Cranial anatomy and implications of *Dolichocebus*, a late Oligocene ceboid primate

THE very scarce fossil record of Cainozoic New World monkeys[1,2] has contributed little to knowledge of the history of platyrrhine primates, an important element of both the neotropical mammal fauna[3] and the pantropical primates, as a whole. Only the affinities of the Middle Miocene Colombian fossils *Neosaimiri*, *Stirtonia* and *Cebupithecia* seem reasonably well established[4], though not without dissent[5], and these are clearly linked with the modern squirrel, howler and saki-uakari monkeys, respectively. After completion of a survey of the morphology and interrelationships of the platyrrhines, to be detailed elsewhere (A. L. R., in preparation), it is now possible to discuss the evolutionary implications of the terminal Oligocene *Dolichocebus gaimanesis* of Patagonia, represented by a nearly complete cranium only recently prepared fully, although first described in 1942 (ref. 6). This specimen strongly suggests that *Dolichocebus* is a member of the *Saimiri* lineage, which thus becomes the oldest generic lineage known for the primates, dating from about 25 Myr ago[7]. Its affinities also imply that the two major monophyletic divisions of Ceboidea were already established by late Oligocene times, as were the marmosets and tamarins.

A restoration of the *Dolichocebus* cranium is presented in Fig. 1. It is close in size to the modern middle-sized ceboids *Saimiri*, *Aotus* and *Callicebus* and the late Oligocene–early Miocene *Tremacebus* and *Homunculus*[8,9]. During fossilisation all permeable cavities were filled with a fine sand that later hardened with the skull into a single mass. Most subsequent damage involved plastic deformation, bilaterally compressing the neurocranial vault asymmetrically above the skull base and partially collapsing the left orbit. The relatively undistorted basicranium affirms Kraglievich's[9] nominal interpretation of the long, narrow skull. Because essentially all tooth crowns are missing and the posterior dental arch was shorn away bilaterally, the number of molars cannot be counted with certainty. However, the highly compact, alveolar-like texture of the exposed bone suggests that third molars were present in life[8], contrary to Kraglievich's interpretation[9].

There are several indications that the masticatory system of *Dolichocebus* was rather lightly built. The anterior and posterior roots of the right zygomatic arch, suggestive of the bending stress imposed by the attached masseter muscles, are quite gracile. Similarly, the pyramidal process of the palatine is slender, providing evidence that the pterygoids were not powerfully developed. The right temporal line is visible along much of the parietal near the midline and on the zygomatic wall of the temporal fossa. It is neither deeply etched nor rugose and the temporal fossa is transversely shallow, suggesting that the temporalis muscle was not well developed. Finally, the glenoid fossa is shallow and lacks an entoglenoid process medially, indicating that the compressive loading borne by the mandibular condyle did not have a strong mediolateral component. This might reflect a relatively small torque of the medial pterygoid-masseter muscular sling, which in turn implies an insertion on a relatively shallow mandibular corpus.

This pattern is very much like that of *Saimiri*. The gracile features of *Dolichocebus* and *Saimiri* contrast with the heavier homologous features of *Callicebus*, *Aotus* and *Pithecia*, for example, whose chewing muscles are correspondingly better developed[10], and probably also of *Tremacebus* and *Homunculus*. The area of the neurocranium of *Dolichocebus* encompassed by the temporal muscles was relatively larger than that of *Saimiri*, however, especially posteriorly, where the fibres of the posterior temporalis converged on the midline and inion. In *Saimiri* the lines sweep ventrolaterally once they cross the coronal suture, delimiting a more limited area of insertion.

These differences correlate with the relatively larger, hence more prognathous, face and enhanced dentition of the fossil. Given the limitations of the material, one can be sure only that the diet of *Dolichocebus* did not consist predominantly of leaves but of insects and fruit, perhaps as with *Saimiri* and/or *Cebus*[11,12].

The structure of the orbits establishes the phylogenetic connection of *Dolichocebus* and *Saimiri* to a very high degree of probability. In both taxa the juxtaposed and fused right and left medial orbital walls are perforated centrally by a relatively large fenestra (in life closed by a sheet of connective tissue). Such a large interorbital fenestra is rare among extant adult mammals[13], and is probably best developed in *Saimiri*. In a randomly selected series of 53 *Saimiri* skulls in the American Museum of Natural History (25 adult male, 17 adult female and 11 juvenile) from Columbia, Ecuador, Guyana and Peru, all individuals have a completely formed fenestra such as no other platyrrhines are reported to have[14].

Although the functional significance of the interorbital fenestra is dubious, its unique structure and rare occurrence suggest that it is a (homologous) shared derived feature of *Dolichocebus* and *Saimiri*, illustrating that they are more closely related than either is to any other ceboid for which cranial material is available. (Specifically, this does not exclude the possibility that *Neosaimiri* or the Hispaniolan *Saimiri bernensis*[15], known by dental remains only, are more recently related phyletically to *Saimiri*.) Other derived features which support *Dolichocebus*-*Saimiri* affinities are the great anteroposterior length of the frontal interorbital process, unique to these species, and the
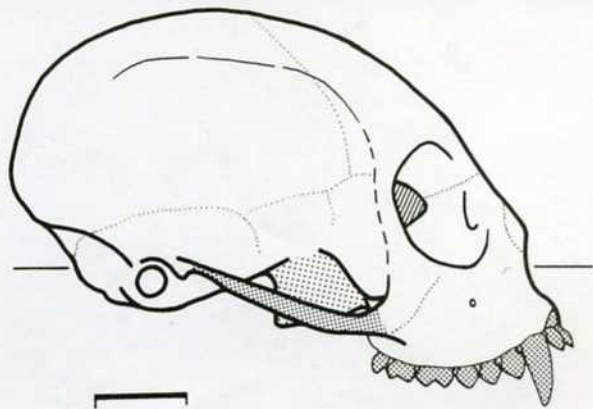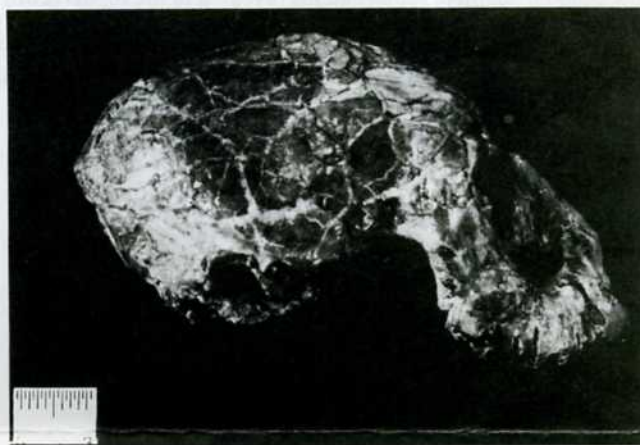

Fig. 1 *Dolichocebus gaimanensis*. Lateral view of original (top) and reconstruction (bottom). The scales are in mm and cm. Stippled areas are restored and hatchures mark the interorbital fenestra.

narrow nasals and reduced petromastoids, both indications of broader cebine affiliations.

Longstanding notions of the interrelationships of New World monkeys due to traditional classifications[16,17], or more modern ideas based on molecular evidence[18,19], are being challenged by cladistic analyses[20] and replaced by a new approach to platyrrhine classification[21]. It has been suggested, for example, that the reduced third molars and enlarged premolars of the cebines *Cebus* and *Saimiri* are indications that they are more closely related to the clawed marmosets (and tamarins) than to any other platyrrhine group with which they have been commonly classified. Furthermore, cebines and marmosets (Cebidae) form a monophyletic assemblage collaterally related to a second monophyletic amalgam composed of all remaining ceboids (Atelidae) with the single exception of the early Oligocene *Branisella*. Some adaptive aspects of this dichotomy are marked by the contrast between light weight, frugivorous–insectivorous, and heavy, frugivorous–folivorous, masticatory systems.

Thus these larger lineages must have differentiated before the Colhuehuapian appearance of *Dolichocebus* in the late Oligocene, approximately 25 Myr ago[7]. This is supported by evidence of the relationships of the roughly contemporaneous *Tremacebus* and *Homunculus* to members of the alternative atelid clade. The living marmoset genera, which according to molecular evidence may have diversified only 7–10 Myr ago[22], must also have differentiated before the late Oligocene. The historical details of this early radiation of the ancestors of modern ceboid primates and their extinct relatives requires the discovery of more fossils. Additional evidence may show that the diversity of living ceboids is a product of their early division into several long-lived, relatively anagenetic lineages, contrasting with the successional adaptive replacements revealed in the fossil record of Old World higher primates[21].

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