# SYSTEMATICS AND PLATE TECTONICS IN THE SPREAD OF MARSUPIALS

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ABSTRACT. Geophysical evidence that the likely route of colonization of Australia by mammals was from South America via Antarctica is accepted. Though conclusive evidence is still lacking, the available evidence suggests that didelphoid marsupials were present in South America before placental mammals. The suggestion that marsupials dispersed to Australia before a climatic or geological change closed this route to the later-appearing placentals remains the simplest explanation of the absence of placentals from Australia.

THE early mammal faunas of the Southern Hemisphere show two peculiarities. First, there is the presence in South America through most of the Tertiary of a mixed fauna of insectivorous, omnivorous and carnivorous marsupials and of herbivorous placentals, whereas in most parts of the world, wherever both stocks were initially present, the marsupials prove competitively inferior to the placentals and die out by the Miocene. The second is the fact that it was the inferior marsupials alone which colonized Australia, the superior placentals (with the exception of a few in the Late Cenozoic) failing to do so at all. This latter problem has been much discussed, and has still not yet been explained conclusively.

I suggested recently (Cox 1970) that continental drift might provide the solution. If marsupials appeared before placentals, as Lillegraven (1969) had argued convincingly, perhaps they entered the Antarctica–Australia land mass before that broke away from the rest of Gondwanaland, and that this in turn took place before placental mammals had evolved; so that, by the time they appeared, Australia was no longer accessible. At that time it seemed likely that drift would have separated Antarctica–Australia from both Africa and South America at approximately the same time. It now appears (Jardine and McKenzie 1972) that this belief was wrong, and that there was a narrow connection between South America and Antarctica–Australia for long after all these had become separated from Africa, in fact, until well into the Tertiary and considerably after the South American placentals had appeared. This reopens the question as to why the placentals did not cross to Australia, but marsupials did. Jardine and McKenzie see no difficulty in this, and merely state 'It is reasonable to suppose that the unspecialized didelphoid marsupials were able to colonize Antarctica, and that the specialized placentals could not' (1972, p. 23). However, though the evolutionary potential of such insectivorous or omnivorous animals as didelphoid marsupials is undoubtedly greater than that of herbivorous forms, they are not 'unspecialized' but merely adapted to a different, specialized, way of life. It is by no means obvious why their ecological adaptations should have made the passage of Antarctica easier for them than for herbivorous placentals. Indeed, the reverse seems more likely. Herbivores are normally larger than insectivores or omnivores, and larger mammals lose heat at a proportionately lower rate than small mammals. As a result, small mammals are usually less tolerant of cold

climates than their larger, herbivorous relatives—as shown in the history of the Bering land bridge where, as the climate became cooler, the larger herbivores were able to cross after other groups had found this impossible. Of course, one must be cautious in arguing that the abilities of modern marsupials are necessarily identical with those of their Early Tertiary ancestors. Nevertheless, Darlington's (1965, p. 19) comments on the fauna of the southern end of South America today are worth noting. 'No marsupials and few other mammals reach the southern end of the virtually continuous forest strip. In fact only the following terrestrial mammals are known to occur as far south as Tierra del Fuego in all habitats combined; one amphibious otter, one fox, one "camel" (the Guanaco), and one cavioid and several cricetid rodents.' Significantly, there are not only no marsupials, but few terrestrial insectivores or carnivores.

To show that it was feasible for any group to spread from one area to another at a particular time it is necessary to prove several things: (1) That the group was then in existence; (2) that there was continuous land, or at least only minor sea crossings (which would probably be almost undetectable geologically) between the two areas; (3) that there was no impassable climatic barrier at the time in question. Finally, even if all these factors would have allowed dispersal, this could still be prevented if the group in question were competitively inferior to group(s) already established in the 'desired' destination. In the present problem the last factor seems to provide no difficulty, since we have no *a priori* reason to believe that the unknown Late Cretaceous and Early Tertiary fauna of Australia offered any greater ecological resistance to mammalian establishment than did that of any other part of the world. The answer to the problem therefore depends on the answers to three questions. When did didelphoid marsupials appear in South America? When did placentals appear on that continent? Finally, when did the land route from South America to Australia finally become impassable to mammals?

The questions as to the time of origins of the two groups are deceptively simple in appearance, but far more difficult in practice. In palaeontology there is frequently a confusion between the earliest specimen which shows any characteristic of the group in question, and the earliest member which had fully developed all the salient features which enabled the group to colonize the mode of life which provided its living and which we recognize throughout the members of its adaptive radiation. The latter form might show a dozen characteristic features. As we go back in time these disappear in turn, until the earliest recognizable relative would have had only one or two. The problem is made more acute by the fact that the earlier material is usually fragmentary, so that it may be impossible to distinguish more than one of the characters, due to lack of many relevant skeletal elements. For example, in early mammal history much of the material consists of teeth. These may show indications of marsupial or placental features, and may therefore be placed in one or other of these groups. It is for such reasons that different Mid-Cretaceous (Albian) teeth from Texas have been placed in both groups (Slaughter 1968a, b), and these *may* indicate the time of divergence of these two lines. But the owners of these teeth almost certainly were not yet fully marsupial or fully placental, with all the advanced features which later characterize these two groups and decide their relative success or failure. In the case of the placentals, this view is supported by another observation. The con-

trast between the variety of Asian early Upper Cretaceous placentals and the more restricted variety of North American forms in the succeeding Campanian, which appear to be immigrants from the Asian placental fauna, has led most workers to conclude that the placentals evolved in Asia. If so, the owner of the North American teeth of primitive placental type can, at most, have been no more than a member of the primitive pre-placental stock from which the definitive placentals later arose as a result of further evolutionary progress.

Hoffstetter (1970a) has commented on the suggestion that placentals evolved from a marsupial-like ancestor. He interprets my (1970) biogeographic theory as implying that the Australian marsupials diverged from the common ancestor before a dichotomy into South American marsupials and the placental stock (text-fig. 1A) and
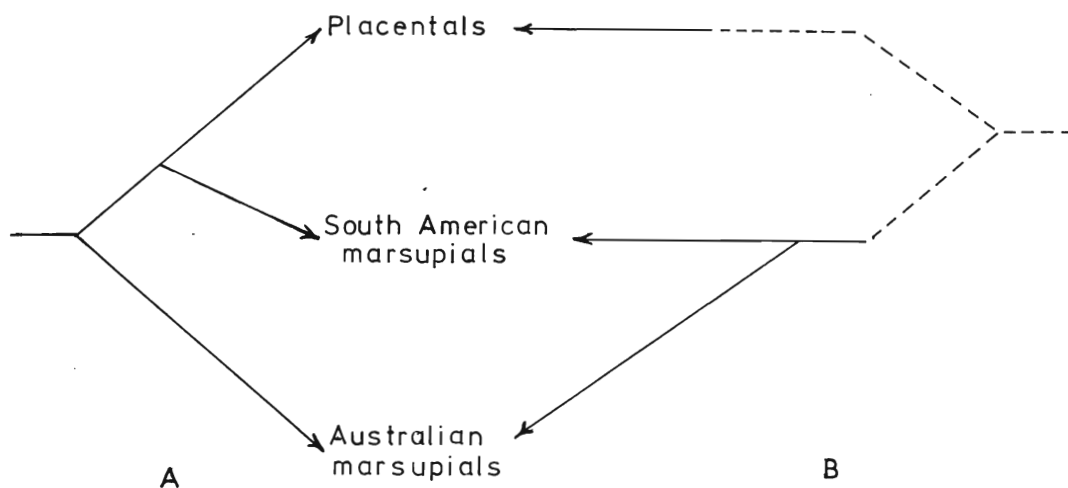


TEXT-FIG. 1. Marsupial–placental phylogeny: A, as inferred by Hoffstetter (1970a); B, as suggested in this paper. (Dotted lines indicate ancestral 'marsupioid' forms, neither fully marsupial nor fully placental.)

very properly points out that this would imply a great deal of convergent evolution between the Australian and the South American marsupials. However, this difficulty is more apparent than real. The supposed phylogenetic pattern is more accurately shown in text-fig. 1B, in which both the ancestry of the placentals and the common ancestor of the Australian and South American marsupials diverge from a common ancestral stock, which in French terminology would be described as 'marsupioid'.

As far as we know at present, the didelphoid marsupials appeared in the Campanian. This is based on the best known record, that of North America, where Fox (1971) has found two genera of didelphoid and four other genera of marsupial belonging to two other families, all in an early Campanian (75 m.y.) horizon. This early diversity in North America led most recent workers to believe that North America was the place of origin of marsupials as a whole. This appeared to be supported by their absence from the early Upper Cretaceous fauna of Asia, which has been sufficiently thoroughly investigated that their absence is unlikely to be merely due to sampling error. However, it is at least as possible that marsupials did not spread to Asia because of a combination of the same barrier that kept many Asian

placental stocks out of North America, and the fact that these placentals were in any case competitively superior to the marsupials, as was shown by the rapid decline of these same marsupials in North America after the placental colonists arrived there. The absence of earlier Asian marsupials does not, therefore, prove that they had not yet evolved anywhere. Furthermore, Upper Cretaceous marsupials are now known from South America (Sigé 1968) and, though their exact age is as yet uncertain, it is possible that marsupials evolved earlier in the Southern Hemisphere and that the Campanian didelphoids of North America are an immigrant stock, as Hoffstetter (1970a) has suggested.

As far as the placentals are concerned, those from the early Upper Cretaceous of Asia, already mentioned, form the first fauna sufficiently varied to suggest that forms possessing an essentially complete range of placental features had appeared. Within South America a single possible placental (*Perutherium*) has been described, and was found in the same Cretaceous deposits as the marsupials mentioned above. The specimen consists of a fragment of jaw containing three damaged teeth, and it has been doubtfully assigned to the Condylarthra, though it is also possible that it is a bunodont marsupial (Hoffstetter, 1970b). Apart from this specimen, placentals are unknown in South America until the Upper Palaeocene, by which time the characteristic South American herbivorous placentals were already so diverse that their ancestors must have entered the continent by the latest Cretaceous (Maestrichtian) or earliest Palaeocene (Patterson and Pascual 1968).

At present, then, there are only two certain palaeontological facts: that marsupials were present in South America in the Late Cretaceous and that the radiation of South American herbivorous placentals was already under way in the Early Palaeocene. (It seems best, for the time being, to ignore *Perutherium*, since its taxonomic position is still uncertain.) These two facts cannot themselves provide an answer to the question as to whether the marsupials or the placentals were the first South American mammals. However, an indirect aspect of the evolution of the two groups may be relevant. It is significant that the placentals are limited to the herbivorous niches in the mammal fauna of South America, though in other continents they radiated widely into many different niches, and in the end supplanted the marsupials. This fact could be explained in one of two ways: either the placentals only colonized the continent after the marsupials had already occupied the insectivorous or omnivorous niches, or the earliest placental colonists were already specialized as herbivores. In the first case there is the clear implication that marsupials were the older inhabitants of South America. In the second case, there is a similar, though less clear, indication of this. In general, herbivorous types of mammal seem to have evolved later than their insectivorous relatives. This is almost certainly because, though it was possible for small insectivorous forms to survive around the feet of the dinosaurs, a larger browsing herbivore would not only have been competing with the herbivorous dinosaurs, but would have been worth the attention of the carnivorous dinosaurs. The alternative small herbivore niche occupied by rodents today was already occupied by another mammalian line, the multituberculates, which survived until the Eocene. No other herbivorous placental or marsupial is known from any Cretaceous deposit; it is important, however, to recognize in scanning the palaeontological literature, that this does not mean that no Cretaceous forms

have ever been placed in any herbivorous mammalian group. Naturally enough, palaeontologists are interested to try to discern relationships between these early placentals and the better-known Cenozoic groups. If such a relationship is established (suspected?), the Cretaceous form is then placed in the appropriate Cenozoic order. The result is an impression of great Upper Cretaceous diversity, whereas in fact Simpson (1971, p. 189) says, 'All these genera are so similar that, if we were dealing only with them it would be unjustified to place them in more than one order; indeed one could defend referring all to a single family of a purely phenetic classification or one ignoring later forms.'

The known history of the marsupials and placentals, and the niches filled by these two groups in South America, thus still suggest (though they are far from proving) that marsupials were present in South America before the placentals. Finally, then, is it possible that the land route to Australia became impassable before the latter evolved?

Jardine and McKenzie (1972) do not support this possibility. They state that South America, Antarctica, and Australia formed a single land mass until the Late Eocene, when Australia separated from Antarctica, i.e. that the South America–Antarctica link was still intact at least until then. This is based on Barker's (1970) work on the Scotia Sea, which suggests that South America and Antarctica have separated since the Middle Tertiary. Barker states that the age of various continental structures in the Scotia Ridge (joining South America and Antarctica via the South Sandwich Islands) argue a post-Cretaceous separation. This in turn is consistent with his sea-floor spreading data, which suggest that the Scotia Sea is of post-Middle Tertiary age, though he states that this estimate is speculative. This area has also since been discussed by Dalziel and Elliott (1971) who agree that the fragmentation of the South America–Antarctica bridge was an Early Tertiary event.

At present there seem to be only two ways out of this difficulty. Either there was a climatic change sufficient to keep out the placentals, or there was a break in the land bridge. As far as climatic change is concerned we know that, though temperatures were high in the Jurassic and Early Cretaceous, they became lower and more zoned in the Later Cretaceous. Jardine and McKenzie (1972) mention that the only known Tertiary flora of Antarctica, that of Seymour Island, indicates a cool temperate forest flora. However, Seymour Island is near the northern tip of the Antarctic Peninsula, and any hopeful emigrant to Australia would have had to go much closer to the South pole to get across Antarctica. McKenzie and Sclater (1971), in their reconstruction maps of the area, show the South pole moving across the narrow connection between East and West Antarctica in the Late Cretaceous–Late Eocene, and even in the latest Cretaceous any migrant would have had to go as far as $c.$ 70° S. on its way to Australia. Significantly, investigations of quartz sand grains and of planktonic foraminifera from Subantarctic deep-sea sediments show that Antarctica was already glaciated in the earliest cores sampled, which were of Lower Eocene age (Margolis and Kennett 1971).

As to a possible break in the South America–Antarctica bridge, one need not suggest that the geological evidence quoted by Barker, and by Dalziel and Elliot is wrong, but merely wonder whether so much is yet known about this region that one can definitely rule out any Late Cretaceous–Early Tertiary marine transgression,

however shallow, across this narrow peninsula. Finally, little is yet known of the history of the connections between East and West Antarctica, and it remains possible (though perhaps unlikely) that it was a break in the connection between these two land masses that barred the land route to Australia (see addendum).

It therefore remains possible that marsupials entered Australia at some time in the Upper Cretaceous, and that the route became impassable shortly afterwards, before placentals appeared in South America. Though Jardine and McKenzie (1972, fig. 5) show the marsupials as entering Australia and beginning their radiation in that continent in the Eocene, there is no firm evidence as to the exact date. As they note, four different marsupial families are known in Australia in the Miocene, and the single Oligocene marsupial specimen known shows several primitive didelphoid features not found in later Australian marsupials. These facts give no evidence upon which to base any estimates of the antiquity of the known Miocene radiation. If anything, the fact that didelphoids alone colonized Australia, and not the South American caenolestid and borhyaenid marsupials, is easier to explain if the latter groups had not yet evolved at the time of colonization. The fact that all three groups are known from the Upper Palaeocene of Brazil (Paula Couto 1970) therefore suggests that this colonization was a pre-Tertiary event.

In conclusion, it is hardly necessary to point out how many gaps there are in this fabric of theory, which has been woven from too few threads of fact. These gaps are as serious in the palaeontological as in the geological field, and all that workers can hope for is gradually to reduce the range of theoretical possibilities. It may be that a final and unassailable answer to the problem will never be found for, in the end, much may depend on subjective judgements on the migratory capabilities and climatic tolerance of very early marsupials and placentals—matters on which the performance of their modern descendants is of doubtful relevance. As always, one searches for a solution which explains the known facts while involving the smallest number of additional assumptions. The aim of this paper has been merely to show that such a simple solution is still compatible with the known facts.

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ADDENDUM

Dalziel (1973) has since modified the opinions quoted above, and suggests that the initial break between South America and West Antarctica could have occurred in the Late Jurassic, but that an archipelagic link between the two continents might have continued into the Cenozoic. This raises two other possibilities: either that this archipelagic route became more hazardous after the marsupials had crossed but before the placentals had appeared, or that it was at all times a difficult route which marsupials by chance crossed but placentals did not. The possible interactions of geological—geographical, climatic and biological—evolutionary factors are, clearly, still complex.

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