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PHYLOGENETIC RELATIONSHIPS OF
PLESIADAPIFORM-TARSIIFORM PRIMATES

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ABSTRACT

All plesiadapiform-tarsiiform primates shared a common ancestry that involved loss of the incisors and development of the canine at the front of the jaw. Their antemolar dental complement is composed of a canine followed by five or fewer premolars. All tarsiiforms are united in having parabolic protocristae on the upper molars and include omomyines and uintasoricines (both *sensu stricto*). All plesiadapiforms have the derived protocone fold on M¹⁻². Among these, two clades are recognized—plesiadapids and paromomyids compose the Plesiadapoidea; microchoerids and anaptomorphids form the Anaptomorphaidea. Generic relationships among all plesitarsiiforms are proposed, based on inferred shared-derived similarities.

INTRODUCTION

Although the systematics and relationships of plesiadapiform-tarsiiform primates have long been the subject of intense research and spirited debate, recognition of these primates as a distinct clade occurred only recently (Gingerich, 1975, 1976). Traditionally, plesiadapiforms have included the families Plesiadapidae, Carpolestidae, Picrodontidae, and Paromomyidae and, because of their essentially Paleocene occurrence, have been accorded the status of archaic pro-

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simians (Romer, 1966; Simons, 1972). Tarsiiforms have usually been defined to include the Omomyidae, Anaptomorphidae, Tarsiidae, and Microchoeridae and portrayed as an essentially Eocene stock of primates that were morphologically intermediate between adapids, lemurs, and lorises and the higher primates, the Anthropoidea. Some authors have united the tarsiiforms and anthropoids as the Haplorhini, because extant taxa in these groups lack a moist, naked rhinarium and have fused nasal processes. In this scheme lorisiforms, lemuriforms, and adapids compose the Strepsirhini (Pocock, 1918; Hill, 1953; Martin, 1972; Szalay, 1973, 1976).

An opposing view of primate relationships recently posited by Gingerich (1975, 1976) is one with which we agree, but, as outlined below, for different reasons. Two major clades compose Primates—the Plesitarsiiformes, including all plesiadapiforms and tarsiiforms; and the Simiolemuriformes, including the strepsirhines and anthropoids.

All primates that show an absence of incisors and the development of the canine at the front of the jaw are inferred to have had a common ancestry and constitute the Plesitarsiiformes. Krishtalka (1978) suggested new relationships among the higher taxa of plesitarsiiforms. These are here explained in greater detail and to the generic level.

The dental characters cited in this study were obtained from personal examination of original and cast material of fossil plesitarsiiforms in the collections of the Section of Vertebrate Fossils, Carnegie Museum of Natural History, as well as from descriptions and illustrations in the literature. Only one conclusion is based on undescribed material.

The abbreviations in this paper are as follows: AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; IRSNB, Institut Royal des Sciences Naturelles de Belgique; MCZ, Museum of Comparative Zoology, Harvard University; PU, Princeton University; UKMNH, University of Kansas Museum of Natural History; USNM, National Museum of Natural History (Smithsonian Institution); YPM, Yale Peabody Museum.

TARSIVUS AND DENTAL HOMOLOGIES

The systematic position of *Tarsivus* has been a moot point in all discussions concerning the relationships among primates. Compared with other extant primates, *Tarsivus* is unique in many ways—in the adult the enormous orbits impinge on the cranium and nasal region as a result of a series of craniogenetic interactions that begin in the fetus (Starck, 1975); unlike catarrhines, in which the tubular ectotympanic extends from an extrabullar tympanic ring, the ring is intrabullar in *Tarsivus* (Szalay, 1975); as far as is presently known, *Tarsivus* is the only extant primate with a compound (petrosal and entotympanic) auditory bulla (Cartmill, 1975; R. D. Martin, personal communication; Schwartz [manuscript—Entotympanic contribution to the auditory bulla of *Tarsivus*]; Starck, 1975; Van Kampen, 1905); although both anthropoids

and *Tarsius* have discoidal, hemochorial placentation, the processes of fetal membrane and placenta development in *Tarsius* are markedly dissimilar (Lockett, 1974, 1975; see Schwartz, 1978; Schwartz et al., 1978, for a more detailed discussion of *Tarsius*).

Dentally, *Tarsius* is especially distinct from other extant primates. Its antemolar teeth, as identified by Schwartz (1978, manuscript—Dental development, homologies, and primate phylogeny) are $C^1, dP_1^1P_2^2dP_3^3P_4^4P_5^5$, unlike the traditional identification of $I^1I_2^2C_1^1P_2^2P_3^3P_4^4$. We think the revised dental formula of *Tarsius* reflects the true homologies of the teeth for the following reasons:

1) *Tarsius* has six upper and five lower antemolar teeth. The upper central tooth is caniniform and is followed by five premolariform teeth, of which the first and third are smallest. The five lower antemolar teeth are similarly premolariform, with the first and third smallest.

2) Comparison of sequences of dental development and eruption between *Tarsius* and other extant primates with incisiform, caniniform, and premolariform teeth in expected positions indicates that the central upper caniniform tooth of *Tarsius* develops and erupts in homologous fashion to the upper canine of these other extant primates. In the latter, the upper canine, P^2 , and P_2 develop and erupt as an integrated unit. In *Tarsius* the homologous integrated unit consists of the central upper caniniform tooth, the third upper tooth and the second lower tooth, implying that these teeth in *Tarsius* are homologous to the upper canine, P^2 , and P_2 , respectively, of extant primates.

3) If the central upper caniniform tooth in *Tarsius* is a canine, the five premolariform teeth that follow it are premolars, as are the five lower premolariform antemolar teeth. As a corollary, the third upper and second lower teeth in *Tarsius* are indeed P^2 and P_2 , respectively.

4) The small first and third premolars in *Tarsius* are not replaced and are therefore retained dP_1^1 and dP_3^3 . Thus the antemolar dental formula of *Tarsius* is properly $C^1dP_1^1P_2^2dP_3^3P_4^4P_5^5$.

5) In primates with three premolars (usually identified as $P_2^2P_3^3P_4^4$) the most frequent sequence of premolar development, eruption, and replacement is $P_2^2-P_4^4-P_3^3$. In *Tarsius* this sequence occurs as third upper tooth/second lower tooth (P_2^2)—ultimate upper and lower antemolar teeth (P_5^5)—penultimate upper and lower antemolar teeth (P_4^4). This implies that P_2^2 , P_4^4 , and P_5^5 in *Tarsius* are homologous with " $P_2^2P_3^3P_4^4$ " of three premolared primates that, according to these homologous sequences, should also be identified as P_2^2 , P_4^4 , P_5^5 . The loss of two premolars in these primates occurred at the P_1^1 and P_3^3 loci.

The occurrence of five premolars in primates is not a *de novo* event. McKenna (1975) has persuasively argued that the primitive eutherian antemolar dental complement included three incisors, a canine, and five premolars—a dental complement preserved in some specimens of

Gypsonictops and *Kennalestes*. Indeed, five premolars also seem to be retained in some erinaceids and dermopterans (Krishtalka, 1976a; Schwartz and Krishtalka, 1976), and possibly in some nyctitheriids and adapisoricids (Krishtalka, 1976a, 1976b).

These revised identifications of the premolars in *Tarsius* ($dP_1^1P_2^2dP_3^3P_4^4P_5^5$) and extant three-premolar primates ($P_2^2P_4^4P_5^5$) is cause to reevaluate the dental homologies of the antemolar teeth of other primates. Examination of plesiadapiform-tarsiiform dental remains indicates that:

1) Like *Tarsius*, all plesiadapiform-tarsiiform primates (except *Ekgmowechashala*) have a caniniform tooth at the front of the jaw followed by five or fewer premolariform teeth. When five premolariform teeth are present, the first and third are smallest. By implication, the caniniform tooth at the front of the jaw in plesiadapiform-tarsiiform primates is a canine and is followed by five premolars, of which the first and third are retained deciduous teeth.

2) The sequence of tooth replacement preserved in a partial dentary of a juvenile *Absarokius* (USNM 19198) is, as in *Tarsius* and three premolar primates: second premolariform tooth—ultimate premolariform tooth—penultimate premolariform tooth, or $P_2-P_5-P_4$. This specimen also preserves the enlarged anterior alveolus for the lower canine, a tiny alveolus for dP_1 and possibly, a small alveolus for dP_3 .

3) As discussed above in point one, in those plesiadapiform-tarsi-

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Fig. 1.—Hypothesized relationships among the major groups of plesiadapiform-tarsiiform primates (Plesitarsiiformes, Gingerich, 1976). *Node 1*—incisors lost; canine develops and erupts at the front of the jaw and is followed by five premolars of which P_1^1 and P_3^3 may be inhibited, with retention of dP_1^1 and dP_3^3 . *Node 2*—paraconid and metaconid smaller on M_{2-3} than on M_1 ; talonid cusps, especially the hypoconulid, reduced on the lower molars; hypocristid on M_{1-2} flexed at a point labial to the midline of the molar. *Node 3*—pre- and postprotocristae form a wide parabola on M^{1-3} enclosing a broad, shallow trigon basin; conules reduced; cingula on M^{1-2} extend around lingual face of the protocone; cristid obliqua on P_5M_1 are buccal to the midline of the tooth; hypoflexid notch shallow; entoconid and hypoconid flattened. *Node 4*—low, weak, lingual ridge connects distinct and well-separated paraconid and metaconid on M_{1-3} . *Node 5*—protocone fold on M^{1-2} continuous with postcingulum and enclosing posterointernal basin; M^{1-2} squared lingually, with longer lingual slope on protocone; trigonid on M_{2-3} compressed. *Node 6*—post-protocrista on M^{1-3} weaker and shorter and does not reach apex of protocone. *Node 7*— M^{1-2} more transverse; protocone with longer lingual slope and some distention of the lingual base; cristid obliqua on M_1 joins metaconid. *Node 8*—upper canine cusperate; P_2 reduced; metacone and paraconule occur on P^5 ; metacone occurs on P^4 ; paraconid reduced on P_5M_{1-3} ; trigonid quadrate on M_1 , anteroposteriorly compressed on M_{2-3} ; M_3 with prominent third lobe and double or large hypoconulid. *Node 9*—rudimentary protocone on P^4 ; less robust lower canine; trigonid on M_{1-3} inclined anteriorly.

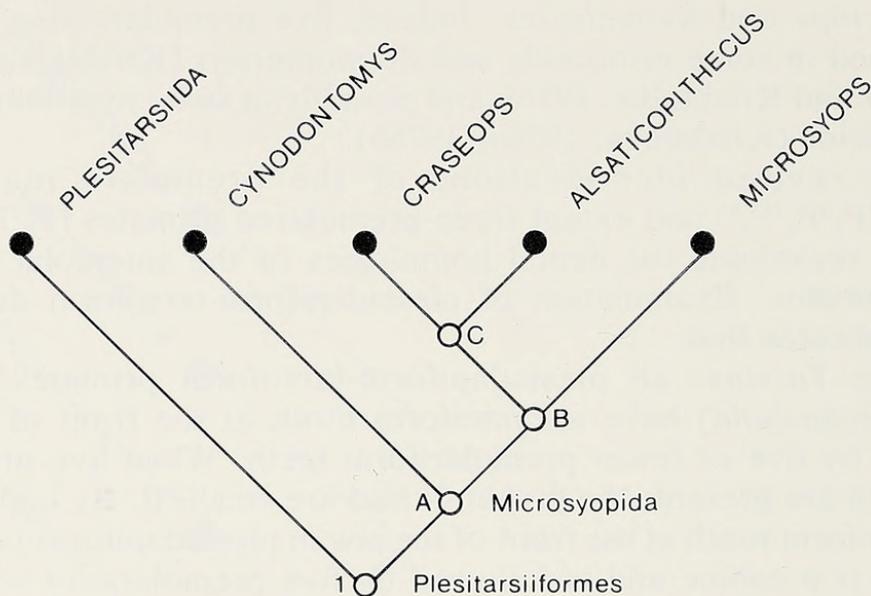


Fig. 2—Suggested relationships among microsyopids. *Node 1*—corresponds to node 1 of Fig. 1. *Node A*—proximal entoconid and hypoconid separated by a deep notch on M_{1-3} ; mesoconid on M_{1-3} ; subcrescentic paracone and metacone on M^{1-2} . *Node B*—reduced, shelf-like paraconid on M_3 ; mesostyle and hypocone on M^{1-2} ; P_5 more molariform. *Node C*—sloping paraconid shelf on M_{1-3} .

iform primates with five premolars, the first and third are smallest. Sequentially, the size of the five premolars from dP_1^1 to P_5^5 is small (dP_1^1), large (P_2^2), smallest (dP_3^3), large (P_4^4), largest (P_5^5). In plesiadapiform-tarsiiform primates with fewer than five premolars, the loci of premolar loss may then be inferred from the comparative size of the remaining premolars. As expected, the most frequent sites of premolar loss appear to be the first and third—loci at which inhibition of the permanent premolars has already occurred in *Tarsius*, *Absarokius*, and, by implication, all plesiadapiform-tarsiiform primates with five premolars.

RELATIONSHIPS

Plesitarsiiformes: Microsyopids and Plesitarsiida

According to our reconstructions of dental homologies (Schwartz and Krishtalka, 1976, 1977; Schwartz, 1978, manuscript) all plesitarsiiform primates (Fig. 1, node 1) have an antemolar dental formula of a canine followed by five (possibly $dP_1^1P_2^2dP_3^3P_4^4P_5^5$) or fewer premolars. The absence of incisors, occurrence of the canine at the front of the jaw and retention of deciduous P_1^1 and P_3^3 are inferred shared-derived similarities of these primates that imply their common ancestry. Gingerich (1975, 1976) arrived at a similar conclusion also on the

basis of the morphology of the antemolar teeth, although he identified these as the traditional incisors, canine and four premolars.

If Schwartz's (manuscript) analysis of the dental homologies is correct, the origin of the plesitarsiiform primates involved loss of the incisors, development of the canine at the front of the jaw and, possibly, inhibition of permanent P_1^1 and P_3^3 . In contrast, origin of the simiolemuriforms (Gingerich, 1976) apparently involved loss of one of the five premolars (P_3^3).

The initial group to differentiate among the plesitarsiiforms were the microsyopids (Figs. 1, 2). They retain such primitive characters as a large hypoconulid, deep hypoflexid notch, and (initially) a large paraconid on the lower molars. If the entotympanic bulla of *Microsyops* (McKenna, 1966) characterizes all microsyopids, it may be a retention from the primitive primate condition or may be derived from an ancestral compound bulla. Also possibly retained is a medial entocarotid artery (McKenna, 1966; Szalay, 1969a). All microsyopids are united (Fig. 2, node A) by possession of a deep notch between the proximal hypoconulid and entoconid on the lower molars, and subcrescentic paracone and metacone on M^{1-3} . In *Microsyops*, *Craseops*, and *Alsaticopithecus* (Fig. 2, node B) M^{1-2} bear a hypocone and a mesostyle, and the paraconid on M_3 is reduced to a shelf-like crest. *Craseops* and *Alsaticopithecus* (Fig. 2, node C) are further derived in that the paraconid on M_{1-2} is also reduced to a ventrolingually sloping shelf.

All other plesitarsiiforms, the Plesitarsiida (Fig. 1, node 2), are united by a number of derived similarities—the paraconid and metaconid are smaller on M_{2-3} than on M_1 ; the talonid cusps, especially the hypoconulid, are reduced on the lower molars; on M_{1-2} the hypocristid (the crest forming the posterior rim of the talonid basin) is flexed at a point that is labial to the midline of the crown, closer to the hypoconid; the lower canine is less trenchant than at node 1. The morphology of the skulls known in a few plesitarsiid genera (*Tetonius*, *Necrolemur*, *Tarsius*, *Plesiadapis*, *Phenacolemur*) suggests that loss of the medial entocarotid artery and development of an intrabullar ectotympanic with an extrabullar tubular extension may also be derived features of this group.

Plesitarsiida: Tarsiiformes and Plesiadapiformes

Within the Plesitarsiida, two major clades are discernible, especially with regard to derived structures on the upper molars. In some plesitarsiids (Fig. 1, node 3) the pre- and postprotocristae on the upper molars form a wide, continuous parabola enclosing a broad, shallow trigon basin. Additionally, the conules are reduced, the cingula extend around part of the lingual face of the protocone, the cristid obliqua on P_5 – M_1 originates more labially so that the hypoflexid notch is shallow,

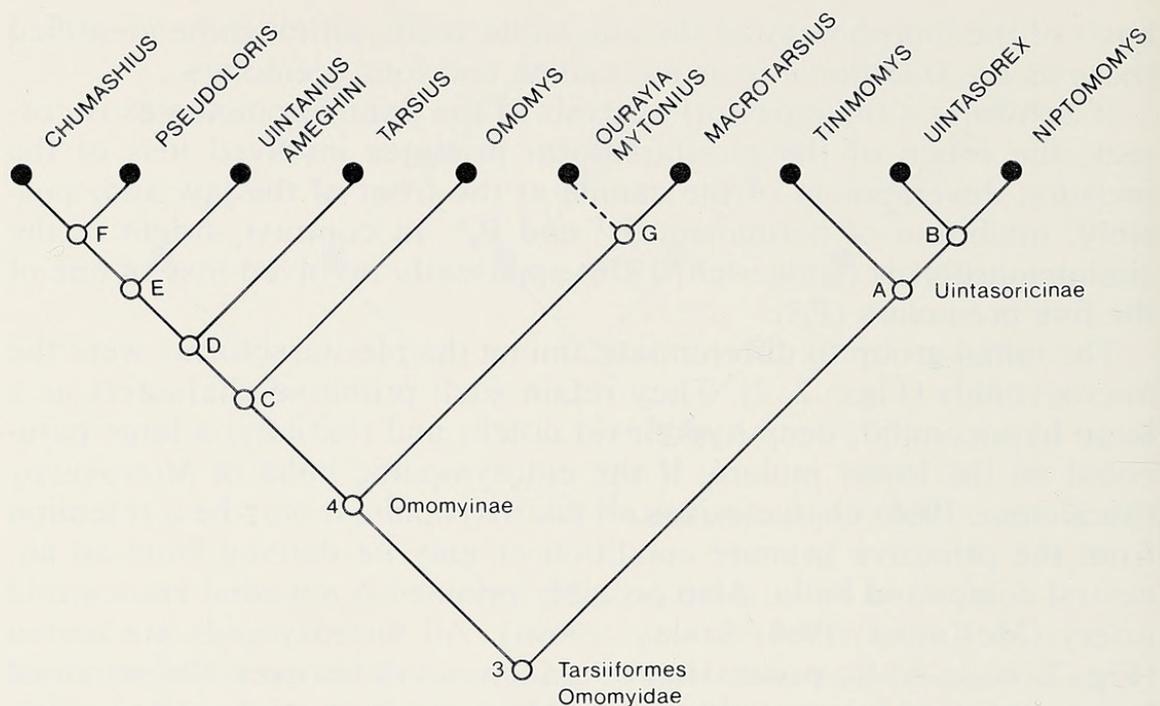


Fig. 3.—Hypothesized relationships among tarsiiforms. *Node 3*—corresponds to node 3 of Fig. 1. *Node 4*—corresponds to node 4 of Fig. 1. *Node A*—enlarged P_5^5 ; loss of premolars at P_1 and P_3 loci. *Node B*—upper molars less transverse; M_{2-3} trigonid compressed anteroposteriorly and paraconid lost; severe reduction of molar cusps. *Node C*—paraconid on M_{2-3} more medial than on M_1 . *Node D*—paraconid more medial on M_1 . *Node E*—paraconid more medial and reduced on M_{1-3} . *Node F*—paraconid closer to protoconid on M_{1-3} . *Node G*— M_{1-2} with buccal contour not emarginate, broader talonid and more lingual cristid obliqua; lower molars quadrate.

and the entoconid and hypoconid on the lower molars are flattened. This suite of derived similarities is unique to the genera in Fig. 3, here referred to the clade Tarsiiformes.

In contrast, on M^{1-2} of all other plesitarsiids (Fig. 1, node 5) the pre- and postprotocristae remain short and V-shaped, but a new crest, the protocone fold, is developed on the posterior face of the protocone. M^{1-2} are squared lingually, the protocone leans labially and has a longer lingual slope and the trigonid on M_{2-3} is anteroposteriorly compressed. Thus, all plesitarsiiform taxa with a protocone fold are regarded to have shared a common ancestry and are referred to the Plesiadaptiformes, cladistically a sister group of the Tarsiiformes.

Tarsiiformes: Omomyidae (Omomyinae and Uintasoricinae)

All genera in Fig. 3 are united by the derived tarsiiform dental morphology outlined above. Among these, *Tinimomys*, *Niptomomys*, and *Uintasorex* (Fig. 3, node A) are unique in that P_5^5 are enlarged and two premolars have been lost, apparently at the P_1 and P_3 loci. These three

genera compose the Uintasoricinae (also see Krishtalka, 1978, for formal diagnosis). In *Uintasorex* and *Niptomomys* (Fig. 3, node B) the upper molars are less transverse, the trigonid on M_{2-3} is highly compressed and lacks a paraconid, and the molar cusps are reduced.

Remaining tarsiiforms (Figs. 1, 3; node 4) have a weak lingual ridge of enamel joining distinct and well-separated paraconid and metaconid on M_{1-3} . As such these genera compose the Omomyinae. A morphocline among one group of omomyines, the Omomyini (Fig. 3, nodes C, D, E, F), involves progressive reduction and more medial occurrence of the paraconid on M_{1-3} . In *Omomys* this occurs only on M_{2-3} , whereas in *Tarsius*, *Uintanius*, *Chumashius*, and *Pseudoloris* it involves M_1 and increases in degree on M_{2-3} . Thus, on M_{1-3} of *Pseudoloris* the paraconid is tiny, anteromedial and closer to the protoconid than the metaconid. *Ourayia*, *Mytonius*, and *Macrotarsius* (Krishtalka, 1978) compose the Macrotarsiini and have more nearly quadrate lower molars, much broader talonids on M_{1-2} , more buccal cristid obliquas and virtually no buccal emargination of the crown between the trigonid and talonid. Unlike the condition in the Omomyini, the paraconid on the lower molars of *Ourayia*, *Macrotarsius*, and *Mytonius* remains in its primitive lingual position.

Tinimomys.—Szalay (1974) identified *Tinimomys* as a paromomyid and Bown and Rose (1976) allocated the genus to the Microsyopidae, *incertae sedis*. The dental remains include a partial maxilla with three teeth described as P^5-M^2 . The alleged P^5 is larger than M^1 or M^2 and is molariform in that it bears well-developed paracone, metacone, paraconule, metaconule, protocristae, continuous cingula, and pericone swelling. Such a degree of molarization commonly characterizes a deciduous ultimate premolar and this tooth may be a dP^5 . Permanent P^5 was also probably larger than M^{1-2} , but more premolariform, as is the morphology of P_5 in relation to M_{1-2} in *Tinimomys*.

Pseudoloris.—In *Pseudoloris*, usually identified as a microchoerid, the upper molars lack the protocone fold of *Nannopithec*, *Necrolemur*, *Microchoerus*, and plesiadapiforms in general. Rather, with parabolic protocristae on M^{1-3} , *Pseudoloris* is a tarsiiform and most closely related to known omomyines.

Ourayia.—The systematics of *Ourayia* have been reviewed and revised elsewhere (Krishtalka, 1978). The associated palate and partial dentaries (PU 16431) previously identified as *Ourayia* (Simons, 1961a; Szalay, 1976) and *Hemiacodon* (Robinson, 1968) are indistinguishable from *Macrotarsius*. The hypodigm of *Ourayia* is limited to the remains of the lower dentition (AMNH 1899, 1900, PU 11236, CM 12309) from the Uintan of Utah. Also *pace* Szalay (1976) *Mytonius* (Robinson, 1968) appears to be generically distinct from *Ourayia* (Krishtalka, 1978).

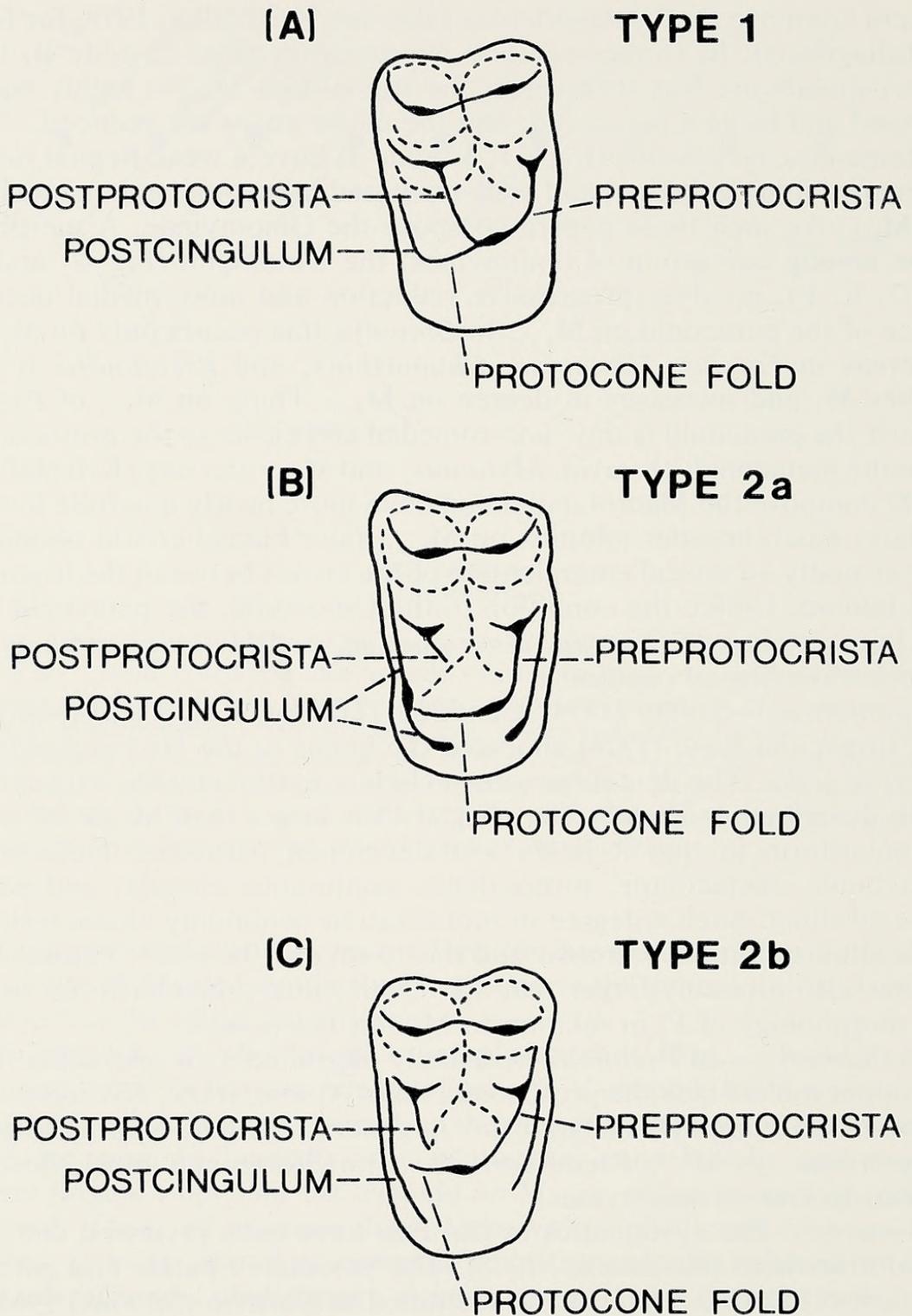


Fig. 4.—Three types of protocone fold-postcingulum configurations on M^{1-2} of plesiadapiforms. (A) Type 1—protocone fold and postcingulum continuous and enclose posterointernal basin. (B) Type 2a—postcingulum extends lingually beyond protocone fold, with weak junction marked by cuspule or wear facet. (C) Type 2b—postcingulum extends lingually beyond protocone fold, with no junction.

Uintanius.—The systematics of this genus are unclear. *U. ameghini* (Matthew, 1915; Robinson, 1966; Szalay, 1976) is known from partial upper and lower dentitions that appear to belong to the same species. This is not the case with “*U. vespertinus*” (Szalay, 1976). The upper molars, with parabolic protocristae (and no protocone fold, *pace* Szalay, 1976), are omomyid-like and may be referable to *Omomys*. The lower molars, with closely appressed paraconid and metaconid on M_{2-3} , belong to an anaptomorphid.

Plesiadapiformes: Anaptomorphaidea and Plesiadapoidea

As described above, M^{1-2} in all genera placed in the plesiadapiforms (Fig. 1, node 5) are squared lingually as a result of the development of a protocone fold. Also the protocone leans labially and the trigonid on M_{2-3} is compressed.

Two major configurations of the protocone fold-postcingulum complex occur among plesiadapiforms—(1) in some the fold is continuous with the lingual end of the postcingulum, and a posterointernal basin is formed (Fig. 4A); (2) in others the postcingulum extends lingually beyond the protocone fold around part or all of the base of the protocone. The latter configuration is also expressed in two ways—(2a) a weak connection between the protocone fold and postcingulum is maintained (Fig. 4B), or (2b) the protocone fold is short and does not reach the postcingulum (Fig. 4C).

Apart from the protocone fold, some plesiadapiform genera share a suite of derived features (Fig. 1, node 8) as follows: the upper canine is cusped; P^5 bears a metacone and paraconule and a metacone occurs on P^4 ; the paraconid is reduced on P_5M_{1-3} ; the trigonid on M_1 is quadrate because the paracristid extends anteriorly from the protoconid, bends lingually, and runs to the paraconid; in contrast, the trigonid on M_{2-3} is highly compressed anteroposteriorly and rectangular so that the paracristid and protocristid are essentially parallel; M_3 bears a prominent third lobe with a broad or double hypoconulid; P_2 is reduced. Possession of these similarities implies a common ancestry for plesiadapids (including carpolestines) and paromomyids—a relationship long recognized by other workers (Simpson, 1937, 1955; Van Valen, 1969; Rose, 1975; Simons, 1972; Gingerich, 1976) and expressed taxonomically by the clade Plesiadapoidea. All plesiadapoids have a type 1 configuration of the protocone fold-postcingulum complex (Fig. 4A)—the protocone fold is continuous with the lingual end of the postcingulum and encloses a posterointernal basin.

All other plesiadapiform genera (Fig. 1, node 6) lack these plesiadapoid features, but have a short, weak postprotocrista on M^{1-3} compared to the two other protocone crests, the preprotocrista and the protocone fold. These genera are united in the Anaptomorphaidea and

exhibit types 1, 2a and 2b configurations of the protocone fold-postcingulum complex on M^{1-2} (Fig. 4 A–C). It appears that a continuous protocone fold-postcingulum enclosing a posterointernal talon is the primitive configuration in plesiadapiforms (Fig. 1, node 5) and is retained in all plesiadapoids and some anaptomorphoids.

○ *Anaptomorphaidea: Microchoeridae and Anaptomorphidae*

All anaptomorphoids are plesiadapiforms that have a weak, short postprotocrista. Among these two clades seem discernible. The four genera referred to the Microchoeridae (Fig. 5) share a suite of derived features that is expressed as a morphocline—increasing size of the hypocone, progressive shortening of the postprotocrista, and development of more nearly square upper molars. In addition, all four genera have lost one of the five premolars, apparently from the P_3 locus. Initially in the morphocline (Fig. 5, node A) the postcingulum extends beyond the protocone fold and ends lingually in a hypocone. In *Necrolemur*, *Microchoerus*, and *Rooneyia* (Fig. 5, node B) P^5M^{1-3} are more nearly square and the hypocone is a broad-based columnar cusp that is nearly as high as the protocone and occupies almost one-half of the lingual margin of the crown. As a result the protocone fold in *Microchoerus* and *Necrolemur* (Fig. 5, node C) extends posterolabially from the apex of the protocone but is interrupted by the enlarged hypocone. Additionally, the postprotocrista is reduced to an isolated cuspule between the metaconule and the protocone, and P^5M^{1-3} are square (Hürzeler, 1948). In *Rooneyia*, the hypocone on M^{1-2} is worn on the only known specimen but is highest and most columnar among microchoerids, and is connate with the equally worn protocone. As a result, the protocone fold is obliterated and, with the increase in size of the metaconule, the postprotocrista is barely discernible.

Remaining anaptomorphoids, the Anaptomorphidae (Fig. 6), are united by the following derived features (Figs. 1, 6, node 7): M^{1-2} are more transverse; the apex of the protocone is more labial and its base is lingually distended so that the lingual slope of the cusp is longer; the cristid obliqua on M_1 joins the metaconid. These genera appear to compose two clades—among washakiines (Fig. 6, node A) the postcingulum on M^{1-2} extends lingually beyond the protocone fold and, although the protocone fold meets the postcingulum, this junction is weak and usually marked by a small cuspule or wear facet (type 2a; Fig. 4B). A hypocone and pericone occur in *Shoshonius*, *Washakius*, *Dyseolemur*, and *Hemiacodon* (Fig. 6, node B) lingual to the end of the postcingulum and precingulum, respectively, and the molar enamel is somewhat wrinkled. *Shoshonius*, *Washakius*, and *Dyseolemur* (Fig. 6, node D) have a lingual crease on the protocone of M^2 and the paraconid is more medial on M_{2-3} . The postprotocrista, a short ridge

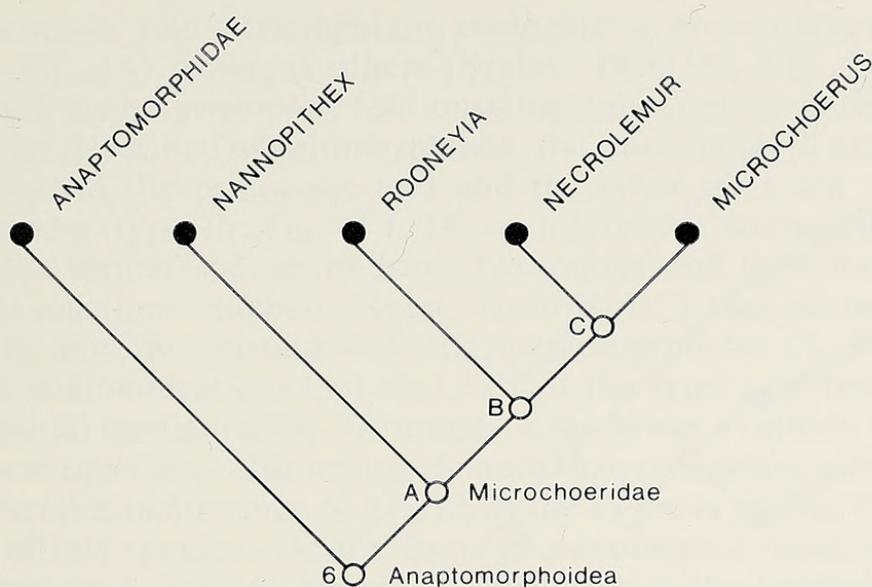


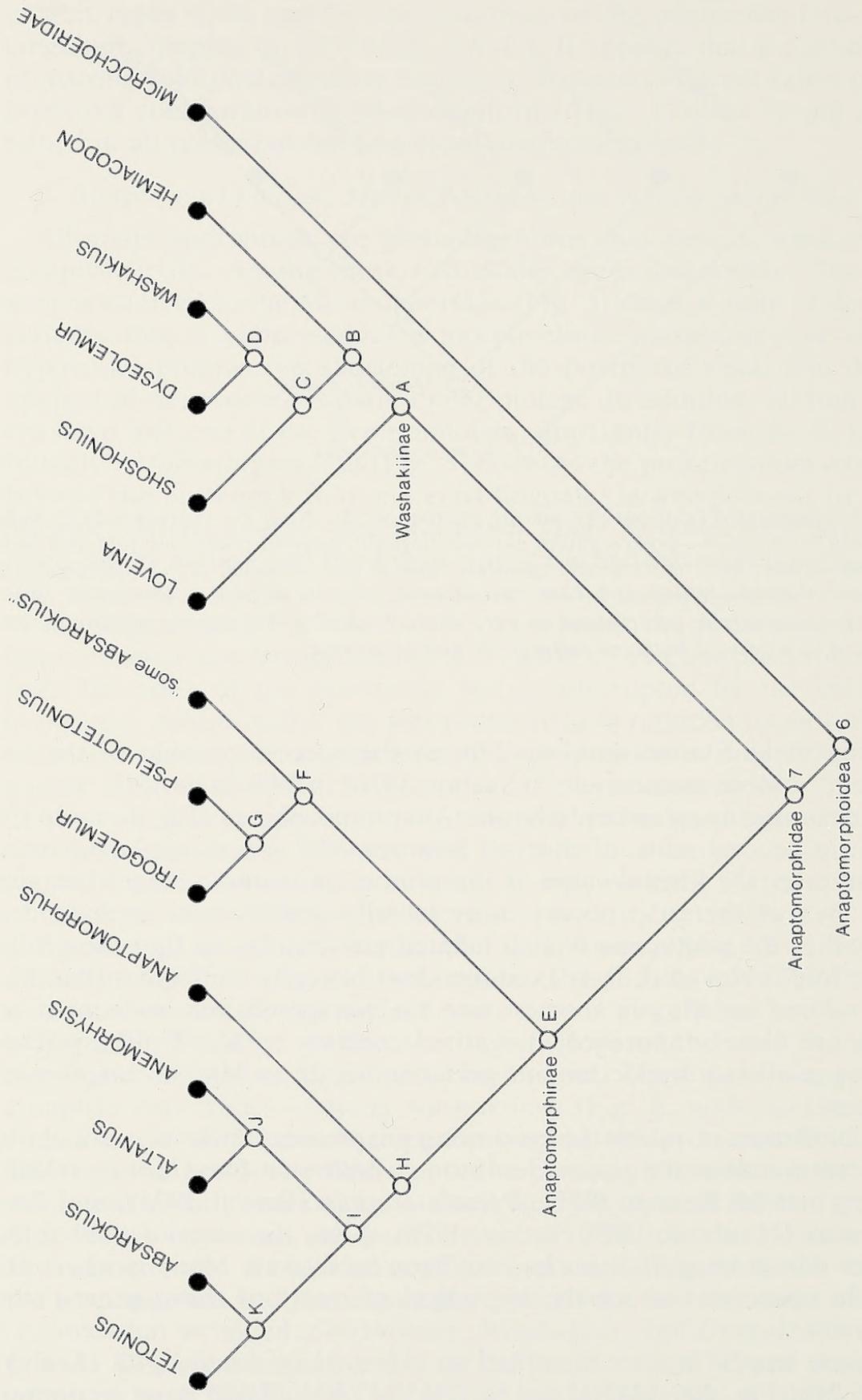
Fig. 5.—Suggested relationships among microchoerids. *Node 6*—corresponds to node 6 of Fig. 1. *Node A*—postcingulum extends lingually beyond protocone fold and ends in a hypocone; M^{1-2} more nearly quadrate; loss of one premolar (P_3); postprotocrista shorter. *Node B*—hypocone on M^{1-2} broad-based, almost as high as protocone, interrupts protocone fold; postprotocrista very short. *Node C*— M^{1-3} square; postprotocrista reduced to a cuspule between metaconule and protocone.

among these five washakiines, forms the second cuspule of the so-called “double metaconule” (Szalay, 1976) in *Washakius*.

Remaining anaptomorphids, the Anaptomorphae (Fig. 6, node E), share a second suite of derived features— M^2 is enlarged and more transverse; the lingual slope of the protocone is much longer because the apex of the cusp occurs more labially and its base is distended lingually; the protocone is also inflated posteriorly, so that the protocone fold is elevated; P_5 is exodaenodont buccally and higher than M_1 ; the talonid on M_{1-2} is shorter; and the paraconid and metaconid on M_{2-3} are closely appressed in marked contrast to M_1 . Unlike washakiines, neither a hypocone nor pericone occur on M^{1-2} of anaptomorphines.

Elucidation of relationships among anaptomorphines is particularly difficult because the upper dentition is unknown for *Altanius* (Dashzeveg and McKenna, 1977), *Pseudotetonius* (Bown, 1974), and *Trogolemur* (Matthew, 1909; Szalay, 1976). Also, the anterior part of the lower dentition of *Altanius* has not been recovered. Many workers are not in consensus about the hypodigm of many of these genera (see below).

Some upper molars identified as *Absarokius noctivagus* (Szalay, 1976:245, Fig. 49, AMNH 55154, 55155, YPM 17488) have a continu-



ous protocone fold-postcingulum enclosing a posterointernal talon (type 1; Fig. 4A), whereas others (Szalay, 1976:246, Fig. 50, USNM 22264) lack such a protocone fold-postcingulum continuum. Rather, as in all other described anaptomorphines, the postcingulum extends lingually beyond the protocone fold and the latter does not reach the postcingulum (type 2b; Fig. 4C). These differences warrant the exclusion of the former specimens from *Absarokius* and their inclusion in a new taxon (here dubbed "some *Absarokius*") that seems closely related to new, as yet undescribed, anaptomorphines (T. M. Bown, personal communication) that also exhibit the type 1 protocone fold-postcingulum configuration. Elements of the lower dentition identified as *A. noctivagus* may also belong to more than one genus, as is implied by the variable occurrence of a tooth at the P_3 locus among the known sample of this species. On the basis of unpublished material (T. M. Bown, personal communication), it appears that the upper molars of "A. *noctivagus*" with type 1 configuration of the protocone fold-postcingulum complex are associated with the lower jaws that lack a tooth at the P_3 locus and have a P_4 with partially fused roots. This material ("some *Absarokius*," Fig. 6) is tentatively considered most closely related to *Trogolemur* and *Pseudotetonius* (Fig. 6, node F), genera that also lack a lower premolar and have a single-rooted P_4 (Fig. 6, node G).

Among all other anaptomorphines in which M^{1-2} is known (Fig. 6, nodes H, I, K), the postcingulum extends lingually beyond the protocone fold—barely so in *Anaptomorphus* (Fig. 6, node H); more so

←

Fig. 6.—Suggested relationships among anaptomorphids. *Node 6*—corresponds to node 6 of Fig. 1. *Node 7*—corresponds to node 7 of Fig. 1. *Node A*—postcingulum on M^{1-2} extends lingually beyond protocone fold; protocone fold-postcingulum junction weak and marked by weak cuspule or wear facet. *Node B*—pericone and hypocone developed at lingual end of pre- and postcingulum, respectively; molar enamel wrinkled; postproto-crista is short ridge or cuspule between metaconule and protocone. *Node C*—metastylid on M_{1-3} . *Node D*—paraconid on M_{2-3} more medial; crease on lingual face of protocone meets pericone. *Node E*— M^2 enlarged and transverse; long lingual slope on protocone due to lingual distension of base and occurrence of apex labially; protocone on M^{1-2} inflated posteriorly so that protocone fold is elevated; P_5 exodaenodont buccally and higher than M_1 ; talonid on M_{1-2} short; M_{2-3} paraconid closely appressed to metaconid in marked contrast to M_1 . *Node F*—roots of P_4 fused, at least labially; loss of one premolar. *Node G*— P_4 single-rooted. *Node H*—postcingulum extends slightly beyond protocone fold on M^{1-2} , with no junction between these two crests. *Node I*—postcingulum extends further lingually beyond protocone fold and around part of the base of the protocone. *Node J*—complete buccal cingulid on M_{1-3} . *Node K*—postcingulum extends around much of protocone; P_5 paracone and P_5 protoconid enlarged.

in *Anemorhysis* (Fig. 6, node I); and much more so in *Tetonius* and *Absarokius* (Fig. 6, node K). The latter also have a larger paracone on P⁵. *Altanius* is provisionally regarded as closely related to *Anemorhysis* (Fig. 6, node J) because both have complete buccal cingulids on the lower molars, a unique feature among anaptomorphines.

Mckennamorphus.—Szalay (1976) named *M. despairensis* from UCMP 44055, a single fragmentary dentary with part of the anterior dentition (McKenna, 1960:69) that Bown (1974) had identified as *Pseudotetonius ambiguus*. Szalay omitted any mention of *P. ambiguus*, and because UCMP 44055 does not differ from other material of this species, *Mckennamorphus* is not considered a valid taxon.

Pseudotetonius.—Of the four specimens Bown (1974) included in *P. ambiguus*, MCZ 19010, a partial left dentary with C₁, P₄₋₅M₁₋₂ and alveoli for dP₁ and P₂, differs from the other three and more closely resembles *Absarokius noctivagus* in the enlarged protoconid and buccal exodaenodonty of P₅. MCZ 19010, with a single-rooted P₄ and four premolars, is referred to "some *Absarokius*" (Fig. 6).

Chlororhysis.—Gazin (1958) identified *C. knightensis* as an omyine from a partial dentary with P₂dP₃P₄P₅, and noted its close similarity to *Loveina*. Later (Gazin, 1962) he allocated a partial dentary with P₅M₁₋₃ to this species. Simons (1972) included *Chlororhysis* in *Tetonius* but Szalay (1976) recognized the genus as a distinct anaptomorphine. Examination of the two partial jaws indicates that, unlike anaptomorphines, the paraconid and metaconid on M₂₋₃ are not closely appressed, and the talonid on M₁₋₂ are not short. This material is not generically separable from *Loveina*.

Plesiadapoidea: Plesiadapidae and Paromomyidae

All plesiadapoids are united by a suite of derived features outlined above and in Fig. 1, node 8. These genera compose two clades—the plesiadapids (including carpoolestines) (Fig. 7) and paromomyids (Fig. 8). All plesiadapids (Fig. 7, node A) lack a paraconid and talonid basin on P₅ and have a paraconule on P⁴, a margoconid on the lower canine and extremely small dP₁P₂dP₃ (Rose, 1975; Gingerich, 1976). As such, *Pronothodectes* appears to represent the ancestral condition of plesiadapines and carpoolestines—a relationship also suggested by other workers (Simpson, 1937; Van Valen, 1969; Rose, 1975; Gingerich, 1976). All other plesiadapids show variable (Fig. 7, node B) or complete (Fig. 7, nodes D, E) loss of a premolar at the P₁ locus. *Elphidotarsius*, *Carpodaptus*, and *Carpolestes* (Carpolestinae, Fig. 7, node C) have long been described as a natural group and their shared-derived similarities are well known (Rose, 1975 and references therein)—P₅ is a laterally compressed trenchant blade; the trigonid on M₁ is also laterally compressed with the paraconid and metaconid more medially

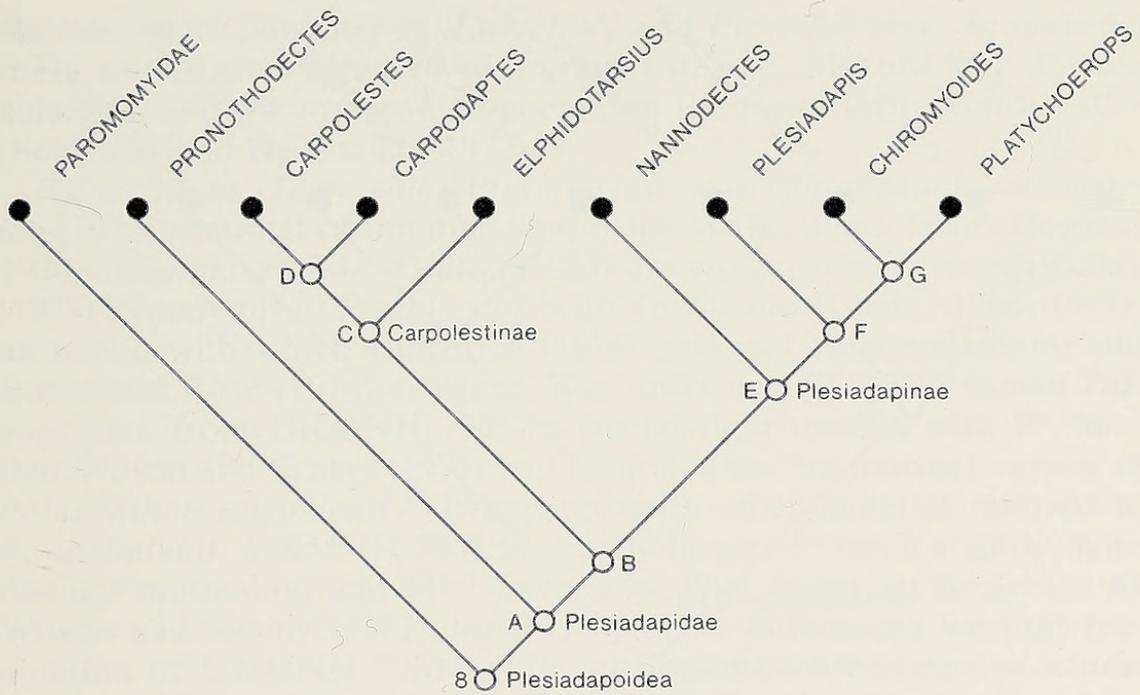


Fig. 7.—Hypothesized relationships among plesiadapids. *Node 8*—corresponds to node 8 of Fig. 1. *Node A*—paraconule on P^4 ; loss of P_5 paraconid and talonid basin; $dP_1P_2dP_3$ extremely small; margoconid on lower canine. *Node B*—variable loss of one premolar at the P_1 locus. *Node C*— P_5 is trenchant blade; M_1 laterally compressed with paraconid and metaconid more medial; P_5 – M_3 exodaenodont; small hypocone on M^{1-2} . *Node D*—loss of premolars at P_1 and P_2 loci; P_4 single-rooted; P_5 enlarged with more apical cusps; M_1 paraconid directly anterior to protoconid; P^{4-5} larger than molars, polycuspidate, with three rows of cusps aligned anteroposteriorly; mandible deeper. *Node E*—loss of a premolar at P_1 locus; upper molars more quadrate, broader; lower trigonid on M_{1-3} . *Node F*—loss of second premolar (at P_2 locus); cheek teeth squared. *Node G*—loss of a third premolar (at P_3 locus).

placed; P_5 – M_3 are exodaenodont; and a small hypocone occurs on M^{1-2} at the junction of the protocone fold and postcingulum. *Carpodartes* and *Carpolestes* (Fig. 7, node D) are more derived—premolars are lost at the P_1 and P_2 loci; P_4 is single-rooted and P_5 is enlarged with more apical cusps; the paraconid on M_1 is directly anterior to the protoconid; the mandible is deeper; and P^{4-5} are larger than the molars and polycuspidate, with three anteroposterior rows of cusps.

Plesiadapines (Fig. 7, node E) parallel carpoleslines in the loss of a premolar at the P_1 (*Nannodectes*) and P_2 (*Plesiadapis*, *Chiromyoides*, *Platychoerops*) loci. The upper molars are broader than in carpoleslines and the trigonid on M_3 is lower. The cheek teeth are squared among more derived plesiadapines (Fig. 7, node F), and in *Platychoerops* and *Chiromyoides* (Fig. 7, node G) a third premolar is lost at the P_3 locus.

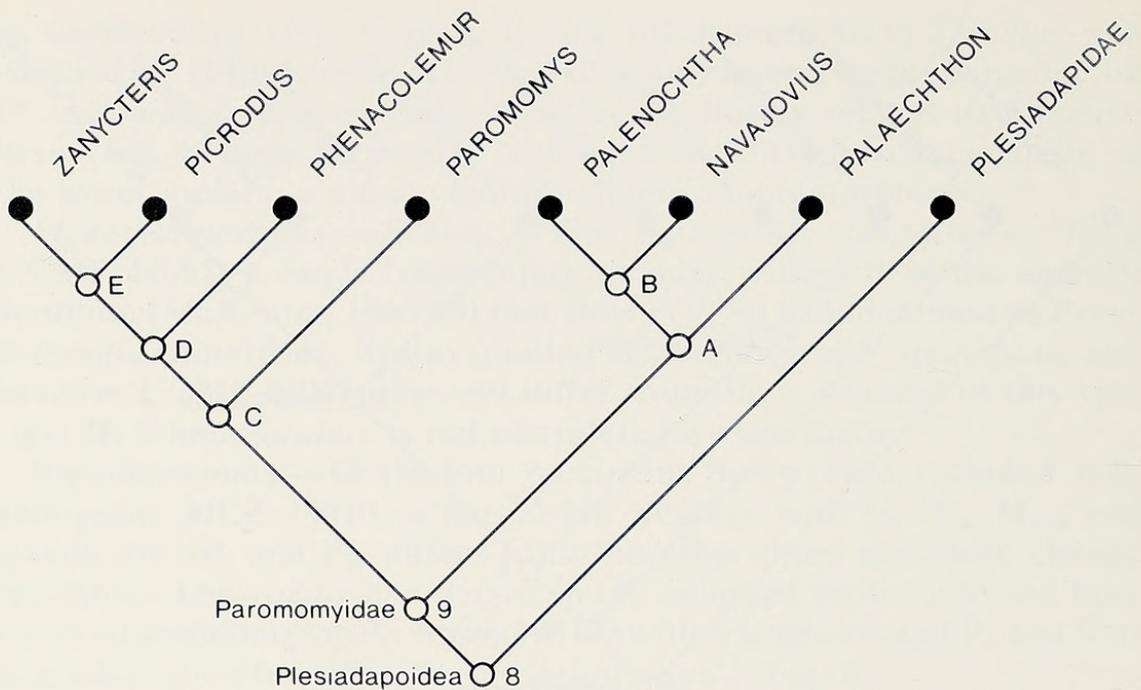


Fig. 8.—Suggested relationships among paromomyids. *Node 8*—corresponds to node 8 of Fig. 1. *Node 9*—corresponds to node 9 of Fig. 1. *Node A*—lower canine lanceolate; M_{1-3} hypoconulid closer to entoconid. *Node B*— M^3 reduced. *Node C*— M^{1-2} more nearly square, with broader and shallower talon and talonid basins, reduced cusps and conules; M_{1-3} trigonid strongly inclined anteriorly; trigonid notch reduced. *Node D*—molar cusps, crests and conules further reduced; cusps occur more marginally. *Node E*— P_5^5 enlarged; P^5 triangular, P_5 greatly elongate; M_3^3 lost; cusps, conules and crests on molars extremely reduced; metaconule marginal on M^{1-2} .

Remaining plesiadapoid genera (Figs. 1, 8, node 9) lack the shared-derived similarities of plesiadapids but are apomorphic in having a reduced P^4 with a rudimentary protocone, a less robust lower canine, and a trigonid on M_{1-3} that is inclined anteriorly. These features imply a common ancestry for the genera referred to the Paromomyidae (Fig. 8), among which two groups are commonly recognized. In *Palenochtha*, *Palaechthon* (= *Plesiolestes*, *Torrejonia*, *Talpothenach*, see below), and *Navajovius* (Fig. 8, node A) the lower canine is lanceolate (Bown and Rose, 1976), M^3 is reduced, and the hypoconulid is closer to the entoconid than the hypoconid on M_{1-3} . *Navajovius* and *Palenochtha* (Fig. 8, node B) have a more reduced M^3 .

Paromomys (= *Stockia*, see below), *Phenacolemur*, *Picrodus*, and *Zanycteris* (Fig. 8, node C) appear to compose a second group of paromomyids: M_{1-2}^{1-2} are more nearly square, with broad shallow basins, reduced cusps, and conules and a rudimentary trigonid notch on M_{1-2} . In *Phenacolemur*, *Zanycteris*, and *Picrodus* (Fig. 8, node D) the upper molars are square, the cusps occur more marginally, and the cusps, conules, and crests on the molars are further reduced, often to

no more than nubbins. In *Zanycteris* and *Picrodus* (Fig. 8, node E) these trends are expressed to a greater degree, M_3^3 are lost, P_5^5 are enlarged, and the metaconule occurs on the posterior margin of M^{1-2} (Schwartz and Krishtalka, 1977).

Palaechthon, *Torrejonia*, *Plesiolestes*, and *Talpohenach*.—Gingerich (1976, personal communication) believes that *Plesiolestes* (Jepsen, 1930) and *Palaechthon* (Gidley, 1923) are congeneric, whereas Szalay (1973) synonymized *Plesiolestes* with *Torrejonia* (Gazin, 1968, 1971), an action with which Gingerich (1976, personal communication) and Bown and Rose (1976) disagree. Kay and Cartmill (1977) named *Talpohenach* from UKMNH 7903, a partial right maxilla with $P^{3-5}M^{1-3}$ that Wilson and Szalay (1972) had identified as "an unusual variant of *Palaechthon nacimienti*." Compared with other material referred to *P. nacimienti*, UKMNH 7903 is slightly larger, P^4 has a slightly more distinct protocone, and M^{1-2} have somewhat larger styler areas. As Wilson and Szalay (1972) concluded, these differences warrant recognition of UKMNH 7903 as ?*P. nacimienti*, or perhaps as a new species of *Palaechthon*, but not generic distinction. Until material referred to these genera is restudied, *Palaechthon* is considered synonymous with *Plesiolestes*, *Torrejonia*, and *Talpohenach*.

Stockia.—*S. powayensis*, usually identified as an omomyid (Gazin, 1958; Szalay, 1976), is known only from two partial dentaries with M_{1-3} and M_{2-3} , respectively, and possibly three isolated teeth, a P_5 , dP_5 , and M_1 . Like *Paromomys*, M_{1-2} are quadrate and M_3 bears a broad third lobe with a double hypoconulid. The trigonid of M_1 is square, whereas that of M_{2-3} is a compressed rectangle with parallel protocristid and paracristid. The talonid basins are broad and shallow and the cusps are reduced, nubbin-like and marginal. These features, in part, unite paromomyines (Fig. 8, node C). *Stockia* closely resembles *Paromomys* in comparable parts of the lower dentition—a similarity also noted by McKenna (1960)—and the two are tentatively regarded as congeneric, at least until more material of "*Stockia*" is recovered. Its late Eocene occurrence parallels that of another paromomyid, *Phenacolemur* (Robinson, 1968; Krishtalka, 1978).

Elphidotarsius.—Rose (1975) described the dental formula of *Elphidotarsius* as 2.1.3.3 (or 0.1.5.3. of this paper). One of the figured partial dentaries of *E. cf. E. florencae* (Rose, 1975:14) appears to lack the alveolus for dP_1 (alveolus in front of I_2 of Rose) and its inferred dental formula is $C_1P_2dP_3P_4P_5M_{1-3}$. Loss of a premolar may be variable in *Elphidotarsius* (Fig. 7, node B).

NOVEL RELATIONSHIPS

Anaptomorphids and omomyids.—The generic composition of and allegedly close relationship between omomyids and anaptomorphids

are commonly accepted (Gazin, 1958; Simons, 1963, 1972; Szalay, 1976; Gingerich, 1976). Neither of these conclusions appear warranted if the relationships proposed above are correct. Some taxa usually identified as omomyids (*Loveina*, *Shoshonius*, *Hemiacodon*, *Dyseolemur*, *Washakius*, *Rooneyia*) have a protocone fold and V-shaped protocristae, whereas others (*Omomys*, *Chumashius*, *Macrotarsius*, *Tarsius*, *Uintanius*) lack such a fold and have widely divergent, parabolic protocristae. Possession of the protocone fold implies a common ancestry for the former genera and all others that have this derived feature and is the basis for their inclusion in the clade Plesiadapiformes. Specifically, *Rooneyia* (Wilson, 1966) is a microchoerid, and *Loveina*, *Shoshonius*, *Washakius*, *Dyseolemur*, and *Hemiacodon* are anaptomorphids (Figs. 1, 5, 6). On the other hand, possession of arcuate protocristae on the upper molars unites *Omomys*, *Chumashius*, *Macrotarsius*, *Uintanius*, *Tarsius*, *Pseudoloris*, and uintasoricines as Tarsiiformes. All anaptomorphids have the derived protocone fold and are more closely related to microchoerids, paromomyids, and plesiadapids than to tarsiiforms. Also contrary to previous conclusions (Simons, 1961*b*; Gingerich, 1977) *Tarsius*, a tarsiiform, and microchoerids (anaptomorphoid plesiadapiforms) do not share a descendant-ancestor relationship among plesitarsiiforms.

Microsyopids and uintasoricines.—Many workers have hypothesized a special relationship between uintasoricines and microsyopids (Szalay, 1969*b*) and between these groups and some paromomyids (Bown and Gingerich, 1973; Bown and Rose, 1976). Krishtalka (1978) dealt with some of the difficulties inherent in these suggestions. (1) A protocone fold and parabolic protocristae are among the derived characters for plesiadapiforms (including paromomyids) and tarsiiforms (including uintasoricines), respectively. Microsyopids are primitive in lacking a protocone fold and in having V-shaped protocristae. (2) The entoconid-hypoconulid complex does not appear to be a derived similarity in microsyopids and uintasoricines. The hypoconulid in microsyopids is large, close to the entoconid and separated from that cusp by a deep notch. In uintasoricines the hypoconulid is extremely reduced (*Uintasorex*) or often lost (*Niptomomys*, some specimens). When present, the hypoconulid is compressed anteroposteriorly to an elongate thickening of the hypocristid, of which the raised lingual end is close to the entoconid. If a notch separates the lingual end of the hypoconulid and entoconid in uintasoricines, it is extremely weak.

GENERA OMITTED

Ekgmowechashala.—Macdonald (1963, 1970) and Szalay (1976) described this Arikareean primate as an omomyid. *E. philotau* lacks the

derived antemolar morphology of plesitarsiiforms and its affinities appear to be elsewhere (Schwartz and Krishtalka, in preparation).

Teilhardina and *Purgatorius*.—Three species of *Teilhardina* have been described—the type, *T. belgica* (Simpson, 1940; Teilhard de Chardin, 1927); *T. ? gallica* (Russell et al., 1967); *T. americana* (Bown, 1976). Szalay (1976) referred *T. gallica* to a new genus, *Donrussellia*, but Savage et al. (1977) maintained that *Donrussellia* is a subgenus of *Teilhardina*. It is clear from examination of figured specimens that *T. (D.) gallica* differs significantly from the type of *T. belgica* and warrants generic distinction as *Donrussellia*, a conclusion also hinted at by Bown (1976). Moreover, Gingerich (1976, personal communication) has identified *D. gallica* as an adapid, and we concur, at least on the basis of the morphology of the lower molars.

Similarly, *T. americana* has a distinctive lower dentition compared with that of *T. belgica*— P_5M_{1-3} of *T. americana* are more robust and bear broader buccal cingulids; the talonid on M_{1-3} is broader and shorter; the paraconid and metaconid on M_{2-3} are closely appressed as in anaptomorphines; and the metaconid on M_{1-3} is not highly inflated. On the basis of the lower dentition "*T.*" *americana* appears to be an anaptomorphine plesiadapiform, and possibly a species of *Ane-morhysis* (see Bown, 1976).

The affinities of *T. belgica* are unclear. As reconstructed by Szalay (1976), and Gingerich (1977) the type specimen (IRSNB 64) appears to have two small anterior alveoli, followed by a huge alveolus for a single-rooted tooth, a much smaller alveolus, and $P_{4-5}M_{1-3}$. If these reconstructions are correct, the relative size of the alveoli implies a lower antemolar dental formula of two small incisors, a large canine, and $P_2P_4P_5$. If "alveolus a" (Gingerich, 1977) is indeed an alveolus rather than a foramen, either P_2 was double rooted, or a dP_1 was present. A second partial lower jaw of *T. belgica* (IRSNB unnumbered, Szalay, 1976:175, Fig. 2) bears a definite alveolus for a single rooted dP_1 or the anterior root of a double-rooted P_2 . Given these reconstructions, the antemolar dental formula of *T. belgica* may be, as in simi-olemuriforms, two incisors, a canine, and either three double-rooted premolars ($P_2P_4P_5$) or two single-rooted (dP_1P_2) and two double-rooted (P_4P_5) premolars. However, if the front of the jaw is reconstructed to accommodate a larger anterior tooth, such as the canine in plesitarsiiforms, the lower antemolar dental complement of *T. belgica* would be C_1 , tiny dP_1 , huge P_2 , and double-rooted P_3 (or dP_3), P_{4-5} .

The most complete described material of *Purgatorius* (Clemens, 1974) is a partial right dentary with three molars, three double-rooted premolars, and two alveoli anterior to the first premolar. The anterior end of the dentary is not preserved. Of the two alveoli, the first is

larger than the second and, as Clemens (1974) concluded, may have contained a canine followed by a single-rooted P_1 . Such a reconstruction yields an antemolar dental formula of one or more incisors (unknown), a canine, and four premolars (as in simiolemuriforms) or, if the anteriormost tooth is the canine, an antemolar dental complement ($C_1dP_1P_2P_4P_5$) found in many plesitarsiiforms. In short, the anterior dentitions of *T. belgica* and *Purgatorius* are too poorly known to confidently identify these genera as simiolemuriforms or plesitarsiiforms on that basis. The morphology of P^5-M^3 may, however, be a clue.

Elements of the upper dentition referred to *T. belgica* (Quinet, 1966a; Szalay, 1976) and *Purgatorius* (Van Valen and Sloan, 1965; Szalay, 1969a; Clemens, 1974) are closely similar. Both have an extremely weak protocone fold and a protocone that leans labially on M^{1-2} , and a metacone on P^5 —features that in part characterize plesiadapoid plesitarsiiforms (Fig. 1, nodes 5, 8). However, lower molars of *T. belgica* (Teilhard de Chardin, 1927; Quinet, 1966b; Szalay, 1976) and *Purgatorius* (Van Valen and Sloan, 1965; Szalay, 1969a; Clemens, 1974) lack the derived features of not only plesiadapoids, but primates in general. The metaconids are highly inflated and dominate the trigonid, and the talonids are not as broad as in primates. In these features the lower molars of *T. belgica* and *Purgatorius* resemble those of *Mckennatherium ladae* and “*Diacodon*” *minutus*, a primitive adapisoricid and ?condylarth, respectively (Krishtalka, 1976a). Lower molars of *T. belgica* and *Purgatorius* lack the L-shaped paracristid and quadrate trigonid on M_{1-3} of plesiadapoids, and the derived lower molar morphology of anaptomorphoids, tarsiiforms, microsypids, or adapids. The crown outlines and presence of moderately low cusps and wider talonid than trigonid on M_{1-2} may possibly imply the primate affinities of the lower molars of these genera. P_5 in both is more nearly primate-like than the molars but not unequivocally so. The talonid slope resembles that of certain adapisoricids. In summary, P_5M_{1-3} of *Purgatorius* and *T. belgica* are similar and primitive, and only their association with respective elements of their plesiadapoid-like upper dentition implies identification of these genera as primates. Many of the similarities between M^{1-2} of both taxa are also primitive—constriction across the conules; marked buccal and posterior emargination of the crown; long postmetaconulecrista and metacingulum; and strong conulecristae, postmetacrista, and metacingulum. The structure of the weak protocone fold may ally *T. belgica* and *Purgatorius* with plesiadapiforms, whereas the occurrence of a metacone on P^5 is possibly a derived feature shared with plesiadapoids. These genera are provisionally identified as primitive, closely related, plesiadapoid primates, pending a better knowledge of their anterior dentitions.

Hoangonius.—Like *Donrussellia*, Gingerich (1976) has identified *Hoangonius* as an adapid simiolemuriform.

Micromomys, *Utahia*, *Saxonella*.—These genera are too poorly known for a confident assessment of relationships (see Szalay, 1973, 1976; Rose, 1975; Bown and Rose, 1976; and references therein).

SUMMARY

The Order Primates appears to consist of two clades—the Plesitarsiiformes (including “plesiadapiforms” and “tarsiiforms”) and the Simiolemuriformes (including strepsirhines and anthropoids). Both evolved from a common ancestor that had a dental complement of two or three incisors, a canine, five premolars, and three molars. Origin of the plesitarsiiforms involved loss of the incisors, development of the canine at the front of the jaw, and, possibly, inhibition of P_1^1 and P_3^3 and retention of dP_1^1 and dP_3^3 . The ancestor of the simiolemuriforms, on the other hand, retained two incisors and the canine and had lost the premolar at the P_3^3 locus.

Apart from the microsyopids, two clades compose the Plesitarsiiformes—the Tarsiiformes, including omomyines and uitasoricines; and the Plesiadapiformes, including anaptomorphids, microchoerids, paromomyids, and plesiadapids. Each of these groups is defined by a common ancestry based on inferred shared-derived similarities, and their generic composition differs from that proposed in previous studies.

The recognition of plesitarsiiform and simiolemuriform clades implies parallel evolution of a number of features—divergent halluces and polleces, a postorbital bar, postorbital closure, a tubular ectotympanic, a petrosal bulla, nails on at least hallux and pollex, fused nasal processes, hemochorial placentation, abbreviation of the snout, and loss of the medial entocarotid artery. As suggested elsewhere (Schwartz, 1978; Schwartz et al., 1978), many of these alleged similarities between plesitarsiiforms and simiolemuriforms may be of different morphogenetic origin and not homologous. Also, some of the oft cited reconstructions of intrabullar carotid circulation for fossil and many extant primates may be erroneous (Conroy and Wible, 1978).

Some of the relationships among plesitarsiiforms proposed in this paper are novel. Determination of their validity will involve the results of new discoveries, and an aggressive frisk of the inferred shared-derived characters and alleged parallelisms.

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LITERATURE CITED

- Bown, T. M. 1974. Notes on early Eocene anaptomorphine primates. Univ. Wyoming Contrib. Geol., 13:19-26.
- . 1976. Affinities of *Teilhardina* (Primates, Omomyidae) with description of a new species from North America. Folia Primatol., 25:62-72.
- Bown, T. M., and P. D. Gingerich. 1973. The Paleocene primate *Plesiolestes* and the origin of Microsyopidae. Folia Primatol., 19:1-8.
- Bown, T. M., and K. D. Rose. 1976. New early Tertiary primates and a reappraisal of some plesiadapiforms. Folia Primatol., 26:109-138.
- Cartmill, M. 1975. Strepsirhine basicranial structures and the affinities of the Cheirogaleidae. Pp. 313-354, in Phylogeny of the Primates (W. P. Luckett and F. S. Szalay, eds.), Plenum Press, New York, xiv + 483 pp.
- Clemens, W. A. 1974. *Purgatorius*, an early paromomyid primate (Mammalia). Science, 184:903-905.
- Conroy, G. C., and J. R. Wible. 1978. Middle ear morphology of *Lemur variegatus*: some implications for primate paleontology. Folia Primatol., in press.
- Dashzeveg, D., and M. C. McKenna. 1977. Tarsioid primate from the early Tertiary of the Mongolian People's Republic. Acta Paleont. Polonica, 22:119-137.
- Gazin, C. L. 1958. A review of the Middle and Upper Eocene primates of North America. Smithsonian Misc. Coll., 136:1-112.
- . 1962. A further study of the Lower Eocene mammalian fauna of southwestern Wyoming. Smithsonian Misc. Coll., 144:1-98.
- . 1968. A new primate from the Torrejon Middle Paleocene of the San Juan Basin, New Mexico. Proc. Biol. Soc. Washington, 81:629-634.
- . 1971. Paleocene primates from the Shotgun Member of the Fort Union Formation in the Wind River Basin, Wyoming. Proc. Biol. Soc. Washington, 84:13-38.
- Gidley, J. W. 1923. Paleocene primates of the Fort Union, with discussion of relationships of Eocene primates. Proc. U.S. Nat. Mus., 63:1-37.
- Gingerich, P. D. 1975. Systematic position of *Plesiadapis*. Nature, 253:111-113.
- . 1976. Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates). Mus. Paleont. Papers Paleont., Univ. Michigan, 15:1-141.
- . 1977. Dental variation in early Eocene *Teilhardina belgica*, with notes on the anterior dentition of some early Tarsiiformes. Folia Primatol., 28:144-153.
- Hill, W. C. O. 1953. Primates, comparative anatomy and taxonomy, Vol. I, Strepsirhini. Edinburgh Univ. Press, Edinburgh, 798 pp.
- Hürzeler, J. 1948. Zur Stammesgeschichte der Necrolemuriden. Schweiz. Pal. Abh., 66:1-46.
- Jepsen, G. L. 1930. Stratigraphy and paleontology of the Paleocene of northeastern Park County, Wyoming. Proc. Amer. Phil. Soc., 69:463-528.
- Kay, R. F., and M. Cartmill. 1977. Cranial morphology and adaptations of *Palaechthon nacimienti* and other Paromomyidae (Plesiadapoidea, ?Primates), with a description of a new genus and species. J. Human Evol., 6:19-53.
- Krishtalka, L. 1976a. Early Tertiary Adapisoricidae and Erinaceidae (Mammalia, Insectivora) of North America. Bull. Carnegie Mus. Nat. Hist., 1:1-40.
- . 1976b. North American Nyctitheriidae (Mammalia, Insectivora). Ann. Carnegie Mus., 46:7-28.
- . 1978. Paleontology and geology of the Badwater Creek Area, Central Wyoming.

- Part 15. Review of the late Eocene primates from Wyoming and Utah, and the Plesitarsiiformes. *Ann. Carnegie Mus.*, 47:335–360.
- Luckett, W. P. 1974. Comparative development and evolution of the placenta in mammals. Pp. 142–234, in *Reproductive biology of the primates* (W. P. Luckett, ed.), Karger, Basel.
- . 1975. Ontogeny of the fetal membranes and placenta: their bearing on primate phylogeny. Pp. 157–182, in *Phylogeny of the Primates* (W. P. Luckett and F. S. Szalay, eds.), Plenum Press, New York, xiv + 483 pp.
- Martin, R. D. 1972. Adaptive radiation and behavior of the Malagasy lemurs. *Phil. Trans. Roy. Soc., London*, 264:295–352.
- Matthew, W. D. 1909. Carnivora and Insectivora of the Bridger Basin, Middle Eocene. *Mem. Amer. Mus. Nat. Hist.*, 9:289–567.
- . 1915. A revision of the Lower Eocene Wasatch and Wind River faunas. Part 4. Entelonychia, Primates, Insectivora (part). *Bull. Amer. Mus. Nat. Hist.*, 34:429–483.
- Macdonald, J. R. 1963. The Miocene faunas from the Wounded Knee area of western South Dakota. *Bull. Amer. Mus. Nat. Hist.*, 125:139–238.
- . 1970. Review of the Miocene Wounded Knee faunas of southwestern South Dakota. *Bull. Los Angeles County Mus. Nat. Hist.*, 8:1–82.
- McKenna, M. C. 1960. Fossil Mammalia from the early Wasatchian Four Mile fauna, Eocene of northwest Colorado. *Univ. California Publ. Geol. Sci.*, 37:1–130.
- . 1966. Paleontology and the origin of the Primates. *Folia Primatol.*, 4:1–25.
- . 1975. Toward a phylogenetic classification of the Mammalia. Pp. 21–46, in *Phylogeny of the Primates* (W. P. Luckett and F. S. Szalay, eds.), Plenum Press, New York, xiv + 483 pp.
- Pocock, R. I. 1918. On the external characters of the lemurs and of *Tarsius*. *Proc. Zool. Soc. London*, 1918:19–53.
- Quinet, G. E. 1966a. *Teilhardina belgica*, ancêtre des Anthropoidea de l'ancien monde. *Bull. Inst. Roy. Sci. Nat. Belgique*, 42(1):1–14.
- . 1966b. Sur la formule dentaire de deux primates du Landenien continental belge. *Bull. Inst. Roy. Sci. Nat. Belgique*, 42(38):1–6.
- Robinson, P. 1966. Fossil Mammalia of the Huerfano Formation, Eocene of Colorado. *Bull. Peabody Mus. Nat. Hist., Yale Univ.*, 21:1–95.
- . 1968. Paleontology and geology of the Badwater Creek area, central Wyoming. Part 4. Late Eocene primates from Badwater, Wyoming, with a discussion of material from Utah. *Ann. Carnegie Mus.*, 39:307–326.
- Romer, A. S. 1966. *Vertebrate paleontology*. Univ. Chicago Press, 3rd edition, viii + 468 pp.
- Rose, K. D. 1975. The Carpolestidae, early Tertiary primates of North America. *Bull. Mus. Comp. Zool.*, 147:1–74.
- Russell, D. E., P. Louis, and D. E. Savage. 1967. Primates of the French early Eocene. *Univ. California Publ. Geol. Sci.*, 73:1–46.
- Savage, D. E., D. E. Russell, and B. T. Waters. 1977. Critique of certain early Eocene primate taxa. *Geobios Spec. Mem.*, 1:159–164.
- Schwartz, J. H. 1978. If *Tarsius* is not a prosimian, is it a haplorhine? *Proc. Vith Congr. Intl. Primat. Soc.*, Academic Press, London, pp. 195–202.
- Schwartz, J. H., and L. Krishtalka. 1976. The lower antemolar dentition of *Litolestes ignotus*, a late Paleocene erinaceid (Mammalia, Insectivora). *Ann. Carnegie Mus.*, 46:1–6.
- . 1977. Revision of Picrodontidae (Primates, Plesiadapiformes): dental homologies and relationships. *Ann. Carnegie Mus.*, 46:55–70.
- Schwartz, J. H., I. Tattersall, and N. Eldredge. 1978. Phylogeny and classification of the Primates revisited. *Yrbk. Phys. Anthropol.*, in press.

- Simons, E. L. 1961a. The dentition of *Ourayia*:—its bearing on relationships of omomyid prosimians. *Postilla*, 54:1–29.
- . 1961b. Notes on Eocene tarsioids and a revision of some Necrolemurinae. *Bull. British Mus. (Nat. Hist.), Geol. Ser.*, 5:45–69.
- . 1963. A critical reappraisal of Tertiary primates. Pp. 65–129, *in* *Evolutionary and genetic biology of Primates*, Vol. 1 (J. Buettner-Janusch, ed.), Academic Press, New York, xiii + 327 pp.
- . 1972. *Primate evolution, an introduction to man's place in nature*. Macmillan, New York, 322 pp.
- Simpson, G. G. 1937. The Fort Union of the Crazy Mountain Field, Montana and its mammalian faunas. *Bull. U.S. Nat. Mus.*, 169:1–287.
- . 1940. Studies on the earliest primates. *Bull. Amer. Mus. Nat. Hist.*, 77:185–212.
- . 1955. The Phenacolemuridae, new family of early primates. *Bull. Amer. Mus. Nat. Hist.*, 105:415–441.
- Starck, D. 1975. The development of the chondrocranium in primates. Pp. 127–155, *in* *Phylogeny of the Primates* (W. P. Luckett and F. S. Szalay, eds.), Plenum Press, New York, xiv + 483 pp.
- Szalay, F. S. 1969a. Mixodectidae, Microsyopidae, and the insectivore-primate transition. *Bull. Amer. Mus. Nat. Hist.*, 140:193–330.
- . 1969b. Uintasoricinae, a new subfamily of early Tertiary mammals (?Primates). *Amer. Mus. Novitates*, 2363:1–36.
- . 1973. New Paleocene primates and a diagnosis of the new Suborder Paromomyiformes. *Folia Primatol.*, 19:73–87.
- . 1974. A new species and genus of early Eocene primate from North America. *Folia Primatol.*, 22:243–250.
- . 1975. Phylogeny of primate higher taxa: the basicranial evidence. Pp. 91–125, *in* *Phylogeny of the Primates* (W. P. Luckett and F. S. Szalay, eds.), Plenum Press, New York, xiv + 483 pp.
- . 1976. Systematics of the Omomyidae (Tarsiiformes, Primates) taxonomy, phylogeny and adaptations. *Bull. Amer. Mus. Nat. Hist.*, 156:157–450.
- Teilhard de Chardin, P. 1927. Les mammifères de l'Eocene inférieur de la Belgique. *Mem. Mus. Roy. Hist. Nat. Belgique*, 36:1–33.
- Van Kampen, P. N. 1905. Die Tympanalgegend des Saugetierschadel. *Morph. Jb.*, 34:321–722.
- Van Valen, L. 1969. A classification of the Primates. *Amer. J. Phys. Anthrop.*, 30:295–296.
- Van Valen, L., and R. E. Sloan. 1965. The earliest primates. *Science*, 150:743–745.
- Wilson, J. A. 1966. A new primate from the earliest Oligocene, west Texas, preliminary report. *Folia Primatol.*, 4:227–248.
- Wilson, J. A., and F. S. Szalay. 1972. New paromomyid primate from Middle Paleocene beds, Kutz Canyon area, San Juan Basin, New Mexico. *Amer. Mus. Novitates*, 2499:1–18.



Krishtalka, Leonard and Schwartz, Jeffrey H. 1978. "Phylogenetic relationships of plesiadapiform-tarsiiform primates." *Annals of the Carnegie Museum* 47, 515–540. <https://doi.org/10.5962/p.330818>.

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