## African marsupials—vicariance or dispersion?

UNTIL recently the marsupials were not recorded in Africa, but two recent discoveries in the Lower Eocene and in Lower Oligocene of North Africa have demonstrated the presence of this group of mammals on the continent. Their phylogeny and palaeobiogeography must, therefore, be reconstructed.

The discovery of marsupials in the Lower Oligocene of Africa has recently been interpreted as indicative of continuous land dispersion across the Tethys from Europe to Africa[1]. Another recent discovery, however, proves that marsupials were present in northern Africa in the late Lower Eocene[2]. The upper molar described from the north-west Sahara displays both primitive characters (the narrowness of the protocone) and very derived characters (dilambdodonty), which could suggest either immigration from a European centre of origin or survival of an ancestral stock common to South America and Africa before the opening of the South Atlantic (vicariance).

A vicariant origin for the African marsupials should not be excluded, because the time when the main marsupial dental characters appeared[3], which would permit an evolutionary evaluation of African Oligocene and European late Eocene marsupials, is unknown. Unfortunately there is no way of testing the phyletic relationships between the Saharan and Egyptian forms, due to the scanty fossil record. On the other hand, European or Holarctic origin is supported by the continuous record of mammals of Holarctic affinities discovered in the Palaeocene[4], Eocene[5,6] and Oligocene[6] of Africa, and by the absence of marsupials from the only known Palaeocene mammal fauna of Morocco[4]. The recent discovery of marsupials in the European Palaeocene[7] reinforces this interpretation. However, several other palaeobiogeographic scenarios might also help to explain their presence in Africa. According to Sigé[8], Africa could have been a land route between South America and North America, but there is no evidence of non-marsupial vertebrate dispersion to support this hypothesis.

Several authors have claimed that Africa could have been a link during early Cenozoic between South America and Europe for phorusrhacid birds[9], mesosuchian ziphodont crocodiles[10], characid fishes[4] and marsupials[7]. As in the case of Africa, models which exclude Asia and the Indian plate need to be reconsidered. No true marsupial has been discovered in the Asian Mesozoic, but very few micromammals have been described from the rich mammalian assemblages of the Chinese early Tertiary. Additional information is provided by molecular data. For example, the structure and sequence of neuropeptides[11] have recently shown that the most primitive living marsupials are Australian, thereby suggesting that Australia could have been the dispersion centre of the group. In conclusion, these new data demonstrate that the phylogeny and palaeobiogeography of marsupials is much more complicated than previously assumed, and should stimulate new research in many fields.

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BOWN AND SIMONS REPLY—Jaeger and Martin suggest a possible vicariant origin for newly discovered marsupials from the Lower Eocene of Algeria and the Oligocene of Egypt[1,2]. These are the only metatherian remains ever recovered from the African continent, and the vicariance hypothesis suggests that these animals are survivors of an ancestral marsupial stock common to South America and Africa before the opening of the South Atlantic (before the early Cretaceous[3]). The distributions of at least the early Tertiary marsupials of Europe and North America might then have been derived from this remnant African stock, rather than having originated in Europe, as we have claimed[2] for the Egyptian marsupial, or in North America, as suggested by others[4,5] for the Euramerican marsupials. Although a vicariance theory of origin of mammalian groups is in vogue, its application to this problem and to others is generally supported only by negative evidence, that is, the absence of a good fossil record. For African marsupials, a vicariant origin is the least parsimonious alternative and requires detailed speculation about the composition of a non-existent fossil record.

First, there are no known pre-late Cretaceous marsupials from South America (the late Cretaceous marsupials from Peru are virtually identical to North American late Cretaceous *Alphadon*[6]). Second, the only proposed marsupial of early Cretaceous antiquity from anywhere in the world is North American *Holoclemensia texana*[7], a form that some feel is of doubtful metatherian affinity[8-10]. Even if *Holoclemensia* is metatherian, vicariance biogeography would place the origin of the Metatheria in North America, in accordance with most current thought. Third, the combination of primitive and derived characters in the Eocene Algerian form is unknown in any other didelphid, including those from South America, and the Egyptian marsupial shares derived characters with late Eocene and early Oligocene marsupials from Europe. By a vicariant origin, the Didelphidae of South America and those of Euramerica would have to be polyphyletic, or else the South America didelphids were at some time reintroduced there from Africa via Euramerica. Fourth, Egyptian *Peratherium* is so like European species of the genus, that had the Old World didelphids originated in Africa and spread to Euramerica, the avenue of dispersal between Africa and Europe must have been irregularly maintained over many millions of years. The first three points are not supported by palaeontological evidence, and the last observation is directly opposed to what is known of Tethyan palaeogeography during the early Tertiary.

Although Jaeger and Martin are correct in observing that a vicariance origin for the African marsupials should be examined, there is no evidence to support their hypothesis involving the composition and dispersion of an unknown fauna. We believe that there is some evidence that the Egyptian marsupial was an early Tertiary immigrant from Europe. Marsupials were probably present in Europe during the Palaeocene[11], although they are as yet unknown from mammalian microfaunas of that age in Africa. The Egyptian marsupial cannot have arrived in Egypt before the latest Eocene because of marine conditions there. Its appearance in the Egyptian continental Oligocene approximately coincides with the Tethyan regression, when Europe and Africa were presumably separated by less water distance than for many millions of years previously.

We also observe that the presence of a single stylar cusp on a narrow stylar shelf, in conjunction with the more or less dilambodont molar structure in the specimen from the Eocene of Algeria, is so unusual for a marsupial as seriously to jeopardize its assignment to the Metatheria. The tooth appears to share at least as many derived characters with European *Remiculus* (Mixodectidae) and *Adapisoriculus* (Insectivora, *incertae sedis*) as it does with any marsupial.

Finally, we did not "... interpret the discovery of marsupials in the Lower Oligocene of Africa as indicative of continuous land dispersion across the Tethys from Europe to Africa", as Jaeger and Martin suggest. Rather, we observed that the palaeogeographical reconstructions do