

owe its origins ultimately to the small private fortifications that first occurred in the Frankish kingdoms in Europe in the later ninth century. But it would be wrong to assume that private fortifications like Goltho are an index of Anglo-Saxon feudalism, as Brown implies. The archaeology of English towns like Lincoln and villages like Raunds reveals another social

pattern, and shows that England was a wealthy country on the eve of the Norman Conquest<sup>10</sup>. □

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## Palaeontology

# Faunas of a southern world

Leigh M. Van Valen

THE mammals of South America look exotic from a northern perspective — anteaters and other edentates, camels called llamas, diverse endemic groups of monkeys, rodents and bats, and so on. It has become reasonably common knowledge that the faunas were even more different before the Pliocene joining of the Americas. But in both areas the mammals were all placentals and marsupials, and comparable similarity has been more or less assumed for earlier times. Two remarkable faunas recently described<sup>1-6</sup> by José Bonaparte at the Museo Argentino de Ciencias Naturales, Buenos Aires, and his collaborators, show that this was not the case.

In the Cretaceous, the mammals of North America consisted mostly of tribosphenids (marsupials and placentals and their immediate forebears) and multituberculates, with a very few rare stragglers from earlier groups. Asia was similar, with more placentals and no marsupials. But in South America we now see a complete absence of tribosphenids and only a very divergent group of multituberculates (if that is what they really are). Multituberculates were the longest-lived order of mammals, vaguely rodent-like in adaptation but part of the pre-tribosphenid basal radiation of mammals.

The bulk of the Cretaceous mammals in South America were of groups which had flourished to the north in the Jurassic: triconodonts, symmetrodonts, dryolestans and amphitherians. These were also part of the basal radiation of mammals and are known mostly from jaws and teeth. The last three groups belong to the pantotheres, the group ancestral to tribosphenids. Most of the families in the South American Cretaceous are unknown elsewhere. The dryolestan *Mesungulatum* partly converged on primitive ungulates (hoofed mammals), and it was even thought to be an ungulate until lower teeth were found. A peramurid-grade amphitherian, *Vincelestes*, a divergent member of the derived group immediately ancestral to tribosphenids, is known from six skulls (the only pantotheres skulls known anywhere) and postcranial material still

undescribed. I have seen much of the material and agree with Bonaparte's interpretations for the most part.

The most extraordinary form, though, is *Gondwanatherium*, which has quite high-crowned (hypsodont) molars. No other Mesozoic mammal was hypsodont, even those in Mongolia, which was arid then as now and where the animals undoubtedly had grit blowing on their food. There were no pampas of grasses with opal phytoliths to wear down teeth; the nature of the ground cover is unknown.

Bonaparte thinks that *Gondwanatherium* was an ancestral edentate because of its hypsodont teeth and geographical location. Its hypsodonty, though, is clearly formed entirely by an upgrowth of cusps and of the lower part of the crown, whereas that of edentates seems to be formed by an elongation of the root. Thus, the similarity is probably non-homologous, not a result of continuity of information. Also, loss of enamel would be dysfunctional for an animal with hypsodont teeth. Indeed, much of the evolution of the edentates is an attempt to compensate for the early and apparently triphyletic<sup>7</sup> loss of enamel in that group. I do not know what *Gondwanatherium* is. Its own order, *Gondwanatheria*<sup>8</sup>, does seem appropriate, though, even if proposed in a fit of oversplitting. Possibly it is even a hypsodont monotreme; its crown pattern has vague resemblances to the early Cretaceous monotreme *Steropodon* of Australia<sup>9</sup>.

The better-known fauna, of the Los Alamos Formation, is late Cretaceous, near the Campanian-Maestrichtian boundary. The other, from the La Amarga Formation, is earlier, about Hauterivian. Their overall aspect is similar and suggests some generality for the southern fauna. Many reptiles and birds are also of endemic groups<sup>3,10</sup>, from these formations and elsewhere.

We know nothing of the Cretaceous mammals of the other parts of the disintegrating Gondwanaland except for *Steropodon*. As Bonaparte notes, the southern fauna of the Cretaceous may

have been more widespread. The reptiles do indicate this; perhaps Africa and India will eventually disclose their own Gondwanatherian mammals. And did primitive therians such as pantotheres reach Australia only to be done in by others, even monotremes?

The Gondwanatherian Fauna did not survive the Mesozoic. One genus, *Sudamerica*, is known from the later Palaeocene<sup>11</sup>. Two earlier Palaeocene<sup>12</sup> faunas (described as Cretaceous<sup>13</sup>) lack any trace, and this is the case after the Palaeocene also. Some of the non-mammalian elements of the fauna did survive, however<sup>3</sup>. It is even conceivable that the enigmatic Miocene genus *Necrolestes*<sup>14</sup>, usually thought to be a marsupial, is a late-surviving Gondwanatherian pantothere. The contemporaneity, precise timing and causes of the extinction remain unknown.

The earlier Palaeocene faunas are interesting in themselves. In addition to the expected precursors of later groups and the possible survival of dinosaurs, there are representatives of two orders of placentals which are otherwise unknown in South America except for a minor Pleistocene incursion of one. The Insectivora and Pantodonta each had appreciable success in Holarctica. That they were rapidly exterminated in the south, as was a smaller group also successful in the north, is another blow to the view that isolated biotas are necessarily inferior adaptively.

The immigration of marsupials and placentals occurred in the early Palaeocene<sup>12</sup>, as part of a larger incursion (and excursion). Together with a more prolonged and sporadic exchange in the last 10 million years or so of the Cretaceous<sup>3,10</sup>, this provides an as yet unappreciated datum for palaeogeographers. It also sets a lower time limit on the autochthonous radiation of marsupials in Australia. That the Cretaceous part of the interchange seems to have involved no mammals is not yet explained. □

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