

of the Canal region. His explanation of the nature of the interchange, complex communities of the Red Sea and establishment of the species that followed that direction. Colonization of the Red Sea by Red Sea organisms has, on the other hand, been a stepwise process of range expansion through the canal. For pointed out that it was probably possible only for a reduced number of species to have successfully settled in the Bitter Sea. For has published extensive subject, but we have chosen to review integrative review *One Hundred Years of Suez Canal—A Century of Migration* (paper 26), in which he discusses the possible pre-canal faunal interchange of 2,000 years and the period of range expansion.

of modern vicariance biogeographic theory of plate tectonics thus put aggregated hypotheses of jump dispersal-oceanic land bridges. Now the

majority of vicariance biogeographers accept that long-distance dispersal exists, but some still believe that it has played only a relatively minor role, superimposed on basic patterns dictated by geological history. However, new, isolated habitats like volcanic islands clearly do receive a biota from jump dispersal, and humans are effectively increasing the rate of such long distance dispersal (Elton 1958). The problem is not whether chance dispersal occurs, but more the extent to which patterns we see have been caused by it rather than by vicariance events. For example, recent studies on chameleon radiation using a combination of molecular and morphological approaches point to a greater role of oceanic dispersal than previously thought (Raxworthy, Forstner, and Nussbaum 2002). The challenge for the future is to evaluate further the influence and scale of dispersal activity, not only over an evolutionary time frame but also on an ecological one, and new and emerging techniques (such as molecular-based technologies) are already helping to make major advances on these age-old questions in biogeography.

Comparative study of present-day animal and plant kingdoms lead to the same result. The species found today on two such continents are indeed different, but the genera and families are still the same; and what is today a genus or family was once a species in prehistoric times. In this way the relationships between present-day terrestrial faunas and floras lead to the conclusion that they were once identical and that therefore there must have been exchanges, which could only have taken place over a wide land bridge. Only after the land bridge had been broken were the flora and faunas subdivided into today's various species. It is probably not an exaggeration to say that if we do not accept the idea of such former land connections, the whole evolution of life on earth and the affinities of present-day organisms occurring even on widely separated continents must remain an insoluble riddle.

Here is just one testimony amongst many: de Beaufort wrote [1895]: "Many other examples could be given to show that it is impossible in zoogeography to arrive at an acceptable explanation of the distribution of animals if no connections between today's separate continents are assumed to have existed, and not only land bridges from which, as Matthew put it, only a few planks have been removed, but also such that joined land masses now separated by deep oceans."¹

Obviously, there are many individual questions which are insufficiently explained by this theory. In many cases former land bridges have been assumed on the basis of very meagre evidence and have not been confirmed by the advance of research. In other cases there is still no complete agreement on the point in time when the connection was broken and the present-day separation began. However, in the case of the most important of these ancient land bridges, there does

¹ Arldt [1895] states: "Of course, there are today still some opponents of the land-bridge theory. Among them, G. Pfeffer is worth special mention. He starts from the point that various forms now restricted to the southern hemisphere are manifest as fossils in the northern hemisphere. This precludes any doubt, he says, that these forms were once more or less universally distributed. If this conclusion is not completely compelling, still less is the further conclusion that we should assume a universal distribution even in all cases where there is a discontinuous distribution in the south but no fossil evidence as yet in the north. If he wants to explain distribution anomalies solely by migrations between the northern continents and their mediterranean bridges, the assumption rests on a very uncertain footing." That the affinities found on the southern continents can be explained more simply and completely by direct land bridges than by parallel migrations from the common northern region will require no further comment, even though in individual cases the process could have been the one that Pfeffer assumed.

From *The Origin of Continents and Oceans* 1924
Alfred Wegener

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4th Ed. London: Methuen,
1929
CHAPTER 2

*The Nature of the Drift Theory
and Its Relationship to Hitherto Prevalent
Accounts of Changes in the Earth's Surface
Configuration in Geological Times*

It is a strange fact, characteristic of the incomplete state of our present knowledge, that totally opposing conclusions are drawn about prehistoric conditions on our planet, depending on whether the problem is approached from the biological or the geophysical viewpoint.

Palaeontologists as well as zoo- and phyto-geographers have come again and again to the conclusion that the majority of those continents which are now separated by broad stretches of ocean must have had land bridges in prehistoric times and that across these bridges undisturbed interchange of terrestrial fauna and flora took place. The paleontologist deduces this from the occurrence of numerous identical species that are known to have lived in many different places, while it appears inconceivable that they should have originated simultaneously but independently in these areas. Furthermore, in cases where only a limited percentage of identities is found in contemporary fossil fauna or flora, this is readily explained, of course, by the fact that only a fraction of the organisms living at that period is preserved in fossil form and has been discovered so far. For even if the whole groups of organisms on two such continents had once been absolutely identical, the incomplete state of our knowledge would necessarily mean that only part of the finds in both areas would be identical and the other, generally larger, part would seem to display differences. In addition, it is obviously the case that even where the possibility of interchange was unrestricted, the organisms would not have been quite identical in both continents; even today Europe and Asia, for example, do not have identical flora and fauna by any means.

already exist today a gratifying unanimity among specialists, whether they base their conclusions on geographical distribution of the mammals or earthworms, on plants or on some other portion of the world of organisms. Arldt [11], using the statements or maps of twenty scientists,² has drawn up a sort of table of votes for or against the existence of the different land bridges in the various geological periods. For the four chief bridges, I have presented the results graphically in Figure 1. Three curves are shown for each

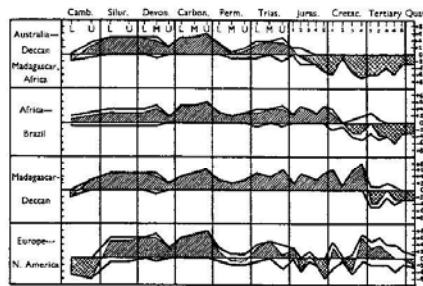


FIG. 1. The number of proponents (upper curves) and opponents (lower curves) of the existence of four land bridges since Cambrian times.

The difference (majority) is hatched, and crosshatched when the majority opposes.

bridge—the number of years, the number of rays and the difference between them, i.e., the strength of the majority vote, which is emphasised by hatching the appropriate area. Thus, the top section indicates that according to the majority of researchers the bridge between Australia on the one side and India, Madagascar and Africa

² Arldt, Burekhardt, Diener, Frech, Fritz, Handlirsch, Haug, von Ihering, Karpinsky, Koken, Kossmat, Katzer, Lapparent, Matthew, Neumayr, Ortmann, Osborn, Schachert, Uhlig and Willis.

(ancient "Gondwanaland") on the other lasted from Cambrian times to the beginning of the Jurassic, but was then disrupted. The second section shows that the old bridge between South America and Africa ("Arch-helienis") is considered by most to have broken in the Lower to Middle Cretaceous. Still later, at the transition between Cretaceous and Tertiary, the old bridge between Madagascar and the Deccan ("Lemuria") is assumed by the majority to have broken (see section 3 of Fig. 1). The land bridge between North America and Europe was very much more irregular, as shown by section 4. But even here there is a substantial measure of agreement in spite of the frequent change in the behaviour of the curves. In earlier times the connection was repeatedly disturbed, i.e., in the Cambrian, Permian and also Jurassic and Cretaceous periods, but apparently only by shallow "transgressions," which permitted subsequent re-formation. However, the final breach, corresponding now to a broad stretch of ocean, can only have occurred in the Quaternary, at least in the north near Greenland.

Many of the details of this will be treated later in the book. Only one point is stressed here, so far not considered by the exponents of the land-bridge theory, but of great importance: These former land bridges are postulated not only for such regions as the Bering Strait, where today a shallow continental-shelf sea, or floodwater fills the gap, but also for regions now under ocean waters. All four examples in Figure 1 involve cases of this latter type. They have been chosen deliberately because it is precisely here that the new concept of drift theory begins, as we have yet to show.

Since it was previously taken for granted that the continental blocks—whether above sea level or inundated—have retained their mutual positions unchanged throughout the history of the planet, one could only have assumed that the postulated land bridges existed in the form of intermediate continents, that they sank below sea level at the time when interchange of terrestrial flora and fauna ceased and that they form the present-day ocean floors between the continents. The well-known palaeontological reconstructions arose on the basis of such assumptions, one example of them, for the Carboniferous, is given in Figure 2.

This assumption of sunken intermediate continents was in fact the most obvious so long as one based one's stand on the theory of the contraction or shrinkage of the earth, a viewpoint we shall have to examine more closely in what follows. The theory first appeared in

Ever since our geological knowledge was made the subject of that impressive synthesis, the four volumes by Eduard Suess entitled *Das Antlitz der Erde*, written from the standpoint of contraction theory, there has been increasing doubt as to the correctness of the basic idea. The conception that all uplifts are only apparent and consist merely of remnants left from the general tendency of the crust to move towards the centre of the earth, was refuted by the detection of absolute uplifts [71]. The concept of a continuous and ubiquitous arching pressure, already disputed on theoretical grounds for the uppermost crust by Hergesell [184] has proved to be untenable because the structure of eastern Asia and the eastern African rift valleys have, on the contrary, enabled one to deduce the existence of tensile forces over large portions of the earth's crust. The concept of mountain folding as crustal wrinkling due to internal shrinkage of the earth led to the unacceptable result that pressure would have to be transmitted inside the earth's crust over a span of 180 great-circle degrees. Many authors, such as Ampferer [18], Reyer [14], Rudzki [15] and André [16], among others, have opposed this quite rightly, claiming that the surface of the earth would have to undergo regular overall wrinkling, just as the drying apple does. However, it was particularly the discovery of the scale-like "sheet-fault structure" or overthrusts in the Alps which made the shrinkage theory of mountain formation, which presented enough difficulties in any case, seem more and more inadequate. This new concept of the structure of the Alps and that of many other ranges, which was introduced by the works of Bertrand, Schardt, Lugeon and others, leads to the idea of far larger compressions than did the earlier theory. Following previous ideas, Heim calculated in the case of the Alps a 50% contraction, but on the basis of the sheet-faulting theory, now generally accepted, contraction of $\frac{1}{3}$ to $\frac{1}{4}$ of the initial span [17]. Since the present-day width of the chain is about 150 km, a stretch of crust from 600 to 1200 km wide (5–10 degrees of latitude) must have been compressed in this case. Yet in the most recent large-scale synthesis on Alpine sheet-faults, R. Staub [18] agrees with Argand that the compression must have been even greater. On page 257 he concludes:

"The Alpine orogenesis is the result of the northward drift of the African land mass. If we smooth out only the Alpine folds and sheets over the transverse section between the Black Forest and Africa, then

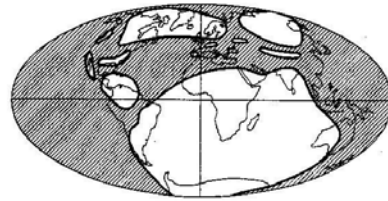


FIG. 2. Distribution of water (hatched) and land in the Carboniferous, according to the usual conception.

Europe. It was initiated and developed by Dana, Albert Heim and Eduard Suess in particular, and even today dominates the fundamental ideas presented in most European textbooks of geology. The essence of the theory was expressed most succinctly by Suess: "The collapse of the world is what we are witnessing" [19, Vol. 1, p. 778]. Just as a drying apple acquires surface wrinkles by loss of internal water, the earth is supposed to form mountains by surface folding as it cools and therefore shrinks internally. Because of this crustal contraction, an overall "arching pressure" is presumed to act over the crust so that individual portions remain uplifted as horsts. These horsts are, so to speak, supported by the arching pressure. In the further course of time, these portions that have remained behind may sink faster than the others and what was dry land can become sea floor and vice-versa, the cycle being repeated as often as required. This idea, put forth by Lyell, is based on the fact that one finds deposits from former seas almost everywhere on the continents. There is no denying that this theory provided historic service in furnishing an adequate synthesis of our geological knowledge over a long period of time. Furthermore, because the period was so long, contraction theory was applied to a large number of individual research results with such consistency that even today it possesses a degree of attractiveness, with its bold simplicity of concept and wide diversity of application.

in relation to the present-day distances of about 1800 km, the original distance separating the two must have been about 3000 to 3500 km, which means an alpine compression (in the wider sense of the word Alpine) of around 1600 km. Africa must have been displaced relative to Europe by this amount. What is involved here is a true continental drift of the African land mass and an extensive one at that.³

Other geologists have put forward similar views, as for example F. Hermann [106], E. Hemig [19] or Kossmat [21], who states "that the formation of mountains must be explained by large-scale tangential movements of the crust, which cannot be incorporated in the scope of the simple contraction theory." In the case of Asia, Argand [20], especially, has developed an analogous theory in the course of a comprehensive investigation to which we shall return later. He and Staub have done the same for the case of the Alps. No attempt to relate these enormous compressions of the crust to a drop in temperature of the earth's core can be anything but a failure.

Moreover, even the apparently obvious basic assumption of contraction theory, namely that the earth is continuously cooling, is in full retreat before the discovery of radium. This element, whose decay produces heat continuously, is contained in measurable amounts everywhere in the earth's rock crust accessible to us. Many measurements lead to the conclusion that even if the inner portion had the same radium content, the production of heat would have to be incomparably greater than its conduction outwards from the centre, which we can measure by means of the rise of temperature with depth in mines, taking into account the thermal conductivity of rock. This would mean, however, that the temperature of the earth must rise continuously. Of course, the very low radioactivity of iron meteorites suggests that the iron core of the earth presumably contains much less radium than the crust, so that this paradoxical conclusion can

³ It seems that estimations of the size of the Alpine compression are always on the increase. Staub wrote recently [214, similarly in 215]: "If we now, however, imagine these Alpine sheets, which are probably stacked twelvefold, to be smoothed out again . . . the solid Alpine hinterland would necessarily lie much further south, and the original distance between foreland and hinterland would probably have been ten to twelve times greater than it is today." He adds: "Formation of a mountain range therefore originates quite clearly and certainly from independent drifting of larger blocks, solely continental blocks by their structure and composition; and thus, starting from Alpine geology and Hans Scharit's sheet theory, we arrive quite obviously and naturally at the acknowledgment of the basic principle of the great Wegener theory of continental drift."

perhaps be avoided. In any case, it is no longer possible, as it once was, to consider the thermal state of the earth as a temporary phase in the cooling process of a ball that was formerly at a higher temperature. It should be regarded as a state of equilibrium between radioactive heat production in the core and thermal loss into space. In fact, the most recent investigations into this question, which will be discussed in more detail later on, imply that actually, at least under the continental blocks, more heat is generated than is conducted away, so that here the temperature must be rising, though in the ocean basins conduction exceeds production. These two processes lead to equilibrium between production and loss rate, taking the earth as a whole. In any case, one can see that through these new views the foundation of the contraction theory has been completely removed.

There are still many other difficulties which tell against the contraction theory and its mode of thinking. The concept of an unlimited periodic interchange between continent and sea floor, which was suggested by marine sediments on present-day continents, had to be strictly curtailed. This is because more precise investigation of these sediments showed with increasing clarity that what was involved was coastal-water sediments, almost without exception. Many sedimentary deposits formerly claimed as oceanic proved to be coastal: one example is chalk, as proved by Cayeux. Dacqué [29] has given a good review of the problem. Only in the case of a very few types of sediment, such as the low-lime Alpine radiolites and certain red clays reminiscent of the red deep-sea clay, is formation in deep waters (4-5 km) still assumed today, particularly since sea water dissolves out lime only at great depths. However, the area of these true deep-sea deposits on present-day continents is so tiny compared with the areas of the continents and the areas of coastal water sediments on them that the theory of the basically shallow-water nature of marine fossil deposits on present-day continents is unaffected. For the contraction theory, however, a considerable difficulty arises. Since coastal shallows must be counted, geophysically, as part of the continental blocks, the nature of these marine fossils implies that these blocks have been "permanent" throughout the history of the earth and have never formed ocean floors. Are we then still to assume that today's sea floors were ever continents? The justification for this conclusion is obviously removed by establishing that the marine sediments found on continents were formed in shallows. But more than this, the conclusion now leads to an open contradiction. If we

lines formed during the process of depression are elevated along with the crust. The "isobase charts" of de Geer [25], drawn up from the shore lines, show for the last glaciation of Scandinavia a central depression of at least 250 m, gradually decreasing towards the perimeter; for the most extensive of the Quaternary glaciations still higher values must be assumed. In Figure 3 we reproduce a chart



FIG. 3. Post-glacial elevation contours (in metres) for Fennoscandia (according to Högbom).

of this post-glacial elevation of "Fennoscandia" (Finland, Sweden and Norway) according to Högbom (taken from Born [48]). The same phenomenon has been proved by de Geer to have occurred for the glaciated region of North America. Rudzki [16] has shown that, assuming isostasy, plausible values for the thickness of inland ice layers can be calculated, i.e., 930 m for Scandinavia and 1670 m for North America, where the depression amounted to 500 m. Because of the viscosity of the substrate the equilibration movements naturally lag far behind: the shore lines generally formed only after the

reconstruct intercontinental bridges of the type shown in Figure 2, thus filling up a large part of today's ocean basins without having the possibility of compensating for this by submergence of present-day continental regions to the sea-floor level, there would be no room for the volume of the world's oceans in the now much reduced deep-sea basins. The water displacement of the intercontinental bridges would be so enormous that the level of the world's oceans would rise above that of the whole continental area of the earth and all would be flooded, today's continents and the bridges alike. The reconstruction would not therefore achieve the desired end, i.e., dry land bridges between continents. Figure 2 therefore represents an impossible reconstruction unless we introduce further hypotheses which are "ad hoc" improbabilities; for example, that the mass of ocean water was exactly the required amount less at the former period than it is today, or that the deep-sea basins remaining at that time were precisely the required amount deeper than today. Willis and A. Penck, among others, have brought up this peculiar difficulty.

Of the many objections to contraction theory, one more only will be emphasised: it has very special importance. Geophysicists have decided, mainly on the basis of gravity determinations, that the earth's crust floats in hydrostatic equilibrium on a rather denser, viscous substrate. This state is known as *isostasy*, which is nothing more than hydrostatic equilibrium according to Archimedes' principle, whereby the weight of the immersed body is equal to that of the fluid displaced. The introduction of a special word for this state of the earth's crust has some point because the liquid in which the crust is immersed apparently has a very high viscosity, one which is hard to imagine, so that oscillations in the state of equilibrium are excluded and the tendency to restore equilibrium after a perturbation is one which can only proceed with extreme slowness, requiring many millennia to reach completion. Under laboratory conditions, this "liquid" would perhaps scarcely be distinguishable from a "solid." However, it should be remembered here that even with steel, which we certainly consider a solid, typical flow phenomena occur, just before rupture, for example.

An example of perturbation of isostasy of the crust is shown by the load to which an inland icecap subjects it. The result is that the crust slowly sinks under this load and tends towards a new equilibrium position to correspond with the loading. When the icecap has melted, the original position of equilibrium is gradually resumed, and the shore

melting of the ice, but before the elevation of the land, and even today Scandinavia is still rising by about 1 m in 100 years, as shown by tide-gauge readings.

Even sedimentary deposits result in a subsidence of the blocks, as Osmond Fisher was probably the first to recognise: every deposition from above leads to a subsidence of the block, somewhat delayed of course, so that the new surface occupies almost the same level as the old. In this way many kilometres' thickness of deposit can arise and yet all the layers are formed in shallow water.

Later on we shall examine the theory of isostasy more closely. Here we shall simply say that it has been established by geophysical observations over so wide a range that it is now part of the solid foundation of geophysics and its basic truth can no longer be doubted.⁴

One can see immediately that this result runs quite counter to the ideas of contraction theory and that it is very hard to combine one with the other. In particular, it seems impossible, in view of the isostatic principle, that a continental block the size of a land bridge of required size could sink to the ocean bottom without a load or that the reverse should happen. Isostasy is therefore in contradiction not only to contraction theory, but in particular also to the theory of sunken land bridges as derived from the distribution of organisms.⁵

⁴ Americans, e.g., Taylor [101], sometimes mean by "isostasy" Bowie's theory of the origin of geosynclines and mountain ranges. According to Bowie [224], the initial elevation of sediment-filled basins, the geosynclines, comes from a rise in their isotherms, and hence a volumetric expansion. Once this has led to a land elevation, erosion sets in and a jagged mountain range is formed, whose substrate continually rises due to reduction in loading. Finally, the isotherms are raised to an abnormal height by this elevation, and begin to move slowly downwards; the block cools and contracts and the surface sinks; a depression is formed from the mountain region and renewed sedimentation occurs. This produces further depression or subsidence until the isotherms are abnormally low in level, then rise again, and so on over many cycles. This concept, which cannot be applied to the great folded ranges with their overthrusts, as Taylor and others have emphasised, does indeed make use of the principle of isostasy but should not be given the simple title of "the theory of isostasy."

⁵ The objections to the contraction theory enumerated here are mainly directed against its typical earlier form. Very recently, attempts have been made to modernise the theory and to answer the objections, partly by restricting it and partly by adding hypotheses; various authors have been involved, such as Kober [24], Stille [22], Nöelke [26], and Jeffreys [102], among others. This is also true of the theory publicised by R. T. Chamberlin [160] which supposes contraction to be caused by "rearrangement" of material in the earth resulting from the planetesimal origin of the earth accepted by this author. Although one cannot deny

In the foregoing, we deliberately reviewed the objections to contraction theory in some detail. This is because in one part of the train of thought discussed here another theory is rooted; this is known as the "theory of permanence" and is especially widespread among American geologists. Willis [27] formulated it as follows: "The great ocean basins constitute permanent features of the earth's surface, and have with little change in shape occupied the same positions as now since the ocean waters were first gathered." In fact, we have already referred above to the fact that the marine sediments on present-day continents were formed in shallow waters, and we deduced that the continental blocks as such have been permanent throughout the earth's history. Isostasy theory proves the impossibility of regarding present-day ocean floors as sunken continents, and this extends the scope of the result based on marine sediments to comprise a general permanence of deep-sea floors and continental blocks. Further, since here, too, the apparently obvious assumption was made that the continents have not changed their relative positions, Willis's formulation of the "permanence theory" appears to be a logical conclusion from our geophysical knowledge, disregarding, of course, the postulate of former land bridges, derived from the distribution of organisms. So we have the strange spectacle of two quite contradictory theories of the prehistoric configuration of the earth being held simultaneously—in Europe an almost universal adherence to the idea of former land bridges, in America to the theory of the permanence of ocean basins and continental blocks.

It is probably no accident that the permanence theory has its most numerous adherents in America; geology developed late there—thus simultaneously with geophysics—and this necessarily led to more rapid and complete adoption by geology of the results advanced by its sister science than in Europe. There was absolutely no temptation to make the contraction theory, which contradicts geophysics, one of the basic assumptions. It was quite otherwise in Europe, where geology already had a long period of development behind it before geophysics had produced its first results, and had, without benefit of geophysics, already arrived at an overall view of

that these attempts show a certain adroitness in pursuit of their aim, one cannot say that they really refute the objections, nor that they have brought the contraction theory into satisfactory agreement with new research, especially in the field of geophysics. A thorough discussion of this neo-contraction theory must, however, be dispensed with here.

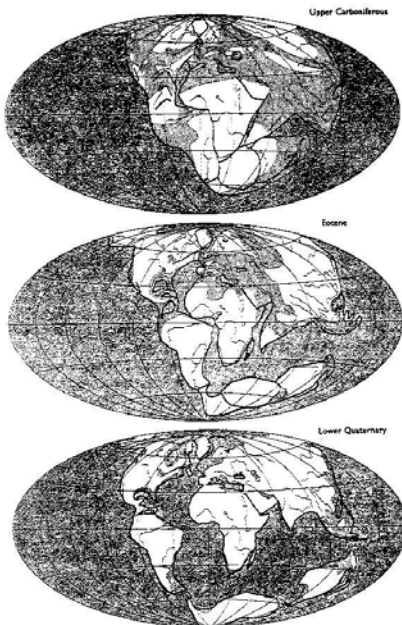


FIG. 4. Reconstruction of the map of the world according to drift theory for three epochs. Hatching denotes oceans, dotted areas are shallow seas; present-day outlines and rivers are given simply to aid identification. The map grid is arbitrary (present-day Africa as reference area; see Chapter 8).

the earth's evolution in the form of the contraction theory. It is quite understandable that it is difficult for many European scientists to free themselves completely from this tradition and that they view the results of geophysics with a mistrust that never completely fades.

However, where does the truth lie? The earth at any one time can only have had one configuration. Were there land bridges then, or were the continents separated by broad stretches of ocean, as today? It is impossible to deny the postulate of former land bridges if we do not want to abandon wholly the attempt to understand the evolution of life on earth. But it is also impossible to overlook the grounds on which the exponents of permanence deny the existence of sunken intermediate continents. There clearly remains but one possibility: there must be a hidden error in the assumptions alleged to be obvious.

This is the starting point of displacement or drift theory. The basic "obvious" supposition common to both land-bridge and permanence theory—that the relative position of the continents, disregarding their variable shallow-water cover, has never altered—must be wrong. The continents must have shifted. South America must have lain alongside Africa and formed a unified block which was split in two in the Cretaceous; the two parts must then have become increasingly separated over a period of millions of years like pieces of a cracked ice floe in water. The edges of these two blocks are even today strikingly congruent. Not only does the large rectangular bend formed by the Brazilian coast at Cape São Roque mate exactly with the bend in the African coast at the Cameroons, but also south of these two corresponding points every projection on the Brazilian side matches a congruent bay on the African, and conversely. A pair of compasses and a globe will show that the sizes are precisely commensurate.

In the same way, North America at one time lay alongside Europe and formed a coherent block with it and Greenland, at least from Newfoundland and Ireland northwards. This block was first broken up in the later Tertiary, and in the north as late as the Quaternary, by a forked rift at Greenland, the sub-blocks then drifting away from each other. Antarctica, Australia and India up to the beginning of the Jurassic lay alongside southern Africa and formed together with it and South America a single large continent, partly covered by shallow water. This block split off into separate blocks in the course of the Jurassic, Cretaceous and Tertiary, and the sub-blocks drifted

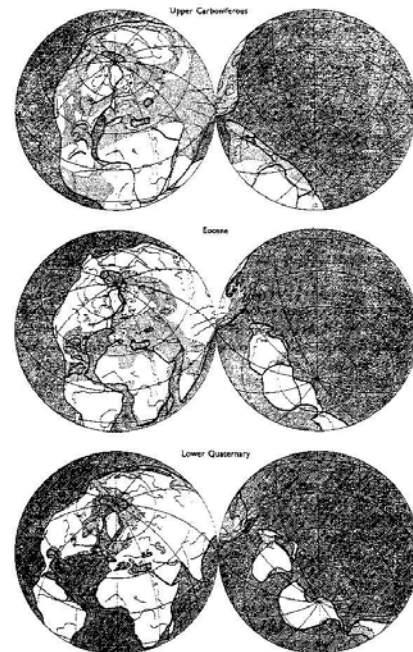


FIG. 5. Same as Fig. 4, in different projection.

away in all directions. Our three world maps (Figs. 4 and 5) for the Upper Carboniferous, Eocene and Lower Quaternary show this evolutionary process. In the case of India the process was somewhat different: originally it was joined to Asia by a long stretch of land, mostly under shallow water. After the separation of India from Australia on the one hand (in the early Jurassic) and from Madagascar on the other (at the transition from Tertiary to Cretaceous), this long junction zone became increasingly folded by the continuing approach of present-day India to Asia; it is now the largest folded range on earth, i.e., the Himalaya and the many other folded chains of upland Asia.

There are also other areas where the continental drift is linked causally with orogenesis. In the westward drift of both Americas, their leading edges were compressed and folded by the frontal resistance of the ancient Pacific floor, which was deeply chilled and hence a source of viscous drag. The result was the vast Andean range which extends from Alaska to Antarctica. Consider also the case of the Australian block, including New Guinea, which is separated only by a shelf sea: on the leading side, relative to the direction of displacement, one finds the high-altitude New Guinea range, a recent formation. Before this block split away from Antarctica, its direction was a different one, as our maps show. The present-day east coastline was then the leading side. At that time New Zealand, which was directly in front of this coast, had its mountains formed by folding. Later as a result of the change in direction of displacement, the mountains were cut off and left behind as island chains. The present-day cordilleran system of eastern Australia was formed in still earlier times; it arose at the same time as the earlier folds in South and North America, which formed the basis of the Andes (pre-cordilleras), at the leading edge of the continental blocks, then drifting as a whole before dividing.

We have just mentioned the separation of the former marginal chain, later the island chain of New Zealand, from the Australian block. This leads us to another point: smaller portions of blocks are left behind during continental drift, particularly when it is in a westerly direction. For instance, the marginal chains of East Asia split off as island arcs, the Lesser and Greater Antilles were left behind by the drift of the Central American block, and so was the so-called Southern Antilles arc (South Shetlands) between Tierra del Fuego and western Antarctica. In fact, all blocks which taper off towards

the south exhibit a bend in the taper in an easterly direction because the tip has trailed behind; examples are the southern tip of Greenland, the Florida shelf, Tierra del Fuego, the Graham Coast and the continental fragment Ceylon.

It is easy to see that the whole idea of drift theory starts out from the supposition that deep-sea floors and continents consist of different materials and are, as it were, different layers of the earth's structure. The outermost layer, represented by the continental blocks, does not cover the whole earth's surface, or it may be truer to say that it no longer does so. The ocean floors represent the free surface of the next layer inwards, which is also assumed to run under the blocks. This is the geophysical aspect of drift theory.

If drift theory is taken as the basis, we can satisfy all the legitimate requirements of the land-bridge theory and of permanence theory. This now amounts to saying that there were land connections, but formed by contact between blocks now separated, not by intermediate continents which later sank; there is permanence, but of the area of ocean and area of continent as a whole, but not of individual oceans or continents.

Detailed substantiation of this new concept will form the chief part of the book.

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PAPER 20

From *Transantarctic Relationships and Their Significance, as Evidenced by Chironomid Midges*

Lars Brundin

IV. THE NATURE OF TRANSANTARCTIC RELATIONSHIPS

CHIRONOMID MIDGES AS INDICATORS IN AUSTRAL BIOGEOGRAPHY

With the above monograph of three comparatively high-ranked midge groups as a background is prepared for a discussion of the true nature of transantarctic relationships and their general sign. Before that it seems appropriate, however, to raise the question: What about the general suitability of midges as indicators in biogeography? Is it, after all, advisable to try to answer intricate questions as to the history of the austral biotas and the existence or non-existence of former land connections on the basis of these small and fragile midges of the cool mountain streams? Are there not many groups which would give a more reliable evidence of general applicability?

We are here touching upon a subject which has been strongly coloured by misconceptions. The common belief that vertebrates and higher plants are the best organisms for biogeographic work they are so "well known". But the knowledge of ecology, biology, and distribution, however deficient for biogeographic analyses. Many biologists realize, it is true, that a proper insight into extrinsic and intrinsic relationships is absolutely essential for the interpretation of the history of but only few seem to be fully aware of the fact that all endeavour to interpret relationships in fact arguments are based on typological thinking. Referring to our discussions in the foregoing chapters it may be stated that the present plant and animal systems still are largely typological, meaning that the five components of the different aggregates generally are parapatrytic. Only few have drawn the line of conclusion of this, Darlington is not among those. He stresses in his *Zoogeography* (1957) that the ships of many groups are still unsettled and continues (p. 28):

"There is not much that zoogeographers can do about this until taxonomists improve the poor classification of many groups. Zoogeographers should work as much as possible with the best-known groups of animals, unless classifications are imperfect, and proceed cautiously. Taxonomic experience is useful, almost essential, to zoogeographers. An experienced taxonomist knows what classifications are and what other taxonomists mean when about relationships. Also (but this is less important) a taxonomist can sometimes suspect unworked classifications of animals with which he is not familiar, much as an engineer might suspect an unworked bridge even if it built it himself."

"But this is the dark side of the matter. The bright side is that the facts now known of the geographical and classification of at least of vertebrates are good enough."

It is significant of the confused situation in biogeography of today that the opinion of Darlington encountered weak resistance. That the interpretation of the phylogenetic relationships is most satisfactory even among the mammals, was demonstrated above in the section on "The shortcoming of the typological method". A principal prerequisite for an understanding of the main trends in the earth of the placentals is of course the establishment of the sister group relationships of such high-ranks as the Insectivora, Primates, Edentata, Glires, Proboscidea, Hyracoidea, Tubulidentata, etc. Relationships are, however, very poorly known. But according to Darlington the classification of vertebrates is "good enough" for biogeographic analysis. This is fatal optimism. When Darlington wrote his dis-