estimate of vertical mixing from a single measurement of <sup>212</sup>Pb may be possible more often. When such ideal conditions do not obtain, the residence time can still be estimated from Eq. 7, provided  $C_0$  is vertically homogeneous and known. On the 2 days for which we have measurements, similar estimates of  $\tau_s$  were obtained, of the order of 4 to 5 minutes. If our conclusion is correct, that the source strength of the city's <sup>212</sup>Pb is relatively constant, then the residence times in the street layer calculated from measurements made on 16 additional occasions during different seasons did not vary by more than a factor of 3 from these values.

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### **References and Notes**

- The radon chain, with half-lives given in parentheses, is <sup>222</sup>Rn (3.8 days), <sup>218</sup>Po (3 minutes), <sup>214</sup>Pb (27 minutes), <sup>214</sup>Bi (19 minutes), <sup>214</sup>Po (164 μsec), long-lived isotopes. The thoron chain is <sup>220</sup>Rn (54 seconds), <sup>210</sup>Po (0.1 second), <sup>212</sup>Pb (10.6 hours), <sup>212</sup>Bi (1 hour).
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- <sup>212</sup>Pb in the urban boundary layer. 10. It is possible that the Empire State Building itself affects the flow of air around it and therefore locally affects vertical mixing. We think that this effect was negligible, as our sampling sites were on the upwind side of the building. In addition the presence of an inversion, detectable at the sampling sites during profiles 1 and 2 on 26 February, argues against vertical mixing induced by the argues against vertical mixing induced by the building itself. The U.S. Weather Bureau

morning radiosonde at La Guardia airport detected an inversion at 170 m; we found this between the 30th and 86th floors of the Empire State Building, when the temperatures were  $10.6^{\circ}C$  and  $12.5^{\circ}C$ , respectively.

- 11. We consider only the advective flux, which is generally much greater than the diffusive flux *(*4).
- 12. The wind sounding at La Guardia airport was given by the U.S. Weather Bureau for 19 March at 100-m intervals. It was 7 m/sec from 130° (surface), 9 m/sec from 137° (100 m), and 11 m/sec from 140° (200 m), 13 m/sec m), and 11 m/sec from 140° (200 m), 15 m/sec from 144° (300 m), 13.5 m/sec from 151° (400 m), and 14 m/sec from 159° (500 m). The geostrophic wind was 16 m/sec from 180° (800 m). The wind profile on that day thus resembled an Ekman spiral, and we applied Lettau analysis [see H. Lettau, Tellus 2, 125 (1950)] to obtain an estimate of the eddy viscosity for the layer between the surface and 400 m. The equation for the eddy

viscosity is  $K_{\rm m} = (1/\rho) (|T|/|dv/dz|)$ , where T is the wind stress vector, z is the horizontal wind vector, and  $\rho$  is the density. From the estimated wind stress at 200 m (5 dyne/cm<sup>2</sup>) and the wind shear between the surface and 400 m (0.02 sec<sup>-1</sup>) we calculate 25  $m^2/sec$ for K

- Supported by AEC contracts AT (30-1) 2663 and AT (30-1) 4055. We are grateful to Dr. M. Bender for taking some of the samples, 13. M. Bender for taking some of the samples, to G. Mathieu for analyses of stable lead, and to Drs, W. Van Pelt and T. Kneip for the volume calibration of our air samplers. We thank Drs, W. Broecker and J. Friend for helpful discussions and criticisms, Mr. Kussman and Mr. Heidelberger of the U.S. Weather Bureau for meteorological data, and T. Sullivan and his staff at the Empire State Building for permission and assistance in taking samples. Lamont-Doherty Geological Observatory contribution No. 1769.
- 13 August 1971; revised 27 September 1971

# Breakup of Pangaea and Isolation of Relict Mammals in Australia, South America, and Madagascar

Abstract. The composition of aboriginal land mammal faunas in Australia and New Guinea (prototherians and metatherians), South America (metatherians and eutherians) and Madagascar (eutherians only) is reconsidered in light of continental drift reconstructions of Mesozoic-Tertiary world paleogeography. It is proposed that these three faunas represent successively detached samples of the evolving world mammal fauna as it existed when each of these land masses became faunally isolated from the rest of the world as a result of the progressive fragmentation of Pangaea. Isolation of aboriginal prototherians and metatherians in Australia and New Guinea may date from the Upper Jurassic-Lower Cretaceous; isolation of aboriginal metatherians and eutherians in South America may date from the Middle Cretaceous-Upper Cretaceous; isolation of aboriginal eutherians in Madagascar may date from the Paleocene-Eocene.

For more than a century zoogeographers have been intrigued by the fact that primitive mammals tend to be concentrated in three widely separated regions in the Southern Hemisphere-Australia and New Guinea, South America, and Madagascar (1, pp. 82, 287). Currently, the most widely accepted interpretation of this distribution is that it is a coincidental result of three independent episodes of "sweepstakes dispersal" across past or present water gaps with world continents and islands assumed to have been fixed in their present positions, at least during the time of dispersal of these groups of mammals (2, pp. 88-105; 3, pp. 363, 522). However, the assumption that continental positions have remained fixed during this period is being called in question by a growing body of geophysical research on plate tectonics. Reexamination of relevant faunal evidence in light of new paleogeographic perspectives that are provided by the continental drift reconstructions of Dietz and Holden (4) suggests that the distribution of relict mammals in the Southern Hemisphere is not the

result of coincidence, but instead that there is a direct causal relation between the early separation of continental masses and the preservation of these relict mammal faunas (Table 1).

According to Dietz and Holden (4, pp. 4943-4952) and many other students of continental drift, at the close of the Paleozoic all of the earth's crust was united to form a single supercontinent, Pangaea (Fig. 1A). Near the end of the Triassic, Pangaea began to split into two parts: (i) Laurasia-West Gondwana, which includes present-day North America, South America, Eurasia (excluding India), and Africa, and (ii) East Gondwana, which includes present-day Antarctica, India, Australia, New Guinea, and New Zealand (Fig. 1B). At about the same time. India began to separate from the rest of East Gondwana and to drift northward. Also at about the same time, as a result of the formation of the North Atlantic rift, present-day North America lost its direct connection to South America and Africa, but retained its connection to Europe. In the Upper Jurassic or Lower Cretaceous, present-day South

America began to split away from Africa (Fig. 1C). During the Cretaceous, Madagascar began to separate from Africa, and Australia-New Guinea began to drift northward away from Antarctica (Fig. 1D). Subsequently, during the Tertiary, North America (including Greenland) separated from Eurasia and ultimately became united with South America; India became united with south-central Eurasia; and Australia-New Guinea approached, without joining (as yet), the southeastern part of Eurasia. Throughout the entire period of fragmentation of Pangaea, Africa maintained a more or less continuous, although sometimes tenuous and shifting, connection with Eurasia. During this period, classical Gondwanaland (South America-Africa-Madagascar-Antarctica-India-Australia) did not exist as an intact unit isolated from Laurasia (North America-Eurasia) (Fig. 1, B and C).

In the following analysis of the mammal faunas of Australia, South America, and Madagascar, bats and marine mammals are omitted because of their special ability to disperse across water gaps. Also excluded are faunal elements that probably or certainly were introduced by man.

The original land mammal fauna of the Australian region evidently consisted exclusively of monotremes (subclass Prototheria) and marsupials (subclass Theria, infraclass Metatheria) (5). Two families of monotremes and seven families of marsupials now inhabit this region. This region also is inhabited by murid rodents, which are a family of placentals (subclass Theria, infraclass Eutheria), but rodents are conspicuously absent from pre-Pleistocene fossil deposits in Australia (5, p. 390) and therefore probably are relatively recent immigrants. The time of the first occurrence in this region of monotremes and marsupials is not documented by the Australian land vertebrate fossil record, which is virtually blank from the Triassic to the Oligocene.

Early South American mammals are known from fossil deposits that extend from the Upper Cretaceous through the Eocene (6). This early fossil fauna includes five families of marsupials (Metatheria) and 21 families of placentals (Eutheria). No prototherians are known in these deposits. Of the placental families, five are assigned to the living order of South American edentates (Edentata) and 16

Table 1. Comparison of dates of initial rifting (4, pp. 4945–4950) and composition of aboriginal mammal faunas (see text) in Australia–New Guinea, South America, and Madagascar.

Date of initial rifting (× 10 <sup>6</sup> years B.P.)	Composition of aboriginal terrestrial mammal fauna
180	Prototheria, Metatheria
135	Metatheria, Eutheria
135-65	Eutheria
	Date of initial rifting $(\times 10^{\circ} \text{ years B.P.})$ 180 135 135–65

\* Originally part of the Antarctica-India-Australia-New Guinea block.

are assigned to seven orders of extinct ungulates (Condylarthra, one family; Xenungulata, one family; Pyrotheria, one family; Litopterna, two families; Astrapotheria, one family; Trigonostylopoidea, one family; Notoungulata, nine families). All seven of these extinct ungulate orders probably originated from radiation of two ancestral stocks, Condylarthra (with five derived orders) and Notoungulata. Absent from this early fauna are caviomorph rodents and primates, which appear relatively suddenly in South America in Oligocene deposits and therefore seem to be mid-Tertiary immigrants. Numerous other placental groups (insectivores; lagomorphs; sciurid, heteromyid and cricetid rodents; carnivores; proboscidians; perissodactyls; artiodactyls) appear first in Pliocene-Recent deposits and therefore apparently are late Tertiary immigrants.

The original land mammal fauna of Madagascar, like that of Australia and New Guinea, is not known directly from early Tertiary fossil evidence, but may be inferred from evidence of the Pleistocene-Recent fauna (3, p. 521). This fauna includes only placentals; monotremes and marsupials are absent. Of 38 genera of living Madagascan mammals, 34 are endemic genera belonging to four placental groups: tenrecid insectivores (Tenrecidae, 10 genera), lemuroid primates (Lemuridae, Indridae, Daubentoniidae, 10 genera), civets and allied carnivores (Viverridae, seven genera), and an endemic subfamily of cricetid rodents (family Cricetidae, subfamily Nesomyinae, seven genera). One endemic genus of aardvarks (order Tubulidentata) is known from the Madagascan Pleistocene (7, p. 712). These five eutherian groups, each represented by endemic Madagascan genera, probably constitute the original land mammal fauna of the island. The few other known Madagascan land mammals, all members of genera that also inhabit Africa, are an extinct Pleistocene pygmy hippopotamus, which probably was a relatively recent immigrant, and one or two species each of shrews, bushpigs, house mice, and house rats, which probably were introduced by man.

Aboriginal land mammal faunas in these three regions may be summarized as follows: Australia and New Guinea, prototherians and metatherians; South America, metatherians and three orders of eutherians, of which one (Edentata) is unique and two (Condylarthra, Notoungulata) are extinct; Madagascar, five orders of eutherians, of which four are broadly distributed outside of Madagascar (Insectivora, Primates, Carnivora, Rodentia) and one is now restricted to Africa (Tubulidentata). Completely lacking from these aboriginal faunas are seven other living orders of eutherians-Dermoptera, Pholidota, Lagomorpha, Proboscidea, Hyracoidea, Perissodactyla, and Artiodactyla, Of the seven missing orders, six (all except Dermoptera) are in Africa but not in Madagascar (3, p. 431). About 22 families of the orders Insectivora (four families), Primates (three families), Carnivora (four families) and Rodentia (11 families) likewise inhabit Africa but not Madagascar (3, p. 431). The rodent family Cricetidae, present in Madagascar, is believed to be ancestral to the family Muridae (8, p. 177), which probably arose in the Miocene and which is spectacularly successful in the Old World, but is not native to Madagascar. As a whole, the eutherian fauna of Madagascar appears to be more primitive than that of Africa (9, p. 282).

The known fossil distribution of the nine aboriginal stocks is indicated in Table 2. Monotremes as such are unknown outside of Australia and New Guinea, but extinct multituberculates are closely related prototherians (10, p. 7; 11, p. 976) and are well known as fossils from the Upper Jurassic to the Paleocene-Eocene in North America, Europe, and Asia; still earlier prototherian orders, Triconodonta and Docodonta, are known from the Upper Triassic-Upper Jurassic in North America, Africa, Europe, and Asia. Metatherians are known outside of the

Australian and South American regions from the Middle Cretaceous to the Miocene in North America and from the Eocene to the Miocene in Europe. Most of the aboriginal eutherian stocks also have early fossil records outside of the Australian, South American, and Madagascan regions.

The prototherian-metatherian aboriginal fauna of Australia and New Guinea is clearly more primitive than the metatherian-primitive eutherian aboriginal fauna of South America, and this in turn is more primitive than the primitive eutherian aboriginal fauna of Madagascar (3, p. 535; 9, pp. 49-50; 12). Closely corresponding to these faunal relationships, geophysical evidence indicates that the Australia-New Guinea land mass was part of the first block (East Gondwana) to detach from Pangaea, that the South American land mass was the second block to detach from Pangaea, and that the Madagascar block was the last of these three to detach (Table 1). The most straightforward interpretation of the zoological and paleogeographical evidence is that the aboriginal land mammal faunas of these three regions represent three successively detached and isolated samples of the evolving world fauna as it existed before each of the respective regional land masses separated from Pangaea. More specifically, the evidence seems to imply that prototherians and metatherians were the dominant mammal groups in Pangaea before separation of East Gondwana interrupted faunal exchange between that land mass and Laurasia-West Gondwana (Fig. 1A). After this separation, prototherians in Laurasia-West Gondwana evidently declined and became extinct as eutherians arose and began their radiation. Meanwhile, prototherians and metatherians persisted in isolation in East Gondwana, which was then inaccessible to the newly evolved eutherians (Fig. 1B). At this stage, South America, bearing a sample of the metatherian-primitive eutherian world fauna, separated from the rest of Laurasia-West Gondwana. Subsequently, paralleling events during the preceding evolutionary stage, metatherians declined and became extinct in the main part of the world (Laurasia-West Gondwana minus South America) as eutherians there continued to radiate and become more dominant. In South America metatherians and the early stock of primitive eutherians survived in isolation (Fig. 1C). Finally, Madagascar detached from the

Aboriational stock				Geological distributi	on	•	
AUUIIBIIIAI SUUA	Australia	South America	Madagascar	North America	Africa	Europe	Asia
Prototheria* Metatheria	PleistR. U. Olig. (5)-R.	U. Cret. (25)–R.		U. JurU. Eoc. M. Cret. (26)-L. Mioc.†	U. Trias.	U. TriasU. Paleoc. M. EocL. Mioc.	U. TriasU. Paleoc.
Eutheria Edentata		II Palence (6)-R		+ (22)			
Condylarthra <sup>‡</sup>		?U. Cret. (6)–Pleist.		U. CretEoc.	?L. Olig?L. Mioc.	U. PaleocL. Olig.	M. EocL. Olig.
Notoungulata		U. PaleocPleist.		L. Eoc.			U. Paleoc.
Insectivora: Tenrecidae			PleistR.	M. EocM. Olig. (28)	L. MiocR.		
Primates: Lemuroidea			PleistR.	L. EocM. Eoc.	L. Mioc.–R.	?L. EocU. Eoc.	Eoc., PlioR.
Carnivora: Viverridae			PleistR.	•	L. Mioc.–R.	U. EocR.	L. OligR.
Rodentia: Cricetidae		-1	PleistR.	L. OligR.	U. MiocR.	L. OligR.	L. OligR.
Tubulidentata: Orycteropodids	e		Pleist.	?L. Eoc.	L. MiocR.	?EocOlig., L. Plio.	L. Plio.

remainder of the main world continent (North America-Eurasia-Africa), thereby isolating a sample of the second stage of primitive eutherian evolution. This sample in Madagascar persisted in isolation as more advanced eutherians evolved and became dominant in the residual main world continent (Fig. 1D).

In the above formulation, groups named as components of world faunas and isolated faunas are to be understood as the most dominant and widespread groups inhabiting the indicated land masses at the indicated evolutionary stages. It is not to be assumed that members of these groups were exclusively or uniformly distributed over the surface of these land masses, any more than living mammalian faunal elements are uniformly distributed in presentday continents or islands. The ranges of ancient mammals presumably were limited geographically and ecologically, as are those of living mammals. The absence of metatherians from Cretaceous-Paleocene deposits in Eurasia, for example, may indicate that this group originated in the southern or western part of Pangaea and that it failed to spread to northeastern Pangaea before metatherians lost dominance to eutherians. A similar explanation may account for the absence of prototherians from Cretaceous-Paleocene deposits in South America.

This hypothesis does not imply that faunal exchange ceases immediately when a rift forms and continents begin to separate. Although the Red Sea rift apparently began to split the Arabian peninsula from Africa in the Oligocene [Dietz and Holden (4), p. 4952; 13, p. 238], faunal exchange between these land masses remains possible up to the present by way of the Isthmus of Suez. Even after rifting completely separates two land masses, some mammals probably continue to disperse between the newly formed continents until the water gap becomes too wide.

In the present hypothesis it is assumed that metatherians originated and dispersed earlier than eutherians (Fig. 1, A and B). Although the known fossil record of both of these groups extends back to the Upper Cretaceous, the Lower Cretaceous record of their derivation from presumed Jurassic panthere ancestors is meager and ambiguous (14, p. 378). Because metatherians retain more primitive characters than eutherians (15, p. 142; 16, p. 90), it seems probable that they originated

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first. Recent comparative study of these two groups has led Lillegraven (16, p. 108) to revive T. H. Huxley's suggestion that metatherians are directly ancestral to eutherians.

Available fossil evidence generally supports the hypothesis presented here (Table 2). Extinct prototherians, metatherians, and primitive eutherians, all related to living Southern Hemisphere relicts, are known from successively more recent deposits in the main world continents. The most important contrary indication is Clemens' (17, p. 10) suggestion that Australian marsupials may be derived from a North American Upper Cretaceous ancestor. If marsupials dispersed from North America to Australia during or after the Upper Cretaceous, this event would have occurred long after the presumed time of separation of East Gondwana and Laurasia-West Gondwana.

As would be expected, the dates of initial rifting indicated by geophysical evidence (Table 1) are somewhat earlier than the respective dates of isolation of relict mammal faunas indicated by paleontological evidence (Table 2). Obviously, knowledge is still far from precise concerning dates of initial rifting, paleogeographic details of final separation, and evolutionary history and relationships of ancient mammals. Based on known fossil evidence, a rough estimate of the chronology of early mammalian zoogeography is that isolation of prototherians and metatherians in Australia-New Guinea dates from the Upper Jurassic or Lower Cretaceous, isolation of metatherians and early primitive eutherians in South America dates from the Middle or Upper Cretaceous, and isolation of later primitive eutherians in Madagascar dates from the Paleocene or Lower Eocene. According to Cooke's (13, p. 238) paleogeographic maps of Africa, Madagascar may have been joined to the African land mass in the Paleocene. The faunal isolation of Madagascar evidently was complete before the Upper Eocene-Lower Oligocene, when proboscidians, hyracoids, and simian primates are dominant elements in the fossil fauna of Africa (13, pp. 240-243). Cricetid rodents may have dispersed to Madagascar later than tenrecids, lemuroids, viverrids, and aardvarks, after a narrow water gap already existed, just as murid rodents have dispersed across a water gap to the Australian region.

Previous continental drift interpretations of mammalian zoogeography have been offered by Kurtén (18) and Hoffstetter (19). Kurtén is primarily concerned with comparing the number of mammalian orders that may have differentiated on isolated land masses and, therefore, he does not attempt to explain specific distributional patterns, such as the occurrence of marsupials in Australia and South America or the occurrence of primitive placentals in Madagascar. Hoffstetter has based his innovative and comprehensive interpretation of early marsupial and placental



Fig. 1. Breakup of Pangaea, simplified from Dietz and Holden (4, figures 2 through 5), with added notations to indicate the hypothetical composition of world mammal faunas and isolated mammal faunas during successive stages of continental fragmentation. [Illustration by Kevin Royt]

dispersal on Wegener's original reconstruction of Cretaceous paleogeography, in which North America, South America, Antarctica, and Australia are assumed to have formed a single connected land mass after South America and Africa had already been separated by the embryonic Atlantic Ocean; this arrangement and the implied dispersal routes are not conformable with modern geophysical evidence (4, pp. 4946-4947).

Cox's (20) interpretation of the early dispersal of marsupials is largely accepted and incorporated into the hypothesis presented here. Martin's (21) suggestion that marsupials reached Australia and the Americas by dispersal from a hypothetical land mass isolated in the South Pacific Ocean fails, as noted by Cox, to explain how the ancestral marsupial stock reached this isolated center of dispersal. Clemens' (14, p. 381) recent suggestion that marsupials may have spread from South America to Antarctica and Australia across a Cretaceous or early Tertiary water gap seems implausible, since it invokes chance to account for the failure of South American placentals to accompany marsupials on this over-water migration and it implies that the occurrence of monotremes and marsupials in the Australian region also is the result of chance.

The hypothesis presented here has several obvious implications that may provide tests of its validity. First, this hypothesis should be applicable to interpretation of later mammalian zoogeography, after the separation of Africa and Madagascar. It should help to explain the Tertiary mammalian faunal history of North America after its separation from Europe and during its subsequent union with Asia via the Bering bridge and with South America via the Isthmus of Panama. It should also apply to the mammalian faunal history of India during the long isolation of that subcontinent and after its union with Asia along the Himalayan suture. Second, the hypothesis developed here for mammals should be applicable to other vertebrates, to invertebrates, and to plants. It should help to explain the distribution of a number of Southern Hemisphere nonmammalian vertebrates, such as lungfishes, osteoglossid fishes, leiopelmatid and hylid frogs, side-necked turtles, Sphenodon, iguanid lizards, booid and elapid snakes, ratite birds, and tinamous. Lynch (22, p. 218) has already inter-

preted the distribution of leptodactyloid frogs in a way that generally agrees with the hypothesis presented here. Finally, this hypothesis implies certain past distributions not yet documented by the fossil record. Marsupials should be anticipated in the African Cretaceous, as postulated by Cox (20, p. 770), and prototherians should be expected in the African Jurassic or Cretaceous. Similarly, prototherians and metatherians should be present in the Mesozoic and early Tertiary of India. Prototherians and metatherians also should be anticipated in Antarctica above the Lower Triassic beds that recently have yielded labyrinthodont amphibians, thecodont reptiles, and therapsid reptiles (23).

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   I thank H. Dybas and P. Hershkovitz, colleagues at the Field Museum of Natural History, with whom I have had numerous of these ideas. I also thank L. ky and L. Van Valen, University discussions B. Radinsky and L. of Chicago, who read and commented on an early version of the manuscript.
- 18 August 1971; revised 1 October 1971

## Cell Aggregation: Role of Acid Mucopolysaccharides

Abstract. Factors that induce cell aggregation are released by several types of chick embryo and mammalian cell cultures. These aggregation factors are also present in some serums. The factors in each of the preparations tested were inactivated by treatment with bovine testicular hyaluronidase. Conversely, hyaluronic acid promoted aggregation of only those cells that were aggregated by media containing the factors. These factors appear to be acid mucopolysaccharides, with hyaluronic acid being a major component.

Dissociated cells from sponges (1), from embryos (2), and from some tissue cultures (3), are able to reassociate to form multicellular structures, or aggregates. From these cells, substances with an aggregation-promoting activity (aggregation factors, or AF's) have been obtained by various methods (4, 5). Some of these AF's apparently exert their effects by interaction with components at the cell surface. For example, AF's obtained after chemical dissociation of sponges or by spontaneous cellular release in monolayer cultures enhance the aggregation of the corresponding mechanically dissociated cells at 4°C (6, 7). On the basis of preliminary evidence, it has been suggested that the sponge AF's, large molecules with a definable ultrastructure, are composed of glycoproteins (8). We now report that the AF's released from mammalian cells and from chick embryo neuroretinal and liver cells in culture and the AF's present in serums appear to be acid mucopolysaccharides (MPS).

To obtain the AF's released from SCIENCE, VOL. 175