The Paleocene Primate *Plesiolestes* and the Origin of Microsyopidae

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**Abstract.** Comparison of the dental morphology of the Middle Paleocene paromomyid primate *Plesiolestes problematicus* with that of the Early Eocene microsyopid *Cynodontiomys latidens* indicates that *Plesiolestes* and *Cynodontiomys* are closely related and that the Microsyopidae are derived from paromomyid primates. The Microsyopidae are, therefore, considered to be primates also. The diagnostic primate molar morphology apparently evolved before the petrosal bulla characteristic of most primates was acquired. Evidence presented here supports a derivation of Primates from leptictid insectivores.

**Key Words**

- *Plesiolestes*
- *Cynodontiomys*
- Paromomyidae
- Microsyopidae
- Leptictidae
- Origin of primates

**Introduction**

Deposits of Middle Paleocene (Torrejonian) age in western North America yield a varied primate fauna. These primates have been assigned to eight genera: *Pronothodectes, Elphidotarsius, Picrodus, Paromomys, Palenochtha, Plesiolestes, Palaechthon* and *Torrejonia. Pronothodectes, Elphidotarsius*, and *Picrodus* are classified, respectively, in the families Plesiadapididae, Carpo- lestidae and Picrodontidae; the remaining genera are placed in the Paromomyidae [Simons, 1972]. Only two of these genera were previously known to have had Eocene descendants. A species of the plesiadapid genus *Pronothodectes* was ancestral to *Plesiadapis* and *Platychaerops* [Russell, 1964]. The paromomyid *Paromomys* probably gave rise to *Phenacolemur* [Simpson, 1955; McKenna, 1960].

With specimens of *Plesiolestes problematicus* Jepson [1930] now available for study, it appears that *Plesiolestes* also had descendants in the Eocene. As is illustrated below, the dentition of the Early Eocene species *Cyno-
*Plesiolestes problematicus* is known at present from maxillary fragments preserving P₄ through M₃, and from numerous virtually complete mandibles, demonstrating that the lower dental formula of this species was 2.1.3.3. Species of *Cynodontomys* and its descendant *Microsops* are known from numerous mandibles and two relatively complete skulls preserving almost the entire dentition [McKenna, 1966; Szalay, 1969a]. The dental formula of *Cynodontomys* species is apparently 1²C₀³P₀⁴M₀². It is thus possible to derive the lower dental formula of *Cynodontomys* from that of *Plesiolestes* by subsequent loss of the lower second incisor and the canine.

In all linear dimensions *Plesiolestes problematicus* is approximately three-fifths the size of *Cynodontomys latidens*. Both species have an enlarged, procumbent lower incisor (fig. 1). The crown of the incisor is pointed at the tip and rounded at the base. The occlusal surface of the crown in both
Fig. 1. Occlusal view of left lower incisors of *Plesiolestes* and *Cynodontomys.* 
*A Plesiolestes problematicus* (Princeton University No. 14149, × 9.6). 
*B Cynodontomys latidens* (Yale Peabody Museum No. 30506, × 5.2).

Fig. 2. Occlusal view of right *P*$_2$–*M*$_3$ of *Plesiolestes* and *Cynodontomys.* 
*A Plesiolestes problematicus* (Princeton University No. 14106, × 8.7). 
*B Cynodontomys latidens* (composite, Yale Peabody Museum No. 27806 and 29759, × 5.2).
species is slightly concave, with an anteroposteriorly oriented central rib which is expanded laterally to form a blade. Medially, the central rib is bordered by a cingulid. Although the lower incisors of *Plesiolestes* and *Cynodontomys* are similarly constructed, the dorsal crest of the blade in the latter genus is relatively higher and more well defined than that of *Plesiolestes*.

The lower premolars and molars of *Plesiolestes problematicus* and *Cynodontomys latidens* are compared in figure 2. In both species, $P_3$ is tall and double-rooted with a prominent protoconid and no metaconid. The paracristid extends forward from the protoconid to a weakly developed paraconid. A crest extends posteriorly from the protoconid to form the lateral margin of a small heel. This heel has a single undifferentiated crest at its posterior margin. In both genera, $P_4$ is molariform with a distinct protoconid, paraconid and metaconid forming the trigonid, and with a basined talonid and distinct hypoconid and entoconid. The $P_4$ of *Cynodontomys latidens* (fig. 2) is relatively wider, and has a somewhat more distinct metaconid and a weaker hypoconid than that of *Plesiolestes*. The relative development of the metaconid on $P_4$ is variable in *Cynodontomys*, *Plesiolestes* and *Pelaechthon*.

The three lower molars of *Plesiolestes problematicus* are of the same proportions and are almost identical in morphology to those of *Cynodontomys latidens* (fig. 2). $M_1$ has a small but distinct paraconid situated medially to the metaconid, while on $M_2$ and $M_3$ the paraconid is reduced to an anterior shelf-like projection of the trigonid. As in *Palenchothra minor*, the protoconid and metaconid are separated by a deep trigonid valley and not joined by a transverse crest as observed in *Paronomys* and *Phenacolemur*. Both *Plesiolestes* and *Cynodontomys* have a well-developed hypoconulid and entoconid which are proximal to each other and form the posteromedial border of the talonid. Both genera have a mesoconid at the anterior end of the crista obliqua. The lower molars of *Plesiolestes* differ morphologically from those of *Cynodontomys* in the presence of a forward extension of the external cingulid, in having a twinned hypoconulid on $M_3$, and in having the hypoconulid and entoconid joined by a crest. Separation of the entoconid and hypoconulid in *Cynodontomys* is functionally related to the development of a hypocone in the upper molars. This hypocone replaces the primitive postprotocingulum (= 'Nannopithec-fold' of SIMPSON [1955], and others) of *Plesiolestes*.

The upper cheek teeth of *Plesiolestes problematicus* are relatively broader than those of *Cynodontomys latidens*, although the relative development and position of the major cusps, conules and shearing crests is essentially the same in the upper teeth of both species (fig. 3). The $P_4$ of *Plesiolestes* differs
from that of Cynodontomys latidens principally in having a small paraconule which is absent in the latter species.

Discussion

Szalay [1969a] recently figured upper fourth premolars from the Four Mile fauna of Colorado which he referred to Cynodontomys ('Microsyops') wilsoni. These premolars are premolariform and have no metacone. Restudy of this sample of isolated upper fourth premolars indicates that they belong to a species of the anaptomorphine primate Tetonius, and are therefore irrelevant to discussion of microsyopids. Several upper fourth premolars which do have a metacone were also found in the Four Mile sample of C. wilsoni and are probably representative of that taxon, although they have not been described or figured. In view of the fact that in no case have upper fourth premolars of Cynodontomys species been demonstrated to be consistently premolariform, the interpretation of McKenna [1960] and Szalay [1969a] that the presence of a premolariform P4 in the Microsyopidae is a primitive characteristic of the family is no longer tenable. As stated above, the development of the P4 metaconid in Cynodontomys species is variable.
Van Valen and Sloan [1965] allocated a premolariform P₄ to their Early Paleocene primate species Purgatorius unio, a species which is known only from isolated teeth. This tooth could well be a P₃ or belong to another species. The isolated premolariform P₄ subsequently allocated to Purgatorius unio by Szalay [1969a] is much too large to belong to that species. Until Purgatorius species are known from jaws preserving serially associated teeth, the morphology of its premolars cannot be determined. It seems more likely, considering known Late Cretaceous insectivores [see Lillegraven, 1969], that the earliest primates had molariform fourth premolars.

The most significant difference between the upper molars of Plesiolestes problematicus and Cynodontomys species is the presence in Plesiolestes of a postprotocingulum connecting the protocone with the postcingulum, whereas in Cynodontomys this connection is broken. In Cynodontomys, the lingual end of the postcingulum bears a distinct cusp, the hypocone. As noted above, the development of the hypocone in Cynodontomys is correlated functionally with development of a notch separating the twinned hypoconulid and entoconid. Hypocones have evolved from the postprotocingulum independently in several lineages of early primates (plesiadapids, adapines, notharctines). Consequently, a similar development in the evolution of Cynodontomys from Plesiolestes is not without parallel.

The morphology of all of the known dentition of Plesiolestes problematicus is closely similar to that of Early Eocene Cynodontomys species. Many of the differences distinguishing the teeth of the two genera are paralleled by evolutionary changes in other lineages of early primates. It therefore seems probable that Plesiolestes problematicus, or a species of a closely related genus such as Palaeochthon, is the Middle Paleocene ancestor of the Eocene Cynodontomys-Microsyops-Craseops lineage.

The discovery that Plesiolestes and Cynodontomys species are closely related provides new, independent evidence supporting the conclusions of McKenna [1960, 1963], Simons [1960, 1963], and Szalay [1969a, b] that the Microsyopidae are primates. McKenna [1966] and Szalay [1971, 1972] have since abandoned this conclusion, stating that similarities of the auditory bulla of microsyopids to the bulla of leptictid insectivores indicate that microsyopids should be considered insectivores also. Plesiolestes problematicus has all of the dental characteristics of the earliest primates, including bulbous cusps, reduced paraconids on M₂₃₄, expanded talonid basins, elongate heel on M₃, presence of a postprotocingulum and an enlarged procumbent lower first incisor. Plesiolestes retains as well some dental similarities to Cretaceous leptictid insectivores, such as Gypsonictops [Lille-
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Graeven, 1969]. Sloan [1969] suggested that *Gypsonictops* may have given rise to the order Primates through a descendant such as the poorly known *Purgatoriidae*, Van Valen and Sloan [1965].

The most reasonable interpretation of these relationships is that both the Middle Paleocene paromomyids (such as *Plesiolestes*) and microsyopids are primates which were derived from leptictid insectivores and retained the entotympanic bulla construction typical of leptictids. It is unlikely that the distinctive molar morphology of early primates was acquired at the same time as the distinctive primate bulla construction. The close relationship of *Plesiolestes* and the Microsyopidae demonstrated above provides evidence that the diagnostic primate molar morphology evolved from that of leptictid insectivores before the characteristically primate petrosal bulla was acquired.

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