale and Evans, 1940, pp. 356–359).

A detailed gravity survey of the oil region of Burma shows that it is the northward extension of the belt of high negative anomalies with values of an order of magnitude

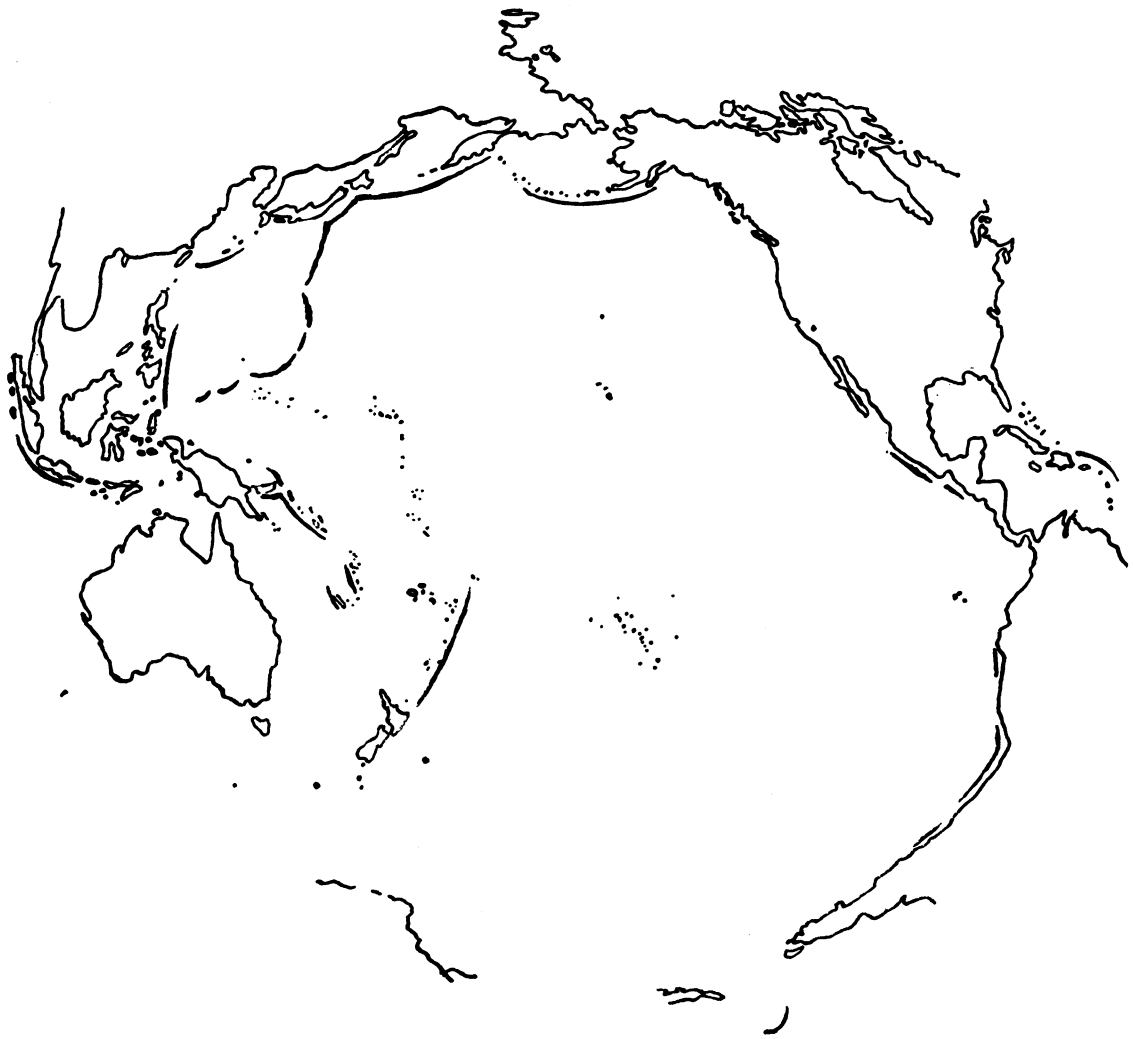

FIG. 4. The major deep-sea trenches of the Pacific Ocean. Redrawn after Stille (1944, fig. 19, p. 65).

comparable[1] to that observed south of Sumatra and Java (Evans and Crompton, 1947, fig. 8, p. 226).

The existence of such large negative gravity anomalies means that beneath the belt along which they occur, the earth's crust is so much lighter than on either side that it would rise high above its present position, if it were not held down as in a vice. If there were a significant difference in the strength of the ocean floor and of the continents, the strong negative anomalies and the deep trenches should be confined to the places where the belt lies between continental shelves or the land mass itself.

The eastern portion of this belt actually lies between two continental shelf areas, viz., the Sunda Shelf, which connects southeast Asia with the Dutch East Indian islands in the north, and the corresponding Sahul Shelf of Australia in the south. At its north-

[1] A belt over 500 kilometers long shows negative isostatic anomalies of more than −75 milligals. Over more than half that distance, the negative anomalies exceed −100 milligals, reaching values of over −125 milligals, i.e., values as high as the greatest recorded by Vening Meinesz in the great belt of negative anomalies south of Java.

west end in Burma, the counterpart of the deep-sea trench (here filled with oil bearing sediments) and the belt of high negative gravity anomalies lie wholly within the Asiatic continent. But between these extremes, it lies where the sialic continental shelf on the north faces the simatic material of the floor of the Indian Ocean. Instead of being absent, both the trench and the negative anomalies are developed even more vigorously here than at the extremities. This can only mean that "the resistance of the Indian ocean floor is not inferior" to that of the continental masses. Vening Meinesz, whose words are here quoted, continues, "We could not well imagine a migration (of continents) through the ocean floor, when this part of the crust can so strongly resist pressure" (Vening Meinesz, 1934, pp. 120–121).

But suppose this conclusion were not justified and the trenches and gravity anomalies were the result of drift, which way would this part of Asia be drifting? If southward, no such effect could develop on the flanks, parallel to the direction of movement, as, for example, in Burma, or should be but weakly expressed. If it were drifting west, how could the same type of belt develop on the east side (beside Celebes and Mindanao), or vice versa?

The same contradictory situation exists, on a still vaster scale, around a large part of the circumference of the Pacific Ocean (fig. 4). Here the deep-sea trenches reach their greatest development and, in the Mindanao Trench off the east coast of the Philippines, the greatest known ocean depths. On the west side of the North Pacific, they lie on the convex side of the great island arcs; in the South Pacific, they parallel outer island chains in the western part and the coasts of Central and South America on the east side. Gravimetric studies in a number of critical places prove that here also large negative gravity anomalies characteristically run beside the deep-sea trenches.[1]

Thanks primarily to the brilliant studies of Gutenberg and Richter (1949), intermediate and deep earthquakes[2] are known to accompany the deep-sea trenches and accompanying terrestrial or submarine mountain chains in a very characteristic way. Figure 5 shows this relation. Where the deep-sea trench borders a continuous land mass, as along the west side of South and Central America, the epicenters of the earthquakes are found farther inland the deeper their centers lie below sea level. This is what might be expected, if the deep-sea trench along the west coast of South America were the "ocean-floor . . . dragged down" with the advance of the westward drifting continent, as Wegener pictured it (Wegener, A., 1924, p. 145). Whether or not the resulting disturbance beneath the continent would and could under the drift hypothesis extend down to a depth of 700 kilometers and as far eastward as figure 5 suggests is left to the reader to ponder. The map raises more direct questions:

First, if the characteristic association of deep-sea trench, belt of high negative gravity anomalies, and shallow earthquakes, followed by successive zones of increasingly deeper earthquake shocks, means westward drift in front of the Andes, it must mean drift towards the southwest in southern Mexico, towards the southeast in the Aleutian and Kurile Islands, towards the east off the Philippines and the Marianas, towards the southwest in the Solomon and New Hebrides Islands, and towards the southeast from the Tonga Islands to the North Island of New Zealand.[3] What kind of drifting is this?

Look especially at the Solomon Islands and New Hebrides, northeast of Australia. Here the arcuate form of the submarine welt of which the islands are the peaks is directed towards the continent, instead of away from it, and the belt of intermediate earthquakes

[1] The essential geophysical and geological facts are summarized systematically in Gutenberg and Richter (1949, pp. 30–64). For graphic representation of transoceanic and transcontinental cross sections and gravity profiles, see Woolard (1949, p. 191). For representative specific data, see Vening Meinesz (1948, vol. 4), Heiskanen (1945), Ewing (1938), and Hess (1938, 1948).

[2] Shallow earthquakes originate above 70 kilometers; intermediate, between depths of 70 and 300 kilometers below sea level; and deep earthquakes, between 300 and 700 kilometers below sea level.

[3] The specific distribution of the intermediate and deep earthquakes vitiates, of course, Wegener's attempt to explain the deep-sea trenches of the west side of the Pacific in a wholly different way from that he had to adopt for those of the east side (Wegener, A., 1924, compare p. 145 with pp. 178–182).

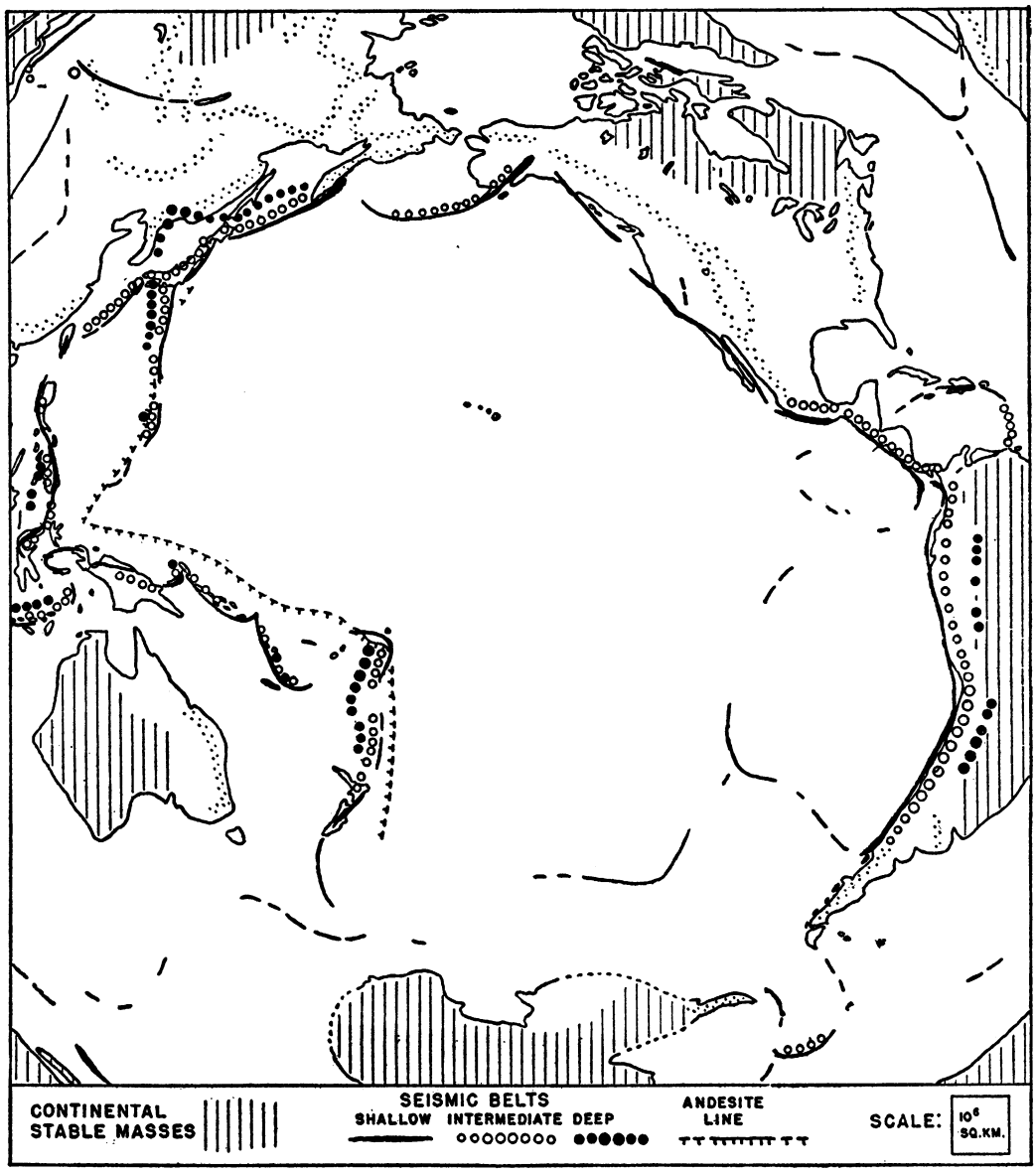

FIG. 5. Distribution of shallow, intermediate, and deep earthquakes in the Pacific Ocean (from Gutenberg and Richter, 1949, fig. 33, p. 90).

lies on the side of the ocean instead of on the landward side. What is it that is drifting here? The same situation exists on the eastern front of the Caribbean island arc (Hess, 1938) and, more striking, on the corresponding front of the startling South Antillean arc that connects Cape Horn with Antarctica (map in Stocks, 1939). In both regions, a conspicuous deep-sea trench lies on the convex side of the arc, exactly as in the normal case where continent and ocean meet; but here, in the North and South Antillean arcs, as in the New Hebrides, deep sea lies on the inside as well as the outside of the arc. In all three cases ocean floor is pitted against ocean floor, with results that are essentially identical with those obtained when a continent presses against the ocean floor.

The same condition is seen on a gigantic scale in the mighty submarine range that extends from the Tokyo Bay area of Japan southward through the Bonin Islands to the southern limit of the Marianas at Guam, and, turning southwestward, continues with characteristic offsets into the Yap and Palau Island chains (Hess, 1948).

This great submarine mountain range, which is double in its central part, compares favorably with the Himalayas in length and height above the surrounding earth surface. Like the Himalayas, it is bordered on its convex side by a long and deep depression which here forms the deep-sea trench, the counterpart of which in front of the Himalayas is filled to great depths with the sediments of the alluvial Ganges Valley. Belts of negative gravity anomalies and of intermediate (and, in the Bonins, deep) earthquake centers are aligned along both in the same way. Yet, in the one case, the belt lies wholly within a continent and, in the other, wholly within an ocean floor over 4000 meters deep on both sides. This can only mean that the ocean floor undergoes the same kind of deformation as the continental platform. Thus the third criterion set up at the beginning of this paper proves as definitely negative as did the first two.

The last of the criteria lies in tangible evidence for a pronounced difference in the mobility of the rocks of the "sima," which are generally dark colored and rich in silicates of magnesium and iron, and the rocks of the "sial," which are light colored and rich in silica and alumina. Evidence of such a pronounced difference in behavior is indeed widespread, wherever the deeper parts of the continental structure are exposed by erosion, as in the ancient Canadian and Fennoscandian shields and in the cores of great mountain ranges. But the evidence is invariably the exact opposite of what should be, if continental drift were a reality. Wherever both kinds of rock are found involved in the same deformation, it is always the simatic materials that break rather than bend, while the sialic rock wraps around the fragments; or they thicken and thin like a stiff plastic, while the light materials flow around them with all the signs of higher mobility. Every field geologist with experience in such regions knows that this is universally true.

All four "decisive criteria," then, point to a power of resistance to deformation ("strength") of the materials of the ocean floors that is at least as great as that of the continents, and probably even greater. The writer, accordingly, believes that a definite answer can be given to the question with which this discussion began: the concept of continental drift cannot be used as a working hypothesis by the student of animal and plant distribution.

This leaves him only the much maligned hypothetical "land bridges," in cases which demand a land connection where none exists today. Whether or not the facts of animal and plant geography make necessary the disappearance of former land connections beyond the submergence of land caused by the rising sea level after a glacial epoch does not concern this discussion. But it must be pointed out that such changes not only are possible, but have actually occurred on a rather large scale. Such vertical displacement of parts of continental surfaces, incidentally, is as contrary to Wegener's basic assumption as the corresponding behavior of the ocean floor.[1]

In the Grand Canyon of the Colorado, for instance, sediments nearly 3 miles thick were once deposited on the old land surface on top of the pre-Cambrian rocks that is exposed for miles in the bottom of the canyon. The flat-lying sediments form the higher canyon walls and the successive lines of cliffs beyond and at varying distances from the rim. About two-thirds of that pile of sediments was laid down below sea level. The old land surface at the bottom, which today lies more than 3000 feet above sea level, must, therefore, at the time have been depressed some 7000 feet below sea level.

Some people think it was the sediments that pushed it down. But a simple considera-

[1] Kurt Wegener (Alfred's brother) for instance, wrote: "The results of pure geophysics . . . have furnished clear proof, that only horizontal movements (of crustal units), if any, are possible . . . and that the emergence and submergence of continents must be relegated to the realm of fantasy" (Wegener, K., 1939, p. 5; translation mine).

tion shows that that is impossible. To do so, the sediments that are laid down on top must push aside heavier rock materials at the bottom of the crust. In order to push aside an equal weight of the heavier material at depth, a greater thickness of the lighter material must be laid down on top of the crust. A land surface that lies near sea level can, therefore, never disappear below the water merely by the piling up of sediment on top of it. The crust must be forced down by other, independent forces. What these may be does not concern us. It is important to realize that sediment-filled basins prove that parts of the earth's surface can and do bend down, and that thick sediments exist because there was a depression, and not that a depression exists because there were sediments.

With this in mind, let us follow the surface of the old rocks east of the Appalachian Mountains as it dips eastward beneath the young marine sediments of the Coastal Plain. Seismic refraction records, checked by scattered bore holes, have traced it down to the coast. Beyond this, the systematic investigations by Ewing and his collaborators have traced it in seaward sections from four points, from Woods Hole, Massachusetts, in the north, to Norfolk, Virginia, in the south, to a depth of about 2½ miles and more below sea level, at distances 60 to 100 miles from shore (Ewing *et al.*, 1950, pp. 887–891). In all sections, the old land surface, at the bottom of the younger sediments, dips seaward at first 40 to 50 feet per mile and steepens gradually to 100 feet per mile and more. Here, then, we have an old land surface that has been depressed to deep sea level on the margin of an ocean, much as the equivalent, though much older, land surface on top of the pre-Cambrian rocks of Wisconsin sinks eastward beneath the Paleozoic rocks of the Michigan basin, sloping about the same amount, steepening downward in the same way, and reaching a similar depth. In both cases, sediments accumulated because they were available, and they could come to rest because the basins held them. But they did not make the basins.

If some sinking were to take place, where no large amount of sediment is available, as, for example, at the site of a land bridge, the sinking would not be compensated by deposits, and the land bridge would vanish.

This may well have happened at the right place more than once in the earth's history. But it is very doubtful if it has ever affected really large areas, such as are implied in the traditional ideas concerning the "foundering" of such hypothetical continents as "Gondwana land." Recent studies by Ewing and Press have shown that, contrary to current belief, over large parts of the Atlantic as well as the Pacific and, by inference, the other ocean floors, sialic rock materials are absent. This was proved by combined direct explosion seismic measurements for a small part of the western North Atlantic and analysis of the dispersion of surface waves. The theoretical (mathematical) basis for the traditional view was shown to be erroneous (Ewing and Press, 1950), and, when reinterpreted in the light of the corrected equations and the experience in the western North Atlantic, the records of world-wide earthquakes led to the conclusion as stated.

The student of animal and plant geography must, therfore, get along without assuming either that vast continental areas have foundered to form large areas of the ocean floor, or that continents and islands have drifted in directions he needs for his purposes. There are no short cuts to the understanding of geographical realities.

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STRATIGRAPHIC AND PALEONTOLOGIC DATA RELEVANT TO THE PROBLEM OF AFRO-AMERICAN LIGATION DURING THE PALEOZOIC AND MESOZOIC

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INTRODUCTION

OVER A LONG TERM OF YEARS there grew up in the minds of geologists a piecemeal appreciation of the fact that there are much the same sequences of strata, fossil plants and animals, and paleoclimatic records preserved in the opposing sides of the South Atlantic basin. It was not until Du Toit (1927) published his synthesis of these comparables that geologists appreciated the detailed degree to which the correlations might in some parts of the geologic record be drawn. Largely due to the antagonism which Du Toit's continental drift interpretation of the close similarities aroused, there has grown up a modern North American tendency to discount the data along with the theory. Despite all the many discoveries made on both continents in what has probably been the most productive quarter century in the history of earth science, the basic fact remains that these two widely separated areas have had over long periods of geologic time intimately related and at times very similar, if not identical, histories. To deny them any continental connection across the area which is now the South Atlantic basin would seem to create even greater problems than the "Gondwanists" and/or "Wegenerians" do.

Since the symposium was aimed at the Mesozoic to Recent history of the basin, little space could be allotted for too deep delving into the remotely antecedent history. Happily, the very closest and most challenging Afro-American comparisons occur in the Devonian-Triassic record.

For perspective it might be well to check on a globe the vast distances involved in these comparisons: from South Africa (Cape Town) to the Falkland Islands; to Paraná, Brazil; to the mouth of the Amazon; to the State of Piauí, Brazil; to Sierra Leone and Morocco; from Amazonas to Morocco; to Colombia; to central United States; to south Brazil; to the Bolivian Andes.

During 1945 to 1948 the writer had the good fortune to be in Brazil with ample opportunity to visit sites of geologic interest in most of the states of that vast country. The results of those travels were in part incorporated as annotations in a Portuguese translation[1] of Du Toit's (1927) "Comparison," and in data furnished for the 1950 Geologic Map of South America. The paleontologic studies based on the Devonian and Carboniferous collections made during the the Brazilian sojourn are now in progress. Thus to a degree a considerable part of the paleontologic comparisons here offered is subject to some modification when the research is completed. However, there seems to be no reason to suppose that the restudy will materially alter the general correlations and over-all opinions here expressed.

This survey was written on the assumption that the reader is conversant with the general field of stratigraphic geology and the broad picture of African and South American geology, such as can be gleaned from the latest geologic maps and the general regional treatises such as Krenkel's (1925–1938) summary of African geology. Reed's (1949) compendium on the geology of the British Empire gives a succinct résumé of the South African relations, which supplements in part Du Toit

[1] "Comparação geológica entre a América do Sul e a África do Sul," a revised and annotated edition of two works by Alexander L. Du Toit, translated by Kenneth E. Caster and Josué C. Mendes, with notes by the author, translators, and Joaquin Frenguelli. Although the book was printed in 1948 in São Paulo, the edition was recalled prior to distribution because of an untenable number of typographical errors. It is now again in press in Rio de Janeiro and will appear in the Boletim series of the Divisão de Geologia e Mineralogia of Brazil.

(1924, 1939). Oliveira and Leonardos (1943) have given a very complete survey of Brazilian geology, as has Ahlfeld (1946) for the Andean sector of Bolivia; Windhausen's (1931) "Geologia Argentina," although somewhat out of date, is a most useful study. Caster (1942) attempted a generalization of the Paleozoic paleogeographic fundamentals of South America; although subject to many modifications of detail, it still forms the general background for the broad discussions of South American paleogeographic relations in this paper. See also Weeks (1947).

Acknowledgments

I am deeply grateful to the various Brazilian agencies, national and state, and the implementing officials of these, many of whom are my good friends, for the opportunities to travel widely in Brazil. Among these many institutions should be mentioned the University of São Paulo and the Instituto Geográfico e Geológico of the State of São Paulo; the Divisão de Geologia e Mineralogia and Conselho Nacional de Petróleo of the Federal Government; and the Instituto de Biologia e Pesquisa Tecnológica of the State of Paraná. Likewise my sincerest thanks go to the many Brazilian colleagues who shared the work in field and laboratory and have remained friends and scientific collaborators over the miles and years. A Fellowship from the John Simon Guggenheim Memorial Foundation (1947–1948) made possible an added year's travels in Brazil and over a large portion of the rest of South America in quest of additional Paleozoic data.

The text figures for this paper were drafted by my wife, Anneliese S. Caster, who also typed the manuscript. For this assistance, as well as for understanding companionship in field and laboratory, I am deeply grateful.

COMPARISONS

PRE-DEVONIAN

The Proterozoic (or late pre-Cambrian)[1] has been widely identified in the maps and literature of both Africa and South America. Judging from the literature (scanty in proportion to the immensity of the areas involved), enormous thicknesses of clastic and chemical sediments are usually involved in each area so denominated on the maps. Some of these areas pertain to ancient orogenic belts and are properly to be denominated geosynclinal; possibly all will turn out eventually to be. In recent years biohermic calcareous organisms, generally identified as *Collenia*, have been discovered in these strata from widely separated areas on all continents. Almeida (1944) described these from the São Roque series of São Paulo, a series presumably to be identified with a band of barren but supposedly Proterozoic sediments extending southward parallel to the southeastern coast of Brazil through Paraná and Rio Grande do Sul and Uruguay. The terrane is undoubtedly allied to the iron-bearing sediments of Corumbá, Mato Grosso, and Minas Gerais. The system extends into the State of Bahía, and towards the mouth of the Amazon. The belt paralleling the southern coast is almost certainly geosynclinal.

In Africa *Collenia* is showing up from the Atlas to the Cape. Young (1932) and Schuster (1933) have described the organism from south equatorial Africa; MacGregor (1941) from Southern Rhodesia; Jamotte (1944) and several others from central Africa. Choubert (1945) described the growths from the eastern Atlas Mountains; Menchikoff (1946) from the Sahara and other areas of North Africa.

Collenia was world-wide in the late pre-Cambrian. It characterizes the Beltian system of Montana, is known in the supposedly equivalent Sinian system of China, and exists in Australia. It characterized the shoal waters of the ancient geosynclines (Fenton and Fenton, 1939), although this may be only an accident of preservation. since almost nothing is known of epeiric (cratonic) Pro-

[1] The strata here considered as Proterozoic in both continents pertain to that problem terrane of sediments which accumulated essentially under Paleozoic geographic conditions, often in Paleozoic troughs, but antecedent to the appearance of characteristic Paleozoic (Cambrian) fossil faunas. Various geologists have proposed that these records, known from all continents, be given a separate system rating, thus making them a pre-Cambrian system at the base of the Paleozoic.

terozoic sediments. Its presence affords the best evidence to date for correlating strata in the oldest terranes on the two sides of the Atlantic basin. The communication routes between the present outcrop areas were most probably shallow water. However, there is no proof that this path lay across the present Atlantic deep.

Obviously, there is also a conspicuous parallelism between the rich iron facies developed in the Proterozoic sediments of both Africa and South America. In the absence of any general consensus, or even favored hypothesis, as to the mode of origin of the world-wide sedimentary iron of this period, this fact cannot be satisfactorily employed in the present connection.

The older Paleozoics are really too inadequately known in South America, and especially in the non-Andean section, to make comparisons with Africa very significant. The very extensive studies now in progress of the North African Paleozoic column are revealing an ever greater North American element in all these faunas. (See, for example, Termier and Termier, 1950.) In fact, it may well be the dominant element (Le Maître, 1950). This fact makes any indications of the same phenomenon in South America very interesting, since the African-North American Paleozoic connection seems certainly not to have been via central Europe. In the Andean geosynclinal belt the older Paleozoics show, even in the preliminary surveys now available, close relationship with the North American faunas. However, no Paleozoics are known in the Andean belt to the east of the general area of Lake Maracaibo. Any relics of Afro-American marine connections across the Atlantic basin in the pre-Silurian would now appear to be best sought north of Brazil, from Venezuela to Florida.

The Silurian system was the first widespread Phanerozoic transgression on both sides of the South Atlantic. Thick and very extensive basal Paleozoic sandstones, lying immediately on the crystalline complex in South America, are usually identified as Silurian. This is also true for vast territory in the cratonic area of Africa. As is shown below, there is some conflict in certain sedimentary basins of both continents as to the Silurian versus Devonian age of these basal sandstones. The only definitely dated Silurian terrane of Brazil forms a narrow band of outcrop for nearly a thousand miles on the north side of the Amazon, from the Rio Branco to near the mouth of the great river. This terrane overlies the crystalline complex and underlies the Lower Devonian. It is chiefly sand and siltstones (Trombetas sandstone) and carries a varied and characteristic benthonic and pelagic fauna (Clarke, 1899a) of Middle Silurian (Clinton and Niagaran) aspect. The affinities of both aspects of the fauna are mainly North American-West Saharan. There are, however, somewhat more axonophorous graptolites present than in the North American Middle Silurian. The Roraimã sandstone of the Guiana shield is usually assigned to the Silurian, but in the absence of fossils and adjacent formations of known age this is a problematical assignment.

The Roraimã formation compares with extensive undated sandstones overlying the crystallines of western equatorial Africa.[1] The Amazonian trough would serve as a satisfactory Middle Silurian link between North America and North Africa. Since there is no coastal equivalent of the terrane known on west coastal Africa, nor west nor north of the Amazon Valley in South or Central America, we cannot speak with any certainty of the actual pathways of North American connection. However, the Amazon trough seems certainly to have connected with the pre-Andean geosyncline. The thick Silurian terrane of Bolivia-Argentina shares faunal elements with both Amazonas and North America.

Strata of possibly Silurian age, but appearing without qualification as Silurian on the current geologic map of Brazil, cover extensive areas of the country south of the Amazon drainage. Most famous of these terranes is the Bambuí series of the headwaters of the Paraná and especially in the São Francisco

[1] A basal conglomerate in the Roraimã sandstone has been suggested (Bucher, 1952) as a possible source of the alluvial diamonds recently discovered on the Orinoco River. In view of the close association in Brazil (see below) between Carboniferous glacial beds and placer diamonds, there is a tantalizing suggestion here that the Roraimã beds may be much younger than is customarily supposed.

Valley of Minas Gerais and Bahía. This is an area of broad synclines[1] and fault blocks preserving extensive remnants of what was certainly a far wider transgression of shallow, lime-depositing waters. The series is almost without fossils. Two alcyonarian coral genera, *Chaetetes* and *Favosites*, have been tentatively identified by Ruedemann for the Brazilian Survey. Both are form-genera, and these type corals are very long ranging. Next to nothing is known of the regional picture of the Bambuí. With no reliable correlation criteria available, none of the South American Silurian labels outside of the Amazon trough and pre-Andean belt are reliable.

The background for the Silurian label attached to a tiny outcrop in Santa Catarina will illustrate this. A small disturbed area of intermediately metamorphosed sandstones, conglomerate, shales, limestone, and dolomite has been called the Itajaí series by Maack (1937, 1939), from the Itajaí-Mirim River. The series emerges from beneath the Upper Carboniferous glacials (Tubarão series), and its structural trend is at an angle to the regional grain of the lithologically similar but supposedly much older strata of the Proterozoic belt (Açunguí series of Paraná and São Roque series of São Paulo). The Itajaí beds appear to align with an isolated outcrop of metamorphosed strata near Anitápolis, Santa Catarina, which, on the basis of degree of metamorphism and trend, Moraes Rego (1926) correlated with the then unnamed Itajaí sequence. The latter he dated as Silurian, since it was: (a) pre-tillite (Carboniferous), and (b) dissimilar in lithology from the Devonian in the adjacent Paraná basin. The Devonian of Brazil is everywhere a shale and sandstone terrane and is undeformed. Thus, Rego's "Silurian" really means "pre-Devonian, probably Paleozoic." He neglected to explain this fact when he turned over a curious oligochaete worm from the Anitápolis beds to Carlotta Maury for description. By coincidence, one of the best-preserved oligochaetes known comes from the Upper Silurian of New York State. Thus it is easily understood why Maury never questioned the Silurian age of her *Oliveirania santacatharinae* (1927). However, such is the power of paleontology, that this unique fossil seemed to establish the age of the Anitápolis-Itajaí metamorphics and to justify a correlation with the Bambuí, the accepted age of which was based on just about as reliable data. Although Carvalho some 10 years later (1936) showed that the Anitápolis dating was a mistake, the formation being in reality metamorphosed Carboniferous varvites (Tubarão series) deformed on a basalt-intruded fault, Rego's uncritical age determination of the Itajaí, fortified by the Anitápolis mistake, lingers on.

When so little is known of these problematical terranes and their age or correlations in Brazil (or Africa), it is indeed hazardous to make transoceanic correlations or even meaningful comparisons. The best that one can say is that there are large areas in southwest Africa where similarly controversial and lithologically more or less analogous sedimentary terranes occur. These are usually labeled "late pre-Cambrian and early Paleozoic." Apparently no fossil data have yet turned up in the African occurrences. Or better, where *Collenia* has shown up, that part of the problematical terrane has been attributed with some certainty to the Proterozoic. Without taking too much stock in actual correlations, there is a gross similarity, both in sequence and lithologies, of the older sedimentary terranes in South Africa and southern Brazil-Uruguay.

All the pre-Devonian terrane in both continents is barren of fossils, except for *Collenia* in the Proterozoic limestones of Africa and presumably equivalent limestones in São Paulo, Brazil (São Roque series = Porongos series, probably). It is quite possible that the Itajaí series of Santa Catarina equals the Camaquã series of Rio Grande do Sul.[2]

[1] There is certainly nothing in the nature of the Bambuí series either in thickness or lithology, imperfectly known though the terrane is, to justify considering it as a geosynclinal accumulation. Since it is the terrane on which the "Franciscan geosyncline" of authors was based, only confusion results from continuing to employ this term in discussing South American paleogeography.

[2] While this paper was in press, a most important study by de Guimarães (1951) on the geological evolution of pre-Cambrian Brazil appeared. De Guimarães develops a convincing argument for close genetic as well as geographic alliance in pre-Cambrian times between South America and Africa.

TABLE 1

EARLY PALEOZOIC PARALLELISM BETWEEN RIO GRANDE DO SUL AND SOUTH AFRICA (FROM OLIVEIRA AND LEONARDOS, 1943)

	South Africa		Rio Grande do Sul	
Upper Carboniferous	Dwyka glacial series		Itararé glacial series	
Devonian	Cape system		Paraná series	
Silurian?	Matsap series	Quartzites Andesitic lava Conglomerates Quartzites Slaty shales Poligenic conglomerates	Camaquã series	Seival conglomerate Andesitic lava Sandstones Shales Poligenic conglomerates
Ordovician?	Rooiberg series	Acid lavas Shales Quartzites	Maricá series	Acid lavas Shales Hard sandstones Conglomerates
Cambrian?	Nama-Transvaal system		Suspiro series of black limestones	
Proterozoic	Ventersdorp system Witwatersrand system		Porongos series	Marbles Phyllites Chlorite schists Quartzites Mica schists

DEVONIAN

Beginning with the Devonian system, the comparison between South America and Africa becomes considerably more specific and the broad transoceanic parallelism consequently much more definitely established. This is due to the widespread distribution of the Devonian system on both continents and the rich marine invertebrate faunas contained. On both continents two very distinct Devonian faunas, one "boreal" and the other "austral," existed synchronously and were intermixed on the periphery. North Africa and northern South America, including the Amazon Valley and the Colombian-western Venezuelan Andes, were "boreal" in faunal pattern. This means really North American in morphologic affinities. As mentioned above, in a discussion of the general Paleozoic of northwest Africa, this "boreal" North American (previously supposed European) flavor is ever more pronounced as paleontologic studies proceed in the Atlas, the Sahara, Algeria, Morocco, and the Gold Coast. South Africa and South America in general, south of the Amazonian Devonian realm, were inhabited by a highly characteristic "austral" fauna, apparently autochthonous to the seaways over the lands adjacent to the present South Atlantic. The "oneness" of this Atlantic-spanning fauna has been appreciated for a long time (e.g., Clarke, 1913).

North American Devonian faunal elements penetrated the Andean geosyncline as far south as the Bolivian *planalto.* Between Bolivia and Colombia they spread eastward in a belt of unknown width along the present Equator in what is now the Amazonian synclinal trough, where they undoubtedly attained the present mouth of the Amazon. This equatorial sea was once far more extensive than the narrow belt of present Devonian outcrop would indicate; an extensive outlier of this sea was recently discovered (Caster, 1947a) in the eastern part of the State of Piauí, Brazil (see 1950, Geologic Map of

South America, ed. Stose).

The coralline, limy facies of the South American Devonian occurs only in the northernmost end of the Andes and wholly in the "boreal" province. In the Sierra de Perijá, on the Colombian-Venezuelan frontier just west of Lake Maracaibo, massive coral-rich limestones are interlarded with shales and might even be termed biostromic. This fauna has been described by Weisbord (1926), Harris (1943), and Wells (1943). The limy facies gives way southward in the pre-Andean trough to clastics. At Floresta, some 250 miles south, in the Cordillera Oriental, the facies is siltstone, shale, and argillaceous limestone (Caster, 1939, 1942). In the same belt, some 200 miles farther south, at Gutierrez, the Devonian is wholly clastic; micaceous shale, siltstone, and sands contain the "boreal" fauna. This condition prevailed over all the remainder of South America during the Devonian. Limestones are unknown, and even non-fossil lime content is uncommon, in the strata. Thus the equatorial boreal belt is wholly clastic and lime free. Presumably temperature has always been the critical lime-controlling and reef-forming factor. Corals, corallines, and bryozoans are so rare as almost to be termed absent from central Colombia south. Since they are known constituents of the "boreal" fauna, their southward disappearance in the clastic boreal realm of the Andes and Amazon is best explained on the assumption of meridionally declining temperatures.

Moreover, the chief distinction between the "austral" and "boreal" faunas is probably likewise temperature-linked. The "austral" fauna is a cold-water assemblage, and the lime-free "boreal" fauna of the equatorial regions a temperate one. In Bolivia and especially in Paraguay and Mato Grosso, Brazil, a slight admixture of the temperate "boreal" and cold "austral" biotas reflects the meeting zone. Apparently no barriers other than distance and temperature existed between the very different contemporaneous faunas.

On the other hand, much of the "boreal" and "austral" distinction stems from the over-all non-contemporaneity of the faunas. The chief "austral" fauna, the Afro-Brazilian, is of Lower Devonian age and may extend back into the uppermost Silurian, whereas the chief "boreal" fauna is Middle Devonian, possibly extending into the Upper Devonian. Only coevals should be compared for most of the analysis pertinent here. Some of the supposed mixing is certainly due to survival of certain Lower Devonian "austral" organisms, such as the brachiopod *Leptocoelia flabellites*, into Middle Devonian times, when it had an almost universal distribution; but some of the supposed commingling may be due to an earlier localized (first?) appearance in the Southern Hemisphere and in the belt where the cold and temperate waters met of certain forms that later became indices of the "boreal" Middle Devonian. *Tropidoleptus* may be such a one.

The principal commingling on the cold-temperate frontier was by plankton or nekton, such as pteropods (*Tentaculites*) and jellyfish (*Conularia*); these ranged widely through all the thermal provinces, although the latter forms had their most numerous expression in the colder regions. Most benthos was apparently too rigidly circumscribed by environment to cross critical temperature frontiers.

The Amazonian Devonian (Hartt, 1874; Rathbun, 1874; Katzer, 1903, etc.) is made up of a clastic series. A basal sandstone, the Maecurú, carries abundant marine fauna, dominantly of "boreal" Lower Devonian make-up (Clarke, 1896, 1899b), but containing some forms prenuncial of the boreal Middle Devonian, e.g., *Tropidoleptus*. It is this mixture, both in Amazonas and Bolivia, that has made actual dating of the strata difficult. The sandstone grades upward into micaceous siltstones and sandstones interbedded with olive shales. The argillaceous facies (Curuá beds) carries mainly a "boreal" Middle Devonian fauna but retains some Lower Devonian carry-overs. The Curuá has often been closely compared with the New York Hamilton. Supposedly overlying the Middle Devonian shales and siltstones are petroliferous black shales (Ererê) which contain concentrations of the plant microfossils *Protosalvinia* (*Orvillia*), which in the Northern Hemisphere "boreal" realm is an Upper Devonian plant. In addition, char-

acteristic black shale marine invertebrates are present, chiefly thalassic forms such as *Orbiculoidea* and *Lingula* and thin-shelled pelecypods. The Ereré has been evaluated as the only Brazilian Upper Devonian. However, field work in the Campos de Ereré in 1948 demonstrated that the Curuá and Ereré beds are coeval intergrading facies variations, rather than sequential deposits.

The Devonian of Piauí (Caster, 1947c) occurs on the eastern edge of the Brazilian Piauí-Maranhão basin and occupies a broad, northeasterly trending belt along the Ceará border for nearly the entire length of the State of Piauí, and may actually attain the Atlantic coast. Although the outcrop is completely isolated from any other Devonian area by great distances, the terrane probably is present deep under the basin. Marine fossils are known from the vicinity of Picos, Piauí. *Tropidoleptus*, camarotoechids, and a large pelecypod fauna are dominants. They occur in hematitic sandstones and pebble beds rather than in the red and green shales which predominate in the terrane. Fish spines occur at one pebble horizon. Two calcareous concretion zones in the shale yield an abundant homalonotid trilobite fauna and sparse eurypterid appendages. Certain horizons of the shale are made carbonaceous by the concentration of eurypterid integument of the *Hastimima* type, a eurypterid hitherto known in Brazil only from the Carboniferous coal strata of the Paraná basin. *Tentaculites* and *Conularia* are the pelagic elements. Curiously, there seems to be no faunal linkage of the Piauí occurrence with the well-known "austral" Devonian of south Brazil, while, on the other hand, the fish and eurypterid remains recall the South African Bokkeveld beds (Du Toit, 1939, p. 214; Haughton, 1929, p. 125). The balance of the Piauí fauna is "boreal" and allied to Amazonas.

From South Africa to the Mediterranean, "boreal" elements are conspicuously present in African Devonian faunas. However, a distinction must be made between the North African and South African "boreal." Whereas the South African "boreal" element is really a "contamination" of a dominantly "austral" fauna, as is shown below, the North African "boreal" is a commingling of conspicuously North American faunal elements with the general Northern Hemisphere Devonian fauna. So far no suggestions of the "austral" fauna have turned up in North Africa.

The conspicuously "boreal" North African faunas extend south to the isolated block of Devonian at Accra on the Gold Coast (e.g., Krenkel, 1925–1938, pt. 3, p. 1349). The limited trilobitic fauna is apparently both North American in bearing and suggestively akin to that of the Amazon clastic sediments. In the Atlas of Morocco (Termier and Termier, 1950), the Sahara (Haug, 1905), and elsewhere, compositely, virtually all marine facies are represented. The more the Devonian faunas of North Africa are studied the more conspicuously North American their relationships become (Le Maître, 1950). Concomitant with the recognition of the North American qualities in the faunas, the supposed European and Eurasian relationships decline. It is significant that Europeans have discovered this strong American "boreal" affinity of the North African Devonian faunas.

Since the well-known European Devonian faunas apparently do not show a conspicuous North American ligation, it would be futile to presume that the Afro-American connection was by way of central Europe and the Appalachian geosyncline. In fact, the American elements recognized in North Africa are principally those of central United States and not of the geosynclinal area in the east and northeast. Moreover, during the Middle Devonian the northern end of the Appalachian geosyncline was largely blocked by deltaic accumulations and orogenic activity through New England and Maritime Canada.

It would appear that there has been no published speculation on the possible route of connection between the shallow benthos of the Mississippi Valley and North Africa. However, it is interesting to note the presence of the same "boreal" fauna in the northern Andes and that the reef (warm-water) facies of the central United States and Canada penetrates southward only to this belt. Hence, it would seem useless to look for any Afro-American, warm-water, calcareous, and biohermic facies connection by way of equatorial America, where, as is pointed out,

temperate and clastic sediment conditions prevailed. Apparently the Devonian epeiric seas extended from the United States over portions of the present Gulf of Mexico and the Caribbean to reach Colombia-Venezuela, where the fauna is a veritable "outpost" (meaning now-isolated portion) of the Kentucky-Tennessee Devonian (Caster, 1942). The climatological evidence would strongly indicate that any Afro-American ligation for this warm benthos must have lain in a completely unrevealed east-west belt between present Florida and Venezuela, a belt that may have been an extension of the pre-Andean trough and adjacent craton (trough on south, craton north).

On the other hand, the cool-water, clastic sediment fauna of the present American equatorial region seems from such scanty data as are available to extend into the Gulf of Guinea area, where the Accra outcrop is the only remnant known.

The absence of any "austral" elements either in the small Accra fauna or in the extensive North African deposits, coupled with the presence of at least two characteristic Bokkeveld forms, the eurypterid remains and the fish spines, in the Piauí fauna, and a large "boreal" element, i.e., Amazonas-Piauí (or Accra) derivatives, in the Bokkeveld (figs. 6, 7), suggest that the hitherto missing avenue of South African "boreal" commingling lay southeast from the Amazon trough across eastern Brazil and thence across the South Atlantic basin.

In all of these isolated remnants of the "boreal" Devonian beyond the North American continent, now separated by really enormous distances, we treat of large sectors of a fauna, mainly benthos, and represented by two great thermal ecologies. Isolated organisms, even benthonic forms, may be able fortuitously to cross vast, inhospitable distances, but to suppose that whole facies can achieve this stretches credulity. The alternative hypothesis consists in restoring between the isolated remnants bridges whereon at the time of distribution the same conditions existed as the remnants themselves now record. The faunas of the Devonian are shallow marine benthos in the main, hence the bridges across areas where now vast deeps prevail, i.e., the Caribbean and Gulf of Mexico, the Central Atlantic basin, and the South Atlantic basin, were presumably continuously benthonic and probably epeiric.

THE AUSTRAL DEVONIAN

By far the most widely distributed and best-known Devonian deposits and marine fauna of the Southern Hemisphere are those known as "austral" (Clarke, 1913). South Africa, the Falkland Islands, the Buenos Aires Department of Argentina, and the eastern chain of the Andes and adjacent piedmont form the south and west perimeter of the broad arc of the "austral" realm. The Andean, and possibly the South African, sectors of the peripheral arc were largely a geosynclinal environment. The Falklands and the vast Paraná basin development of Brazil (Paraná-São Paulo, Goiás, and Mato Grosso States plus parts of Uruguay and Paraguay) are, on the other hand, the cratonic expression of the realm. There seems to be no ground for doubting that over this vast area the synchronous history was very much the same both physically and biologically. The fauna is one of the best defined and most characteristically autochthonous of any known. The pre-Andean geosyncline afforded localized entry of the coeval "boreal" fauna into the southern realm as reflected by the Bolivian faunas (e.g., Steinmann, 1892; Kozłowski, 1923). Unknown connections, possibly across northeastern Brazil, as suggested above, permitted "boreal" elements to reach South Africa. In Mato Grosso, on the north side of the Paraná basin, a few "boreal" species from the Amazonian or pre-Andean trough appear in association with the southern epeiric fauna. Reed (1925) has revised the South African fauna (Bokkeveld); Clarke (1913) and Kozłowski (1913) have done the major paleontologic work on the South American "austral." Moraes Rego (1940) has compiled the stratigraphic and paleontologic data with special interest in the Brazilian expression.

THE SOUTH AFRICAN DEVONIAN

The Cape system of the Union of South Africa (e.g., Haughton, 1929; Du Toit, 1939) and the Argentine-Bolivian sequence in the

Andes are the thickest expressions of the "austral" Devonian. Certain parallelisms can be drawn between their sedimentary sequence and especially between their faunal records; both contain the same rich marine invertebrate fauna (the "austral" assemblage), and both show a conspicuous element of "boreal" admixture. Statistically the degree of mixing is much the same, though qualitatively the "boreal" migrants were quite different. Thus in this parallelism we do not appear to treat of an intra-geosynclinal migrational phenomenon. Neither the Argentine trough nor the Falkland epi-sea accumulation shows "boreal" elements in this sector of the peripheral belt.

The Cape system is three-fold; it embraces the basal Table Mountain series, the intermediate Bokkeveld series, and the terminal Witteberg series. In southernmost Africa these sediments are folded into the east-west "Cape folded belt."

The Table Mountain series attains a maximum of 5000 feet, of which four-fifths is sandstone, or quartzite. Although it is initiated by a discontinuous basal shale containing "unidentifiable" pelecypod fragments and contains another, the "upper shale," band about 1000 feet below the top, the series is mainly comprised of white quartz sandstone; there is some arkose; conglomerates are rare. Cross-bedding is usual, and rounded white quartz pebbles up to an inch or so in diameter are commonly scattered through the series. The series rest unconformably on a great erosion plane. But, curiously enough, as Du Toit (1939) points out, nowhere is there a basal conglomerate.

One of the curious developments of the Table Mountain terrane is the presence of the "upper shales," from 150 to 300 feet in thickness, overlying a well-defined tillite (see Du Toit, 1939, p. 210, pl. 18, for photograph of striated pebbles) which locally attains a thickness of 100 feet. Haughton reports that subglacial folding of the Table Mountain sands occurs locally beneath the tillite, which shows a west-to-east ice movement over the partially consolidated sandstone, although Du Toit says nothing about this. The presence of this glacial zone in the Table Mountain series has long been a challenge to those who would find a meticulously close physical comparison between Africa and South America. So far, it might be said that no undisputed Devonian tillites are reported from South America (see Paraná basin discussion below), although two possible horizons have been suggested.

Owing to the unidentified status of the sparse fauna occurring in the basal shales of the Table Mountain series and the complete absence of all other faunal data, the age of the series is somewhat in question. It is commonly assigned to Lower Devonian or uppermost Silurian, and it may well transgress the systemic boundary in the same manner as the basal sandstone of the Paraná terrane definitely does towards the Andes. The tillite horizon would make a convenient demarcation plane between the African development of the systems, if the lower four-fifths of the Table Mountain sequence could definitely be established as Silurian.

The Bokkeveld series of shales and sandstones, some 2500 feet in maximum thickness, conformably but not gradationally overlies the Table Mountain series. Shales dominate in the terrane, there being five thick argillaceous bands separated by four sandstones in the series. Sands, greywackes, and mudstones replace shales towards the northern border of the present east-west outcrop belt of the Cape. This apparently indicates a northern sedimentary source area. The shales vary from black carbonaceous deposits to greenish and bluish micaceous. Although limestone is unknown in the whole area of the "austral" fauna, fossiliferous calcareous concretions do occur in certain shale horizons of the Bokkeveld (as in Piauí). The lower three-fifths of the Bokkeveld terrane contains a marine Lower Devonian fauna, whereas the upper part contains only badly preserved fragments of terrestrial plants. There is no sharp break known between the marine and continental beds.

The Bokkeveld fauna has been extensively studied. Reed (1925) gives the latest extensive revision. Clarke (1913) made a thorough analysis of the whole "austral" fauna, as then known, and was the first to suggest a transoceanic "Flabellites land," on the southern edge of which the highly isolated south-

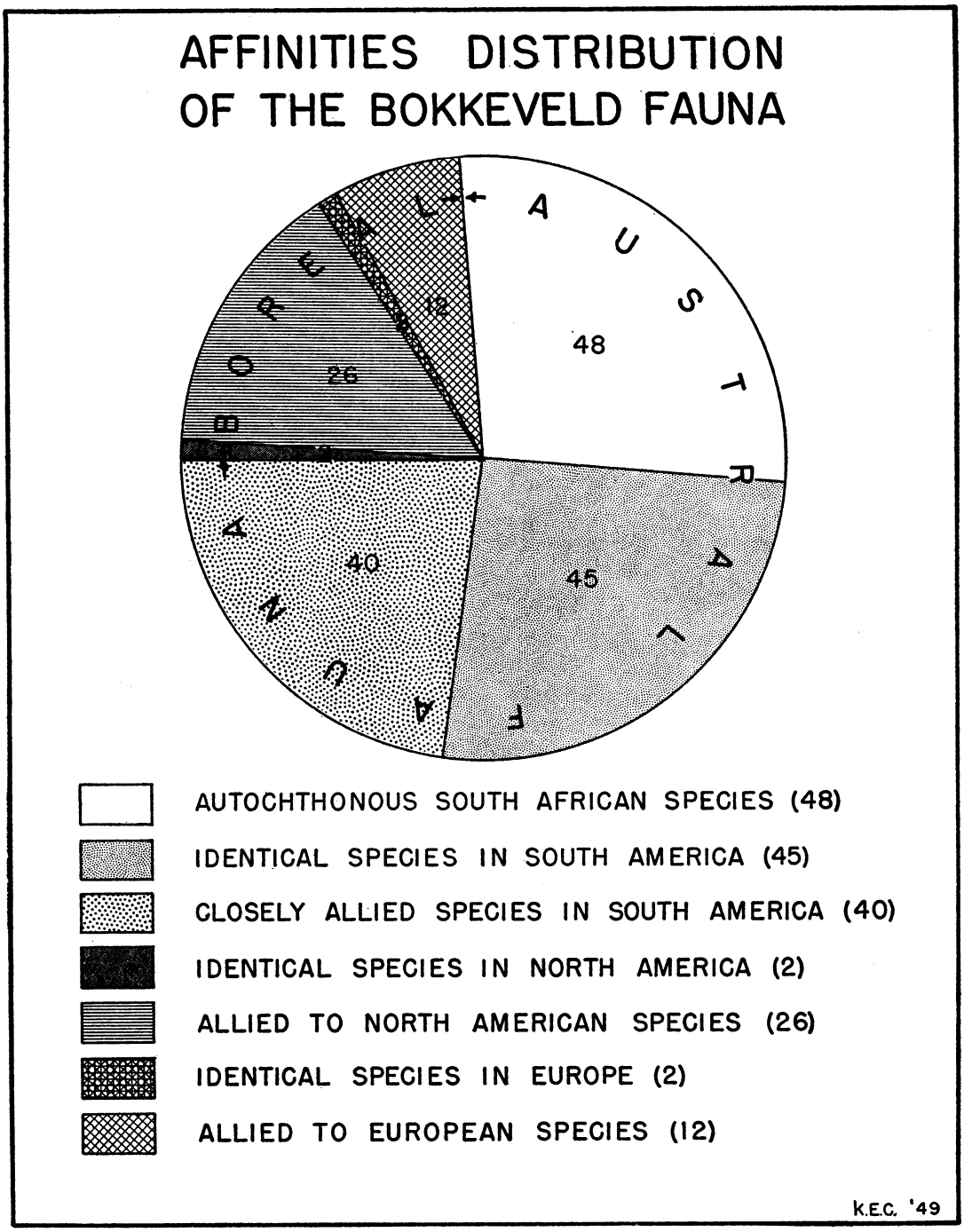

FIG. 6. Qualitative world analysis of the affinities of the Bokkeveld Devonian fauna of South Africa. Presumably a restudy of the fauna in the light of modern work in North Africa will materially reduce the supposed European "boreal" aspects of the fauna and by that much, at least, enhance the North American "boreal" flavor.

ern fauna developed. The Bokkeveld fauna is the most diversified expression of this biota. However, it has also the largest "boreal" admixture of any of the present "austral" regions, nearly a quarter of the species having northern affinities, as can be seen in figure 6. The route by which this large northern element reached so far into the southern realm is still unknown. Haug (1905) has identified several Bokkeveld species in the Sahara Devonian. Unfortunately this deposit has not yet been studied in detail, and it is not known if any truly "austral" elements of the Bokkeveld fauna occur in the Sahara. In the light of the recent studies in the Atlas area, it appears more likely that the Sahara species shared with South Africa fall in the "boreal" quarter of the Bokkeveld fauna and, if so, probably in the North American "boreal" affinity sector. Such as is known of the Accra Devonian sliver would suggest this kind of restricted "unilateral" overlap, for no "austral" species have yet been reported from the Gold Coast intermediate area. What may have been the ligation role, if any, of the Brazilian deposits in the State of Piauí (see above) remains to be seen. At one time it was supposed by Du Toit, Grabau, and others that there were connections ("Samfrau geosyncline") between South America, South Africa, and the present South Pacific. However, Allan (1942, 1947) has repudiated his former comparisons (1935) between New Zealand and "austral" brachiopods and thus eliminated the evidence on which the "geosyncline" was constructed. It now appears that the Australo-New Zealand Devonian connections were via Asia (and possibly North America) and the fauna is wholly of "boreal" extraction.

In figure 7 the South African fauna is graphically compared with the faunas of the other "austral" and adjacent areas of Devonian development. The overlaps refer to shared species. Unfortunately it is not possible to bring out the large "boreal" element in the Bokkeveld fauna in this diagram, an element that attained South Africa by other channels (and unknown) than those considered here. In this figure, moreover, no attempt is made to show to what degree the same species participates in the various overlaps of the circles. As might be expected, certain elements of the fauna are "universal," i.e., were easily and widely distributed. However, only a small number of species pertaining to such thalassic organisms as pteropods and jellyfish (*Conularia*) occur in the fauna[1]; most of the common, widely distributed forms were shallow benthos: brachiopods, gastropods, pelecypods, and trilobites. Unfortunately, study of the Piauí fauna has not proceeded far enough to make a final count possible. Its circle would largely overlap the Amazonas circle and subtend a somewhat larger South African arc than does the Amazonas one.

The closing phase of the Cape system is a supposedly non-marine terrane known as the Witteberg series. Neither its upper nor lower boundary is clearly established, but the sequence shows no break with the marine Bokkeveld or with the overlying lower Dwyka shales (Carboniferous). Although some 2500 feet are usually assigned to the Witteberg series, there are about 4000 feet of non-marine strata between the Bokkeveld and the Dwyka glacial beds. The Witteberg series is dominantly a white quartzite series, with interbedded shales and micaceous flags. As with the other Cape units, the sediments grow finer towards the south.

In the transitional (or undelimitable zone) from the Bokkeveld into the Witteberg sequence, certain of the sandstones carry spiral or "rooster-tail" (*Taonurus* or *Spirophyton*), supposed worm burrows in profusion. These "problematica" characterize near-shore marine sands elsewhere, from the Lower Devonian to the Pennsylvanian (or possibly higher). They are best known in North America in the upper Lower Devonian ("Cauda-galli" grit at the base of the Onondaga limestone) and Lower Mississippian (e.g., Berea-Bedford formations of Ohio and Pennsylvania). Contrary to the interpretation of South African geologists, their presence suggests at least a partially marine environment for the Witteberg series, although other marine evidence

[1] It now appears that there were actually fewer species of the planktonic-nektonic element in the "austral" fauna than present lists would seem to indicate. In other words, there was free access over vast distances for the same species to travel in the "austral" sea and into the bordering warmer "boreal" waters.

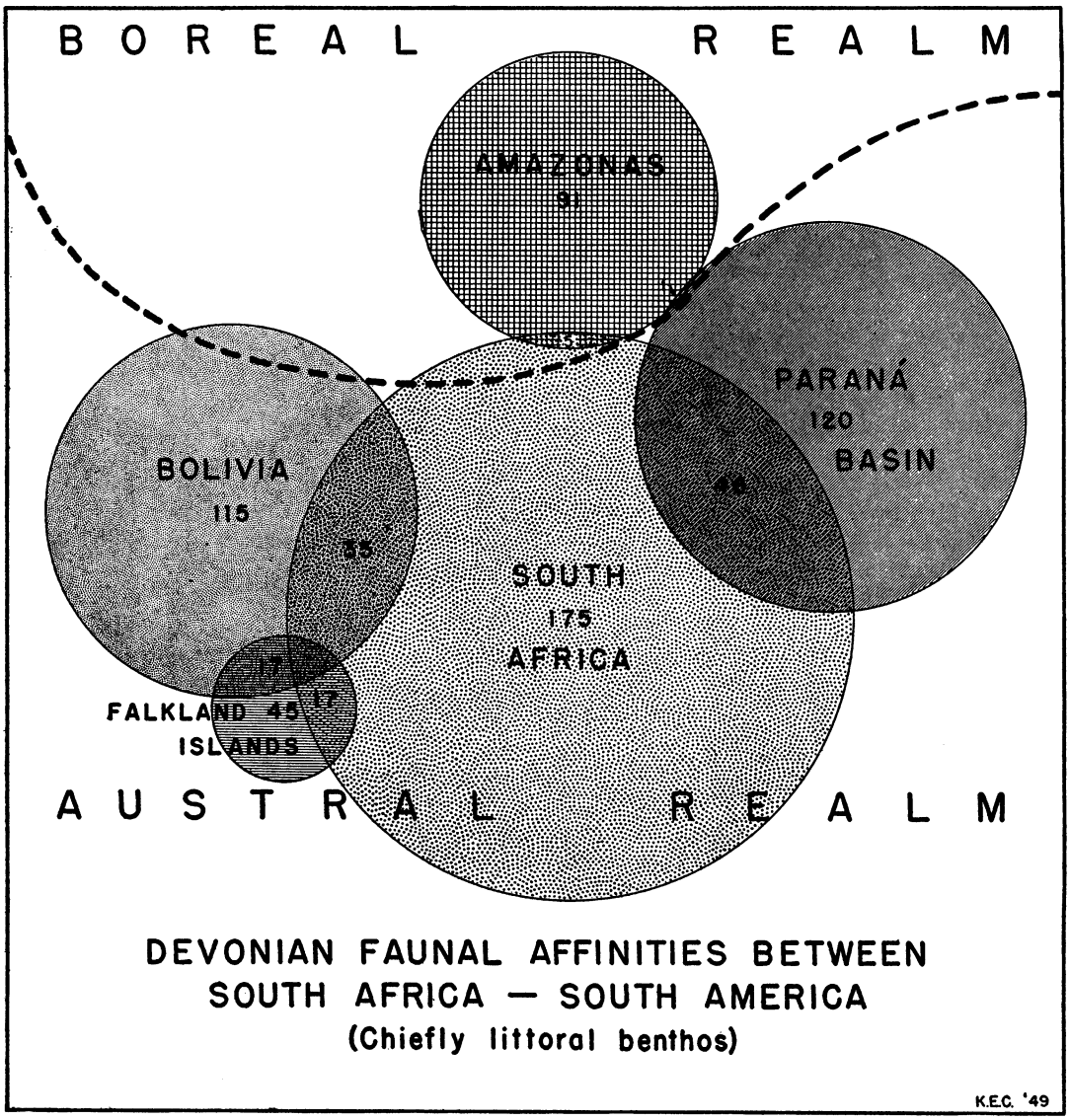

FIG. 7. South African species shared with meridional South America and the Falkland Islands. The circles are drawn on radii proportional to the number of species in each faunal province.

is sparse. In this connection the scraps of the same kind of eurypterid integument, *Hastimima*, as occurs in the Piauí deposits may be significant. Until the discovery of the same integument in the undoubtedly marine Devonian of the State of Piauí, Brazil (mentioned above), this form-genus was known only from the coal-producing interglacial beds (Tubarão series) of the Carboniferous sequence in south Brazil. A single fish spine (inadequately known) is the only biotic element shared by the Witteberg and the marine Bokkeveld beds; here again, the Piauí marine beds afford the only South American comparisons.

Certain graphitic shales of the Witteberg series are filled with triturated vegetable matter; so much so, in fact, that there have been many fruitless searches for coal in the terrane (Du Toit, 1939). From these carbonaceous

shales a rather imposing list of plant genera has been given in the literature. If the determinations are reliable, these genera certainly bespeak a very close alliance with the Carboniferous (in fact, Upper Carboniferous): *Bothrodendron, Didymophyllum, Cyclostigma, Halonia, Haplostigma, Knorria, Lepidodendron, Lepidostrobus, Selaginites, Sigillaria,* and *Stigmaria.* On the other hand, if carelessly identified, or based on too imperfect material (as was probably the case), most of these Carboniferous form-genera might be confused with cognates in known Middle and Upper Devonian floras. South African geologists, at any rate, have suggested that the Witteberg terrane (4000 feet of "non-marine" strata between the marine Bokkeveld and the Dwyka conglomerate) may extend from Middle Devonian into Mississippian time. The only other comparable Southern Hemisphere terrane is in the Buenos Aires district of Argentina (and possibly in Bolivia), where there is a similar lithic sequence and a newly discovered and rather large Devonian (and possibly Mississippian) flora (Frenguelli, 1946a, 1951).

THE DEVONIAN OF THE PARANÁ BASIN

The vast Paraná basin of south Brazil, Uruguay, eastern Argentina, and Paraguay represents the largest area continuously underlain by Devonian strata in the Southern Hemisphere. The general stratigraphic relations of this Paraná (or Campos Gerais) series as developed in Brazil (largest share of the area) have been summarized by Moraes Rego (1940) and Oliveira and Leonardos (1943, pp. 309–318). Petri (1948) has done some of the most detailed stratigraphic work on the series as developed in the Brazilian State of Paraná. Vast though this area of Devonian is, the outcrops cover but relatively small peripheral areas, and the sub-surface aspects are unknown owing to the enormous thickness of the Paraná lavas and Gondwana sediments which overlie the Devonian. Uruguay and Paraguay have extensive areas of outcrop; those of the former show no characteristics especially different from Brazil; unfortunately, the Paraguayan deposits are very imperfectly known, but appear to show a gradational change into the pre-Andean geosynclinal facies of Argentina and Bolivia. Most data have come from the narrow cuesta arc of outcrop in the Brazilian States of Paraná and São Paulo on the south side of the basin, and from a corresponding, but more extensive cuesta in Goiás and Mato Grosso on the north and northwest rim, respectively.

Throughout the basin the series begins with a basal white quartz arenite deposit, usually referred to as the Furnas sandstone, which is overlain by an argillaceous sequence with sand lenses known as the Ponta Grossa formation. Unfortunately, each country has its own names for these two basic lithologic units of the series. Throughout the basin the Devonian rests unconformably upon the crystallines or older sedimentaries, and is discordantly, albeit often conformably, topped by the Gondwana glacial beds (figs. 11, 12). The structural basin is apparently of post-Devonian origin; in Devonian time what is now the basin was part of the widely submerged craton of the Austro-Brazilian shield, which was depressed westward into the pre-Andean geosyncline of Argentina-Bolivia, whence came the original epeiric transgression.

The Paraná series was the first extensive epeiric transgression of the Paleozoic seas over the southern Brazilian shield. Although there is no present way of telling how much farther east beyond the present subsurface distribution of the series the transgression may have extended, it seems probable that the Devonian seas did not reach deeply into northern Minas Gerais beyond the present boundary of São Paulo. But there is nothing in the sediments of the southern cuesta overlooking the Curitiba basin in Paraná to intimate that the Devonian terrane did not once extend over the top of the present Serra do Mar and indefinitely beyond over the area now downfaulted into the Atlantic Ocean. The Curitiba basin exposes the pre-Devonian peneplane surface over the Açunguí metamorphic series of ancient (Proterozoic?) sediments and intrusives. Northward the epeiric sea presumably was confluent with the Amazonian "boreal" waters, but possibly only by way of the western geosyncline.

The Furnas sandstone seldom attains a

thickness of 900 feet and averages about 850 on the south side of the Paraná basin. At Aragarças, Goiás, on the northern edge it may exceed 1000 feet. It is a very pure and widely uniform white quartz sandstone which is locally conglomeratic. In Goiás and Mato Grosso red facies appear and sometimes dominate the basal Devonian sandstone. Current cross-bedding is everywhere usual, as are deep scour and fill phenomena, all being suggestive of beach or near-shore oscillation and sorting. The grains are usually well rounded. Detailed analyses have been given for Paraná by Maack (1946a). The basal zone is often coarsely conglomeratic in Paraná. The whole formation, wherever known, appears to be marine, although the lower nine-tenths of the Furnas is usually barren of fossils, other than possible trilobite trails, *Fraena furnai* Lange (1942). The top one-tenth, however, carries a sparse Ponta Grossa fauna in the sandy matrix [e.g., at Tibají, Paraná (Petri, 1948); Rio Bonito, Goiás; Santa Ana da Chapada, Mato Grosso (Caster, 1947a)]. The contact with the overlying shales is relatively sharp, but a narrow transitional zone sometimes occurs.

There seems to be no basis for questioning the wholly Devonian age assignment of the Furnas sandstone in the Paraná basin. Westward, towards the pre-Andean geosyncline, fossil data exist which indicate the presence of progressively older sub-Furnas but Furnas-like sandstones. In Paraguay (Harrington, in letter, May 6, 1949) one such facies equivalent of the Furnas even carries *Climacograptus* of European Lower Silurian aspect (Valentian). This facies relation is brought out diagrammatically in figure 9. It has been a matter of no small confusion in Brazilian stratigraphy that the main essentials of the Furnas facies are developed with amazing fidelity in the marine-washed, fluvio-glacial sediments of the Carboniferous Itararé series of the Paraná basin. Where the sandstones are isolated in the Campos Gerais of Paraná they have often been mistaken for each other, and several sharp arguments on stratigraphy have resulted. Maack (1946a), in a truly classic study based on clues first furnished by Lange (1944), resolved one of these: the unfortunately still current confusion of the Vila Velha Carboniferous fluvio-glacial sandstone with the Furnas. Both were probably derived from the same peneplaned surface on the shield of Brazil and its then Atlantic extensions, hence the close similarity. The Carboniferous sequence does yield an occasional "foreigner," however, of granite, basalt, or quartzite; such extraneous boulders are apparently not present in the Furnas. The characteristic appearance of the Vila Velha glacial outwash deposit is shown in plate 17. The curious imbrication of the weathered bedding and the castellated quartz and iron-cemented top surface weathering prove quite reliable gross distinguishing characters even over the vast distance across the basin, for the same problem exists on the Goiás border.

When this close similarity in facies between the Devonian and Carboniferous quartz sands, of supposedly such different origins though presumably in the main derived from the same source area, both coming from the southeast, i.e., area now Atlantic basin, is considered, it is natural to wonder if their environments may not actually have been much more similar than is apparent. Is there a possible glacial element in the Furnas? Could it have been, as was its certainly partial equivalent Table Mountain sandstone of Africa, in part derived from a continental glaciation? As can be seen in figure 9, there are extensive Upper Devonian (and possibly older) glacial beds in western Argentina (Frenguelli, 1946a). While these have no direct bearing on the Furnas, they attest to at least local Devonian frigidity in South America. As a matter of fact, the whole succeeding "austral" marine Devonian fauna bespeaks cold water.

As will be seen in the same figure, a questioned infra-Furnas tillite horizon exists in Brazil. This is based on a unique, controversial occurrence. Oppenheim (1936) and others have called attention to an "arkose" which underlies supposed Furnas sandstone in the cuesta overlooking the Curitiba basin, Paraná. The sole exposure is at the foot of the cuesta on the Castro to Tibají Road (the Lapó formation, Maack, 1947b). The writer visited this site with Reinhard Maack in 1947, accompanied by Mrs. Caster and Setembrino Petri. The party concurred with

Vila Velha sandstone, a fluvio-glacial deposit of the Carboniferous, Vila Velha State Park, Paraná, Brazil. Except for the presence in this sandstone and conglomerate of an occasional erratic boulder, the deposit is almost indistinguishable from the Devonian Furnas sandstone which underlies it by some 800 to 900 feet, but with which it has often been confused. Note the people at top of the photograph, for scale. Photograph by Lange da Morretes

Varvites in the Itararé (glacial) group-facies, lower Tubarão series (basal Gondwana), near Itú, State of São Paulo, Brazil. Occasional faceted and striated "flat-iron" pebbles and boulders occur as ice-rafted erratics in these otherwise fine silts. The exposure is a freshly cut face of a flagstone quarry. Photograph by Caster

Mrs. Caster in defining this deposit as a tillite rather than an arkose. Striated rounded pebbles to boulders are common here as are "flat-iron shaped" pebbles. The till is sharply delimited from the overlying white quartz sandstone and lies above the Castro porphyry, rounded blocks of which are incorporated in it. Since the cuesta has always been supposed to be due to the Furnas sandstone, it would appear that this is a pre-Furnas tillite. This is Maack's (1947b) contention. Caster and Petri (1947) and Petri (1948), however, point out the block-faulting which is characteristic of this area and which had previously passed unnoticed to the extent of seriously confusing stratigraphers (e.g., Maack, 1946a, 1947a). Itararé glacial sandstones have been mistaken for the Furnas sandstone within a short distance (north end of the Serra de Monte Negro) of this spot, as Petri (1948) has brought out. There is still a possibility that the supposed Furnas of this spot is a down-dropped block of the Itararé formation and that the Castro porphyry is post-Devonian. The age of this intrusive is not established, for this is the only place where it has been supposedly demonstrated that the porphyry directly underlies the Furnas. Furthermore (and this is the crux of the writer's skepticism), the sandstone above the tillite here shows the characteristic imbricate bedding and surficial castellate weathering elsewhere so characteristic of the Itararé beds (see pl. 17). On the other hand, no erratic boulders were seen in the sandstone, but the discovery of these in the Itararé (e.g., Vila Velha) often requires long search (Maack, 1946a).

In the Mato Grosso development of the basal Devonian sandstone, at the northwest "corner" of the Paraná basin (see 1950, Geologic Map of South America, ed. Stose), occurs the largest Devonian outcrop in Brazil. In this area, the relations of which are shown in figure 8, a red facies replacement of the typical Furnas enters from the northwest (current foresets dominantly from the northwest in the whole Chapada de Santa Ana, just east of Cuiabá). This, with an antecedent pink phase, virtually constitutes the basal Devonian sandstone in the famous scarp facing the Rio Cuiabá and exposed on the old road via Burití to Santa Ana da Chapada. Here only 1 to 3 feet of basal white quartz conglomerate represent the normal facies of the Furnas. The red replacement continues apparently through the east-west length of the Serra Azul, along the Rio das Garças to Aragarças at the junction with the Rio Araguaia, where only the upper fifth of the basal Devonian terrane is red, the inferior remainder being of the typical white Furnas facies of south Brazil. Turning south from either end of this east-west line, the red beds rapidly disappear upward from the Furnas terrane. As soon as the red facies is absent, the marine fauna begins to appear in the upper limits of the white sandstone. In the Rio Bonito area of Goiás it descends for more than 100 feet into the upper Furnas, just as in Paraná.

Where the red facies replaces the typical Furnas, the "austral" fauna appears abruptly in greenish and bluish paper shales, apparently following a diastemic hiatus. Thus, in the Paraná basin, just as in South Africa, where the cratonward expression (as, it is assumed, the western source must indicate the red beds are) of the geosynclinal facies is developed, the marine fauna comes in sharply, without downward transition into the arenaceous facies.

The Furnas sandstone and the Table Mountain sandstone occupy the same basal position with respect to the well-known "austral" Devonian faunas. However, they cannot possibly represent the same sweep of time; both are coarse clastic facies in the main, and the Table Mountain sequence is more than five times as thick as the Furnas. In figure 9 approximately 1000 feet of upper Table Mountain are suggested as representing the time of true Furnas deposition in South America. This is essentially the post-tillite phase of the Table Mountain terrane. The pre-tillite phase may well have time equivalents, and even facies equivalents, in the imperfectly known trough phase of the sub-Furnas in Argentina, Bolivia, and Paraguay. The essential distinction between the Table Mountain terrane as a whole and the Furnas is the difference in setting of the two. The former is a trough accumulation not too far removed from a source-land to the north of the present area of South African outcrop.

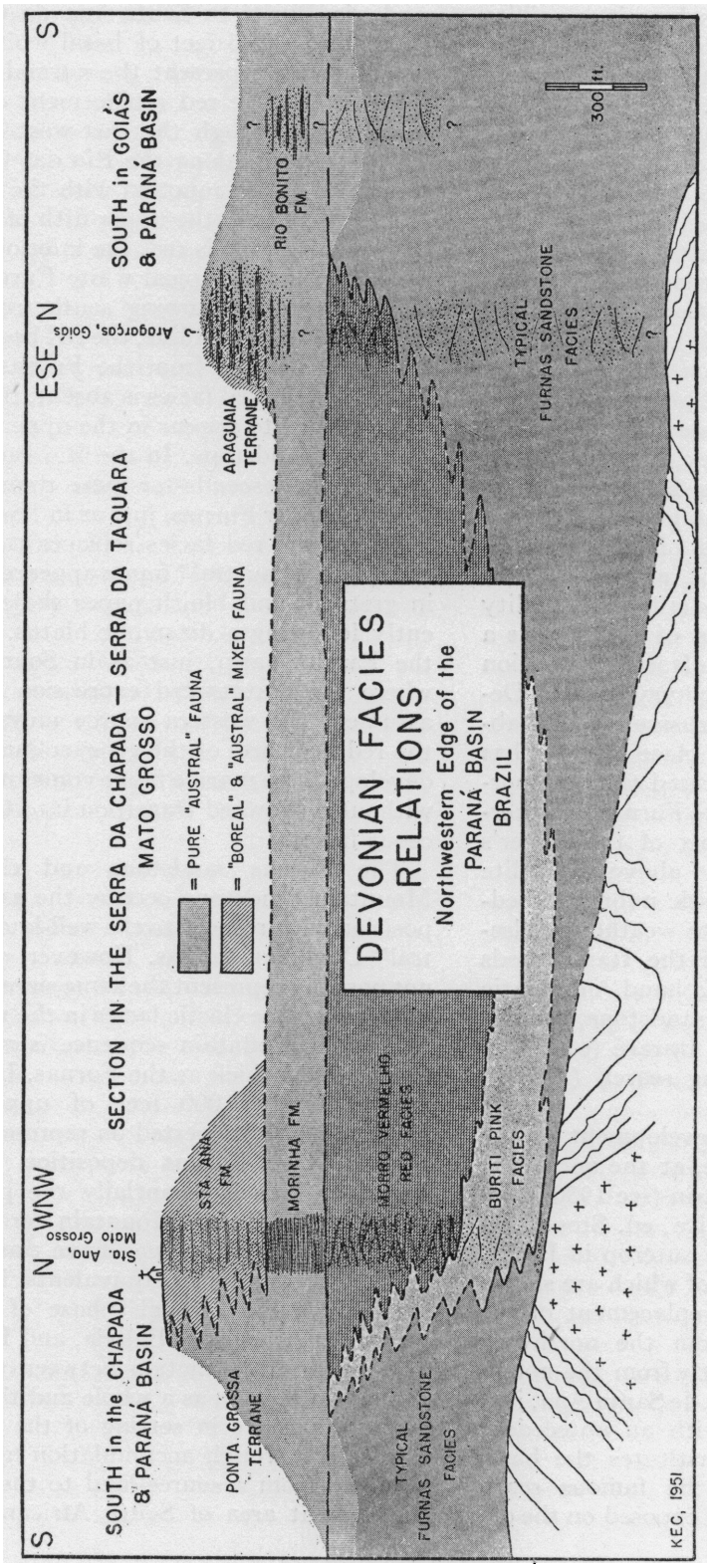

FIG. 8. Intermingling of cratonic and geosynclinal litho-facies in the Devonian on the northwestern edge of the Paraná basin. The white Furnas sandstone represents the transgressive, cratonic phase, derived from the Brazilian shield, whereas the red litho-facies apparently had its origin in the mobile belt to the west. The "boreal" faunal invasion of the "austral" fauna in the upper part of the section probably represents a later faunal duplication of the same phenomenon. Based on original observations in Brazil in 1947. Note that this diagram makes a right-angled bend at each end.

It grades southward into a finer and deeper (but still trough) facies; its true cratonic transgressive expression is apparently unknown, since it should lie to the south of the present South African Devonian outcrop and continent. The Furnas facies of the Paraná basin is the American development of the precise analogue of the cratonic facies which is missing in South Africa. Thus ecologically the two terranes are not comparable. Whereas the Lower Devonian marine fauna appeared in the cratonic deposits in Brazil while the coarse clastics were still accumulating, they reached the South African geosynclinal belt suddenly, and apparently only after an abrupt change from terrestrial to marine setting, and the establishment of at least partial "cratonization" of the previous geosynclinal belt. Moreover, the very presence of the Bokkeveld fauna is indicative of the existence beyond the present area of South African outcrop of the missing true cratonic realm to which the Bokkeveld, like the Ponta Grossa, pertains. The same broad paleogeographic relations may well have existed and even synchronously in the mirrored sides of the craton, without, however, any iso-facieological sedimentary continuum existing or ever having been present between them.

In other words, the South African (Cape) and pre-Andean deeps are fundamentally mirror-images rather than disjunct continuations; the Cape source-land was to the north and northeast, whereas the pre-Andean source was to the west and southwest, and cratonic or epeiric conditions (Bokkeveld-Ponta Grossa) afforded the connecting link between these opposing troughs. Moreover, there is no reason to suppose that these geosynclinal troughs necessarily ever had any great extensions into the present oceanic areas; quite the contrary, indeed, so far as the American trough goes. The southeast to northwest Ventana Range of Buenos Aires, a continuation to the Atlantic coast of the pre-Andean trough, apparently disappears within the present continental shelf, unless it doubles back sharply on itself for an unknown southward continuation under Patagonia. At any rate, the Falkland Islands, which are an emergent portion of the Patagonian Shelf, are covered by a cratonic expression of the Furnas sandstone and succeeding fossiliferous shales, with no signs of a geosyncline on either side. In fact, the Falkland Islands would conform both lithologically and faunally to the hypothetical characteristics of the missing South African craton. Ecologically, despite their position so far south and across the axis of the pre-Andean trough, the Devonian of the Falklands matches the Paraná basin. The fauna (fig. 7) contains the largest percentage of African species of any of the Western Hemisphere developments of the "austral" fauna. Du Toit (1927), of course, "floated" the islands northward so that they would come to lie directly between the Paraná basin and the Cape system in his readjusted continents.[1]

The Ponta Grossa shales and their equivalents carry the well-known "austral" marine Devonian fauna. The southern expression of the shales is thickest, with columns over 850 feet thick being known in Paraná; on the northern edge of the basin, in Goiás and Mato Grosso, the total Devonian fossiliferous column (only part of which can definitely be identified as Ponta Grossa) above the Furnas sandstone seldom exceeds half this figure. Whereas in the north the shale phase is either very pure and restricted to less than 200 feet (Morinha formation, fig. 8) or an alternation of micaceous shale and sandstones (as in the Rio Bonito beds, Goiás, fig. 8), in the south it is a rather uniform shale terrane with lenticular sandstones (see Petri, 1948; e.g., the Tibají) which are often literally charged with the same arenaceous fossils, chiefly spirifers, as similar lenses in the Bokkeveld beds. Petri (1948) gives a thorough faunal listing for the Ponta Grossa; over 120 species are now known (fig. 7), none of which

[1] Personally, if I were inclined to float continents about, I would be willing to have the Falklands where they are with respect to Argentina; they would fit quite nicely south and west of the present remnants of the Cape system and provide a scrap, at least, of the shield across which the cratonic element (Paraná) of the Bokkeveld fauna transgressed to reach the Cape. Yet they would need to be remote enough geographically from the present expression of the Cape system not to have been contaminated by the "boreal" elements acquired by the Bokkeveld fauna by the time it reached the present South African land area.

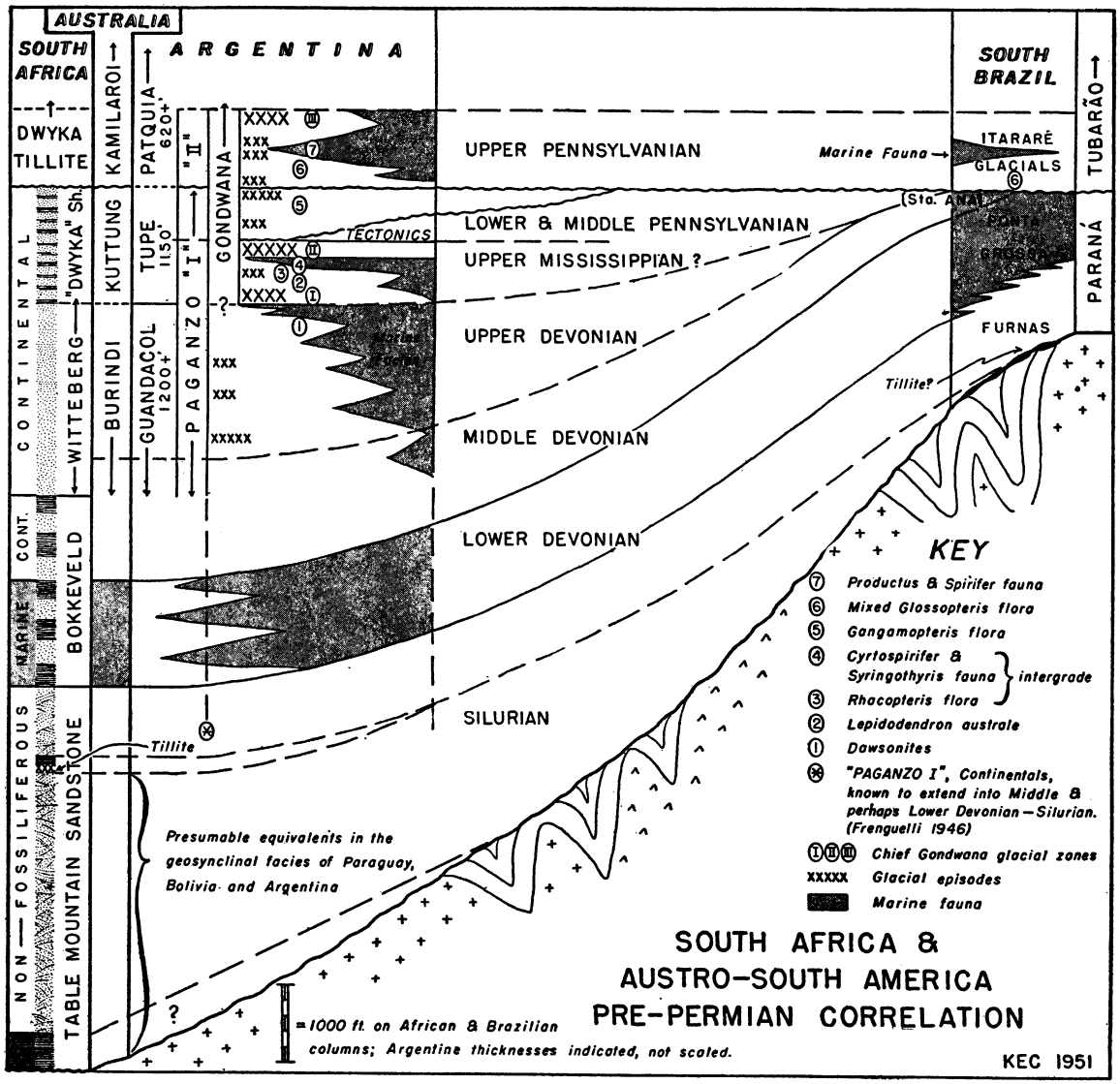

FIG. 9. The possible relation of the cratonic sediments of the Paraná basin, the Cape system of South Africa, and the pre-Andean geosynclinal facies of Argentina-Bolivia. The "Paganzo" relations in Argentina, and the correlations with Australia, are taken from studies by Frenguelli, Harrington, Leanza, and others; all other suggested correlations are original.

in the typical area is of northern affinity. About one-third of the species is closely allied to or identical with Bokkeveld species; however, it is significant that the two formations do not share any of the characteristic "boreal" quarter of the Bokkeveld fauna.

It is in the Paraná basin (including the Falkland Islands) that the pure "austral" fauna is found; out of a western Atlantic-Brazilian center the fauna becomes contaminated by other facies faunas, both towards Africa and westward in America. In other words, the so-called "austral" fauna is a geographically extensive facies fauna and in no sense a complete fauna (not even the complete southern fauna). The fauna called "austral" evolved in, and characterized the shallow waters of, the cratonic (epeiric) ex-

pression of the southern Lower Devonian transgression. The fauna appears to be unique and amazingly homogeneous only because, in the main, but one facies expression has been extensively preserved, and that studied in great detail.

On the peripheries of the cratonic development (areas now largely eroded) one should expect gradations into other facies expressions of the whole southern fauna. At the extreme limits, east and west, the epeiric benthos should give way to geosynclinal facies where mobile belts were present. In these belts, possibly because of their far-reaching (northward) linear extensions and especially because of their shores, migrants from distant centers of evolution might enter. This seems to be precisely what did happen. Many of the species differences between South Africa and Brazil-Falklands probably correlate with the closer proximity to the trough and the consequently somewhat less cratonic setting of the former (i.e., more coarse clastic contamination, for one thing). This seems also to be the key to the species differences, essentially of the same order of magnitude as between the typical Paraná basin expression of the Devonian fauna and the Paraguayan-Bolivian expression. If the Paraná basin circle of figure 7 were superimposed appropriately, in accord with the faunal comparisons, on the Bolivian circle, the overlap would be of about the same magnitude as exists between the Bokkeveld and the Bolivian fauna and probably for exactly the same ecologic reason: synchronous homotaxis.

On the northwest border of the Paraná basin (fig. 8) there is preserved a unique remnant of the inter-facial gradation between the cratonic and mobile belt litho-facies and faunas. This condition presumably existed all the way south along the now eroded western edge of the basin in Paraguay and Argentina. Presumably when the Devonian of the eastern Bolivian Montañas is better known, it will help to bridge still better the gradation between the peripheral zone and the Devonian geosynclinal belt now preserved in the present high Andes.

No marine Middle Devonian apparently is known south of Bolivia; this may be a reflection of the evanescence of the pre-Andean geosyncline southward, as is suggested above. In Argentina, however, above a "boreal" Middle Devonian marine fauna, Middle Devonian continental beds (Frenguelli, in letter, 1951) are turning up in the geosynclinal belt, as are Upper Devonian and Mississippian (Frenguelli, 1946a, 1951). The fossil floras seem to be quite positive as to age. Moreover, there are at least two pre-Pennsylvanian glacial episodes recorded. There seems to be close parallelism with Australia in this respect (Frenguelli, 1946a).

In the typical (south Brazilian) development of the Paraná basin, the sequence terminates with the Ponta Grossa shales (Petri, 1948) which are overlain by Itararé glacial beds. The Itararé sequence is highly variable laterally, embracing as it does every aspect of continental glaciation from the diverse fluvio-glacial deposits to the till itself. Moreover, this is the superior contact everywhere throughout the Brazilian expression of the Paraná basin Devonian, even on the northern border, in Goiás and Mato Grosso, where the Aquidauana deposits were shown by Almeida, Barbosa, Caster, and Petri (Caster, 1947a) to be fluvio-glacial. This is the relation shown in figure 9.

In the region of Tibají-Lambedor, Paraná, Maack (1946b) has given the name Barreiro to a sandstone and conglomerate formation lying directly above the Ponta Grossa shales. It is his contention that this formation represents a non-marine regressive phase of the Lower Devonian of the basin analogous to an upper sandstone, capping the Falkland terrane. Caster and Petri (1947) and Petri (1948) have argued that this is apparently a fluvio-glacial deposit and attributable to the Itararé Carboniferous (more or less equals Vila Velha sandstone), and that no regressive or upper sandstone phase of the Devonian exists in this part of the Basin.

In Bolivia, the Huamampampa sandstone (e.g., Steinmann, 1892; Kozłowski, 1923) of the Andes carries *Tropidoleptus* with a sparse "austral" (or "australoid") fauna and is succeeded by characteristic Middle Devonian faunas, closely allied to North America (admixed with "austral" elements). The situation in the Chapada de Santa Ana, in Mato Grosso (fig. 8), and in the highest part of the

Devonian column suggests affinity to the Huamampampa-Icla terrane of Bolivia. On the Chapada there is an abundant *Tropidoleptus* fauna in the Santa Ana formation [presence reëstablished by Almeida, Barbosa, Caster, and Petri (Caster, 1947a) after more than half a century of serious doubt (Clarke, 1913, p. 45) as to its presence], associated with many undescribed invertebrates, some of which are certainly "austral" but many of which are "borealoid." The Santa Ana overlies the Morinha formation (Caster), with no apparent transition. This formation carries a characteristic and pure "austral" (Ponta Grossa) shale fauna. The age of the Santa Ana beds may prove to be Middle Devonian. On the other hand, this aspect may reflect homotaxis, with the geosynclinal facies developing meridionally in later Lower Devonian time a fauna, or faunal elements, which were to be widely characteristic of the Middle Devonian elsewhere. Beder and Windhausen (1918) and others since (e.g., Bonarelli, 1921) have reported seemingly similar "austro-boreal" and Lower–Middle Devonian faunal associations in Paraguay.

In South Africa and the Falkland Islands a clastic sequence intervenes between the marine Lower Devonian and the first great glacial terrane (Dwyka-Lafonian). In South Africa many insufficiently determined plant fragments are reported from the sequence; the Falkland terrane seems to be barren. Whereas in the Falklands the strata are often interpreted as the regressive facies of the Lower Devonian, there is no general consensus for the South African deposits. In view of the isofacial and homotaxial similarity already seen to exist between the geosynclinal facies of the synchronously deposited Lower Devonian of the Cape system and the pre-Andean terrane, it is particularly challenging to observe the remarkable discoveries in recent years of the Argentine geologists with respect to the reinterpretation and clarification of the supposedly older Gondwana terrane.

Frenguelli (1946a, 1951) and others show most convincingly that the older "Gondwana" of Du Toit (1927) and others, the Paganzo system, bed I, of Bodenbender (1897, 1902), which both correlated with basal Gondwana beds (Du Toit, with the Dwyka; Bodenbender, with the Talchir glacials), descends far below the Permo-Carboniferous true Gondwana terrane, to embrace Mississippian and probably Middle and Upper Devonian units. Moreover, Frenguelli (1946a) says that it may even descend to include Lower Devonian and the Upper Silurian. The terrane represents a continental and glacial sequence in the western border of the pre-Andean geosyncline. Several marine incursions in the later part of the terrane give reliable dating horizons. No Gondwana floral elements exist in this very thick sub-Gondwana terrane. Figure 9 suggests a possible correlation of the lower part of this Argentine terrane (Guandacol series) with the upper Bokkeveld and Witteberg sequence of the Cape system. Frenguelli makes a categorical correlation with the now generally recognized pre-Gondwana sequences in Australia, the Guandacol being in every respect comparable with the Australian Burindi. The Argentine sequence, which varies from 300 meters to more than 1000 meters in thickness, carries, as does the Burindi, the Devonian plant *Dawsonites* in its upper part and appears to grade into known Middle Devonian marine beds locally in Argentina (and Bolivia, in all probability). The Guandacol terrane is conspicuously glacial. This terrane, and the ensuing Mississippian one of Argentina, are represented by the Devono-Carboniferous hiatus in Brazil.

The present remnants of the "austral" Devonian sediments show every sign of structural interruption at the present coast lines. On both sides of the South Atlantic the Devonian epicontinental seas must have extended into the area now occupied by deep ocean basin. In South Africa this means a geosynclinal extension westward (? northwestward) of the Cape trough; in South America the Paraná basin epi-sea reached far beyond the present continent. As is brought out in the preceding paragraphs, the biotas on the two sides of the Atlantic share identical ("austral") cratonic elements, rather than geosynclinal. Such geosynclinal similarities as exist are, on one hand, coevally homotaxial derivatives of the austral fauna itself and, on the other, "boreal" migrations into the en-

tirely distinct and actually opposed troughs. There is absolutely no evidence of a "Samfrau" or any other geosyncline crossing the Atlantic area to connect the pre-Andean and Cape geosynclines.

The South African "boreal" migrants (trough facies elements) necessarily entered from a northern center; the fauna shows that the nearest outpost of that center was in equatorial Brazil and North Africa. This means apparently that the Cape trough did extend over a great distance into the present deep South Atlantic basin area, to connect with the eastern Brazil (Piauí) "boreal" development, which shares some striking faunal similarities with the Bokkeveld-Witteberg, or with the mouth of the Amazon (and extension of the Maecurú-Curuá-Ererê fauna), or with the Gold Coast (Accra remnant). Such a geosyncline must apparently have a sialic floor; at least the preserved remnant does. Such troughs pertain to the continental sectors of the earth's surface, rather than the oceanic, and probably are never half one and half the other.

Moreover, it seems inescapable that the Paraná basin elements (true "austral" elements) in the Bokkeveld fauna reached South Africa via an epeiric sea; i.e., over craton; i.e., over sial. These facts leave us with very little alternative other than to "bridge" the South Atlantic basin with "continent." At the present time, it is largely a matter of faith, belief, or prejudice whether or not one makes this continental ligation coextensive with the present ocean basin or introduces rifting and "drift" to increase the area of the modern basin over the former "bridge." Whatever the manner of achieving present geography, the inference remains: in the Lower Devonian there was no "South Atlantic basin" in existence in any dimension or condition which would justify applying the modern name to it, especially with all the semantic associations that go with the name.

PRE-GONDWANA CARBONIFEROUS

The Argentine Tupe formation (Frenguelli, 1946a), from 120 to 200 meters in thickness, lies disconformably above the Guandacol series, and continues the pre-Gondwana chapter of Windhausen's old Paganzo series, unit I (figs. 9, 15). It is characterized by fluvio-glacial beds at the bottom, with striated boulders, out-wash gravels, varved deposits, and characteristic "Marlekor" glacial concretions. Some coaly layers occur in the sandy terrane, and in the upper part of the lower section many triturated plant zones appear. These carry a very characteristic non-Gondwana, non-*Glossopteris* flora, which Frenguelli identifies, in many cases to species, with the flora of the glacial stage of the Australian pre-*Glossopteris* Kuttung series. *Lepidodendron australe*, *Rhacopteris circularis* (European Kulm), *Sphenopteridium cuneatum*, *Sphenopteris*, and *Calamites peruvianus* are some of the commoner representatives. Frenguelli (1946a, p. 304) dates this as a Viséan flora. In places the plant zone carries a characteristic Mississippian marine fauna.

In the middle of the Tupe comes a massive "greywacke," or tillite, clearly of glacial origin, which bears scattered calamite fragments. Above this comes a now well-known marine zone (Herradura and Tontal faunas), characterized by *Syringothyris keideli* and the Upper Devonian carry-over, *Cyrtospirifer* (Harrington, 1939; Leanza, 1945, 1948). *Chonetes scitula*, *Spirifer pericoensis*, and *Streptorhynchus inaequiornata* are some of the marine dominants here. In the Tontal section *Rhacopteris ovata* occurs in the marine zone. The age again seems to be Dinantian (Du Toit, 1937, p. 67; Keidel and Harrington, 1938, p. 190; Keidel, 1939a, p. 128; 1942, p. 102) or older (Heim, 1945, p. 265). The Tupe series in the Quebrada de Herradura type section terminates with a 10-meter tillite bed, above which the 1000-meter thick Patquia (Paganzo, unit II) terrane follows disconformably.

However, in the Bajo de Velis and Bonete sections of Argentina there intervenes an "Upper Tupe" continental sequence (Frenguelli, 1946a), of some 190 meters in thickness, between the normal disconformable top of the Tupe and the "great glacial" series (Gondwana) of the lower Patquia (Paganzo II). In the lower part of this upper Tupe terrane Frenguelli finds definite Westphalian (Muscovian) plants; in the middle, a Lower Stephanian (Lower Uralian) flora, and, still higher, an Upper Stephanian (Middle Ura-

lian) one. Thus, in the complete Tupe terrane, the Lower, Middle, and lower Upper Carboniferous seem clearly to be represented. As Frenguelli points out, the Upper Tupe sequence is a unique record for "Gondwanaland,"[1] where this long time stretch was characteristically erosional; e.g., in Australia, where an unconformity marks the break between the Lower Marine series (=basal Patquia) and the Kuttung glacials (=lower Tupe).

There is a strong temptation tentatively to correlate the new Argentine (Tupe) findings with the little-known 1500 feet of lower Dwyka shale in South Africa. It is critical to such a correlation that the little-known terrestrial flora of the Dwyka and the contiguous Witteberg terrane be restudied.

The brief marine incursion in the Paganzo I (Tupe series), and possible earlier similar incursions, still inadequately understood, establish the presence of a recurrent marine center, joined northward with the marine seaway in Bolivia and Peru, whence during the ensuing Gondwana time periodic transgressions reached eastward across the adjoining Brazilian craton. Marine beds interstratify with the Gondwana glacials and intergrade with them when the ice front pushed out into the western sea from the emergent shield. This marine element is essentially missing in the African development of the post-Bokkeveld. The one exception is seen in figure 15 in the upper Lower Beaufort.

Whatever the detailed Afro-American correlations prove to be, it seems clear that the broad South Atlantic structural relations that were established in the Lower Devonian (or Silurian) continued throughout the Upper Devonian, Mississippian, and probably the whole of Gondwana time. Thus, one should expect to find not evidence of a former lithic continuum between the geosynclinal deposits of Africa and Argentina, but only at best a homotaxial similarity and possibly equivalence in time. Their actual scenes of sedimentary accumulation were separated by a vast craton. Apparently during most of post-Bokkeveld Paleozoic and Gondwana time this was an emergent shield. Across it, floral and terrestrial faunal migrations were possible, and upon this emergent "bridge," whereon the Lower Devonian epeiric sea had been, various continental glacial centers may have developed through the Devonian and Mississippian, just as they were later certainly to develop during the "Permo-Carboniferous." It is suggested above that there may exist a continental glacial chapter in the ultimate background of the sediments now constituting the Furnas sandstone.

The existence of cratonic continental glaciers is now suggested especially for the time embraced by the hiatus between the Ponta Grossa and the Itararé (=Upper Pennsylvanian) because of the presence of several glacial horizons in Argentina during this time. Although these particular tills are probably (though not necessarily) of source-land (i.e., mountain glacier) origin, coeval continental glaciers may very well have existed on the adjacent emergent shield areas. Possibly the strange dominance of white quartz in the Pennsylvanian (Itararé) fluvio-glacial sand and gravel deposits of the Paraná basin, which renders them so strangely similar to the Furnas sandstone, is in part attributable to the reworking of glacial materials left on the craton by post-Ponta Grossa continental glaciers. The white quartz residua from the chemical weathering of various continental glaciers between Africa and South America would afford at least a plausible explanation for the overloading of the Itararé glacial beds with this material. The possibility of a glacial element in the Furnas itself is discussed above.[2]

GONDWANA DEPOSITS

Under the head of Gondwana deposits only

[1] As Dr. Curt Teichert has recently pointed out (oral communication), the term "Gondwanaland" is redundant, inasmuch as the word Gondwana means "land of the Gonds."

[2] This same principle may prove eventually worth considering in connection with the perennial difficulty all geologists have in attempting to account for a terrane so rich in vein quartz and so enormous in volume as the North American Pottsville (Lower to Middle Pennsylvania) facies. There may well be a much larger glacial element in the whole Pennsylvania-Permian terrane of eastern and mid-continental United States than has heretofore been suggested; far more than is implied by the almost certain glacial origin of the cyclothems and megacyclothems in the waxing and waning of "austral" and perhaps more widespread continental ice caps.

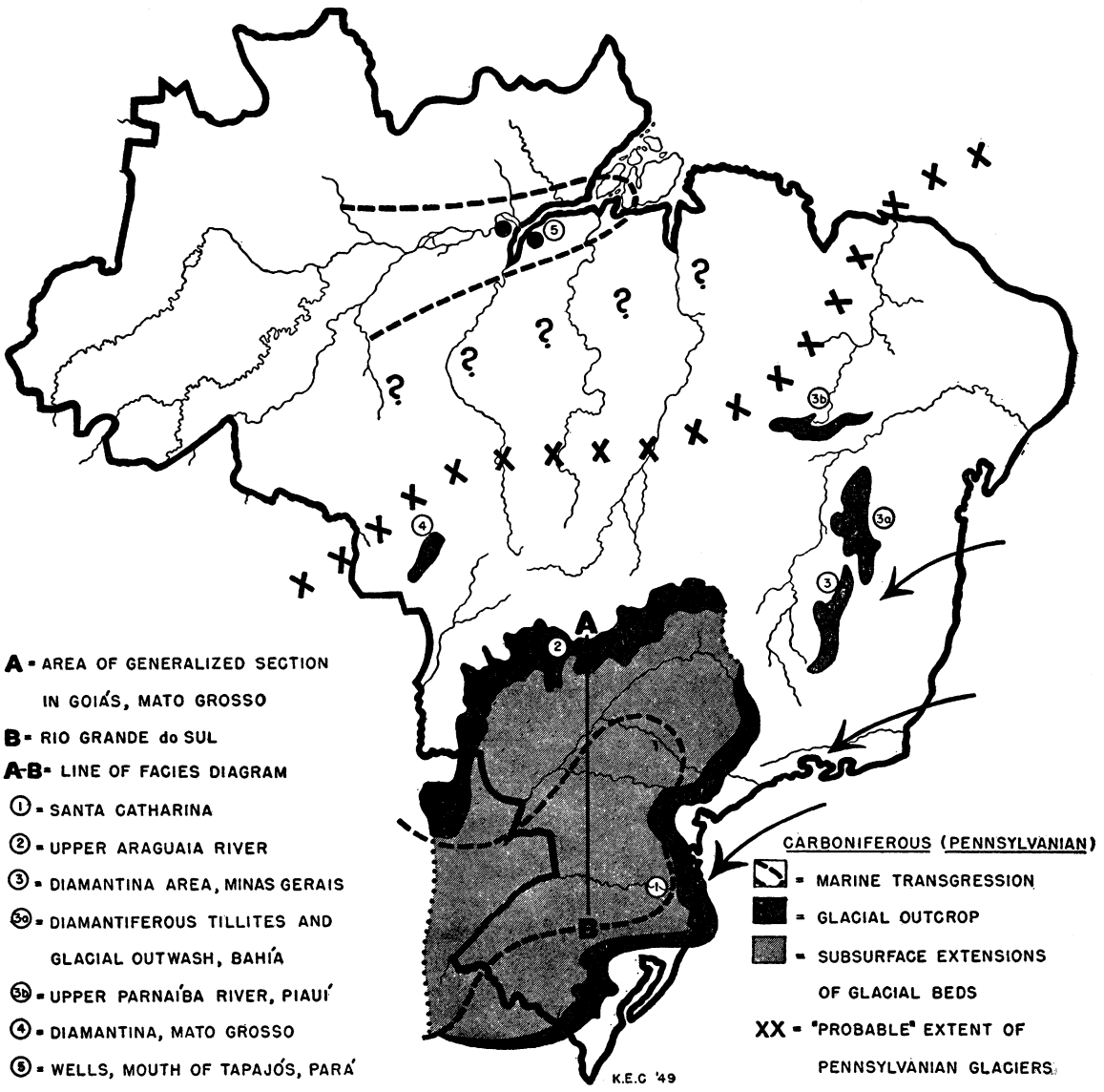

FIG. 10. Distribution of glacial deposits in the lower Gondwana terrane of Brazil. The eastern Brazil glacial areas have usually been classified as older Paleozoic, and the Amazonian occurrences glossed over in modern literature. Incidentally, these surface occurrences of glacial deposits furnish the chief, if not the exclusive, source of Brazilian diamonds.

far-flung terranes characterized by some aspect of the *Glossopteris* flora are here considered legitimate. This restricts the term essentially to those "austral" deposits found in both geosynclinal and cratonic expression and long known as the sequence initiated by the "great glacial" episode. This includes the equivalents known in South Africa as the Dwyka tillite, in Brazil as the Itararé, and in the Falklands as the Lafonian tillite. As is demonstrated above and is more fully documented by Argentine geologists, the geosynclines carry older glacial deposits, physically indistinguishable from the true Gondwana terrane and often in earlier times identified with it. However, the *Glossopteris* flora is

unknown in these older, pseudo-Gondwana beds, where a wholly Carboniferous and typically "austral" flora, without "Gondwana" contaminants, prevails. Moreover, as Frenguelli (1946a) shows emphatically, there is no "boreal" admixture in this (or for that matter the subsequent) flora; it may well be described as autochthonously "austral," but not "Gondwana," although it certainly existed over all of "Gondwanaland." Even the initial Gondwana terrane can hardly be described as characterized by other than an "impure" *Glossopteris* flora.

Brazilian Gondwana Deposits

Gondwana deposits have their most extensive South American development in Brazil. Figure 10 shows the areas of glacial terrane which the present writer, after having examined the evidence in the field, judges to be assignable to the Gondwana. Many will disagree, both as to the dating and the actual glacial nature of some of the deposits outside the Paraná basin. The basin itself extends into the adjacent countries of Uruguay, Argentina, Paraguay, and Bolivia, where the characteristically cratonic expression of the Gondwana terrane assumes the geosynclinal expression best known in Argentina. The Falkland Islands again pertain to the Paraná basin setting, as they did in the Lower Devonian.

The classic section of the Brazilian Gondwana is in south Brazil, from Rio Grande do Sul through Santa Catarina and Paraná to São Paulo. A generalized graphic representation of this terrane, chiefly based on the Santa Catarina expression, is shown in figure 11. Details of the column are given in various current publications, such as the compendium of Oliveira and Leonardos (1943), and splendid papers by Maack (1937, 1939, 1946a, 1946b, 1947a), Gordon (1947), and Barbosa and Almeida (1949), etc. The classification and the broader dating on this figure are those current in Brazil today.

The Tubarão series includes the glacial and interglacial beds of the "great glacial" episode at the base of the Brazilian Gondwana terrane. At least five tillites occur in the sequence in São Paulo (Barbosa and Almeida, 1949), and most of the Brazilian coal deposits occur in the Bonito formation as interglacial accumulations (Almeida, 1945). The former distinction of Itararé (glacial) and Tubarão (non-glacial) is facieologic rather than stratigraphic. The whole terrane is of glacial origin or was deposited while the ice cap waxed and waned. Plate 17 shows a characteristic fluvioglacial deposit of the Itararé facies, and plate 18 a varvite of lacustro-glacial origin. Whereas in the south the later phase of the series is chiefly silts, deposited during the waning stage of the "great glacial," in São Paulo the till and fluvio-glacial terrane persists to the end. Barbosa and Almeida (1949) have reported an enormous thickness of about 3650 feet for the series in São Paulo. Towards the south it is only a fraction as thick. The São Paulo thickness compares favorably with the maximum for the coeval Dwyka tillite in South Africa (fig. 15).

The Tubarão series is characterized by an "impure" *Glossopteris* flora. Among the characteristic plants are: *Glossopteris* (four species), *Gangamopteris*, *Gondwanidium*, *Noeggerathiopsis*, *Sphenopteris*, *Phyllotheca*, *Taeniopteris*, *Lepidodendron*, *Lycopodiopsis derbyi*, and *Rhacopteris* (Dolianiti, 1946). Relics of an older austral Carboniferous flora predominate, and typical Gondwana plants are just entering. Read (1941) pronounced this Tubarão flora as Pennsylvanian in age, with which most South American students now agree in general (e.g., Maack, 1947b).

Throughout the southern exposures of the Paraná basin glacial terrane a marine horizon appears near the middle of the sequence, usually between tillites, and occasionally associated with fossil insect remains (*Phylloblatta*) (Carpenter, 1930; Petri, 1945; Mezzalira, 1948). Ruedemann (1929), Oliveira (1930b, 1936), Reed (1930), Kegel and Texeira da Costa (1951), and others have described occurrences of the marine fauna. Barbosa and Almeida (1949) have carried the marine horizon for the first time into São Paulo. Although the assemblage appears to be brackish and frigid, hence atypical, certain brachiopod species of the Itaituba fauna of Amazonas (Tapajós) appear here, as they certainly do in Argentina in the medial marine transgression of the basal glacial terrane of Paganzo I (basal Patquia

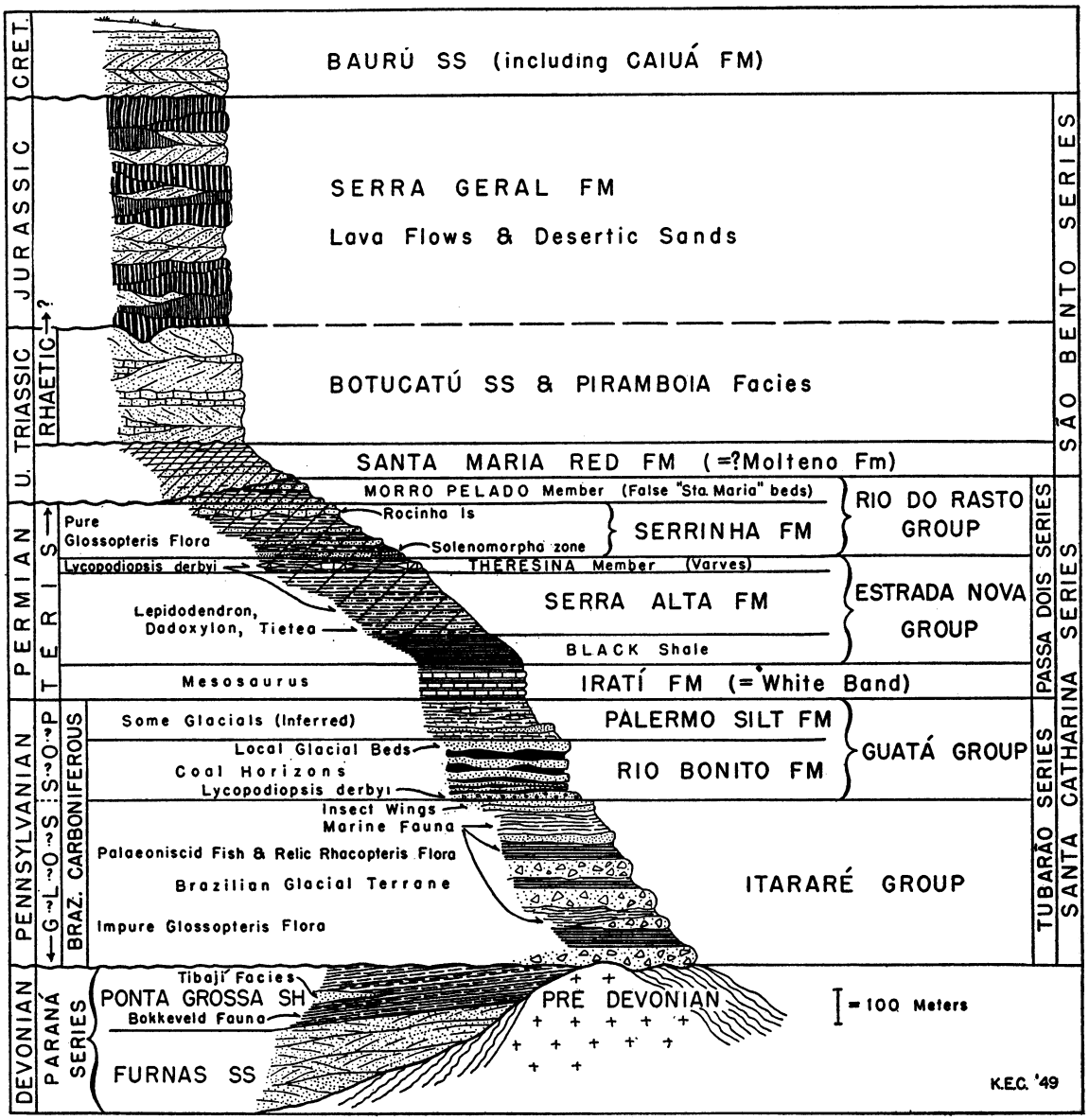

FIG. 11. The Gondwana terrane in southern Brazil. Classification based on Gordon (1947) and Maack (1947b).

of Frenguelli, 1946a). (See fig. 15.) The Argentine marine horizon seems to correlate (Frenguelli, 1946a) very well with the fauna (and adjacent flora) of the *Euomphalus subcircularis-Spirifer supramosquensis* zone of the European Uralian (uppermost Carboniferous). Marine beds appear in the South African Dwyka apparently at approximately the same position.

Overlying the glacial terrane and without gradation abruptly appears the bituminous shale and dark limestone alternation of the Iratí. This is the famous *Mesosaurus* horizon and apparently is a true "geological moment" marker on both sides of the South Atlantic basin, for it corresponds in position, physical character, and fauna with the White Band at the top of the upper Dwyka shales of the

South African Karroo. Although the little aquatic reptiles have been assigned to different species on the two sides of the basin, present geography seems to have played a prominent part in determining this taxonomic difference. The Iratí seems to be the most convenient datum for beginning the Permian period. Starting here, the "pure" *Glossopteris* flora appears, and *Mesosaurus* seems certainly to be Lower Permian (von Huene, 1941).

Although commonly interpreted as a freshwater series of beds, the presence of *Conularia*, *Schizodus*, and *Myalina* in the Iratí of Brazil seemingly bespeak marine origin, as does the widespread uniformity of the formation over the whole Paraná basin. Whereas it is classified as the top horizon of the Dwyka in Africa, it appears best allied with the Estrada Nova (Passa Dois series) of Brazil, with which it intergrades, rather than with the glacial series. The horizon has not been identified in the pre-Andean geosyncline. Apparently *Mesosaurus* throve on an abundant crustacean fauna (Clarke, 1920, 1948; Beurlen, 1931, 1936, 1937) in the open clear waters and did not venture into either the sapropeltic bottom zone or the (unidentified) roily shore environment.

The Passa Dois series, 900 to 1000 feet in thickness, is a predominantly red and green shale and siltstone terrane. It grades downward through a basal black shale member into the Iratí, and terminates above in the Triassic (pre-Keuper) erosion. Mendes (1944, 1945a, 1945b, 1949, 1951) gives the latest analyses of the Estrada Nova formation, and Maack (1937, 1939, 1947a) and Gordon (1947), of the Rio do Rasto. The Terezina member at the top of the former is a cherty-oölitic calcareous horizon filled with a pelecypod fauna which is in large part duplicated downward in cherty lenses deep into the Estrada Nova red beds. There seems no question of the essentially marine nature of the whole Passa Dois, yet the fauna has been found to be largely unique, hence of little extra-basin stratigraphic value. Mendes (1945a) summarizes the controversy as to the Triassic, Permo-Triassic, or Permian age of the sequence as adjudged by the fauna. He concludes from a thorough study of the whole biota (and the plants seem more critical than the fauna so far) and the stratigraphic relations that it is wholly Permian. This is now the generally accepted dating.

At the top of the series the Morro Pelado red beds have often been misconstrued as the reptile-bearing Santa Ana beds of Rio Grande do Sul, from which, however, they prove to be separated by a great hiatus, the Santa Ana beds being Keuper in age (Gordon, 1947; Maack, 1947a). With the top of the Passa Dois, the pure *Glossopteris* flora terminates. The floral data suggest the heterofacial, time equivalence of the Passa Dois and the upper Patquia of Argentina (Frenguelli, 1946a, 1948). Despite the absence of any terrestrial vertebrate remains in the Rio de Rasto terrane of the Paraná basin, the plant data suggest that this correlates, likewise, with the Lower Beaufort of Africa. The Estrada Nova presumably likewise has an equivalent in the lower Patquia and seems to be contemporaneous with the coal-bearing Ecca formation of the South African Karroo (see figs. 13, 15). Some of the more significant correlation data are suggested in figure 15.

In the belt of outcrop, labeled A on figure 10, the Gondwana sediments emerge as a broad band in the Brazilian States of Mato Grosso and Goiás. Prior to an expedition of the Brazilian Geological Survey in 1947, in which the writer participated, the age and relations of the thick terrane between the great lavas and the imperfectly known Devonian were somewhat uncertain. A general schematic representation of this sequence is shown in figure 12; the scale is the same as in figure 11.

Although the outcrop belt of the Gondwana terrane in Goiás and Mato Grosso is known but little better than in a reconnaissance manner, yet the essential faunal, floral, and physical facts in hand make possible the north-south correlations across the Paraná basin represented in figure 12. The key horizon is the Iratí carbonaceous shale and interlaminated cherty limestones which are rich in *Mesosaurus* remains. This formation shows almost no lithologic variation over the broad extent of its development, in Uruguay and Paraguay and throughout the basin states of Brazil. In the little-explored vast-

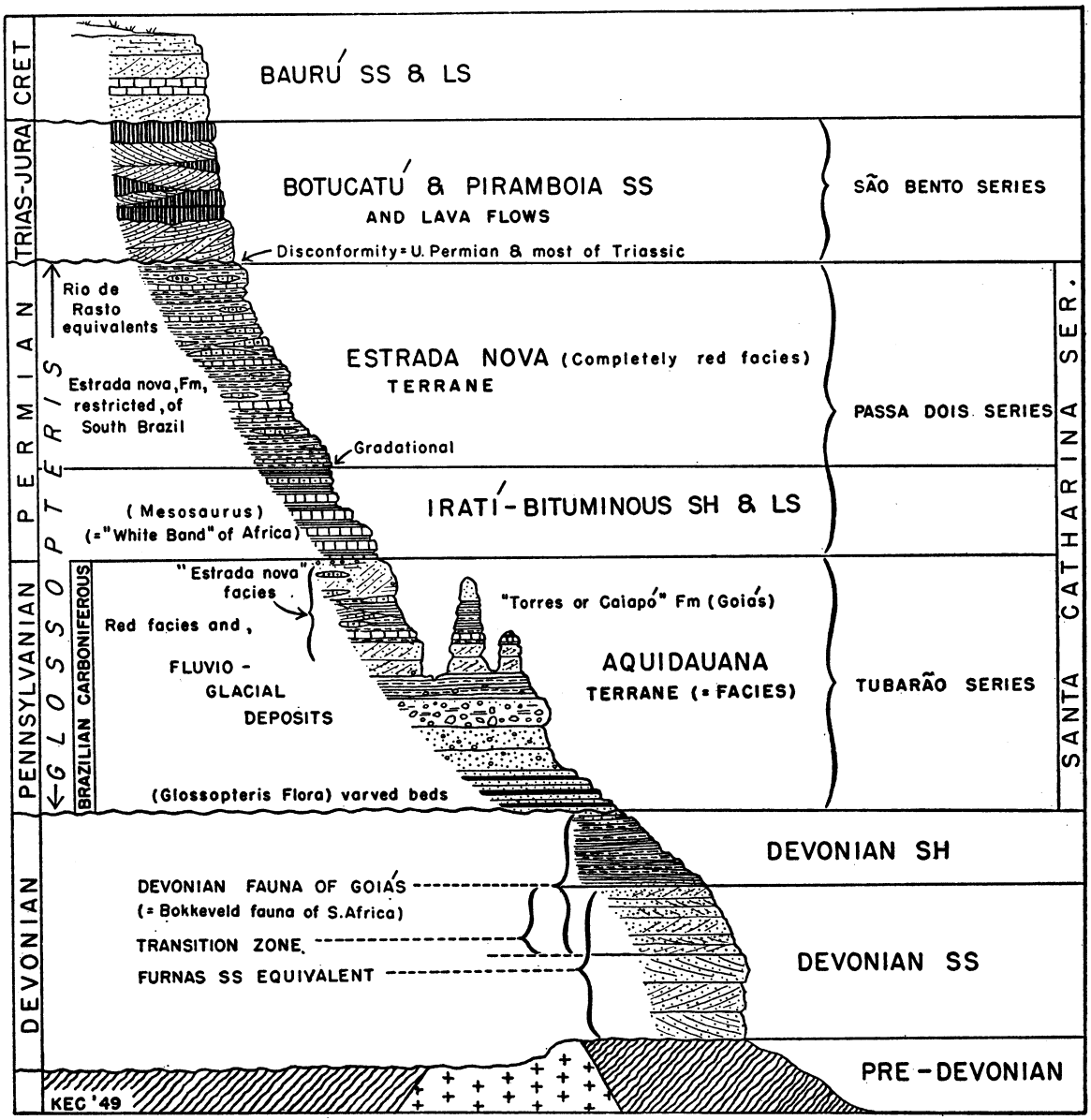

FIG. 12. The generalized Gondwana terrane in Goiás and Mato Grosso, Brazil. Based on the 1947 observations of Almeida, Barbosa, Caster, and Petri. Compare with figures 11 and 13. Same scale as figure 11.

ness of the Mato Grosso and Goiás savanna the Iratí has been spotted in a few places, as has also the Estrada Nova formation, with its characteristic oölitic silex and abundant pelecypod fauna. But the mystery terrane was a thick sequence of gravels and red beds, sandstones and shales, the relation of which to both the Iratí and the Estrada Nova was unknown, although various correlations had been suggested. The 1947 expedition was able to show that this is continuous with the Aquidauana series on the northwestern side of the basin and that on the Goiás-Mato Grosso frontier it underlies the Iratí. Moreover, it was shown to contain in the Serra dos Caiapós and the Torres do Rio

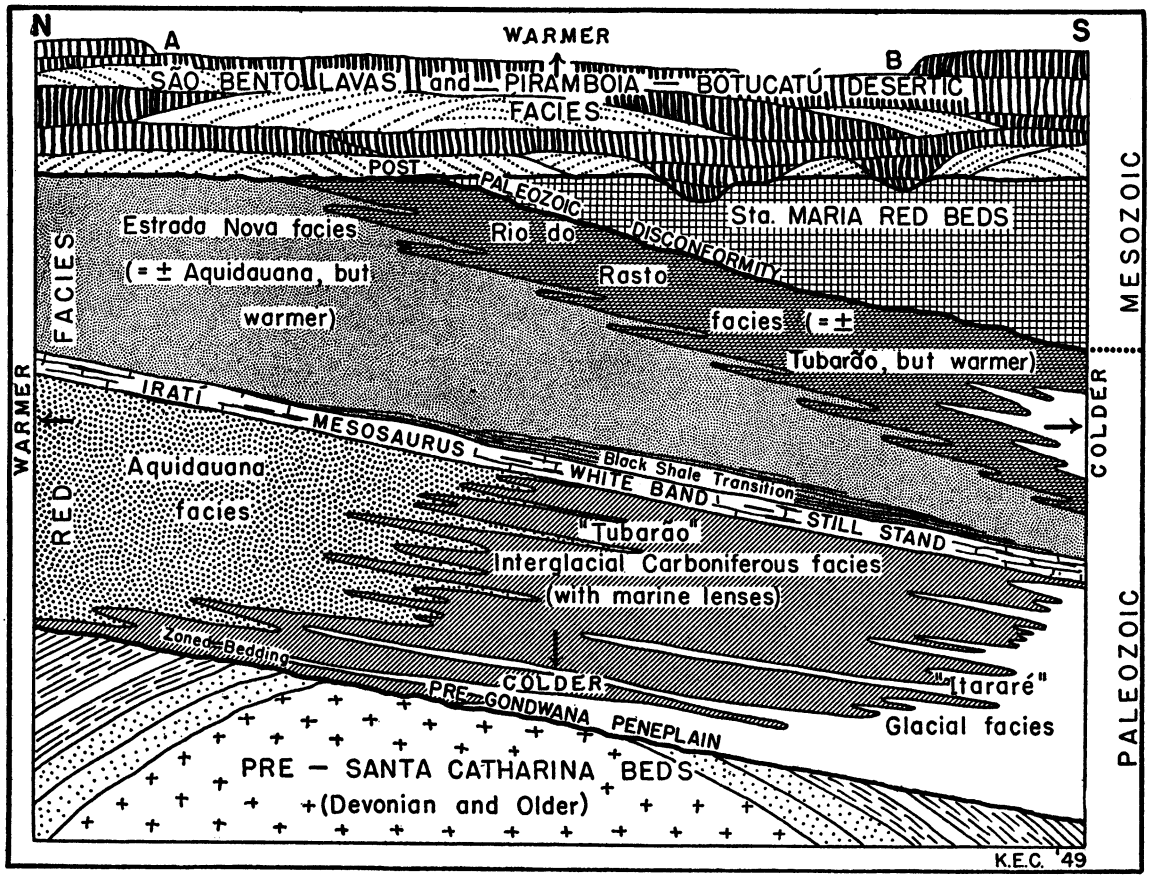

FIG. 13. Facies relations in the Brazilian Gondwana terrane along the line A–B of figure 10. The stippling represents the red magnafacies; the difference in the sizes of the stipples distinguishes the two red parvafacies. The three fundamental hiatuses of the Paraná basin sediments are apparently of very wide extent in southern South America and "Gondwanaland" in general. It is assumed that conditions were colder both towards the south and towards the bottom of the Gondwana column.

Bonito a glacial facies and an "impure" *Glossopteris* flora similar in both respects to the Tubarão series of south Brazil. Equally interesting was the discovery that the larger, red, part of the Aquidauana more or less facieologically duplicates the Estrada Nova beds of the south. Even oölitic cherts, replete with pelecypods, round out the facies similarity. However, the faunas of the two chert developments are quite different, i.e., they are different parvafacies (fig. 14) expressions.

The supra-Iratí sequence is uniformly red in color, a thick terrane of sandstones, siltstones, and shales, with a great quantity of oölitic chert which is replete with the characteristic fauna of the cherty zones of the Estrada Nova-Terezina formations of the south. The red beds terminate above with the deeply eroded unconformity at the base of the Botucatú sandstone and Paraná lavas, and grade downward into the bituminous shales of the Iratí, just as the type Estrada Nova does in Santa Catarina. While it may be that the red terrane carries a time equivalent of the supra-Terezina beds (Rio do Rasto, false Santa Maria) of the southern outcrop belt, no basis for the identification appeared in the rapid survey of 1947. Hence the whole upper red sequence appears in figure 12 as Estrada Nova.

The facies relations of the Brazilian Gondwana across the Paraná basin are shown

diagrammatically in figure 13. This is the section along line A–B of figure 10. Apparently there existed in the Paraná basin during Gondwana time two great lithologic and faunal phases, i.e., magnafacies (fig. 14), one glacial, with various subfacies such as continental till, pro-glacial deposits (fluvio-glacial, lacustro-glacial, and marginal marine), and one ferruginous and atypically marine (as part of which there were colder and warmer subfacies expressions, probably in correspondence with proximity to the Gondwana ice front). The facies-formation nomenclature is explained in figure 14. Apparently the "great glacial" or initial tillite stage of the Gondwana terrane traversed the whole basin and probably reached far beyond (see Amazonas, below). This glacial phase occupies the whole sub-Iratí Gondwana in the southern limits of the basin and in the Falkland Islands and Argentina. However, on the northern edge of the basin a regressional phase, represented by the red marine magnafacies, progressively replaces the glacial beds southward. Possibly originally, beyond the present limits of the basin outcrops, the subfacies of the red magnafacies now preserved in the Aquidauana formation merged northward into a warmer water red subfacies, having the occasionally limy character of the upper Estrada Nova formation in the southern Brazilian states.

This regressional closing stage of the Tubarão series was interrrupted by a rapid cratonic submergence over a vast area which extended far beyond the present basin. This gave the setting for the black muds and petroliferous limestones of the Iratí formation. (See South African Gondwana Deposits, below.) It is interesting that this new ecologic condition grades downward into the upper Dwyka shales of South Africa (initial transgression stage?), but comes in sharply, nonconformably, in South America where it grades upward into the overlying terrane. The Iratí and White Band fulfill the sedimentary role of a rapidly attained "still stand" of a sedimentary cycle. So far no

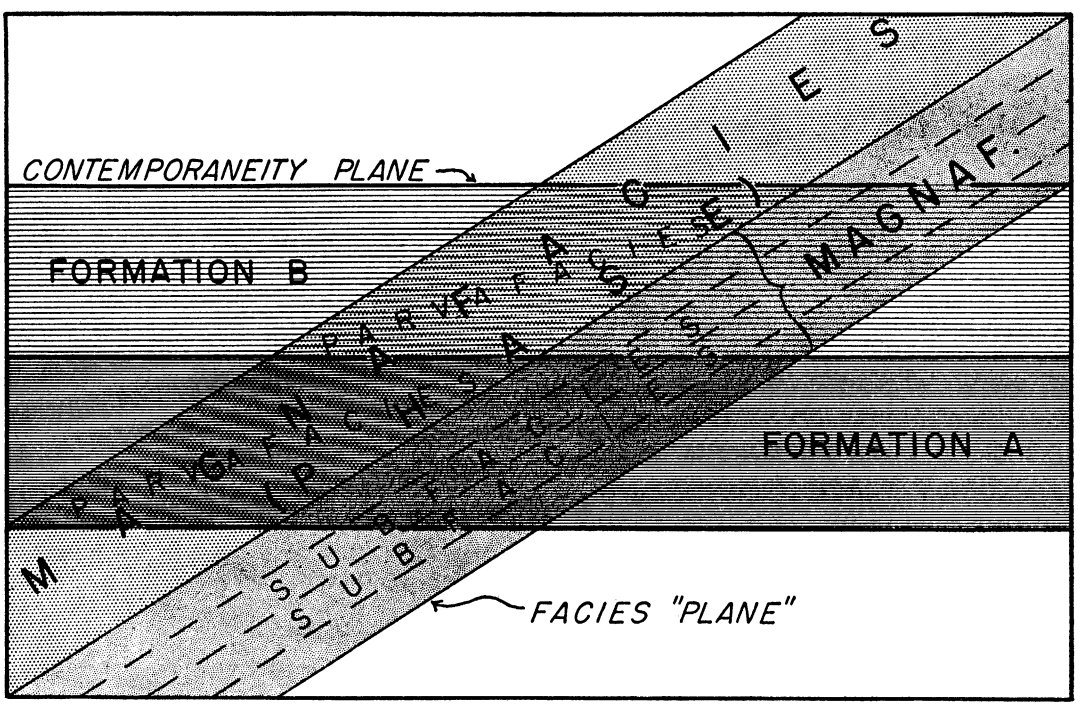

FIG. 14. Facies and formation relations and nomenclature as employed in this paper. Modified from Caster (1934).

lateral facies change of the Iratí has been identified, although lateral transitions almost certainly did exist beyond the present outcrop area.

In figure 13 it is assumed that south or southwest, beyond the present limits of the Paraná basin, glacial or subglacial conditions were again developed following the Iratí transgression. Actual glacial beds of this time are now known (Frenguelli, 1946a) from the lower middle Paganzo II (Patquia) of Argentina (fig. 15). Moreover, the Argentine deposits seem to furnish a red subfacies analogous to the red development in the Aquidauana formation in Mato Grosso and Goiás. This is the colder subfacies of the Estrada Nova formation which in theory should next succeed iceward beyond the southernmost preserved outcrops of the Paraná basin, in the "colder" direction of figure 13. In addition to the coeval temperature variations, with respect to proximity to the Gondwana ice cap, figure 13 suggests that there was a progressive amelioration of the Gondwana climate with the progress of time. Thus the Rio do Rasto beds in the upper middle Passa Dois series may be a new subfacies of the usually red marine magnafacies, conditioned by this broad regional warming, concomitant with the retreat of the Atlantic (?) continental ice cap. At any rate, there does not appear to be a subfacies in the Aquidauana expression of the red magnafacies which resembles the Rio de Rasto sediments. Whatever the explanation, the "false Santa Maria" beds (Morro Pelado), at the top of the Passa Dois series in the south, are a closing return of the typical red facies (Estrada Nova conditions) and may well reflect a temporary deterioration of the Gondwana climate at the end of the Permian. Possibly the Ecca shales of South Africa represent in some part an older expression of this same Rio de Rasto subfacies. The true Santa Maria beds, on the other hand, seem to reflect completely different environmental conditions and have no part in the ferruginous magnafacies picture of previous time. They appear to be wholly continental.

Incidentally, this discovery of the lateral assumption of a red facies by the Tubarão series of south Brazil, and that that facies is essentially of the same nature as the younger Estrada Nova formation, may help to explain one of the most striking differences in the South African and South American Gondwana terranes. The Gondwana coals on the two sides of the South Atlantic basin are not synchronous; the Brazilian is sub-Iratí, whereas the African is in the Ecca division of the Karroo, above the *Mesosaurus*-bearing White Band. On a floral basis, as well as superposition, the Ecca seems pretty satisfactorily correlated with the Estrada Nova and the lower middle Patquia (fig. 15). The coals may now well be considered as homotaxial, isofacial equivalents; possibly the Argentine glacial episode had a coeval counterpart in South Africa. The Estrada Nova terrane of south Brazil might be thought of as bearing facieologically to the Ecca of Africa very much the same relation as the Aquidauana of the north side of the Paraná basin does to the typical Tubarão of south Brazil.

On the lower Amazon, centering on the lower Tapajós and opposite bank of the Amazon, there occurs the best known marine Carboniferous terrane of South America. This is the Itaituba series (Hartt, 1874). It is comprised of some 150 to possibly 600 meters of marine sediments which overlie a discontinuous tillite that intervenes between the basal white sandstone (30 meters thick) of the Itaituba series and the so-called Upper Devonian black shales (see Ereré, above). The tillite is known only from well cores on the lower Tapajós (Moura, 1933). The Itaituba is chiefly black and brown shales with some gypsum. At the top comes an impure bituminous limestone terrane, 15 to 20 meters in thickness, some zones of which carry a very rich silicified marine fauna. The affinities of this fauna, according to Hartt (1874), Katzer (1903, 1933), Duarte (1938), and others, is largely with the North American mid-continent upper Pennsylvanian (approximately Uralian of Europe). *Lepidodendron* is the only plant so far identified from the terrane. However, the presence of coals in what is probably a terrestrial phase of the same series in Pará, on the upper Xingú River (not shown in fig. 10), Potí series, some 1000 kilometers above the confluence

with the Amazon, promises floral data for the future. It is a dilute and chilled Itaituba fauna which occurs in the midst of the glacial series of south Brazil (Itararé) and Argentina (lower Patquia) (see position in fig. 15) as well as in the midst of Stephanian plant-bearing strata of the State of Piauí, Brazil (Duarte, 1936; Kegel, 1951). The presence of a tillite on the lower Amazon, at the base of the Carboniferous terrane, has been largely overlooked since it was first discovered and published. However, the well-core samples still extant in the Geological Survey in Rio de Janeiro seem to the writer fully to substantiate Moura's (1933) interpretation.

The areas labeled as 3a and 3b in figure 10 are the famous diamond mining areas in the Serra do Espinhaço belt of Minas Gerais and Bahía. This is especially the tillite area whence fluviatile diamonds come.[1] Although always currently identified as pre-Gondwana, there is a good chance (contrary to most published opinion) that they are wholly, or partially at least, of Tubarão, Carboniferous age. This was Branner's opinion in his 1919 survey of Brazilian geology for the first geologic map of the country. The degree of metamorphism or deformation has been the chief basis for considering them older (usually Cambrian or pre-Cambrian). However, it is significant that in the Chapada de Diamantina (von Freyberg, 1932; Moraes, 1934), metamorphosed graphitic coal beds occur in association with the supposedly Cambrian Lavras diamantiferous tillites and fluvio-glacial deposits. Apparently there is no exposure known which shows these (Lavras and Diamantina series) beds as underlying the Bambuí series of the São Francisco Valley (supposed Silurian terrane), except under deformational circumstances. From personal reconnaissance of the terrane, the writer can see no reason for abandoning Branner's concept and for not considering these as part of the vast Gondwana glacial terrane, and therefore presumably correlates of the Tubarão series in the southern states of Brazil. This would be in keeping with the widespread distribution of the "great glacial" terrane over the country, far beyond the Minas Gerais-Bahía area. Moreover, the continental glaciers must presumably have occupied this area in order to have attained the Amazon Valley and Goiás-Mato Grosso.

[1] It appears that all commercially recovered diamonds of Brazil occur either in fluvio-glacial beds or in tillites, or in subsequent stream deposits derived from these "primary" sources. The original source of these transported stones is not known, and no commercial diamond "pipes" have yet been found in Brazil.

Argentine Gondwana Deposits

As figure 15 brings out, the "Piso II" of Bodenbender's (1897, 1902) Paganzo system in the Argentine pre-cordillera, now labeled Patquia formation by Frenguelli (1946a), is a sequence of over 3000 feet in thickness which contains the equivalents of the Gondwana terrane. There is a glacial flavor to the whole formation apparently, but aside from the basal terrane, which is the "great glacial" unit of "Gondwanaland," the underlying Lower Tupe series, of Lower Carboniferous age, is an even more thoroughly glacial record. The unconformity at the base of the Patquia coincides with that at the base of the Gondwana terrane everywhere. It has been tentatively correlated with the Asturian orogeny in Europe.

In the midst of the "great glacial" series of the Patquia there was a marine incursion into the geosyncline. This is the much-discussed (Stappenbeck, 1910; Keidel, 1922; Keidel and Harrington, 1938; Keidel, 1939b, 1942; Gerth, 1932; Fossa-Mancini, 1943b, 1944; Heim, 1945; Leanza, 1945) *Spirifer supramosquensis-Euomphalus subcircularis* fauna, several elements of which identify it as the southern expression of the Amazonian Itaituba fauna despite its frigid depauperateness. It seems to be Uralian, as Du Toit (1927), Read (1941), and Frenguelli (1946a, p. 338) concluded, and the correlate also of the even less typical marine invasion of the basal glacial terrane of the south Paraná basin. The rather abundant fossil flora associated with the marine beds and occurring in the glacials both above and below is characterized by Frenguelli (1946a) as a "mixed Carboniferous and *Glossopteris* flora" closely similar to the older Gondwana flora of Brazil and transoceanic "Gondwanaland." Frenguelli gives the floral age as either upper Gshelian or Sakmarian.

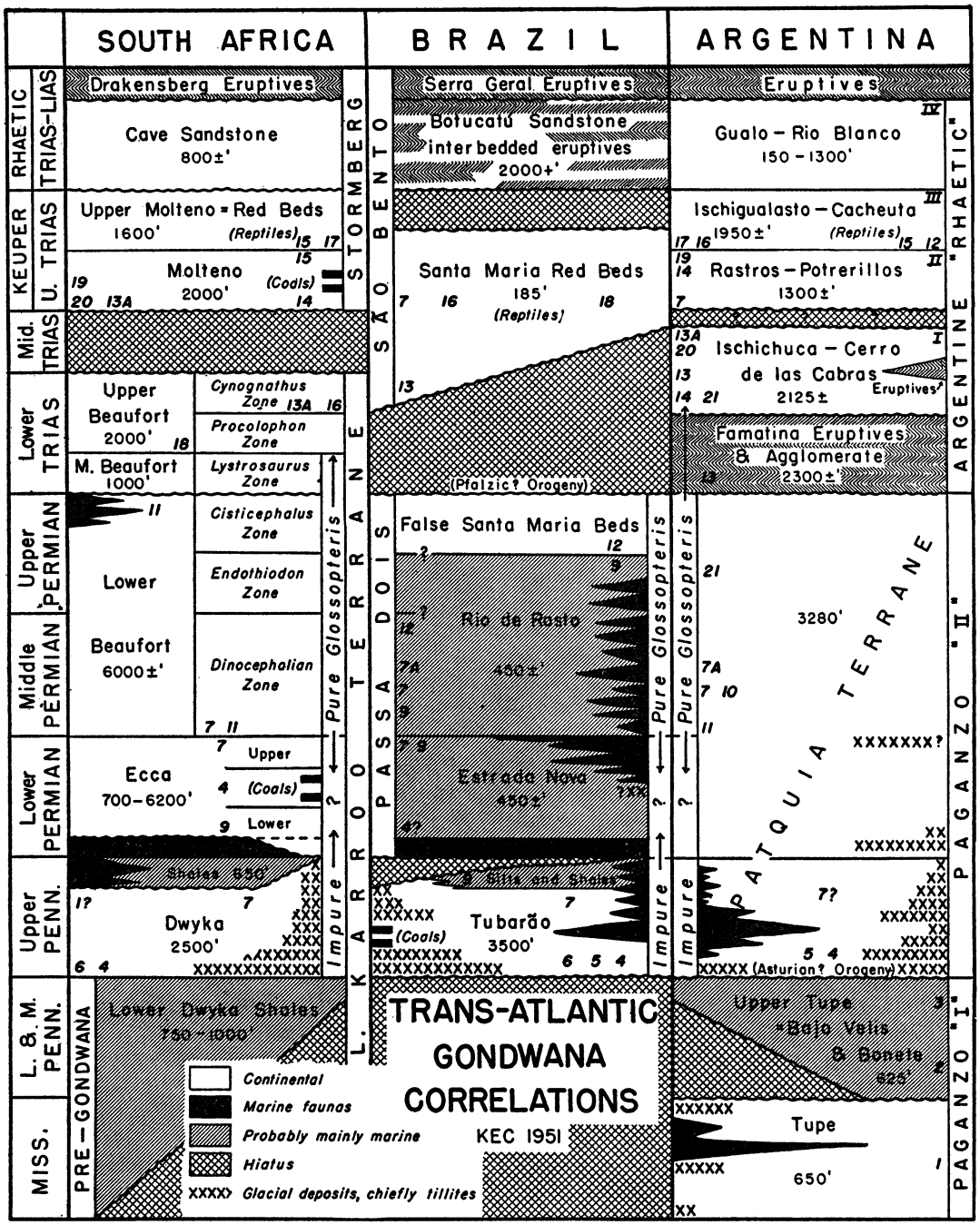

FIG. 15. Correlation of the South African, Brazilian, and Argentine Gondwana beds according to floral and faunal evidence. Compare with Du Toit (1927) for changes made since his study. Key to some of the significant fossil data: 1. *Lepidodendron australe.* 2. Westphalian plants (Frenguelli). 3. Stephanian plants (Frenguelli). 4. *Gangamopteris.* 5. *Noeggerathiopsis.* 6. *Phyllotheca.* 7. "*Dadoxylon.*" 7A. *Dadoxylon nummularium.* 8. *Spirifer supramosquensis-Euomphalus subcircularis* zone (=Tapajós fauna of the Amazon). 8A. Marine horizons. 9. *Lycopodiopsis Derbyi.* 10. *Mesosaurus fauna.* 11. *Palaeanatina.* 12. *Estheria* fauna. 13. *Zuberia* (false *Thinnfeldia*). 13A. *Zuberia Feistmantelli.* 14. True *Thinnfeldia.* 15. *Dicroidium* flora. 16. *Cynognathus* zone reptiles. 17. Archosaurian reptiles. 18. Upper Beaufort reptiles. 19. *Podozamites.* 20. *Neocalamites.* 21. *Walkomia.* I–IV. Frenguelli's (1946a) age determinations based on fossil flora of the "Rhaetic" of Argentina: I, not younger than Middle Triassic; II, at least Lower Keuper; III, Upper Keuper (Noric); IV, true Rhaetic.

The overlying strata are apparently largely continental up to a medial glacial zone. This whole sequence, however, abounds with varved deposits, characteristic glacial concretions (Marlekor), and fluvio-glacial deposits. In this terrane the "pure *Glossopteris* flora" prevails (fig. 15) and continues through to the top of the Patquia terrane. The "pure *Glossopteris* zone" is adjudged to be Permian, and, on the basis of close similarity in flora, is correlated with the Passa Dois series in the Paraná basin. Some of the more striking correlation data are given in figure 15. Above the upper glacial horizon (tillite), *Palaeanodonta* appears in the continental deposits, with the long-ranging *Dadoxylon* trunks, suggesting correlation not only with the Rio de Rasto of the Paraná basin but with the upper part of the Lower Beaufort of the Karroo system. This Argentine terrane offers the glacial elements necessary for the facieological understanding of the Brazilian Passa Dois series (fig. 13) and also makes it possible to relate the Ecca formation of South Africa, with its coals, to the general South Atlantic Gondwana facies pattern.

Overlying the Patquia comes a thick terrane of strata commonly referred to as "Rhaetic" by workers in the Argentine. (The Patquia has often been also so referred.) Frenguelli (1946a, 1948) makes a brilliant analysis of the stratigraphy and floras of this supposed Rhaetic and shows the presence of four sequential floras here, only the uppermost of which is genuinely Rhaeto-Liassic. These floras are indicated by Roman numerals in figure 15, and Frenguelli's age assignments are given in the legend. Apparently the whole range of the Triassic period is represented in the sequence containing floras I to III. The plants are mainly cosmopolitan Gondwana species. Of the 55 unequivocal plant determinations by Frenguelli, only eight species are exclusively Argentinean. Seventeen of the forms are known from South Africa, and seven are closely allied to African species; 23 are known from Australia, and eight additional forms are closely allied to Australian plants (here, in fact, is one of the peculiarities of the whole Argentine Gondwana terrane: it is more closely similar to the Australian Gondwana than to any other); eight species are shared with India, and five are closely allied to Indian forms; two are shared with New Zealand; one is shared with Europe, and one species has European allies; three are known from Indo-China; one is known from Grahamsland; and two are known from Japan.

The Argentine Triassic begins with a profound erosion which Frenguelli suggests may correspond to the Pfalzic diastrophism in Eurasia. The first deposits are agglomerates and pyroclastics. *Zuberia*, one of several false thinnfeldias, first appears here in the column. (Wrongly identified *Thinnfeldia*-like fossil plants have seriously hampered the past understanding of the Argentine column. Apparently *Thinnfeldia, sensu stricto*, descends not much, if any, below the Keuper.) The pyroclastic episode and antecedent erosion seem to fall into the great hiatus at the top of the Passa Dois series in south Brazil. There is no real basis for judging how far down the Brazilian column the wedging terrane of the red Santa Maria reptile beds may eventually be shown to extend in Rio Grande do Sul, where it comes in on this same hiatus. *Zuberia* appears near the lowest base so far known for these transgressive strata.

South African Gondwana Deposits

The Gondwana terrane of South Africa is represented by the enormously thick Karroo system. Through various compendia (e.g., Du Toit, 1939) the data on this sequence are so readily available that only a brief summary is needed here. Part of this is represented by figures 15 and 16, although the age determinations there have been somewhat modified in line with general Gondwana stratigraphy and biologic affinities as now understood. Apparently only the Middle Triassic is without record in the terrane from the presumably Pennsylvanian-Mississippian Lower Dwyka shales through the Cave sandstone and Drakensberg eruptives of Rhaetic-Lias age.

The Karroo sequence varies enormously in thickness; it is far thicker towards the south, as seen in figure 16, and thins notably northward. The thickest development of the terrane has its best South American comparison in the Argentine section of the pre-cordil-

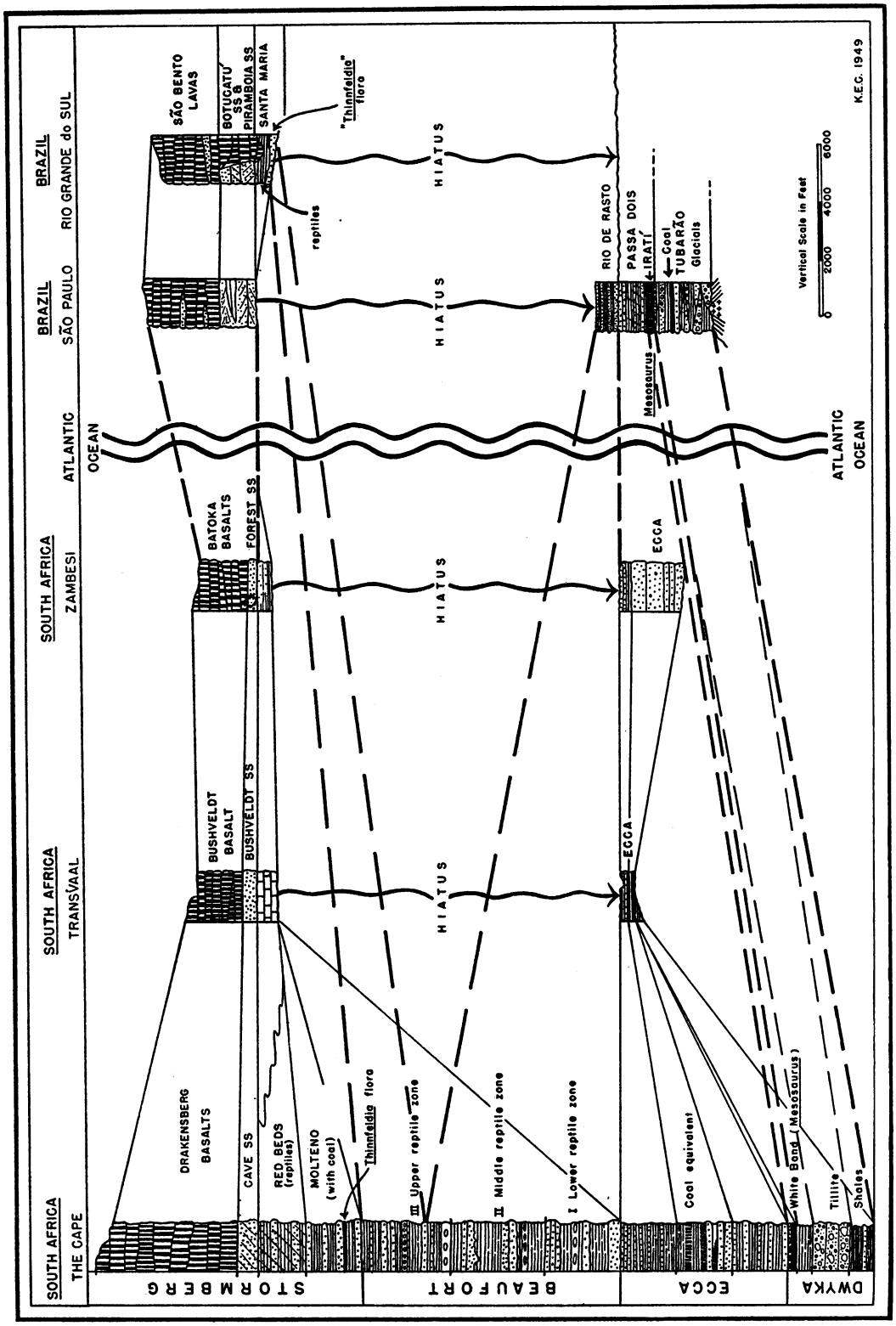

FIG. 16. A summary of the correlations across the South Atlantic basin between the Gondwana terrane of South Africa and the Paraná basin of Brazil.

leran geosynclinal belt; whereas the thinner aspect compares better with the Paraná basin cratonic Gondwana sediments.

The Lower Dwyka shale lies below the "great glacial" series and in that sense is pre-Gondwana. Like the Tupe series of Argentina (Frenguelli, 1946a), it appears to correlate (Du Toit, 1939) both in its sub-Gondwana position and through a sparse and poorly known pre-*Gangamopteris-Glossopteris* flora with the Kuttung series of Australia. Although the shale terrane in South Africa is considered pre-glacial, this is apparently only a local circumstance, since its Argentine and Australian paleobotanical coevals are replete with glacial records. The age of all three deposits is apparently Lower Carboniferous.

The great Dwyka tillite is perhaps the most famous of all Gondwana glacial formations. As do the glacial terrane in the base of the Argentine Patquia and the Itararé glacials of the Tubarão series in the Paraná basin, it marks the commonly accepted beginning of the Gondwana terrane and carries the "impure" early aspect of the *Glossopteris* flora. The São Paulo glacial sequence (e.g., Barbosa and Almeida, 1949) compares favorably in thickness with the middle Dwyka. The Dwyka tillite is evaluated as Upper Pennsylvanian by virtually all students of the Gondwana terrane today. Moreover, there seems to be no good reason for not considering the Upper Dwyka shales of latest Pennsylvanian age. The Upper Shales, and the White Band into which they grade, are often represented in South Africa only by a hiatus separating the Lower Ecca shales from the great tillite. In contrast with the Paraná basin no coals occur in the Dwyka series.

The later Tubarão silts and shales of Paraná-Rio Grande do Sul would seem to occupy the same position as the Upper Dwyka shales. However, as figure 16 brings out, there is such an enormous difference in thickness that one would be very daring indeed to make any correlations on pure stratigraphic position. As a matter of fact, the Brazilian Palermo silts and so-called Tubarão beds, restricted, intergrade in many places with typical glacial beds—tillites or fluvio-glacial deposits. Whereas the Paraná basin-Argentina marine invasion of the older Gondwana always occurs in the midst of the "great glacial" terrane, the South African marine invasion (Keetmanshoop) of the Dwyka is in the midst of the Upper Dwyka mudstones and shales. This invasion is but little known, and only *Eurydesma*, a thick-shelled clam, a straight-shelled nautiloid cephalopod, and *Conularia* have been reported. Apparently the Upper Dwyka shales do not grade into the tillite series but sharply overlie it, thus recalling the Iratí-Tubarão relations in Brazil.

The White Band is a white-weathering bituminous shale, capped by a white chert layer; it is the closing phase in the top of the Upper Dwyka shales. It carries the famous *Mesosaurus* fauna of the Iratí formation in the Paraná basin. The facies is nearly identical in Africa and Brazil except for the prominent calcareous content of the Iratí. *Mesosaurus* occurs in both the limestone and the foetid shales, and sometimes in bone-breccia quantities. Although the Brazilian species have been referred to two genera and the African to three distinct species, in reality the differences are far more artifactual than natural.[1] It is one closely allied aquatic reptile assemblage; moreover, the curious crustacean fauna (presumably the food of *Mesosaurus*) is likewise as endemic as though no Atlantic basin intervened. Unfortunately no attempt has been made as yet to correlate the White Band-Iratí Crustacea, although cursory scanning of the papers by Woods (1922) on the White Band and by Beurlen (1931, 1934, 1935, 1936, 1937) on the Iratí brings out much the same relation between the arthropods as the swimming reptiles show, with, however, some Northern Hemisphere crustacean elements, not known in the Paraná basin, appearing in the White Band. Benthos is unknown in either expression.

As is mentioned under the discussion of the Iratí formation of Brazil, despite close similarity in facies and probable equivalence in time of the *Mesosaurus* horizons of South

[1] Maniero (1951) described the new fossil wood *Parataxopitys brasiliana* from the top of the Iratí limestone of Brazil, pointing out a very close morphologic similarity to the genus *Taxopitys* Kraus of Southwest Africa. *Taxopitys africanus* occurs in the *Mesosaurus* association in the White Band of Africa.

Africa and the Paraná basin, the Iratí lithology grades upward into the Estrada Nova formation, whereas the White Band grades downward into the Upper Dwyka shales. A hiatus marks the base of the Iratí and the top of the White Band.

This relation becomes understandable when one recalls that a hiatus appears also to exist at the base of the Upper Dwyka shales at the contact with the Dwyka tillite. This now seems to be one of the critical sedimentary breaks in the lower Karroo, although probably no great amount of time is involved, considering the seemingly uninterrupted continuity of the "impure" *Glossopteris* flora across it. The chronologic paleogeography would seem to have been as follows:

A. Following the "great glacial" episode, represented by the Dwyka tillite and the Tubarão series, marine waters entered South Africa with the sparse Keetmanshoop fauna. The Upper Dwyka shales record this progressive transgression across the low-lying craton, including the Afro-American ligation belt. This phase appears to have been wholly erosional in the cratonic area now known as the Paraná basin, but a largely continental sedimentary phase of this time may well exist in the lower Patquia of Argentina.

B. By the time the transgression had reached the Paraná basin, submergence of the whole craton had proceeded so far as to create a subabyssal deep, cut off from normal marine waters and analogous to the Devonian and Lower Mississippian black shale sea of interior United States. Foetid muds and sulphureted and lethal sapropeltic sediments prevailed over a vast epi-sea. It was now at the acme of the transgression that *Mesosaurus* throve in really phenomenal abundance, possibly developing regional morphologic differences. In the Paraná basin this "still-stand" is the sole record; it is characterized by much bituminous and cherty limestone, interbedded with petroliferous black shales; in Africa only black shales and cherts now record the still-stand.

C. Broad cratonic warping, essentially the reverse of the beginning of the transgression, brought South Africa above sea level. Broad erosion ensued, often removing the whole White Band and Upper Dwyka record down to the Dwyka tillite. Meanwhile, on the submerged craton of the Paraná basin, sedimentation continued. Much of the Paraná basin sediment of this phase may be derived from the African erosion. However, for reasons unknown, when Africa emerged the *Mesosaurus* fauna succumbed throughout the American relic of the Iratí-White Band "black sea." Perhaps the extinction was due to the lethal nature of the products thrown into suspension by the stirring up of the emergent sapropel in Africa.

D. While erosion proceeded in Africa, a lithologic facies analogous to, if not actually the same magnafacies as, the Upper Dwyka shales gradually replaced the black muds of the Iratí. These would be in part a redeposition of the eroded Upper Dwyka and White Band. More and more fine clastics entered the relic sea—a sea that may actually have had no oceanic connections, judging from the anomalous invertebrate faunas that characterize the Passa Dois series of Brazil and post-"great glacial" phase of the Patquia, as well as the Ecca and most of the Beaufort in Africa. Shallowing of the water body would seem also to have characterized the progressive entrance into the Estrada Nova terrane, as slowly the primary or reworked sapropels were replaced by fine red clastics, deposited in waters of moderate depth.

E. The Lower Ecca shales may represent an eastward shallow "marine" transgression from the Paraná basin across the South African post-Iratí hiatus. However, in the main, the Ecca would seem to furnish the largely terrestrial phase of the anomalous Estrada Nova formation in Brazil.

The Ecca series is an extremely variable terrane, made up of a basal blue-green fissile shale and flags, which often rest non-conformably directly on the Dwyka tillite. The great body of the Ecca pertains to the middle, "Coal Measures" sequence. This is the great productive coal terrane of South Africa. The mixed *Glossopteris-Gangamopteris* flora of the older Gondwana prevails throughout the Ecca. *Dadoxylon* occurs in the upper shale sequence, which is essentially a recurrence of the lower Ecca shale facies. The Brazilian early Gondwana plants *Lycopodiopsis Derbyi* and *Lepidodendron Pedroanum* occur in the Ecca.

The Ecca coals are remarkably extensive and attain considerable thicknesses. They clearly pertain to the Permian side of the Gondwana terrane, although exhibiting more the floral characteristics of the South American sub-Iratí than of the Passa Dois-upper Patquia—a recurrent magnafacies phenomenon. The "Coal Measure" grits interbedded with the Ecca coals recall in a most remarkable degree the glacially derived sediments of the Brazilian sub-Iratí, in association with which the Paraná basin coals are developed. For example, Du Toit illustrates by a sketch (1939, p. 254, fig. 36) the highly characteristic and quite remarkable weathering of one of these grits. The writer can duplicate this phenomenon from both the north and the south sides of the Paraná basin and has found this weathering a completely reliable criterion for the identification of the Tubarão fluvioglacial deposits. The Vila Velha sandstone of Paraná and the Aquidauana terrane of Goiás-Mato Grosso are similarly fractured in polygonal joints, imbricate partings, and castellated (quartz cementation) sandstone cuesta crests. This observation tends to support the thesis, which is developed elsewhere in this paper (fig. 13), that the Ecca Coal Measures are facieologic equivalents of the Tubarão series of the Paraná basin and that a dominantly glacial element lies unrecognized in this African sequence. The Ecca appears to represent the geographically low-lying terrestrial expression of the continent on which the Passa Dois of South America was the dominantly shallow marine expression and the Patquia the western geosynclinal continental equivalent. Apparently the upper shales of the Ecca pass without significant interruption in sedimentation into the Beaufort terrane, just as do the two divisions of the Passa Dois and the various stratigraphic members of the Patquia. However, it appears that *Gangamopteris* does not even attain the top of the Ecca. The Lower and Middle Beaufort constitutes the "pure" *Glossopteris* zone of Africa.

Clearly, South Africa was a paleobotanical "laggard" during Ecca-Estrada Nova time. It preserved Carbonic and early Gondwana floral elements far longer, apparently, than did the marine stratigraphic equivalents in the Paraná basin or the coeval terrestrial deposits of the Argentine geosyncline. Quite probably, the water-logged Estrada Nova woods were derived from western forests, and no relic of the northern shore of the Estrada Nova sea has yet been identified; to the south, it now appears that the Estrada Nova sea was at least intermittently fronted by continental ice fields. With these paleogeographic probabilities, plus the element of considerable distance, in mind, one can better understand such floral discrepancies as seem to exist between the coal terrane of Africa and the post-Iratí of South America.

The thick and largely terrestrial Beaufort terrane succeeds conformably upon the Upper Ecca shales. Six archaic reptile zones characterize the Beaufort. The three lower pertain to the Lower Beaufort and are usually judged as Middle and Upper Permian. The faunal affinities of the two lower reptile zones of the Lower Beaufort terrane are chiefly with Russia. A marine incursion in the higher beds of the Lower Beaufort carries an Upper Permian invertebrate fauna which helps materially to corroborate the dating. The pure *Glossopteris* flora has its African expression in the Lower and Middle Beaufort, a fact that has been responsible for correlating the Lower Beaufort with the Upper Passa Dois of Brazil and upper Patquia of Argentina. In the American deposits nothing of the reptile facies is known.

Apparently a hiatus marks the contact of the Lower and Middle Beaufort, although the deposits are conformable. The Middle Beaufort introduces red beds in the section. It corresponds with the zone of *Lystrosaurus* and carries the last of the pure *Glossopteris* flora. This has been evaluated as an erosional (Brazil) or eruptive (Argentina) episode in South America. Despite the floral affinities with the underlying Permian, the Middle Beaufort reptiles are judged by vertebrate paleontologists as Lower Triassic.

The Upper Beaufort is conformable upon the Middle and is characterized by two reptile zones, likewise evaluated as of Lower [and sometimes extended to include Middle (e.g., Romer, 1945)] Triassic age. *Zuberia Feistmantelli*, a characteristic "false *Thinnfeldia*" (Frenguelli, 1944), comes in the *Cynognathus*

beds, the upper of these two reptile zones. The closest direct connection between the Brazilian reptile beds (Santa Maria and São Pedro deposits of Rio Grande do Sul) comes through the dicynodonts, from the Middle and Upper Beaufort beds. The gigantic *Kannemeyeria* of the Upper Beaufort is apparently closely allied to Brazil's *Stahleckeria* (Loefgren, 1937), and the bizarre primitive archosaur, *Erythrosuchus*, to Brazil's famous *Scaphonyx*. The long-ranging *Dicynodon* is the only "genus" common to the Santa Maria beds and South Africa. This form-genus extends all through the Beaufort and is clearly a Permian derivative. According to Frenguelli (1948) the Upper Beaufort reptile fauna has allies in the Argentine Cacheuta formation. Apparently this horizon and certainly the Santa Maria beds carry a proportionately large (nearly half the fauna) archosaurian (Thecodontia: Pseudosuchia) content. The thecodonts had their first great development in the Lower Beaufort. A lone saurischian gives the Santa Maria fauna a late Triassic aspect. Apparently on this genus, plus the red color of the beds, several geologists have made direct correlation between the Santa Maria and the African Red Beds. Thus the Santa Maria is given an enormous spread on the correlation table (fig. 15) in order to show the mixed affinities of its reptile assemblage. Unfortunately not enough is known of the flora of the Santa Maria as yet to make this very useful in correlation. *Zuberia* in the lowest Santa Maria beds bespeaks an older rather than a younger equivalence. On the other hand, the fact that there are no reptile species and almost no genera common to South America and Africa suggests that the Santa Maria and Argentine reptile assemblage is a derivative one, separated by sufficient time and distance for considerable taxonomic differentiation to have occurred. This would argue for later rather than earlier age assignment. Probably it is best visualized as overlapping the uppermost Beaufort, occupying the Middle Trias hiatus, and extending into the time of the Molteno, *sensu stricto*.

There is apparently no evidence of the Middle Triassic in the Karroo terrane. The hiatus at the top of the Beaufort matches the post-Passa Dois erosion of Brazil. The interlude was partially filled by pyroclastics at the base of the Argentine "Rhaetic" beds, which Frenguelli dates as mid-Triassic in part.

The Molteno, basal formation of the Stormberg series, follows conformably upon the Upper Beaufort. This is a thick continental terrane which is separated into the Molteno proper and the overlying Red Beds. In the midst of the former comes the upper coal horizon of South Africa. The Molteno flora is of post-*Glossopteris* aspect, in accord with the latest Gondwana floras. It is characterized by the Upper Triassic (Keuper) true *Thinnfeldia* association. Yet, as is generally the case throughout "Gondwanaland," in company with Rhaetic-pointing genera, such as *Podozamites* and *Dicroidium*, there are many laggards, such as *Dadoxylon* and *Zuberia*, which hark back to the Middle and Lower Trias or earlier. There may be some confusion in South African correlations owing to the presence of these Upper Beaufort relics in the Molteno beds, giving rise to a current idea that the Beaufort and the Molteno may be in part dissimilar contemporaneous facies. On the other hand, there may exist in South Africa an unrecognized transitional unit, comparable in age and flora to the Argentine Ischichuca-Cerro de las Cabras sequences, which Frenguelli (1948) evaluates as bridging the Middle Triassic hiatus. The Molteno beds proper carry no reptiles.

The Red Beds, in contrast, preserve a large and important reptile fauna, in which saurischian (theropod) dinosaurs, rather than the therapsids of the Beaufort, dominate. Such of the latter as are present belong to the advanced and aberrant ictidosaur end product of the therapsid line, which was widely distributed over the world in the latest Triassic. The theropods *Gryponyx* and *Thecodontosaurus* are apparently the only Red Bed genera shared with other South African deposits; they cross upward into the Cave sandstone. The second of the two is also widely distributed in the world Rhaetic.

It would appear that the Santa Maria-Karroo relations are best comprehended by continuing the same trans-Atlantic cratonic

history postulated for the Iratí-White Band time. Beginning in Middle Beaufort time and accentuated in the Upper Beaufort, a red, Molteno-like facies began to make its appearance in Africa. The non-correlation, yet inherent similarity, between the archaic reptile faunas of the Beaufort and the Santa Maria (and São Pedro) of south Brazil could be explained by a progressive westward migration of this red facies across an Atlantic craton in Upper Beaufort and Middle Triassic time, including the restricted Molteno. On the western edge of the craton and adjacent foothills of the Argentine geosynclinal zone, further evolution of this archaic lineage of Beaufortian therapsids (cynodonts and dicynodonts) and pseudosuchians (thecodont archosaurs) produced what now appears to be the highly autochthonous Santa Maria (and São Pedro)-Cacheuta fauna. Probably, according to this picture, the Santa Maria episode is more nearly equivalent to the Middle Triassic hiatus and the Molteno, *sensu stricto*, than to anything else in South Africa. During Santa Maria time, South Africa saw a reoccupancy by the long-antecedent Ecca environment but probably without the glacial overtones that seem to accompany the typical Ecca parvafacies.

Spondylosoma of the Santa Maria (São Pedro) beds is therefore apparently the oldest and correlatively the most primitive "sauropod" dinosaur (although considered systematically as a "prosauropod" of the theropod line of the Saurischia). At least nine genera of these prosauropods make up the dominant reptile fauna of the Red Beds and give to these Keuper beds the same aberrant, insular ("South African") flavor that the therapsids do to the Beaufort. Such a florescence could have been achieved, out of the Santa Maria beginnings, during the slow eastward migration of the New World red facies in post-Santa Maria time, i.e., during the late Molteno sedimentation and sub-Red Bed hiatus.

As is mentioned above, at least two of the Red Bed theropod dinosaur genera carry across the post-Red Bed hiatus and into the Cave sandstone. This culminating sediment of the Karroo system certainly appears to be both paleobotanically and zoologically assignable to the Rhaetic. Moreover, it now appears that the true Rhaetic-Liassic record in South Africa and South America is restricted to this desertic sandstone and the associated vast Drakensberg lava outpourings. These Rhaetic records seem precisely to match the Botucatú-Piramboia sandstones and Serra Geral lavas of the Paraná basin and the Gualo-Rio Blanco and their associated eruptives of the Argentine. Here again, at the top of the Gondwana column, in all three areas there seems to be the same kind of close, coeval, isofacial correlation seen in the "great glacials" at the bottom.

TRANS-ATLANTIC GONDWANA CONNECTIONS

Although it is not possible now to make the *lit-par-lit* correlation across the South Atlantic basin that Du Toit and other defenders of Wegenerism pictured for the Gondwana terrane, the colossal fact remains that the two sides of the ocean are astoundingly similar in over-all sequence both of sedimentation and of flora and fauna. Moreover, they require cratonic ligation in order repeatedly to complete the sedimentary and general ecological picture. The same magnafacies seem clearly to have been developed on the two sides, sometimes simultaneously, more commonly heterochronously, as one might expect in accordance with crustal warpings and the geographic shifting of climatological belts through time. Apparently the most important of these factors in the Permo-Carboniferous (and Triassic?) were the waxing and waning of continental ice caps and slow shift of centers of ice-cap accumulation. Concentrically with the ice caps there seem to have persisted essentially the same magnafacies belts through the whole of the Mississippian-Permian inclusive. However, some of the magnafacies are not common to the two sides of the South Atlantic, e.g., the Beaufort reptile parvafacies of Africa is not known in South America (or anywhere else precisely). Nonetheless, some of the organisms from this assemblage do appear later in quite different appearing strata in the Brazilian Santa Maria beds and the Argentine Ischigualasto-Cacheuta formations. There is no such close generic identity between these

reptile beds of Africa and South America as existed with respect to *Mesosaurus* of the White Band-Iratí.

Distance, as well as time, presumably enters the picture here. The White Band-Iratí was an identical coeval trans-Atlantic facies, and the nektonic way of life of *Mesosaurus* compensated for what must still have been considerable distance separating South Africa and South America. One has only to look at the cumbersome weightiness of the Beaufort tetrapods to appreciate that they would require far more time to cover the same distance; moreover, the lithic facies difference between their home habitat in the Beaufort and the New World scene of the Santa Maria clearly shows that they were not only covering distance but making conquest of a new environment. Time, distance, and environment, the usual evolutionary selective factors, achieved the remolding of the Beaufort fauna now found in the Santa Maria beds of south Brazil.

When the climate and/or geography changed and the New World red magnafacies transgressed eastward across the Atlantic craton, the Santa Maria fauna, with the newly evolved "germs" of sauropod development in its midst, regressed towards Africa. Distance, as well as time, again seems clearly in evidence through the diversification and extinction achieved in the fauna by the time of its arrival in the Red Beds of South Africa. As the prosauropods "took over," ever more as South Africa and the Rhaetic were approached, the relics of the metamorphosed Beaufort therapsid and thecodont fauna waned.

CONCLUSIONS

To this writer there seems to be no satisfactory manner of accounting for the Carboniferous-Rhaetic relations as preserved in South Africa and South America without intimately connecting their history across the South Atlantic basin. This history requires the absence of oceanic deep where now the basin exists. This means restoring a continental, cratonic sector between the present borderlands. The general Gondwana history of this cratonic link, as reflected by the peripheral remnants, was that of an emergent shield area.

When shoal waters (epi-sea) covered the "bridge," as in the Devonian and the Iratí-White Band episode of the Gondwana, nektonic-pelagic communication was rapid. Yet the fact that coeval differences do exist in an identical magnafacies expression between the mesosaurs of Africa and South America (albeit the differences are perhaps less striking than the present taxonomy might suggest) intimates that the distance was considerably greater between the present transoceanic outcrops than the mere contiguity of opposing present coast lines would afford. Distance would seem to be the chief selective factor in the morphologic variation observable in this instance, just as in the Devonian marine faunas.

During the predominant, emergent history there were apparently repeated recurrences of continental ice on the trans-Atlantic craton. Terrestrial flora, possibly of less exacting environmental requirements than the archaic reptiles, crossed freely and rapidly during every ice-free period, or possibly even outflanked the ice. This results in the abundantly documented fact of a Gondwanaland-wide, uniform, and constantly evolving *Glossopteris*-Gondwana flora through its three conditions of initial impurity, medial purity, and terminal impurity.

The African Permian reptiles never achieved a South Atlantic crossing; at any rate, no record of such has yet turned up in South America. Even the Lower Triassic (Middle and Upper Beaufort) forms suffered a morphologic (and especially taxonomic) "sea change" by the time (Santa Maria) they reached Brazil, and an even greater one before they had an opportunity to return with the New World red facies to post-Molteno Africa.

An Afro-South American "Gondwanaland" seems, from the stratigraphic and paleontologic data now available, to have been a reality. Furthermore, this trans-Atlantic ligation seems to have existed far back into the Paleozoic; so far, in fact, as to make any

discussion of a South Atlantic Ocean impractical until after the Rhaetic. Whatever seaways occupied the area where now this ocean exists bore in extent, outline, or bottom profile apparently no resemblance to the present deep. Moreover, the evidence, as outlined above, is against any marine waters in this sector of the globe during enormous stretches of Paleozoic and early Mesozoic time.

It would seem (from a considerable body of comparable stratigraphic and fossil data not here the subject of review) that, following the great lava outpourings of the Rhaetic-Lias on both sides of the present South Atlantic, fundamental separation rather than ligation became the controlling factor. Thereafter, dissimilarity rather than similarity, independence of sedimentary and biotic history rather than a linked development seem to be the characteristics of Africa and South America. Certainly the most vast lava outpourings and basaltic intrusions in earth history (Woodworth, 1912), which these Drakensberg-Serra Geral (or Paraná) lavas signify, must reflect some profound tensional phenomenon affecting Afro-American "Gondwanaland." By Cretaceous time the Atlantic Ocean and basin were in existence, and its waters were transgressing the opposing continents; no Jurassic marine sediments are known yet on either side of the whole Atlantic, outside the "Tethyan"-Caribbean belt. It is "struthiomimic" to gloss over this.

It would appear that the marginal "foundering" of the Afro-American linking craton has continued throughout the post-Rhaetic. In fact, the very late Cenozoic block-fault subsidence of the whole south Brazilian coast from Bahía to Rio Grande do Sul forming the present narrow continental shelf appears to be the latest expression of this craton-sapping or foundering process. Whether or not there has been actual drifting apart of the two continents is a subsidiary detail and one towards the investigation of which this survey was not directed. Indeed, it is doubtful if the stratigraphic record and associated fossils in the relic masses of the present continents would give much reflection of continental drifting if it has occurred.

The present consensus of geophysicists seems to be that it is equally impossible (possible?) to founder as to drift areas of continental character and proportions. Certainly a bridge across the present South Atlantic basin would be a respectable piece of craton. Perchance the real explanation of the coming into existence of the South (and North?) Atlantic basin is progressive growth through the operation of both "impossible" processes.

The Atlantic basin history may have been in essence this: After a long and essentially "normal" cratonic (epeirogenic) history of emergence and subsidence with respect to sea level, for causes unknown, great tension was set up in what are now South Africa and southern South America and in the intervening area especially. The great lava series of South Africa and the Paraná basin resulted. Possibly the known tension of the relic areas was surpassed in the bridging zone and far vaster basaltic flooding resulted there (and "flooding" would accurately describe some of the Paraná lava episodes). Subsidence and even vast foundering along the length of the bridge might be easily imagined under these circumstances; assimilation of the base of the basalt-laden sialic sector by the "sima" appears possible (to a paleontologist). Certainly the long-known and disconcerting sialic quality in the mid-Atlantic eruptives would not necessarily argue against this idea. Drift may or may not have occurred (but very likely did) in this process by which the Atlantic basin was apparently initiated in latest Triassic time. Probably the progressive enlargement of the basin was achieved after the initial rupture and profound subsidence mainly by a process of peripheral (bilateral) foundering which might be compared to progressive step-fault "grabening" on a gigantic scale. Such progressive basin enlargement by continent sapping through normal faulting continued until very recent times. The elevated coastal wall of mountains of south Brazil and down-dropped continental shelf block might be compared to one side of a vast graben, the upthrow side of which has been longitudinally arched. Possibly the over-steep continental shelf of Brazil (Shepard, 1948) is the shallow-

ly sediment-masked fault plane of a previous normal-fault sapping.

The disruption of trans-Atlantic ligation came prior to the appearance of most of the dominants in the modern biota. According to the historical geology data above outlined, it would appear almost futile to search among such living groups as the flowering plants, the teleost fishes, anuran Amphibia, lepidosaur reptiles, birds, or placental mammals for any reflection of Afro-American junction. For most, if not all, of these groups the terrestrial connections appear to have been north-south rather than east-west (present coordinates). On the other hand, those relics that persist in the modern flora and fauna, which had already been differentiated in the Paleozoic or early Mesozoic and existed in Gondwanaland, might be expected in some instances to reflect their present disjunctness. Of particular significance would be any archaic remnants of the autochthonous Gondwana biota. Apparently such supporting data are in existence.[1]

SUMMARY

The middle and late Paleozoic and earliest Mesozoic records of southwestern Africa and southeastern South America have long been known to show a degree of parallelism. This paper aims at a summary restudy of this situation and particularly at a qualitative appraisal of the data.

The terranes that may appropriately be called "parallel" commence on both sides of the South Atlantic with the Lower Devonian (possibly uppermost Silurian). The sequences begin with a coarse basal conglomerate of quartz sand which lies unconformably over older and usually deformed rocks. The clastics grow finer upward, as they are replaced by micaceous shales, sandstones, and siltstones. The finer clastics carry an abundant cold-water marine fauna of shallow benthos and a minor pelagic constituent. This is the "austral" or Malvino-African Devonian fauna. It is, despite its wide dispersal, a single homogeneous assemblage. The morphologic variation in genera and species is amazingly small, considering the distances involved, nor does this appear to be artifactual.

There is nothing in the fauna as a whole to suggest the existence of any barriers, other than distance, between the African and American scenes during the Devonian. The setting seems, moreover, to have been that of a shallow epeiric basin, or continental shelf rather than a geosyncline.

The Gondwana (Carboniferous-Triassic) parallelism involves very similar stratigraphic and biotic sequences on the two sides of the basin; glacial deposits and interglacial coal deposits and thin limestones characterize both sides. New Brazilian facies data seem to resolve the one seeming discrepancy in strict parallelism of the terranes.

The Keuper and Rhaetic (late Gondwana) terrestrial vertebrate faunas continue the same close facies parallelism, as do their enclosing strata and associated volcanics. But this phase marks the end of the close parallelism and consequent argument for close ligation across the South Atlantic.

The stratigraphic and paleontologic data now available still are best accounted for by the assumption of a broad continental linkage between South Africa and South America until the end of the Triassic, or possibly into the early Jurassic. By Cretaceous time there is abundant transgressive evidence of the Atlantic Ocean. The history of the "austral" Atlantic is essentially the history of the North Atlantic basin as well. The "boreal" connection was in part geosynclinal, however, whereas the "austral" one seems to have been solely epeiric, when marine.

If the Atlantic basin did not originate until the early Mesozoic, it would not be surprising therefore if previous records on the two sides of the basin were to reflect this fact; or, contrariwise, if present-day biotas, largely derived since the Mesozoic, gave little indication of the fact. Only the most ancient elements and the most conservative of existing flora and fauna might be logically expected to present evidence of the time of ligation. So far, these potentially promising neontologic clues have been insufficiently pursued.

[1] Of great interest in this connection is a paper by Fulford (1951) dealing with the world distribution pattern of leafy Hepaticae of South America. Distributional data such as these would appear to have especial relevance to the current problem.

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DISCUSSION

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WE ARE INDEBTED to Caster for his study of the data bearing on possible land connections across the South Atlantic basin during Paleozoic time. His extended sojourn in South America has given him acquaintance with the Spanish and Portuguese literature, personal contacts with many of the workers in the area, and wide experience in the field. These advantages have greatly enriched his provocative summary.

As he clearly shows, there are some parallels in the Paleozoic rocks and fossils of South America and South Africa that cannot be attributed to coincidence and may have deep significance. They deserve unfettered study and objective analysis. Until we know much more about the earth's interior and the fundamental causes of diastrophism it is unsafe to reject, *a priori*, either continental drift or foundering of broad land bridges. This seems, however, to be a heady subject that suffuses its devotees with strong enthusiasms, and Caster, like Du Toit, has gone all out to show that South America and South Africa have been broadly connected. But unlike Du Toit, who was convinced of continental drift, Caster believes the continents were never contiguous, but were joined by a broad land bridge in the form of a craton that has since foundered to make the South Atlantic basin. The writer assumes the role of critic with some reluctance and with all good will in the hope of serving as a counterbalance, for the arguments made by both Du Toit and Caster seem in large part irrelevant, inconclusive, or contradictory.

Caster's comparisons of the pre-Devonian record, for example, lead to the conclusion that "Without taking too much stock in actual correlations, there is a gross similarity, both in sequence and lithologies, of the older sedimentary terranes in South Africa and southern Brazil-Uruguay." Yet the similarity consists of such generalities as the mere presence of Proterozoic rocks bearing *Collenia*, notwithstanding the facts that Proterozoic rocks occur in every continent and that *Collenia* is admittedly world-wide in distribution. The presence of iron in the Proterozoic rocks of Brazil and South Africa is also cited. If these deposits were sufficiently alike, they might be used as an argument for continental drift, but since Caster believes that a great craton lay between the present continents, he must assume that the ore deposits were formed far apart, and it is difficult to see what possible significance they might have with respect to land connections. To be sure he admits, with disarming frankness, that "this fact cannot be satisfactorily employed in the present connection." Nevertheless it is in the record as a part of the parallelism. This is in a class with the discussion of the "strata of possibly Silurian age" which leads to the conclusion that "When so little is known of these problematical terranes and their age or correlations in Brazil (or Africa), it is indeed hazardous to make transoceanic correlations or even meaningful comparisons. The best that one can say is that there are large areas in southwest Africa where similarly controversial and lithologically more or less analogous sedimentary terranes occur." Although the argument is too weak to stand alone, the inference is there. It would have been literally true and much more objective to reduce the whole discussion of the pre-Devonian record to a single sentence to the effect that in the light of our present knowledge it has no bearing whatsoever on the problem in hand.

The insidious way in which such irrelevant data creep into the argument is illustrated by the first sentence in the next section, as follows: "Beginning with the Devonian system, the comparison between South America and Africa becomes *considerably more specific* and the broad transoceanic parallelism consequently *much more definitely established*." The words I here italicize beg the question, by making the wholly unjustified inference that a case has already been made for pre-Devonian land connection.

The arguments for Devonian ligation rest entirely on the "austral" marine fauna which

is shared by parts of South America and South Africa. It is correctly interpreted as a shallow benthonic fauna, and Caster argues that "the bridges across areas where now vast deeps prevail . . . were presumably continuously benthonic and probably epeiric." In this he completely deprecates the possibility of migration via island steppingstones. At present South Africa and Brazil are in the same temperature belt, and the westerly winds drive a surface current from southern Brazil directly towards the tip of South Africa. If comparable relations prevailed in Devonian time, a few widely spaced islands or submarine shoals would have provided adequate steppingstones to account for the admitted faunal similarities on the two sides of the South Atlantic.

This means of migration has been amazingly effective in the island-studded Pacific during later geologic time. To the writer, one of the most impressive experiences of a trip through the Pacific in 1946 was to see so many of the same familiar shells on the beaches of Hawaii, Bikini, Kwajelein, and Guam. Almost 2000 miles of deep ocean separates the Hawaiian chain from the Marshall group where Bikini and Kwajelein lie, separated by 200 miles of deep water. Guam is still another 1500 miles farther west across deep water broken only by widely spaced and tiny volcanic islands. All these islands lie in the same temperature belt, however, and the trade winds keep a surface current streaming westward from the southern end of the Hawaiian chain towards the Marshalls and the Marianas. Small collections which the writer made while combing the beaches of Bikini, Kwajelein, and Guam have been compared by my colleague, Percy A. Morris, with other collections from Hawaii, and the following is a partial list of species common to two or more of these remote islands, as indicated by the letters following the names (B, Bikini; G, Guam; H, Hawaii; K, Kwajelein):

Lioconcha heiroglyphica: B, H, K
Tellina rugosa: H, G, K
Tellina scobinata: B, H, K, G
Codakia punctata: B, H, K, G
Corbis fimbriata: K, G
Garfrarium pectinatum: K, G
Hippopus hippopus; B, K
Tridacna gigas: B, K, G
Conus hebraeus: H, G, K
Terebra crenulata: B, H, K
Terebra maculatus: H, K
Cyprea caput-serpentis: B, H, K
Strombus samar: H, K

These are all benthonic and shallow-water, shell-bearing mollusks. The list is by no means exhaustive. It includes only forms that appeared in two or more of my collections and could be accurately identified at sight. Exhaustive collections would certainly increase greatly the list of species that are widely distributed across great spans of deep water. Vaughan's study of the corals of the Hawaiian Islands (1907) showed also that numerous species and varieties of reef corals are found elsewhere in the Pacific and in the Indian Ocean. No former bridges of continuously shallow water can be invoked for the Pacific islands; many of the shallow, benthonic, shell-bearing animals have managed by means of meroplanktonic young, or otherwise, to cross impressive expanses of deep water. Undoubtedly many species are limited to smaller hops, and the faunas are far from uniform across the broad Pacific, but those that can cross are among the most prolific and conspicuous species. Indeed the local bottom ecology exerts a far more impressive control over the distribution of these faunas than large stretches of deep water.

Although suitable steppingstones are now lacking in the South Atlantic, a map published by Gutenberg and Richter, in 1949, shows a nearly unbroken ridge crossing the Atlantic basin between southern Brazil and South Africa. It is now deeply submerged, to be sure; but if we may assume that in mid-Paleozoic time it was much shallower, we have a bridge quite as adequate for the dispersal of the austral Devonian fauna as a craton connecting the continents. If there be any evidence for a broad land connection between South America and South Africa it must be sought, therefore, in the terrestrial fossils of the post-Devonian record.

The presence of *Mesosaurus* in similar environment in South Africa and Brazil has previously been considered one of the most telling arguments for continental drift. This rested on the assumption that *Mesosaurus*

was a fresh-water reptile and, therefore, could not have crossed open ocean. But Caster points out that it occurs in a fetid limestone along with several forms of marine invertebrates and correctly infers that it was a pelagic animal inhabiting a seaway with a stagnant and poisonous bottom which excluded a normal benthonic fauna. If *Mesosaurus* was thus adapted to marine water and to a pelagic life, it may well have made long journeys to sea, as do the modern seals and sea lions, and crossing of the Atlantic without a land bridge seems not improbable. The type of rock in which these reptiles are preserved indicates an unusual environment and probably a specialized food supply. If so, they would thrive only locally, even though capable of long journeys by sea, and their present restriction to beds of similar lithology in South Africa and Brazil offers no particular problem. That migration from one region to the other was not simple and direct is indicated by the fact that the African and South American species are distinct and that two of the three African genera have not been recognized in South America.

In seeking evidence of direct land connections we are thus reduced to the *Glossopteris* flora and to the terrestrial vertebrates of the Upper Permian and the Triassic rocks. The wide distribution of the distinctive *Glossopteris* flora in the Southern Hemisphere is indeed remarkable. But if a land bridge is needed to get these plants from South America to Africa, other land connections to India and Australia and Antarctica are necessary. Unfortunately, in spite of the abundant and widely distributed foliage of these plants, their mode of reproduction is not yet certain and their place in the plant kingdom is still obscure. During recent years Virkki (1937) has found peculiar double-winged spores in such abundance in association with the leaves of *Glossopteris* and *Gangamopteris* that the Indian paleobotanists believe they belong to these plants (Sahni, 1938). Such winged spores were presumably specialized for transportation by the wind. But whether these plants were distributed by spores or by seeds, when we consider the endless adaptations of animals and plants, it appears not improbable that this peculiar and highly specialized tribe had developed some device that permitted their transportation across open water. The cocoanut and other modern plants of the Pacific islands at least show us that such adaptations are possible. Until we know more about the manner of reproduction within the *Glossopteris* flora it is hardly necessary to drift continents or to place a craton between them to form a broad land bridge.

Unlike the *Glossopteris* flora, which shows such monotonously similar composition from one land mass to the next in the Southern Hemisphere, the reptiles and labyrinthodonts show marked regional differentiation, South Africa having a diverse fauna of which only a few genera and no species occur in South America. Critical analysis of these faunas is beyond the writer's competence and is treated by Colbert in another part of this Symposium. It may be noted here, however, that Simpson, in his penetrating analysis of the mammals in Cenozoic rocks (1943), points to the fact that of the known Triassic reptiles of South America only 43 per cent of the families and 8 per cent of the genera are known in Africa, and no species are common to the two continents. "These figures," he concludes, "are decidedly inconsistent with any direct union of corresponding parts of South America and Africa. The resemblance is greater than between South America and Africa today, but its small degree opposes a direct land connection, even a connection by a direct bridge."

Simultaneous glaciation on the two sides of the Atlantic, of course, has no bearing on the question of land bridges. It is now clear, at least, that during Pleistocene time continental ice sheets developed simultaneously on opposite sides of the North Atlantic, and it is generally conceded that even the glacial and interglacial ages can be correlated on the two sides. Lying as they do in the same latitude and in the same belt of atmospheric circulation, northern Europe and northeastern North America had many environmental features in common. If South America and Africa had their present respective positions in late Paleozoic time they, too, should have experienced parallel temperature changes.

Of course the presence of late Paleozoic

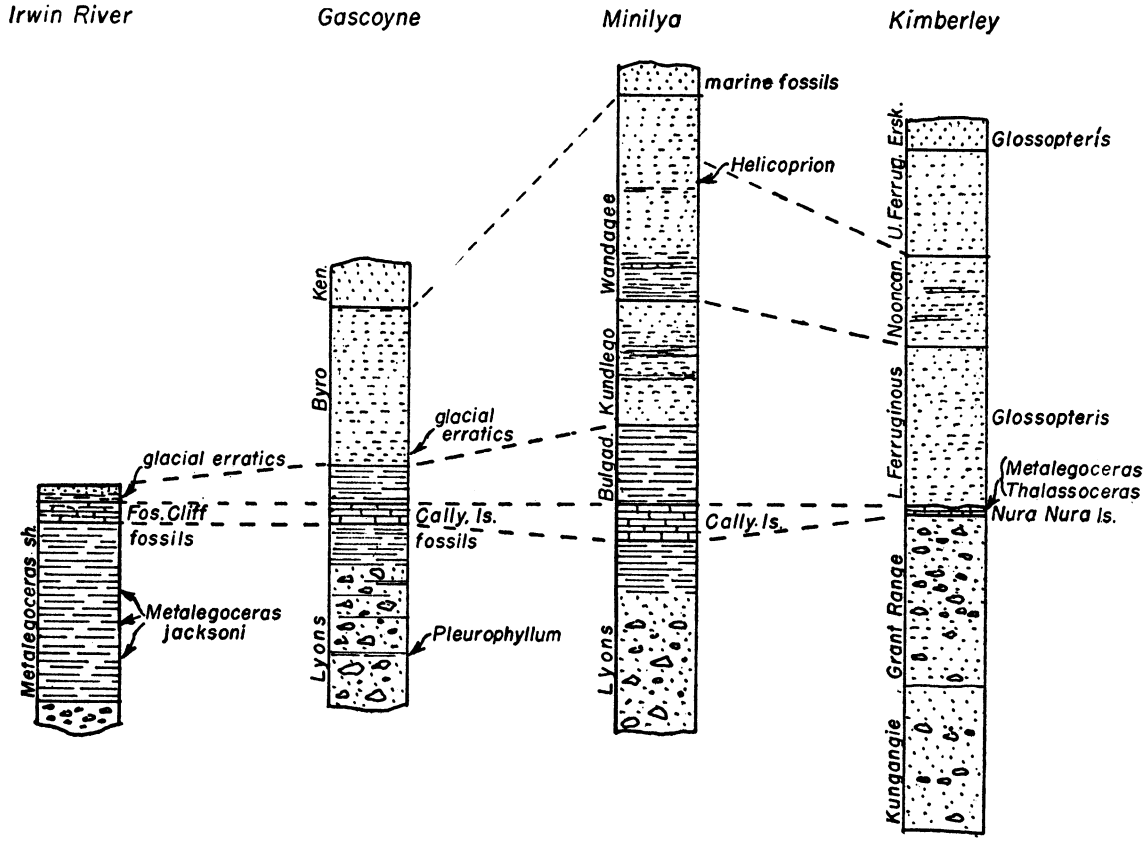

FIG. 17. Correlation of important sections of late Paleozoic rocks in Western Australia. After Teichert (1941).

glaciation in low latitudes is a problem still unsolved, unless we accept continental drift. But as for evidence of a craton between the present continents, the evidence from glaciation is wholly irrelevant.

Thus, when critically analyzed one by one, the arguments for a broad land connection across the South Atlantic basin appear to be irrelevant, altogether dubious, or definitely invalid, and, taken together, they do not gain strength.

The geologic date of the glaciation has no relevance to the problem of land connection, but it does have great interest in respect to earth's history. For reasons that seem tenuous and obscure, Caster takes the extreme view that the "great glaciation" of the Southern Hemisphere (Tubarão series of Brazil, Dwyka tillite of South Africa, Talchir tillite of India, and the great tillites of Australia) occurred during Upper Carboniferous (Pennsylvanian) time. In so doing he ignores completely recent discoveries that strongly indicate a post-Carboniferous and Early Permian date. This has long been a controversial subject, and critical review of the evidence would go far beyond the limits of this paper. Since Schuchert's analysis of 1928, further critical evidence has been presented by Teichert in Australia and by Sahni and his associates in India. In this connection the following summary by Teichert in 1946 (p. 102) is significant:

"At first they [the Permian rocks of western Australia] were regarded as Carboniferous. At a later stage they were, in common with contemporaneous sequences in eastern Australia referred to as 'Permo-Carboniferous.' In this case the question of the boundary between the Carboniferous and Permian was

usually left open, but sometimes the lower tillites and the lowest fossiliferous horizons were more specifically assigned to the Upper Carboniferous. . . . It was only when ammonoids and other fossils of great chronological value were discovered in western Australian Permian in great numbers (Teichert 1940c, 1942a, 1944a) that it was possible to put the correlation of these beds on a more exact basis.

"The main glacial period during which most of the glacial sediments (tillites, etc.) were deposited is of Lower Permian, or Sakmarian, age."

The figure from Teichert (1941, fig. 5; reproduced here as fig. 17) will clarify his arguments. The thin calcareous formation succeeding the great tillites throughout Western Australia provides a key horizon for correlating these sections one with another. Although given local names (Fossil Cliff beds, Callytharra limestone, Nura Nura limestone), it represents a single marine invasion that introduced a prolific fauna of over 100 species, a number of which occur also in the Permian of Timor. This is an early Artinskian, not a basal Permian, fauna.

In Northwest basin the underlying Lyons series includes a succession of tillites alternating with marine shales whose faunas have not yet been adequately studied but which include some species, as the coral *Pleurophyllum australe*, that recur in the higher beds, thus tying the glacial deposits to the overlying Permian. In the Irwin River area, where the glacial beds are thin, the *Metalegoceras* shale occupies the interval of the Lyons series and at three horizons carries abundant specimens of the ammonite *Metalegoceras jacksoni* which Miller (1932) has compared with closely similar species in the Lower Permian, Somohole, beds of Timor. Throughout Western Australia the great tillites rest on Devonian or older beds and are tied to the overlying Permian beds as explained. Glacial erratics in the shale above the Fossil Cliff limestone in the Irwin River area and in the base of the Byro beds in the Gascoyne area show clearly that glacial conditions persisted locally, or recurred, after the early Artinsk invasion.

The *Glossopteris* flora is closely associated with the great glacial deposits in Australia as elsewhere, and it ranges up through beds admitted by all to be Permian. In most places it comes in a little above the tillite, but *Gangamopteris cyclopteroides*, a distinctive member of the *Glossopteris* flora, has been found between the base of the Dwyka tillite and its striated floor near Strydenburg in the Karoo Basin of South Africa (Du Toit, 1926, p. 214). During recent years also, Sahni and his students have found the distinctive spores of the *Glossopteris* flora in the uppermost part of the Talchir tillite and in the shales immediately above in India, in the Bacchus March tillite of southeastern Australia, and in the Dwyka tillite of South Africa (Sahni, 1938, 1940).

On the contrary, outside of South America at least, the *Glossopteris* flora has nowhere been found in beds distinctly older than this great glaciation. In southeastern Australia, where the section is uncommonly thick and complete, the *Glossopteris* flora comes in with this final glaciation; it is not represented in the older beds, the Upper Kuttung and correlatives, that are admittedly Carboniferous.

Notwithstanding these circumstances, Caster recognizes in Brazil an "impure *Glossopteris*" flora in the great glacial (Tubarão) series and a "pure *Glossopteris*" flora in the overlying series, referring the former to the Pennsylvanian and the latter to the Permian. This he does apparently only because the earlier flora includes Pennsylvanian holdovers along with the *Glossopteris* assemblage. The problem of age determination thus appears to hinge upon evaluation of the significance of holdovers as against the appearance of the *Glossopteris* flora which elsewhere characterizes the Permian. Unfortunately no ammonites have yet been found in these beds in South America, and the marine faunas thus far described are hardly diagnostic. Obviously the problem needs further study. So far as the South American floras are concerned, the evidence appears equivocal, but when the "Gondwana deposits" of all the Southern Hemisphere are considered, the scales are tipped strongly to favor the view that the rise of the *Glossopteris* flora was associated with the "great glaciation" of the Southern Hemisphere and that both came at the beginning of, or early in, the Permian.

My extended criticisms relate almost wholly to two of Caster's interpretations. They should not obscure the fact that in summarizing the Paleozoic stratigraphy of a large part of South America and adding his own knowledge to many recent discoveries not easily available in this country, Caster has placed us all in his debt. One could only wish that observation and interpretation had been more clearly segregated.

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STRATIGRAPHIC EVIDENCE BEARING ON THE HYPOTHESIS OF CONTINENTAL DRIFT

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STRATIGRAPHIC EVIDENCE suggesting continental drift consists essentially of the presence of closely similar faunas or lithologic sequences on continents separated by present oceans. Interpretation of drift relates the similarities to closer proximity of the rocks at their deposition than in the present geography. Identical organisms in separate localities lived at times sufficiently contemporaneous that significant or recognizable differences had not evolved, habitats had ranges within the tolerances of the compared organisms, and migration routes were free of geographic or environmental barriers either continuously or interruptedly within any elapsed time; faunas are controlled by time, environment, and geographic province. Differences in faunas show lack of one or more of the controlling elements, or additional exigencies of chance. Close similarities of stratigraphic sequences imply comparable deformations of sources and sites of deposition, the latter affecting comparable local habitats. Faunal and stratigraphic identities can be explained most readily by assuming that the compared localities originally were in geographic juxtaposition, though alternate interpretations may be more reasonable explanations with consideration of other evidence. Early Paleozoic faunas on the two sides of the Atlantic illustrate the sort of facts that suggest drift. Knowledge of American continental development reveals reasons for hesitancy in accepting drift as a preferred hypothesis. Reference here is to only a limited part of extended literature, little of which is concerned directly with the analysis of the hypothesis; the theory has been discussed in several publications (Wegener, 1924; American Association of Petroleum Geologists, 1928; Bucher, 1933; Du Toit, 1937).

The theory that South America drifted relatively from Africa carries the corollary that North America similarly separated from Europe, whether as postulated by Wegener (1924) or at some other time. The lower Paleozoic faunas of Europe and North America are quite suggestive that the two continents were once in close proximity. The Cambrian succession in Sweden has been the subject of studies since the days of Linnaeus, and has yielded a sequence of faunas particularly characterized by trilobites (extinct arthropods) and brachiopods. Successive distinctive forms are related for the most part only remotely; for whatever reason, each association was replaced by another with few genetic descendants. Virtually identical successions are found in similar rocks in Wales, some 800 miles westward, and in Poland, to the southeast. In the later years of the last century, very similar faunas in similar sequence were discovered in northeastern Newfoundland, Cape Breton Island off Nova Scotia, and southeastern New Brunswick, interruptedly for some 600 miles. The dispersal of virtually identical faunas of graptolites, extinct hydrozoans, in succeeding beds does not seem so significant, for they probably were planktonic, whereas trilobites and brachiopods were presumably benthonic; the presence of a belt of similar environment across the Atlantic is implied. The fact that some 800 miles of the European dispersal and some 600 miles of the North American lie within the respective continents shows that the organisms had extended geographic range in the time of their existence. Certainly the virtual identities (Howell, 1937b) are in accord with the hypothesis that the separation of Newfoundland from Britain took place by drift subsequent to early Paleozoic.

Cambrian faunas of western Newfoundland and western New England are quite like those of the western part of the continent, from Arizona and Nevada to British Columbia. The two "provinces," which have been called Atlantic and Pacific, were not totally isolated by land, for some Atlantic forms are present with the Pacific, and in Vermont the Middle Cambrian is of Atlantic type (Howell, 1937a), whereas the Lower and Upper Cambrian are

Pacific. Such contrasts might be taken to support the hypothesis that western Newfoundland was originally far separated from the eastern part of the province and has subsequently moved into proximity; but such has not been considered, and the differences have been attributed to environment or possibly time.

Some years ago a large fauna of trilobites from northwestern Argentina (Harrington, 1938) was found to be similar to those in Sweden, and similar forms were found in eastern Colombia (Trumpy, 1943). It is not conceived that Colombia has drifted from Acadian Canada, so the conclusion must be that through early Paleozoic time conditions permitted dispersal of faunas between Baltic Europe and Argentina.

The faunas on the two sides of the North Atlantic in the Cambrian and lower Ordovician are very similar, and their characters are compatible with the hypothesis that original close geographic association has been broken by later drift. On the other hand, faunas considered approximately synchronous and extending from western Newfoundland and New England to western North America contrast markedly, but differences are not attributed to original separation. Cambrian faunas in South America are of the Atlantic province; similarity does not in itself require subsequent separation by drift. Unascertained environmental controls must have been responsible for the broad geographic dispersal and contrasting assemblages of contemporaneous lower Paleozoic forms.

Stratigraphic sequences can also give strong suggestion of the necessity of original juxtaposition, later broken. On coastal Norway, in southwestern Scotland, and in northeastern Newfoundland are Ordovician sequences of thousands of feet of argillites, volcanic rocks, and intercalated conglomerates with some plutonic pebbles. Each locality was one of deep subsidence, with associated volcanism and rising near-by land having exposed intrusive rocks. It is not surprising that each area of like history had similar environments and faunas; only geographic dispersal requires explanation.

The writer (Kay, 1944, 1947) reached the interpretation from the stratigraphic record that such belts are ancient island arcs homologous to the modern festoons of the Antilles, Indonesia, and the western Pacific (Eardley, 1947), and that such distinct belts developed systematically from the beginning of their geologic record, at least from the early Paleozoic; other types of information lead to the same conclusion (Hess, 1939). The Atlantic belt may have passed around the Gulf of Mexico into the Antilles and recurved into the eastern Andes. The Pacific belt may continue into the western Andes. Parts of each belt are in differing states of development. There were other more ancient belts in the Protozoic (pre-Cambrian) eras that crossed the craton of the present continent (Pettijohn, 1943), so that it is the theory that volcanic belts have decreased in number and continuity through time, present volcanic festoons being vestiges of once more extensive trends of such character. The theory has been discussed recently (Kay, 1951).

Sequences such as those in the Ordovician of Norway, Scotland, and Newfoundland are no more to be taken as evidence of original close proximity than is the similar section of southeastern Alaska; all are in belts of like stratigraphic character, parts of the great mobile belts (Bucher, 1933). Mountain making within them produced erosion products that spread on the continental (cratonal) blocks. Though similar belts on two sides of an ocean may only suggest drift, synchronous incidents in their histories seem more impressive. The theory that mountain building is synchronously world-wide has been disputed (Stille, 1941; Gilluly, 1949). It is at least regionally periodic and may be synchronous in widely separated areas. There is no uncertainty that there are periodic marine encroachments on the continents; if these be due principally to rise of sea level (eustatic movements), they are synchronous and have controlled climates and influenced lithic sequences in all continents at the same time in the same way. Hence similarities in sequences in different continents have been attributed to spread and retreat of seas controlled by rise and fall of sea level rather than original proximity of regions of similar sections (Grabau, 1936). Some have postulated that sea level responds

to mountain-making (orogenic) movements.

With present understanding of island arcs, some of the explanations given in the original hypothesis of continental drift (Wegener, 1924) seem fantastic. The arcs were thought to have formed in the lee of drifting continents, and the mountain chains to have risen along the margins of advancing blocks. Both coasts of North America seem to have had island arcs prior to the postulated time of drift. The hypothesis would require multiple advance and retreating movement on both sides of North America and along western South America. And the development would have proceeded from at least early Paleozoic time, rather than have the short span originally attributed to it. The development of both coasts has been essentially similar, though stages have been somewhat retarded along the Pacific as compared to the Atlantic. Could North America have drifted from Europe without resulting in contrasting histories on the two sides of the continent? The arcuate pattern of the festoons may better be compared to the subsiding bands between the welling areas of convection in a boiling fluid than to the sinuous eddying of drift.

Wegener considered the Himalayan chain to have formed from a shallow trough within a continent, the Indonesian arcs, now considered to be continuents of the same stratigraphic and orogenic belts (Stille, 1943), to have resulted as eddies in the drift of Australia, and the western Pacific festoons to have been lagging slivers of the receding Asia, though they are geophysically similar (Hess, 1948). He had to give exceptional treatment to the Mediterranean chains, which seem to lack continuents on the American side of the Atlantic, by hypothesizing that they passed into a relatively ancient Atlantic rift. Either the hypothesis is erroneous, or the more recent studies of stratigraphy, tectonics, and geophysics of island arcs have been interpreted poorly; the latter have reached integrated conclusions from independent types of evidence.

The writer is not sufficiently informed to analyze the stratigraphic and faunal evidence that leads to the impression that South America has drifted from Africa, but North America and Europe have similiarities that are strongly suggestive of separation. But the hypothesis has required interpretations that are so in contradiction with knowledge of continental development that it scarcely seems that they can be compromised.

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PROBABILITIES OF DISPERSAL IN GEOLOGIC TIME

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ALL-OR-NONE VERSUS DEGREES OF PROBABILITY

MOST OF THE LARGE AND WORDY LITERATURE of historical biogeography concentrates on the most basic but most gross of problems in this field. It is concerned mainly with the major biogeographic units, especially the past and present continents, and with inferences as to land connections between these. The discussion has involved postulates that are commonly unformulated and only rarely made explicit as working hypotheses. These hidden premises frequently are "all-or-none" propositions, in the form of Aristotelian "either-or" dichotomies.

The most usual of these propositions, when brought out into the open, will readily be recognized as permeating a large part of the literature. Formal statement of this usually unstated proposition might be made as follows:

PREMISE: The dispersal of a given group of organisms either (a) requires a land connection, or (b) does not.

OBLIGATORY ALTERNATIVES: (a) If dispersal does not require land, distribution of the group has no bearing on past land connections; (b) if dispersal does require land, disjunctive areas occupied by the group have been connected by continuous land.

Although it does not follow from this premise, a frequent addition to the second alternative is that the connection was more or less direct or, at least, that it did not traverse land areas where the group in question is not known to occur.

This sort of logic reduces the whole problem to delightfully simple form. It makes every man his own paleogeographer. To reconstruct a land connection one needs only a map, a ruler, and the information that, for instance, tapirs occur in tropical America and southeastern Asia or that mallows (of the genus *Malvastrum*) with 12 chromosomes occur in the tropics through South America, Africa, and the East Indies to Australia. That something is wrong with the procedure becomes evident when the results of different students are superposed, or when one student applies the methods to many different groups. Then the seemingly simple method leads to conclusions that are extremely complicated and contradictory, to the point of utter chaos. One is reminded of the facetious restatement of Grimms' law (in phonetics) as being that any consonant may change to any other. The biogeographers' equivalent is that any continent may be connected to any other (at any time).

Not many students are really so naive as to use this procedure in its simplest and most overt form. Review of the literature gives the impression, nevertheless, that a majority of biogeographers have been influenced to some extent by the "either-or" way of looking at things. A few have avoided this, and probably most of them would have if they had stated the premise and examined it sensibly. The fact is, of course, that its alternatives are false. There is no group of organisms that cannot be dispersed across water. Less striking but equally true is the factual contradiction of the other branch of the dichotomy: there is no group of organisms the dispersal of which is not influenced in some way and to some degree by the presence of intervening water. The fact of actual past dispersal of any one group of organisms across water may be determined and dichotomous; either it occurred in a given case or it did not. But in most cases of biogeographic study, the fact is sought, not given. The predictive or inferential situation is not one of absolute alternatives but one of degree. It is a matter of probability.

There are some cases in which over-water dispersal is effectively impossible or effectively certain, or, in terms of probability theory, in which the probability is practically zero or practically one. Even these cases are only the extremes in an infinitely graded series of probabilities and it is doubtful whether

there is ever justification for concluding that the probability is rigidly, precisely, mathematically either one or zero. It merely approaches these limits under unusually favorable or unfavorable conditions. Perhaps the elephants provide as good an example as any, because it is usually assumed, and with justification, that they are among the animals giving most conclusive evidence of overland dispersal. Yet a water barrier a foot wide obviously is no real barrier at all to an elephant. Probability of dispersal across such a strip of water can reasonably be taken as one for practical purposes, other things (such as ecological conditions on the two sides) being equal.

On the other hand, dispersal across 150 or 250 miles of water or, say, from Africa to Madagascar (in their present geographic relationships[1]) is evidently so nearly impossible for an elephant that equating the probability with 0 would seem to be justified. But just where does the shift from $p=1$ (i.e., probability of occurrence amounting to certainty) to $p=0$ (amounting to impossibility) occur? At a water barrier width of 100 yards? One mile? Five miles? Evidently at intermediate distances the dispersal is neither certain nor impossible but of intermediate degrees of probability varying inversely with the width of the barrier. Consideration of these facts also strongly suggests that dispersal across 1 foot of water is not really certain but merely highly probable, with, say, $p=.9999999$, and that dispersal across 200 miles of water, more or less, is not really flatly impossible but only highly improbable, say, $p=.0000001$. For some other animal, the probabilities may have the same trend but different values. The amphibious hippopotamus, for instance, crosses water more readily than an elephant, and therefore its dispersal across a water barrier of given width is more probable. Dispersal across a strait 150 to 250 miles in width may still have very low probability, but it is more likely than for the elephant. Rounding both probabilities to zero may lead to wholly false inferences.

Probabilities for other groups of organisms will certainly depart still more widely from those for the elephant. It is unlikely that probabilities are precisely the same for any two groups. Following the "either-or" implications that the probability may be taken as either one or zero for all groups or, indeed, for any group is logically unjustified and factually unrealistic. Biogeographic inferences will lead to false and contradictory conclusions unless some account is taken of probability in each case. The picture cannot be painted in black and white when nature has neither, but only infinite gradations of darker and lighter gray.

DIRECTIONS OF INFERENCE

In the particular sort of problem here under discussion there is one constant or known element, and there are two variables, one or usually both of which are unknowns for which values should be sought. The constant is represented by what is actually known of the geographic distribution of organisms, often including uncertainties (especially in past distributions) and shifting factors (especially in taxonomy), yet in the procedure of inference necessarily taken as given fact. One variable is geographic, especially the presence or absence of land connections, in the usual basic form of the gross problem. The other variable is biological, or more properly, broadly ecological, the probabilities of dispersal by various means for various groups of organisms.

It is impossible to solve a single equation with two unknowns. The only way to obtain a fixed value for either unknown is arbitrarily to assume a value for the other or to assign it a series of possible values. Similarly in this biogeographic problem it is impossible to infer from the distributional facts simultaneous conclusions as to land connections and probabilities of dispersal. It is necessary either to postulate the existence (or absence) of land connections or to postulate probabilities of dispersal. Distributional facts

[1] The water distance is now 230 miles and would be 160 with only slight lowering of relative sea level.

plus a postulate of geographic land and sea configuration permit inferences as to probabilities of dispersal. These facts plus a postulate as to dispersal probability permit inferences as to land and sea configurations. Of course the postulate need not be guesswork in either case and may exceptionally approach the level of fact. Geology may supply preferable postulates for geographic configuration, and biology may supply the same for dispersal probabilities.

As an example of this question of direction of inference, it is a fact that Madagascar has a small number of groups of land mammals related, in varying degrees, to a few of the far more abundant groups in Africa. From this fact alone, it is impossible to conclude anything about the dispersal of these animals (except that it occurred) or about former relationships of Africa and Madagascar, unless some assumption is made about one or the other of these two elements in the problem. It may be postulated that the configuration of the land in that region was about the same throughout the Cenozoic as it is now. Then inference leads to a definite conclusion regarding the other variable: that over-water dispersal for these animals has a small but definite probability. (Means of making such an inference are discussed below.) On the other hand, the postulate may be that the probability of over-water dispersal for these animals is effectively zero. Then inference in the other direction is made possible and leads to the conclusion that the present configuration of the lands did not characterize the whole Cenozoic but that Africa and Madagascar were connected at some time in that era.

The literature of the subject abounds in inferences in the second direction illustrated above and contains few examples of the first. With rare exceptions, a postulate is made as to probabilities of dispersal, and inferences are drawn as to geographic relationships. As emphasized in the preceding section, this is often done without particular notice that the probabilities of dispersal are variables also to be investigated and seldom factually established. The opposite direction of inference, towards investigation of dispersal probabilities in given cases, has rarely been employed. Among the few exceptions are cases in which the geological evidence practically forces establishment of a geographic postulate and does not permit serious consideration of this as a variable. An example is the case of the Hawaiian Islands. On geological grounds alone, it is virtually impossible that these islands were ever connected by land with any continent. Therefore most recent students have taken this as established, or have taken it as a postulate eliminating the geographic unknown in the figurative equation to be solved, and their inference has been directed towards interpretation of positive and negative features of the Hawaiian biota in terms of probabilities of dispersal over wide stretches of ocean.[1]

Some reasons for this preferred but not necessary orientation in the direction of inference can be seen. Most students of the problem have been zoologists and botanists, and they have tended to assume that they could evaluate, *a priori*, the biological element of means of dispersal or, at least, have been likely to take this for granted rather than the geological elements. Being biologists they have also usually failed to see that their estimates of probabilities of dispersal, even when least subjective, might be wholly invalidated by the effect of geological time. (This is an extremely important point which is considered in more detail below.) The geologists have reënforced this tendency by their failure to produce a conclusive theory of continental evolution and in some cases by their uncritical readiness to accept ill-understood biological evidence in favor of one theory or another. For instance, Wegener's and Du Toit's emphasis of biological evidence to support the theory of continental drift (see Du Toit, 1937) seems to have en-

[1] Even here there have been and in decreasing numbers still are students who approach the problem in the traditional but here almost certainly inappropriate direction. Among these is Crampton, who took it as established that probability of overseas dispersal of land snails is precisely zero and inferred from this a great series of Pacific land bridges, instead of taking the geographic evidence as indication that the probability, although small, is not zero and using distributions as a means of evaluating that probability. The whole subject of the Hawaiian biota is discussed with care and skill by Zimmerman (1948).

couraged some biologists to think that their premises as to dispersal required no investigation and that the only problem was to determine how and when the continents moved about.

Another factor in the odd one-sidedness of much of this study is that many of the leaders in the development of biogeography, particularly as this science arose in the last century, were mammalogists. On an average, the probabilities of overseas dispersal for mammals are very low. These students therefore had some justification for proceeding as if zero probability were an established fact or, at least, the best working hypothesis. (Even so, it now seems clear that some serious errors arose from confusing "very low" with "zero," say, $p = .00000001$ with $p = 0$, in mammalian dispersal.) In some cases this encouraged students of other groups to adopt the same hypothesis, even when the probabilities of dispersal for their groups were manifestly not so low as for mammals.

It is an instructive experiment to try reversing the time-hallowed approach to these problems, to start with the hypothesis that land and sea have always been about as they are now, and to try to infer from this the probabilities of dispersal by various means, instead of going at it the other way around. The distribution of mammals as a whole will be found so consistent with present land configurations as to indicate for most of them dispersal by land routes only. The only apparent discrepancy in the broad picture is that the probability of crossing Bering Strait turns out to be much higher than that of crossing water barriers of similar width elsewhere. This inconsistency warrants reversal to explain the exception: the inference that the strait was narrower or non-existent in the past is suggested. A few other minor irregularities occur, as in the East Indies where the independent evidence of local geology shows that our geographic hypothesis is not warranted. On the other hand, on this basis it becomes necessary to conclude that overseas dispersal had a probability still low, yet significant, for a few sorts of mammals.

Despite explicable exceptions, the mammalian pattern is mainly consistent with land distribution over the present configuration of the lands. In the particular case of South America, for instance, mammalian faunal relationships are much the closest with North America, the actually connected land mass. They exist but are less close with Europe and northern Asia. They are minimal, almost nonexistent, with Africa and Australia, the two continents most distant by the most nearly continuous existing land routes but not most distant by over-water routes. Moreover, every group of mammals that South America shares with the Old World is also present in North America, on the land, not over-water, route to the Old World, with two exceptions. These exceptions are the camels and the tapirs, and paleontological evidence shows that they are not real exceptions in a historical view: they formerly abounded in North America, and the South American forms certainly came from there.

When the same method is applied to the flowering land plants, for instance, the results seem to be different. Distributions of many plants are consistent with the minimal postulates for land dispersal of mammals. Others are not. Many plants are distributed zonally around the world without apparent regard for intervening seas. There are no pan-tropical mammals, but there are many pan-tropical plants. No South American mammals are as closely related to African as to North American allies,[1] but a number of plants show this trans-Atlantic relationship. In other words, the distribution of mammals seems to be conditioned primarily by land connections essentially as these now are, only secondarily by climate and other factors, while the distribution of many plants seems to be conditioned primarily by climate and only secondarily by land connections as these now are. Following the present direction of inference, the conclusion is that the probability of over-water dispersal is significantly higher for many plants than for most mammals. As is demonstrated below, the proba-

[1] An apparent exception has been among certain of the so-called hystricomorph rodents, but recent work seems to be confirming an older suspicion that this was a taxonomic mistake, the apparent relationship being due only to convergence of two quite separate groups of ultimately North American and Eurasian origin, respectively.

bility for these plants may still be very low when time is not considered. For other plants, many of which do show distribution patterns not radically unlike those for mammals, still lower probabilities may exist, approaching zero about as closely as do the probabilities for most mammals. Still the conclusion stands that the evidence, viewed in this way, suggests that numerous plants have significant probability of overseas dispersal.

Of course many botanists, following the methodological lead of so many zoologists, have approached this problem from the other side, have assumed a zero probability of overseas dispersal, or near it, and have inferred the existence of trans-Atlantic or pan-tropical land connections. From this has arisen a fundamental conflict between these botanists and most mammalogists, because the distribution of the two groups simply cannot be explained on the same land configuration except by the postulate of greater probability of overseas dispersal for plants. It is not proposed to carry this discussion farther here, but the results of revising the direction of inference may provide some food for thought.[1]

The following three quotations require no comment:

"Therefore it would seem only logical that a true interpretation of zoogeography must be based on a correct understanding of phytogeography; it must be a BIOGEOGRAPHY" (Camp, 1947).

"A comparison of phytogeographic and zoogeographic maps indicates that it is impractical at the present time to construct biogeographic maps, that is, maps that intend to illustrate simultaneously the distribution of plants and of animals" (Mayr, 1944).

"The order of importance of the natural barriers to spread varies with the means and methods of dispersal and with the tolerance and adaptability of the plant or the animal to the different barriers. For plants climatic barriers come first, then edaphic, biotic, and geographic obstacles. . . . In case of mammals the order of barriers is: geographic, climatic, and biotic or environmental" (Antevs, 1947).

DETERMINANTS OF PROBABILITY OF DISPERSAL

Stress on probability of dispersal as an essential element in zoogeography requires some notice of the factors that determine this probability. Considerable attention has been given to this subject, mostly as regards specified taxonomic groups and particularly those that are in fact widely dispersed, especially to oceanic islands. A general review is not called for at this point, but a summary from the present point of view may be suggestive. Of all determinants, time may be the most important and this is given special consideration. First, however, some of the non-temporal, especially biological and geographical, factors are noted.

In general the broad factors of dispersal probability at any one time involve:

The source area and population
  Dispersal stimulus
  Means of dispersal
The intervening or, in special cases, barrier region
The colonization area
  Climatic, edaphic, or general environmental receptivity
  Ecological receptivity

"Dispersal stimulus" is taken to subsume a variety of quite distinct factors, any one of which tends to make dispersal more likely because of conditions within the existing range. Deterioration of environment is one such factor, tending to induce actual migration rather than the more usual spread. Population growth is an essential element in most cases of spread or continuous dispersal; an increasing population naturally tends to spread and a decreasing population to dwindle not only in size but also in area. Even if a population is not increasing and is not significantly overcrowded, its absolute size has a decided effect on probability of dispersal. The number of individuals that might be dis-

[1] It is hoped that this point may be considered by other contributors to this Symposium in discussion of supposed Gondwanaland, an ancient pan-tropical continent inferred from the evidence of fossil plants on the usual postulate that overseas dispersal of these plants was impossible. May it not be equally valid to infer from these ancient pan-tropical distributions that overseas dispersal of plants was then (as now?) sufficiently above zero probability to become significant in a long span of geological time?

persed corresponds with number of trials in probability theory and therefore has a strong influence on total probability, especially when the basic probability of dispersal of any one individual is low. The nature of this influence is further discussed in the next section of this paper. In passing, it is noteworthy that population size in this connection means the number of individuals in the stage or condition when successful dispersal actually does or may occur. In plants, this normally means the number of viable seeds, usually a number greatly exceeding that of established, resident individuals. In invertebrates it might mean number of fertilized eggs or of larvae, etc. At the other extreme, in mammals under some quite special conditions it might mean at most one-half of the number of gravid females.[1]

More attention has been paid to means of dispersal than to most other factors, and these means are rather well known, although not always fully evaluated, for most groups. For the special case of transoceanic dispersal for land organisms, the means must usually involve some stage in the life history when the organism is, or can be, air-borne, water-borne, or ferried.

There are numerous organisms for which one of these conditions is normal or usual, and of course this increases the probability of dispersal. Many plant spores and seeds, all volant animals, and even some non-volant animals (i.e., some spiders) are regularly air-borne. Parasites of volant animals are regularly ferried, within the meaning of the word here intended. Even animals for which such transport is highly unusual may have a low but real probability in this respect, for instance in the air-borne transportation of fishes by tornadoes. Although the list is not exhaustive, the following characteristics may be noted as among those that would tend to increase the probabilities of dispersal by these means among organisms not normally so transported:

Small size (important for air, to less extent for ferry transport)
Low specific gravity (important for air and for water transport by floating)
Protective coating (important for all, and especially for water transport)
Dormant stage (also of some possible importance for all)
Possible attachment to volant animals (burrs, mucilaginous eggs, etc., also seeds ingested but not digested; important for ferrying)
Habitat in trees, brush, or aquatic vegetation (important for ferrying)

It is evident that very few non-aquatic, non-volant vertebrates are normally air-borne, water-borne, or ferried, but that a few groups have members with characters tending to increase probability of accidental transport by these means, for instance small, arboreal rodents which do, in fact, seem to have dispersed over seas more often than most other mammals. On the other hand a large percentage of land plants, as spores or seeds, have most of the characteristics that tend to promote overseas transport. This supports the previous deduction from distributions, on the postulate of stable continents, that mammals rarely and plants rather frequently have overseas dispersal.

The effect of the region intervening between source area, from which dispersal occurs, and the area colonized is rather obvious. This region may have the same characteristics as the source area, in which case probability of dispersal will depend almost entirely on population increase and will occur at steady, determinate speed. This is the situation, really not very common, in which the "age and area" rule may actually work out in a regular way. Every gradation may occur from this condition to nearly absolute impassability, a continuous series of decreasing probabilities for dispersal in which it is difficult to designate the point at which the intervening region ceases to be a "migration route" and becomes a "barrier." Although this is a continuous series, it is legitimate and useful to distinguish between barrier regions where continuous residence or

[1] The special conditions: dispersal so improbable that overlapping dispersal of two individuals practically will not occur, and a species of mammals bearing only one young (or young all of one sex) at a time. Colonization may then be effective only by a gravid female carrying a male foetus, and then only if the female continues to be fertile until her offspring reaches sexual maturity. The example is given to illustrate an extreme, yet it is probable that such events have occurred in the long course of time since (therian) mammals arose.

population maintenance of the organisms in question is impossible and those in which (even though it may be difficult, or may not occur in fact) it is possible. The distinction can usually be made.

Concentration of attention on oceans, seas, or salt-water straits has perhaps been overdone. There are rather numerous instances in which land organisms have dispersed freely over salt water but not over continuous land connections. Yet this special case, an example of which is the subject of the present Symposium, is the one of greatest interest to geologists and has outstanding importance for broader features of biogeography. Some normally fresh-water organisms, among plants, invertebrates, fishes, and even mammals, can live for rather long periods in sea water, and a few can maintain populations there. Then the probabilities of transoceanic dispersal are enhanced, sometimes to such a degree that it is doubtful whether the sea should be designated "barrier" or "migration route." This is the basis of the distinction made by Myers (1938) between a primary [or obligatory] and a secondary [non-obligatory] division of fresh-water fishes. For many fresh-water, and the great majority of land, organisms, however, there is a clear distinction: they cannot live long or develop normally in, on, or above the sea, let alone maintain populations there. These organisms are the crucial ones in dealing with transoceanic dispersal or land bridges, and some confusion has arisen from failure to be certain that particular groups (for instance among fresh-water fishes) do really belong in this category.

Even regarding those organisms for which the sea is an impossible habitat, it is wrong to designate the oceans, or branches of them, as "absolute" barriers, a point established in the first section of this paper. The real situation is that in such cases the effect of the intervening region on probability of dispersal is fully determined by the width of that region (although the function is not linear). This is the simplest relationship between a barrier and dispersal probability, which is doubtless one of the reasons why it is most studied.

Dispersal can occur only if there is a colonization area previously unoccupied by the group in question but habitable by that group. The conditions making for habitability are fairly well understood in most cases. It is unnecessary to enumerate them here beyond pointing out that they fall broadly into two categories. First are the more strictly environmental conditions: suitable food, climate, soil (for plants and, through plants, indirectly for animals), and the rest. Second, there must be an open (unoccupied) ecological niche, or else the colonizing organism must be able to oust an established group from such a niche. (This is what is designated as "ecological receptivity" on a previous page.)

In high-probability dispersal, regular spread of organisms over regions generally favorable to them, invasion of an occupied niche is by the usual process of inter-specific selection. The outcome, hence the effect of colonization area on probability of successful dispersal, may be taken as fully determined by "fitness" in the Darwinian sense. In low-probability dispersal, including among others overseas dispersal of land organisms, another factor enters. The incoming groups will be few in numbers, perhaps only one individual at any one time, and may arrive in weakened condition. The presence of ecologically similar, competing organisms already established will then significantly lower the probability of colonization, and the outcome may not correspond with fitness under conditions of equal opportunity. Here again the probabilities are radically different for different sorts of organisms. Chances of survival will be much higher when there are numerous simultaneous arrivals, as is frequently true for plant seeds, for instance, than when only one or a few potential colonists arrive at any one time, as must commonly be true of mammals and other relatively large organisms normally dispersed in adult form.

Known distributions amply testify to the importance of conditions in the colonization area. In plants, especially, this frequently seems to be the decisive factor. Of two regions, one of which is set off by no geographic barrier but is ecologically unfavorable while the other is separated by a strong barrier (even a major ocean) but is ecologically

favorable, plants will often colonize the latter and not the former. Probabilities related to the colonization area may thus outweigh those related to source area, population, and intervening region, although all have some role in the determination of total probability.

The effect of colonization area on dispersal probability also forms a continuous series. No sharp line can be drawn between an area impossible of colonization by a given group and one merely difficult, or between difficult and easy, easy and certain.

Even so brief a review of the determinants of probability of dispersal shows how exceedingly numerous and complex these are. Many act simultaneously, like the source area factors that determine how many (and what sort of) attempts or trials occur towards dispersal from that area. Others act sequentially, like those arising in source area, intervening region, and colonization area. Theoretically it would seem possible to evaluate each of these factors and to obtain a concrete, reasonably accurate numerical estimate of the total probability for a given group of organisms and a defined episode of its dispersal. Actually this has never been done, as far as I know, and there does not seem to be any group for which all the required data are available, even as approximations. The problem is so extremely intricate that the labor of gathering and treating such data may not be considered worth while unless, possibly, in a few of the least complex cases by way of example. This does not mean that it is futile to list and to study these determinants. Even though more precise values are unavailable, broad, subjective estimates of these probabilities enter into almost every study of biogeography. These are sure to be more reliable in proportion to the amount of conscious attention and thought given to the determinants underlying them.

On the other hand, empirical, *a posteriori* estimates of probability of dispersal can be made in many cases and even quantified in numerical terms, at least as to orders of magnitude. It is possible to take examples of dispersals that have, in fact, occurred, to determine or postulate the conditions under which these took place, and to derive reasonable estimates of the total probability involved. On a more theoretical plane, it is also possible to set up hypothetical models with assumed values for the various determinants and to calculate total probabilities for these. Such models may then assist materially in the sound interpretation of actual biogeographic occurrences. Both of these procedures require estimation of the effects of multiple trials and of geologic time, a subject that must now be more particularly considered.

PROBABILITY AND TIME

The whole argument as to whether there was or was not a land connection between two continents at a given time usually depends on the probability of dispersal from one to another without a land connection. There is actually no way in which this probability can be directly measured, or at least this has not been done, so that this basis for the argument is never precise, quantitative, and objective. Each student states his subjective judgment in the matter. If all do not agree (and they seldom do), there seems to be no decisive way to settle the question. Camp (1948) believes that bird-ferrying of *Rhipsalis* across the South Atlantic is so improbable that it is only a "glib explanation" unworthy of serious consideration. Therefore he invokes a geologically recent land connection between South America and Africa. Anthony (1948) believes that if bird-ferrying occurred at all, dispersal would be too probable. It should then (he says) have led to colonizations of *Rhipsalis* more numerous than actually occurred, but he concludes that introduction by man is likely and no land connection is required. Roland-Gosselin (1947) thinks that the probability of bird-ferrying is just about right to account for the facts without, again, any land bridge.[1]

[1] On *Rhipsalis*, see also Backeberg (1948). This genus includes cacti with small but attractive blossoms, sometimes raised as house plants. It grows wild in warm parts of the Americas and also in Africa and beyond into the eastern tropics, the only cactus that seems to be

No one really knows what the probability of bird-ferrying is for *Rhipsalis*. Whose opinion should prevail?

In such a case, the logic of the conclusion depends on what is really meant by the vague words "probable" or "improbable," and on how well their implications have been understood. Few would insist that bird-ferrying for *Rhipsalis* is utterly, absolutely impossible. Almost everyone would agree (with Camp) that it is extremely improbable, as we usually use the word and relate it to any one time or to such spans of time as we personally experience. But Anthony has brought in another element: the problem does not necessarily involve one time or such periods as come under human observation. It may involve millions of years. Anthony's argument implies that a possible event, however improbable it may be as an isolated occurrence, becomes probable if enough time elapses. Here, at least, is something that can be precisely evaluated in theoretical terms and that does not have to be merely a matter of opinion and subjective estimation.

For any event, there is a definite probability of occurrence. In flipping a coin, the chance of getting heads is one in two, or the probability is one-half. In simple mathematical conventionalization, $p = .5$. This is an exact, true statement of probability (if the coin is theoretically perfect). It is true, however, only if the coin is flipped once and no more, just as it may be true that spread of organisms across a barrier is improbable only if we think of a single individual or of one population over a short period of time such as a year or a century. If the coin is flipped 10 times in succession, or (what amounts to the same thing as far as probability goes) 10 coins are flipped once, then the probability of getting heads at least once is far greater than one-half, or .5. In fact, it is greater than .99, and a gambler would be justified in taking this as a sure thing. Statements of probability in coin-flipping mean nothing unless they take into account the number of trials or opportunities for occurrence. Similarly, statements of probability of dispersal are meaningless unless they take some account of analogous effects tending to change the value of total probability.

Probability of dispersal is affected in this way by the size of the population subject to dispersal. If the chance that any given individual will cross a geographic barrier is, say, one in a million, $p = .000001$, then in a population of a million individuals the chance that at least one will cross the barrier is almost two in three, $p = .63$. An event so extremely improbable for a single individual that most of us would think of it as impossible becomes more likely than not for the population as a whole. The passage of time has the same effect: it multiplies the opportunities for occurrence, whether one considers this as giving the same individuals (or their successors) more opportunities for dispersal or as increasing the number of successive individuals that have such opportunities. If the probability that some member of a population will cross a barrier is .000001 in any one year, in a large population this means that the probability for any one designated individual is almost infinitesimally small, so much so that it would seem absolutely impossible to even the best qualified observer in the field. Yet during the course of a million years the event would be probable, $p = .63$, again. In the course of 10 million years the event would become so extremely probable as to be, for most practical purposes, certain, $p = .99995$. In other words, there would be only about one chance in 20,000 that it would not occur. One million or 10 million years is not a particularly long time, as time goes in dealing with many problems of historical biogeography. This example, in itself, should give pause to those who speak of the "improbability" of transoceanic dispersal on the basis of their observations of a few individuals for a few years.

The calculation of such probabilities is fairly simple and is explained in innumerable books touching on statistics or probability, but it is not familiar to all biologists, so may be briefly explained here. The symbol for

growing as a native plant in the Old World. Dozens, probably hundreds, of other cases could be cited in which authorities have differed radically as to the probabilities of various means of dispersal for organisms with transoceanic distributions. *Rhipsalis* is cited in order to have a concrete example and because the case is fairly typical and is the subject of recent, vehement dispute.

probability of occurrence is p, and that for probability of non-occurrence is q. Values of p lie between 1, certainty of occurrence, and 0, impossibility of occurrence. The value of q is always $(1-p)$. The probability in multiple trials or opportunities for occurrence is obtained by expanding the binomial expression $(p+q)^t$, where t stands for the number of trials or opportunities. For instance, for two trials this expression becomes

$$(p+q)^2=p^2+2pq+q^2$$

The first quantity, p^2, is the probability that the event will happen twice in two trials. The second quantity, $2pq$, is the probability that it will happen once, and the last, q^2, is the probability that it will not happen at all. For three trials the expression gives

$$p^3+3p^2q+3pq^2+q^3$$

The successive terms give the probabilities that the event will occur three times, twice, once, or not at all.

In consideration of dispersal, p may represent any basic probability such as (a) the probability of successful dispersal of a single individual, or (b) the probability of dispersal from a given population in any unit of time such as a year. In case a, t may be taken as the number of individuals in a population.[1] In case b, which is perhaps the more enlightening model for considering biogeographic events, t should be taken to represent the number of years (or other time units) involved.

In either case, in biogeographic problems the pertinent values of t will commonly run into millions. Expanding the expression

$$(p+q)^{1,000,000}$$

is a formidable undertaking, but fortunately this is not necessary. In these problems what we usually want to know is the probability that the event will not occur at all or that it will occur at least once. The probability of non-occurrence is the last term in the expanded binomial, and this is always simply q^t. Raising such a fraction as, say, .99999 to the millionth power may still seem unduly formidable, but this can easily be done with a table of logarithms to a sufficient number of places. The probability of occurrence one or more times is necessarily one minus the probability of non-occurrence, or $(1-q^t)$. In some cases, probability of occurrence just once or of occurrence more than once may also be of interest, and the binomial gives fairly simple formulas for these values, too. In all, the following symbols and formulas are useful:

p = probability of dispersal analogous to a single trial, e.g., for one individual or for a population in one year, one fruiting season, etc.
$q=1-p$ = probability of non-occurrence, of failure in dispersal
t = a quantity analogous to number of trials: the number of individuals in the population, number of years or seasons, etc., as appropriate
a = total probability of non-occurrence $=q^t$
b = total probability of occurrence at least once $=1-q^t=1-a$
c = total probability of occurrence just once $=tpq^{(t-1)}$
d = total probability of occurrence more than once $=(1-q^t)-tpq^{(t-1)}=b-c$

For accuracy, the values of a, b, c, and d must of course be worked out by formula from separate values assigned to t and to p (the value of q being fixed by that of p). Since, however, the total probabilities sought tend to depend on relative values of t and p, a rough and ready approximation can be worked out more simply from the single value representing the product of these numbers, tp. Such approximations have so much bearing on judgment of biogeographic probabilities that a brief table is submitted:

$tp=$	.001	.01	.1	.5	.7	1	1.5	2	5	10
$a=$	.999	.99	.90	.61	.50	.37	.22	.135	.007	.00005
$b=$	.001	.01	.10	.39	.50	.63	.78	.865	.993	.99995
$c=$	.001	.01	.09	.30	.35	.37	.33	.270	.034	.00045
$d=$	.000	.00	.01	.09	.15	.26	.45	.595	.960	.99950

[1] Probabilities calculated will then apply to a unit of time equal to the average length of time during which dispersal is possible for an individual, perhaps the average span of individual life or perhaps, more commonly, a shorter period. To take longer periods into account, this result would then have to be treated as in case b, using a new value of t equal to the total length of time expressed as the number of the units implied in treatment a.

These values are close enough as basis for general judgment for values of p from .1 to about .00000001, although there may be an error in the last place for extreme values of p. For values of tp smaller than .001 or larger than 10, the values of a, b, c, and d so closely approach either 1 or 0 that in most cases they can be taken as virtually equal to one or another of those extremes, although it is well to remember that these probabilities never literally and precisely amount either to certainty or to impossibility. The interesting value $tp = .7$ is included, because this is approximately the point at which non-occurrence and occurrence (at least once) become equally probable.

Two simple examples illustrate use of the table:

1. If the chance that a species of plant will be dispersed across a barrier in any one fruiting season is one in a million, what is the chance over a period of a million fruiting seasons?

$p = .000001$ (given)
$t = 1{,}000{,}000$ (given)
$tp = 1$
$b = .63$ (table)

The chance is approximately two in three, or odds are about two to one—a noteworthy probability for what would seem to the observer of one or a few seasons as a virtually impossible event.

2. If the chance of crossing a particular barrier for a given group of animals is one in a million in any one year, how long a time must elapse before the chances of crossing or not crossing are equal?

$p = .000001$ (given)
$tp = .7$ (as shown in table for $a = b = .50$)
$.000001t = .7$
$t = 700{,}000$ years—geologically a brief time

In a given case, the subjective statement that an event is "improbable" may correspond (if the statement as made is true) with $p = .49$, or with

$$p = .0000000000000001$$

The implications are extremely different for these two values, which nevertheless can hardly be distinguished in many arguments about dispersal. Even though the values cannot (at present) be calculated exactly for particular cases, it is possible to judge their orders of magnitude under given circumstances.

To return to *Rhipsalis*, let us test certain assumptions by finding their relationship to probabilities of dispersal. Suppose that the genus has existed for about a million years, which is a conservative guess likely to be of the right order of magnitude. Suppose, then, that the probability of dispersal from South America to Africa in any one fruiting season or for any one annual seed crop had been on the order of, say, .0001.

$$tp = .0001 \times 1{,}000{,}000 = 100$$

Probability of at least one colonization (b in the table) would be far in excess of .9999, hence virtually certain. This is all right, as colonization did occur. More than that, however, colonization in any one period of 10,000 years would be more probable than not, and colonization within 50,000 years would be nearly certain. One would expect that colonization would have occurred at least 20 times, and 100 or more times would be likely. But the botanical evidence is that only one or, at most, a few colonizations occurred. Too much has been proved, and the most likely true value of p was evidently smaller than .0001.

Suppose, now, that p was as small as .00000001. Then $tp = .01$ and, from the table, probability of colonization in the last million years would be only about .01, in other words, truly very improbable. It is likely that p had a higher value than .00000001. Similar calculation on the postulate of $p = .000001$ indicates probability of at least one colonization as .63, of just one as .37, and of more than one as .26. These figures agree very well with what actually happened: colonization, which factually occurred, is indicated as probable; colonization just once (as some authorities consider to be the case) is more probable than multiple colonization; colonization two or three times (as others think correct) is still not markedly improbable; but really numerous colonizations (which seem not to have occurred) are prohibitively improbable.

Evidently in the case of *Rhipsalis*

$p = .000001$ is of the right order of magnitude, and the correct value was probably smaller than .00001 and larger than .0000001. These limits are likely to include the true value, even if the estimate of age as a million years is badly mistaken and this figure should be as large as 10 million or as small as 100,000.

Is a probability of dispersal in any one year of .000001 (or thereabouts) too large to involve transoceanic bird transport, or too small for spread overland?[1] I do not propose to answer this question, which is the business of the authorities or disputants in this particular case. My point is that when the question is put in this way, they will have a much more definite basis for judgment and we will have some idea what is meant by the improbability of one means of dispersal or another.

SOME IMPLICATIONS OF DISPERSAL PROBABILITIES

It is meaningless to speak of probability unless this is for some sort of one-trial situation (one individual, one population, one species, etc., within one season or other time unit) or for an explicitly stated number of trials (defined population size, number of species, etc., through a given period of time). Such specification is seldom found in discussions of dispersal. Frequently the implication is that some sort of one-trial probability is intended, although this is seldom appropriate in dealing with dispersal taking place over long spans of geological time. Such a typical statement as that "overseas transport is so improbable that even the lapse of Cenozoic time is not long enough to make it probable" seems to indicate that the "improbable" refers to some indefinite and unspecified one-trial probability and that an effort is being made to evaluate the effect on this of multiple trials or opportunities with the passage of time. The examples given in the preceding section suggest how wide of the mark such subjective or instinctive evaluations may be. Students unacquainted with formal multiple-trial probability theory almost always have erroneous judgments on such questions as the effect of a thousand, a million, or 10 million trials on probability when this is one-millionth for a single trial. Most students seem to underestimate the effect of multiple trials, although this may also be overestimated.[2]

Camp's opinion that bird-transport for *Rhipsalis* remains negligibly improbable despite the long period of available time may be a subjective underestimate, and Anthony's opinion that if the event were possible at all the passage of time would make it too probable to fit the facts may be a subjective overestimate. At least one or the other of these discrepant opinions must be a radically erroneous estimate. In fact in this case, as is shown, reasonable postulates as to time and probability can be made such that the multiple-trial probability is neither too small nor too large to fit the facts.

Any event that is not absolutely impossible (and absolute impossibility is surely rare in problems of dispersal) becomes probable if enough time elapses. One chance in 100 million seems negligibly small, but, if this is the chance in any one year, the event would be more likely than not within the span of the Mesozoic or of the Cenozoic. At first sight this may appear to prove too much. If geologic time so radically increases the probability of crossing barriers, doubts may arise as to whether any barriers have in fact been effective over long periods of time. If, however, this objection arises, it merely exemplifies the habit of all-or-none postulates and of inference from probability of dispersal to

[1] Application to overland spread is complicated by the fact that, if that occurred, the whole distance probably was not traversed in any one year, but this complication does not particularly change the basis for judgment, as the event corresponding with overseas migration would simply be an annual spread such that completion of the migration would ensue in due course.

[2] There was a local crisis during the war when some pilots, ordered out on their tenth mission, concluded that they were sure to be killed. Losses had been averaging about 10 per cent on each mission.

$$10 \times 10\% = 100\%$$

Presumably, no biologists are so mathematically unsophisticated, but the anecdote illustrates the difficulty that almost all of us share in some degree of making intuitive judgments of multiple-trial probabilities.

distribution rather than the reverse.

If a land bridge endures for a geologically long time, the probability that it will be crossed by any or all pertinent land organisms will become very high, approaching certainty, as far as the effect of the dispersal route alone is concerned. Under such conditions, failure of a given group to spread across the land bridge is sufficient evidence that absence of a water barrier is not the effectively crucial element in its dispersal probabilities. Again, when the nature of a dispersal route is unknown, the fact that it was followed by only a few land organisms over a long period of time indicates extremely low basic dispersal probability. Such low probability is itself an essential and positive datum in the biogeographic problem. It may be decisive in inferences as to the nature of the dispersal route.

Available evidence indicates that there have been about a dozen or fewer successful colonizations of mammals in Madagascar by dispersal from Africa during a span of some 75 million years and that these colonizations have been scattered at random throughout that time. Probability of such dispersal must then have been exceedingly low, or, in other words, there must continuously have been a highly effective barrier to spread of mammals between Africa and Madagascar. Existence of a land connection is almost impossible in view of these considerations, and it can be taken as practically proved that a sea barrier existed throughout the Cenozoic. Such dispersal as did occur, because of its low probability and random timing, is positive evidence against, not for, a land dispersal route. Existence of such a route would have made dispersal of many groups practically certain and determinate, which is contrary to the given biogeographic data.

The effects on regional biotas of very low probabilities of dispersal are peculiar in some respects and enlightening in many biogeographic problems. If a strong barrier exists, such as an ocean between Africa and South America or a strait between Africa and Madagascar, dispersal probabilities within a limited length of time will be very low for most land organisms. For some groups, probabilities may be so extremely low that geological lapse of time does not, in fact, produce any dispersals. For others, the time involved may suffice to make the probabilities high enough for dispersal to have been virtually certain. There will, however, be many other groups (for instance among some non-volant animals and many plants) for which the probabilities of dispersal in geologic time remain low but become appreciable.

Among these groups, the probability that some will cross the barrier becomes high over a long period of time. The number of such groups that will cross is not fixed, but it tends to be determinate. It is a function of p, the dispersal probability for any given group, and of t, the length of time involved. But among groups for which p and t have about the same values, just which forms do in fact cross and when they cross will be random.

The random nature of selection of migrants (among small or amphibious mammals) and of time of dispersal is clearly evident in the mammalian fauna of Madagascar. It also seems to me to be a plausible explanation of many resemblances and differences of the tropical floras of the various continents, although my lack of botanical competence makes this only a suggestion for testing by the phytogeographers. With somewhat more confidence, it may be advanced as a possible explanation of the long-puzzling fact that marsupials, only, entered Australia at an early date (perhaps late Cretaceous or Paleocene) and placentals (murid rodents) much later (probably Miocene or early Pliocene). If the colonization of either marsupials or placentals was exceedingly improbable throughout pertinent geologic time, the random temporal spacing of the two dispersals and the random selection of marsupials first would be in accordance with the implications or probability theory.

Conversely, when the evidence indicates that incidence of particular groups dispersed and of times when they were dispersed was scattered and random rather than concentrated or determinate, then this is strong evidence that probabilities of dispersal were exceedingly low. It suggests that dispersal crossed a major barrier rather than followed a usual migration route. In the case of land

organisms, it suggests overseas dispersal as against existence of a land bridge.

All this emphasizes the need to evaluate the total situation. Taken by itself, presence of a group of land organisms on two continents inevitably suggests a land connection, and such cases have been cited with this conclusion in innumerable biogeographic studies. Within the total picture, the particular case may join with others as an item of the evidence for a land bridge or it may actually become evidence against that inference.

As a final point, when evidence from different types of organisms seemingly conflicts, the negative evidence of one group may actually be stronger than the positive evidence of another. Many students in the two respective fields believe that the flowering plants indicate a land connection between Africa and South America in the Cenozoic but that the mammals indicate the absence of such a connection. Consideration of dispersal probabilities seems to establish almost conclusively that existence of a land connection would have led to much greater resemblance in the mammalian faunas than actually exists but that absence of a connection would not necessarily preclude the existing degree of floral resemblance. Therefore, there was no such connection during this time. Application of such considerations to earlier times, the late Paleozoic and the Mesozoic, is left to the other contributors to this Symposium. It is suggested here that failure to approach the problem from all sides and to make conscious evaluations of all premises and particularly of the effects of probabilities is the main reason for continuing disagreement regarding these broad aspects of biogeography.

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VARIABLES AFFECTING THE PROBABILITIES OF DISPERSAL IN GEOLOGIC TIME

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INTRODUCTION

ONE OF THE IMPORTANT PROBLEMS raised by Simpson for discussion centers on the variables affecting the probabilities of dispersal in geologic time. The two major variables that have largely controlled the distribution of land life are the climatic on the one hand, and the topographic (principally water barriers) on the other. Although these variables have largely determined the effectiveness of migration during geologic time, the influence of each has differed greatly for angiosperms and for land mammals. As Simpson points out, the distribution of plants is determined primarily by climate, next by edaphic and biotic factors, and lastly by land connections. But the continental connections are of first importance in controlling the distribution of land mammals; the environmental conditions often are secondary. This leads Simpson to the conclusion that in the problem of over-water dispersal the likelihood of becoming established in a distant area is much greater for a plant than for an animal.

While this is true in general terms, two important qualifications must nonetheless be made for probability so far as plants are concerned. In the first place, since plants are controlled largely by climate, and since climate has been changing during geologic time, it follows that plants comprising different communities have had different probabilities at different times. In other words, we must always distinguish clearly between the general kinds of plants we are making reference to, whether the species concerned represent rain forest, temperate forest, steppe, or desert vegetation. In the second place, it must be emphasized that in the problem of over-water dispersal the factor of distance, even within a span of geologic time, does impose a real barrier Plant dispersal across water is not unlimited with respect to whole floras, for beyond certain distances it becomes random and accounts for waif assemblages. My views regarding the role that these climatic and topographic variables have had in determining migration are discussed under two topics, (1) climates and probabilities, and (2) water barriers and probabilities.

CLIMATES AND PROBABILITIES

At any particular time plant distribution will largely be a reflection of the climates available for occupancy. As related to dispersal probabilities, population size will be a critical factor, for the larger the population, the greater the numbers of seeds that will be supplied to the environment for dispersal. Thus at times when plant communities have had a wide (subhemispheric or subcontinental) geographic distribution, owing to a maximum extent of favorable climate, we may infer that dispersal probabilities have been highest. In other words, dependent upon the character of the paleoclimate, the probability may be relatively high in one epoch, although in a succeeding epoch the same plant (or its close lineal descendant) will have a very low probability for long-distance migration. This is because climate, the principal factor controlling migration, has changed in a given area relative to the adaptability of the species concerned. This point can be illustrated by reference to dispersal probabilities for plants making up three general types of Cenozoic vegetation: (1) tropical to subtropical forest, (2) temperate hardwood-deciduous and coniferous forest, and (3) desert scrub.

1. Early in the Tertiary, widespread tropical to subtropical climate permitted moist, lowland floras to extend much farther north and south than at present (Chaney,

1947). Tropical to subtropical forests then occupied regions now covered by desert, steppe, arid subtropical scrub, semi-arid woodland and temperate forest vegetation, extending poleward to about latitude 45° or 50°. Tropical forests today are confined largely to within 20° of the Equator, and their distribution on a given continent is not continuous but is interrupted by various types of subhumid tropical climates in which occur open forest and scrub communities of tropical derivation. During Eocene time individuals of tropical species were generally more numerous than their present-day derivatives. Furthermore, since greater numbers of seeds were being supplied to the environment, chances for dispersal (and hence successful migration) were considerably higher. In addition, environments suitable for colonization were much larger in area. Thus tropical and subtropical Eocene species had a higher probability of long-distance migration than any modern equivalent on two counts: there were many more individuals supplying seeds to the various agents of transport, and areas suitable for colonization were greater in extent. Under such conditions the time factor would also assume additional significance in making dispersal more effective, for a given time lapse under Eocene climate would result in many more chances than under a similar amount of time for the present conditions of restricted tropical climates and comparatively fewer individuals. Whereas in Eocene time any lowland area within 45° to 50° of the Equator could be colonized by tropical plants, at the present time such plants survive in a more limited region because arid and temperate climates now characterize areas formerly tropical. These relations indicate that probabilities for long-distance migration were much higher for tropical plants in the Eocene than they are today.

2. A similar conclusion is reached from an analysis of the temperate conifer-forest and hardwood-deciduous trees and shrubs which formed the Arcto-Tertiary Flora. This Flora was widely spread across Holarctica north of latitude 55° early in the Tertiary when milder climate extended poleward (Chaney and Hu, 1940). During the Tertiary this Flora gradually shifted southward to middle latitudes, as winter temperatures were lowered. From the outset of the Tertiary, and continuing well into the Miocene, communities of the Arcto-Tertiary Flora occupied every available ecological site in the temperate and cool temperate portions of the Northern Hemisphere. Commencing in the later Miocene and continuing through Pliocene time, this Flora was restricted gradually into successively more localized climatic areas (Chaney, 1940). Its descendants now survive in the temperate forests of western North America, eastern North America, eastern Asia, and Europe. These are all areas where more localized climates have selected species of suitable tolerance range for survival. That ancestors of species now in any one of these regions and absent in others were common to all or nearly all of these areas and occupied also the present intervening regions of non-forest is a fact that cannot be disputed. One need only examine the fossil record of species of alder, beech, birch, elm, katsura, hornbeam, Chinese redwood, swamp cypress, red maple, and a host of others to be convinced of this fact.

Although the immediate ancestors of ten's of species now occurring in Virginia and Szechwan lived side by side during the early and middle Tertiary, the likelihood of reassembling any of them by long-distance migration today amounts to zero. There is, of course, no need to explain the present patterns of distribution of the temperate segregates of the Arcto-Tertiary Flora by long-distance migration; the fossil record demonstrates that this Flora was once continuous across the northern regions where no forest lives today. In the temperate regions of early and middle Tertiary time there were literally millions of trees, each producing ten's of thousands of seeds yearly which were being dispersed widely. Not only the continental areas but the islands of the North Atlantic and Arctic oceans were populated as well. It seems clear that today the probability that *Metasequoia* (Chinese redwood) might live again on Greenland, Spitzbergen, Novaya Zemlya, or Grinnell Land is zero for present conditions. Only a few living trees are producing seeds in the deep valleys of east-

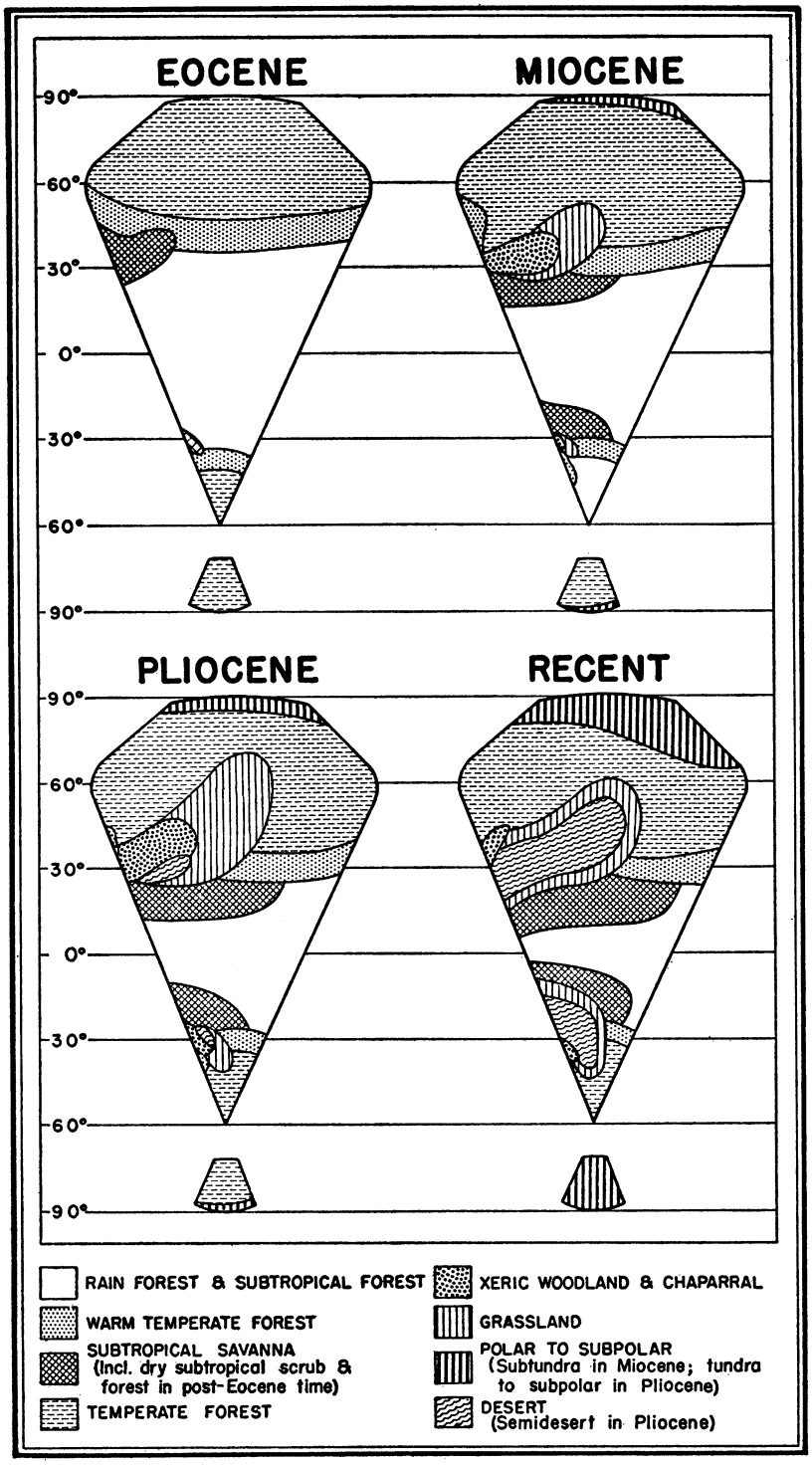

FIG. 18. Changing patterns of some generalized Tertiary environments. Highest probabilities for long-distance migration have coincided generally with maximum distribution of particular communities. Since their areas have varied with time, probabilities must also have varied with time for species of any given ecologic type.

central China. The probability of dispersal for its light seeds to those regions is very low, but even if it could be raised to probable, the climate would never permit establishment and hence successful migration. Until more favorable climate exists in those regions, no forest trees can live there. Whether this will be in a million years or in 10 million years is uncertain.

3. The third example of changing probabilities in time is provided by the relations of the present desert floras of the world, which now cover about one-fourth of the land surface. The likelihood of interchange between the present desert regions is more probable today than it has been at any time in the past. This follows from the fact that desert environments are phemonena of latest Cenozoic time (Axelrod, 1950). At the present time there are more individuals representing any one desert species than there have ever been since angiosperms first appeared in the record. This is because the present areas suitable for colonization are subcontinental in extent. During middle Tertiary time subdesert regions apparently had a highly restricted occurrence, but there is no evidence of them earlier in the period. Throughout most of the Tertiary, ancestors of desert plants apparently were integral parts of woodland, grassland, scrub, and forest vegetation which then dominated the areas now desert. Thus it is useless to postulate Cretaceous or Tertiary migrations between supposed desert areas, as some biogeographers have done, because the desert climates and the plants and animals which are confined to them were not yet in existence. The problem of probabilities of dispersal for the plants comprising these floras is clearly one of the late Cenozoic, not earlier.

SUMMARY

With respect to climates and probabilities, the general conclusion seems warranted that probability of effective migration for plants has varied with time and also with the kinds of plants that make up the different vegetation types which are determined by climate. At any one time probability has been highest for species of those vegetation types having maximum distribution. In general, species of tropical forests have a low probability today in comparison with Eocene time. Temperate forest species had a high probability from the late Cretaceous to the middle Tertiary, but it is low today. Steppe plants had a higher probability during the Pliocene than at present. By contrast, desert species have a higher probability today than at any time since angiosperms have been in existence.

These relationships are shown in diagrammatic form in figure 18. The north-south continental area is of the hypothetical type usually depicted by geographers to show the distribution patterns of vegetation and climate, in which the land area has generally low relief so that the idealized patterns are not disrupted by topographic factors. The maps, which illustrate average conditions for three epochs of the Tertiary, show the gradual contraction of rain forest and subtropical forest environments during the period as successively drier and drier environments gradually expanded. The maps serve to emphasize the point that probabilities of long-distance dispersal for species representing different plant communities have varied with time, and that highest probabilities have generally coincided with the maximum distribution of particular communities.

WATER BARRIERS AND PROBABILITIES

The known Cenozoic record shows clearly that the effective (normal) migration of seed plants and land mammals differs considerably with the width of water barriers. A good number of water barriers are now known to have hindered continental faunas from migration into adjacent areas. These include the following:

North Atlantic: apparently prevented interchange between North America and Europe throughout the Cenozoic

Beringia: formed a sporadic barrier between North America and Asia during the Cenozoic

Central America: submergence of portions of the region prevented normal migration between North and South America from the early Tertiary to the late Pliocene

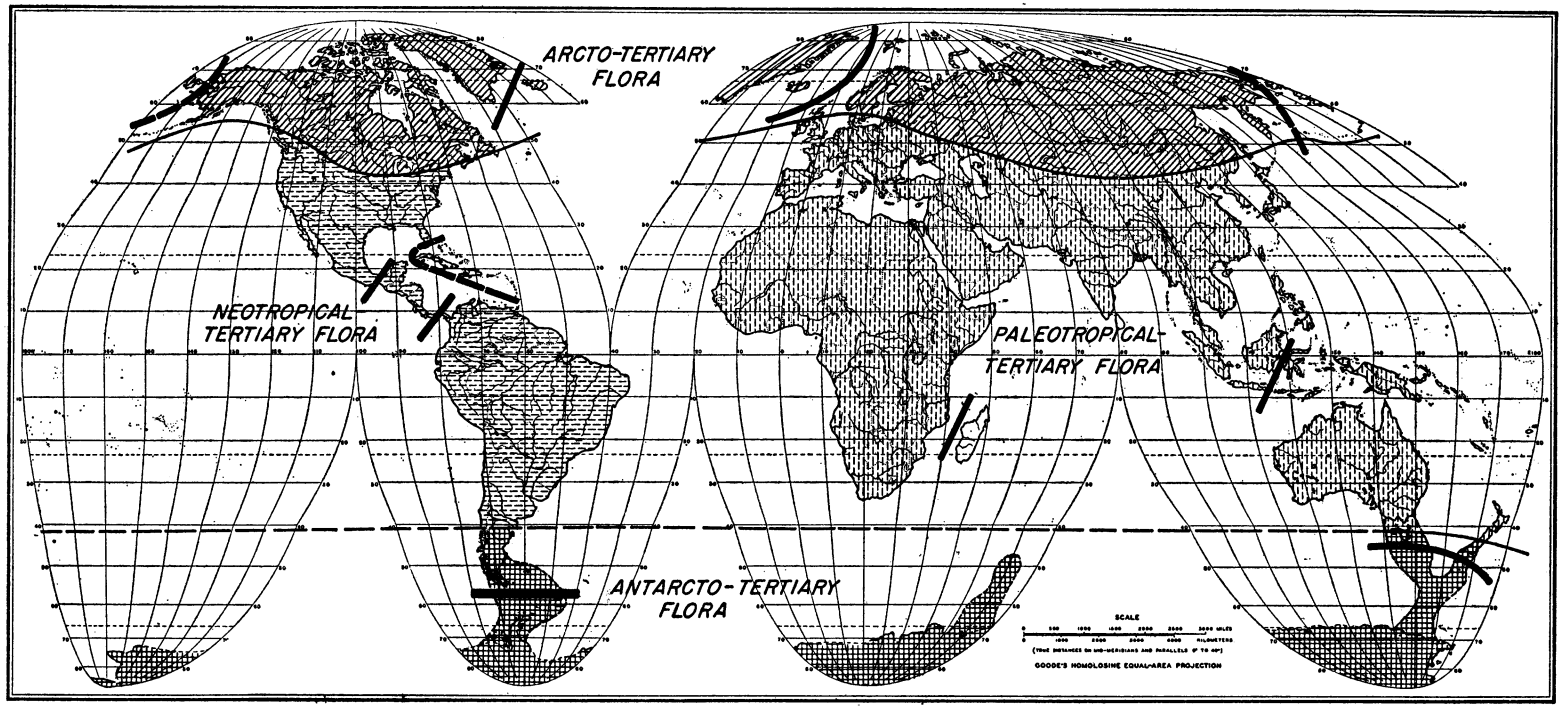

FIG. 19. Distribution of Tertiary floras across water barriers for land mammals during the early Cenozoic. Although plants have spanned water barriers that have effectively restricted normal mammalian migration, this is not considered to mean that plant migration has been unlimited with respect to over-water movement during geologic time. Beyond certain distances, over-water migration has also resulted in the random assemblage of waif floras, floras fully comparable to the waif faunas of Madagascar and other islands. Based on Goode Base Map No. 201HC. Copyright by the University of Chicago. Used by permission of the University of Chicago Press.

Caribbean Sea: water isolated the West Indies from North, Central, and South America during most of the Cenozoic

Mozambique Channel: effectively prevented normal interchange between Madagascar and Africa throughout the Cenozoic

Wallacea: isolated Australia from Asia throughout the Cenozoic

Drake Passage-Macquarie Passage: isolated Antarctica from South America and the Tasman region[1] during the later Cretaceous and Cenozoic

These same barriers, however, apparently had little effect on the migrations of Tertiary Floras. All evidence indicates that they occurred contemporaneously as similar floristic units on both sides of the barriers, as shown in figure 19. Time is available to discuss briefly only three of these barriers: Beringia, North Atlantic, and Drake Passage-Macquarie Passage.

Beringia

Simpson (1947) has recently reviewed the mammalian evidence which shows that on several occasions during the Cenozoic (early Eocene, late Eocene, early Oligocene, late Miocene, middle to late Pliocene, Pleistocene) intense migration took place between North America and Asia. These migrations were across the present area of Bering Strait, which is now the site of a 70-mile water barrier that effectively prevents Recent mammals from crossing. During the stages of Tertiary interchange between North America and Asia it is believed that the present barrier was not in existence, or at least that it was so narrow as to be ineffective. On other occasions during the Tertiary (middle Eocene, middle and late Oligocene), and in Recent time, there apparently was no or little interchange. An effective water barrier has been inferred for these stages, though one that was probably not much wider than it is today.

There is no evidence to suggest that Beringia was a barrier to plant migration during the Tertiary. Early in the period this northern region was dominated by the temperate Arcto-Tertiary Flora, made up of hardwood-deciduous and conifer-forest trees similar to those now surviving in the temperate portions of North America and Eurasia. The similarity of the fossil floras in northeastern Asia to those in northwestern North America during the Tertiary is so great that we must infer continuous migration across this area during the early and middle Tertiary. If an effective barrier had been in operation, we might expect to find evidence of migration waves of different elements representing this Flora entering one continent or the other. The floristic unity of the Arcto-Tertiary Flora across this region clearly suggests uninterrupted migration through the area.

[1] As used here, the term refers to New Zealand, southeastern Australia, and Tasmania, all bordering the Tasman Sea.

North Atlantic

Simpson (1947) has also presented clear evidence to show that a trans-Atlantic bridge is not required to explain the distribution of Tertiary mammalian faunas. The record can be explained adequately on the basis of a bridge in the Beringian area at the required times. There are, however, large and well-preserved early Tertiary floras known from Greenland, Iceland, and Spitzbergen, and they are much alike in composition. Furthermore, they are so similar to the temperate floras of North America and Eurasia that all of them are grouped together to form the Arcto-Tertiary Flora, a major continental Tertiary Flora which maintained its general over-all identity throughout the Tertiary.

The Tertiary floras of these islands are preserved in sediments interbedded in the North Atlantic basalt plateau, parts of which occur also in the Faeroe and Shetland Islands and in Scotland. Geologic evidence shows conclusively that this plateau had a greater extent during the Tertiary than it does at the present day. This has led some authors to suggest that it formed a continuous bridge across the North Atlantic. Should this have been the case, then the early Tertiary faunas of North America and Europe might be expected to show greater resemblances. As Simpson has indicated, the low relationships between the continental faunas argue strongly for water barriers of sufficient width across this region to hinder effectively their migration. But the Arcto-Tertiary Flora populated the region, and apparently by normal disper-

sal to judge from the fact that all its important floristic elements are represented in the fossil floras recorded from these island areas. The present water barriers across the North Atlantic are not very wide: Canada (Baffin Land) to Greenland, 200 miles; Greenland to Iceland, 190 miles; Iceland to the Faeroes, 270 miles; the Faeroes to the Shetlands, 170 miles. Although the structural relations of the basalt plateau show that these present barriers were narrower during the Tertiary, the width of the Tertiary water barrier (or barriers) that blocked migration of land mammals is not known. It seems likely that the cumulative effect of two rather narrow barriers would be as important as a wider one in limiting the migration of land mammals. Either case would easily explain all the facts of vertebrate distribution and still permit plants to populate the area with no particular difficulty.

Drake Passage-Macquarie Passage

Simpson (1939) has also discussed the record of land animals that have been supposed to demand a connection between Magellanica and Australia by way of Antarctica. He shows rather conclusively that there is no need to postulate an effective land bridge for them across this region. Yet the record of the temperate Antarcto-Tertiary Flora on Australia, New Zealand, Tasmania, Kerguelen Island, Seymour Island, Patagonia, southern Chile, and southern Argentina during the early and middle Tertiary is one of floristic unity in all these scattered regions. Such similarity over widely separated localities shows that the floras do not represent waif assemblages brought together by chance dispersal. This suggests, therefore, that there was an effective migration route for plants across Antarctica during earlier times. The floras provide clear evidence of favorable climate at high southern latitudes, and geological evidence permits the reasonable inference that there was more land there during the Cretaceous and Tertiary than exists today.

Archipelagos of only slightly greater extent than those now present could account for the continuity of the Antarcto-Tertiary Flora in all these regions during the early and middle Cenozoic. Examination of the revised chart of Antarctica (United States Hydrographic Office, No. 2562) shows the probable sites for wider land areas across the southern regions. The Macquarie Swell and the New Zealand Plateau link Australia and New Zealand with Antarctica; the Kerguelen-Gaussberg Ridge ties Herd and Kerguelen to Antarctica; and Antarctica is easily united with South America, either directly or else by island arcs through the Falklands, South Georgia, and the South Sandwich Islands, to the Palmer Peninsula on Antarctica. Waters are of only moderate depth along all these tracts today, and at distances of 200 to 300 miles the higher parts rise to within 1000 feet of sea level. All these regions could easily have been archipelagos at various times during the history of angiosperms, according to geophysicists and structural geologists with whom I have discussed the problem. Thus islands scattered some 200 to 300 miles apart, or less, would readily provide stepping-stones for migration of the Antarcto-Tertiary Flora and at the same time effectively hinder continental faunas.[1]

Summary

With respect to water barriers and probabilities, the conclusion seems warranted that forests have readily crossed water barriers that have effectively blocked migration of continental faunas for epochs, or for fully a period of geologic time.

DISCUSSION

This brief discussion of the two important variables determining the distribution of land life indicates that angiosperms and land mammals have been controlled by wholly different factors. In the case of the climatic factors, which are paramount for plant distribution, widest occurrence for species of any given ecologic type (temperate forest, rain forest, steppe, desert) has corresponded with times when analogous climates have had their widest extent. But even at such times

[1] In connection with this discussion, see a recent article by Fairbridge (1949), which was received after the present manuscript was submitted for publication.

the angiosperm floras (Arcto-Tertiary, Neotropical-Tertiary, Antarcto-Tertiary, Paleotropical-Tertiary Floras) have never been able to occupy more than a subhemisphere in a latitudinal direction. This is because climates have always been zoned with respect to latitude. Limits on poleward extension by tropical floras have been imposed by temperate climates at higher latitudes, and the Equator-ward distribution of temperate plants has been restricted by tropical climates. The drier regions at low to middle latitudes have had warmer and wetter climatic boundaries lying to the south, and cooler and moister ones to the north. Within any of these regions, whose areas have varied with time (fig. 18), the lowland floras have always been sharply confined.

Thus even at times when continental floras have had a maximum distribution, they have not been able to spread so widely as continental mammalian faunas. The land mammals have largely transgressed the climatic belts which have restricted plant distribution whenever and wherever land connections have been present in meridional or latitudinal directions.[1] At times of widest plant distribution, therefore, and hence the time of greatest probability for long-distance migration, angiosperms have never had a distribution equaling that of the mammals. Mammoths ranged across Holarctica and southward into Africa and South America during the Early Pleistocene, transgressing major vegetation types and the climates responsible for them. Similar or comparable distributions are known for other mammals, such as horses, camels, and tapirs. But a trans-tropic migration of a Tertiary Flora, a migration analogous to the invasion of South America by the placentals in the latest Pliocene, has never been recorded for angiosperms living outside the equatorial zone. The Tertiary Floras of temperate (Arcto-Tertiary, Antarcto-Tertiary) or semi-arid (Madro-Tertiary, Andeo-Tertiary) requirements have always had boundaries coinciding with the warmer latitudes. Although some plants seem to have transgressed the tropical zone along the meridional cordilleran chain, which rose to its present heights during the latest Cenozoic, they have been few in number. Transgression of climatic zones by land mammals has been determined largely by the presence of land connections in meridional directions, not by the climates that have controlled the distribution of plants.

Nonetheless, within any given climatic province plants have easily crossed narrow water barriers that have effectively blocked the invasion of near-by land areas by continental faunas for fully a period of geologic time. The Arcto-Tertiary Flora readily spanned the North Atlantic during the early Tertiary, but the mammalian fauna did not. The Paleotropical-Tertiary Flora ranged southeastward into Australia, but no mammals other than a few placental rodents are known to have crossed (presumably rafted) the unstable land area of Wallacea during this period. Likewise, the inference can be made that the Paleotropical Flora extended across the Mozambique Channel to Madagascar during the early Tertiary, but mammals have been rafted only occasionally over this area. The Antarcto-Tertiary Flora clearly demands free, uninterrupted migration between South America and the Tasman region by way of Antarctica along the orogenic chains connecting these continental areas, yet the vertebrates provide no clear evidence for effective migration along a southerly route.[2]

Although these data show that a higher probability exists for over-water dispersal of plant species, it probably has not been sufficient to account for the modern discontinuous patterns shown by plants of distant continental areas. This is because of the fact that within any given climatic region distance will finally impose a barrier to migration. The water barrier that a continental flora can transgress within an epoch of time (say, 10 to 15 million years) is not unlimited. The point where normal migration during geologic time becomes difficult for a continental Ter-

[1] There usually is not complete faunal interchange across a land bridge, owing to the filtering effect of different environments, biological pressure, and other causes (see Simpson, 1940, pp. 148–152).

[2] Simpson (1943, p. 14) grants that the relations between South American and Australian marsupials (one family, one suborder) may be explained on the basis of island chains, though a Holarctic radiation is preferred.

tiary Flora, and where the factor of probability for chance dispersal to the nearest land area comes into play, is not now known. Some data suggest that at distances lying apparently up to 200 or 250 miles probability is sufficiently high to amount to reasonable certainty of colonization by the complete flora within an epoch of time. But for more distant areas probabilities are lower, and chance dispersal comes into play. As a result, the more distant shores are populated by waif assemblages. Floras of ocean islands, such as those of Hawaii, Ascension, or St. Helena, regularly lack floristic balance in that large groups (classes, orders) are commonly absent, and certain floristic elements are poorly or not at all represented. Up to these distances (200 to 250 miles), however, probabilities seem sufficiently high so that in time a whole flora can transgress the barrier without the loss of any significant floristic units. Evidence of paleoclimate suggests that probabilities for tropical and subtropical plants were generally best in the later Cretaceous and early Tertiary, for temperate plants from the late Cretaceous to the middle Tertiary, and for semi-arid to arid types late in the Cenozoic. Long-distance, over-water migration, therefore, cannot explain the present-day normal patterns of distribution shown by continental floras. The repeated patterns of existing discontinuous distribution scarcely show relationship to chance dispersal, but rather to floristic evolutionary phenomena by which Cretaceous and Tertiary Floras of wide distribution have gradually become restricted in response to a greater zonation and diversification of climates.

From the Middle Cretaceous on down to the present day, the angiosperm flora of the world has been differentiated into broad floristic regions which have maintained their separate identities. The temperate floras of northern and southern latitudes were already differentiated by the Middle Cretaceous. The temperate Arcto-Tertiary and Antarcto-Tertiary Floras derived from the Cretaceous vegetation at the north and south attained a distribution that was subhemispheric in extent during the earlier half of the period. Later in the Cenozoic, in response to lowered precipitation and lowered temperatures, these Floras were confined to temperate regions which are now largely latitudinal in relation to one another (Axelrod, 1948). The tropical and subtropical floras of the Old World and the New were also largely distinct in the Cretaceous, although they were more similar then than they are today in having a larger pan-tropic element. The derivative tropical vegetation of the Tertiary, as represented by the Paleotropical-Tertiary and Neotropical-Tertiary Floras, ranged north and south to latitude 50° under the influence of mild, early Tertiary climate. Later Equator-ward restriction in response to lowered temperature largely accounts for the meridional patterns, as well as for those of pan-tropic or interrupted pan-tropic occurrence (Axelrod, 1948, 1950).

Thus if there has been any time during the history of angiosperms when long-distance migration has been effective in controlling distribution patterns, it must have been prior to Middle Cretaceous time. The suggestion that long-distance migration may have been more effective during the Lower Cretaceous than at any later time finds some support in certain inferences we can make from modern ecology and past floras. During that epoch the highly adapted angiosperms were beginning to compete successfully in lowland regions with the older Mesozoic floras dominated by ferns, cycadophytes, and coniferophytes, and were gradually supplanting them. As the older types were being displaced, angiosperms may well have entered upon a stage of general widespread random migration (by all available means of dispersal) which has never been equaled since that time. Sites suitable for occupancy by angiosperms were now to be found everywhere, for the older flora was on the wane. Ecologic competition was at a minimum, for there were no closed communities to hinder establishment. Climates were rather widespread and generalized in type owing to generally low continental regions and wide marine embayments. The suggestion is that the lowland continental floras were first assembled during the Lower Cretaceous as angiosperms were replacing the older Mesozoic flora. Selected at random by the generalized environments of early Cretaceous time, three basic continental floras were early differentiated over the low-

lands. A tropical to subtropical flora characterized the lower to middle latitudes throughout the world, and it was more nearly a pantropic flora than has ever existed since that time. Although there were differences between the floras of the Old World and the New, they apparently were not so great as those which had developed by the early Tertiary, when the Neotropical-Tertiary and the Paleotropical-Tertiary Floras can be recognized. At higher latitudes, northern and southern, the temperate Cretaceous floras were early assembled as distinct floristic units. Their derivatives, the Arcto-Tertiary and Antarcto-Tertiary Floras, were likewise widely divergent with respect to their floral elements, and these differences have largely been maintained down to the present day.

These data suggest that by the end of the Lower Cretaceous the stage was already set for the floristic evolution of angiosperms. During the succeeding 100 million years these generalized patterns in distribution have been slowly modified by changing climate, changes that have gradually selected species suited to successively more and more limited regions during the middle and later Cenozoic. There is not space here to describe and illustrate the nature of the floristic evolution which seemingly accounts for the modern patterns in distribution. In way of generalized summary, however, it is suggested that the facts of modern plant distribution are best explained on the thesis that (a) during the history of angiosperms the continents have had essentially the same spatial relations as now; (b) climate was favorable for forests in the far north and south during the Cretaceous and early Tertiary; (c) during these times access to all continents was made possible by migration across Holarctica in both easterly (North Atlantic) and westerly (Beringia) directions, and across Antarctica from both Magellanica and the Tasman region by archipelagos of only slightly greater extent than those now present; and (d) the present-day patterns are the consequence of Cenozoic climatic changes of a type that may be inferred from the fossil record of diverse types of vegetation, in which extinction in areas of former occurrence are explained by a climatic trend towards increasing continentality, a trend characterized by lowered rainfall, shifting seasonal occurrence, and greater ranges of temperature.

Such an interpretation does not preclude effective long-distance migration in both latitudinal and meridional directions during long spans of geological time. Actually, the critical question is not, Did it take place?, but rather, How much has actually taken place? In applying this question to an analysis of floral relationships, we must always distinguish clearly between floras of continents (and continental islands) and those of ocean islands, for the problem differs greatly for each. For oceanic islands we know that the result has been the stocking of isolated regions by long-distance migration from various sources, with resultant waif assemblages lacking floristic balance.[1] For such cases probabilities were most likely highest for new islands rising out of the sea, before competition by closed communities had developed. The times mentioned above seem to have afforded highest probabilities for long-distance derivation of tropical, temperate, and semi-arid types. But the net effect on continental floras seems to have been that only occasional examples appear to require such an explanation. The species making up these floras show repeated patterns in distribution which are scarcely related to chance, but rather to floristic evolution in time, an evolution controlled and directed by changing climate. Although at certain times suitable environments have been subcontinental in extent (Eocene-tropical; Pliocene steppe), and plants have had suitable means of dispersal, it would appear that long-distance, over-water migration has not been generally effective in populating widely separated continents. The significance of closed communities to invasion by migrants, even though the migrants possess similar ecological requirements, may be a decisive factor in frequently preventing establishment. Some data suggest that long-distance migration is most likely to be successful at times of climatic shift, when closed or saturated communities

[1] See, for example, the recent analysis of the Hawaiian flora by F. R. Fosberg, *in* Zimmerman (1948, pp. 106–119).

temporarily are not in existence, and competition is low. Such shifts are known for the early Tertiary (expansion of tropical climate), the middle Tertiary (expansion of semi-arid climate), the late Tertiary (maximum steppe climate), and the Pleistocene (glacial-pluvial, desert).

As for the problem in hand, the floras of the south Atlantic islands are typically of waif character, with relations both to Africa and to South America. This suggests derivation from distant continental shores. Furthermore, if we consider the total present-day floras of South America and Africa, and not a few selected genera or families, we find that there is a relatively low relationship between them, and that both have higher affinities with the Australasian region than with one another.[1] The inference is that South America and Africa have been widely separated by water during the history of angiosperms.

CONCLUSIONS

1. Highest probabilities for dispersal of angiosperms have corresponded with times of maximum extent of favorable climates, and with the widest distribution of particular plant formations (rain forest, temperate forest, steppe, desert). By contrast, the climatic factor seems to have had but little effect on the distribution of mammalian faunas during the long time they have been in existence.

2. Migrations of mammalian faunas have been effectively blocked by rather narrow water barriers for epochs, or for fully a period of geologic time. But plants have transgressed these same barriers with no particular difficulty in both latitudinal and meridional directions. In all these cases the water barriers have been within a given climatic province characterized by a particular Tertiary Flora (Arcto-Tertiary Flora: Beringia, North Atlantic; Neotropical-Tertiary Flora: Central America-Panama; Paleotropical-Tertiary Flora: Tethys Sea, Wallacea, Mozambique Channel; Antarcto-Tertiary Flora: Drake Passage-Macquarie Passage).

3. There are, however, no plant migrations known that correspond to the great migrations from Holarctica into the Southern Hemisphere during the Cretaceous (marsupials into Australia, South America, Madagascar) or late Cenozoic (placentals into South America). The belt of tropical climate, which has always occupied a much wider zone throughout the history of angiosperms than it does today, formed an effective barrier to migration of temperate or semi-arid plants in north-south directions through the Cretaceous and most of the Cenozoic. Only in the late Cenozoic, as the meridional cordillera was elevated to great heights and tropical climates were restricted in area, did a few plants transgress the tropical barrier.

4. Plants have always enjoyed a wider and easier means of over-water dispersal than land mammals. Within an epoch of time probabilities seem in general to have been sufficiently high so that continental floras have transgressed water barriers up to 200 to 250 miles in width. At greater distances lower probabilities have resulted in a random dispersal of migrants, a dispersal which accounts for waif floras lacking floristic balance.

Although plants have populated ocean islands, this is not considered to mean that over-water dispersal can account for most modern patterns in discontinuous distribution shown by continental floras. These are to be explained largely by the evolution of continental Cretaceous and Tertiary Floras in response to changing climates, changes which during geologic time have restricted species of wider range to more localized environments, and have also permitted species of formerly narrow distribution to spread more widely.

5. The distribution patterns shown by modern and fossil angiosperm floras are consistent with the data of present and past mammalian faunas in demonstrating that the continents have been in their present

[1] Acknowledgment is due Prof. Carl Epling for this information which is clearly demonstrated by a large series of maps he has recently prepared showing the distribution of plant groups (genera, tribes, families) throughout the world.

positions since the Middle Cretaceous and probably earlier. The floras and the faunas, not the continents, have been moving during the past ages. For the floras, the mechanism of movement has been provided by the compulsion of changing climates; for faunas, migration has been determined largely by the presence of well-recognized land bridges.

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FOSSIL FLORAS OF THE SOUTHERN HEMISPHERE AND THEIR PHYTOGEOGRAPHICAL SIGNIFICANCE

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"IT HAS BEEN REMARKED that if the science of botany had grown up in the southern hemisphere, it would be now a very different science" (Bews, 1925). The appropriateness of this comment is constantly being demonstrated by our rapidly increasing knowledge of the living and extinct floras of the Southern Hemisphere. In recent years intensified exploration has disclosed many new and exceedingly fertile localities and the presence of new plant groups previously unknown from the Northern Hemisphere.

Despite these hopeful signs, any comprehensive treatment of the fossil floras of the Southern Hemisphere may appear daring and disproportionate, were it not for the fact that the late Paleozoic and early Mesozoic (or Mesophytic) ones have long been regarded as constituents of the *Glossopteris* flora and its descendants. Yet even a brief survey of these fossil floras, particularly those of Africa and South America, is indispensable in any discussion of their bearing on biological and geological theories (Dalloni, 1948; Darrah, 1939; Feruglio, 1951a; Frenguelli, 1949, 1950; Furon, 1949; Rodin, 1951; Seward, 1933a, 1933b; Sherlock, 1948).

Unfortunately, fewer fossil floras are known from the Southern Hemisphere and peninsular India than from the Northern. Moreover, the former do not compare favorably with their northern counterparts either in numbers of species recorded or the amount of research devoted so far to their study. For instance, Darrah (1945) published a map of South America showing the then known localities where fossil plants had been collected, and Seward (1933a) mapped some of the Mesozoic floras of the Southern Hemisphere, yet no map showing all known localities of the Southern Hemisphere is available at the moment. The limited numbers of fossil plant species reported per period from Central and South America and the Antilles are evident from Berry's (1942) calculations (the area in question covers nearly 8,000,000 square miles): Triassic and Jurassic, one species to 160,000 square miles; Lower Cretaceous, one species to 100,000; Upper Cretaceous, one species to 300,000; Paleocene, one species to 600,000; Eocene, one species to 320,000; Oligocene, one species in 400,000; Miocene, one species in 20,000; Pliocene, one species in 40,000. Similar computations for the Paleozoic of this area or the fossil floras of Africa and other parts of the Southern Hemisphere would be even more out of proportion. Consequently conclusions based on such limited data are at best tentative rather than convincing.

To this difficulty must be added the great problem of correlating floras of roughly comparable ages but distant geographical locations. For example, after discussing "Stratigraphical problems in the coal measures of Europe and North America," Trueman (1946, pp. lxxxvii–lxxxix) concluded: "Any interpretation of the relationships between the two sides of the Atlantic is necessarily influenced by the acceptance or rejection of the hypothesis of continental drift. Certainly the explanation of the relationships is greatly facilitated by the assumption that during the Carboniferous North America was situated much closer to western Europe than at the present time, but even if the drift hypothesis is rejected, it is no less desirable to estimate the nature of the links between the two continents."

With few modifications this statement could be equally well applied to South America and Africa and indirectly to the other land masses of the Southern Hemisphere, where some problems of dating and correlating fossil floras are being resolved, but many more remain. Thus paleobotanical evidence indicates that the early vascular floras of Tasmania, supposedly of Cambro-Ordovician age, are now referable to the Silurian (Cookson, 1937), and those of Victoria are likewise referred to the Upper Si-

lurian and Lower Devonian (Cookson, 1945, 1949). Of paramount importance are the age of the *Glossopteris* flora, formerly regarded as Permo-Carboniferous and now placed in the Permian or Permian-Triassic (Dixey, 1936; Du Toit, 1927; Gothan, 1930), and the correlation of the strata in the now widely separated areas occupied by it (Feruglio, 1951a; Sahni, 1927; Walkom, 1944, 1949).

PALEOPHYTIC FLORAS

Although the oldest plant fossils known from South Africa are of algal nature (MacGregor, 1941; Vasconcelos, 1949; Young, 1949) and either Cambrian or pre-Cambrian in age, comparable records from other parts of the Southern Hemisphere seem to be quite sparse. It is therefore better to limit the following discussion to vascular floras.

Outstanding is the fact that the oldest pteridophyte (psilophyte) floras, ranging from Silurian to Lower Carboniferous, show a remarkable degree of uniformity, almost global in extent. These early vascular plants (psilophytes) ranged from the Upper Silurian to the Middle Devonian. The same degree of uniformity is seen even in the pteridophyte floras of the Upper Devonian and Lower Carboniferous, irrespective of which area is studied, whether Europe or North America, Siberia and eastern Asia, or South America, South Africa, and Australia (Hirmer, 1938).

This uniformity of early paleophytic floras and their subsequent differentiation are well illustrated by the succession of Carboniferous and Permian floras in Australia. In this succession Walkom (1937, 1944) recognizes three distinct fossil floras, namely, (1) the *Lepidodendron Veltheimianum* flora, composed of 12 species, the oldest one of this succession and very distinct from the Upper Devonian flora; (2) *Rhacopteris* flora, made up of 25 species, of Lower Carboniferous age, lacking distinctly northern Carboniferous genera, such as *Alethopteris*, *Neuropteris*, *Pecopteris*, and containing the genera *Rhacopteris*, *Cardiopteris*, *Sphenopteridium*, *Adiantites*, and *Noeggerathia;* and (3) *Glossopteris* flora, consisting of 48 species and varieties, abundant in Gondwanaland, and in Australia present in Lower (Creta) and Upper (Newcastle) Coal Measures. Taken as a whole, this flora is completely different from the *Rhacopteris* flora, although they have a few genera in common. But these two floras are also separated by a considerable break in time. Although the Lower Carboniferous flora of Australia can be compared with floras of the Northern Hemisphere, especially the European ones, the *Glossopteris* flora can be compared only with itself as represented in other parts of Gondwanaland. Significantly no trace of the *Rhacopteris* flora has so far been found in southern Africa, a fact that "needs some explanation" (Walkom, 1949). The absence of the *Glossopteris* flora in New Zealand also requires an explanation, if that country "occupied the position shown on Wegener's maps well into the Mesozoic Era" (Walkom, 1949, p. 12; see also Fleming, 1949; Oliver, 1950).

If the world be taken as a whole, distinct floras can first be distinguished in late Upper Carboniferous or shortly before the beginning of Permian (Darrah, 1937; Gothan, 1930; Jongmans, 1937, 1942; Read, 1947). These floras and their corresponding provinces can be traced from Stephanian to the beginning of Triassic. In accordance with Halle (1937) four major floras and provinces are now recognized, as follows (see fig. 20):

1. European Permo-Carboniferous (= Euramerican) flora, which extended throughout Europe to the Ural Mountains, Iran, Turkestan, and the eastern United States. This large area is today divided by the Atlantic Ocean.

2. Angara (=Siberian=Kusnezk) flora, which ranged from the Ural Mountains to the Pacific coast of Asia, from Vladivostok to Bering Strait, from the North Polar Sea to the Targatabai Mountains in the south and west to Turkestan and Kashmir. This is the best-defined natural area and includes the great Siberian coal basins of Kusnezk and Minussinsk.

3. Cathaysia flora, which extended from Shansi and Korea to Sumatra, New Guinea and western North America as far as Colorado, Oklahoma, and Texas, where it met the Euramerican flora; in Kansu, its western

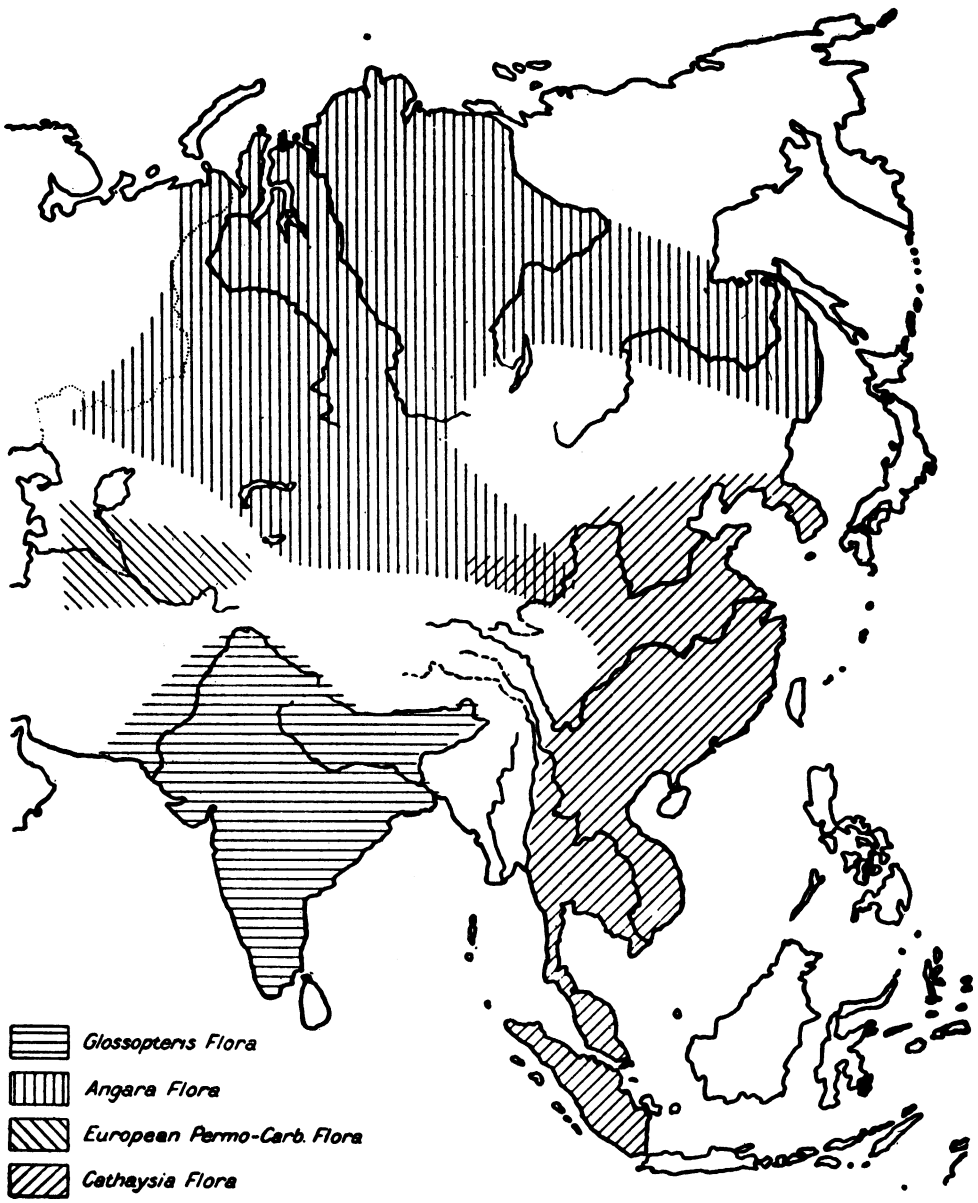

FIG. 20. Distribution of late Paleozoic floras in Asia (from Halle, 1937).

border, this flora was replaced by the invading Angara flora during Upper Permian. As is most likely, the large region occupied by this flora has always been divided by the Pacific Ocean. The Cathaysia flora was formerly called *Gigantopteris* flora, which begins in Middle Permian. The theory of continental drift does not seem to offer any better interpretation in regard to this region than it seems to offer in connection with the problem of the origin of modern Pacific floras. This point has apparently not been stressed by other authors.

Provinces 1 to 3 are often treated collectively as the "northern or Arcto-Carboniferous province of warm-climate, rain forest coal floras" as compared with the "southern or Antarcto-Carboniferous province of cool-

climate, rain forest floras" (Read, 1947, p. 273). The Carboniferous and Permian floras of the large area extending from eastern Europe to eastern Asia and south to New Guinea have been carefully mapped and correlated by Jongmans (1942).

4. *Glossopteris* flora, which occupied Gondwanaland, including sections of central and southern South America, central and southern Africa, Australia, Antarctica, and India south of the Himalayan arch. During Permian the *Glossopteris* flora was in contact with the Angara flora in northern India, with the Euramerican flora in southern Rhodesia (Walton, 1929), Transvaal (Le Roux, 1949), Mozambique (Teixeira, 1947), Madagascar (Boureau, 1949), and with the Cathaysia flora in Dutch New Guinea (Jongmans, 1940). In Triassic times, elements of the *Glossopteris* flora were exchanged with Euramerican ones. One of the main arguments for continental drift is derived from the *Glossopteris* flora and its distribution.

Botanically speaking, the Angara flora is of real interest, as it contains elements of the other floras surrounding it. The mixed character of this flora is easily explained by its central position. It is noteworthy that it contains fewer elements of the *Glossopteris* flora than of the other two. Despite its synthetic composition, the Angara flora included many genera and species peculiar to it.

GLOSSOPTERIS FLORA

Although Gondwanaland was probably quite isolated, the *Glossopteris* flora had some contact, during early Permian at least, with the Angara flora in India, with the Euramerican flora in South Africa and South America, and the Cathaysia flora in Dutch New Guinea (see fig. 21). The few Euramerican elements present may be regarded as survivors of earlier cosmopolitan floras. The presence of an intermediate or transition flora in Kashmir suggests a northward migration of older Gondwana elements. The *Glossopteris* flora supposedly never invaded the Cathaysia flora despite the present proximity of areas once occupied by these floras. This fact is often construed as an argument in favor of drift (Holland, 1941, 1943; Sahni, 1936). However, a fossil flora containing Cathaysia elements has been reported from Dutch New Guinea, and *Vertebraria*, an important element of the *Glossopteris* flora, has been found in a near-by locality (Jongmans, 1940).

Comparison of the succession of Carboniferous and Permian floras in Australia with that of other parts of Gondwanaland was attempted by Walkom (1930, 1944). As pointed out above, only the Lower Carboniferous floras of Australia can be compared directly with those of the Northern Hemisphere. Permian floras of Australia, on the other hand, are directly comparable with those of western Argentina, because these Argentine floras "are almost identical with our Australian floras of the same succession." The South African succession, by comparison, is not so well represented as that of Australia. Interesting in this connection is the presence in the Lower Permian in Southern Rhodesia of "a very pronounced northern element" of Upper Carboniferous species (Walton, 1929) and of *Pecopteris* in Transvaal (Le Roux, 1949). *Sphenopteris*, *Asterotheca*, *Sphenophyllum*, and other elements of northern Permo-Carboniferous floras occur "together with the *Glossopteris* flora" in Mozambique (Teixeira, 1947, p. 28). This proves that "the gondwanean flora does not really exhibit the characters of independence which, years ago, many authors deemed it possible to ascribe to it." According to Walkom (1949, p. 12) this occurrence of northern species is "a result of slow migration southward from Europe. This migration appears to have been limited to this one line from Matthew's Holarctic region since so far this Upper Carboniferous flora is not known to have penetrated to the *Glossopteris* bearing areas of South America or Australia." Actually northern elements have been reported from Rio Grande do Sul, Brazil (Lundquist, 1919), and Dutch New Guinea (Jongmans, 1940), as indicated by arrows in figure 21. Finally, comparison with the small Carboniferous assemblage from India is barely possible, as the latter consists of only three species. How-

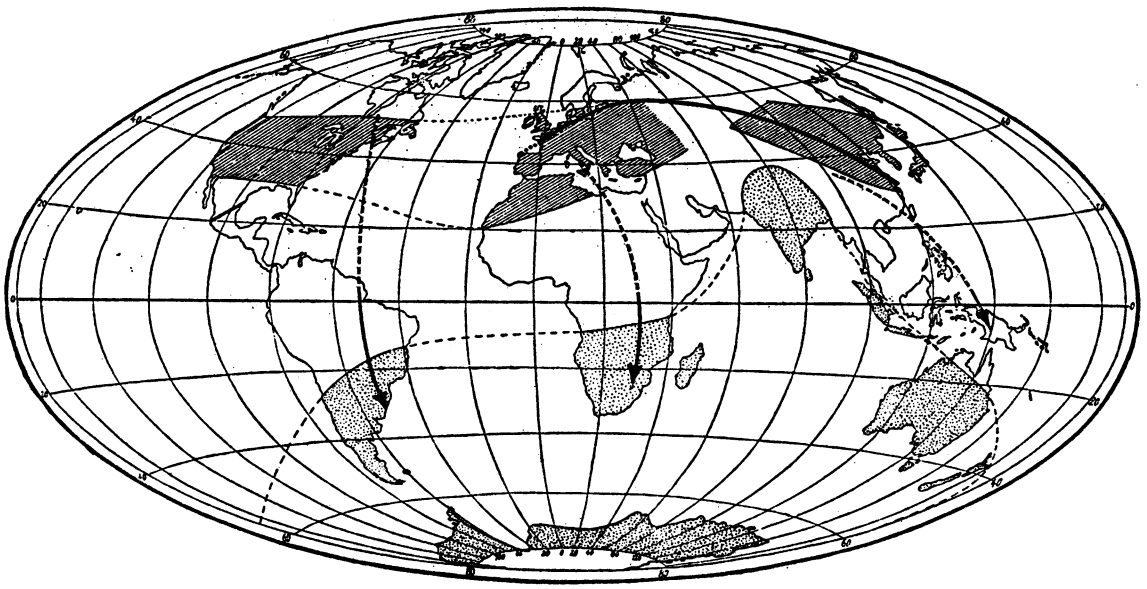

FIG. 21. Distribution of late Paleozoic floras. The continents are shown in their present position and size. The hatched area indicates "northern" floras; the stippled area shows the distribution of the "southern" or *Glossopteris* flora. The three arrows point to the localities where mixed floras of southern and northern elements have been found (modified from Zimmerman, 1930). Mixed floras have also been reported from Patagonia (Feruglio, 1951a), Mozambique (Teixeira, 1947), and Madagascar (Boureau, 1949). For further discussion, see Dalloni (1948).

ever, the Permian succession is well represented in India by the *Glossopteris* flora, which in younger strata is associated with the *Thinnfeldia* flora (Triasso-Rhaetic). The restricted occurrence of certain species in the Indian succession may be valuable in dating isolated Australian finds.

Recent discoveries of new South American localities may eventually throw additional light on the entire succession (Dolianiti, 1946; Feruglio, 1951a; Jongmans and Gothan, 1951; Martins and Sobrinho, 1951; Mendes and Mezzalira, 1946; Mezzalira, 1949; Read, 1941). Detailed study of the plant microfossils of Gondwana deposits may greatly increase the roster of species attributed to the *Glossopteris* flora. Thus Ghosh and Sen (1948) recorded as new to the Lower Gondwanas almost all microfossils isolated by them from the Raniganj coal field in Bengal. They described over 50 spore types, 11 wood fragments, 31 cuticles and related structures, and eight unknown plant fragments. Although the characters seen on spores may be of little use as indicators of past climates, extensive analyses of microfossils of widely separated areas are bound to be immensely useful in correlating strata of comparable age (Virkki, 1939, 1945).

Actually our knowledge of the origin and fate of the *Glossopteris* flora is quite inadequate. Its origin can probably be connected with the cooling of the climate towards the end of the Carboniferous, resulting in large-scale extinction of pre-Gondwana cosmopolitan elements, including those of the Northern Hemisphere. Thus the *Glossopteris* flora lasted apparently from the Upper Carboniferous to the Triassic, representing a cold temperate flora in contrast to the Cathaysia flora, and becoming richer with the increasingly warmer climate of the Permian. At its maximum it was certainly not a glacial flora (Boutakoff, 1948; Du Toit, 1940; Fox, 1940; Jamotte, 1929, 1933; Sahni, 1939; Seward, 1931).

One of the greatest problems is the origin of the glossopterids. Did they originate in Argentina or South Africa, and in which direction did they migrate? Gondwanaland was well isolated from the rest of the world by the Tethys Sea occupying the geosyncline

from which the Himalayas arose. However, Kashmir and Assam were promontories via which the contact with the Angara flora must have taken place (Sahni, 1936). On the whole, evolution in Gondwanaland was fairly uninterrupted, whereas major changes must have occurred in the north. A notable fact is the great impoverishment of the *Glossopteris* flora during Lowest Triassic, leaving *Dadoxylon*, two species of *Glossopteris*, and *Phyllotheca* or *Schizoneura*. During this time Brazil and South Africa probably occupied the heart of Gondwanaland, and plant migrations occurred more readily near the periphery of the continent (Du Toit, 1930). During late Triassic the flora became more numerous, reaching its peak during Upper Keuper in the Molteno stage of South Africa and corresponding stages elsewhere in the Southern Hemisphere. Pteridosperms were then largely replaced by ferns, ginkgophytes, and cycadophytes, whereas *Glossopteris* remained in South Africa and Tonkin and possibly left as its successor the genus *Linguifolium* of Chile, Tasmania, and New Zealand (Berry, 1945).

This famous Molteno flora has been dated by Du Toit (1927) as essentially of Upper Triassic age, containing some Permian survivors and many new and abundant elements, especially ferns and ginkgophytes which migrated north to form Rhaetic assemblages in the Northern Hemisphere. Or as Du Toit (1927, p. 290) puts it: "The rather poor Permo-Triassic '*Glossopteris* assemblage' of Gondwanaland has indeed now been replaced almost entirely by the more abundant and cosmopolitan Trias-Rhaetic '*Thinnfeldia* Flora.' " *Thinnfeldia* and other frond genera are now believed to represent the foliage of the Mesozoic pteridosperm family Corystospermaceae described from the Molteno beds by Thomas (1933).

Effective comparison of the *Glossopteris* flora as represented in various parts of Gondwanaland is greatly hindered by the profound taxonomic problems encountered. For instance, Jones (1949) and Jones and de Jersey (1947) pointed out that much of the Australian *Thinnfeldia* material might profitably be treated as a single species rather than divided up among five of the eight species customarily recognized in Australia. Generic segregation of the complex into geographical groups, as proposed by Frenguelli (1943) on external morphological grounds, is opposed by Jones and de Jersey (1947). Cuticular analysis of all, or the major part of, the genera of the *Thinnfeldia* series (T. M. Harris, 1931–1937, pt. 1) is bound to result in different generic assignments and delimitations (Lundblad, 1950). Actually, Jacob and Jacob (1950) accept the inclusion of the southern thinnfeldias under *Dicroidium* on the strength of their study of the cuticular characters of eight species of this genus. Contrary to Jones and de Jersey (1947), they recommend that the five species of *Dicroidium* combined by these authors be maintained as separate entities.

Whence did the thinnfeldias come? Did they originate in the Northern Hemisphere from Permian ancestors like *Supaia* as represented in the Hermit Shale of Arizona? "If some of the Hermit Shale plants are the ancestors of the Thinnfeldias, their distribution could be explained either on the theory of isthmian links of Willis and Schuchert or on Wegener's theory." Walkom (1949) favors the former.

MESOZOIC FLORAS

Beginning with the well-known Rhaeto-Liassic floras of the Northern Hemisphere, especially those of Greenland, it is possible to distinguish three main floral regions (T. M. Harris, 1931–1937, pt. 5; Hirmer, 1939):

1. Northern province: which ranged from eastern Greenland (latitude 70° N.), through Sweden to France, Rumania (latitudes 45°–56° N.), Poland, Russia, Siberia within the same latitudes to western Japan (about latitude 35° N.) (see Kobayashi, 1942, for Mesozoic floras of eastern Asia).

2. Middle province: which extended from Tonkin to certain localities in China proper, Pamir, Iran, Armenia, Mexico, and British Honduras.

3. Southern province: various floras of

South Africa, Australia (Queensland), and Argentina may eventually be referred to this province after their correct age has been established (see Feruglio, 1951b, for map of Mesozoic floras of Argentina).

The northern province is marked by the presence of a uniform flora, extending 160° in longitude (from 25° W. of Greenwich to 135° E.), and 35° in latitude (between 70° and 35° N.). Characteristically this province ran obliquely across present climatic and latitudinal belts. The same phenomenon is seen with regard to the central province. Hirmer (1939) believes that this position is in agreement with the distribution of land at the end of Triassic and the beginning of Jurassic, as postulated by Köppen and Wegener (1924).

As the exact age of the floras of the southern province is still doubtful (Frenguelli, 1948; T. M. Harris, 1931–1937, pt. 5; Fossa-Mancini, 1940; Teixeira, 1943), additional information is badly needed, before this province can be satisfactorily defined. This aim will not be materialized until critical collections from these areas have been studied in detail by methods employed by Harris on his Greenland material or by Lundblad (1950) in the description of the Rhaeto-Liassic floras of Sweden.

Not many Jurassic floras are known from the Southern Hemisphere, and none is so well represented as the famous British flora. Edwards (1934) analyzed the known Jurassic plants from New Zealand, comprising 40 to 50 species from six localities and possibly several horizons. He found that half that number (20 to 25) was also known from Australia, one-third from India, and one-fourth from Graham Land. A new Jurassic flora has been reported from the Esquel schists of Argentina (Cazoubon, 1947). Comparison of such recently discovered floras with well-known ones may provide the necessary information to resolve the long controversy concerning the reputedly uniform climate of the Jurassic which was apparently more imaginary than real (Florin, 1940b).

CRETACEOUS AND TERTIARY FLORAS

For practical as well as scientific reasons late Cretaceous and Tertiary floras are often treated together. On the whole, floras of these periods found in the Northern Hemisphere are also better known than their contemporary floras in the south. How much uncertainty surrounds many of these southern floras is seen from Gerth's attempt (1941) to appraise all Tertiary floras of southern South America. He placed the known floras in two groups, both of which have descended from a common ancestor, an Upper Cretaceous subtropical flora found throughout South America: (1) *Maytenus-Zamia* flora, which was limited to humid subtropical or tropical climates, and originally described from a locality south of Concepción, Chile; and (2) *Nothofagus-Araucaria* flora, found in humid but cool climates and first reported from Tierra del Fuego and Antarctica; *Nothofagus* and *Araucaria* are still living in the area. While this flora arose at the extreme southern tip of South America, the *Maytenus-Zamia* flora arose at about the same time but much farther north. As the climate deteriorated during Tertiary times the *Maytenus-Zamia* flora retreated and the *Nothofagus-Araucaria* flora advanced northward. This trend in the change of climates has apparently not been altered since the middle of Tertiary. Gerth construes this fact as an argument against the changes of the South Pole postulated in connection with continental drift.

Another interesting discovery was recently announced by Selling (1947). A collection of Cretaceous plants from Patagonia contains among conifers, various dicotyledonous leaves, etc., and flowering and fruiting spikes of a species of *Aponogeton.* This family (Aponogetonaceae) had so far not been reported from the Western Hemisphere, either living or extinct. Moreover, the species represented seems to be related to a species of *Aponogeton* endemic in tropical Africa rather than species found in Australia or Asia. This discovery as well as relationships existing among modern plants found in South America and Africa disqualifies Berry's (1942) contention that the Tertiary floras of South

America were as American as the African ones were African. But he is undoubtedly correct in stating that considerable north and south migrations occurred at least during early Tertiary both in the New as well as in the Old World. In each case, however, the Miocene seems to mark the beginning of dissimilarity, especially in the Americas; in short, the floras assume their modern aspect (Hirmer, 1939).

In all probability, our knowledge of Tertiary floras will be greatly increased as soon as more extensive studies of spores and pollen (palynology) from various parts of the world are made and supplemented by anatomical studies of fossil woods (W. F. Harris, 1950). Some examples may illustrate this. In Africa some significant data have come from Egypt where floras dated as Middle Cretaceous furnished the first fossil record of a predominantly austral angiosperm family, the Proteaceae, from the Northern Hemisphere. These floras consisted largely of forests made up of many species of this family (represented by woods and fruits). Although the distribution of the modern members of this family has often been used in support of drift, Kausik (1943) concluded that drift alone could not account for all peculiarities of distribution of this family, past or present. Consequently, he asked for more data, particularly on fossil members. Lately Cookson (1950) and Cookson and Duigan (1950) published exemplary studies on fossil members of this family as represented in Tertiary deposits of Australia, carefully based on analyses of and comparisons with living species, particularly of their cuticular characters. These authors are of the opinion that most extra-Australian records of fossil Banksieae (Proteaceae) are based on misidentifications.

Two similar instances of regressive areas are well documented. Hofmann (1948) proved convincingly that mangrove occurred in the late Cretaceous in Central Europe (Austria) by detailed comparisons of leaf fragments, pollen, and wood samples. This mangrove included species now limited either to Old or New World tropics. The second instance concerns the past and present distribution of the austral family Dipterocarpaceae. Although its present center of distribution lies in southeastern Asia, fossil woods belonging to this family have been recorded from western Europe. Recently discovered fossil woods from Egypt referable to this family now link these widely separated localities (Hirmer, 1939).

These cases are so striking because they represent definitely or predominantly austral angiosperm families, which in the past occupied larger areas frequently extending into the Northern Hemisphere. By comparison, loss of area by many fern and gymnosperm groups is to be expected as a result of the general decline of these groups during the explosive expansion of the angiosperms in the Cretaceous and early Tertiary. An excellent example of loss of area was provided by Hirmer and Hörhammer (1936) who studied the past and present distribution of the Matoniaceae, a family of tropical ferns. Today this family occupies only the equatorial portion of its former large tropical area.

Antarctica has long been regarded as a major center of origin and distribution of modern plant groups (Darrah, 1936; Hill, 1929; Wade, 1941; *et al.*). For instance, Copeland (1947) now estimates that "practically the whole fern world of the tropics is descended from the ferns of old Antarctica"; to be specific, nine-tenths of the tropical fern flora.

Not all migrations followed this direction, as many occurred from north to south and may even be going on today. Diels (1942) has shown how far south certain pioneers of the Holarctic realm may penetrate into tropical areas such as the Philippines or Central America. These migrations were probably induced by climatic changes during late Tertiary or Pleistocene times and thus are not very old. The remarkable fact about them is that these pioneers have hardly changed in the process, and their variability has apparently not increased beyond the range known in their normal habitats and concentrated areas of distribution.

The contrast between tropical and temperate floras in the past, at least since the late Cretaceous, has remained essentially unchanged, e.g., the tropical zones and the Equator have remained in their present position, according to evidence adduced by

Kaul (1943, 1945) from the study of fossil palm stems collectively referred to the genus *Palmoxylon*. However, Kaul explains the pre-Tertiary distribution of temperate and tropical floras on the basis of drift, at least "in Asia from the Tertiary backwards to the Carboniferous period." Obviously many more data from such critical areas will be needed before such far-reaching conclusions can be regarded as safely established. Such analyses should include extensive ecological and geographical accounts of living tropical floras, notably those of the Far East (Airy Shaw, 1942; Gordon, 1949; W. F. Harris, 1950; Richards, 1942). Gordon (1949) advocates "two lines of research; firstly the continued and intensified study of fossil angiosperm floras and contemporary faunas all over the world, with strict insistance on reliable identification or none at all, and secondly a detailed investigation of the geological structure and origin, and the botanical history, of isolated oceanic islands, especially Hawaii. When we can explain how *Astelia* and other sub-antarctic genera reached Hawaii, I don't think we will have so much difficulty in accounting for their distribution in the southern continents."

DISTRIBUTION OF GYMNOSPERMS

In addition to the tracing of the history of entire floras it is often equally instructive and profitable to examine the records of important groups. The history of the gymnosperms is of particular interest here, as their rise and subsequent decline either coincided with or, as is more likely, preceded the spectacular ascent of the angiosperms in late Mesozoic times (for summary, see Just, 1948). Moreover, some of the most important recent advances in paleobotany pertain to the Mesozoic history of the gymnosperms.

The present distribution of the Cycadaceae shows remnants of an area undoubtedly much larger in the past (Suessenguth's Schollenareale or Vester's pluricontinental area). Apparently the cycads originated from Permian pteridosperms (late Paleozoic taeniopterids). Although they were never so numerous as their contemporaries, the Cycadeoidales (Bennettitales), the cycads survived until the present, whereas the cycadeoids vanished completely in the Upper Cretaceous. This phenomenon always elicited considerable speculation regarding the causes of extinction. In preference to the old stories of insect attacks, ill effects of injurious volcanic gases, etc., Ridley (1938) offered a rather plausible explanation, namely, "The evolution of the broad-leaved dense forest is, I think, enough to account for the disappearance of the Mesozoic Cycads and gymnosperms." According to him, some living species are actually near extinction, as the Christmas Island cycads, and other species which propagate mostly by vegetative means rather than by sexual reproduction (*Cycas Rumphiana*). The distribution of the cycads has been interpreted on the basis of drift and also used as an argument against it. As far as is known, both lines of Cycadaceae, namely, the Cycadoideae and Zamioideae, are equally old, dating from the end of the Triassic (Rhaetic) (Florin, 1933; T. M. Harris, 1941) and, paradoxically enough, are better represented by Mesozoic fossils than Tertiary records.

The case of the Ginkgoales is equally interesting and significant (Florin, 1936, 1940c, 1949). Well-established fossil representatives of this order belonging to some 15 genera ranged from the Lower Permian to the Upper Pliocene. The order originated from the same ancestors from which the Cordaitales came and not from the latter, as commonly held. *Ginkgo*, often listed as the oldest known plant genus, dates from the Middle Jurassic and comprises seven fossil species and the type species, *Ginkgo biloba*. Beginning with the Upper Triassic, the evolution of the Ginkgoales is marked by the rapid appearance of new forms represented by many individuals. The order reached its greatest development during Jurassic and Lower Cretaceous. Then all genera disappeared except *Ginkgo*, *Ginkgoites*, and *Torellia*. Like the cycadeoids they show a marked decline during the Middle Cretaceous. This decline, too, may well have been associated with the explosive evolution of the angiosperms during the Cretaceous.

The Tertiary conifers of the Southern Hemisphere (Florin, 1940b) have been more carefully studied than any other large systematic group. Florin (1940a) has shown that the origin of the conifers must probably be dated back to Westphalian, as the conifer floras of the Upper Carboniferous and Permian are as clearly separated as are the other elements of these periods.

During late Paleozoic the conifers of the Northern Hemisphere progressed far more than their southern contemporaries and were more widely distributed than the latter. Beginning with the Permian, and especially since the Jurassic, the conifers of the Southern Hemisphere became more and more differentiated from their northern counterparts. Apparently contact between these two groups existed across trans-tropical bridges. However, northern genera rarely over-stepped the Equator, whereas southern genera probably migrated more often to the north. Few conifer genera are represented in both hemispheres. The great uniformity of climate and world-wide distribution of Jurassic floras postulated by many paleobotanists can no longer be substantiated by recourse to the conifers.

The traditional view of the north temperate (or even Arctic) origin of conifers is apparently in need of some revision. As far as southern conifers are concerned, Florin (1940b, p. 92) assumes former land connections "or at least much closer proximity, between Antarctica and the adjacent southern ends of South America, Australia, New Zealand, and South Africa."

SUMMARY

Modified drift theories continually attract favorable comment from many paleobotanists and botanists (for summaries, see Just, 1947; Good, 1950). However, not all problems of origin and distribution can be explained on the basis of continental drift, certainly not at our present state of knowledge. In many instances, we need more fossil records of critical groups from critical areas and periods, especially of early angiosperm types. Surprises may also be in store, such as the discovery of a new gymnosperm group, the Pentoxyleae, so ably described by the late Professor Sahni from Jurassic beds of India (1948). Our rapidly growing knowledge of plant microfossils will be an indispensable aid in solving problems of correlation. Progress may also result from reorientation and new interpretations. The dramatic reclassification of the large cycadophyte complex by Florin and Harris is an excellent example in point (see summary in Just, 1951). Ecologists, too, may soon be able to give us more information regarding the effects of microclimate on local distribution and survival of many important species. Thus the vestiges of our kaleidoscopic picture of the fossil floras of the Southern Hemisphere will be removed, the sequence of events established, and the panorama completed.

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PHYTOPHYLETIC PATTERNS ON LANDS BORDERING THE SOUTH ATLANTIC BASIN

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A WELL-DEFINED GROUP of plants, in general, holds to much the same basic ecological conditions. The outlying north temperate species of mainly tropical, herbaceous plant genera often are summer annuals, thereby achieving ecological compatibility with their groups; our northern summers may be quite as "tropical" as the real tropics, and from the standpoint of persistence through northern winters versus dry seasons in the tropics, the mechanisms of dormancy and hardiness of the seed are physiologically quite comparable. Likewise, the living forms of ancestral types of north temperate woody genera often are to be found on the higher mountains of the tropics where frosts sometimes occur or, on occasion, in south temperate regions. It should be clearly understood that the opening statement does not in any way imply a supposition on my part that living organisms today necessarily occupy the same geographical ranges as their precursors; to do so would be utterly naive.

The elucidation of the problems of ancient distributions and dispersals should, if possible, be derived from the study of a consistent, world-wide fossil record. Unfortunately, however, the great majority of flowering plant groups have left nothing like an adequate fossil record behind them, particularly in the present-day tropics where we need it most. Because of this I have attempted to shed some light on the question of the broad pattern of past dispersals by another method, in spite of its obvious imperfections and possible interpretational pitfalls. It is the only method available until we know more of the fossil record. This method consists of analyzing the phyletic trends of a group as indicated by living members, then plotting the generalized direction in which the major phyletic divergences appear to have taken place. A little circle in eastern Brazil on our map, marking the area where the evolutionarily specialized genus *Hydrothrix* occurs today, means little unless we consider it against the phyletic pattern of its own group. Therefore, let us examine the family to which it belongs, the Pontederiaceae[1] (fig. 22).

Of the many examples that might have been used, I have purposely chosen the Pontederiaceae, since it is an aquatic, freshwater group. We are so prone to assume that such plants are dispersed over long distances by our avifauna that there is no point in avoiding the issue. It is freely admitted that aquatic and wading birds might easily carry the seeds of this group about. Therefore, I would not consider it of undue significance that *Eichhornia* and *Heteranthera* were found to have their primary distributions associated with the Afro-American area if these were instances isolated from the general pattern; they might then be dismissed as being probably no more than the result of interesting accidents of dispersal. To me the significant thing is that there is an obvious trend of phyletic divergence, as demonstrated by standard and generally accepted botanical criteria, which sweeps from somewhere in the Pacific area across India and Africa into South America, beginning with the patently primitive *Monochoria* and ending with the highly divergent *Hydrothrix* and *Pontederia*. The chart indicates only a few of the obvious morphological divergences and specializations. The progressional nature of the phyletic pattern would seem to be too regular to be chance and the distances too great at the present time to lend much credence to the theory that birds are a logical vector of dispersal between Africa and South America.

Transportation by wind and water also should be seriously considered. These dispersal factors are taken up below. Here, I would point out only that I am unable to

[1] The common pickerel-weed (*Pontederia cordata*) of our northern waters and the water-hyacinth (*Eichhornia crassipes*), native in tropical America but introduced into Florida and perhaps even partially native in the Everglades, are familiar members of this plant family.

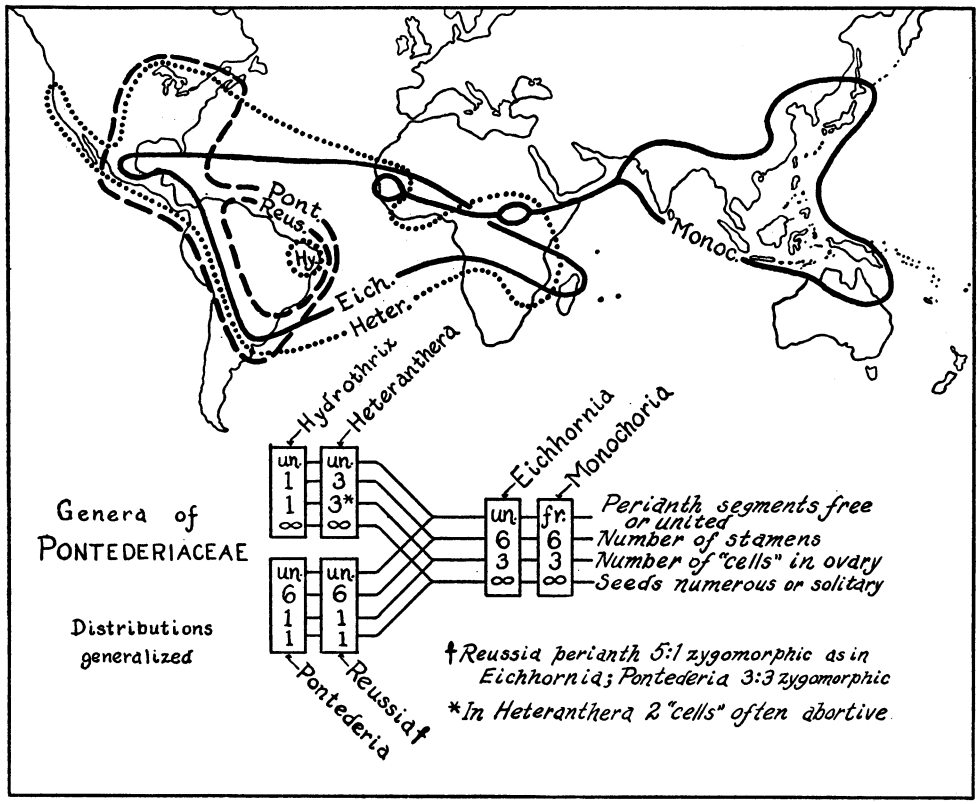

FIG. 22. Genera of Pontederiaceae showing (below) the trend of phyletic specialization from *Monochoria* to *Hydrothrix* and *Pontederia* and (above) the generalized distributions of the six genera of the family. Other phyletic trends such as specialization of the plant body and additional modifications of the perianth are not indicated, but closely parallel the items listed on the chart.

see how this series of genera, in its present distribution and phyletic pattern, could have come down out of the north, off of Holarctica, except by a most unusual series of coincidences. It is what we would expect of a normal trend in phyletic divergences and dispersals if it occurred on a single large and essentially continuous land mass. The phyletic trend pattern of the Pontederiaceae is by no means unique; were it so, we might disregard it as the result of chance. In another place I have delineated others that show the same general type of trend (Camp, 1947), and these examples are only a fraction of those that might be demonstrated. It also is to be noted, in addition to pertinence for our general topic, that this chart of the Pontederiaceae indicates the general method by which the abbreviated analyses of this paper have been made and which, with a considerably larger number necessarily here omitted, are the basis of the present discussion.

The oft-repeated east-west phyletic trend is by no means the only one that has contributed members of a plant family to Africa and South America. The Escalloniaceae and its derivatives appear to have quite a different pattern (fig. 23). Of the 25 genera in the family, *Tetracarpaea*, of Tasmania, appears to possess the primitive characters for the group. To conserve space I cannot here list all genera or give their ranges; these can be found in standard works. Ten of the genera occur within the central complex (indicated by the circle). Four are found along the trend line leading into Holarctica; of these *Itea* is most interesting for it occurs from the eastern Himalayas to Japan and then, after a large

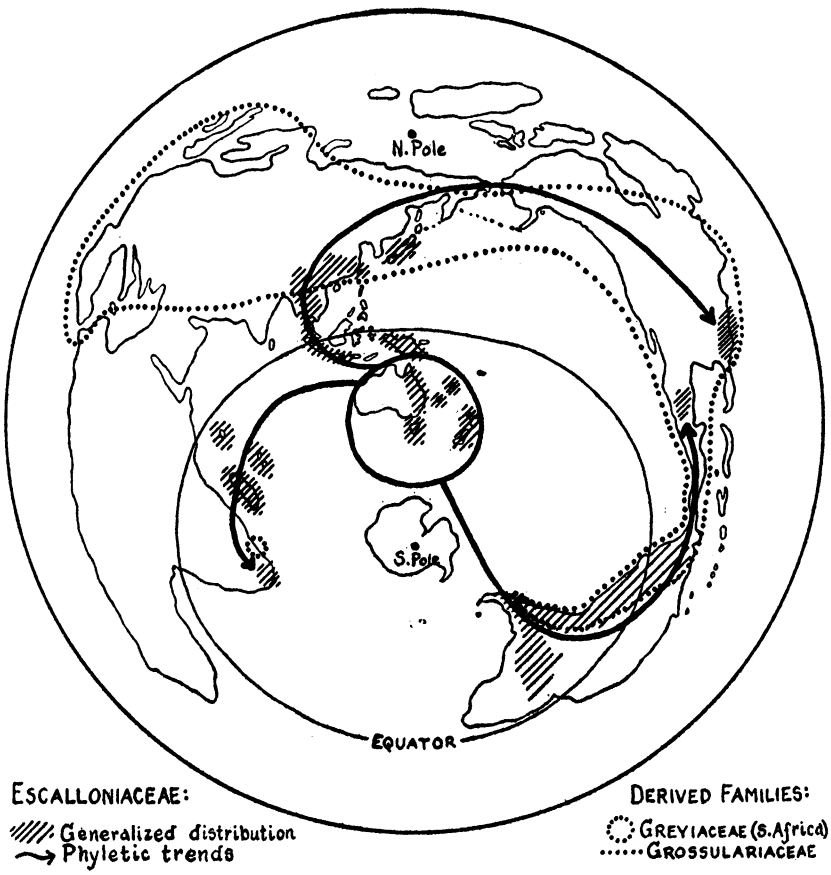

FIG. 23. Phyletic trends in the Escalloniaceae, leading to the derived families Greyiaceae and Grossulariaceae. The map, an oblique azimuthal equi-distant projection, is designed so as to be centered on Tasmania, the home of *Tetracarpaea*, the most primitive living member of the group.

disjunction, in eastern North America. The trend line to Africa has along it seven genera; at the end of the line can be found the monotypic family Greyiaceae, apparently derived from the Escalloniaceae.

The remaining trend line reaches into South America where there are four genera; an attenuated extension of this line occurs in Mexico. Of these *Escallonia* is the most widely dispersed and morphologically variable. At the higher altitudes in the Andes south of the Equator, again near the end of a trend line, its most divergent members form almost a direct link with the primitive members of the derived Grossulariaceae. Our cultivated gooseberries and currants are Holarctic members of the Grossulariaceae, but their phyletic roots are to be found among the high mountain escallonias south of the Equator. Contrary to the Matthewsian dictum, the advanced and highly specialized northern members of the Grossulariaceae seem not to have driven the primitive members southward into the Andes; apparently that is where the group arose. The early divergent members of the group, with their new genetic potentials, migrated northward into new territory, leaving their ancestral forms behind them.

Lacking opportunity, it is impossible in this place to present any large number of analyses of angiospermous groups to indicate the data from which the broader conclusions have been reached. However, from a compilation of them we might at least present a

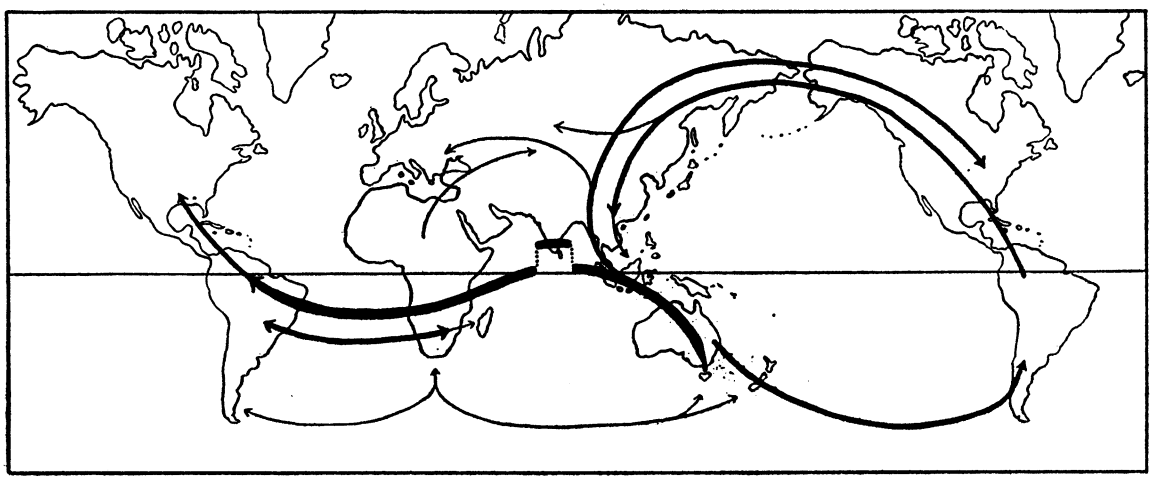

FIG. 24. The major phyletic trend lines of the world's families of flowering plants. For the sake of clarity, the trend lines surrounding the Pacific basin have been kept separate from these pertinent to the problem of the South Atlantic basin by the simple expedient of adding an additional Western Hemisphere. The phyletic trend lines among the plants of the oceanic islands of the Pacific are outside the present discussion, so have been omitted.

preliminary summary of the evidence (fig. 24). There is an "Antarctic" series, so poorly developed that I am unable to ascertain which way the trend goes. An Australo-Patagonian trend is very much in evidence. The trends (going both ways) between North America and Asia are obvious. There is a series of groups which seem not to be intimately connected with the main transtropic trend and which trend from South America to Africa as often as in the reverse direction. Other minor trends and offshoots are evident. But, with all these, the main phyletic trend seems to swing from Australia (and so often from Tasmania or southeastern Australia) across Africa and into South America.

In general, the Indian members of the basic groups of flowering plants have been linked to the Malayan offshoots of their phyletic complexes. However, as I check the data, it becomes increasingly evident that, when we extract the divergent members of the groups now in India and consider only the apparently basic, more primitive members, these are not so much part of the Malayan portion of the complex as part of the great phyletic trend line between Australia and Africa. I have drawn the line as being disjunct for only one reason. The great crumpled mountain ranges north of tropical India for the most part are considerably more recent than the advent of true flowering plants. It is, therefore, only proper to assume that India was covered with ample vegetation of a surprisingly modern aspect during much of the time the earth movements in that area were taking place. Let us then, metaphorically, smooth out the once flat-bedded sedimentaries of these great ranges, much as we would smooth out the crumples in a sheet of paper. With this, India moves back into place on the major trend line of phyletic development which appears to have swept across the warmer parts of the Southern Hemisphere.

The importance of the basic phyletic elements on this major trend line cannot be ignored. A few examples must here suffice. The Magnoliaceae have long been troublesome to students of phylogeny; the recently discovered monotypic Degeneriaceae (known only locally from Fiji, and roughly adjacent to one end of the major trend line as here drawn) may go far in resolving this problem. Elsewhere I have suggested that the great tropical family Annonaceae has too long been overlooked as a primitive group of angiosperms. I have been told by morphologists working on such matters that, like *Degeneria*,

the carpels of various tropical Annonaceae are open at anthesis, the pollen falling between the carpel margins rather than penetrating through the specialized stigma, as is usual with angiosperms. *Xylopia*, probably the most primitive living genus of the group, occurs from Australia into Africa and is also in South America.

We are prone to think of the heath family (Ericaceae) as being essentially temperate, yet the central complex of the most primitive of its living genera, *Befaria*, is at the end of the major trend line in the northern Andes. Some of the more primitive species of the geographically sprawling genus *Rhododendron* are found near it in the mountains of the Netherlands Indies, and the most primitive of the multitudinous true heaths (*Erica*) are on the trend line in Africa. Likewise, our northern plums, cherries, and peaches (Amygdalaceae), if extracted from the Rosaceae where they do not belong, have phyletic coherence with their obviously ancestral geobalanids, a group found on the basic trend line in South America and Africa and from thence to Australia. The mostly temperate Fagaceae—the beeches (north and south temperate of both Eastern and Western Hemispheres), oaks, chestnuts, etc.—disappear as well-marked groups in an apparently common complex in southeastern Asia, with incompletely known material from the mountains of New Guinea giving us our first real clue as to what is primitive in the group. The Balanopsidaceae, in various features an even more primitive group, sitting athwart the major trend line in the same general area southeast of Asia, also are part of the general phyletic pattern of the Fagaceae.

It would appear, then, that the majority of primitive members of our basic groups of flowering plants are today located somewhere along this major trend line. Furthermore, as intimated above and so far as plants are concerned, I am unable to accept the Matthewsian dictum that the primitive members of a group occur at the outer margin of a group's range because they were forced there by the later developed and more aggressive members. This is equally true of genera and of larger taxonomic units. For example, of the approximately 300 families of flowering plants about two-thirds are widely dispersed. The majority of these are essentially tropical, with their basic members somewhere along the main trend line; the remainder, which may be widespread in temperate areas (mainly in Holarctica), have their phyletic roots in existing tropical or Southern Hemisphere groups (as is noted above in the relation between the Escalloniaceae and Grossulariaceae). After the few primitive ones, such as the Degeneriaceae, are extracted, the remaining one-third, or exactly 100 families, usually are highly specialized, at least when compared with their evolutionary precursors, and often relatively limited in geographic range. Of these specialized and geographically limited offshoots of the basic groups, only 16 are to be found on Holarctica, and the majority of these have definite southern affinities. The remaining 84 families (which should be farthest away from their primitive precursors) are associated with the land areas of Australia, India, Africa, and South America, only occasionally sending a few inconsequential species northward onto Holarctica. It is of further interest to note that, of these 84 families, 11 have a common Afro-South American range.

Because of this array of evidence I can do no more than rephrase what has been stated elsewhere (Camp, 1947): that, in my opinion, not only have the lands crossed by this great phyletic trend line been the ancestral homes of our flowering plant groups, but the bulk of their primary evolutionary divergences also took place in these same areas. In this chart (fig. 24) two correlations become evident: one is that the major phyletic trend line binds together the hypothetical old land of Gondwana; the other is that the several trend lines south of the Equator closely parallel the wind drifts and major ocean currents of that hemisphere.

A series of questions therefore confronts us. (1) Are the major groups of flowering plants much older than we have ever dared suppose? Or (2), did Gondwana really exist as a land area and, if so, did it break up much more recently than its proponents thought? Standing apart from these is another question: (3) Are we forced to conclude that the vast transoceanic distances of the Southern

Hemisphere are fundamentally ineffective as barriers to plant dispersal? A final question, closely related to the second, would be: (4) Is it possible that the configuration of land surfaces in the Southern Hemisphere in the not-too-distant geological past was quite different from what it is today?

It is my considered opinion that the major groups of flowering plants may be more ancient than we have supposed, that the genetic patterns of the basic angiospermous families already were in existence early in the Mesozoic. Spectacular as was the rise and decline of the Mesozoic reptiles, it might not be amiss to think that possibly the major biological event of the Mesozoic was the rise and elaboration of the angiosperms, their more nutritious tissues and faster growth (in comparison with that of the characteristic gymnospermous Mesozoic vegetation) making possible the development of the highly metabolic mammalian type. This rise of the angiosperms probably took place mainly on the uplands where chances for preservation of a fossil record were at a minimum; in spite of the complexities of many tropical lowland floras, the angiosperms still are basically an upland group of organisms.

The possible existence of an old land mass in the Southern Hemisphere and the date of its break-up must be left to the geologists. It will perhaps be classed merely as wishful thinking on my part, or at best dismissed as ignorance of the known fossil record, yet I honestly cannot see any great obstacles for a working hypothesis to the effect that an old continental mass did exist at one time in the Southern Hemisphere and that its segmentation, in whatever manner, did not take place until some time in the Mesozoic, with certain parts having become disjunct perhaps even much later.

The third question cannot be passed over so easily. I would not for a moment discount wind and ocean currents as effective agents in the dispersal of certain forms, often for long distances. Even without the numerous examples given by Ridley (1930), common experience would make this evident. However, it would take a volume of almost equal size to set down certain facts and demonstrate a fundamental point which begins to be evident as one analyzes the data against the phyletic patterns of various groups, which Ridley did not do. One searches in vain for examples among particular groups and critical forms in Ridley's voluminous compilation; furthermore, he was quite aware of lack of evidence where various of these were concerned and often commented on the wide dispersal of such materials with no apparent means to accomplish it. As one analyzes such groups it becomes increasingly evident that those mechanisms permitting effective dispersal either by wind or salt water are special, secondary adaptations, rarely to be found associated with their more primitive members. One might then legitimately question whether the earlier and patently widespread dispersals of the more primitive members of the basic groups of flowering plants were primarily through the agencies of winds and ocean currents.

Since I am supposed to be dealing only with living floras perhaps I should ignore my last question: whether land configurations in the not-too-distant geological past might have been considerably different from what they are today. But having gone this far, it would be only proper that I present a last set of correlates. In our analyses it soon became evident that, in the main, the basic elements of the South American flowering plant groups are not in the lowlands but associated with the four major upland areas.[1] One of these is the northern Andes. Another is the southern Andes and adjacent Pata-

[1] The flora of the tropical South American lowlands, especially that of the central Amazonian basin (and to a lesser extent the Orinoco basin), is highly heterogeneous, yet it is not a centrifugal flora; it is a centripetal flora, obviously having been derived (as are the majority of lowland floras) from what might be called the "piedmont areas" of the surrounding uplands. Furthermore, it is a recent flora, many groups being characterized by series of often poorly delimited genera and species, apparently the result of yet active genic introgressions and unstabilized segregations. The flora of the central Amazonian basin appears to be no older than the late Pliocene, or perhaps even the Pleistocene, and for general complexity has its analogous counterpart in the Northern Hemisphere in the areas into which a similar but less rich heterogeneous assemblage migrated following the last glacial retreat. The reason for this is the relatively recent emergence of the central Amazonian basin following a series of inundations during the Tertiary.

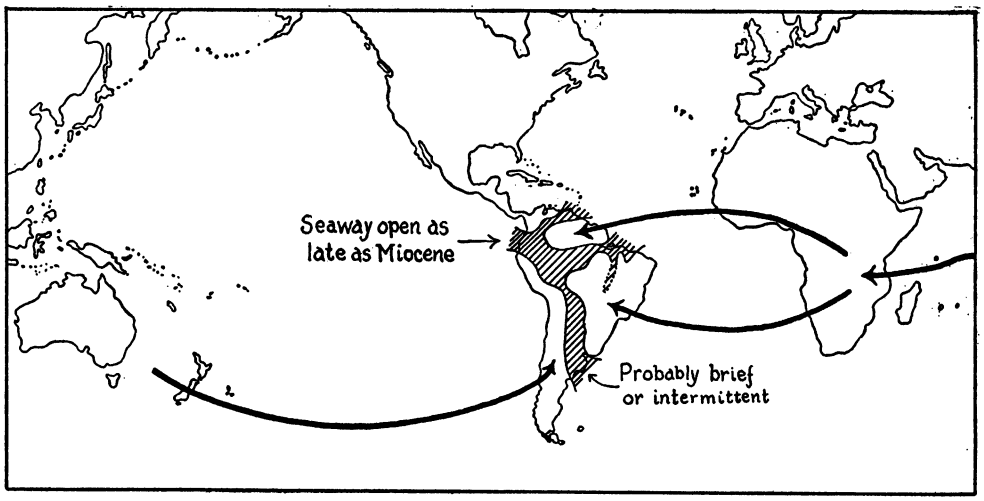

FIG. 25. The major Tertiary sedimentaries of South America (shaded) with indications (heavy arrows) of the more important phyletic connections of the flowering plants of the Guiana shield, the Planalto do Brasil, and the southern Andean-Patagonian areas; the northern Andean area is briefly discussed in the text. These four basic upland areas of the early Tertiary were the primary sources, perhaps as late as the Pleistocene, of the present South American lowland floras. The acknowledged complexity of the present flora of the central Amazonian basin is the result of its recent origin from a series of much older and markedly different ancestral floras.

gonian region. The other two are the Guiana shield and the Planalto do Brazil; floristically, these two have much in common, yet they contain certain basic elements which they do not share. Let us now place the major Tertiary sedimentaries on the map of South America and see what happens (fig. 25).[1]

The basic phyletic trends associated with the northern Andes (which are not here indicated since they are not part of our topic) appear to be quite strongly linked both with those of Holarctica and a specialized and secondarily derived trans-Central American-Caribbean flora. The basic elements of the

[1] Figure 25 was derived from a consideration of material from various sources, especially from a preliminary copy of the geologic map of South America released in 1945 by the Geological Society of America, a more complete edition of which has since been issued. Since figure 25 was prepared and the accompanying text completed, A. A. Olsson, who has had extensive geological experience in the northern Andes, called my attention to the extended paper by Weeks (1947) on the paleogeography of South America. In carrying out certain plant explorations, I recently spent a year and a half in the field in Ecuador, crisscrossing the Andes, from the Pacific lowlands into the Amazonian lowlands. One who, like myself, has had some previous training in field interpretation of geological structure and who long has correlated geological formations and plant associations, could not help being interested by the geological structure of the region. The high-altitude sedimentaries of the Cuenca and Loja basins especially impressed me; it is my lasting regret that, then, I could do no more than enviously pass by the Tertiary, angiosperm-bearing fossil beds on the upper rims of the Loja basin. These would be estuarian deposits on the southern margin of the seaway indicated in figure 25. The Tertiary fossiliferous strata of Ecuador and adjacent Colombia, especially at the higher elevations, are considerably obscured by intrusives and extensive superposed extrusives and volcanics, so that only rarely can a satisfactory section be obtained. Recently, Mr. Olsson has discovered additional fossiliferous beds at high altitudes in southern Colombia, somewhat south of the northern margin of the seaway indicated by the present chart, and therefore within it. This information was not then available to Weeks for his interpretations of that part of the area. Mr. Olsson has kindly given me permission to note, ahead of publication of the data, that these high-altitude, fossil-bearing strata "are marine beds of the late Oligocene or early Miocene." It seems quite probable that the Amazon is a reversed river, which once flowed westward. Those who delight in speculation on continental displacement might well wonder whether the Niger River could possibly be the headwaters of a once westward-flowing Afro-South American river system. This much is fact: Almost every botanical expedition to critical areas in South America

southern Andean-Patagonian flora are considerably more linked with those of New Zealand and Australia than with those of the rest of South America, and appear mainly to have been derived from that direction. If the basic floras of the Guiana shield and the Planalto do Brazil were derived from Africa we should expect that they would have considerable similarity; if, however, they arrived by somewhat different routes, we should expect to find certain differences. As already noted, these floristic similarities and differences are evident.

[The botanist who delves into these matters often has the feeling that he is standing alone. Since this paper was submitted for publication, my attention was called to a work on the dispersal of non-marine mollusks (Pilsbry, 1911), which anticipated some of the present conclusions. By combining phyletics and distribution (an unusual approach for that period) Pilsbry concluded that the evidence indicated land connection between Africa and South America "enduring from at least Paleozoic to near the end of Cretaceous time" (i.e., throughout the Mesozoic) and, further, "strong evidence that a few groups passed by the Antarctic route to Australasia." His maps and phyleto-dispersal summaries often are surprisingly similar to my own concepts of the phyleto-dispersal patterns of certain groups of flowering plants. This perhaps indicates that the Mesozoic was a critical time in the elaboration and dispersal of the basic elements of both the present non-marine molluscan and angiospermous groups. This hypothesis of the elaboration of the flowering plants in the Mesozoic from an existing, widespread, angiospermous, tropical, upland flora has only recently been critically discussed and documented by Axelrod (1952).]

With this I present such data as are possible within the space at my disposal regarding the phyto-phyletic patterns on lands bordering the South Atlantic basin. I have but one conclusion pertinent to the topic of this symposium: If any significance is to be placed on the sequences of phyletic patterns among our basic groups of flowering plants it would seem evident that they did not come down out of Holarctica but originated and underwent their primary development and early dispersal on a common land mass within the Southern Hemisphere. This early dispersal within the Southern Hemisphere is tentatively placed at some time in the Mesozoic.

and Africa returns with additional material ever more closely linking the plants of the mountainous areas north of the Gulf of Guinea with those of the mountains of the Guiana shield. Some have attempted to dispose of the problem by claiming that these are examples of parallel, or perhaps convergent, evolution. These instances are now so numerous and in so many groups of plants that botanists are no more willing to accept this as a tenable hypothesis than are zoologists the hypothesis that the interfertile races of man are the result of convergence, having descended from different kinds of ape-like creatures. Such speculations, which only obscure the problem, would be unnecessary if it were to be ascertained that the basic elements of our angiospermous flora already were present in the Mesozoic and that the final segmentation of Gondwana did not occur until the same time. Considerable patience and tolerance towards exploratory hypotheses will be necessary until additional paleogeographical facts are uncovered.

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LIVING INVERTEBRATES AND MESOZOIC SOUTH AMERICA

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THERE ARE, I SUPPOSE, something like 150,000 known kinds of living invertebrates in South America—perhaps not quite so many, perhaps many more. Obviously I cannot discuss them all. The best I can do here is to say a very little in general about a few main groups, to discuss one small group of beetles in a little more detail as an example, and finally to suggest a few general propositions about living invertebrates and ancient South America.

According to Stephenson (1930) the native terrestrial earthworms of the tropical part of South America are a highly endemic lot. Most of the groups are unrepresented in the north temperate zone. A few have tropical African relatives. The native earthworms of the cool southern tip of South America are strikingly different from those of the tropical zone and are related towards Australia, New Zealand, and South Africa.

Pilsbry (1911) has listed various groups of mollusks common to South America and Africa. Some of the groups occur nowhere else. They include various land snails, fresh-water snails, and fresh-water mussels. It is the fresh-water forms that most often show South America-African relationships. Pilsbry and Bequaert (1927) note that these forms are large or moderately large and that they usually occur in abundance where they occur at all, so that their absence in the north temperate zone, both living and fossil, is significant.

Insects are enormously diverse in South America, as elsewhere in the tropics. Many insect groups of the American tropics occur also in the Old World tropics, but not in the north temperate zone. Some of the groups are characteristic chiefly of South America and Africa, but, in the case of the insects, I think that the South America-African groups are usually represented in the Oriental region too. The cool southern tip of South America has an insect fauna which is in part fundamentally different from the tropical fauna, with many relationships towards Australia and New Zealand and a few towards South Africa. (This general statement of insect relationships is based on my own knowledge and reading.)

Many marine invertebrates (mollusks, crustaceans, etc.) of shallow coastal seas of the opposite sides of the tropical Atlantic Ocean, that is to say of the coasts of West Africa and of eastern tropical America, are related. Many of the groups are entirely confined to coastal waters, at least as adults. The latter cannot cross deep seas except perhaps by rare accident. But most of the groups have a free larval stage which may last for at least several weeks, and it has not been settled whether or not some larvae may be carried across the Atlantic by ocean currents. Schuchert (1932) has thought not, but his long argument does not seem to me to be very convincing.

These few fragments of fact make up a most inadequate survey of South American invertebrates. There is a huge endemic element in the South American invertebrate fauna that I have barely mentioned, and there is also a large North American element, or perhaps it would be better to say that there are many groups which are represented in North as well as South America. That many South American groups are related towards tropical Africa or towards temperate Australia, New Zealand, or South Africa, is certain. But these relationships involve only parts of the South American fauna, and the relationships are often not very close and can often be accounted for in any of several different ways. It seems to me that each case should be studied separately and thoroughly before we can decide even what the likely alternatives really are. I shall discuss one small group of beetles, the paussids, as an example of what I mean.

Paussids are small or medium-sized beetles that live with ants. Many of them have conspicuous trichomes and distorted antennae, as other myrmecophilous beetles so often do. My interest in paussids began by accident. I happened to look at a few from the

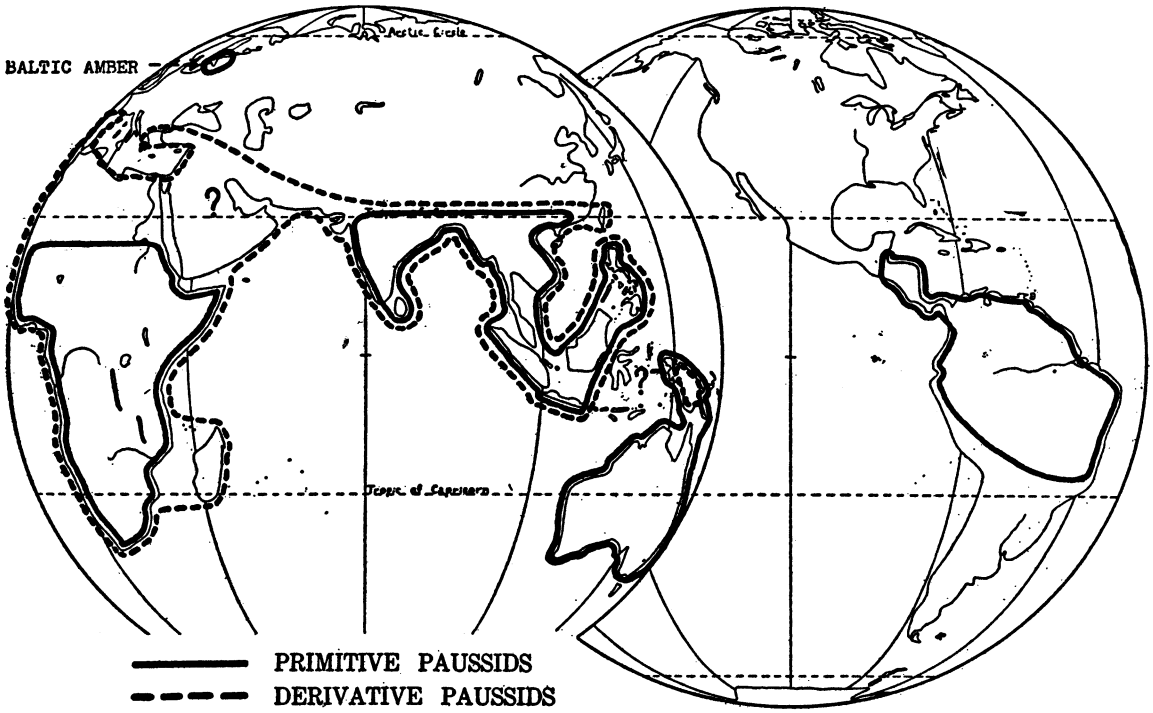

FIG. 26. Approximate known limits of distribution of primitive and derivative paussids. Location of Baltic amber, with fossil primitive paussids, is indicated.

Philippines and discovered the fact, new at least to me, that they were just extraordinarily modified Carabidae or ground beetles. I set out first to discover the geographical relationships of the Philippine forms and then, impelled by growing interest, to get some idea of the distribution of paussids as a whole. Finally I was driven by necessity to go fairly deeply into the external comparative anatomy of paussids, their probable phylogeny, their fossil record, and their classification, in order to get a reasonably satisfactory idea of their geographical history. The work took about a year and has recently been published (Darlington, 1950). Of course I mention this personal history to show how much time and work have been necessary to get a reasonable understanding of the zoogeography of a single small group of beetles, of which the South American representatives number only about a dozen species.

The accompanying map (fig. 26) outlines the distribution of paussids, distinguishing the primitive ones (with antennal segments still free) from the derivative ones (with the segments of the antennal flagellum soldered or fused together, and with other derivative structural characters). It will be seen that paussids inhabit all the main tropical regions of the world, but are absent over most of the north temperate zone, including all of North America. The few that occur in tropical America belong to a single primitive subtribe (Cerapterina) which is also widely distributed in the Old World tropics.

Attempts have been made to use the paussids as evidence of ancient land connections involving South America. Kolbe (1920) suggested that the South American forms were related to Australian ones and derived from them across an Antarctic land bridge, but it seems to me that the South American and Australian genera are not directly related, and the South American paussids are exclusively tropical, not south temperate as they might be expected to be if they had come over an Antarctic bridge. Kolbe thought, too, that he had a derivative paussid from South America and another from Australia, that the two were related, and that one had been

derived from the other across the Antarctic bridge. This was a dreadful mistake. The two species proved not to be related and both had wrong localities. Both were really African. As Wasmann (1929), who had bitter arguments with Kolbe, said about these paussids after correcting the erorrs, "Die Hypothese seiner Einwanderung ist damit erledigt."

Jeannel (1942, 1946) tries to use paussid distribution as evidence for continental drift. He assumes that paussids originated early in the Mesozoic, and he assumes a direct relationship between one South American and one African genus, and cites this in favor of a Mesozoic union of part of South America with Africa. But paussids probably did not come into existence until almost the end of the Mesozoic, and it is only a guess, and I think a wrong guess, that there is a direct relationship between the South American and African forms. Moreover, although the group of paussids in question (the subtribe Cerapterina) does not now occur north of the tropics, it is well represented in the Baltic amber and therefore occurred in northern Europe at least as late as the late Eocene, and may conceivably have dispersed by northern routes.

For several reasons given in detail elsewhere (Darlington, 1950, pp. 86–88), including the primitive nature of all the paussids in the Baltic amber, the dependence of paussids on ants (which are unknown before the Tertiary), the distribution of the paussids themselves, and the pattern of their evolution, I think that paussids probably did not originate until very late in the Cretaceous and that the greater part of their evolution occurred within the Tertiary. As to their dispersal, I think (1950, p. 113) that they probably originated and evolved chiefly in the great land areas of the Old World tropics; that the first important subtribe, the primitive Cerapterina, spread from there over most of the rest of the world except Madagascar, reaching South America (by whatever route) about the beginning of the Tertiary, and later leaving fossils in the Baltic amber; that the cerapterines later withdrew from northern areas into their present discontinuous but nearly tropicopolitan range; and that the derivative paussids arose in the Old World tropics in the middle or late Tertiary, became more numerous than the primitive forms in the main tropical regions of the Old World, and spread over as much of the rest of the world as was then suitable and as they could reach, but that they were too late to reach America or even the continent of Australia. All this will be best understood if the map (fig. 26) is referred to. The reasons for my conclusions are given at length in the paper cited above.

What I want to emphasize is not that Kolbe and Jeannel were wrong in attempting to explain the presence of paussids in South America by means of a southern land bridge or drifting continents. The point is the amount of work that has been necessary to uncover what seem to be more likely probabilities in the history of this one small group of invertebrates. Even now, supposing that my conclusions are correct, the paussids tell us almost nothing about the history of South America. It is the other way around. The known history of South America, particularly its isolation during most of the Tertiary, tells us something about the probable time of arrival of the paussids, and if we knew the history of South America in more detail, we could probably fit paussid history to it in more detail. But the paussids do not tell us much about South America. So far as I can determine, the South American paussids are not directly related to any other living ones. Existing genera of Cerapterina on different continents seem in general not to be directly related to one another but to be scattered survivors of a formerly larger and more diverse group (Darlington, 1950, p. 95). The South American paussids have no close relationships to suggest the direction from which they have come, and they tell us nothing precise about their time of arrival. So far as the evidence of the South American paussids themselves goes, they might have reached the continent by any route that was open to winged land animals, and they might have come at any time at least from the late Cretaceous to well into the Tertiary.

To return to a more general view of living

invertebrates and Mesozoic South America, I repeat that it is a fact beyond argument that some living South American invertebrates are related to tropical African forms or to south temperate Australian or South African forms. But these relationships involve only parts of the South American fauna; the relationships are often general rather than direct; and they can often be explained in several different ways. Each separate case should be carefully studied, and conclusions should be reached with caution. This common-sense rule of procedure seems so obvious that it is hard to understand why zoogeographers so often ignore it. My present conclusions are that living invertebrates tell us very little about South America in the Mesozoic, or rather that they give us little or no first-line evidence about it. The ancient history of South America must be worked out (has been worked out in part) by study of geology and of fossils, especially vertebrate fossils. However, once the main history is known, invertebrates, even living ones, may be useful in the working out of details.

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THE BIOGEOGRAPHY OF TERMITES

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THE HISTORICAL FACTORS that have influenced present distributions of plants and animals are difficult to determine without direct knowledge of former distributions as evidenced by authentic fossils. However, when one examines the existing geographical and ecological patterns in relation to the phylogenetic sequences, it is possible to detect correlations. These give some indication of the time, place, and ecological conditions associated with the origin of many existing genera and other taxonomic groups.

Natural controls over certain factors of dispersal occur among termites. These social insects are relatively sedentary except during the colonizing flight. There is little variation in flight adaptation throughout the order which consists of about 1800 species grouped into about 150 genera and five families (Snyder, 1949). All are weak fliers, and all mate after the colonizing flight, so that a female accidentally carried by the wind for a hundred miles would have to attract a male landing close to her after the flight in order to establish a colony successfully. Such double accidents are very unlikely, and present distributions indicate that water gaps more than 50 miles wide are effective barriers to termite dispersal. The great majority of termites are distributed over water solely by means of flight, but a few genera may be dispersed by floating logs or by human transport.

In addition to the limitation of vagility, termites have not adaptively radiated into widely different climatic and food niches. They are largely tropical insects. A few genera occur in warm temperate regions, and only four genera are confined to temperate regions (Emerson, 1936): *Archotermopsis* (one species), *Hodotermopsis* (two species), *Zootermopsis* (three species), and *Reticulitermes* (13 species). Their food is primarily cellulose and may be eaten in the form of dead wood or dead leaves of plants. A few genera live primarily in dry habitats, but the large majority are found only under relatively moist conditions of forests and grasslands. They reach their greatest abundance of individuals and species in the rain forests of the tropics. The microclimate of individual termites is highly humid. The higher termites (Termitidae) live in a socially controlled humidity close to 100 per cent saturation, and even the "dry wood termites" (Kalotermitidae) probably live under fairly humid conditions within their excavations in wood. The social life enables these insects to control and stabilize the conditions of their existence (social homeostasis) which they do by defending their colonies by means of the specialized soldier caste, by constructing nests and sealed passageways, and sometimes by storing or growing their food supply. Construction and feeding activities are primarily the result of the caenogenetic evolution of the behavior of nymphs and workers.

The unique combination of factors influencing the distribution and evolution of termites may be expected to result in geographic patterns somewhat different from all other types of organisms. At the same time, some of the same factors undoubtedly have affected some other organisms in a similar manner, so that comparative studies of both similarities and differences of the causes of geographic distribution are possible. Some of the theory and conclusions based upon termite studies were initially suggested from studies of paleontology and biogeography of other organisms, particularly mammals.

The few existing species of the primitive termite families Mastotermitidae and Hodotermitidae show every indication of being relicts of groups formerly more widely distributed. One hodotermitid genus, *Porotermes*, contains three living species. One species

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is found in Australia, one in South Africa, and one in Chile (Emerson, 1942, 1947). From consideration of the obvious primitive morphology of these termites, comparison of their distribution with other termites, and the peculiar discontinuous occurrence at the southern tips of what may be called the continental peninsulas of the northern world mass, a theory may be tentatively set forth that *Porotermes* was distributed in the north in early Mesozoic times, and that the present species are relicts of a group that has become extinct over most of its ancient range.

The Kalotermitidae ("dry wood termites") consist of a number of genera living without necessary soil connections and utilizing metabolic water to some extent. They are primitive in their social life and also in their morphology, but on the whole represent an evolutionary advance over the Mastotermitidae or Hodotermitidae. The most primitive living genus is *Kalotermes* (probably soon to be divided into several related genera). The species are found in the Neotropical region (14), Nearctic region (seven), Indo-Malaya (seven), Australia and Tasmania (10), Papuan region including the South Sea islands (four named species and one new species), New Zealand (one), Ethiopian and Malagasy region (13 named species and five new species), and Palearctic region (six). Although a fairly successful group under present conditions, *Kalotermes* shows indications of becoming extinct in areas of high competition in the central continental regions of the tropics. It survives only on islands and continental edges in the tropics and occurs only in the warmer parts of temperate regions where it may be found in central continental areas (Allee *et al.*, 1949, p. 660). The even distribution of numbers of species probably indicates a very ancient origin (possibly mid-Mesozoic), but does not give us data on the place of origin.

Derived genera such as *Cryptotermes*, *Neotermes*, and *Glyptotermes* show a similar world-wide occurrence, but are somewhat more successful genera in central tropical continental regions (Allee *et al.*, 1949, p. 661).

Cryptotermes is a genus derived from a *Kalotermes*-like stock. It is capable of living under dry conditions in a piece of wood, and its soldiers have a phragmotic head adapted to defensive plugging of the passageways. The species are easily transported by man in wood and have often been introduced into foreign continents and islands. The distribution of native species is Neotropical (five), Nearctic (one), Indo-Malayan (five), Australian (three, including a new species), Papuan and South Seas (two), Ethiopian (four), and Malagasy (two, including a new species). The genus is primarily tropical, and no region has a comparatively large number of species. Like *Kalotermes*, *Cryptotermes* is largely confined to continental edges. Up to date there is only a single record of the natural occurrence of a species in the interior of a continent (Ituri Forest of the Belgian Congo).

Neotermes is separately descended from *Kalotermes* and differs adaptively from its ancestors by its limitation to damper wood. Occasionally it invades living plants. It is found in continental interiors far more often than either *Kalotermes* or *Cryptotermes*. The distribution of species is: Neotropical (13, including two new species), Indo-Malayan (22), Australia (one), Papuan and South Seas (19, including four new species), Ethiopian (14, including one new species), Malagasy (seven, including a new species), and Palearctic (one). Like *Cryptotermes*, *Neotermes* is largely tropical, but may invade warm temperate regions. Its distribution pattern in the South Sea islands indicates that it may occasionally be transported in floating logs or by man. Possibly the large number of species in Indo-Malaya is indicative of the place of origin, but with errors in taxonomy and insufficient collecting it is still too early to hazard a guess. The tropicopolitan distribution indicates an origin in Mesozoic times.

Glyptotermes is descended from *Kalotermes* possibly from near the base of the *Neotermes* branch. *Glyptotermes* possesses a soldier with a phragmotic head adapted to the defensive plugging of small passageways in the wood. This adaptation is convergent to the more specialized head of *Cryptotermes* soldiers. The genus can live in drier wood than *Neotermes*, but not in as dry wood as *Crypto-*

termes. The distribution of species of *Glyptotermes* is: Neotropical (23, including two new species), Indo-Malayan (13), Australian (five), Papuan and South Seas (four, including one new species), Ethiopian (seven, including five new species), and Malagasy (one). The genus does not invade northern temperate regions bordering the tropics, and it is not so easily transported by man as is *Cryptotermes*. The relative number of species indicates possible origin in either the Neotropical or Indo-Malayan region. Its wide distribution indicates an origin in Mesozoic times.

Calcaritermes is directly derived from *Glyptotermes* and is closely related in both its morphology and ecology. With the exception of a single species in north and central Florida, this genus is wholly Neotropical, with the center of dispersal in Central America. Eleven species are known, including two new species awaiting description. With the exception of one new species from the vicinity of Rio de Janeiro, all the records are from northern South America and Central America. Because of its limited distribution, it may be postulated that the genus arose in the New World, probably in Central America, during Tertiary times.

We may thus detect gradations in the present successful survival of the genera of the Kalotermitidae, and these gradations are often correlated with the phylogenetic position of the group.

The Rhinotermitidae consist of several genera showing more of a tendency for recent continental endemism than the three families already discussed. *Coptotermes* is tropicopolitan and is similar in its broad distribution to the primitive genera of the Kalotermitidae, but, in contrast, it is abundant and successful in central tropical continental regions. Introductions by man become successfully established in man-modified environments and produce much economic destruction. *Heterotermes* is tropicopolitan except for Africa where its relative, *Psammotermes*, seems to occupy the same ecological niche in arid regions. *Prorhinotermes* is primarily confined to islands and is absent on all continents except on the coast of Central America and southern Florida (Allee *et al.*, 1949, p. 725). It is found in the West Indies, Pacific islands, East Indies, and islands of the Indian Ocean including Madagascar. Contrary to most groups of termites, this genus seems to be distributed in floating logs. It survives on islands where competition is weak, but is eliminated on the continents where these termites must often be washed ashore. The center of dispersal seems to be the islands of the Pacific, including the East Indies, and the genus probably reached the West Indies at the time of sea connections through Panama during Tertiary times.

A group of closely related genera of the Rhinotermitidae shows a directional evolutionary trend from monomorphic soldiers to dimorphic soldiers, and an increasing specialization of the minor soldier towards reduced mandibles and prolongation of the labrum for the dispersal of a repellent volatile fluid. The most primitive genus of this sequence is *Parrhinotermes* (five species), with monomorphic soldiers. It is found in Queensland, the East Indies, and Malaya. The next most primitive genus is *Schedorhinotermes*, with dimorphic soldiers including a mandibulate minor soldier. It is found in Australia, the western Pacific islands including New Guinea, the Indo-Malayan region, and Africa. The larger number of species centers in the Indo-Malayan region (17 species), and only three are found in Africa. The hypothesis seems tenable that the genus arose in Mesozoic times in the region of the East Indies, spread to Australia, New Guinea, and the Solomons in Cretaceous times, and spread to tropical Africa in Tertiary times. The fact that the genus is absent from Madagascar indicates that it had not reached Africa by the early Tertiary.

Two derived genera, *Rhinotermes* and *Dolichorhinotermes*, have dimorphic soldiers with reduced mandibles in the minor soldier (Snyder, 1949). These genera have four species each, and both are confined to the Neotropical region. It may be postulated that these genera originated from an Indo-Malayan *Schedorhinotermes*-like base in Cretaceous times, passed to the New World over the Bering land bridge under tropical conditions in pre-Tertiary times, and differentiated further in the New World. Because

of the phylogeny and distribution, we may assume that the direction of dispersal was eastward over the Bering connection with a tropical climate. In Tertiary times, another derived genus with a monomorphic soldier of the minor soldier type probably originated in South America. This latter genus with one species is *Acorhinotermes*, so far known only from British Guiana.

From a consideration of the distribution and limitations of dispersal correlated with the clear phylogenetic stages and direction of evolution, one may find some indications of place of origin, time of origin, and direction of ancient dispersion.

The highest termites belonging to the family Termitidae are obviously the most successful living termites. They are most abundant in numbers of individuals and numbers of species in the grasslands and forests of the lowland tropics. They decrease in proportion to other families of termites in temperate zones, in deserts, and at high altitudes. The family contains about three-fourths of the known species of termites. Their social life is by far the most advanced within this order of social insects.

Certain principles of distribution are well illustrated by the subfamily Nasutitermitinae. This subfamily is characterized by the well-adapted nasute soldier among the specialized genera. This soldier has reduced, functionless mandibles, and the front of the head is prolonged into a "nasus" or snout, with the opening from a gland at the end enabling the forceful ejection of an irritating and repellent sticky fluid. The primitive genera of this subfamily have soldiers with functional biting mandibles and proportionately small glandular projections. Gradations occur in the reduction of the mandibles and the enlargement of the gland projection in various primitive genera, and it is also clear from the morphology of the imago mandibles that the nasute soldier is diphyletic and represents a convergent evolution towards this type of defensive adaptation (Allee *et al.*, 1949, p. 727).

The most primitive genus of the Nasutitermitinae is *Syntermes*, composed of 20 species entirely confined to the grasslands and forests of tropical South America (Emerson, 1945). A rough phylogenetic sequence of genera with mandibulate soldiers indicates an evolution from a *Syntermes*-like base towards the genus *Nasutitermes* with a nasute soldier. These genera with mandibulate soldiers are *Procornitermes* (six species, including two new species, all found south of the Amazon in South America), *Cornitermes* (15 species, including seven new species in tropical South America north to Costa Rica), and *Rhynchotermes* (two species, one in southern tropical South America and the other in Central America).

Nineteen genera with nasute soldiers have arisen from this stock of Neotropical genera with mandibulate soldiers. The phylogenetic relationships between these 19 genera are somewhat obscure, but there is little doubt that all have come from the *Syntermes-Rhynchotermes* branch. *Nasutitermes* is a tropicopolitan genus and contains the largest number of species of any genus of termites. Altogether there are 195 named species distributed over the tropical world—Neotropical (68), Indo-Malayan (61), Ethiopian (28), Malagasy (eight), Australian (17), and Papuan (13). It seems consistent with the facts to postulate that *Nasutitermes* arose from the primitive Neotropical genera of Nasutitermitinae with mandibulate soldiers, and that the largest number of existing species are still found at the center of the origin of the genus. Being essentially tropical in its adjustment, it probably moved to the Indo-Malayan region at the time when a tropical climate prevailed in the latitude of the Bering land bridge. There is some evidence from plant fossils that such a climate occurred this far north in Cretaceous times, but not during the Tertiary or Quaternary, so it is presumed that the dispersal of nasute termites westward occurred in late Mesozoic times. This theory is further corroborated by the occurrence of many species of the genus in the Australian region and in the Papuan region as far east as the Fiji Islands. The genus probably moved into tropical Africa at least by early Tertiary times or in the late Mesozoic, as is evidenced by its occurrence in Madagascar and neighboring islands of the Indian Ocean.

With this genus of termites were dispersed

many termitophilous staphylinid beetles that are host specific. Dr. Charles Seevers is engaged in making a phylogenetic study of these beetles. The indications are that the postulated direction and time of dispersal are corroborated by the phylogeny and dispersal of the beetles. It should be pointed out that this is an instance of the evolution of an interspecies relationship that is ecologically stable through long periods of geological time. Such cases may be used as a basis for the study of the evolution of unitary ecological systems.

Following the tropicopolitan dispersion of the basic stock of nasute termites, many genera arose that indicate an origin in late Cretaceous or early Tertiary, and others that possibly arose in mid-Tertiary times.

Several genera are endemic in the Neotropical region. These, together with their respective numbers of species, are *Rotunditermes* (one), *Diversitermes* (five), *Velocitermes* (five), *Tenuirostritermes* (four), *Parvitermes* (six), *Obtusitermes* (two), and *Constrictotermes* (three). *Tenuirostritermes* is known from four species in Central America and southwestern United States. Several new species await description, including one from Venezuela. It may be postulated that this genus arose in Central America following the early Tertiary isolation of South America. The lone new species from Venezuela may be explained as a southern dispersion from Central America at the time of the Pliocene connection with North America. *Constrictotermes* shows relationships with the slightly more primitive Indo-Malayan genera *Grallatotermes* and *Lacessititermes*. It is possible that *Constrictotermes* came from a nasute stock that underwent specialization in the tropical orient in late Cretaceous times and subsequently reinvaded the New World after the early Cretaceous dispersion of the basic nasute termites. However, the evidence for such an hypothesis is very meager at present. The other Neotropical genera of nasutes could have arisen from primitive nasutes in Cretaceous or Tertiary times, with the indications pointing to a Tertiary origin. If a genus is South American and does not extend farther north than Costa Rica, it may be postulated that it originated in South America after the early Eocene isolation from North America. If the genus is distributed in South America south of the Amazon and in tropical Central America, the origin may be prior to the Eocene isolation of South America.

Six genera of nasute termites on the *Nasutitermes* branch are endemic in the Indo-Malayan region. These, together with the numbers of species now known, are *Hirtitermes* (three), *Longipeditermes* (one), *Havilanditermes* (one), *Ceylonitermes* (one), *Bulbitermes* (17), and *Lacessititermes* (15). It may be suggested that these genera originated from the basic nasute stock reaching Asia from the New World in Cretaceous times. Differentiation in the Indo-Malayan region may have occurred in late Cretaceous or Tertiary times. Two genera, *Grallatotermes* (six) and *Hospitalitermes* (21), seem to be primarily Indo-Malayan, but two species of *Grallatotermes* and two species of *Hospitalitermes* (Ahmad, 1947) are known from the Papuan region and not from Australia. Possibly these Papuan species were "island hoppers" during the late Tertiary or Pleistocene, but very few termites have been dispersed in this manner. One new species of *Grallatotermes* on the east coast of Africa on Mafia Island and in Portuguese East Africa extends the range of the genus to the Ethiopian region.

One genus, *Tumulitermes*, differentiated from the *Nasutitermes* stock in Australia and is confined to this continent.

One genus, *Trinervitermes*, is a grassland group of harvesting termites with dimorphic nasute soldiers. It contains 54 species in the Ethiopian region and six in the Indo-Malayan region, particularly in India proper. Because of the ecological restriction, it may be assumed that *Trinervitermes* arose in Africa during the Miocene establishment of tropical savannas and that a few species were able to reach India from this African group during a Miocene or Pliocene connection of tropical grassland. The fact that this common African genus did not reach Madagascar indicates an origin later than early Tertiary.

One genus, *Coarctotermes*, has 11 species in tropical Africa, including five new species, and four species in Madagascar, including one new species. This distribution is indica-

tive of the origin in Africa during late Cretaceous or early Tertiary times. The reason for the failure of this genus to reach India is obscure.

Turning back to the other branch of the Nasutitermitinae, we again find several genera with mandibulate soldiers that indicate stages in the evolution of the nasute soldier (Allee *et al.*, 1949, p. 727). All of these genera with mandibulate soldiers are confined to the Neotropical region. The list with the number of species known in each genus contains *Paracornitermes* (two) from southern Brazil, *Labiotermes* (five species, including three new species) from both northern and southern tropical South America, *Armitermes* (15) from northern Argentina to Spanish Honduras, and *Curvitermes* (four species, including two new species) from Mato Grosso, Brazil, to British Guiana. There would seem to be no doubt that these primitive genera with mandibulate soldiers form a second branch from the *Syntermes-Procornitermes* stock in South America. The evidence of phylogeny and distribution indicates that both branches of the Nasutitermitinae originated in South America in Mesozoic times.

Several nasute genera have developed from this second branch. *Angularitermes* (one) is known only from northern South America. *Mimeutermes* (two) is known from Guinea and the Gold Coast in Africa. A new genus with one species awaits description from the Belgian Congo rain forest. *Subulitermes* (soon to be divided into several related genera) is known from 22 species, including 11 Neotropical, six Indo-Malayan, one Papuan, and four Australian. *Convexitermes* is a close relative of *Subulitermes* and is known from nine species from tropical South America and Panama. *Occasitermes* is known from one species confined to Australia. Two new genera closely related to *Subulitermes* with one species each from the Belgian Congo await description. *Eutermellus* (two named species and one new species) is known only from the west coast of Africa. And finally another new genus with a single species from the Belgian Congo showing relationship to this series of genera awaits description.

In both branches of the Nasutitermitinae we see the primitive genera with mandibulate soldiers confined to the Neotropical region. One genus (or more) of nasute soldiers in each branch moved west from South America (where the largest number of species are still found) over the Bering land bridge under tropical conditions, presumably in the Cretaceous. Species of each of these dispersing genera now exist in the Indo-Malayan region and in Australia, and also either the same genus or closely related genera reached tropical Africa. No species of the *Subulitermes* branch has yet been reported from Madagascar, but this may be due to incomplete collections or it may mean that the ancestors of these genera did not reach Africa until after the separation of the Malagasy fauna. In both branches, numerous genera of nasute termites are endemic in various regions, including the Australian, Ethiopian, and Neotropical.

No known geographical or physical ecological barrier prevented the genera with mandibulate soldiers from moving to other continents at the same time that some of the nasute genera dispersed, and the mandibulate genera or their immediate ancestors surely existed at the time of this world dispersal of nasute genera in Mesozoic times. Therefore it is postulated that a biotic barrier prevented this dispersal of primitive genera. The most obvious adaptive difference between the mandibulate soldiers and the nasute soldiers is the augmentation of the "squirt gun" apparatus for ejecting a defensive fluid. Experiments using ants as predators give some indication of a greater defensive effectiveness of the nasute soldier compared to related mandibulate soldiers. It seems reasonable, therefore, to postulate that the genera possessing nasute soldiers could push through barriers of predators (biotic barriers) that prevented the dispersal of the genera of Nasutitermitinae with mandibulate soldiers. Once the nasute genera had become established in other tropical continental areas, they evolved numerous endemic genera adjusted to local conditions during the Tertiary periods when geographical and climatic conditions prevented dispersal to other continents.

Predator pressures, of course, are not the only biotic barriers to termite distribution.

About 15 cases of introduction by man to various parts of the world indicate that successful establishment is often possible in climatic areas similar to the native environment, but that these foreign termites remain confined to man-modified habitats on continents. Natural biotic habitats are seldom invaded except in the simpler communities of islands. Complex natural communities of great continental areas exclude those species that have not evolved in close association with the community in question. Little is known concerning the details of the factors involved, but it seems reasonable to guess that competition between ecological equivalents may be the biotic barriers, and ecological equivalents may often be closely related species or congeners (Allee *et al.*, 1949).

The geographical patterns here correlated with phylogeny, historical ecology, and ancient highways of dispersal are repeated in many other cases of termite distribution too numerous to be given in detail in this brief summary. The additional cases illustrating each major conclusion, however, add credence to the hypotheses stated. At the same time, the theoretical discussion is based upon our understanding of termite phylogeny through the study of the morphology of existing termites, with only slight supplemental evidence from a few temperate Tertiary fossils. The verification of many of the postulates must await the discovery of fossils from the Mesozoic strata of the major continental masses, and it now seems unlikely that many such fossil termites will ever be found. So our conclusions must rest upon circumstantial evidence, with many gaps, and consequently will probably remain tentative for a long time.

In spite of the tentative nature of the theories, they may be used for suggesting relationships and correlations into which much further information can be fitted or inconsistencies noted. With further information on variations in vagility, ecological adaptations, and geological origins, a comparison can be made between termite distribution and the biogeography of other organisms, both plant and animal. Comparative biogeography should give us a reasonable understanding of the intricate events determining patterns of distribution.

Some of the suggested tentative conclusions that are capable of verification or refutation by accumulating data may be listed as follows:

1. It is unnecessary to postulate any great change in continental masses and their connections since early Mesozoic times.
2. All five families of termites now living were in existence and were dispersed over the great land masses by late Mesozoic times.
3. Patterns of distribution of living forms indicate the origins of extant subfamilies and included genera of termites at various times in both the Mesozoic and Tertiary periods.
4. Faunal connections of Australia and Indo-Malaya are postulated for Cretaceous times, and these have been severed for termites since that time.
5. Faunal connections between South America and other continents including Australia were present over a Bering land bridge with a tropical climate during Mesozoic times. Faunal connections between the Old and New Worlds have not occurred during Tertiary times for those termites confined to tropical terrestrial habitats.
6. During the Mesozoic, dispersion of termites originating in the Old World introduced elements into the South American fauna, and dispersion of termites originating in South America introduced elements into Australia, Indo-Malaya, and Africa.
7. Certain genera (or their close relatives) that were in existence in Mesozoic times were unable to move over land connections under favorable physical conditions because of biotic barriers to their dispersal, while other genera that had evolved special defensive adjustments were able to pass through these biotic barriers.
8. In order to explain present distributions of termite genera, it is necessary to invoke three major factoral complexes in their historical settings. a. Close land approximations or connections existed between South America and North America over the Isthmus of Panama prior to early Eocene times and again since the late Pliocene; between North America and Asia over the Bering Strait

under tropical conditions at various times during the Mesozoic, but not during Tertiary or Quaternary times; between Indo-Malaya and Australia in Cretaceous times but not later; between tropical Asia and Africa under comparatively moist conditions in Pliocene times or earlier; and between Africa and Madagascar in late Cretaceous or early Tertiary times, but not during post-Eocene times. b. Warm temperate climates in some cases and tropical climates in other cases existed at the times of the land contiguities or connections. c. Favorable biotic conditions, including food, defense against predators, and lack of competition between close ecological equivalents, accompanied dispersal. The biotic conditions are about equal in importance to land connections and climates in the explanation of modern distributional patterns.

9. Because of the uniformity in their terrestrial adjustment, in their dependence upon a humid microclimate, in their powers of flight (weak), in the necessity for males and females to attract each other after the colonizing flight, in the food (cellulose of wood or leaves), in the social control over fluctuating conditions in their habitat, and in their limitations to warm or tropical temperatures, termites are less likely to present complexities and variations in their ability to disperse than do many other organisms. A few genera may be dispersed in floating logs, but the large majority are dispersed only by land or over narrow water gaps. Accidental or chance dispersals during Mesozoic, Tertiary, or Quaternary times seem to be extremely rare.

10. Because of the Mesozoic origin of a large number of existing genera, the present patterns of distribution differ strikingly from other genera of termites and from other organisms with a Tertiary origin.

11. Although there is no reason to suppose that termites are not continuing to speciate and to evolve further adaptations, there is circumstantial evidence that some highly specialized types (i.e., those with nasute soldiers or with snapping mandibles) had become established by late Mesozoic times. Many Mesozoic genera are persistent and successful at the present time (Emerson, 1950, 1951). A large number of existing genera seem to show very slow or bradytelic evolution.

12. Percentages of endemic genera and species of termites in the fauna of a region compared to the percentages of shared subfamilies, genera, and species between two faunas give an indication of the relative geological times of isolation of the faunas. For example, such data can be construed to mean that the Australian termite fauna became isolated from that of Indo-Malaya before the separation of the Indo-Malayan and Neotropical faunas. These events were followed in chronological order by the faunal separations of Madagascar from Africa, of tropical Africa from Indo-Malaya, of Ceylon from India, of Java from the Malay Peninsula, of Borneo from the Malay Peninsula, and of Sumatra from the Malay Peninsula. Studies of percentages of endemic and shared groups combined with phylogenetic sequences indicate that the Neotropical termite fauna is closer to that of Indo-Malaya than to any other major faunal region (Emerson, 1928), and that the relations of the Neotropical and Ethiopian faunas are through the Indo-Malayan region and not by any dispersion over an Atlantic connection.

13. The highest number of species in a large successful genus with marked faunal differences in numbers indicates the region of origin of the termite genus.

14. Patterns of distribution indicate (a) relative competitive success or failure, (b) place of origin, (c) time of origin, (d) ancient land connections or contiguities, (e) ancient climatic conditions and changes, and (f) different histories of associated species in the same ecological community.

15. There are many exceptions to the "Age and Area" concept (Willis, 1922). Older groups have the widest dispersal, all other factors being equal, but all other factors are seldom equal.

16. The emphasis given by Matthew (1915) upon northern dispersal is substantiated by the distribution of termites. However, there is no indication that termites that originate in north temperate regions have any superiority in adaptive evolution. In fact, the adaptive evolution of tropical groups of termites has progressed in general much

further than that of temperate groups.

17. Special cases may be exceptions to these broad and simple statements, but these general conclusions are indicative of some important aspects of ancient geography and ecology. A more complete knowledge of all the factors of biogeography will probably show many complexities not emphasized in these over-simplifications, but nevertheless these incomplete generalizations contain much truth.

18. Increased information and understanding of the paleontology, phylogeny, taxonomy, distribution, and ecology of plants and animals, and a comparison between groups in relation to geological and geographical barriers and means of dispersal should enable scientific investigators to find convincing answers to many problems of biogeography that are now unknown or obscure. It is not surprising that our ignorance is vast. It is surprising that the data already gathered are enabling us to detect order and to piece together bits of evidence left by events that occurred many millions of years ago.

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THE EVIDENCE OF THE FRESH-WATER FISHES

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INTRODUCTION

THE TERM "FRESH-WATER FISHES" cannot be defined on the basis of a simple, unqualified statement. For this reason, the Recent fresh-water fishes have been divided by Norman (1931) and Myers (1938, 1949) into two major categories: (a) a primary division consisting of fishes physiologically restricted to fresh water throughout their life cycle, and (b) a secondary division including fishes that may spend some part of the life cycle in a marine environment.

With some exceptions, the Recent fresh-water fishes can readily be placed in one or the other of these major divisions. Available evidence also indicates that the Tertiary fresh-water fishes can be arranged in the same manner. This is, of course, not unexpected, as there are relatively few families represented in the Tertiary that do not have modern representatives, and apparently a number of typically fresh-water genera have persisted from the Eocene to the present.

The fresh-water fishes of the Mesozoic are, on the whole, poorly known, and, with the exception of certain Triassic formations, there are no continental deposits that have yielded a reasonably representative fish fauna. Because of this lack of basic data, it is difficult to divide the known Mesozoic fresh-water forms between the above categories or, for that matter, to determine when in the Mesozoic the various groups of fresh-water teleost fishes, already well established at the beginning of the Cenozoic, originated.

During the Mesozoic there was an important alteration in the complexion of the known fish faunas, reflecting profound evolutionary change in all the major groups of fishes. By Permian time the dominant marine groups of the Paleozoic were almost eliminated. In fresh waters, the rhipidistian crossopterygians (which gave rise to the tetrapods) were about gone, although the coelacanths and dipnoans persisted, and the most primitive group of ray-finned fishes, the palaeoniscoids, were dominant. During the Triassic, the coelacanths apparently developed a marine tendency as did many of the ray-fins. Fresh-water ray-fins were still abundant, however, and were represented mainly by a somewhat higher level of organization, designated the subholostean. The Jurassic is unfortunately almost a complete blank in regard to fresh-water fishes, except for the dipnoans, although Jurassic marine formations are replete with sharks, holosteans (a still more advanced level in ray-fin evolution), and the first of the true teleosts. The same uninformative picture holds for the Cretaceous, with the teleosts forming the dominant marine group. Continental Cretaceous deposits occasionally yield fish remains, but they offer little evidence on the evolution and dispersal of the fresh-water types then existing.

In spite of this rather unpromising situation, some pertinent conclusions may be drawn, particularly bearing on the dispersal of fresh-water faunas at the beginning of the Mesozoic. Fishes found only in continental deposits are here regarded as being restricted to fresh water unless there is direct evidence to the contrary. This is admittedly a rather weak assumption, but there appears to be no logical alternative. Although this discussion is primarily concerned with a consideration of Mesozoic fresh-water fishes from South America and of their affinities with fishes of similar age in Africa, a brief consideration of the pertinent Permian and Cenozoic fishes is included in order to present a more complete picture of the changes in the Neotropical fresh-water fish assemblage.

DISPERSAL FACILITIES OF PRIMARY DIVISION FRESH-WATER FISHES

The problem of fresh-water fish dispersal in relation to migration from one continental mass to another or across a continent involves mainly a consideration of the fishes in the primary division. Fishes that are able to enter salt water voluntarily are obviously in a position to migrate from one river mouth to another through coastal waters and thus extend their range.

The stage or stages in the life cycle of the various primary fresh-water fishes at which dispersal may be accomplished will vary, to a greater or lesser extent, according to the breeding habits and behavior patterns of the adults and the structural variations of the eggs, larvae, and adults. In general, however, the eggs are large and heavy compared with those of marine fishes and sink to the bottom (demersal) upon extrusion. They are covered, in many cases, with an adhesive substance which holds them to some submerged object. The larvae of both oviparous and viviparous types are normally capable of only very localized movement associated with obtaining food. It is evident, therefore, that the eggs and larvae of fresh-water fishes have no effective dispersal facilities available to them unless supplied by some external agent such as current action. As various mechanisms are employed in these stages to prevent such transportation, it normally does not occur except possibly in time of flood. Furthermore, most larval fishes are probably unable to survive under flood conditions.

Ichthyologists have long been aware that primary fresh-water fishes, even in the fully adult stage, do not travel long distances. There is usually some change of location during the breeding period, but it may be a very short distance into quiet water and, at best, rarely more than a few miles. Furthermore, there is a rather well-defined ecologic zoning of the fish fauna within a particular drainage system (Hesse, Allee, and Schmidt, 1937). Fishes occurring at or near a river mouth do not move upstream where the current is swifter, the water cooler, and the food different; likewise, fishes existing in the headwaters or in a lake on the same drainage are prone to remain in their respective habitats. As many as five such zones have been recognized for some drainage systems. Although the extent, order, and composition of these zones may vary considerably, depending largely on the maturity of the drainage system, they are consistently present and must be considered in connection with the dispersal problem. Within broad limits, the fishes inhabiting a particular zone have a characteristic body form[1] and fin form. That similar ecologic zoning existed in the past history of fresh-water fishes will probably never be adequately demonstrated, although observed differences in body form among contemporaneous fishes as far back as the Paleozoic make it a reasonable inference.

The dispersal of fresh-water fishes over a large continental area and across a land bridge from one continent to another has long been a puzzling problem. The rate of dispersal must be exceedingly slow compared with that of mammals, reptiles, or even amphibians. Since the reestablishment of the Panamanian bridge near the end of the Pliocene, a few primary division representatives of the South American fresh-water fauna (characins) have migrated northward, and one species (*Astyanax mexicanus*) has reached Texas and Mexico, presumably the limit of its temperature tolerance. This northward dispersal, involving a land bridge, may have required the greater part of a million years, which is, incidentally, the maximum time interval available.

The physical basis for the dispersal of most fresh-water fishes is undoubtedly intimately related to the slowly but constantly changing physiography of the land surface. Any change that brings about even a brief union of parts of adjacent drainage systems may permit further migration of new faunal elements. It is usually not possible to follow the history of drainage systems through millions of years or to determine exactly by what routes fresh-water fishes were distributed over a continent during a particular geologic time interval. It is possible, however, to

[1] Some differences in body form are apparently nongenetic, indicating that subadults transported from other zones may assume the body form of an entirely different zone.

visualize the probable major factors that have permitted this dispersal.

Throughout geologic time most parts of the various continents have been subjected to periods of elevation, depression, abundant rainfall, aridity, and changes in temperature. These events have without question had a profound effect on the interior drainage systems—creating new ones, connecting or subdividing established ones, or eliminating them entirely. In spite of the fact that fresh-water fishes (in the broad sense) have probably been more or less restricted to particular ecologic zones within a drainage system since their appearance in the early Paleozoic and that dispersal dependent on geologic change would be slow and haphazard, no other basic explanation seems possible, without involving the morphology or physiology of the fishes themselves, to explain the dispersal that is known to have occurred in the past.

The specific circumstances that may permit or explain the dispersal of fresh-water fishes across suitable land bridges or within the limits of a single continent might be listed as follows:

1. Otherwise separate drainages united at their sources or elsewhere along their courses by an interconnecting swampy area.

2. Interception of one drainage system by another through stream capture. The interception may occur anywhere along the course of the captured stream by the headwater erosion of the captor, or by a meander of the captor impinging against some section of the captured.

3. Tongues of fresh water discharged into the sea by large rivers (e.g., Amazon) and deflected along the coast by off-shore currents as far as the mouths of other rivers.

4. Previous connection of now isolated coastal drainage systems which were formerly tributaries of a much larger single river system that existed prior to the submergence of an extensive land mass, e.g., connection of Great Britain with Europe in the Pleistocene.

5. Transportation of post-larval fishes by cyclonic storms, by birds, or other sweepstakes methods is not probable, but is statistically possible over long periods of time.

6. Favorable climatic change, particularly affecting the dispersal of tropical or semi-tropical fresh-water fishes by any of the above means.

7. Finally, the possibility that certain groups of primary division fishes have had salt-water-tolerant representatives in the past cannot be lightly dismissed. There is actually no positive evidence for or against this assumption, and practically nothing is known about the habits of most pre-Tertiary fishes.

GEOLOGICAL SETTING

Rather extensive continental deposits are known to occur in South America for the Permian, Triassic, late Cretaceous, and all of the Tertiary except the Eocene and Oligocene (see Weeks, 1947). Fishes from these deposits are, however, exceedingly rare, and, with the exception of a reasonably adequate representation from the middle and late Triassic, satisfactory faunas are unknown. The same situation, in general, exists for Africa.

The Permo-Carboniferous Itararé and the Lower Permian Irati beds of Brazil (Oliveira and Leonardos, 1943), and Upper Permian beds in Mendoza, Argentina (Rusconi, 1949a, 1949b), have produced the only known late Paleozoic fishes in South America. In Africa they occur sporadically throughout the Permian sequence, in the Dwyka, Ecca, and Lower Beaufort (Du Toit, 1939).

The Middle and Upper Triassic beds of Mendoza and San Juan, Argentina, have yielded relatively large faunas (Cabrera, 1944; Rusconi, 1946a, 1946b, 1947, 1948). The Lower Triassic portion of the Upper Beaufort series of South Africa has produced a rich and well-described fauna which must be considered as the foundation for an understanding of the fresh-water fishes of this period (Brough, 1931). Members of this fauna are also found in the Upper Triassic Stormberg series.

Two isolated occurrences in South America, both in the state of Chubut, Argentina, represent the only possible fresh-water fishes from the late Cretaceous of this continent. One is from a probable continental

facies in the Formación Guaranitico (Ameghino, 1899), and the other from beds of Senonian age in the valley of the Rio Chubut (Bordas, 1943). The possibility that both of these are brackish-water deposits cannot be eliminated with the evidence at hand. For Africa, in the Baharije stage of western Egypt (Stromer, 1936), there is a fluvio-marine facies, considered to be Lower Cenomanian, that has yielded fishes.

Fishes have been found in the continental Tertiary of South America in lower Eocene (Casamayoran) beds in Patagonia (Schaeffer, 1947a), in the possibly Lower Eocene Série Celagaos of Brazil, in the questionably Pliocene lacustrine deposits at Taubaté and Tremembé, São Paulo, and at Nova York, Maranhão, Brazil (Schaeffer, 1947b).

DISTRIBUTIONAL PATTERNS AND FAUNAL SOURCES

There are no known genera of Paleozoic, Mesozoic, or Tertiary fishes from either marine or continental beds that are peculiar only to South America and Africa. A number of genera have been found in only one of these continents, and a smaller number occur also in Australia or in the Northern Hemisphere. In confining attention here to fishes from the continental deposits, it should again be emphasized that the identifications must often be regarded with suspicion and that it is rarely possible to demonstrate that a particular genus is exclusively a member of the primary division of fresh-water fishes.

The Permian genera common to both South America and Africa have been identified as the palaeoniscoids *Elonichthys* (Hussakof, 1930; Broom, 1913) and possibly *Acrolepis* (Bryant, 1929; Woodward, 1891). Both occur in Permian fresh-water deposits in Europe and North America. *Palaeoniscus*, which is characteristic of late Permian fresh-water and marine formations in Europe, is reported from the early Permian of South Africa (Broom, 1913), but is unknown in the Western Hemisphere.

The large early Triassic fauna from South Africa (Brough, 1931) includes a coelacanth referred to the Permian genus *Coelacanthus*, the palaeoniscoid *Oxygnathus*, and the subholostean *Cleithrolepis*. The last two genera occur in the late Triassic or early Jurassic of Europe but are unknown in South America, while marine coelacanths are first recorded in South America in the Cretaceous. Other palaeoniscoids and subholosteans from this fauna, such as *Atherstonia*, *Colobodus*, *Australosomus*, and *Pygopterus*, are found in Europe in marine deposits but again are unknown in South America. The middle and late Triassic faunas from Argentina described by Rusconi and Cabrera unfortunately cannot be properly evaluated on the basis of the published descriptions. With the possible exception of the holosteans, *Semionotus* in Brazil (Geinitz, 1876) and *Pholidophorus* (Rusconi, 1946, 1947) in Argentina, there is no apparent faunal duplication with South Africa. Both these genera occur commonly in marine deposits, the latter almost exclusively so in Europe and North America. The lungfish *Ceratodus* has been recovered in the early (Broom, 1909) and late Triassic (Woodward, 1889; Seeley, 1897) of South Africa and in rocks of the same age in Europe, Asia, North America, and Australia, but not in South America.

There are no satisfactory records of fishes from the limited Jurassic fresh-water deposits in either South America or Africa.

For the entire Cretaceous of South America, *Ceratodus* (Ameghino, 1899, p. 10) is the only primary division fish on record. The primitive teleost *Tharrhias* has been recovered from late Cretaceous continental beds in Chubut, Argentina (Bordas, 1943), but it also occurs in marine beds of similar age in Brazil (Jordan and Branner, 1908). The rather typical late Cretaceous fauna from the Serié Baia, Brazil, has been compared to a fauna of approximately the same age from Rio Muni and French Equatorial Africa (Arambourg and Schneegans, 1935). Both are probably brackish water, and both contain genera that are widely distributed in Eurasia and North America or are very closely related to contemporaneous northern genera. The one common occurrence of possible significance is the coelacanth *Mawsonia*

in the Serié Baia (Woodward, 1908) and in the Baharije stage of Egypt (Weiler, 1935). Although this genus has not been found in Eurasia or North America, the known coelacanths of the Cretaceous were entirely marine, and the presence of *Mawsonia* in the Serié Baia suggests that this genus was also probably a sea inhabitant.

Although the evidence summarized above does not permit a decision regarding the sources of the various groups of fishes occurring in the Mesozoic continental deposits of South America, the following tentative conclusions may be drawn:

1. There is no faunal resemblance among the probable primary division fishes peculiar to South America and Africa during the Mesozoic such as occurs in the Cenozoic.

2. Fishes occurring in continental deposits in both South America and Africa, without known marine representatives, are also found in rocks of nearly the same age in some parts of Eurasia and North America.

3. The lungfish *Ceratodus*, which is the only reasonably certain member of the primary division, had an almost world-wide distribution in the early Mesozoic, and its dispersal into South America could have been from the north.

4. On the basis of the sporadic and fragmentary record, there is no evidence of direct primary fresh-water fish interchange between South America and Africa during any part of the Mesozoic.

5. As the centers of origin are unknown for any of the groups of fishes here considered, regardless of taxonomic category, it can only be stated that the evidence for the Mesozoic suggests a dispersal relationship between South and North America on the one hand, and Africa and Eurasia on the other.

THE CENOZOIC PRIMARY DIVISION NEOTROPICAL FISH FAUNA

The origin of the Cenozoic primary fresh-water fish fauna of South America has recently been the subject of critical discussion by Myers (1938), Gosline (1944), and Schaeffer (1947b). It is becoming increasingly evident that at least some elements, if not all, were already present in this continent at least by the late Cretaceous. The sources of the fauna are still entirely unknown, and the paleontological evidence is not available to present more than a few reasonable working assumptions.

The characins from South America (*Brycon*) and Africa (*Brycinus* and *Alestes*) that have been regarded as closely related are generalized types (Myers, 1938), which may well have persisted with little modification since the beginning of characin differentiation, presumably in the Cretaceous. The only fossil characins thus far discovered in South America are of late Tertiary age (Schaeffer, 1947b) and are closely related to living Neotropical forms. Since the available geological evidence strongly supports the thesis that South America and Africa had no connections from at least the Cretaceous to the present time, the dispersal of the characins must have been accomplished either through unknown marine types (possibly pre-characin?) or via Holarctic fresh-water routes. Wood's (1950) analysis of the Neotropical and African hystricomorph rodents represents an interesting parallel to the characin problem.

The semimarine Ariidae is the only catfish family common to South America and Africa. *Arius* occurs in the Tertiary of Brazil and Argentina and could have reached South America by a marine route. Dolgopol de Saez (1941) reports silurid catfish remains from the Tertiary of Chubut, Argentina. As the Siluridae, either fossil or recent, have not been found elsewhere in the Western Hemisphere, this taxonomic allocation must be regarded as very tentative.

Osteoglossid intergeneric relationship and dispersal have been considered by a number of ichthyologists in the last 50 years. There have been many differences of opinion on both these topics, neither of which has reached a satisfactory solution. The oldest unquestionable members of the Osteoglossidae are *Phareodus* from the Middle Eocene of North America and the Oliogocene of Australia (Hills, 1934), *Musperia* from the early Tertiary of Sumatra (Sanders, 1934), and *Scleropages*, now living in Australia and parts

of the East Indies, but also from the early Tertiary of Sumatra. The genus *Eurychir* (Jordan, 1925) from the marine Cretaceous of Kansas and *Brychaetus* from the Eocene London Clay are not surely osteoglossids and at the present time cannot be seriously considered, in spite of their interesting marine implications. Sanders is of the opinion that *Musperia* and *Phareodus* are closely related, and these in turn to the living African genus *Heterotis*. De Beaufort (1925) and also Sanders believe that *Scleropages* shows affinity with the recent South American *Osteoglossum*. Myers (1938), as did Boulenger and Arldt, considers *Scleropages* to be similar to *Phareodus*. The only tentative conclusion that can now be drawn from this somewhat confused picture, which incidentally a thorough study of *Phareodus* may help to clear up, is that the living South American genera *Osteoglossum* and *Arapaima* show no close relationship to the North American *Phareodus*.

The cyprinodonts and cichlids are members of the secondary division of fresh-water fishes and are hence salt water tolerant. A marine dispersal cannot, therefore, be ruled out.

The South American fresh-water fishes formerly included in the Nandidae are now placed in a separate family, the Polycentridae. The Nandidae are restricted to West Africa, India, and parts of Malayasia. Although the two families are apparently closely related (Myers, 1938), fossil representatives are unknown, and there are no clues regarding dispersal routes.

The modern *Lepidosiren* of South America is the most specialized of the Dipnoi (Westoll, 1949). Fossil remains of this genus have not been recovered,[1] and there is no direct evidence concerning its ancestry. Romer and Smith (1934) have suggested that *Lepidosiren* and the living African *Protopterus* may be descended from the early Permian *Gnathorhiza* of North America. Stromer (1938) has expressed the opinion that *Lepidosiren* may have evolved from *Protopterus* which, he believes, was derived from some *Ceratodus* stock.

[1] Since this paper was submitted for publication, *Lepidosiren* has been reported from the late Miocene of Colombia (Savage, 1951).

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DISCUSSION OF THE EVIDENCE OF FRESH-WATER FISHES

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SCHAEFFER'S PAPER includes a summary of our present knowledge of the fossil fresh-water fishes of South America, and it appears unnecessary either to qualify or to augment any of the specific points offered by him. Rather, I propose to comment on some general paleo-ichthyological matters that bear on the broader aspects of the problems under discussion. It is hoped that the very brevity and generality of these comments will serve to indicate the incompleteness of the data now available to the paleo-ichthyologist and to suggest the caution with which the facts must be employed biogeographically.

The question of the origin of the fresh-water fishes of South America has long been a provocative and stimulating topic for speculation. All earlier attempts at solving the problem were based entirely upon the living fauna. It is only within recent years that geologic and paleontological data have been given consideration in this connection. The known fossil fish faunas of South America certainly are not inconsiderable either in the diversity of taxonomic entities recognized or in the number and kinds of stratigraphic occurrences. However, Dr. Schaeffer's foregoing conclusions cannot be overemphasized. Our present knowledge of the Mesozoic faunas offers little insight into the origins and modes of dispersal of the primary division fresh-water fishes that previously have inhabited and now occupy that continent. With a very few exceptions, it is perhaps legitimate to doubt that at this time comparable detailed biogeographic analyses of the Mesozoic primary division fishes in any region of the earth would be any more productive of conclusive information.

During the past 30 years the study of fossil fishes has experienced an expansion of unprecedented magnitude. In fact, so great has been the record of accomplishment in the field that modifications, as well as some complete reversals, in our fundamental concepts of fish morphology, phylogeny, and evolution throughout the geographic column have been necessitated. If some figures will be pardoned, an excellent example of one of the advances in fossil fish knowledge during this period is perhaps reflected in the refinement of taxonomy in one group of bony fishes. A few scant years ago the family Palaeoniscidae, the most primitive group of ray-finned fishes, was composed of approximately 25 genera, ranging in age from the middle Devonian to the lower Cretaceous. At the present time, this one family has been raised to the level of an order and with various deletions and additions has been subdivided by some workers into as many as 27 families which include upward of 69 genera.

The recently amassed information on fossil fishes, although sometimes unwieldy, is greatly facilitating research in this field, and detailed data are now available for virtually every period of the geologic past. Unfortunately, world-wide progress in research is not equal. In most cases the known facts concerning any given period are based on materials from local stratigraphic occurrences, and more often than not contemporaneous faunas from other parts of the world remain only superficially understood. This applies especially to South America. Coupled with this difficulty is the virtual impossibility of drawing valid vertical lines of descent.

Until true phyletic lines can be determined in some detail, patterns of distribution will remain inconclusive; the biogeographer will be in constant danger of drawing conclusions from incorrect data; "faunal elements," those presumed identical forms common to widely separated regions, may well prove to be abstractions; and the always difficult establishment of centers of dispersal may be rendered an impossibility.

The answers to these problems ultimately lie in the availability of additional data and in the more adequate coverage of existent materials. Recommendations in both these respects can scarcely be specific, because the problems have cosmopolitan ramifica-

tions. Comprehensive collecting even for the proper elucidation of the problems discussed cannot be confined exclusively to the continental deposits in South America, Africa, or any other continental area. For reasons already mentioned, all future work must be carried on in world-wide scope and in marine sediments as well as fresh-water ones.

THE MESOZOIC TETRAPODS OF SOUTH AMERICA

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INTRODUCTION

AS COMPARED WITH WHAT we know about the Mesozoic land-living vertebrates in the rest of the world, our knowledge of these animals in South America is not very extensive. This is a fact that must be kept in mind by the student who attempts to make an evaluation of the Mesozoic amphibian and reptilian faunas of South America as they are related to contemporaneous faunas in other continental areas. On the other continents, with the exception of Australia, the Mesozoic faunas are known from fairly representative sequences of amphibian and reptilian assemblages that indicate various levels in the succession of Triassic, Jurassic, and Cretaceous sediments. Gaps do exist, of course, and some of the gaps are indeed large, but on the whole the Mesozoic faunas of North America, Europe, Asia, and Africa are much more complete and varied than are these faunas in South America.

In South America there are essentially only two horizons in which Mesozoic land-living tetrapods are adequately known from fossil materials. One of these is of Middle or Upper Triassic age, the other of Upper Cretaceous age. It should be said here that recently there has been reported a sauropod dinosaur of Jurassic age from southern Argentina (Cabrera, 1947). This discovery, while indicative of the possibilities for future explorations in search of Jurassic land vertebrates in South America, does not constitute a record comparable to the Triassic and Cretaceous faunas which are the subject of this paper. Therefore it can be given passing consideration but hardly more than this in the present contribution. In addition there are isolated occurrences of Mesozoic marine reptiles, such as the plesiosaurs and the ichthyosaurs, at scattered localities around the margins of the continent, but marine vertebrates are outside the scope of this particular study. Of course there is every reason to believe that as time goes on additional fossil-bearing horizons will be discovered in the continental Mesozoic sediments of South America, but at the present time our knowledge is limited, and it is upon the basis of this limited knowledge that the discussion must rest.

Triassic amphibians and reptiles have been found in Rio Grande do Sul and far along the upper reaches of the Amazon River of Brazil, and in the States of Mendoza and La Rioja in the western part of Argentina. The fossils from southern Brazil comprise a considerable fauna, which has been collected at several localities, from the Santa Maria formation of the Rio do Rasto group. (In a recent paper by MacKenzie Gordon a division of the total sequence of these sediments is made with the name Rio do Rasto limited to beds of upper Permian age, while the vertebrate-bearing Triassic sediments are called the Santa Maria formation.)

Cretaceous reptiles are known from the southern part of Argentina, especially from Nequen and from thence south through Patagonia. In this region a considerable fauna has been found, dominated by dinosaurs but containing also crocodilians, lizards, and turtles. In recent years a few Cretaceous reptiles have been found in the Baurú formation of São Paulo, Brazil, and in Uruguay.

What light do these limited Mesozoic amphibian and reptilian faunas of South America throw upon the large subject of tetrapod distributions during the age of dinosaurs? Are the Mesozoic tetrapods of South America more nearly related to the tetrapods of North America or to those of the so-called Gondwanaland continents, Africa, India, and Australia? How did the land-living tetrapods migrate back and forth between South America and other continents during Mesozoic times? Do the Mesozoic amphibians and reptiles of this region afford any information on the theory of continental drift as opposed to that of the per-

manence of continental blocks and oceanic basins? If the continents occupied essentially the same positions in Mesozoic times that they do today, what were the connections between them? Was there a Gondwanaland, uniting South America with Africa, India, and Australia? Do the recent amphibians and reptiles of the Neotropical region indicate anything as to the distribution of tetrapods during the Mesozoic era?

These are some of the questions that arise when one approaches the general problem of the Mesozoic tetrapods of South America. It is doubtful whether our knowledge is complete enough at the present time to give satisfactory answers to many of these questions, but at least the evidence can be scrutinized and evaluated.

THE TRIASSIC FAUNA

The Triassic tetrapods of South America, as known from southern Brazil, and from the States of La Rioja and Mendoza in Argentina, can be listed by genera as follows:

Amphibia
- Stereospondyli, Triassic labyrinthodonts
  - *Pelorocephalus*, a brachyopid or short-headed stereospondyl

Reptilia
- Cotylosauria, primitive reptiles
  - *Candelaria*, a procolophonid
- Therapsida, mammal-like reptiles
  - *Dicynodon*, *Stahleckeria* } dicynodonts
  - *Belesodon*, *Chiniquodon*, *Gomphodontosuchus*, *Traversodon*, *Exaeretodon*, *Theropsis* } cynodonts
- Rhynchocephalia, rhynchocephalians, persisting to recent times
  - *Cephalonia*, *Scaphonyx* } rhynchosaurs
- Thecodontia, ancestral archosaurs
  - *Hoplitosuchus*, *Prestosuchus*, *Rauisuchus*, *Rhadinosuchus*, *Procerosuchus*, *Cerritosaurus* } pseudosuchians
- Saurischia, dinosaurs
  - *Spondylosoma*, a prosauropod dinosaur

What is the significance of this fauna in relation to Triassic faunas in other parts of the world? Perhaps the answer to this question is best found in an analysis of the assemblage not by genera but rather by higher categories, on the level of families or suborders. The several Triassic faunas of the world are so varied that extensions of a single genus from one continental area to another are not at all common. On the other hand, closely related genera are found rather frequently in different continental areas, and these genera, even though not identical, are diagnostic and valid in establishing faunal relationships between widely separated regions. Indeed, considering the world-wide distribution of the faunas under examination and the time differences that inevitably must exist between these faunas, even if they are not always apparent, it would be exceptional if many generic identities could be established among the tetrapod assemblages in different parts of the world. A tetrapod, in spreading from one continental region to another through an appreciable lapse of time, would under ordinary circumstances undergo various mutations in response to new environmental conditions, so that in the end there would be developed related but not identical genera in the two regions. Where an identity of genera in separate continental areas can be found, one must suppose that the intercontinental passage was relatively rapid, or that the genus in question was an unusually stable one. Therefore, the presence of closely related but not identical genera in different continents should be regarded as the normal condition, from which perfectly valid conclusions can be drawn.

When we turn to an examination of the Triassic land animals of South America, listed above, it is seen that to date there is known a single labyrinthodont amphibian, described by Cabrera under the generic name of *Pelorocephalus*. Although this fossil is not so well preserved as might be wished, it is sufficiently complete to show that it is a characteristic brachyopid, or short-faced

stereospondyl. The brachyopids were Triassic labyrinthodont amphibians characterized by very short and broad skulls. In addition to the South American genus, the brachyopids are known from the lower or middle Triassic Moenkopi formation of the southwestern United States, from South Africa, from India, from Australia, and especially from central Europe, where a number of genera are represented. Consequently it is apparent that this South American amphibian is closely related to genera that were rather widely distributed in other continental areas.

A rather similar picture of distribution to that outlined above is seen when we examine the procolophonid reptiles. This group is represented in Brazil by the single genus *Candelaria*, recently described by L. I. Price. The Procolophonidae were the last of the cotylosaurs, the most primitive of the reptiles, and characteristically of Permian age. Although the cotylosaurs enjoyed the culmination of their evolutionary development in Permian times, there was this one family, the Procolophonidae, that originated in late Permian times and continued on through the extent of the Triassic period. The first known Permian procolophonids are found in two widely separated regions—South Africa and Russia. From these primitive forms the Triassic procolophonids evolved and spread to various parts of the world, where they have been discovered in South Africa, central Europe, Scotland, North America, and of course South America.

The dicynodonts were highly specialized therapsid reptiles characterized by the rather bizarre skull in which all of the teeth were suppressed except for two large tusks in the upper jaws of the male animals. Dicynodonts are found in incredibly large numbers in the Permian and Triassic of South Africa, and because they have been known for such a long time from that particular region they are generally thought of as characteristic Karroo reptiles. The presence therefore of two genera of dicynodonts in the Triassic of Brazil, *Dicynodon* itself and a giant form, *Stahleckeria*, might be considered as indicative of especially close relationships between South America and South Africa during Triassic times. Yet it should be noted that dicynodonts are well known from the Triassic sediments of such widely separated areas as northern Russia, western China, and the southwestern United States. Therefore it is apparent that the distribution of the dicynodonts in Triassic times was similar to the distributions already reviewed for the brachyopid labyrinthodonts and for the procolophonids. In other words, these reptiles were rather cosmopolitan in their distribution.

There is a series of cynodont reptiles from the Triassic of Brazil and Argentina. These reptiles, best known from South Africa, were quite advanced towards the mammals in their structure. It is interesting to see that the only known Triassic cynodonts outside of Africa are those found in Brazil.

The rhynchocephalian reptiles are represented at the present time by a single genus, *Sphenodon*, living on a few islands off the coast of New Zealand, but during much of the Mesozoic era these reptiles were widely distributed, as is illustrated by the evidence of the Triassic genera. Triassic rhynchocephalians belonging to a distinct family, the Rhynchosauridae, are found in Brazil, where they are represented by two genera, in South Africa, in India, and in Scotland.

As in the case of the cynodonts, there are several genera of thecodont reptiles known from the Triassic sediments of Brazil. The thecodonts were characteristic Triassic reptiles, appearing at the beginning of this geologic period and becoming extinct at its conclusion. There was a considerable amount of adaptive radiation within the Thecodontia, while in addition this order of reptiles served as the stem from which several of the dominant orders of Mesozoic reptiles arose—reptiles such as the crocodiles, the two orders of dinosaurs, and the pterosaurs or flying reptiles. The Brazilian thecodonts belong for the most part to the family Staganolepidae, a group of small- to medium-sized reptiles in which the body was protected by a heavy armor plate of overlapping bony scutes. In Triassic times the staganolepids were living, on the basis of the known evidence, in South America as well as in central Europe and England, in eastern North America, in the southwestern part of the United States, and

TABLE 2

DISTRIBUTION OF TRIASSIC LAND-LIVING TETRAPODS IN SOUTH AMERICA AND IN OTHER CONTINENTAL REGIONS

	North America	South America	Africa	Europe	Asia	Australia
Amphibians						
Stereospondyls						
Brachyopids	x	x	x	x	x	x
Reptiles						
Cotylosaurs						
Procolophonids	x	x	x	x		
Therapsids						
Dicynodonts	x	x	x	x	x	
Cynodonts		x	x			
Rhynchocephalians						
Rhynchosaurs		x	x	x	x	
Thecodonts						
Pseudosuchians	x	x	x	x		
Dinosaurs						
Thecodontosaurs	x	x	x	x	x	

in Africa. So here again we see repeated the pattern of widely distributed reptiles, living in most of the large continental areas during Triassic times.

The Triassic period was the beginning of the age of dinosaurs, but at that time the dinosaurs were for the most part rather small and primitive. It was not until later phases of Mesozoic times, the Jurassic and Cretaceous periods, that the dinosaurs attained the dominance and in many cases the gigantic size that were so characteristic of these reptiles as a group. One might say that the Upper Triassic dinosaurs show the beginnings of the evolutionary trends that were to lead to such spectacular results in the following two periods of geologic history.

A single dinosaurian genus, *Spondylosoma*, has been described by von Huene from the Triassic of Brazil on the basis of rather fragmentary evidence. This dinosaur (if the identification of the material is correct) was a prosauropod belonging to the family Thecodontosauridae. Thecodontosaurs are well known from the Upper Triassic of Europe and from eastern North America as well, while in addition they are found in the Triassic fauna of South Africa. Evidently these early dinosaurs were widely distributed in Triassic times.

Such is a summary of the Triassic land animals of South America and their relationships to closely related forms in other parts of the world. Perhaps this summary can best be presented in graphic form (table 2).

This gives us a picture of the Triassic land animals of South America as being members of a fauna of essentially world-wide distribution. In only one instance, that of the cynodont reptiles, are the distributions limited to only two continents, South America and South Africa. And it is quite possible that even in this case the limitations are caused in part by the imperfection of our knowledge.

It may be helpful to make a comparison between the several Triassic faunas here discussed, by means of the formula suggested by Simpson in 1947 whereby the common elements in two regions at a given taxonomic level are set against the total faunal units at that level in the smaller of the two faunas. The formula is

$$\frac{100C}{N_1}$$

in which C represents the number of faunal units at the given taxonomic level and N_1 is the total number of units at this level in the smaller of the two faunas.

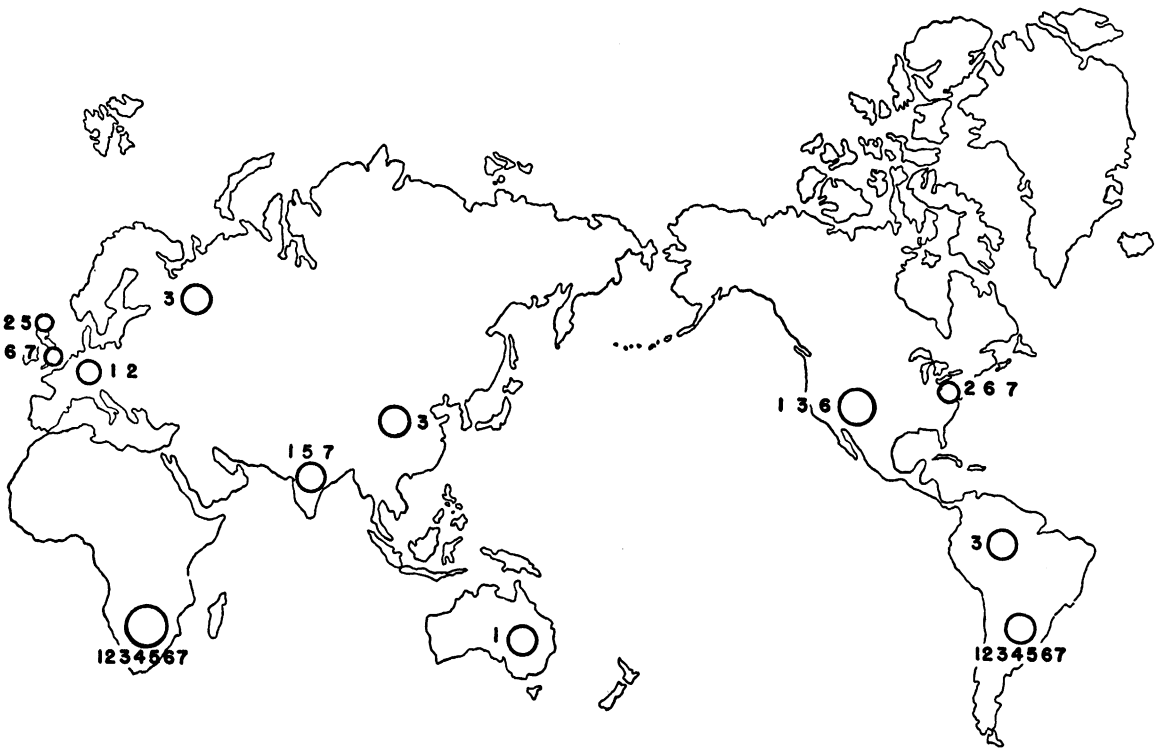

FIG. 27. The distribution of certain amphibians and reptiles during the Triassic period. Amphibians: 1, stereospondyls, brachyopids. Reptiles: 2, cotylosaurs, procolophonids; 3, therapsids, dicynodonts; 4, therapsids, cynodonts; 5, rhynchocephalians, rhynchosaurs; 6, archosaurs, staganolepids; 7, archosaurs, thecodontosaurs.

In a comparison of the Triassic faunas of the different continents it is rather pointless to attempt the use of genera, since there are hardly any genera in common between the various continental areas. Consequently it is necessary to utilize the larger taxonomic categories, the families and suborders.

The suborders and families contained within the Triassic fauna of South America are as follows:

SUBORDERS	FAMILIES
Stereospondyli	Brachyopidae
Diadectomorpha	Procolophonidae
Dicynodontia	Dicynodontidae
Theriodontia	Chiniquidontidae
Theriodontia	Traversodontidae
Rhynchocephalia	Rhynchosauridae
Pseudosuchia	Staganolepidae
Theropoda	Thecodontosauridae

The faunal resemblances between South America and other continental areas during Triassic times on the basis of the categories listed above are as follows:

	SUB-ORDERS	FAMI-LIES
South America—Africa	100%	75%
South America—Europe	86	75
South America—North America	71	63
South America—Asia	43	37
South America—Australia	14	12

These figures must be used with some caution. They indicate that on the whole the relationships between South America and South Africa were possibly closer than those between South America and other continental areas. Yet at the family level there is no difference in the above analysis between Africa and Europe in this respect. Moreover, on the basis of the tabulation above the differences at the family level between Africa and Europe on the one hand and North America on the other are hardly significant,

and such differences as do exist are largely the result of the presence of cynodont reptiles in South America.

The distribution of the Mesozoic tetrapods, as we know them at the present time, might have been brought about in part by the existence of a land connection between Africa and South America. This would have allowed a faunal flow between the continents. But the South American fauna might have been the result of migrations through Eurasia into North America and from thence southward into South America. Of course there are no cynodont reptiles and rhynchosaurs so far known in North America, so one must suppose on the basis of present evidence that these animals have been lost in the fossil record in North America if the movement was through this region.

In short, a broad analysis of the evidence of the South American land vertebrates during Triassic times seemingly is not conclusive in either direction. On this basis a South Atlantic land bridge is not absolutely essential to explain the relationships of the Triassic vertebrates of South America to those of the Old World, but the evidence would seem to be slightly in favor of such a connection. Of course, if one maintains that the two Americas were completely separated from each other throughout the extent of Triassic times, then a South Atlantic bridge is necessary to account for the presence in South America of various reptilian genera closely related to genera in Africa and in other parts of the Old World.

Did the Tethys Sea extend across the present isthmian region during the Triassic period to isolate South America completely from North America? On this point there is no general agreement. Some paleogeographers and paleontologists do indicate such a separation, in which case a South Atlantic connection between Africa and South America would be necessary (Wurm *in* Salomon, 1926; Boule and Piveteau, 1935; Swinton, 1934; Moore, 1949). With other authorities the relationships between the two continents during the Triassic are questioned (Schuchert and Dunbar, 1933). Still others would regard or consider the presence of an isthmian link between the two continents during Triassic times as probable (Grabau, 1921).

If it be supposed that North America was completely separated from South America in Triassic times by an extension of the Tethys Sea across the isthmian region, it does not necessarily follow that there was a broad Gondwana land in Triassic times, stretching between all the southern continents. But there very well may have been an isthmian or island bridge between South America and Africa, across which intercontinental movements of land-living tetrapods could have taken place. A more detailed consideration of Triassic faunas in the several continental regions would seem to indicate, as Romer points out below, that the evidence strongly favors a South American-African land bridge in Triassic times.

THE JURASSIC SAUROPOD

As mentioned above, Cabrera has described a single sauropod, *Amygdalodon*, from the Jurassic of Chubut, southern Argentina. This single genus indicates that in Jurassic times, as was the case in the preceding Triassic period, there were in South America animals of world-wide distribution. We now know that the sauropod dinosaurs were living during the Jurassic period in South America, in North America, in Europe, in Africa and Madagascar, and in Australia; consequently the evidence of *Amygdalodon* corresponds with the evidence afforded by the Triassic fauna that is discussed above and with that of the Cretaceous fauna next to be considered.

THE CRETACEOUS FAUNA

Let us now turn to a consideration of the Cretaceous tetrapods of South America, to see if they offer additional evidence on this perplexing problem. These animals are known

for the most part from Argentina, especially from Patagonia and from Nequen. Four genera have been recorded from Brazil, and there is good reason to think that as more work is carried on in Brazil a considerable Cretaceous fauna will be made known from this country. The Cretaceous land-living tetrapods from South America can therefore be listed by genera as follows:

Reptilia
- Chelonia, turtles
  - *Niolamia*, a primitive turtle
  - *Podocnemis*, *Naiadochelys* (probably *Podocnemis*), *Taphrosphys*[a,b] — pleurodires, or side-neck turtles
  - *Osteopygis*, *Gyremys* (very doubtful) — cryptodires, or vertical-neck turtles
- Squamata, lizards and snakes
  - *Dinilysia*, a snake
- Crocodilia, crocodiles
  - *Baurusuchus*,[a] an aberrant crocodilian, peculiar to South America
  - *Notosuchus*, *Cynodontosuchus*, *Goniopholis*[a] — mesosuchians, or archaic crocodiles
  - *Leidyosuchus*, a "modern" crocodile
- Saurischia, dinosaurs
  - *Clasmodosaurus*, *Loncosaurus* — small, frugivorous, theropod dinosaurs
  - *Genyodectes*, a large, carnivorous, theropod dinosaur
  - *Titanosaurus*[a]
  - *Laplatasaurus*
  - *Antarctosaurus*, gigantic, marsh-dwelling, herbivorous sauropod dinosaurs
  - *Argyrosaurus*
  - *Campylodon*
- Ornithischia, dinosaurs
  - *Loricosaurus*, an armored dinosaur
  - *Notoceratops*, a horned dinosaur (based on fragmentary and questionable evidence)

[a] Brazil.
[b] Hitherto not known below the Eocene.

From the above list it can be seen that there was a considerable dinosaurian fauna in South America during the Cretaceous period. This fauna, known at the present time mainly from southern Argentina but supplemented by a few discoveries from Brazil, is interesting in that it contains an overwhelming proportion of saurischian dinosaurs. In most Cretaceous dinosaurian faunas, especially those from the upper Cretaceous, the ornithischian dinosaurs are preponderant, the saurischians being represented usually by the carnivorous theropods. In the South American Cretaceous fauna, however, there is quite an array of sauropod dinosaurs, and these together with the theropods make up the bulk of the dinosaurian representation. The ornithischians are present as a single genus of armored dinosaur and a very questionable ceratopsian or horned dinosaur.

Two genera of ornithomimids are present among the theropod dinosaurs of South America. These were theropods of medium size, comparable in this respect to the modern ostriches. They had a long flexible neck and a comparatively small, bird-like skull, and it would seem that these dinosaurs probably filled an ecological role similar to that occupied by the modern "ratite" birds; they were swift-running animals that probably fed upon fruits, insects, and other such small fare. The presence of these dinosaurs in the Cretaceous fauna of South America constitutes a strong link to the Cretaceous faunas of the Northern Hemisphere, where the ornithomimids are well represented in North America and Eurasia. They have also been found in Australia.

Genyodectes is a large, carnivorous, theropod dinosaur. The ecological role played by these reptiles in Cretaceous times was a dominant one, for they were giant, meat-eating dinosaurs that preyed upon other large dinosaurs with which they were contemporaneous. They seemingly were upland forms, as were the ornithomimids, and it is not likely that they went very far out into the water or into swampy regions. Since they were upland predators they were probably capable of extensive wanderings, not only as individuals but also as species. Consequently it is not surprising to find them occupying most of the land areas of the world during Upper Cretaceous times, and the world-wide distribution of these reptiles shows that there were adequate avenues open for the dry-land dispersal of large reptiles between all of the large continents. They are found

in Upper Cretaceous sediments in South America, North America, Europe, Asia, and Africa.

The sauropod dinosaurs, so characteristic and dominant in the Cretaceous fauna of South America, can be considered as a relict group in a rather isolated part of the world. By Cretaceous times the sauropods were virtually extinct in North America, although the evidence indicates that they still did persist here and there as greatly reduced remnants of what had once been a widely spread and numerous group of animals. In Eurasia and Africa the sauropods were rather better off during Cretaceous times than they were in North America, so that they formed appreciable segments of the faunas of those regions.

The giant sauropods were swamp-dwelling and swimming dinosaurs, which sought not only their food but also protection from the giant predatory theropods of the time in shallow waters. Consequently it would seem likely that the opportunities for the dispersal of these giant dinosaurs from one region to another were more extensive than for the theropods, which were confined to relatively dry ground. It is certainly true that except for North America the sauropods spread to many parts of the world during Cretaceous times, and in some cases the broad distribution of these reptiles extended to the categories of genera. Thus the genus *Antarctosaurus* is found in South America and India, the genus *Titanosaurus* is found in South America, Europe, and India, while the genus *Laplatasaurus*, so characteristic of the Cretaceous of southern Argentina, is found as well in East Africa, Madagascar, and the Indian peninsula.

These genera have been used by various authors to indicate the close relationships of the southern continents in Cretaceous times. Yet it must be remembered that they are but part of a broad distribution of Cretaceous sauropods. *Titamosaurus* is found in Europe as well as in the southern continents, while the family Cetiosauridae, to which these genera belong, is very widely distributed in Cretaceous deposits.

The only South American ornithischian dinosaur that is well enough known to permit speculation is a nodosaur, a heavily armored dinosaur that probably lived in an upland environment. The nodosaurs were cosmopolitan in their distribution during Cretaceous times, being present, on the basis of available evidence, in Europe, Asia, and North America as well as in South America. Thus the range of these dinosaurs parallels that of the other dinosaurs in that it shows essentially a world-wide distribution of the animals in question.

There was a variety of crocodilians in South America in Cretaceous times, including representatives not only of the mesosuchians, so typical of the Mesozoic, but also of the eusuchians, the modern crocodilians, which went through the initial phase of their long evolutionary history during the Cretaceous period. In addition there was one genus of the two known genera of sebecosuchians, representative of an aberrant group of crocodilians confined to South America. Since the crocodilians have been for the most part aquatic reptiles it must be supposed that facilities for the dispersal of these reptiles may have been comparatively broad during Cretaceous times. True, most modern crocodilians are confined to rivers and lakes, so that they may be fairly considered as continental vertebrates, but certain forms, such as the salt-water crocodile, cross open stretches of the sea. Therefore it is reasonable to conclude that some of the Mesozoic crocodilians followed not only drainage patterns during the course of their distributional expansion from one region to another, but also sea coasts. This may account in part for the world-wide distribution of the mesosuchians during the Cretaceous period. The eusuchians, which occur in South America, are also found in North America and Europe, and it is probable that their absence from the fossil record of Asia and Africa is the result of our imperfect knowledge—a condition that may be corrected by future collecting.

The Sebecosuchia constitute a different problem. These crocodiles were highly specialized along lines quite apart from all of the other crocodilians. Whereas the common trend among the crocodiles throughout their

TABLE 3

DISTRIBUTION OF CRETACEOUS LAND-LIVING REPTILES IN SOUTH AMERICA AND IN OTHER CONTINENTAL REGIONS

	North America	South America	Africa	Europe	Asia	Australia
Reptiles						
Turtles						
Meiolanids		x				
Pelomedusids	x	x		x		
Thalassemydids	x	x	x	x		
Snakes						
Anilids		x				
Crocodilians						
Sebecosuchians		x				
Mesosuchians	x	x	x	x	x	
Eusuchians	x	x		x		
Dinosaurs						
Ornithomimids	x	x		x	x	x
Deinodonts	x	x			x	
Cetiosaurs	x	x	x	x	x	
Nodosaurs	x	x		x	x	
Ceratopsians	x	x?			x	

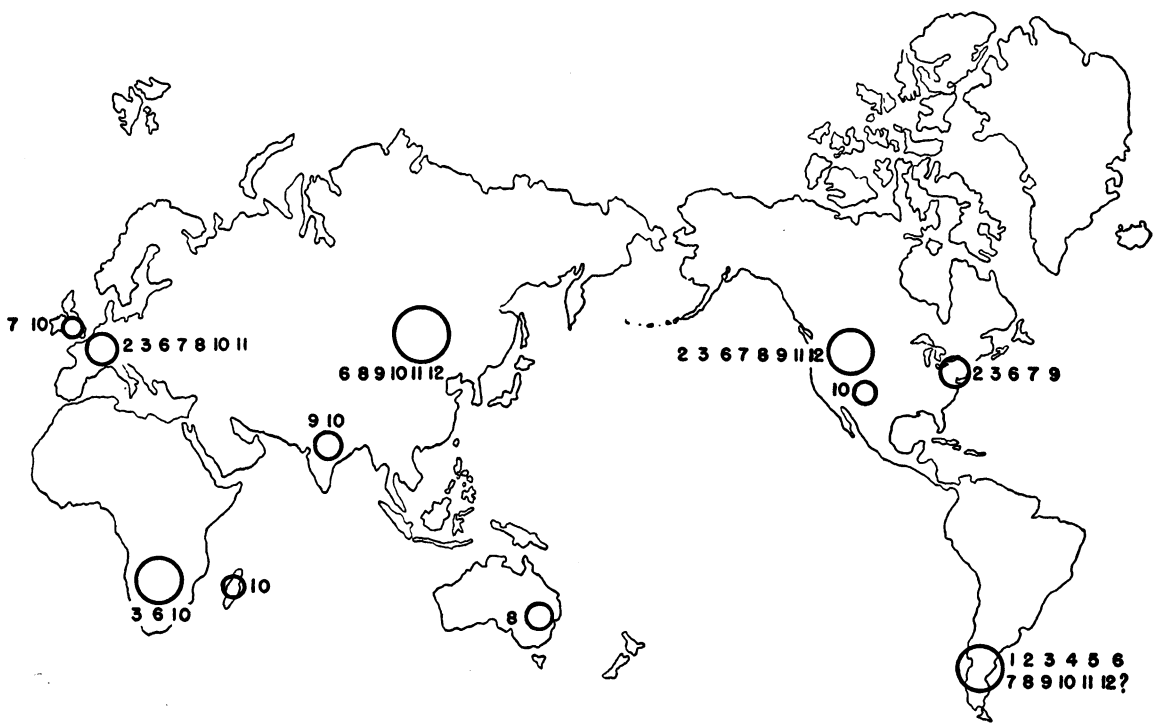

FIG. 28. The distribution of certain reptiles during the Cretaceous period. Turtles: 1, meiolanids; 2, pelomedusids; 3, thalassemydids. Snakes: 4, anilids. Crocodilians: 5, sebecosuchians; 6, mesosuchians; 7, eusuchians. Dinosaurs: 8, ornithomimids; 9, deinodonts; 10, cetiosaurs; 11, nodosaurs; 12, ceratopsians.

history was towards a flattening of the skull and the development of long jaws with many teeth, the sebecosuchian trend was in the direction of a high, narrow skull with compressed teeth, sometimes limited in number and highly specialized in form. This would point to the possibility that these crocodilians may have been more completely adapted to land life than were their contemporary relatives. If such were the case, then these crocodilians would have been more limited as to the possibility of wide distribution than were the other crocodilians living at that time. Whether or not such an explanation is valid, it seems probable that the sebecosuchians constituted a rather limited assemblage of reptiles, peculiarly adapted to certain restricted environments.

Like the crocodilians, the turtles living during Cretaceous times in South America were varied. There was one genus, *Niolamia*, representative of the *Meiolaniidae*, a peculiarly distributed group of primitive turtles, while in addition there were side-neck turtles, or pleurodires, and vertical-neck turtles, or cryptodires.

The pleurodiran *Podocnemis* was present in the Cretaceous fauna of South America, and it persists in that continent at the present time. It belongs to the Pelomedusidae, a family of turtles that was present not only in South America but also in North America and Europe in the Cretaceous period.

The thalassemydids, of which *Osteopygis* occurs in the Cretaceous fauna of South America, were likewise widely spread in late Mesozoic times. These were rather primitive cryptodirans. The description of *Gyremys*, an emydid cryptodire from the Cretaceous sediments of Argentina, is based on such doubtful evidence as to have little value in this evaluation of the Cretaceous fauna of South America.

A summary of the distribution of Cretaceous land-living tetrapods is given in table 3.

Once again, as in the case of the analysis of the Triassic tetrapods of South America, we see the Cretaceous fauna from this continent as part of a large fauna of world-wide distribution. Generally speaking, the Cretaceous land-living reptiles of South America had close relatives in most of the other continental areas, so that their presence in South America reflects the broad distribution of many reptiles during the upper part of Mesozoic times.

It may be useful at this point to attempt a comparison of South America with other continental areas in a manner similar to that utilized in the discussion of the Triassic vertebrates. Again, this comparison is made on the basis of suborders and families, which are contained within the Cretaceous fauna of South America as follows:

SUBORDERS	FAMILIES
Theropoda	Ornithomimidae
Theropoda	Deinodontidae
Sauropoda	Cetiosauridae
Ankylosauria	Nodosauridae
Ceratopsia?	Ceratopsidae?
Sebecosuchia	Sebecidae
Mesosuchia	Notosuchidae
Mesosuchia	Goniopholidae
Eusuchia	Crocodylidae
Serpentes	Anilidae
Amphichelydia	Meiolanidae
Pleurodira	Pelomedusidae
Cryptodira	Thalassemydidae
Cryptodira	Emydidae?

On the basis of these categories, the faunal resemblances between South America and other continental regions might be as follows:

	SUB-ORDERS	FAMILIES
South America—Africa	80%	33%
South America—Europe	90	58
South America—North America	90	66
South America—Asia	70	42
South America—Australia	10	8

It is seemingly apparent that in Cretaceous times the relationships between South America and the northern continental land masses were closer than those between South America and the other southern continents. Here we see a definite foreshadowing of modern faunal relationships that were inaugurated at the opening of Cenozoic times and that have developed since then. It would appear that in the Cretaceous period, as in later times, the interchange of land vertebrates between South America and other continental regions took place by way of an isthmian bridge to

North America and from thence into the Old World. Perhaps different continental relationships had been established by this geologic period as compared with the Triassic period. If there was a South Atlantic connection between South America and Africa in Triassic times, it probably had foundered by the Cretaceous period, for the evidence here is all in favor of a northern connection.

The Triassic fauna of South America has something of an African cast to it, especially by reason of the presence there of various therapsid reptiles. But the Cretaceous fauna of South America is essentially similar to the northern faunas, especially those of North America and of Europe. It is interesting to note in the distribution of the Cretaceous reptiles, as was the case in that of the Triassic forms, how little relationship there is between South America and Australia.

THE RECENT FAUNA

At this point it may be interesting to consider briefly the bearing of the Mesozoic tetrapod faunas of South America on the recent tetrapods of that continent. Of course most of the faunal categories that were present in South America in Mesozoic times have long since become extinct. Between the Triassic fauna of South America and the recent fauna there is a complete break, so that there are no animals now living in the Neotropical region which are related to the amphibians and reptiles that inhabited this area 175 million years ago. Of the Cretaceous fauna, however, there are still some representatives to be found in South America, namely, the turtles, snakes, and crocodilians.

Of the turtles, only *Podocnemis* is represented in the modern fauna. Here we see the survival not only of a family but also of a genus in modern times that was present in the same general region in Cretaceous times. The longevity of the genus *Podocnemis* is in itself a criterion of the evolutionary success of this particular form through a considerable segment of geologic history, and it is possible to say quite definitely that the presence of *Podocnemis* in the modern Neotropical fauna represents an archaic holdover that has maintained its ecologic position in spite of the influx of other faunal elements from other regions.

Niolamia is distantly related to *Meiolania* of the Pleistocene of Australia, but obviously has nothing to do with the recent fauna of South America. The supposed emydid *Gyremys* in the Cretaceous of South America is too doubtful to permit valid speculation with relation to the recent fauna.

The single snake, *Dinilysia*, described from the Cretaceous of South America, belongs to the Anilidae, a family which is still to be found in the Neotropical region as well as in Asia. Therefore it is valid to assume that the modern Anilidae in South America represent a group persisting from Cretaceous times.

Among the crocodilians, most of the Cretaceous genera belong to families and even suborders that have since become extinct. In the latter category are the Sebecosuchia and the Mesosuchia. The eusuchians, the modern crocodilians, were present in the Cretaceous of South America as the genus *Leidyosuchus*, a crocodylid. *Crocodylus*, and in addition various eusuchians belonging to the family Alligatoridae, are found at the present time in the Neotropical region. The presence of crocodylids in the Cretaceous of South America represents in effect a part of a world-wide distribution of these successful and ubiquitous reptiles.

CONCLUSIONS

Such is the evidence afforded by the Mesozoic land-living tetrapods of South America as to the relationships of this continental area to other continental regions during Mesozoic times. All in all, it would appear that during the Mesozoic era the land-living vertebrates of South America were essentially parts of widely distributed faunas of world-wide extent. In a majority of the cases, the Mesozoic genera found in South America are closely related to genera living in most of the other great continental areas. Thus it

would appear that there were adequate avenues for the distribution of tetrapod faunas between the several continents, and that South America shared to a very considerable degree in the movements of the terrestrial vertebrates from one region to another.

There may have been a connection of sorts between South America and Africa during the Triassic period. If other evidence indicates that South America was completely cut off from North America by the Tethys Sea throughout the extent of the Triassic period, then such a southern land connection would be necessary to account for the South American Triassic fauna. But if the separation of the two Americas was not complete, no such southern connection is essential, though the evidence would seem to indicate that it probably existed.

By Cretaceous times the relationship of South America to North America seems to have been definitely established, and the interchange of faunal elements between these two regions foreshadowed the periodic interchanges that were to take place throughout later geologic history.

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DISCUSSION

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COLBERT GIVES ABOVE an admirable summary of the Mesozoic faunas of South America. I find myself in hearty agreement with his conclusions with regard to the Cretaceous; there is nothing in the fauna to indicate closer relationships with one continent than another, and no reason why the non-autochthonous elements present could not have arrived via a "normal" North American connection, if such existed. There is, as Colbert notes, almost no evidence regarding the Jurassic.

The Triassic is a more difficult problem. Colbert lists and describes the tetrapod groups then present in South America, tabulates their distribution in the Triassic of other continental areas, and summarizes these occurrences on a percentage basis. From this he reaches the "Scotch verdict" that the question of a possible South Atlantic connection is an open one, and that while the evidence is somewhat in favor of such a connection, arguments can be brought forward to show that the various elements of the South American fauna might have reached that continent over "orthodox" migration routes.

With this conclusion I mildly disagree. I have been reared in the tradition of continental stability and was early impressed by Matthew's demonstration (ably reënforced by Simpson in recent years) that most if not all Tertiary land bridges are not merely delusions but snares to the unwary. However, I find myself here, after consideration of the evidence, rather strongly inclined towards belief in the existence of a southern intercontinental connection between South America and South Africa in the Triassic. To my embarrassment; for in such a "leftish" position I am disturbed (like many a liberal in political circles) by the company (of bridge-builders, radical continent shifters, and Gondwanaland collectivists) which this may entail.

As Colbert tabulates the evidence, his conclusion seems reasonable enough; in a comparison of the South American fauna with that of other continents for the Triassic as a whole, it appears that the evidence for African connection is very slight. But such tabulations are valid only if the entities compared are truly comparable. This does not appear to be the case here. There is no single "Triassic fauna" with which that of South America can be compared. During the Triassic there occurred a major revolution in vertebrate life. Reptile faunas of the early Triassic are essentially late Paleozoic in type, with therapsids as the dominant forms. Those of the late Triassic are, in strong contrast, typically Mesozoic in nature, with dinosaurs as dominant elements. If such faunas are "lumped" the resultant is a meaningless composite. We must compare the South American forms, if possible, with faunas of a similar stage of the Triassic. If we were to assess the relationships of the fauna of the North American Miocene by comparing it with, say, the Pliocene fauna of Eurasia on the one hand and the combined Oligocene and Pleistocene faunas of South America on the other hand, any numerical data obtained would obviously be of little significance, if not positively misleading. It would appear that we are in danger of finding ourselves in a similar situation here.

At what positions within the Triassic lie the faunas of other continents which Colbert has compared with that of South America? For Africa, there are included two very different assemblages—a therapsid fauna of early Triassic age, from the Upper Beaufort beds,[1] and a second late Triassic fauna from the upper Stormberg with dinosaurs as the principal element (an East African fauna of intermediate age is included as well). For Europe the story is similar; there are here lumped the rather sparse fauna of the early Triassic (the Bunter) and the dinosaur fauna of the Upper Triassic Keuper which follows after the gap of the marine Muschelkalk. Remains from Asia are few but also include early and late elements. From North America the rec-

[1] Von Huene, in contrast to other workers, considers the Cynognathus zone at the top of the Beaufort as Middle Triassic, with a consequent effect of scaling upward other faunas advanced beyond this level.

ord is composed of late Triassic faunas, plus a very few elements of earlier age.

With which of these two major contrasting age groups, early or late, is the fauna of the South American Triassic properly compared? With neither, it would appear.

Of the Triassic tetrapods of that continent, a few are from localities of somewhat uncertain stratigraphic position in Argentina. They are not considered here; their absence does not affect the argument, since recognizable forms include only remains of cynodonts comparable to those of Brazil and the skull of a brachyopid, a labyrinthodont type found in various areas and stages of the Triassic and not of importance in a time determination. The major fauna, to be discussed here, is that from the Santa Maria beds of Brazil. Two main collecting areas are known. There is considerable difference in the faunal content of the two, but it seems to be generally agreed that there is no major difference in age between them. Von Huene (1935–1942) has described in monographic form a large collection of material from these beds; a considerable collection, mostly undescribed, was made by Price and White for Harvard in 1936; subsequently, Price has made large collections for the Brazilian geological survey but has as yet published only a small part of the data on them.

Von Huene originally claimed the Santa Maria beds to be Upper Triassic in age, basing this opinion, it would appear, on the rather advanced character of the rhynchosaurs, the first described elements of the fauna. As he has himself pointed out, however, the degree of specialization of a rhynchosaur type gives little indication of its stratigraphic position. Von Huene has since modified this opinion to some extent. He recognizes (1950) that this fauna is only a little later than that of the Cynognathus zone of South Africa, generally considered as early Triassic. But since, as noted, he considers the Cynognathus zone to be Middle, rather than Lower, Triassic, he compromises by bringing the Brazilian fauna down merely to the earliest Upper Triassic.

Analysis of the fauna clearly indicates a Middle Triassic age, somewhat above the Cynognathus zone of South Africa but far earlier than the dinosaur assemblages typical of the Upper Triassic.

Two types of reptiles make up the greater part of the material from these beds: rhynchocephalians of the rhynchosaur group, and dicynodonts. The rhynchosaurs *Scaphonyx* and *Cephalonia* (if the latter be distinct) are large and apparently rather advanced members of their family which indicates Middle or Upper, rather than Lower, Triassic age. Few of the dicynodonts have as yet been described. As far as I am familiar with them they appear as a whole to be rather primitive in nature, although some have grown to large size and would not seem inappropriate in a Lower Triassic (or even Upper Permian) fauna; none appears to be so specialized as the one genus (*Placerias*) known to have survived into the late Triassic.

Two other groups are moderately abundant: pseudosuchians and cynodont therapsids. Pseudosuchians appeared in the Lower Triassic and had become abundant and diversified in late Triassic times. The forms present are more advanced than would be expected in the early Triassic, and a middle or late Triassic age is indicated. Cynodonts are unknown beyond the Lower Triassic in any regions other than Brazil and Africa; by the Upper Triassic they had been succeeded by a miscellaneous assemblage of other therapsid forms grouped currently as the Ictidosauria, which are structurally far more advanced towards a mammalian condition. The Brazilian cynodonts appear to be a little, but only a little, more advanced than the Lower Triassic members of the group from the Cynognathus zone of the South African Beaufort series. They cannot be conceived of as later than Middle Triassic.

There remain two rarities: a dinosaur and a procolophonid reptile. The dinosaur is of a primitive saurischian type. Dinosaurs are unknown in the Lower Triassic, abundant and rather diversified in the Upper Triassic. Presumably they began their history in the Middle Triassic; the presence here of a single (and seemingly rare) form agrees well with assignment of the beds to this level in the period. The procolophonid, *Candelaria*, is a member of a cotylosaurian group that ranges widely in space and in time from the Permian

to the Upper Triassic; its describer (Price, 1947) notes, however, that it appears to be closer to the Lower Triassic genera than to those of the Middle and Upper Triassic.

It is thus with Middle Triassic faunas that this Brazilian assemblage should be compared, most particularly with faunas of this age in Africa and North America. Not too many years ago we would have been blocked here through the fact that such comparable faunas were quite unknown. Today, while there are still many gaps in our knowledge, a fair body of data is at hand which bears on this subject.

In South Africa the Middle Triassic deposits are the Molteno beds, barren of vertebrates. In East Africa, however, the Manda beds of Tanganyika are considered to be equivalent to the Molteno. They have yielded in recent years a considerable fauna. Much of the material is as yet undescribed, but its general nature is clear from various accounts by Haughton, Parrington, and von Huene (summarized by von Huene, 1950). As the last writer, who is familiar with both areas, notes, the fauna is very similar to that of Brazil. As there, the most abundant forms are rhynchosaurs and dicynodonts. The rhynchosaur (a different genus) is somewhat more primitive than the rhynchosaurs of Brazil, but there is little correlation between age and degree of specialization in rhynchosaurs. The dicynodonts are varied and generally of medium to large size, as in Brazil, and von Huene states that one of them closely resembles the Brazilian *Stahleckeria*. Also present in some variety, as in Brazil, are thecodonts and cynodonts. Von Huene notes that the thecodonts are rather comparable to those of Brazil, and one genus is very similar to *Rauisuchus* of Brazil. As in the latter region the cynodonts are but little advanced over the forms of the Cynognathus zone, and one is closely related to a Brazilian form. Also as in Brazil, there is a solitary primitive dinosaur; the two are closely related and members of the same primitive family. There is thus a remarkable similarity between South American and African reptilian faunas in the Middle Triassic; the differences are no greater than might be expected between two portions of a single continental area.

The problem of comparison with North America is more difficult. Until recently, no Triassic vertebrate fauna was known from this continent other than the faunas of the Upper Triassic, with dinosaurs and their footprints, phytosaurs, and metoposaurid amphibians as the prominent components. But persistent work by University of California parties has uncovered vertebrate remains and numerous footprints in the Moenkopi formation of the Southwest, described by Welles (1947) and Peabody (1948). The Moenkopi has been regarded as a Lower Triassic formation. The amphibian material suggests, however, that the Upper Moenkopi is rather later than had been thought, and, if not so late as Middle Triassic, is certainly close to it in time. The small amount of reptilian skeletal material so far described is not revealing. The abundant footprints, thoroughly studied by Peabody, are important for our study when the time and region of their occurrence are considered. It seems that they should literally show us the footsteps of emigrants to South America if the Brazilian Triassic fauna entered from the north. Of the footprint types most are those of chirotheres and related forms. Chirothere footprints are well known from various stages of the European Triassic; it is currently agreed that most if not all of these were made by thecodonts. Thus there is evidence of the presence in North America of forms which might have invaded South America to become the pseudosuchians of the Brazilian fauna. But what of the rhynchosaurs, dicynodonts, and cynodonts which comprise the other major elements in Brazil? Had they entered South America circuitously via the northern continents, they should be in evidence in North America at the time of deposition of the Moenkopi. The material shows no trace of any of these groups. Apart from the pseudosuchian prints, there is found a great number of footprints of lizard-like appearance, but there is not a print of the sort expected of a rhynchosaur, and there is no print that could be attributed in any way to any therapsid—dicynodont or cynodont. This is negative evidence, but rather good negative evidence. If we look to the succeeding North American fauna of the Upper Triassic, cyno-

donts and rhynchosaurs are again absent; one large dicynodont was present in this region. The absence of cynodonts is to be expected, since they nowhere survived that late. But we may note that no cynodont is known from any Triassic stage in any northern continent. If they migrated from Africa to Brazil via the north, they must have covered an immense amount of territory without leaving a trace behind. The absence of Upper Triassic rhynchosaurs appears significant, since they were present elsewhere in late Triassic times and might reasonably be expected to have survived had they been present earlier. The one dicynodont in the American Upper Triassic would seem to have been a stray invader from some other region—Asia, or possibly from South America itself.

To sum up, it is difficult to furnish Brazil with a Triassic reptile fauna from North America, since there is no evidence that most of the groups needed to stock that fauna were present in the north at the appropriate time. On the other hand, we have in Africa a contemporary fauna almost identical in nature with that of South America. To apply to the actually comparable Middle Triassic reptile faunas the type of treatment used by Colbert, the matter of identities stands as follows:

	SUB-ORDERS	FAMILIES
South America—Africa	83%	72%
South America—North America	33	?14

The evidence as it now stands strongly supports the hypothesis that some type of connection existed between Africa and South America in Middle Triassic times; the burden of proof rests upon those who wish to deny its existence. Evidence to support or refute this hypothesis should be found from the study of sediments, of paleobotany, and of invertebrate paleontology. If, as I rather suspect, objective consideration of this evidence should tend on the whole to be favorable, we may regard the hypothesis as one reasonably well established.

While the mammalian evidence seems to show clearly and decisively that in the Tertiary as now the Atlantic Ocean formed a practically impassible barrier to the passage of terrestrial organisms, the situation becomes less clear as we pass backward in time. The vertebrate evidence from the Paleozoic, as from the Triassic, suggests that in early times this barrier was, at the most, one that was readily crossed and may then have been non-existent. I have (1945) commented on the similarity between European and North American vertebrate faunas at the general level of the Pennsylvanian-Permian boundary. American faunas of the Pennsylvanian are quite similar to those of Europe (Nopcsa, 1934; Westoll, 1944). Late Devonian fish faunas of these continents are quite similar. Possibly these similarities may be due to a nearly uniform circumpolar distribution via Asia, but this is somewhat difficult to believe.

The strongest single piece of evidence for South American transatlantic connections is, of course, the case of *Mesosaurus*. This was a small, fresh-water, fish-eating reptile, whose remains are found in rocks which were close to the Pennsylvanian-Permian boundary in age. It is known in but two parts of the world: in South Africa in the Dwyka, and in Brazil in an equivalent formation. *Mesosaurus* was adapted in a moderate degree to an aquatic life, but no one would contend that it was capable of breasting the waves of the South Atlantic from one continent to the other. If we assume that its migration route between these two areas (absolute geographical extremes under orthodox theory) passed through the northern continents, it is difficult to understand why absolutely no trace of this very distinctive form has ever been found elsewhere. It has been suggested that *Mesosaurus* may have lived under environmental conditions not represented in other deposits. But we have today a great number of faunas and collecting localities of appropriate age in both North America and Europe which appear to represent a considerable variety of environments and yet with no record of the presence of *Mesosaurus*. Maintenance of orthodoxy is difficult. In the Paleozoic, or even the early Mesozoic, the present Atlantic basin may have been passable for continent dwellers without the intervention of a Mosaic miracle.

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CONCLUSION

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THIS SYMPOSIUM shows that we are in the (for a scientist) always happy situation of still being confronted by unsolved problems. However, in addition to this perhaps somewhat negative conclusion, the Symposium has also resulted in a good deal of clarification of fact and concept.

First of all, it is now universally realized that zoogeographical conclusions must be based on biological (including paleontological) evidence, and geological conclusions on geological evidence in order to avoid circular reasoning (Rensch, 1936). Subsequently, the independent conclusions of both fields must be compared to see whether or not they are in agreement. If several solutions are equally probable according to the evidence of one field, the one should be favored that is most probable according to the evidence of the other field.

Furthermore, the shortcomings of each field must be clearly realized. The zoogeographer may be able to present weighty evidence in favor of a former (more or less direct) connection between two areas, but he cannot decide between the various possible geological means (land bridge or pre-drift contact) by which such a contact could have been achieved.

The geologist must realize that there are many potential pitfalls in the interpretation of the biological evidence (Mayr, 1951). The three most common mistakes made in the course of zoogeographical research are to draw conclusions from faulty classifications, to underestimate the changes in the ranges of species and genera through geological time, and to underestimate the powers of dispersal. Simpson's illuminating discussion of dispersal (this Symposium) will go a long way towards clarifying this field. Darlington (this Symposium) shows that mere occurrence of related groups, primitive paussids, in Africa and America tells us next to nothing about the past history of Africa and South America or, for that matter, of the evolutionary history of these beetles themselves.

It is extremely difficult, if not impossible, to reconstruct former distributions and colonization routes, if there is no fossil evidence and if all conclusions must be based on the distribution pattern of the surviving living forms. Each case must be evaluated on its own merits. Not even dispersal facilities are predictable. Species of the same genus, with the same locomotor equipment, often differ strikingly in this respect. Among the 14 superspecies of drongos (Dicruridae, Aves) only three have pronounced facilities of crossing water gaps (Mayr and Vaurie, 1948). Among the white-eyes (*Zosterops*, Aves) one species (*lateralis*) bridged the more than 1000-mile gap between Australia and New Zealand within historical times (1856), while a closely related species (*rendovae*) seems to be unable to cross water gaps of less than 5 miles in width. It is therefore nearly impossible to generalize on the dispersal facilities of a given group. If one species is a poor colonizer, it does not necessarily follow that its relatives are also poor colonizers.

The difficulties of the geologist are perhaps even greater than those of the biologist. They are two-fold. He does not know to what extent similar stratigraphic sequences are the result of the same or of merely analogous events. And, secondly, he does not, or at least until recently did not, know what is under the sea. Ewing's revealing researches more than anything else have placed us on the threshold of a new era in geology. This work, together with the Bikini work (Ladd *et al.*, 1948; Dobrin *et al.*, 1949) and much other recent geological and geophysical work, has resulted in posing some challenging geological questions.

The theory of continental drift is a brilliant and very persuasive attempt to explain many puzzling situations in the history of the earth. However, as Bucher (this Symposium) shows, the facts of submarine geology cannot be harmonized with drift. There is no geological

evidence for large-scale horizontal movements.[1] On the other hand, there is a rapid accumulation of evidence for recent large-scale vertical crustal movements in the Caribbean, in the central Pacific, and in the East Indies. It is to be hoped that these recent findings will not precipitate a new boom of land-bridge constructions.

In view of these many uncertainties it becomes especially important to gather well-established facts, and the presentation of such facts is one of the notable achievements of this Symposium. Instead of a merely philosophical discussion of drift, polar shifts, and land connections *per se*, it tackled the very specific problem of history of the South Atlantic and the possibility of a direct former land connection between South America and Africa, particularly during the Mesozoic.

What light is shed on this problem by the geological, the zoological, and the botanical evidence? We are indebted to Caster (this Symposium) for an exceedingly useful summary of the South American and other geological literature dealing with this problem. He comes to the conclusion that there is considerable, if not complete, parallelism between Africa and South America from the Devonian to the end of the Triassic. "The stratigraphic and paleontological data now available still are best accounted for by the assumption of a broad continental linkage between South Africa and South America until the end of the Triassic . . . " (Caster, p. 146). Dunbar, in his discussion of these conclusions, emphasizes that other interpretations are also possible. In particular, some of the faunas of the respective period were rather widespread and others have such dispersal facilities as to disqualify them as indicators of former land connections.

Caster points out that the period of probable connection antedates the time of origin of many of the groups of animals and plants that are now flourishing. This is especially true for mammals and birds and also presumably for the angiosperms. Simpson (1940) has shown that all the South American mammals can be derived from North American ancestors. The only apparent exception, that of the hystricomorph rodents, was cleared up by Wood (1950). As far as birds are concerned, there is not a single group of South American birds the distribution of which would require a former land bridge with Africa. Whenever similar faunal elements occur in both areas, the distribution can be interpreted in terms of either one or the other of the following two explanations. Either there has been transoceanic dispersal (as, for instance, in the case of the Whistling Duck, *Dendrocygna viduata;* see Mayr, 1951) or there is a linking of the ranges via Central America and southeastern Asia. How the pan-tropical fauna could have gotten from southeast Asia to Central America is still an unsolved problem (Mayr, 1946), but it is virtually certain that no trans-Atlantic bridge is involved.

The evidence is now quite clear cut that there is no need to postulate a former connection between South America and Africa to explain the distribution of mammals or birds. In fact, all the available facts are diametrically opposed to the possibility of such a connection. However, since the main evolution of mammals and birds took place during the Tertiary and latest Mesozoic, these two groups are suitable to test continental connections in the Tertiary, but not in the earlier periods of the Mesozoic. Fishes and reptiles, on the other hand, had most of their evolution in the latter part of the Paleozoic and in the Mesozoic and are therefore specially suited for zoogeographical analyses during these periods. Since the Mesozoic is the geological period on which this Symposium concentrates, special reports were made on reptiles and fishes.

Colbert (this Symposium) gives us a most useful, concise summary of our knowledge of the distribution of the Mesozoic reptiles. For the mid-Triassic the evidence favors a trans-Atlantic African-South American connection, as admitted by Colbert and strongly emphasized by Romer (this Symposium), although additional discoveries in the very poorly known North American Triassic may lead to a modification of this conclusion.

[1] For the sake of completeness, I wish to call attention to some recent papers that have bearing on the drift problem (Knaul, 1945; Umbgrove, 1946; Himpel, 1947; Wundt, 1948; Fairbridge, 1949; Schwarzbach, 1949; Durham, 1950; King, 1950; Umbgrove *et al.*, 1951).

The evidence for the Jurassic period is insufficient for any conclusions, while in the Cretaceous the evidence is rather unequivocally in favor of an active faunal interchange between South and North America, as well as for the absence of a faunal connection between South America and Africa. These facts allow us to make a rough chronological estimate of the faunal connection between South America and Africa. It seems to have existed until at least 180 million years ago, but was no longer in existence 130 million years ago. Schaeffer (this Symposium) gives a most valuable summary of the current knowledge of the Mesozoic fishes of South America and Africa, but, as he and Dunkle (this Symposium) emphasize, the field is still too much in a flux to permit solid conclusions. The rapid advance in the knowledge of fossil fish may soon add materially to our knowledge of former continental connections.

Our knowledge of the history of faunas has been greatly enriched since the publication of Matthew's classic treatise "Climate and evolution" (1915). Matthew was inclined to consider the vast northern continents as great, if not virtually exclusive, evolutionary centers. Camp (this Symposium) points to the importance of the southern continents. It appears that the tropics (lowlands and mountains) are the greatest center of diversity, and it is possible that most temperate-zone groups can ultimately be traced to an ancestral group in the tropics. The much greater extent of the tropical belt in former periods must have enhanced this function of the tropical belt.

The problems of the former distribution of plants are more controversial than those of animals. The evidence available up to now appeared rather confusing and often in conflict with the zoological evidence. However, a consideration of the ecological factors of plant dispersal and colonization is beginning to lead to a substantial clarification (Axelrod, this Symposium). Plants are far superior to most animals in dispersal facilities but colonize much less easily and are more quickly stopped by climatic barriers. Axelrod analyzes these various factors in detail and can reconstruct a story of the evolution of the angiosperm floras that is largely consistent with the faunistic evidence. He believes that more favorable climates in the Antarctic region and an approach of the land masses to within 200 to 300 miles of each other during the Mesozoic would explain the origin of the Southern Hemisphere flora and the lack of a corresponding mammal fauna. However, it appears to me that matters are not quite so simple. Birds have the same ability as plants to cross rather easily water gaps of the order of magnitude of 200 miles, but did not develop an "antarctic type" of bird fauna. Perhaps the gaps were much wider than postulated by Axelrod, or perhaps the time of the evolution of this flora was earlier, or both. Perhaps also no circumtemperate bird fauna evolved in the Southern Hemisphere because in birds there is a more active faunal interchange between tropic and temperate zone than in plants.

Since the known history of the angiosperms does not date back beyond the middle of the Mesozoic, it is not to be expected that this group of plants will shed light on earlier land connections. Just (this Symposium) gives us an informative summary of the older plant groups, the history of which will be more decisive for this problem. In these earlier geological periods also plants will presumably be more useful for the delimitation of climatic belts than for the actual determination of connections and discontinuities. The exploration of Paleozoic and Mesozoic floras has proceeded at a sharply accelerated rate during the past two decades, and much additional important information can be expected in the future.

Even less can be said about the Paleozoic. The available zoological, botanical, and geological literature does not seem to contain sufficient data to permit us as yet to decide unequivocally on such questions as: Were the poles at the same location as they are today? Were the continents (although somewhat differently connected with each other) at approximately the same position as they are now? How far north did the tropical zones extend? Was there a Gondwana continent, and was it clearly separated from a northern continent? There is little doubt in my mind, however, that an accumulation of fossil evidence combined with an improved evaluation

of the biogeographical factors will lead to a similar clarification as has already been achieved for the Cenozoic and, as this Symposium shows, to a lesser degree also for the Mesozoic.

This much is clearly established for all geological ages, that a discontinuity in the range of a taxonomic group of animals or plants is not always best explained by postulating a direct former land bridge. The thesis of a direct connection is to be accepted only if it is consistent with the total evidence.

The scientist can be compared to the explorer who works in large mountainous regions. No sooner has he conquered one mountain than he gets the view of a whole new set of ridges and peaks which, in turn, block the view to still farther ranges. We can summarize the achievements of this Symposium by stating that we have climbed some new peaks and are now enjoying a clear view of previously obscured peaks. Let us be on our way to conquer these also so that we can see what is hidden by them!

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