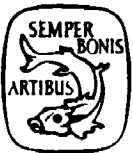


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Biology of Tarsiers

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3. Paleobiology of tarsiiiform primates

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Introduction

Fossil tarsiiiform primates have been known for more than 100 years. These were first found in Eocene strata in Europe and shortly afterwards in North America. It is now clear that during the Eocene there was a major radiation of fossil Tarsiiformes in North America and a lesser one in Europe. Recent work in Mongolia and in Pakistan indicate that tarsier-like primates inhabited Asia during the Eocene as well, but Asian micromammalian faunas are not yet sufficiently well sampled to give a reliable indication of diversity on that continent.

All of the known fossil tarsiiiform primates are included in one family, Omomyidae, which is generally divided into three subfamilies: Anaptomorphinae, a cosmopolitan primitive stem group with 12 genera; Omomyinae, a North American endemic group with 13 genera; and Microchoerinae, a European endemic group with 4 genera. No Omomyidae have been found in Africa, South America, Australia, or Antarctica. An outline classification of Omomyidae is presented in Tab. 3-1.

Previous studies of Omomyidae have been concerned almost exclusively with the systematic relationships of species and genera. In recent years much has been learned about the functional morphology, ecology, and behaviour of living primates, and it is now possible to apply behavioural and ecological generalizations derived from living primates in interpreting the paleobiology of Omomyidae. The reader is referred to Gazin (1958), Simons (1961a), Louis and Sudre (1975), Szalay (1976), Krishtalka (1978), and Bown (1979) for detailed systematic treatment of Omomyidae. The relationships of Omomyidae to other primates are discussed by Simons (1961a, 1961b, 1972), Szalay (1976), Cartmill and Kay (1978), Gingerich and Schoeninger (1977), Gingerich (1978, 1981), and Krishtalka and Schwartz (1978). There is a general consensus that Omomyidae are closely related to *Tarsius*, but as yet little agreement on their relationships to more primitive plesiadapiform and more advanced simiiform primates. In this chapter I would like to outline evidence bearing on the dietary, sensory, locomotor, and social adaptations of Omomyidae.

Dietary adaptations

There is a close relationship between tooth size and body size in living primates (Kay, 1975; Gingerich *et al.*, 1981), and with few exceptions tooth size can be used to give a reliable estimate of body size in fossil primates. This relationship is illustrated in fig. 3-1, where the correlation between tooth size and body size is 0.976 and the principal axis accounts for 99% of the observed variance. For purposes of

Tab. 3-1: Outline classification of fossil tarsiiform primates (Omomyidae), including all genera, number of species currently recognized in each genus, age, geographic distribution, and estimated body size (from Gingerich, 1981).

Genera and number of species	Age	Geographic distribution	Body weight (gm)
Omomyidae Trouessart, 1879			
Anaptomorphinae Cope, 1883			
<i>Altanius</i> Dashzeveg & McKenna, 1977 (1 sp.)	Early Eocene	Asia	10
<i>Teilhardina</i> Simpson, 1940 (2 sp.)	Early Eocene	Eur.-N. Am.	35
<i>Tetonoides</i> Gazin, 1962 (2 sp.)	Early Eocene	N. Am.	30–40
<i>Tetonius</i> Matthew, 1915 (2 sp.)	Early Eocene	N. Am.	80–85
<i>Absarokius</i> Matthew, 1915 (3 sp.)	Early Eocene	N. Am.	75
<i>Anemorhysis</i> Gazin, 1958 (1 sp.)	Early Eocene	N. Am.	20
<i>Uintalacus</i> Gazin, 1958 (1 sp.)	Early Eocene	N. Am.	30
<i>Chlororhysis</i> Gazin, 1958 (1 sp.)	Early Eocene	N. Am.	50
<i>Uintanius</i> Matthew, 1915 (2 sp.)	Middle Eocene	N. Am.	40–45
<i>Anaptomorphus</i> Cope, 1872 (4 sp.)	Middle Eocene	N. Am.	45–120
<i>Trogolemur</i> Matthew, 1909 (1 sp.)	Middle Eocene	N. Am.	25
Anaptomorphinae (?)			
<i>Kohatius</i> Russell & Gingerich, 1980 (1 sp.)	E.-M. Eocene	Asia	55
Omomyinae			
<i>Arapahovius</i> Savage & Waters, 1978 (1 sp.)	Early Eocene	N. Am.	80
<i>Loveina</i> Simpson, 1940 (1 sp.)	Early Eocene	N. Am.	50
<i>Shoshonius</i> Ganger, 1910 (1 sp.)	Early Eocene	N. Am.	45
<i>Omomy</i> Leidy, 1869 (5 sp.)	E.-M. Eocene	N. Am.	30–85
<i>Utahia</i> Gazin, 1958 (1 sp.)	Middle Eocene	N. Am.	30
<i>Washakius</i> Leidy, 1873 (2 sp.)	Middle Eocene	N. Am.	40–50
<i>Hemiacodon</i> Marsh, 1872 (1 sp.)	Middle Eocene	N. Am.	240
<i>Stockia</i> Gazin, 1958 (1 sp.)	Late Eocene	N. Am.	125
<i>Ourayia</i> Gazin, 1958 (2 sp.)	Late Eocene	N. Am.	270–480
<i>Chumashius</i> Stock, 1933 (1 sp.)	Late Eocene	N. Am.	80
<i>Dyseolemur</i> Stock, 1934 (1 sp.)	Late Eocene	N. Am.	50
<i>Macrotarsius</i> Clark, 1941 (2 sp.)	Late Eocene	N. Am.	370–550
<i>Rooneyia</i> Wilson, 1966 (1 sp.)	E. Oligocene	N. Am.	340
<i>Ekgmowechashala</i> McDonald, 1963, (1 sp.)	L. Oligocene	N. Am.	420
Microchoerinae			
<i>Nannopithec</i> Stehlin, 1916 (3 sp.)	M. Eocene	Eur.	40–50
<i>Pseudoloris</i> Stehlin, 1916 (4 sp.)	M.-L. Eocene	Eur.	15–35
<i>Necrolemur</i> Filhol, 1873 (2 sp.)	L. Eocene	Eur.	80–85
<i>Microchoerus</i> Wood, 1844 (3 sp.)	L. Eoc.-E. Olig.	Eur.	225–400

the discussion here, it is important to note that *Tarsius* does not follow the normal body size/tooth size relationship in primates, but it has teeth significantly larger than one would predict given its body size. Or conversely, predictions of body size from tooth size in *Tarsius* will significantly overestimate the former. In the analysis presented here, a tarsioid regression axis has been constructed parallel to the general primate regression in such a way that it passes through the two points representing *Tarsius*. This new line yields predicted weights that are consistent for *Tarsius*, but significantly less than those predicted using the general primate regression.

Body weights for species of Omomyidae predicted from the tarsioid regression are listed in the right hand column of Table 3–1, and these values are shown graphically for all species of each subfamily in fig. 3-2. Note that Omomyidae range from an estimated body weight of about 10 g (*Altanius*) to an estimated body weight of about 550 g (*Macrotarsius*). Anaptomorphines have a modal body weight of

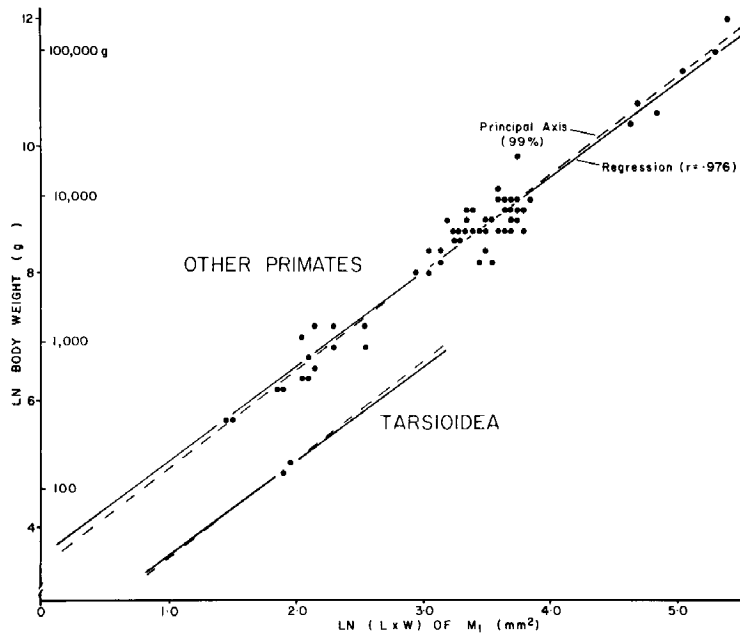


Fig. 3-1: Allometric scaling of tooth size and body size in 42 species of living primates, excluding *Tarsius* species. Abscissa is the natural logarithm of length (mm) multiplied by width (mm) for the first lower molar (M_1). Ordinate is the natural logarithm of body weight (g). The principal axis (dashed line) has a slope of 1.56 and accounts for 99% of the total variance of «other primates» (excluding *Tarsius*). The regression of body weight on tooth size (solid line) is $Y = 1.50X + 3.52$ for «other primates», where X is the abscissa and Y is the ordinate. The equation $Y = 1.50X + 1.96$ yields a line passing through the points representing *Tarsius* and parallel to the «other primate» regression. This «Tarsioida» line was used to predict body weights for Omomyidae given in Tab. 3-1. Measurements used to construct this figure and to calculate the principal axis and regression are given in Appendix I. See Gingerich et al. (1981) for further discussion.

about 30 g. Omomyines tend to be larger, with a modal weight of about 60–80 g. Microchoerines appear to encompass a broader range, with one modal group at about 30 g and another at about 250 g.

There is, of course, an important assumption implicit in the above analysis. This is that tooth size and body size in Omomyidae scale with the same slope as living primates in general, but with a lower body size intercept consistent with the position of *Tarsius*, i. e. that the tarsioid line in fig. 3-1 is reasonably accurate. This assumption is very difficult to test, given only one living genus of Tarsioida. An investigation of body size/tooth size scaling in insectivorous mammals is presently underway to see how *Tarsius* compares with other insectivores—its dentition certainly does not conform to the body size/tooth size relationship of normal primates.

If the above assumption about body size/tooth size scaling in Omomyidae holds, then it is possible to make a very interesting inference about dietary adaptations in these extinct primates. Kay (1975), Kay and Hylander (1978), and Fleagle (1978) have shown that there is a dichotomy in the distribution of primate body sizes. Primates smaller than about 500 g usually feed on some combination of insects and fruits, whereas those larger than 500 g generally feed on a combination of leaves and fruits. Large primates cannot live on a diet of insects because it is too difficult to find and catch enough of them to maintain their body mass. Conversely, small primates cannot live on a folivorous diet because they are not large enough to carry a stomach of sufficient complexity to digest leaves. This 500 g threshold,

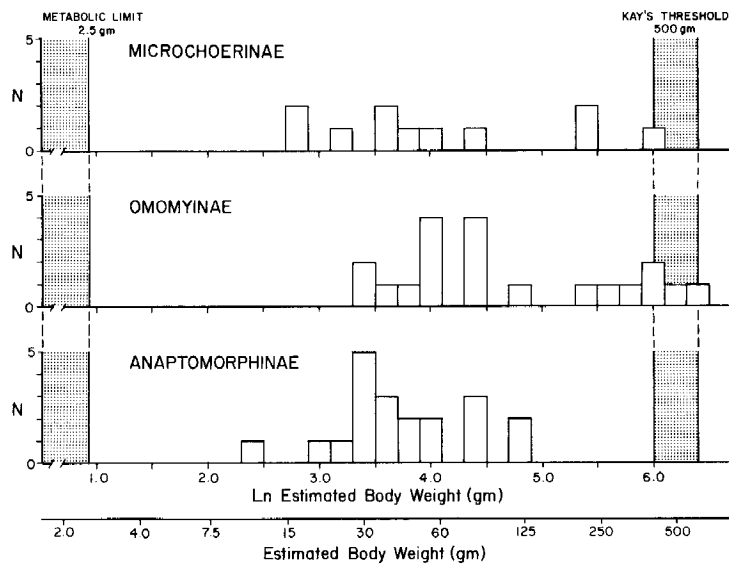


Fig. 3-2: Distribution of body size in Omomyidae. Each square represents one species. Body size is estimated from tooth size using the tarsioid regression equation in fig. 3-1. Note that omomyids fall between the theoretical metabolic limit of minimum size in mammals (2.5 g; Pearson, 1948) and Kay's (1975) threshold separating insectivorous-frugivorous from frugivorous-folivorous primates. Data from Gingerich (1981).

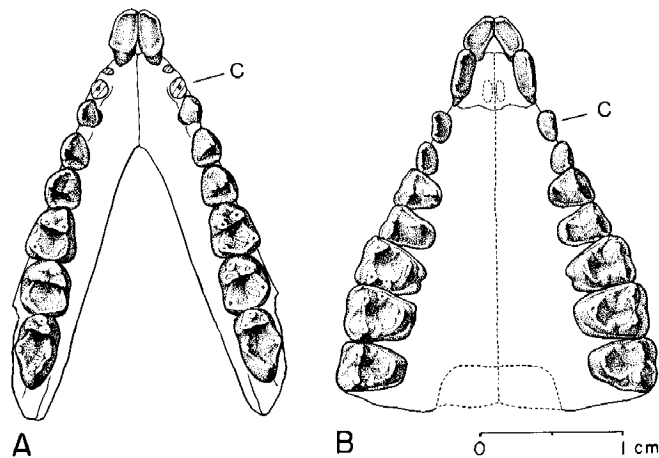


Fig. 3-3: Reconstructed lower (A) and upper (B) dentition of *Ourayia uintensis*, based on Princeton University specimen 16431. Note the large upper and lower central incisors, small upper and lower canines, and the unfused mandibular symphysis. This species has the most broad-crowned upper and lower incisors of any fossil or living tarsioid, but these are still more pointed than spatulate, and differ markedly in form from the spatulate incisors of Adapidae and higher primates. Note also the broadly basined upper and lower molars of *Ourayia*, indicating that fruit was probably an important component in the diet of this large omomyid.

«Kay's threshold,» is an important empirical dichotomy in living primates that applies equally well in the fossil record. In body size, Omomyidae are centered between the theoretical metabolic minimum body size in mammals of 2.5 g (Pearson, 1948) and Kay's insectivorous-folivorous threshold of about 500 g. The implication is that Omomyidae represent a radiation of largely insectivorous and frugivorous rather than folivorous primates.

The dentition of omomyids also indicates insectivorous-frugivorous adaptations. Kay (1977) discussed the functional morphology of molar form in two omomyids, *Tetonoides* and *Hemiacodon*, showing that they are designed for a combination of shearing and grinding. Omomyids have tritubercular molars with three distinct cusps (protoconid, paraconid, and metaconid) on lower molar trigonids, broad lower molar talonids, and three distinct cusps (protocone, paracone, and metacone) forming a broad, basined trigon on the upper molars. The presence of sharply pointed premolars and sharply pointed molar cusps is consistent with insectivory, and the presence of broadly basined molar trigons and talonids is at the same time consistent with frugivory (fig. 3-3).

Omomyidae are characterized by having enlarged, pointed, procumbent upper and lower central incisors, and all lack symphyseal fusion of the mandibular rami (fig. 3-3). In these characteristics Omomyidae resemble plesiadapiform primates, and some of the smaller, insectivorous and frugivorous phalangeoid marsupials. The latter, along with *Tarsius*, may be the best living models for omomyids. As in phalangeroids, some omomyids have unusually modified pointed or bladelike lower fourth premolars (see especially *Tetonius*, *Absarokius*, and *Uintanius*).

Sensory adaptations

A reconstruction of the skull of *Necrolemur* is illustrated in fig. 3-4. Two additional genera of Omomyidae, *Tetonius* and *Rooneyia*, are also known from nearly complete skulls. All three genera have a skull with a short, tapered snout. The infraorbital foramina are small, resembling those in extant lemuriform primates in relative size, indicating that nerves and blood vessels supplying the

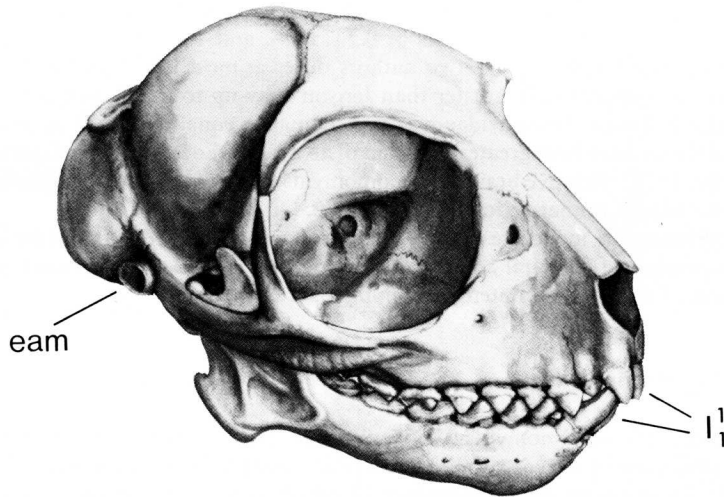


Fig. 3-4: Composite reconstruction of the skull of *Necrolemur antiquus*, an omomyid from the late Eocene of Europe. Note the enlarged, procumbent, pointed central incisors (I_1^1) in this genus. Note also the tubular external auditory meatus (*eam*), the large orbit indicating nocturnality in this species, and the very small infraorbital foramen visible below and in front of the orbit. Figure approximately 3× natural size. Reproduced from Simons and Russell (1960) by permission of the authors and the Museum of Comparative Zoology, Harvard University.

upper lip, rhinarium, and facial vibrissae were reduced by comparison with generalized mammals (Kay and Cartmill, 1977). However, it is possible that omomyids retained well-developed vibrissae and perhaps even a naked rhinarium not seen in *Tarsius* or extant simiiform primates (Cartmill and Kay, 1978).

The relative size of the orbit (orbital diameter compared to cranial length) in *Necrolemur* is comparable to that of extant nocturnal prosimians, while *Rooneyia* has orbits consistent in size with those of diurnal prosimians (Kay and Cartmill, 1977). Orbital convergence is about 55° in both of these genera, and the orbits of *Rooneyia* are somewhat more frontated than those of *Tetoniuss*. The relative size of the orbit in *Tetoniuss* is more difficult to estimate, due to deformation of the cranium, and its diurnal or nocturnal preferences remain ambiguous.

The morphology of the brain in Omomyidae has recently been reviewed by Radinsky (1977, 1979). Natural endocasts of the brain are preserved in skulls of *Tetoniuss*, *Necrolemur*, and *Rooneyia*. *Tetoniuss* has a more expanded neocortex (especially in the occipital and temporal regions) than is characteristic of most insectivores. The brain of *Tetoniuss* has a relatively small frontal lobe compared to that of modern prosimians. The olfactory bulbs also appear to be relatively small, and the neocortex is unconvoluted except for the faint impression of a sylvian fissure. The brain of *Necrolemur* appears to have been relatively larger than that of *Tetoniuss*, but was structurally similar. The brain of *Rooneyia* is more advanced than that of either *Tetoniuss* or *Necrolemur* in being larger, having a relatively larger frontal lobe, and having relatively smaller olfactory bulbs. The only convolution in the neocortex of *Rooneyia* is the sylvian fissure (Hofer and Wilson, 1967; cf. Stephan, this volume).

Relative brain size can be calculated when brain weight and body weight are known, using Jerison's (1973) encephalization quotient ($EQ = E / 0.12 P^{2/3}$ (where E = estimated brain weight in g, P = estimated body weight in g). This encephalization quotient is adjusted so that an average living mammal has an EQ = 1.0. Extant tree shrews have an EQ of about 1.0; and EQ ranges from about 1.1–1.4 in *Tarsius* (Jerison, 1973). Endocranial volume (and hence brain weight) can be estimated relatively easily in crania like those of *Tetoniuss*, *Necrolemur*, and *Rooneyia* in which a natural endocast of the brain is preserved. Estimation of body weight is more difficult and this has led to some disagreement. Radinsky (1977) calculates EQs of 0.42 in *Tetoniuss*, 0.79 in *Necrolemur*, and 0.97 in *Rooneyia*, while Jerison (1979) gives values of 0.71, 0.94, and 1.23, respectively, for these three genera. Brain weights estimated by the two authors differ at most by 7%, while Radinsky's body weight estimates are systematically greater than Jerison's, by up to 216% in the case of *Tetoniuss*. Relative brain size in Eocene Omomyidae was approximately equal to that of an average mammal living today, and it may have been greater than that of an average Eocene mammal (Jerison, 1973; but see also Radinsky, 1978). Relative brain size in omomyids appears to have been greater than that of contemporaneous adapid primates (for which EQ = 0.4–0.6; Jerison, 1979).

Small infraorbital foramina, moderate to large convergent orbits, and reduction of the olfactory bulbs coupled with expansion of occipital and temporal neocortex are all characteristics consistent with visual domination of the sensory system in Omomyidae.

Locomotor adaptations

The postcranial skeleton of Omomyidae is relatively poorly known. The most complete remains consist of associated parts of the vertebral column, pelvis, and hind limb of *Hemiacodon* described by Simpson (1940). Descriptions and illustrations of other postcranial remains of Omomyidae are included in Schlosser (1907, *Necrolemur*), Szalay (1976, *Teilhardina*, *Tetoniuss*, *Hemiacodon*), Savage and Waters (1978, *Arapahovius*, *Tetoniuss*), Schmid (1979, *Necrolemur*, *Microchoerus*), and Szalay and Dagosto (1980, genus not identified). As with skulls and dentitions, the preserved postcranial remains of omomyids are relatively uniform and stereotyped in morphology.

Appendix I

Primate body weights and tooth measurements used to calculate the regression and principal axis shown in fig. 3-1. Body weights (kg) from Harvey, Kavanagh, and Clutton-Brock (1978). Tooth measurements (mm) are length (L), and width (W) of first lower molars (M_1) from Swindler (1976).

Genus & species	Males			Females		
	Wt	M_1L	M_1W	Wt	M_1L	M_1W
<i>Tarsius sp.</i>	.14	2.97	2.42	.12	2.81	2.38
<i>Lepilemur mustelinus</i>	.61	3.50	2.25	.64	3.56	2.36
<i>Propithecus verreauxi</i>	3.70	7.00	4.97	3.50	6.69	4.66
<i>Nycticebus coucang</i>	1.30	3.40	2.90	1.20	3.40	2.90
<i>Perodicticus potto</i>	1.20	3.20	2.70	1.10	3.10	2.50
<i>Galago senegalensis</i>	.30	2.30	1.90	.30	2.20	2.00
<i>Galago crassicaudatus</i>	1.20	3.90	3.30	1.00	4.00	3.20
<i>Saguinus geoffroyi</i>	.50	2.80	2.30	.51	2.90	2.30
<i>Aotus trivirgatus</i>	.92	3.30	3.00	1.00	3.30	3.00
<i>Alouatta villosa</i>	7.40	7.10	6.00	5.70	6.80	5.70
<i>Alouatta seniculus</i>	8.10	7.58	5.93	6.40	7.20	5.50
<i>Saimiri sciureus</i>	.75	2.90	2.80	.58	2.90	2.80
<i>Ateles geoffroyi</i>	6.20	5.20	5.00	5.80	5.30	5.10
<i>Macaca nemestrina</i>	10.40	7.50	5.80	7.80	7.30	5.60
<i>Macaca fascicularis</i>	5.90	6.50	5.10	4.10	6.40	5.10
<i>Macaca mulatta</i>	8.20	7.20	5.60	7.50	7.70	5.50
<i>Cynopithecus niger</i>	10.40	7.10	5.30	6.60	6.60	4.90
<i>Cercocebus albigena</i>	9.00	6.88	5.67	6.40	6.49	5.33
<i>Cercocebus torquatus</i>	8.00	7.30	6.10	5.50	7.30	6.00
<i>Cercocebus galeritus</i>	10.20	7.40	6.40	5.50	7.00	5.90
<i>Cercopithecus aethiops</i>	5.00	5.88	4.49	3.75	5.59	4.19
<i>Cercopithecus cephus</i>	4.10	5.60	4.20	2.90	5.40	4.00
<i>Cercopithecus mitis</i>	7.40	6.20	4.60	5.30	6.00	4.50
<i>Cercopithecus neglectus</i>	7.00	6.30	4.60	4.00	5.90	4.50
<i>Cercopithecus nictans</i>	6.60	5.70	4.20	4.20	5.50	4.20
<i>Cercopithecus ascanius</i>	4.20	5.20	3.98	2.90	5.01	3.77
<i>Presbytis aygula</i>	6.30	5.50	5.00	6.20	5.40	4.70
<i>Presbytis cristatus</i>	8.60	6.12	4.86	8.10	5.98	4.88
<i>Nasalis larvatus</i>	17.70	7.30	5.70	10.00	6.90	5.30
<i>Colobus badius</i>	10.50	7.20	5.20	5.80	7.10	5.20
<i>Colobus polykomos</i>	10.40	7.20	5.70	8.40	7.00	5.50
<i>Hylobates moloch</i>	6.00	6.40	5.20	5.70	6.20	4.90
<i>Hylobates agilis</i>	6.00	6.00	5.10	5.70	6.00	5.20
<i>Hylobates klossii</i>	5.90	6.00	4.80	5.70	5.80	4.70
<i>Pongo pygmaeus</i>	69.00	13.40	11.90	37.00	11.40	11.30
<i>Pan troglodytes</i>	43.90	11.00	10.20	31.50	10.80	9.60
<i>Gorilla gorilla</i>	160.00	16.20	13.70	93.00	15.40	13.20

Proximal and distal ends of the femur are preserved in *Hemiacodon*; the head is somewhat cylindrical and the patellar groove high and narrow (Simpson, 1940; Napier and Walker, 1967; Szalay, 1976) as in *Tarsius*. The tibia and fibula are fused distally (but not proximally) in *Tarsius* and the fibula is much reduced in diameter compared to the tibia. These characteristics have been reported in both *Necrolemur* (Schlosser, 1907) and *Nannopithec* («*Pseudoloris*,» Weigelt, 1933; see also Simons, 1961a, p. 53). Only the proximal end of the tibia is preserved in *Hemiacodon*. The calcaneus and navicular are both elongated in Omomyidae, as in *Tarsius*. The calcaneus is known in *Arapahovius*, *Hemiacodon*, *Microchoerus*, *Nannopithec*, *Necrolemur*, *Teilhardina*, and *Tetonius*. In these genera the portion anterior to the tibial axis varies in length from two (*Arapahovius*, *Hemiacodon*) to three (*Necrolemur*) times that found in generalized primates (cf. Jouffroy *et al.*, this volume). In *Tarsius* the segment in front of the tibial axis is approximately four times the length of that in a generalized primate. The navicular in omomyids is correspondingly elongate.

The entocuneiform and first metatarsal of *Hemiacodon* articulated in a broad saddle joint, like that of *Tarsius*, permitting rotation and extreme abduction of the hallux. A greatly enlarged tubercle on the first metatarsal for insertion of *m. peroneus longus* indicates that the hallux was also capable of very powerful grasping in *Hemiacodon*.

Taken together, these characteristics indicate that *Hemiacodon* was arboreal and probably practiced some form of specialized vertical clinging and leaping locomotion (Napier and Walker, 1967; Walker, 1973). The marked calcaneal elongation seen in all other omomyid genera for which foot bones are known further suggests that this specialized foot structure, mode of locomotion, and arboreality was probably shared by all members of the family.

Social adaptations

Very little can be said at present about social adaptations in Omomyidae. In my experience, omomyid fossils are never found in associated groups representing single species as, for example, fossil horses sometimes are. There is thus no positive evidence to suggest that omomyids lived in social groups. On the other hand, being arboreal, it is possible that omomyids would rarely die in groups and be preserved together even if they lived in groups.

By comparison with Eocene Adapidae, omomyids are conspicuous in lacking sexual dimorphism and this has implications for understanding their behaviour and social adaptations. Judging from their small body size, insectivory, arboreality, and nocturnality, Omomyidae clearly fall into Crook and Gartlan's (1966) primate adaptive «Grade I.» This grade includes genera such as *Microcebus*, *Cheirogaleus*, *Phaner*, *Galago*, *Aotus*, and *Tarsius* (Niemitz, 1979a), all of which are typically solitary or live in pairs (for discussion see chapter 8). There is little differentiation of social roles and little or no sexual dimorphism. Reproductively, Grade I primates are monogamous or live in dispersed and poorly defined reproductive groups. All of these characteristics probably apply to Omomyidae. For monogamy and social organisation of the extant species see MacKinnon and MacKinnon (in press), Niemitz (1979b) and chapter 8.

Omomyidae in time and space

In addition to their morphological, ecological, and behavioral characteristics, the temporal and spatial distribution of Omomyidae is important for understanding their paleobiology.

Origin of Omomyidae

The earliest Omomyidae appear in Europe at Dormaal (Belgium), in Asia at Tsagan Khushu (Mongolia), and in North America at several localities in the Clark's Fork and Bighorn Basins (Wyoming). The earliest omomyid in North America, *Tetonoides tenuiculus* (or *Teilhardina*

americana), appears in the early Eocene at the beginning of the Wasatchian land-mammal age, which is well defined faunally and corresponds to a radiometric age of about 53 Ma (million years before present; Gingerich, 1980). The earliest omomyid in Europe (*Teilhardina belgica*) also appears in the early Eocene (Sparnacian), but at possibly a slightly earlier time, dated radiometrically at about 53.5 Ma, which may be equivalent to the North American late Clarkforkian land-mammal age (Godinot *et al.*, 1978; Godinot, 1981). The earliest omomyid in Asia (*Altanius orlovi*) appears in the early Eocene in the highest part of the White Beds of the Naran Bulak Formation in a fauna that is possibly also a temporal equivalent of the North American late Clarkforkian (Dashzeveg and McKenna, 1977). No precursors of Omomyidae are known in the well sampled middle and late Paleocene mammalian faunas of North America, and it is unlikely that omomyids originated in North America. The latest Paleocene and early Eocene represents an interval of significant worldwide climatic warming (Wolfe, 1978), and it is more likely that omomyids originated in the late Paleocene in more tropical latitudes and environments to the south of those sampled in Europe or Asia. An African or South Asian origin of Omomyidae from a *Purgatorius*-like Paleocene ancestor is likely.

Diversification

Omomyidae reached their maximum known diversity in North America during the middle Eocene (about 8–9 lineages) and in Europe during the late Eocene (about 5 lineages). By the end of the Eocene only two lineages are known in North America and two are known in Europe. Asian micromammalian faunas are not yet sufficiently well sampled to permit any estimation of omomyid diversity during the Eocene in Asia. The very high degree of endemism of European and North American Omomyidae during most of the Eocene, following an initial faunal exchange in the early Eocene, is undoubtedly due to rifting of the North Atlantic Ocean causing complete separation of these two continents by ocean for the first time in the Cenozoic.

It is interesting to note that Eocene lemuriform primates (Adapidae) reached a greater diversity in Europe than in North America, complementing the pattern seen in Omomyidae. Since Adapidae are larger and inhabited the frugivorous-folivorous side of Kay's threshold (discussed above), this inverse relationship of adapid diversity relative to that of smaller Omomyidae is probably not simply an historical accident and it must reflect some difference in ecological conditions in Europe and North America during the Eocene.

Diversity in both Omomyidae and Adapidae generally follows the pattern of climatic warming and cooling and of climatic equibility during the Eocene; diversity was highest during the warmest parts of the middle and late Eocene (Wolfe, 1978).

Extinction of Omomyidae

One of the most important events in the Cenozoic was a rapid decrease in mean annual temperatures worldwide in the early Oligocene (Eocene-Oligocene boundary of some authors; Buchardt, 1978; Wolfe, 1978). Increasing seasonality accompanied this change, and the effect on mammalian faunas was marked. A major faunal turnover occurred in Europe known as the *Grande Coupure* (Stehlin, 1909), after which a diverse representation of modern families of rodents first appeared. No Omomyidae are known in Europe after the *Grande Coupure*. It is almost certain that they were replaced ecologically by rodents, which are morphologically and reproductively better suited to temperate, seasonal, and unstable environmental conditions. Rodents feed predominantly on seeds and grains that are less perishable and less seasonal in their availability than insects and fruits. Rodents typically have more and larger litters with less parental investment than primates do, which is also advantageous in unstable environments.

The only omomyid to reappear at all after the early Oligocene cooling event was *Ekgmowechashala*, which is known from a very short interval of the late Oligocene (23.5 Ma) in the Western Interior of North America. Presumably it survived most of the Oligocene evolving in a subtropical or tropical

Central American habitat and reinvaded North America during a brief warm interval near the end of the Oligocene.

The extinction of Omomyidae is almost certainly a «pseudoextinction» in that this is the group from which Tarsiidae evolved. However, by the end of the Oligocene all known genera that are classified as omomyids had become extinct. Living *Tarsius* is the only relict of what was formerly a diverse evolutionary radiation and an important component of Eocene mammalian faunas.

Summary

As presently known, Omomyidae range from early Eocene to late Oligocene in age, a temporal span of about 30 million years. During the Eocene, omomyids became diverse in North America, Europe, and possibly Asia. Omomyidae range in body weight from an estimated 10 g in the smallest species to 550 g in the largest species. Judging by their body size and dental morphology, omomyids were insectivorous and frugivorous. They were apparently visually oriented and at least partly nocturnal, vertical-clinging-and-leaping, arboreal primates with moderately developed brains. Omomyids apparently were not sexually dimorphic, and lived in monogamous or dispersed and poorly defined reproductive groups. *Tarsius* is the best living model for omomyids and it is probably their only living descendant.

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