TINDALE, N. B. 1957.—Culture succession in south-eastern Australia from late Pleistocene to the present. *Rec. S. Aust. Mus.*, 13: 1-49.
WOODWARD, H. B. 1900.—*Zoo-geographical provisional sketch map of Western Australia.* Government Photolithographer: Perth, W.A.

ARE MARSUPIALS "SECOND-CLASS" MAMMALS ?

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Under the heading of the "evolutionary position of the marsupials" Colbert (1955) writes: "it appears that the marsupials have been and are 'second class' mammals as compared with the placentals," and later: "it is probably valid to think of the marsupials and placentals as arising at about the same time, during the Cretaceous period. They developed two quite dissimilar methods of reproduction, as well as various anatomical differences. During the early stages of their evolutionary histories they were probably well matched, so that marsupial adaptations were about as efficient as placental adaptations. But as time went on, and especially at the opening of the Cenozoic era, the placentals became dominant. There were probably various factors that led to the dominance of the placentals over the marsupials, but of these it is likely that the superior intelligence of the placental mammals was of particular importance."

Beliefs essentially similar to these are frequently expressed or implied by zoologists and palaeontologists. That the marsupials are considered to have an inferior organisation has not arisen directly from a comparative study of their organisation; it has been inferred from the supposition that marsupials become extinct when exposed to competition from placentals. Such suggestions as the marsupials having inferior intelligence and methods of reproduction are usually offered as explanations for their succumbing to competition and predation by placentals, rather than as opinions based on disinterested comparisons of those systems.

I do not quarrel with this approach. Indeed, it seems to be the only one. For we cannot isolate an organ or adaptation and assess its survival value *in vacuo*; we must first observe how well it serves the animal in nature. If a certain species withstands competition from another, it is axiomatic to say that its organisation and therefore all its organs and adaptations individually are adequate. We might also be able to say that its organisation is as good as that of the second species. Conversely, if it does not survive, we will conclude that the first animal was generally not so well adapted as the second; though in what particular way or ways it was inferior will not be so readily ascertained.

So much for methodology, but what of our materials? We can observe in Australia the effect of placental carnivores and herbivores on their marsupial counterparts. But what will we learn from this of the relative merits of placental and marsupial organsation? Before comparing say, the inherent sprinting ability of two

human races, we would ensure that our samples had equal opportunities to develop and train. So too in comparing fundamental eutherian and marsupial organisation we must consider whether the compared species have had roughly equal opportunity to modify their basic pattern. As will be shown, the placentals, to continue the sporting analogy, have had much the better training grounds.

Except for one marsupial (*Didelphis* in the U.S.A.) the present mammalian fauna of Africa, Eurasia, and North America, is wholly placental and, compared with the remainder of the world, fairly homogeneous. However, regional differences throughout this large area are sufficiently marked for the recognition of four zoogeographical regions: Ethiopian, Oriental, Palaearctic, and Nearctic. These faunal regions pertain only to recent times and depend on recent distributions of land and sea and of climatic zones. During the Tertiary climates were generally more uniform throughout this area, and isolation in any part of it was effected mainly by water barriers, such as the one that has recently and occasionally in the past separated north-eastern Asia from north-western America. The greater part of placental evolution took place in what was, in effect, a huge continent. Various stocks, such as the ancestral equids and camelids, might develop in a temporarily isolated North America, but eventually with the re-emergence of the Bering and perhaps other bridges they would be tested by the competition and predation of animals from the Afro-Eurasian land mass. We may call this continental evolution and contrast it with the mammalian evolution on islands and insular continents.

It is highly improbable that Madagascar and Papuo-Australia have been directly connected with the "super-continent" since the Mesozoic. Though each area has a fairly rich mammalian fauna so far as number of species is concerned, these embrace relatively few orders. It is probable that each has been colonised by an extremely limited number of mammals. Apart from rodents the present fauna of Madagascar could be explained as the adaptive radiations of three immigrations, namely of a lemur, a tenrecid insectivore, and a viverrid. The present Australian mammalian fauna (again excepting rodents) might have derived from the chance entry of a monotreme and a polyprotodont marsupial (we are on less firm ground here because of our almost total ignorance of Tertiary mammals in Australia). The modern West Indian fauna is likewise extremely poor in ordinal variety and consists only of Insectivora, Edentata, bats, and three groups of Neotropical rodents.

One of the features of island evolution, as we see from the above outline, is that adaptive radiation, if it occurs at all, necessarily proceeds from a limited number of ancestral species which themselves reached the island by chance. On the other hand, in any one region of the "super-continent" a much greater variety of animals are in a position to occupy a new niche. More important than this is that faunal interchange will sooner or later test all local evolutionary experiments.

Consider the evolution of carnivores. In Australia the role

could only be filled by descendants of either the original marsupial or monotreme that arrived here by what Simpson (1953) would call "sweepstakes routes." Perhaps some of the early monotremes "attempted" a solution and failed (lacking fossil evidence we cannot know). What we can infer with some safety is that one or more insectivorous marsupials were able to evolve carnivore adaptations, that is sufficiently well to get a living by preying on other marsupials and monotremes. But by the time the common ancestor of living dasyurids was evolved this carnivore stock had probably too big a lead in the way of carnivore adaptations to allow other marsupials to embark on a similar evolutionary venture. Thus at this stage, probably an early one in Australian mammalian history, all future evolution of carnivorous types was confined to a single stock.

Now at first sight it might seem that much the same has happened in the Eutheria, for in the remainder of the world, including Madagascar and South America, land carnivores are represented solely by Carnivora Fissipeda. There is this difference, however: before they achieved dominance the fissipedes had to compete with and finally replace such other carnivores as the placental creodonts and miacids and the marsupial borhyaenids. Similarly the recent dominance of the Artiodactyla as grazing animals in Afro-Eurasia and America has been concurrent with the decline in Perissodactyla and the complete extinction of several other orders of ungulates. We must therefore bear in mind their evolutionary past when we observe the impact of, say, modern Carnivora and Artiodactyla on their Australian counterparts, the dasyurids and kangaroos.

A formidable array of exotic mammals are now well established over a smaller or greater part of Australia. They include Lagomorpha (European rabbit and hare), Rodentia (brown rat, black rat, and house-mouse), Carnivora (dingo, European red fox, cat), Perissodactyla (horse and ass) and Artiodactyla (three species of deer, European pig, dromedary, and Asiatic buffalo). During this time a large number of Australian mammals have become extinct or nearly so, every family of land mammals being affected (Harper, 1945).

Apart from his introductions European man has been otherwise destructive. With his traps and guns he has directly exterminated much of the fauna, while his agricultural and pastoral activities have rendered a lot of country unsuitable for indigenous mammals. It is not easy now to discover among the many changes of scene resulting from European settlement the part played directly by introduced placentals in the decline of the indigenous mammals. It is clear however that the introductions are much better adapted to prevailing conditions than is most of the native fauna.

A similar decline among insular mammals can be observed throughout the world. The greater part of the West Indian fauna has become extinct since European settlement. Yet this fauna was entirely placental. In contrast none of the South American relatives of these animals nor any of that continent's marsupials have died out in historical times. Similarly in Australia the indigenous plac-

entals appear generally to possess no more resistance to change than the marsupials. Half of the species of Victorian rodents are now extinct (Brazenor, 1950). About the same proportion of South Australian rodents had died out by 1920, including species of *Rattus* (Wood Jones, 1925). This last, the fact that Australian species of *Rattus* are dying out while introduced continental species of the same genus are flourishing, illustrates better than anything else the futility in searching for fundamental defects in marsupial organisation.

The fate of the Australian species of *Rattus*, animals that were barely distinguishable morphologically or anatomically from the introduced species, suggests that the superiority of the introduced placentals might lie not so much in the gross differences that characterise placentals and marsupials but in small scarcely measurable refinements of their organisation.

While there can be little doubt, for example, that the dingo was in some way responsible for the disappearance of *Thylacinus* and *Sarcophilus* from the Australian mainland, one cannot thereby assume that it was a simple matter of placental versus marsupial organisation. Even if it were demonstrable that marsupial stocks could under no conditions evolve carnivores as efficient as modern canids and felids, it does not follow that marsupial organisation was inherently defective as compared with placental organisation. In the first place it was only the ferrungulates among the Eutheria that evolved carnivores. Secondly there are at least a few niches that marsupials seem to occupy as well as placentals.

Consider the brush-tailed possums. One species, *Trichosurus vulpecula*, ranges over the whole of Australia, including islands. It is adapted not only to a wide variety of climates but also in any one place to a wide range of foods. It is an expert climber and its strong teeth and sharp claws provide it with a pretty good defence against predators, such as feral cats, as large as itself. It has adapted well to European settlement, being able to live in suburban buildings and in rabbit burrows where its natural shelter has been destroyed (Troughton, 1943). In many parts of Australia it has maintained its numbers in the face of heavy trapping. The species was introduced into New Zealand where during the last thirty years it has increased its numbers and range enormously despite intensive trapping (800,000 skins were taken in 1946) and the presence of numerous introduced placentals (Wodzicki, 1950).

In South America similar niches (i.e., arboreal omnivore) have been occupied by marsupials since the Cretaceous. These animals have withstood competition from not only the early Tertiary placental inhabitants of the continent but also the two waves of northern immigrants that followed the restoration of land connections between South and North America in Pliocene and Pleistocene times. Indeed, the last land-bridge allowed one of them, *Didelphis*, to expand its range as far north as the U.S.A.

We may consider here some other aspects of mammalian evolution in South America. As we have just implied, South America was

an island during the greater part of the Tertiary. Yet its early mammalian history is not of the island type we found characteristic of Australia and Madagascar. Island faunas, it will be recalled, are typically derived from a few immigrants. South America, on the contrary, was well stocked with mammals when it was separated from the "super-continent" in the Eocene. But because of its relatively small area and long isolation and the consequent absence of faunal interchange its pre-Pliocene mammalian evolution had much in common with that of islands. Since the Pliocene, however, the archaic elements of the South American fauna have steadily declined, and the fauna has become increasingly pan-continental in composition. And though the marsupials have maintained themselves at roughly their Eocene proportion (i.e. 10%, fide Simpson, 1953) of the total mammalian fauna, their adaptive radiation ceased with the arrival of large numbers of continental animals.

Now South America was the only other region than Australia where any considerable amount of marsupial evolution occurred. Marsupial evolution has therefore generally been of the island type; and, as we have shown, island-evolved faunas, whether marsupial or placental, quite understandably make few contributions to continental faunas. This, I think, is a better explanation for the absence of marsupials from the pan-continental fauna than their being "second-rate mammals."

Similarly the present contest between Australian marsupials and introduced placentals is more reasonably regarded as one between island-evolved and continent-evolved animals.

SUMMARY

It is contended in this paper that the Australian marsupials are generally dying out not because they are marsupials (and thereby inferior to the introduced placentals) but because their past and recent evolution has taken place on an island, where, compared to those of the large Afro-Eurasian land-mass, evolutionary processes are understandably weak and restricted. The principal arguments are the following:

(1) The mammals of islands generally, and of Australia particularly, are dying out regardless of their being marsupial or placental.

(2) No South American mammal (marsupial or placental) has become extinct in historic times.

REFERENCES

BRAZENOR, C. W. 1950.—*The Mammals of Victoria.* Brown, Prior & Anderson: Melbourne.

COLBERT, E. H. 1955.—*Evolution of the Vertebrates.* Wiley: New York. Chapman & Hall: London.

HARPER, F. 1945.—*Extinct and Vanishing Mammals of the Old World.* New York.

SIMPSON, G. G. 1953.—*Evolution and Geography.* Condon Lectures: Eugene, Oregon.

TROUGHTON, E. Le G. 1943. *Furred Animals of Australia.* Angus & Robertson: Sydney.

WODZICKI, K. A. 1950.—*Introduced Mammals of New Zealand.* Wellington.

WOOD JONES, F. 1925.—*The Mammals of South Australia.* Part III. Monodelphia. Govt. Printer: Adelaide.