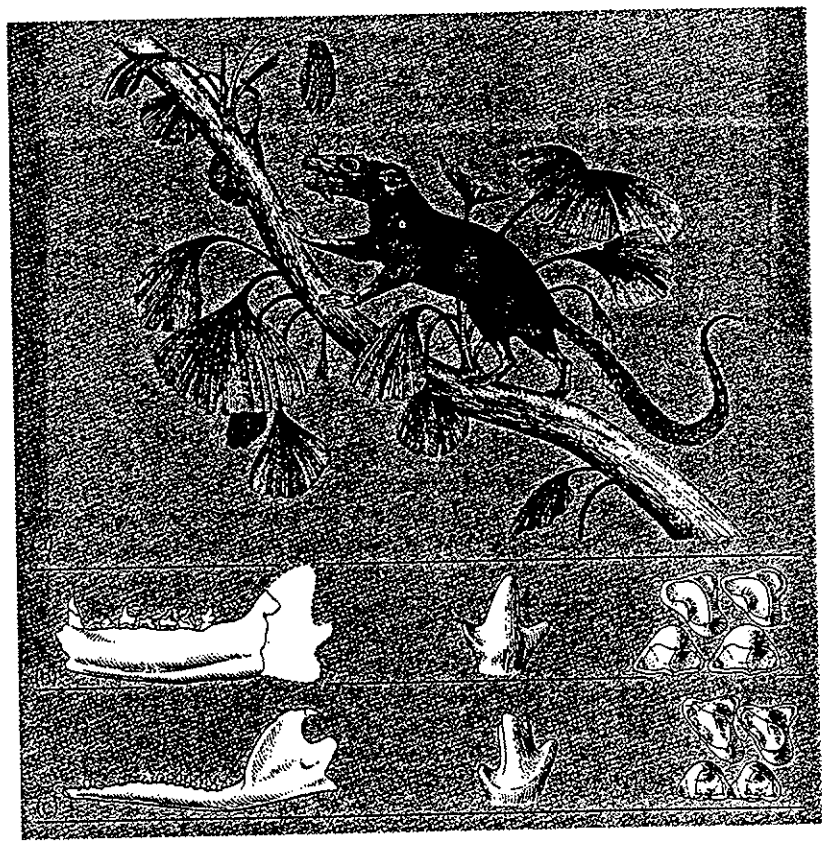
In Parker, S.P. (ed.) *McGraw-Hill Encyclopedia of Science and Technology* (9th ed.), McGraw-Hill, Inc., New York, 2002, v. 5, p. 697-698.

Dryolestida

The Dryolestida (formerly known as the Pantotheria or Eupantotheria) are an extinct order of mammals related to the living marsupials and eutherian (placental) mammals. Along with the closely related symmetrodonts, they were the most diverse group of mammals during the Jurassic. They are often found in some of the same quarries that yield the giant sauropod dinosaurs. Most were about the size and shape of a shrew or mouse, with teeth adapted for chopping up a diet of insects, and they apparently were adapted for living in trees like squirrels. *See* EUTHERIA; MARSUPIALIA; SYMMETRODONTA.

The earliest known dryolestoid is *Amphitherium*, first discovered in the Middle Jurassic Stonesfield Slate of England in 1838. This was an important specimen for historic reasons, proving that mammals once coexisted with the dinosaurs (at a time when it was thought that dinosaurs had died out before mammals appeared). By the Late Jurassic, dryolestoids were the most common mammals in both North America and Europe. They had seven genera of the family Dryolestidae in Europe and six in North America, as well as nine genera of the family Paurodontidae (mostly in North America). By the Early Cretaceous, dryolestids had been replaced in the Northern Hemisphere by the earliest relatives of marsupials and placentals, but they persisted until the Late Cretaceous of South America.

Of the 26 currently known genera of dryolestoids, all but one (*Henkelotherium*) are known only from remnants of teeth and jaws (see **illus.**). The teeth are very distinctive, with a number of unique specializations. The upper and lower molar teeth were made of tall triangles of three cusps, connected by crests between them. These molars were very compressed in a front-to-back direction, allowing as many as seven to nine molars in the cheek tooth row (marsupials typically have four molars; placentals have only three). The upper molar triangles (trigons)



Dryolestids. (a) Reconstruction of *Henkelotherium* (*after Krebs, 1991*). (b) Side view of jaw, side view of teeth, and crown view of upper and lower molars of the paurodonts *Paurodon* and *Pelicopsis*; (c) side views for the dryolestids *Laolestes* and *Melanodon* (*after Prothero, 1981*).

interlocked with the lower molar triangles (trigonids) like the teeth on a zipper, so that shear developed between the molars when the jaw closed. This type of dentition is similar to that found in living insectivorous mammals, and strongly suggests that dryolestoids were insectivorous as well. The upper molars have a large cusp on the exterior edge, which is called the stylocone, and another large cusp at the internal apex of the triangle, the paracone. In more advanced (tribosphenic) mammals such as marsupials and placentals, the paracone shifts to the outer edge and replaces the stylocone, and a new cusp, the protocone, develops in its place. The lower molar trigonids have a small ledge, the talonid, on the back end of the tooth, which occludes with the basin of the upper molar trigon. The paurodonts had a very similar dentition, but the cusps were lower and blunter. The teeth were less compressed in a front-to-back direction, and there were only four or five molars.

For over a century, dryolestoids were known only from dental remains. However, in 1991 a complete articulated skeleton of the paurodont *Henkelotherium* from the Late Jurassic beds of the Guimarota coal mine in Portugal was described. This skeleton was about the size of a small mouse, but was clearly adapted for living in trees, having long clawed fingers for gripping bark and a long, slender tail for balance. The hip and shoulder bones were remarkably modern and like those of most living mammals. Many of the reptilian bones of the shoulder girdle (still found in primitive mammals such as the egg-laying platypus, and some other Mesozoic mammals) were lost. However, the marsupial bones, which project forward from the pelvis in marsupials and help support the pouch, were retained. In addition, rudimentary vestiges of some of the reptilian jaw bones (such as the coronoids and splenials) were still present, although most of the lower jaw was still made of a single bone, the dentary, as in most other mammals. *See* DENTITION.

Dryolestoid diversity peaked in the Late Jurassic, and only one Early Cretaceous dryolestid (*Crusafontia* from Spain) was known. Then, in 1991, a peculiar form, *Donodon*, was described from the Early Cretaceous of Morocco. Between 1986 and 1992, a number of new dryolestoids from the Late Cretaceous Los Alamitos Formation of Argentina were described. At least four different families are represented, and they show a much greater variety of types of teeth than are known from the Jurassic. They include normal-looking dryolestids (*Leonardus* and *Groebertherium*) like those known from the Late Jurassic, as well as the much larger, blunt-cusped *Mesungulatum* (originally mistaken for an ancient hoofed placental mammal) and *Reigitherium*, with its flat-crowned teeth. These specimens show that dryolestoids lingered on in South America long after the northern continents were dominated with marsupials and placentals, and long after the dryolestid heyday in North America and Europe in the Late Jurassic and Early Cretaceous had passed.

For over a century, dryolestoids were placed in the order Pantotheria, a taxonomic wastebasket for Mesozoic mammals that were not members of other groups. In the older literature, one can still find statements that the "pantotheres" were ancestral to marsupials and placentals. Since 1981, the taxon Pantotheria has been abandoned, because it was a mixture of unrelated animals, and also because there was a tendency to use it uncritically as an ancestral group without detailed analysis of its members. Recent research has shown that the dryolestoids were primitive in many features but highly advanced in others. Their complex mosaic of features showed the transition from archaic mammals such as the platypus and some extinct Mesozoic mammals (which still retain reptilian characteristics) to the marsupials and placentals. In addition, their unique specializations (such as seven to nine highly unusual molars) show that they were not ancestral to marsupials or placentals, but an early side branch of mammalian evolution that lived before and then contemporaneously with the earliest marsupials and placentals. *See* THERIA.

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