Folia primat. *19:* 1–8 (1973)

The Paleocene Primate *Plesiolestes* and the Origin of Microsyopidae

T. M. BOWN and P. D. GINGERICH

Division of Vertebrate Paleontology, Peabody Museum of Natural History, Yale University, New Haven, Conn.

Abstract. Comparison of the dental morphology of the Middle Paleocene paromomyid primate *Plesiolestes problematicus* with that of the Early Eocene microsyopid *Cynodontomys latidens* indicates that *Plesiolestes* and *Cynodontomys* 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
Cynodontomys
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 Plesiadapidae, Carpolestidae 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* JEPSEN [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-*

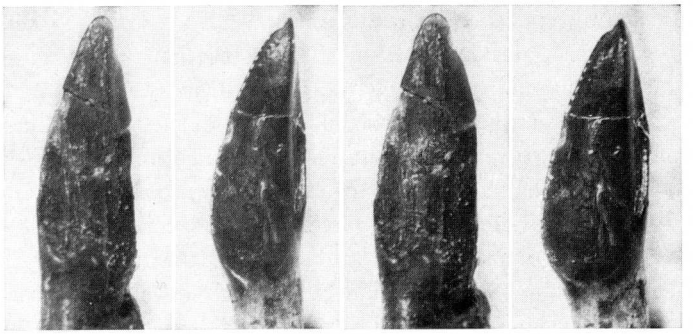
dontomys latidens (family Microsyopidae) is very similar to that of *Plesiolestes problematicus*, indicating that *Cynodontomys* was probably derived from a species of *Plesiolestes* or the closely related Middle Paleocene primate *Palaechthon*. This relationship is important both for the classification of the family Microsyopidae and for problems concerning the origin of the order Primates.

The Microsyopidae are a family of early mammals having molars characteristic of primates and middle ear morphology most similar to that of leptictid insectivores [McKENNA, 1966]. They are thus of particular importance to studies of the origin of primates. At least two evolutionary lineages of the family are present in the Eocene. The *Cynodontomys-Microsyops-Craseops* lineage (subfamily Microsyopinae) is the best documented [McKENNA, 1960]. *Niptomomys doreenae* and *Uintasorex parvulus* (subfamily Uintasoricinae) constitute an additional lineage [SZALAY, 1969b; BOWN and GINGERICH, 1972]. SZALAY [1969a] compared the Late Paleocene and Early Eocene species of *Navajovius* with other early primates and concluded that *Navajovius* was more closely related to *Cynodontomys* than to any other genus; however, it now appears to the present writers that *Navajovius* is more closely related to the *Niptomomys-Uintasorex* lineage. *Plesiolestes* and the less well known, possibly congeneric *Palaechthon* [see SIMPSON, 1937] appear to be more closely related to *Cynodontomys*, although they may prove to be ancestral to all of the Microsyopidae.

Dentition of Plesiolestes *and* Cynodontomys

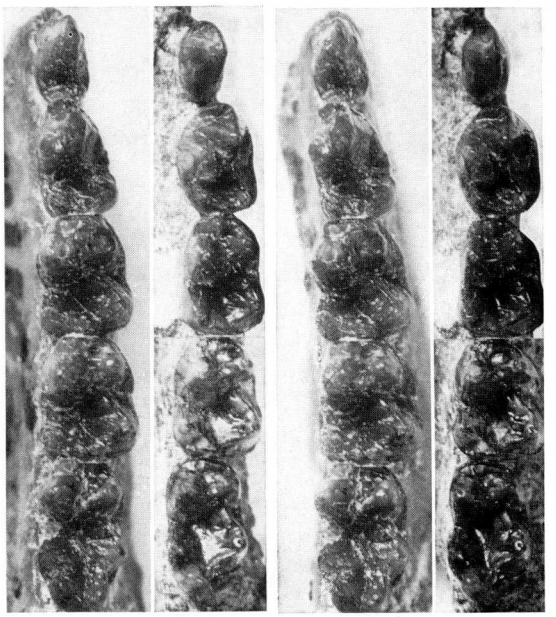
Plesiolestes problematicus is known at present from maxillary fragments preserving P^4 through M^3, and from numerous virtually complete mandibles, demonstrating that the lower dental formula of this species was 2.1.3.3. Species of *Cynodontomys* and its descendant *Microsyops* are known from numerous mandibles and two relatively complete skulls preserving almost the entire dentition [McKENNA, 1966; SZALAY, 1969a]. The dental formula of *Cynodontomys* species is apparently $I^1_1\, C^1_0\, P^4_3\, M^3_3$. 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



A *B*

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).



A *B*

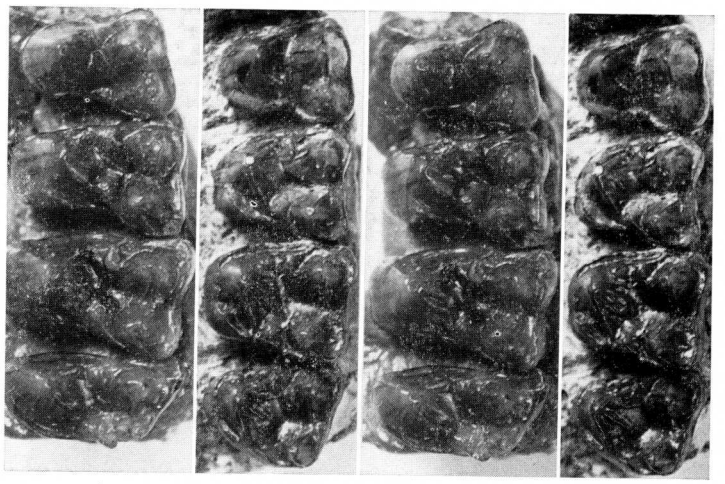
Fig. 2. Occlusal view of right P_{3-4}, M_{1-3} of *Plesiolestes* and *Cynodontomys*. *A Plesiolestes problematicus* (Princeton University No. 14106, × 8.7). *B Cynodontomys latidens* (composite, Yale Peabody Museum No. 27806 and 29759, × 5.2).

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 *Palaechthon*.

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 *Palenochtha minor*, the protoconid and metaconid are separated by a deep trigonid valley and not joined by a transverse crest as observed in *Paromomys* 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 cristid 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 (= '*Nannopithex*-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



A *B*

Fig. 3. Occlusal view of left P^4, M^{1-3} of *Plesiolestes* and *Cynodontomys*. *A Plesiolestes problematicus* (Princeton University No. 14304; metacone on M^3 is broken; × 8.3). *B Cynodontomys latidens* (Yale Peabody Museum No. 27880; reversed; × 5.2).

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 P_4^4 in the Microsyopidae is a primitive characteristic of the family is no longer tenable. As stated above, the development of the P_4 metaconid in *Cynodontomys* species is variable.

VAN VALEN and SLOAN [1965] allocated a premolariform P_4 to their Early Paleocene primate species *Purgatorius unio*, a species which is known only from isolated teeth. This tooth could well be a P_3 or belong to another species. The isolated premolariform P^4 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 *Palaechthon*, 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 M_{2-3}, expanded talonid basins, elongate heel on M_3, 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-

GRAVEN, 1969]. SLOAN [1969] suggested that *Gypsonictops* may have given rise to the order Primates through a descendant such as the poorly known *Purgatorius*, 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.

Acknowledgements

We are especially grateful to Prof. ELWYN L. SIMONS, Yale Peabody Museum, for his helpful comments on the manuscript; and to Dr. M. C. MCKENNA, American Museum of Natural History, and Dr. V. J. MAGLIO, Princeton University, for the loan of specimens in their care. We would also like to acknowledge informative discussion with Mr. RICHARD KAY and Mr. KENNETH ROSE.

References

BOWN, T. M. and GINGERICH, P. D.: Dentition of the Early Eocene primates *Niptomomys* and *Absarokius*. Postilla *158:* 1–10 (1972).

JEPSEN, G. L.: Stratigraphy and paleontology of the Paleocene of northeastern Park County, Wyoming, Proc. Amer. Phil. Soc. *69:* 463–528 (1930).

LILLEGRAVEN, J. L.: Latest Cretaceous mammals of upper part of Edmonton Formation of Alberta, Canada, and review of marsupial-placental dichotomy in mammalian evolution. Paleont. Contr. Univ. Kans. *50:* 1–122 (1969).

MCKENNA, M. C.: Fossil mammalia from the Early Wasatchian Four Mile fauna, Eocene of northwest Colorado. Univ. Calif. Publ. geol. Sci. *37:* 1–130 (1960).

MCKENNA, M. C.: The early Tertiary primates and their ancestors. Proc. 16th Int. Congr. Zool., Washington *4:* 69–74 (1963).

MCKENNA, M. C.: Paleontology and the origin of the primates. Folia primat. *4:* 1–25 (1966).

RUSSELL, D. E.: Les mammifères Paléocènes d'Europe. Mém. Mus. Nat. Hist. Natur. (série C) *13:* 1–324 (1964).

SIMONS, E. L.: New fossil primates: a review of the past decade. Amer. Scient. *48:* 179–192 (1960).

SIMONS, E. L.: A critical reappraisal of Tertiary primates; in BUETTNER-JANUSCH

Evolutionary and genetic biology of primates, vol. pp. 65–129 (Academic Press, New York 1963).

SIMONS, E. L.: Primate evolution, an introduction to man's place in nature (Macmillan, New York 1972).

SIMPSON, G. G.: The Fort Union of the Crazy Mountain Field, Montana, and its mammalian faunas. Bull. U.S. nat. Mus. *169:* 1–287 (1937).

SIMPSON, G. G.: The Phenacolemuridae, new family of early primates. Bull. Amer. Mus. nat. Hist. *105:* 415–441 (1955).

SLOAN, R. E.: Cretaceous and Paleocene terrestrial communities of western North America. Proc. N. Amer. Paleont. Convention, vol. E, pp. 427–453 (1969).

SZALAY, F. S.: Mixodectidae, Microsyopidae, and the insectivore-primate transition. Bull Amer. Mus. nat. Hist. *140:* 197–330 (1969a).

SZALAY, F. S.: Uintasoricinae, a new subfamily of early Tertiary mammals. Amer. Mus. Novit. *2466:* 1–19 (1969b).

SZALAY, F. S.: The European adapid primates *Agerina* and *Pronycticebus*. Amer. Mus. Novit. *2466:* 1–19 (1971).

SZALAY, F. S.: Paleobiology of the earliest primates; in TUTTLE The functional and evolutionary biology of primates, vol. 1, pp. 3–35 (Aldine, Chicago 1972).

VALEN, L. VAN and SLOAN, R. E.: The earliest primates. Science *150:* 743–745 (1965).

Request reprints from: THOMAS M. BOWN, Department of Geology, University of Wyoming, *Laramie, WY 82071*, and PHILIP D. GINGERICH, Division of Vertebrate Paleontology, Peabody Museum of Natural History, Yale University, *New Haven, CT 06520* (USA)