

# American Journal of Science

JANUARY 1943

---

## MAMMALS AND THE NATURE OF CONTINENTS.

GEORGE GAYLORD SIMPSON.

**ABSTRACT.** There are three alternative fundamental hypotheses as to the nature of continents: that they are crustal segments permanent as entities but variable in position (drift hypothesis), that crustal positions do not vary significantly but continental segments and ocean basins do (transoceanic continents hypothesis), and that neither crustal positions nor the major distribution of continental and oceanic segments have varied greatly during at least the later stages of earth history (stable continents hypothesis). Biological data are important in choice between these hypotheses, but their compilation and treatment in the paleogeographical literature are usually inaccurate and often quite irresponsible. One part of this evidence, that derived from mammalian distribution, is here reviewed.

The broader outlines of the past and present distribution of mammals on northern and on southern continents are separately examined, as far as they bear on choice between the three basic hypotheses. Examples of miscomprehension and misquotation are given. The evidence definitely opposes drifting or transoceanic continents and favors stable continents. Statements of intercontinental faunal resemblances are often misleading and their interpretations have usually been subjective, unreliable, and unscientific. A possible valid and more objective method is suggested and it is shown that preliminary study along these lines again favors stable continents.

The history of a widely accepted but manifestly ill-founded transoceanic connection is sketched and the related theory of accordion continents is mentioned. Attempts to relate drift theories to the mammalian fauna of Madagascar are adversely criticized.

### INTRODUCTION.

IN the course of repulsing an attack on the Wegener theory, W. A. J. M. van Waterschoot van der Gracht (1928, p. 224) annihilated the paleontological arguments by saying, "There are few subjects where there exists a greater diversity of opinions regarding practically everything than in paleontology." The remark was made in the course of a symposium on continental drift that exemplified greater diversity of opinions than paleontology can offer. Doctor van der Gracht's dictum becomes amusing when it is noticed that on his particular

subject the verdict of paleontologists is practically unanimous: almost all agree in opposing his views, which were essentially those of Wegener. For instance in canvassing opinions at some length, Du Toit (1937, Chapter II) was able to cite no paleontologists as active protagonists of continental drift and only one as sympathetic with it—this one, Seward, is a specialist on the anatomy of primitive plants and as regards the drift theory he disagrees with a clear consensus of the paleobotanists more immediately concerned with phytogeography (e. g., Berry, 1928; Chaney, 1940).

The fact that almost all paleontologists say that paleontological data oppose the various theories of continental drift should, perhaps, obviate further discussion of this point and would do so were it not that the adherents of these theories all agree that paleontological data do support them. It must be almost unique in scientific history for a group of students admittedly without special competence in a given field thus to reject the all but unanimous verdict of those who do have such competence.

Aside from the perennial subject of continental drift, it is true that paleontologists disagree as to the nature of past connections between the continents. The most fundamental of all questions of paleogeography and historical biogeography deals with the past stability of continental areas and the nature of their relationships to each other. There are innumerable theories as to details, but all may be classed under three heads with respect to this fundamental point. One school maintains that the continents are permanent crustal segments but that their positions relative to each other have changed radically—the hypothesis of continental drift. A second school believes that the relative positions of points on the globe have not changed significantly but that the configuration of land and sea has been radically altered and specifically that continental areas have extended right across the present major ocean basins—this may be called the hypothesis of trans-oceanic continents. The third school supposes that the present relationships of major lands and great sea basins have been approximately constant, aside from rather local changes of contour and changes of relative level—the hypothesis of stable continents. The second and third schools are not mutually exclusive or sharply defined, but together they stand in absolute contrast to the first.

Unlike geological paleogeographers, the students of land faunas are not directly or greatly concerned with the details of coastlines. Their conceptions of continental individuality and stability are broad and relative. For instance an extension of a land area even for several hundred miles beyond a present coast is not likely to be detectable in their materials or to concern them unless this extension was a separate center of evolution or was a path of migration between lands separate at other times. Their continents are diagrammatic, not pictorial, and the paleozoölogist's use of such a term as "stable continent" may lead to misunderstanding unless this distinction of viewpoint is recognized.

To avoid becoming too diffuse, this discussion will refer principally to particular forms of the highly varied theories representative of each school. The leading exponents of continental drift are Wegener, especially 1924, and Du Toit, especially 1937. Advocates of transoceanic continents are legion, but particular reference will be made to J. W. Gregory, especially 1929 and 1930, with some notice of von Ihering, especially 1927, whose work strongly influenced Gregory. The postulate of stable continents is supported by many biogeographers and most paleomammalogists, among whom may be mentioned Osborn, especially 1910, and Matthew, especially 1915. Some of these cited works are old, but the subject is decidedly current as shown, for instance, by the cautiously Wegenerian review by Holland (1941) and much other recent discussion.

The study of continental relationships involves so broad a synthesis of so many different fields that it is not surprising to find that the large, growing literature abounds in mistakes and misapprehensions. Once in print, such ill-advised or erroneous statements seem to take on a life of their own and to be almost impossible to eradicate. A striking example, the *Hipparion*-bridge, will be reviewed in this paper. Many of these lamentable items have arisen and all of them have been perpetuated by the uncritical acceptance of irresponsible or obsolete publications and by the frequently inaccurate copying of the compilers one from another without examination of the original data. It is therefore clear that study of the evidence in a single field and from the sources is now more useful than another compilation and will help to provide a better basis for future compilations.

The evidence of mammals on these questions is limited both in time and in scope. It must be judged in the light of other biological and geological data and cannot be presented without some implications as to these broader fields. It is not claimed that the mammalian evidence alone is conclusive for the Cenozoic or that if it were, the same conclusions would have to be extended to previous eras. This evidence is nevertheless both pertinent and indicative, as has been recognized by leading advocates of all three schools.

#### TIME AND PLACE OF INTERCONTINENTAL CONNECTIONS.

It is universally admitted that the distribution of land mammals and of other forms of terrestrial life is only explicable if some continents now separate, e. g. North America and Asia, have formerly been united and if some now united, e. g. North and South America, have formerly been separate. Much of the discussion of paleontological evidence for and against particular sorts of connections have been devoted to the proposition that stated connections did or did not exist. In so simple a form, this discussion is not always pertinent to the problem, because all paleogeographic systems admit and demand that connections did exist. Holland, who does not take much account of land faunas in his tentative advocacy of drift, says (1941, p. 151), "Evidently the facts of life distribution, whether past or present, would fit equally both parties." One of the purposes of the following discussion is to demonstrate that this is not true. Different paleogeographic theories provide continental connections different in kind and in sequence. These differences would tend to produce different sorts of faunal relationships. The observed faunal relationships are more consistent with some connections than with others and therefore do not fit equally drift and stable continent theories, even though they might possibly be made to fit either to some extent.

Drift theories do not necessarily but do usually involve fairly uniform motion for each crustal segment, at least during that part of geological time in which mammalian distribution was effected. Some irregularities may be permitted, but the mechanics of drift, already sufficiently obscure, would almost defy rational explanation if segmental oscillation were postulated. (Such a theory as that of Joleaud's accordion con-

tinents, mentioned on a later page, can here be dismissed as an aberration). The usual drift theories start later Paleozoic to Recent history with one (Wegener) or two (Du Toit) continental masses which then split. The fragments drift apart and this relative motion may also tend to bring some fragments together in a different order. The exact sequence of splitting and drifting is subject to secondary interpretation. An essential point for present purposes is not so much this sequence as the inference that such making and breaking of contacts is not cyclic. Subject to various modifications and supplements, a given connection has but two phases, union-separation or separation-union, during the time of land vertebrate dispersal.

Theories of transoceanic continents have some of the same implications as drift theories. They also start with continents, now separate, then broadly and firmly united. The oceans now intervening are supposed to have developed by the foundering of large segments of these old continents. In general this foundering is represented as progressive and definitive, but some cyclic action is not wholly excluded.

There are students, land-bridge makers, who take various intermediate positions between the adherents of transoceanic continents and those of stable continents. They tend to accept the same positions for the connections as transoceanic continents, routes crossing what are now major oceans, but suppose the connections to have been less definitive, more fluctuating, and narrower. On purely biological grounds, their intermediate character leaves few definite criteria to distinguish such connections from transoceanic continents, on one hand, or the migration routes between stable continents, on the other.

Advocates of stable continents believe that intercontinental routes were approximately fixed in position, through the land vertebrate phases of history, at least, but fluctuated in their availability as migration routes because of repeated, often roughly cyclic, relatively shallow flooding. The number of such routes to be admitted is held at a minimum. The present connection of Europe and Asia, now at its greatest, that of Africa and Eurasia, formerly greater, and that of North and South America, now somewhat but not much below its maximum, are obvious. The now inoperative but still quite obvious Bering route is admitted by all. An older and now

more obscure North America-Europe connection over Greenland is usually, but not universally accepted. Fewer students of this school than of the others admit direct land migration routes between the southern continents, but those who do admit them usually place these through Antarctica. Except for the Eurasia-Africa mass, all the connections postulated in this type of theory approximate isthmian links as defined by Willis (1932).

#### THE NORTHERN CONTINENTS.

Turning more particularly to the mammalian evidence, it proves in the first place that all the northern continents (including India) and also Africa have had some intermigration of mammals during the Cenozoic. Between Europe, North America, and Asia communication had already occurred in the Paleocene. The latest connection between North America and Europe was perhaps Pleistocene, but probably Tertiary and possibly well down in the Tertiary. The latest between North America and Asia was surely Pleistocene. The earliest between central or southern Africa and Eurasia positively established by evidence in hand was Miocene, although there had been an early Tertiary connection of some sort for North Africa and the uncertainty for the rest of the continent is due to lack of evidence, not to opposing evidence.

Thus these continents have been connected, off and on, through most of the Cenozoic. The second important point is that the connections have not in any case, not even for Europe and Asia, been continuous but have fluctuated rather irregularly, with some tendency toward cycles. For instance the North America-Eurasia exchange has tended to be accentuated toward the beginning of each Cenozoic epoch, although not confined to these times.

Drifting and stable continent theories recognize connections between these continents at about the same times and about the same places, disagreement on these points arising rather from differences of knowledge and judgment of the data than from the basic postulates as to the nature of continents. The intermittent nature of the migrations is most simply and completely explained by the theory of stable continents which postulates only connections that are reversible by nature and that would tend to be made or broken at each important tectonic episode.

On the other hand, the usual drift theories cannot explain these facts because they allow only for one definitive break or one definitive contact of each connection. This inadequacy of drift theory is noticed even by its strongest advocates, although they do not emphasize the point. They have succeeded in bringing the facts into consistency with the theory, which, contrary to implications and statements in the literature, is entirely different from the theory's explaining the facts or the facts' supporting the theory. Wegener eliminated positive inconsistency by supposing these continental connections to have been continuous since the Paleozoic except for North America and Europe, which did not break apart until the Pleistocene, at least. The intermittent nature of migration is explained by periodic flooding on, not strictly between, the continents. But this is virtually identical with the stable continent explanation and really eliminates all bearing of the drift theory on these data, and all bearing of the data on the theory.

Du Toit adopts much the same sort of non-drift explanation, except that he concludes that some intercontinental connections arose after fragmentation (1937, e. g. p. 294). Whatever they are called, such connections differ in no important way from non-drift land-bridges. That so ardent an advocate of drifting finds it necessary also to advocate bridges emphasizes how inadequate and unnecessary the drift theory is to explain these particular facts. Most anti-drift paleogeographers agree with Du Toit's strictures against the reckless and unnecessary proposal of bridges, but this is beside the point. It happens that Du Toit himself adopts one of the most ill-founded of all bridges, as will be shown on a later page.

Given the stable continent connections that are now real and visible, with the partial exception of Europe-North America, there is no warrant to postulate any others unless the evidence requires connections in different positions from those now existing or plainly having existed. Thus the fact of connection offers no support to the theory of northern transoceanic continents, although often stated as if it did, and the only biological evidence that bears on that theory must relate to the position, not only the existence, of the connections. In the Atlantic the principal postulated connection south of the Greenland route is the *Hipparion*-bridge, which is a figment of

the imagination as will later be shown.<sup>1</sup> Gregory (1930) has given some arguments from mammalian distribution for a former trans-Pacific connection south of the Bering bridge. His northern Pacific continent is said to be indicated by the late Eocene titanotheres of the Indian Manha and Uinta and by *Brontotherium* and *Embolotherium* in the Oligocene, because these animals are not known much north of 50°N latitude and because a Bering connection in 65°N "may have been inaccessible to this fauna owing to the direct and indirect effects of climate." *Hipparion* and *Hyaenarctos* are said to have followed the same route in the Pliocene.<sup>2</sup>

The resemblance of Mongolian and American titanotheres is rather broad (see Granger and Gregory, 1942). Few appear congeneric and none conspecific. *Embolotherium* happens to represent a very divergent line that did *not*, as far as known, migrate between Asia and America. Nevertheless some connection is indicated, as it is more strongly by the later *Hipparion* and "*Hyaenarctos*" (*Agriotherium* and *Indarctos*). These animals have been found about as far north in both North America and Asia as there are any known strata in which they could possibly be preserved. Their non-occurrence as fossils in regions where there are no fossil deposits of appropriate age and character is used by Gregory as if it were a positive datum on the distribution of the living animals—a procedure so thoroughly unsound as to require no refutation, but one that appears over and over again in the literature of transoceanic continents and bridges. In fact when we do have north-south sequences of land mammals on the two continents it is the rule (with exceptions such as would be expected from chances of preservation and discovery) that the more strictly and typically southern mammals of each continent did not migrate but only the practically continent-wide or typically

<sup>1</sup> The wonderful legend of Atlantis is here avoided, not overlooked. Biological evidence is regularly introduced in the effort to substantiate this Platonic myth. It suffices for present purposes to say that the discussions of such evidence in the most nearly scientific of the Atlantis literature are even less accurate and logical than the inaccurate, illogical presentations of supposed evidence for Tertiary transoceanic continents of which examples are reviewed in this paper. Anyone who wishes to risk his reason in the study of Atlantis may make a comparatively sober start by referring to Chatwin, 1940; Bramwell, 1938; Termier, 1916; Scharff, 1903. The whole literature of the subject includes at least 2000 titles.

<sup>2</sup> In the previous year, however, Gregory had *Hipparion* migrate across the Atlantic.



northern forms. This evidence strongly favors a northern route. The Bering route at full emergence had its southern shore nearer  $55^{\circ}\text{N}$  than  $65^{\circ}\text{N}$ . It is, moreover, generally agreed that the climate of that region was milder during most of the Tertiary than in the Pleistocene or Recent. For instance the Alaskan early Tertiary floras were temperate to warm temperate, not cool temperate to boreal, as now (Chaney, 1940). There is no real reason to doubt the competence of that route to account for the observed faunal relationships.

This is, indeed, tacitly admitted by Gregory, himself, on another page of the same paper (1930, p. cviii) where he supposes that *Protylopus* crossed by the Bering route, without mentioning that *Protylopus* lived with the very titanotheres that he had previously said (page c) could not cross by that route.<sup>3</sup> Gregory here adds that a more southern route must later have been available because the later camels migrated in the Miocene when Bering Strait was submerged. It is accepted and insisted that the Bering connection has been intermittent. There is, however, no reason to think that it was submerged throughout the Miocene and there is much evidence that it was not. Gregory's only contrary evidence was to say that this is "shown by H. F. Osborn's figure" in Osborn, 1910, p. 294. That figure shows the skeleton of *Merycodus*, which does not have the most remote bearing on this question. The really pertinent figure in Osborn, 1910, is on p. 245 and shows America and Asia fully connected across Bering Straits. Space will not be taken for all examples, but this is only one of many cases in which the paleogeographic compilers have cited previous works as authority for statements which the authors of those works did not make and, in some cases, as here, to which they were categorically opposed.

Gregory's final argument (1930, p. cx) is the close affinity of some recent mammals on opposite sides of "the tropical Pacific." Aside from rodents unspecified, the examples are *Blarina*—*Blarinella*, *Zapus*, and *Urotrichus*—*Neurotrichus*. *Blarinella* is not specially related to *Blarina* despite the resem-

<sup>3</sup> As a matter of fact there is no evidence that *Protylopus* ever migrated from America to Asia and this is extremely improbable, but the point here is Gregory's admission of the competence of the Bering route. His cited authority for the supposed migration is Osborn, 1910 (with incorrect page reference), but Osborn made no such statement. On the contrary, Osborn knew and stated (e.g. 1910, p. 299) that the first known appearance of camels in Asia was millions of years later than *Protylopus*.

blance of its name, but is an exclusively Old World derivative of a world-wide stock. Far from being tropical, it occurs at elevations of 10,000 feet in latitude 35°N (Allen, 1938). (It may incidentally be noted that *Blarina* ranges well into Canada and is quite absent in the tropics). *Zapus* does occur on both sides of the Pacific, with a well-distinguished subgenus on each side, but it is decidedly not tropical and is, indeed, chiefly boreal. The Chinese *Zapus* (*Eozapus*), with patently relict distribution, occurs in two small areas, latitude 30°-35°N, in cold situations at great altitudes, above 10,000 feet (Allen, 1940). The American *Zapus* (*Zapus*) ranges from the latitude of North Carolina and California (in the colder situations of its southern range) to the Arctic Circle in Alaska (see, e. g. Anthony, 1928). The accessibility of the Bering Bridge is entirely obvious for this form; it still lives at one end of the bridge. *Urotrichus* and *Neurotrichus* represent relicts of an ancient, primitive, widespread group the fossil history of which is very little known. On both sides of the Pacific their present associations are boreal to cool temperate, distinctly not warm or tropical. They do not in the least suggest a southern bridge.

These facts have been analyzed as an example and it is seen that they are utterly worthless as support for the thesis they were meant to prove and that, indeed, they have some validity as evidence directly against that thesis. This is only one case of the irresponsibility of so much of the paleogeographic and zoögeographic literature, which consists too largely of statements that are demonstrably untrue or illogical but that are endlessly copied from one work to another and that can assume, to the unwary and uninformed, the appearance of an impressive body of evidence in favor of almost any hypothesis.

#### THE SOUTHERN CONTINENTS.

Supposed southern continental connections have been more stressed than northern in the discussion of these fundamental paleogeographical theses, because the southern continents are now widely separated and evidence of their former union would therefore more clearly and conclusively bear on the geological nature of continents than in the case of the northern continents, all now united or nearly so. It has long been noticed that South America, Africa, Australia, and India have some resem-

blances in flora and fauna that are not shared by northern lands. The claimed resemblances are sometimes erroneous, some of them do not necessitate land connections, and many have been grossly exaggerated, but there is a residuum of genuine cases of southern disjunctive distribution of strictly terrestrial forms of life.

According to the drift theory, this is explained by the former union of all these dispersed areas into one. Advocates of transoceanic continents seek to explain the distribution by vanished continents across all or any of the South Atlantic, South Pacific and Indian Oceans. The proponents of stable continents are divided, some believing in former isthmian connections of various southern continents with Antarctica and hence with each other through that continent and others maintaining that the connections were made by way of the northern continents.

The first problem, whether or not intercontinental migration routes involving only the southern lands did exist, has been discussed to some extent elsewhere (Simpson, 1940b) and the conclusion was reached that they probably did not exist during the Cretaceous and Cenozoic, at least. Since this is not the universal opinion of competent paleontologists, the possibility is not excluded by this adverse personal opinion and still requires brief consideration, with reference to the earlier study for the details.

Some paleogeographers (e. g. Du Toit, 1937, p. 53 and elsewhere; Chatwin, 1940, p. 39) classify as "paleontological" the evidences of groups for which fossils are nearly or quite lacking. They thus confuse the issue by failing to make a distinction that is not only important but also indispensable. As far as I know, when fossil evidence has been found for a recent group of southern disjunctive distribution it has always turned out that this group also occurred in the north. In several cases it is established beyond any possible doubt that distribution was by northern, not southern connections, e. g. the tapirs.<sup>4</sup> When such fossil evidence is found, that particular group is eventually omitted from the evidence for southern routes, but analogous groups not known as fossils continue to be cited.

There is, nevertheless, some evidence for such routes among extinct groups of organisms. The best of this evidence

<sup>4</sup> Yet Gregory (1930, p. cx), citing Blanford, still mentions the tapirs as if they favored southern connections.

comes from the Permo-Carboniferous and Triassic. The evidence is not as strong as is usually said and it is far from conclusive, but it is valid, under competent revision, and some of it does favor southern connections although some does not. This is pre-mammalian and is only incidental to the present discussion.

The later Tertiary and Recent mammals of Africa resemble those of the eastern Mediterranean and southern Asia to some extent. The present Arabian and former Mediterranean connections explain this so fully and simply that no question of previous union of markedly different sort or position is raised. African mammals, recent or fossil, have absolutely no special affinities with those of Australia. African and South American mammals, also, are and, as far as known, have always been so distinct that they are more often cited as evidence that a previous union (if any) had been broken by the Tertiary than as evidence in favor of such union, even by students like Gregory and Du Toit who think that South America and Africa had been essentially parts of a single continent in earlier times. The older idea of community of origin of these two faunas needs no present discussion.

One Tertiary connection of Africa and South America is, however, still debated. This is supposed to have existed in the Miocene between northeastern South America and northwestern Africa and to have been a migration route for the manatees and hystricomorph rodents. The evidence is very equivocal and the reality of the route a bare possibility, at best. If it did exist, it was exceptional under all theories (least so under stable continent land-bridge theories) and does not help to choose among them.

Although African mammals thus have no conclusive bearing on the present problem, the case of Australia is very different. Its mammals are always cited by advocates of drift, trans-oceanic continents, and southern bridges as favoring their views. Wegener (1924, pp. 85-89) particularly emphasizes this evidence. He concludes that the Australian fauna as a whole consists of three different elements (one might call them faunal strata) of different ages. The first is said to date from the time when all southern continents were one, before the Jurassic. This stratum is postulated as pre-mammalian and does not concern us here, but I may add that neither its existence as a real unit nor its date follow from the supposed evi-

dence. The second faunal stratum is said to include the marsupials and monotremes, to show relationships with South America, and to date from a time between early Jurassic and Eocene when Australia and South America were still attached (Antarctica intervening) but Australia was separated from other continents. The third fauna is said to include the dingo, rodents, and bats, among mammals, to have come by an island route from the Sunda Islands (hence ultimately from Asia), and to be recent, i. e. definitely post-Pleistocene. Most compilations overlook, or do not seek to explain, the fact that Australia does have an abundant and differentiated placental mammalian fauna, although one peculiarly limited in scope. Wegener's emphasis of this fact is in his favor, although his interpretation of it is demonstrably erroneous in some respects. Du Toit's views on Australian-South American mammalian relationships are almost exactly those of Wegener, but Du Toit does not discuss the Australian placentals.

The same supposed relationship of South American and Australian marsupials is used as evidence for a land-bridge connection through Antarctica. Advocates of transoceanic continents (von Huene, 1929, pp. 93-94; Gregory, 1930, p. cii) have developed a peculiar modification according to which marsupials migrated across the Pacific from Asia to South America and then returned across the Pacific to Australia, apparently by a different route. Ihering (1927) had a similar idea, but had the marsupials circle around the Pacific clockwise instead of doubling across it.

Fossil marsupials are not known in Asia, but this is likely to be an accident of non-discovery, as is admitted by many advocates of trans-Pacific connections, like von Huene, Gregory, and Ihering. Early and primitive forms are known in North America and Europe. The only strength of marsupial evidence for a southern connection would be the establishment of some differentiation not merely analogous or similar but homologous or the same in both places, or of special affinities closer than would be likely to arise through northern late Cretaceous forms.

Here may be exemplified the tendencies of both drift and transoceanic continent theorists greatly to exaggerate the affinities of the groups they discuss. For instance Du Toit (1937, p. 53) speaks of the "diprotodonts" of Australia and South America as belonging to "identical or allied species."

This is so far from the truth that even the zoölogists most convinced of the reality of the relationship never place the Australian and South American forms in the same families. Most students place them in different superfamilies or suborders. Similarly Wegener (1924, p. 79) referring to another supposed connection, quotes from Arldt what he, Wegener, says are percentage figures for "identical" mammals and reptiles on the two sides of the Atlantic. Reference directly to Arldt (1919, pp. 89-91) shows that these figures (which, incidentally, were unreliable to begin with) are for families or subfamilies, which gives them implications decisively different from those carried by Wegener's word "identical" (or "identisch" in German). Such looseness of thought or method amounts to egregious misrepresentation and it abounds in the literature of this perplexing topic.

The claimed special resemblance of South American and Australian marsupials does not, in any zoölogist's opinion, extend to identity of species or genera but consists at the very most of the possession in common of one family, *Dasyuridae* or *Thylacinidae*, and one advanced suborder, *Diprotodontia*. My own opinion (e. g. Simpson, 1939, 1941) is that even this degree of affinity is not supported by the evidence, which is entirely consistent with affinity only through the little-differentiated Holarctic marsupial stock. For the purpose of argument, however, the evidence may tentatively be granted this maximum possible weight. At this evaluation, it still does not support but on the contrary opposes the idea of a direct, practicable land route between Australia and South America. That such a route should exist and should produce only this rather distant resemblance in only two groups among faunas otherwise so completely different is so improbable as to be almost inconceivable. If any southern connection is indicated, this cannot be continental or a practicable, fully emerged land-bridge, but something on the order of discontinuous, evanescent island chains. Even granting extreme value to these facts, they still favor the hypothesis of stable continents and not those of drift or transoceanic continents as has so often been claimed.

The problem of the Australian placentals involves another special difficulty for drift theories, but not necessarily for the other theories here considered.

The placental mammals of Australia certainly came from

Asia, as all zoölogists agree and Wegener accepts. Although he is not explicit as to his reasons, Wegener evidently placed their immigration in the post-Pleistocene because he thought that this could not occur until Australia was as close to Asia as it is now and he wished to allow as much time as possible for the long drift from Antarctica and not to allow subsequent time for closer approach. As it happens, fossil placental rodents are abundant in the Pleistocene of Australia. This is not a fact discovered since Wegener's work, but was already well-known and in print some forty years before Wegener first conceived the idea of continental drift. With a single unimportant exception, Tertiary mammals are still unknown from Australia (although they certainly occurred there), so that the evidence as to the time of entry of the rodents is indirect. Some Australian rodents are perhaps fairly recent immigrants but others have developed endemic genera and subfamilies—according to some classifications even families—in the Australian region. Such divergence suggests immigration not later than early Pliocene, and Miocene is more likely. As to the earliest possible time of immigration, this cannot have been before the Oligocene and the migration is more likely to have begun in the Miocene.

Wegener held that the Australian-Antarctica connection broke in or after the Eocene. Therefore the most probable interpretation of the faunal evidence leaves him only about the span of the Oligocene for the whole drift of Australia from Antarctica to its present position. If Du Toit's opinion (1937, p. 118) is accepted that Argentina-Antarctica-Australia were connected "down to the Oligocene at least," exceedingly little time is left for Australia's supposed shift from the Neotropical to the Oriental faunal sphere—the continent must have been speeding rather than drifting. An adjustment of the general drift theory—like so many others that have had to be made—could remove the inconsistency involved in these particular drift theories, but there is another point still harder to reconcile with any such theory: after drifting to about its present position in the Miocene, and doing so with most remarkable rapidity, Australia's drift relative to Asia would then have to stop. If it had not been about as close to Asia as it is now, the rodents could not have reached it, but if it had gone on drifting it would either be closer now than it is or would, by a radical change in the theory, have been closer

in the immediate past and then would certainly have lost the degree of faunal isolation that it actually has.

The faunal relationships of Australia are completely and simply explained by the view that Australia has had about its present relationships to other continents since the Cretaceous, at least, that the marsupials entered by the island route from Asia, and that rodents entered later over the same route.

#### DEGREES OF SIMILARITY OF FAUNAS.

Relationships between two land areas may theoretically vary from complete isolation, with intervening water too wide to be crossed by a land animal in any way, to complete union, with true continuity of all land animal populations. Any migration that occurs from one area to another will be partly determined by the nature of the migration route. Although each properly embraces considerable variety in this respect, different paleogeographic theories do to some extent provide different sorts of migration routes. The effects that the routes have had on faunas are therefore important criteria for judging the various sorts of paleogeographic theories. These effects will involve not only the kinds of animals concerned but also resemblances of individual groups and the characters and similarities of faunas as a whole.

The most essential conclusion of all drift theories is that continents now separate have been in actual contact, at least along the edges of their continental shelves, with no greater distances then intervening between their present land surfaces than the approximate width of those shelves. It would be both possible and probable that groups living on what are now separated lands but living there when the lands were united would be really identical, not merely similar or of the same families but interbreeding parts of the same subspecific populations. This need not be universally true, but even if local differentiation happened to coincide with the subsequent line of separation of the lands, the distinctions in fauna should be of a minor order. The actual breadth of the connection could tend to narrow in the course of time, if, as is usually postulated, the rift were accompanied by a rocking or rotating motion of the land masses. The breadth could also fluctuate considerably due to epeiric flooding, and the connection could be as narrow as an isthmian bridge, but in all cases the connections involved in the drift theory are shorter than those



provided by any other theory. Even when narrow, such connections should interpose relatively little obstacle to intermigration and should produce practically no evolutionary differentiation of animals in transit.

The broad transoceanic continents of some paleogeographers likewise provide the means of free faunal interchange, but the routes between areas now land are supposed to be longer than in the drift theories. Such routes, to much greater extent than in drift theories, provide the possibility, but not the necessity, of marked selective action by climatic and other non-marine barriers and also of considerable evolutionary change or genetic differentiation between the animals of common descent at the two ends of the migration route.

The theory of stable continents provides connections that are like those of transoceanic continents and unlike those of drift theory in length because they postulate that present lands were separated by approximately the same distances as they are now, throughout at least the later phases of geological history. Like all the other types of theory, this naturally assumes the possibility of immediate, free interchange between continents now connected: Europe, Asia, and Africa. The connection could be greater or less in the past. Between continents now separated, the connections postulated by this theory would be, at most, limited corridors. As migration routes, these would differ from transoceanic continents mainly in having their abutments, as a rule, against a more limited climatic or environmental zone, with resulting selection. For animals adapted to that zone, they would make intermigration possible, but not for the other land animals of the masses concerned.

If narrower, and hence probably more tortuous, more varied longitudinally and less varied transversely, these corridors would grade into isthmian links. These links would still provide for the sure and relatively rapid migration of certain types of animals, but they would be markedly selective as to which animals migrated and the evolutionary effect on the migrating forms could be considerable. Finally these links would grade into connections with discontinuity, usually by water barriers (island chains), but possibly also sharp discontinuity of land environments. On these, which I have called

"sweepstakes routes" (Simpson, 1940a), a distinctly limited series of land animals can migrate, but the migration is not directly determinate; whether, when, and in what order migrations occur would be the result of chance.

Advocates of continental drift have recognized that drift should be reflected by closer faunal resemblances than are likely under other theories. They have repeatedly claimed that resemblances so strong as to require drift for their explanation do, indeed, occur, but I have not seen any convincing evidence for these personal opinions. Du Toit (1937, p. 294) is one of the few who have made any really definite statements as to the probable biological effects of different types of continental connections. He says:

"(1) Migration along a link need not be equally effective in both directions, whereas our palaeontological studies commonly favor a two-way exchange; and (2) faunal differences at the ends of a link, as von Ubisch (quoted by Wegener) has pointed out, ought to be appreciable owing to the differentiation that must have occurred along the bridge itself, whereas a close specific relationship or even identity of forms may indeed characterize the life of the now-opposed lands."

As an argument in favor of drift, the first of these points is so clearly an example of non sequitur that it merits little attention. Aside from this lack of logic, the fact is, as I have elsewhere pointed out (Simpson, 1940a), that links, like the existing Panamanian isthmian link, do normally facilitate migration in both directions. I have suggested that this fact is a strong argument against some postulated land-bridges supposed to have been one-way routes. At the same time, the fact also eliminates all need for any route shorter or wider than an isthmian link in order to account for a two-way exchange.

As regards Du Toit's second point one may readily grant, and even insist, that faunal differences at the ends of a link ought, indeed, to be appreciable. Du Toit's statement is likely to mislead an unwary reader (I think that it has misled Du Toit, himself), because it shifts subjects inadvertently. He speaks first of faunal differences, i. e. differences in the composition of an animal community, and then of identity of forms, i. e. of particular species within the community, as if the latter were the opposite of, or contradictory to, the first. In reality, radically different faunas may and often do contain

closely related or identical species. Canada and Patagonia, thousands of miles apart and placed by everyone in different faunal realms, certainly have different faunas, but they also have identical and related species. If Du Toit means to imply that any identity of species on different continents constitutes a closer faunal resemblance than is consistent with present continental positions, then he is flatly wrong. If, as the logical alternative, he means to say that identical faunas have been found on separate continents, then he is even farther from the truth.

No two local faunas, even if near each other and separated by no barrier, are likely to be composed of exactly the same species. On the other hand faunas on opposite sides of the earth and connected only indirectly and imperfectly may have species in common. Nothing as to the nature and length of a continental connection can be inferred from the usual vague statements, on one hand, that the faunas are different or on the other that they have some similarities. Absolute qualitative resemblances and differences hardly exist. The pertinent data are the degrees of similarity.

Sufficient analysis of data on degrees of faunal resemblances would far exceed the scope of a single paper. The inadequacy and rarity of such analyses in the literature is an indication of how speculative most of this work is and how arbitrary are the usual conclusions. Wegener and his followers assume, for instance, that if 35 per cent of the known families of mammals were common to North America and Europe in the Eocene, this proves that the continents were then nearer each other and united, but they do not think to check any example of what percentage of families in common might really characterize such a situation.

The introduction of the decidedly incomplete but concrete and definite examples given in the following table will serve to suggest how gratuitous are the vague statements and sweeping claims of past faunal resemblances so great as to be inconsistent with the present positions of the continents. The data refer mainly to mammals, but I think them similar to those for most land vertebrates and I introduce one older reptilian comparison as a hint of this.<sup>5</sup>

<sup>5</sup> Comparisons of this sort involve more complete analysis and presentation than the single percentage figures given here for the sake of brevity. When such a single figure is used for cursory exemplification it is common

	A	B	C	D	E	F	G	H
Families	100	92	89	67	95	61	4	43
Genera	82	67	64	24	45	15	0	8
Species	65	18	26	5	0	0	0	0

A. Percentage of recent Ohio mammals also occurring in Nebraska. Same faunal zone. Complete continental union, with only slight climatic and geographic barriers. Distance about 500 miles.

B. Percentage of recent Florida mammals also occurring in New Mexico. Same faunal region, different zones. Complete continental union, with distinct climatic differences and minor geographic barriers. Distance about 1000 miles.

C. Percentage of recent French mammals also occurring in northern China (proper). Same faunal region, different zones. Complete continental union, minor climatic differences, marked geographic barriers. Distance about 5000 miles.

D. Percentage of recent New Mexican mammals also occurring in Venezuela. Different faunal realms. Connected by isthmian link. Marked climatic and geographic barriers. Land distance about 3300 miles.

E. Percentage of known early Eocene (Sparnacian) European mammals also known from beds of the same age in North America. Present distance between pertinent collecting areas about 5000 miles (by route passing through southern Greenland, in most probable position for postulated connection).

F. Percentage of known early Pliocene North American mammals also known from beds of approximately the same age (Pontian) in Europe. Distance between pertinent fossil fields about the same as for E.

G. Percentage of known early Pliocene North American mammals also known from beds of approximately the same age in South America. Present distance between pertinent fossil fields about 6000 miles (by way of Panamanian isthmus; slightly shorter by great-circle route).

H. Percentage of known Triassic South American reptiles (descriptions incomplete but based on latest published lists) also known from the Triassic of South Africa. Present shortest distance between pertinent fossil fields about 4750 miles.

In all cases the animals counted are native terrestrial forms, omitting bats, strongly amphibious or definitely aquatic types, and mammals known to have been introduced by man.

Many more data of this sort should be compiled and they

---

to give the percentage of total known groups of the two faunas that occurs in both of them, e.g. Arldt and, following him, Wegener. Such figures may, however, greatly obscure the relationship being studied. For instance if fauna A has 50 known species and fauna B has 20, all of which also occur in fauna A, the data do not suggest any barrier or selective differentiation between the faunas and are consistent with the hypothesis that B is a sample from a population the same as that of A. But the percentage-of-total method would represent this by the figure 40 per cent and suggest a well-marked faunal distinction. It is clearer to say that 100 per cent of the species of B are also known in A. I have followed this method in the table, comparing the smaller fauna with the larger when their sizes are markedly disparate.

should be more fully analyzed, but these figures appear to be fairly representative of the stated conditions.

*A* is such a resemblance as should frequently appear between directly opposite points on different continents that were, according to drift theory, in former contact. The intervening distance is sufficient to allow for the widths of the continental shelves. But *no fossil land faunas resembling each other to a degree at all comparable with this have ever been found on continents now separated.* Only evidence of this kind would be more consistent with drift theory than any other, and no such evidence is known.

*B* and *C* are representative of the mammalian faunas of distant parts of the same continent (or of fully united continents). Resemblances of this order of magnitude may be about the least to be expected between continents united according to the drift theory and about the greatest to be expected between distinct continents, or comparably distant parts of fused continents, according to non-drift theories. *Resemblances of this degree are altogether exceptional among fossil vertebrate faunas of continents now distinct* (the only example known to me is given under *E*). This is consistent with stable or transoceanic continent theories, but inconsistent with drift theory.

*D* is the resemblance between two areas united by a land-bridge, definitely beyond the ends of the bridge, proper, but near its abutments, where the two regions had almost completely different faunas before the bridge arose (compare *G*) and the intermigration and its ecological effects are now essentially complete, with faunal equilibrium reestablished. Resemblances far less than this have repeatedly been given as conclusive evidence for drift or transoceanic continents. The example shows that the evidence leads to no such conclusion.

*E* represents the closest resemblance known to me ever to have occurred between terrestrial vertebrate faunas of two continents now separated. This is the best fossil mammal evidence for the drift or transoceanic continent theories that has ever been found, but even this really tends more to oppose than to favor those theories. These figures appear to be consistent with full continental union only if the areas in question were very distant, more distant than drift theory postulates. The figures definitely tend to favor the postulates that the two areas derived their faunas from a common source

and were connected or had been not long before, but by a long route or one definitely restricting interchange. These are the postulates of stable continent theory.

*F* might be consistent with direct connection of a sort more highly selective than that of *E*, but is more favorable to the theory that the connection was still more distant, as through Asia (a theory also supported by other evidence for this example).

*G* represents an approximate minimum resemblance. Compare especially the figures *D*, for (more restricted) parts of the same continents after their land-bridge union.

*H*, to be considered merely preliminary but indicative, is inserted for comparison and to support the incidental statement that the supposed pre-mammalian resemblances of southern faunas have been grossly exaggerated. These figures 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.

A weakness of this sort of evidence, and one of the reasons why it requires care in interpretation and should be made more extensive, is that it does not directly take into account the effects of non-marine barriers to faunal mixture, barriers familiar enough in the contrasts between the northern and southern mammals of Asia or of Africa. The theory of continental drift, for the most part, and that of transoceanic continents, almost entirely, do, however, postulate latitudinal connections that would have about the same ecological conditions as the areas surviving unflooded at the two ends. The demonstrably very selective nature of intermigration is hard to explain on this basis, but is explicable by the necessarily varying conditions of north-south connections and the restricted conditions of the east-west links between stable continents.

#### THE *Hipparion*-BRIDGE AND ACCORDION CONTINENTS.

Considerations like those exemplified in the preceding section are as opposed to many hypothetical land-bridges between supposedly stable continents as they are to the drift theory or to transoceanic continents. Dozens of bridges have been postulated without any consideration for their possible bear-

ing on faunal relationships as a whole and with no apparent idea of the adequacy and evaluation of evidence. One example will be traced, because its history is peculiarly instructive for zoögeographers and because it has come to be related to the discussion of both drift theories and transoceanic continents.

In 1907 Gidley (1907, pp. 868-869, 905-906) placed the American fossil horses previously referred to *Hipparion* in two genera: *Neohipparion* and *Hipparion*. Most American species were placed in the former genus, confined to America, and in *Hipparion*, proper, were placed a few teeth from South Carolina and Florida considered as "not improbable" members of "an American branch of the *Hipparion* group of the Old World." Gidley did doubtfully report *Hipparion* from Texas and he definitely recorded *Neohipparion* as well as *Hipparion* in Florida. (It happens that his evidence on this last point was incorrect, but it was prophetic because *Neohipparion* does occur there.)

In 1918, Osborn (1918, pp. 173, 175) followed Gidley to the extent of placing the Florida species in a "Group" with protocones as in some European species. He stated, however, that "it has not been found practicable to maintain a clear line of definition between species belonging to *Hipparion* and to *Neohipparion*."

On Jan. 20, 1919, the land-bridge here in question was born when Joleaud (1919a), citing Osborn but not Gidley, concluded that the affinities of the Florida *Hipparion* with European forms and the absence of such affinities for *Neohipparion*, of western United States, contradicted the old idea of migration of *Hipparion* to the Old World through Asia. He said (in French), "In reality, it must be that these equids reached Europe directly from Florida." He accordingly erected, in his fancy, a land-bridge running Florida-Antilles-North Africa-Spain, late Miocene in age.

This infant bridge grew lustily in the following month. By Feb. 10 (Joleaud, 1919b) its duration was given as middle Miocene to early Pliocene and on Feb. 24 (Joleaud, 1919c) this was early Miocene to late Pliocene, with a brief interruption in part of the middle Miocene. The bridge had also acquired new passengers: *Anchitherium*, *Lepus*, *Xerus*, and a procyonid from North America to the Old World, *Hystrix* from South America to the Old World, and *Neotragocerus*,

*Ilingoceros*, and mastodons from the Old World to North America. These additions confused an issue already becoming obscure. They have been cited as strong confirmation of the reality of this bridge. Some of them, not all, do confirm a New World-Old World faunal exchange, an idea neither new nor extraordinary, but these do not at all require or confirm a bridge in this position. The bridge was placed just here, i. e. this particular bridge was erected, because of *Hipparion*. Once having such a bridge, Joleaud proceeded to assume that most New World-Old World migration took place over it. All of the animals noted are as much western as eastern in North America and several are now or were then known only from the West.

Keeping clearly in mind that this particular bridge derives its being from *Hipparion*, the confusion may be minimized by briefly considering the other animals mentioned. *Xerus* and the mooted procyonid are too dubious to warrant the long digression that would be necessary to show how invalid is their supposed evidence. *Anchitherium* and the mastodons certainly did migrate, the first to and the second from the Old World, but both were present in western United States and eastern Asia at the time of probable connection, and the simplest route to postulate is the Bering bridge.

Joleaud held that *Neotragocerus* belonged to the mainly Mediterranean and African group Hippotraginae and *Ilingoceros* to the mainly African group Tragelaphinae. If true, this would to some extent support a trans-Atlantic bridge, although not too clearly since both groups do also occur in Asia. But more than seven years before Joleaud made these statements, the original describer of *Ilingoceros*, Merriam (1911), had decided that his first identification of this genus as a true antelope was wrong and he showed, with new, more complete material, that it probably was an antilocaprid and hence an autochthone in North America giving no evidence of migration. This has ever since been the opinion of everyone who has studied the genus at first-hand, although some authors of compilations still cite the African affinities of *Ilingoceros* as a fact. *Neotragocerus* was based on a broken horn-core and a doubtfully referred set of upper molars (Matthew and Cook, 1909). As one of its authors later remarked (Matthew, 1924), "to discuss palaeogeographic theories based upon such flimsy evidence appears...an utter waste of time." Since then



only one other horn-core has been found. It now seems probable that the teeth referred to the genus belonged to entirely different animals (Frick, 1937, p. 544). Still too dubious to warrant theorizing, the genus may well turn out to be one of the bovids, like *Oreamnos*, that crossed the Bering bridge from Asia in late Pliocene and early Pleistocene times. It does not and never did afford the slightest valid evidence for African connections.

The case of *Hystrix* is more peculiar and complex but space must not be taken here to discuss the different problem of a South American-African bridge. Joleaud ran *Hystrix* across the *Hipparion* bridge only because he had the bridge handy. From a psychological point of view it is noteworthy that he remarks that *Hystrix* could not have gone to the Old World by way of North America because no South American animals reached North America until long after *Hystrix* had gone from South America to Africa. He apparently felt that this statement (which, incidentally, is untenable on other grounds as well) supports his Florida-Africa bridge, and J. W. Gregory (1929) follows him in this. Yet, in conjunction with his other claims and theories, this means that the bridge was connected at its western end with both North and South America but did not connect those two continents to each other. Joleaud provided no diagram of his solution of this apparently insoluble topological problem.

In 1924 Joleaud returned to his bridge in some detail. Its growth had continued at a rapid rate during the intervening five years, for at this later date it was supposed to have endured practically throughout the Tertiary, except for a temporary interruption in the middle Miocene. In the Eocene it was supposed to have extended as far north as northern France on one side and Maryland on the other, but thereafter it ran only from Aquitania and the European and African countries bordering the Mediterranean to Florida, the Antilles, and Brazil. This evidence is the same as before except that he now has rodents migrating to Africa from South America both in the Eocene and in the late Tertiary. (Again, temptation to discuss this separate problem is avoided, but it may be noted that no rodents are known among the abundant South American Eocene mammals).

At this time (1924) Joleaud was inclined to accept the theory of continental drift and he believed that these trans-Atlantic

relationships support that theory, but he remarked that the intermittent character of the faunal exchange was contrary to the idea of Wegener, which allows one definitive split between these masses, followed by steadily increasing distance between them, at least since the Paleozoic. Joleaud therefore proposed what seems to me the climax of all drift theories: the drifting continents are supposed to have had an *accordion movement* back and forth, "*un mouvement en accordéon des aires continentales*" (Italics his).

Joleaud's bridge would probably have been forgotten—certainly paleontologists find it more embarrassing than useful and are not inspired to faith by his obvious misunderstanding of the paleontological data—but in 1929 the able and eminent British geologist J. W. Gregory delivered his famous presidential address, "The Geological History of the Atlantic Ocean," to the Geological Society of London. In this (Gregory, 1929, pp. xcix-c), he reviewed Joleaud's evidence of 1919, concluded that the *Hipparion*-bridge was geologically probable, and showed it on one of his paleogeographic maps (p. cxviii). An avowed enemy of the drift theory, Gregory did not mention Joleaud's accordion-continents. Neither did he form or seek an independent opinion on the paleontological basis of the *Hipparion*-bridge.

The strength of this authority placed the bridge firmly and, it is to be feared, permanently in the literature. It has since been cited as well-established by compilers who give Gregory as their source and authority, without going back to his source, Joleaud, and still less back to Joleaud's original basis, the classification and distribution of *Hipparion*. To give an eminent example, there is no more bitter opponent of land-bridges in general than Du Toit, who misses no opportunity to emphasize the lack of agreement, the undue multiplicity, and the slender evidence for the land-bridges of some non-drift paleogeographers, but he accepts this *Hipparion*-bridge as an exception (Du Toit, 1937, p. 297). Had Du Toit wanted an example to point his arguments against such connections, this would have been perfect, and his acceptance of it is among the most striking examples known to me of the indestructibility of error.

The plain fact is that this bridge was a fantastic blunder from the moment of its birth in Joleaud's mind. I have shown that the only real basis for localizing it was Gidley's identifica-

tion of a few *Hipparion* teeth. Joleaud's inference would not logically follow in any case, and even if the facts as stated by him were all granted really to be facts the theory would still be more romantic than scientific. But regardless of logical considerations subsequent study decisively showed that the basic datum on which Joleaud depended was simply wrong (e. g. Matthew, 1924, Simpson, 1930, Stirton, 1940). Gidley's opinion was partly based on an inaccurate figure of a specimen now lost, partly on incorrect ideas about the European forms, and partly on inadequate knowledge. The Florida *Hipparion*'s (and allied horses) are not especially related to those of Europe. They are almost identical with those of western North America. Finally, the New World forms that do happen most nearly to resemble those of the Old World are known almost exclusively from the opposite side of the continent, in Washington, Oregon, and California.

#### MADAGASCAR.

The strange Malagasy fauna has long been a puzzle to zoögeographers. It is difficult to explain by any usual sort of land connection and some of the advocates of drift have paid particular attention to it. The Malagasy land mammals include among Insectivora only tenrecs and one shrew, among Primates only a number of lemuroids, among Rodentia only an unusual, delimited series of cricetids, among Carnivora only some peculiar viverrids, and among Artiodactyla only a bush-pig and a hippopotamus (now extinct). This extraordinary assemblage differs sharply, but mostly in a negative way, from the recent African fauna and it does not hang together, so to speak: in comparison with known continental faunas its assemblage is not of one age. It contains early Tertiary groups without their later Tertiary relatives abundant on adjacent continents, mid-Tertiary groups with neither their early nor their late Tertiary allies, and late Tertiary to Recent groups such as are always, elsewhere, accompanied by members of other groups here quite lacking.

Matthew's theory (1915) was that these various Malagasy groups represent the occasional, accidental overseas introduction of single elements from Africa at different times, each subsequently expanding and, except for the latest, differentiating in the insular environment. I have elsewhere (Simp-

son, 1940a) expressed my adherence to this theory and I have emphasized that the improbability of such overseas migration, urged against Matthew's theory by its opponents, is really an essential and positive part of the theory, not only consistent with the facts but also necessary to explain them. That aspect of the discussion need not be resumed here, but what the principal drift theories have made of the problem will be mentioned.

For both Wegener and Du Toit, Madagascar was originally sandwiched between the tip of India and Africa when those two masses were united, but these two leading advocates of drift differ as to the sequence of separation and its bearing on mammalian faunas. Wegener (1924, p. 62) supposes that India first broke away from Madagascar and Africa in pre-mammalian times and that Madagascar became separated from Africa in the Triassic by a flooded fault trough, but did not break away definitively until the middle Tertiary or later. The trough separation is said to be "demanded by the land fauna," but the bearing on mammals is obscure. The mid-Tertiary as the earliest time for the definitive break is set by the bush-pig and hippopotamus, said to have swum from Africa at that time and to be able to swim only 30 kilometers, on the authority of Lemoine. The date is certainly too early and this immigration must have been latest Tertiary or Quaternary. Wegener leaves almost all the mammals unexplained and his data are wrong for the two that he does seek to explain.

Du Toit (1937, pp. 120-125) has Madagascar breaking away first from Africa, soon after the Jurassic, but remaining attached to India and South America until late in the Cretaceous, at least, largely on dinosaurian evidence which is, incidentally, misinterpreted. In the Oligocene Madagascar is supposed to have been temporarily reunited to Africa. The drift mechanics of this reunion after such old separation are not explained. The evidence is said to be "the well-established faunal relationships that are exemplified by the lemurs, monkeys, tortoises, hippopotami, etc., as cited by Gregory."<sup>6</sup> The fact that there are no monkeys in Madagascar is, of course, one of the striking anomalies requiring explanation, and, again, if the hippopotamus crossed on a bridge, this connection was certainly much later than Oligocene.

<sup>6</sup>The reference is not given and I cannot find such a statement in Gregory's works.

In spite of the fact that Du Toit has recourse to a weakening supplement to his drift theory in order to explain the Malagasy fauna, it remains unexplained and inexplicable on this basis. On a later page of the same work (1937, p. 297) he suggests a different and contradictory explanation. In support of his belief that Madagascar separated from Africa before it did from India, he cites Lydekker (1911, p. 1009) to the effect that the Malagasy mammals are Oriental rather than Ethiopian. This is definitely a misquotation of Lydekker, who did not in the place cited (or anywhere else, that I can find) say anything that can be construed as meaning that the Malagasy fauna is more Oriental than African in affinities. On the contrary, as more clearly stated in an earlier work (1896), Lydekker was thoroughly aware that the Malagasy mammalian fauna was and could only be derived from Africa. This is still universally admitted by competent students. The question is not "Whence?", but "By what means?", "At what dates?", and "How were the more abundant African groups excluded?"

The drift theory offers no possible answers and its exponents become contradictory and incorrect as to fact when they try to apply it to Madagascar. Matthew's is as yet the only theory that gives logical answers to all these questions in combination.

#### CONCLUSION.

The known past and present distribution of land mammals cannot be explained by the hypothesis of drifting continents. It can be accommodated to that hypothesis only by supplementary hypotheses effectively indistinguishable from those involving stable continents and not really involving or requiring drift. This distribution could be explained in terms of transoceanic continents but it is more consistent with fully stable continents. There appear to be no facts in this field that are more completely or more simply explicable by transoceanic than by stable continents and the supposed evidence of this sort is demonstrably false or misinterpreted. The distribution of mammals definitely supports the hypothesis that continents were essentially stable throughout the whole time involved in mammalian history.

## WORKS CITED.

- Allen, Glover M.: 1938, 1940. The mammals of China and Mongolia. Nat. Hist. Cent. Asia, Vol. XI, pts. 1 and 2. Amer. Mus. Nat. Hist., New York.
- Anthony, H. E.: 1928. Field book of North American mammals. G. P. Putnam's Sons, New York and London.
- Arlt, Theodor: 1919. Handbuch der Palaeogeographie. Band I. Palaeozoologie. Gebrüder Borntraeger, Leipzig.
- Berry, Edward W.: 1928. Comments on the Wegener hypothesis. In, "The Theory of Continental Drift," Amer. Assoc. Petrol. Geol., Tulsa and London, pp. 194-196.
- Bramwell, James: 1938. Lost Atlantis. Harper and Bros., New York and London.
- Chaney, Ralph W.: 1940. The bearing of forests on the theory of continental drift. Sci. Monthly, Dec. 1940, pp. 489-498.
- Chatwin, C. P.: 1940. The lost Atlantis. South-eastern Nat. and Antiq., Vol. 44, pp. 41-51.
- Du Toit, Alex. L.: 1937. Our wandering continents. Oliver and Boyd, Edinburgh and London.
- Frick, Childs: 1937. Horned ruminants of North America. Bull. Amer. Mus. Nat. Hist., Vol. 69, pp. i-xxviii, 1-669.
- Gidley, James Williams: 1907. Revision of the Miocene and Pliocene Equidae of North America. Bull. Amer. Mus. Nat. Hist., Vol. 23, pp. 865-934.
- Gracht, W. A. J. M. van Waterschoot van der: 1928. The problem of continental drift. [And] Remarks regarding the papers offered by the other contributors to this symposium. In, "The Theory of Continental Drift," Amer. Assoc. Petrol. Geol., Tulsa and London, pp. 1-75 and 197-226.
- Granger, Walter, and Gregory, William K.: 1942. Revision of the titanotheres of Mongolia. Bull. Amer. Mus. Nat. Hist., in press.
- Gregory, John Walter: 1929. The geological history of the Atlantic Ocean. Quart. Jour. Geol. Soc. London, Vol. 85, pp. lxxviii-cxxii.
- : 1930. The geological history of the Pacific Ocean. Quart. Jour. Geol. Soc. London, Vol. 86, pp. lxxii-cxxxvi.
- Holland, Thomas H.: 1941. The evolution of continents: a possible reconciliation of conflicting evidence. Proc. Roy. Soc. Edinburgh, Section B, Vol. 61, pp. 149-166.
- Huene, Friedrich von: 1929. Versuch einer Skizzen der paläogeographischen Beziehungen Südamerikas. Geol. Rundschau, Vol. 20, pp. 81-96.
- Ihering, Hermann von: 1927. Die Geschichte des Atlantischen Ozeans. Gustav Fischer, Jena.
- Joleaud, L.: 1919a. Relations entre les migrations du genre *Hipparion* et les connexions continentales de l'Europe, de l'Afrique et de l'Amérique au Miocène supérieur. Comptes Rend. Acad. Sci., Vol. 168, pp. 177-179.
- : 1919b. Sur les migrations à l'époque néogène des *Hipparion*, des *Hippotraginés* et des *Tragélaphinés*. Comptes Rend. Acad. Sci., Vol. 168, pp. 310-312.
- : 1919c. Sur les migrations des genres *Hystrix*, *Lepus*, *Anchitherium* et *Mastodon*, à l'époque néogène. Comptes Rend. Acad. Sci., Vol. 168, pp. 412-414.
- : 1924. L'histoire biogéographique de l'Amérique et la théorie de Wegener. Jour. Soc. Amér. Paris, n.s., Vol. 16, pp. 325-360.

- Lydekker, R.: 1896. A geographical history of mammals. University Press, Cambridge.
- : 1911. Zoölogical distribution. *Encyclopedia Britannica*, 11th ed., Vol. 28, pp. 1002-1018.
- Matthew, William Diller: 1915. Climate and evolution. *Ann. New York Acad. Sci.*, Vol. 24, pp. 171-318.
- : 1924. Third contribution to the Snake Creek fauna. *Bull. Amer. Mus. Nat. Hist.*, Vol. 50, pp. 59-210.
- : 1939. Climate and evolution. 2nd ed., revised and enlarged. *Spec. Pub. New York Acad. Sci.*, Vol. I, pp. i-xii, 1-223.
- Matthew, W. D., and Cook, Harold J.: 1909. A Pliocene fauna from western Nebraska. *Bull. Amer. Mus. Nat. Hist.*, Vol. 26, pp. 361-414.
- Merriam, John Campbell: 1911. Tertiary mammal beds of Virgin Valley and Thousand Creek in western Nevada. *Univ. California Pub., Bull. Dept. Geol. Sci.*, Vol. 6, pp. 199-304.
- Osborn, Henry Fairfield: 1910. *The Age of Mammals*. Macmillan, New York.
- : 1918. Equidae of the Oligocene, Miocene, and Pliocene of North America, iconographic type revision. *Mem. Amer. Mus. Nat. Hist.*, n. s., Vol. 2, pt. 1, pp. 1-217.
- Scharff, R. F.: 1903. Some remarks on the Atlantis problem. *Proc. Roy. Irish Acad.*, Vol. 24, sect. B, pp. 268-302.
- Simpson, George Gaylord: 1930. Tertiary land mammals of Florida. *Bull. Amer. Mus. Nat. Hist.*, Vol. 59, pp. 149-211.
- : 1939. The development of marsupials in South America. *Physis, Rev. Soc. Argentina Ci. Nat.*, Vol. 14, pp. 373-398.
- : 1940a. Mammals and land bridges. *Jour. Washington Acad. Sci.*, Vol. 30, pp. 137-163.
- : 1940b. Antarctica as a faunal migration route. *Proc. 6th Pacific Sci. Cong.*, pp. 755-768.
- : 1941. The affinities of the Borhyaenidae. *Amer. Mus. Novitates*, No. 1118, pp. 1-6.
- Stirton, R. A.: 1940. Phylogeny of North American Equidae. *Univ. California Pub., Bull. Dept. Geol. Sci.*, Vol. 25, pp. 165-198.
- Termier, Pierre: 1916. Atlantis. *Ann. Rept. Smithsonian Inst. for 1915*, pp. 219-234.
- Wegener, Alfred: 1924. *The origin of continents and oceans*. Methuen and Co., London.
- Willis, Bailey: 1932. Isthmian links. *Bull. Geol. Soc. Amer.*, Vol. 43, pp. 917-952.