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The Distal Tibia of Primates with Special Reference to the Omomyidae

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The morphology of the distal tibia and its joint surfaces is described in the late Eocene European Necrolemur, *the middle Eocene North American* Hemiacodon, *and an omomyid species from the lower part of the Bridger Formation of North America.* Necrolemur, *like* Tarsius, *exhibits tibiofibular fusion, although to a less advanced degree. The Bridger omomyids, however, show no evidence of fusion but are similar to galagos in the conformation of this joint. The distal tibia of euprimates is distinguished by several derived features. These correlate with derived features of the astragalus and are functionally related to the abduction of the foot that accompanies dorsiflexion in primates.* Tarsius, *omomyids, and anthropoids share a suite of features which distinguish them from strepsirhines; these* may *be haplorhine synapomorphies, but the polarity of these features is difficult to determine. If they are synapomorphies, abduction accompanying dorsiflexion and movement at the inferior tibiofibular joint were restricted in ancestral haplorhines. In living primates such restriction is associated with small body size and saltatorial locomotion.*

KEY WORDS: tibia; ankle joint; primates; Omomyidae.

INTRODUCTION

The great numbers and diversity of omomyid dentitions thus far recovered prove that these extinct primates "once flourished in spectacular

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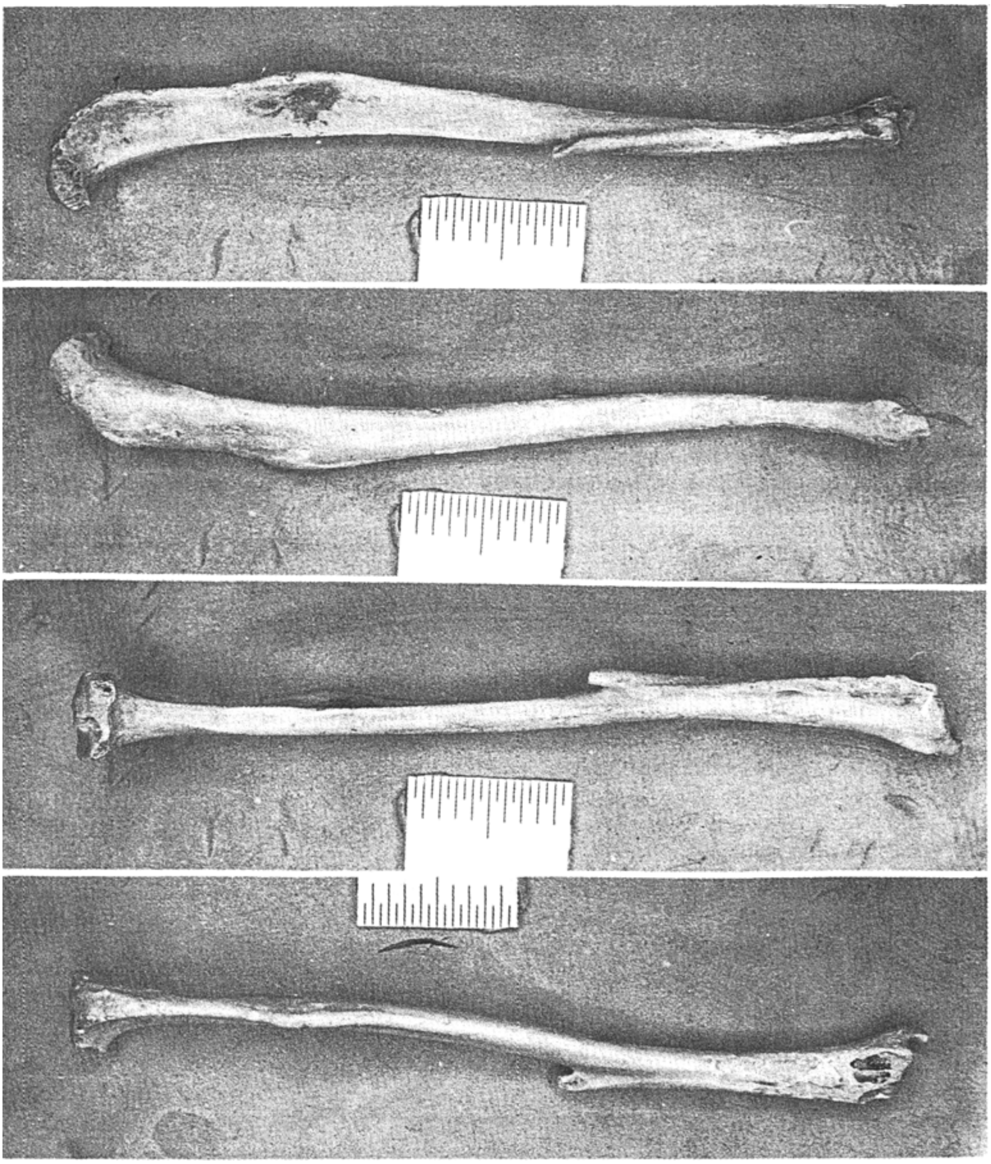

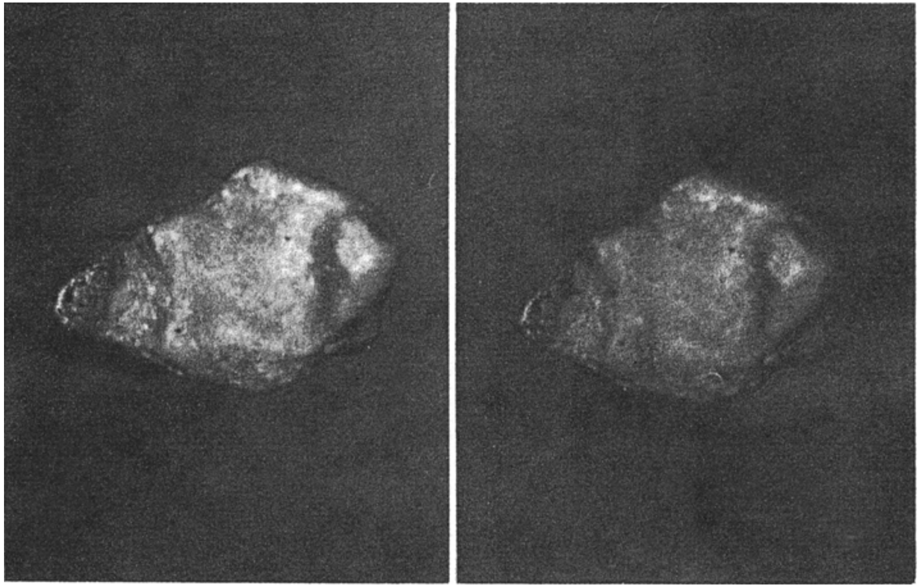

Fig. 1. Tibiofibula of late Eocene *Necrolemur* from the Bayerisches Staatsammlung fur Paläontologie, Munich (Schlosser, 1907). Top (left to right): anterior, posterior, medial, and lateral view. Bottom: inferior (stereopair) views. Scale in millimeters.

variety and abundance" (Szalay and Delson, 1979, p. 199). Compared to this wealth of dental remains, the postcranial anatomy of omomyids is poorly known. To date, the most complete omomyid postcranium is that of *Hemiacodon gracilis* (Simpson, 1940), represented by most of the hind limb. Some postcranial elements are known for microchoerines (Schlosser, 1907; Weigelt, 1933; Schmid, 1979; Szalay and Dagosto, 1980; Godinot and Dagosto, 1983), and Wortman (1903), Teilhard de Chardin (1927), Savage and Waters (1978), and Szalay (1976) have described foot bones of some nonmicrochoerine omomyid genera. This paper offers a description and comparative analysis of some previously unremarked aspects of distal tibial morphology in *Necrolemur,* in *Hemiacodon,* and in other unallocated North American middle Eocene omomyids.

MATERIALS

Primate tibiofibulae from the Phosphorites du Quercy deposits of France (Fig. 1) have been described by Schlosser (1907), Schmid (1979), and Godinot and Dagosto (1983). A similar, previously undescribed specimen (Fig. 2) is housed in the Musée d'histoire Naturelle, Montauban. All of these specimens are about as big as, or a bit smaller than, a tibiofibula of *Tarsius.* Schlosser (1907) referred his material to *Necrolemur antiquus.* This is a reasonable generic assignment, since the other microchoerine genera from the Phosphorites are either too small (*Pseudoloris*) or too large (*Microchoerus*) to be associated with these tibiofibulae. However, two similar-sized species of *Necrolemur, N. zitteli* and *N. antiquus,* have been reported from Phosphorites collections, and assignment of unassociated limb bones to one or the other of these species is not warranted at present. More controlled recent excavations (Crochet *et al.*, 1981) have yielded material that may resolve this question.

The tibia of *Hemiacodon gracilis* is represented by AMNH[2] 29158, the distal third of a right tibia, with the medial malleolus broken off (Fig. 3). This tibia is allocated to *Hemiacodon* on the basis of its size (approximately that of *Galago senegalensis*) and its provenance [LSV-H Ridge C, an Upper Bridger site (West 1976)]. The tibia of another middle Eocene North American omomyid is represented by one proximal end and two distal ends which are probably the right and left tibiae of the same individual (Fig. 4). These specimens, collected in 1965 by C. L. Gazin from Little Dry Creek,

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[2] Abbreviations used: AMNH, American Museum of Natural History; USNM, United States National Museum, Smithsonian Institution; UWA, Thomas Burke Memorial Washington State Museum.

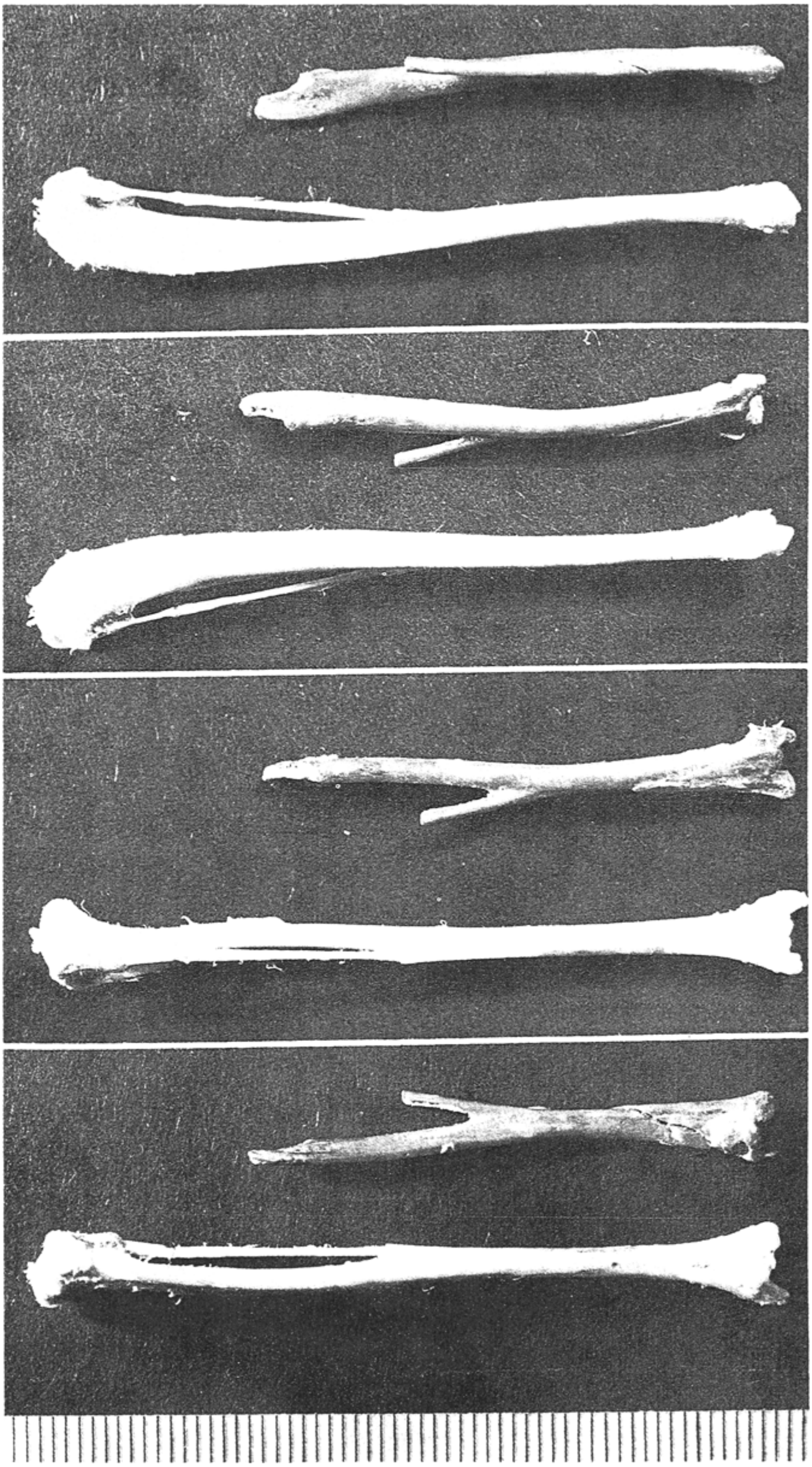
Grizzly Buttes, Bridger Formation, level B, are almost identical in size to AMNH 29158. Other omomyid postcranial bones from the same collection (a proximal tibia, USNM 336188, and the proximal part of a first metatarsal, USNM 336191) are slightly smaller than known *Hemiacodon* material in size but resemble *Hemiacodon* in morphology. A USNM (uncatalogued) omomyid calcaneum collected at a different time, but also from Grizzly Buttes, measures 13 mm in length, compared to 15–19 mm for *Hemiacodon*. These data suggest that the Grizzly Buttes omomyid is an animal similar in size to, or just slightly smaller than, *Hemiacodon*. Neither of the known Grizzly Buttes omomyids (*Omomys carteri* and *Uintanius turriculorum*), however, is nearly *Hemiacodon*-sized, but they are closer to the much smaller *Tetonius*, judging by lower first molar modules and estimated body size (Table I). In fact, none of the known lower Bridger omomyids is as large dentally as *Hemiacodon*, with the possible exception of very large individuals of *Anaptomorphus westi* or *A. amplus*. Dental remains of *Hemiacodon* have never been recorded from lower Bridger beds, but there are several *Hemiacodon*-sized astragali and calcanea known from lower Bridger sites (unpublished specimens collected by Dr. R. West from Sage Creek, Trap, and East Hill localities). Given these limitations, it is impossible at this time to refer these lower Bridger tibiae (and the other material) to a known, dentally defined genus or species, although both *Hemiacodon* and *Anaptomorphus* are reasonable possibilities.

Additional postcranial remains of a large-sized lower Bridger (B level) omomyid are found in the collections of the UWA from Crooked Canyon and Mountain View localities, Wyoming. In addition to several astragali and calcanea, there is one distal half of a left tibia (Fig. 3).

IDENTIFICATION OF PRIMATE DISTAL TIBIAE: COMPARISON WITH OTHER EUTHERIANS

Despite the common assumption that the primate postcranium is "primitive" or "generalized," most of the limb bones of primates have distinctive, derived features or combinations of features related to unique locomotor adaptations. Euprimates in particular have dramatically transformed the tarsus and distal humerus from the primitive eutherian condition in response to the adoption of a distinctive form of arboreal locomotion involving a strong pedal grasp and a reliance on leaping (Decker and Szalay, 1974; Szalay and Decker, 1974; Szalay and Dagosto, 1980). The distal tibia of euprimates is also distinctive, reflecting the changes in astragalar structure and ankle function that characterize euprimates.

The form of the distal tibia was observed in members of most families of extant mammals and in all Paleocene and Eocene mammals with



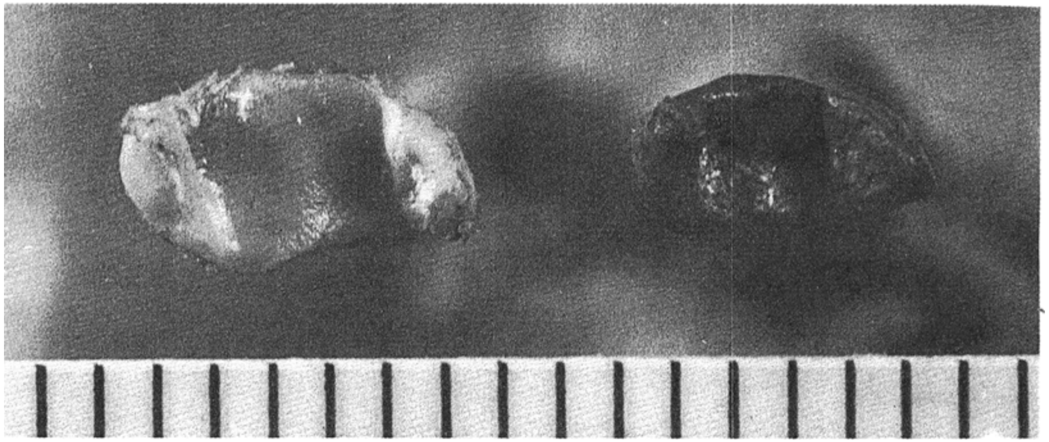


Fig. 2. Tibiofibula of *Necrolemur* from the Musée d'Histoire Naturelle, Montauban (right), and of *Tarsius* (left). Top (left to right): anterior, posterior, medial, and lateral views. Bottom: inferior view. Scale in millimeters.

Fig. 3. Distal tibiae of *Hemiacodon gracilis* AMNH 29158, upper Bridger (Middle Eocene, North America) (left of each pair), and unallocated omomyid UWA 36483 from Crooked Canyon, Wyoming (lower Bridger) (right). (A–D) Anterior, posterior, medial, and lateral views; (E) close-up of anterior aspect of USNM 36483; (F) close-up of lateral side of USNM 36483. Scale in millimeters. In D, the arrow points to a secondary (? ligamentous) attachment of the tibia and fibula.

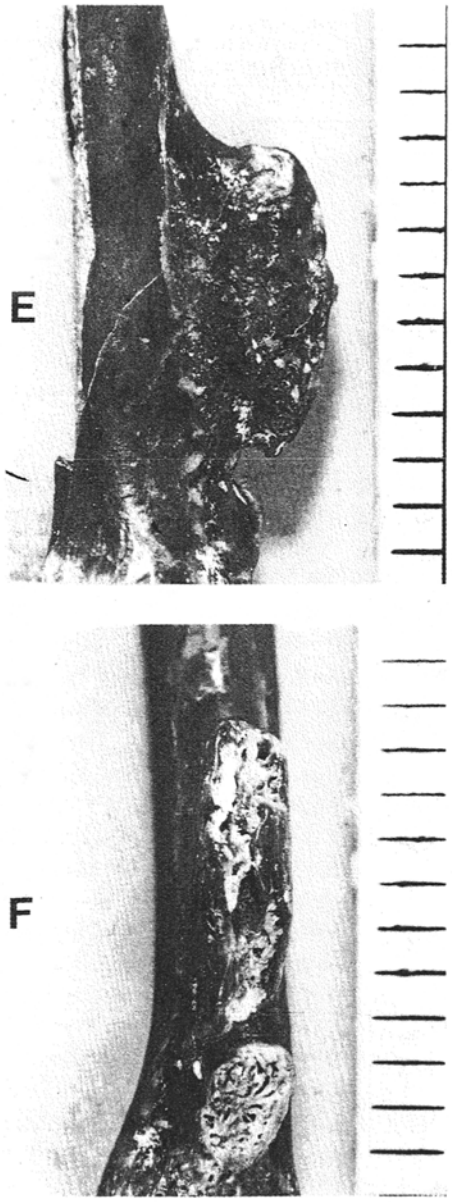


Fig. 3. Continued.

Table I. M_1 Module (Length × Width; mm^2) and Estimated Body Size (Based on a Tarsioid Regression Model) of Lower Bridger Omomyids (1–9) and Two North American Omomyids for Which Astragali Are Known (10–11)[a]

	M_1 module	Estimated body size
1. *Trogolemur myodes*	2.23	25
2. *Utahia kayi*	2.58	30
3. *Unitanius turriculorum*	3.35	45
4. *Washakius insignis*	3.56	50
5. *Omomys lloydi*	3.74	50
6. *Omomys carteri*	5.16	85
7. *Anaptomorphus aemulus*	4.80	75
8. *Anaptomorphus westi*	6.62	120
9. *Anaptomorphus amplus*	(no M_1)	120
10. *Hemiacodon gracilis*	10.49	240
11. *Tetonius homunculus*	4.95	85

[a] Data are from Gingerich (1981).

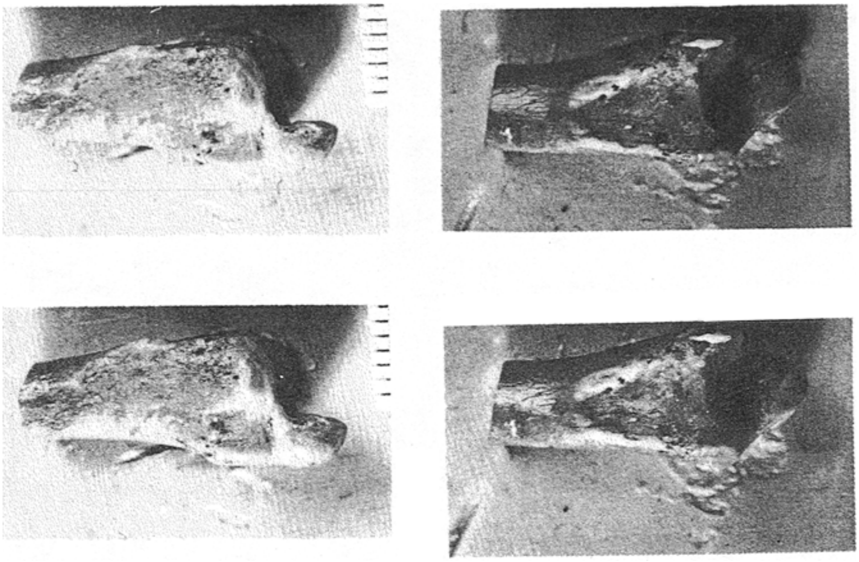
associated postcranial bones. The distribution of character states discussed in this paper is summarized in Tables II and III, and illustrations of selected specimens are presented in Figs. 6 and 7. In the majority of nonprimate eutherians, the medial malleolus is of moderate extent inferiorly and is aligned on a parasagittal plane so that its nearly flat articular surface [for the medial astragalotibial joint (ATiM)] faces directly laterally. (Anatomical abbreviations used here are defined in the legend to Fig. 5.) The articular surface for the lateral astragalotibial joint [ATiL(Ti)] is wider (mediolaterally) than long (anteroposteriorly). The posterior edge of the distal tibia slants anteriorly, so that the anterior and posterior edges converge laterally. The tibia of the ancestral eutherian is also likely to have had an ATiL(Ti) which was fairly flat with no pronounced anterior or posterior processes. The condylarth *Loxolophus* and the carnivoran *Miacis* exhibit most of these primitive eutherian conditions (Figs. 6A and B). That these features are likely to have been part of the primitive eutherian morphotype is supported not only by their wide distribution within eutherians, but also by the fact that relatively primitive eutherian groups such as condylarths, creodonts, and some insectivorans (e.g., *Tenrec, Erinaceus*) exhibit most of these features. Astragali of *Protungulatum* and *Cimolestes,* animals with primitive eutherian astragalar structure (Szalay and Decker, 1974; Szalay, 1977), exhibit anatomical features which suggest that their tibiae also fit this description.

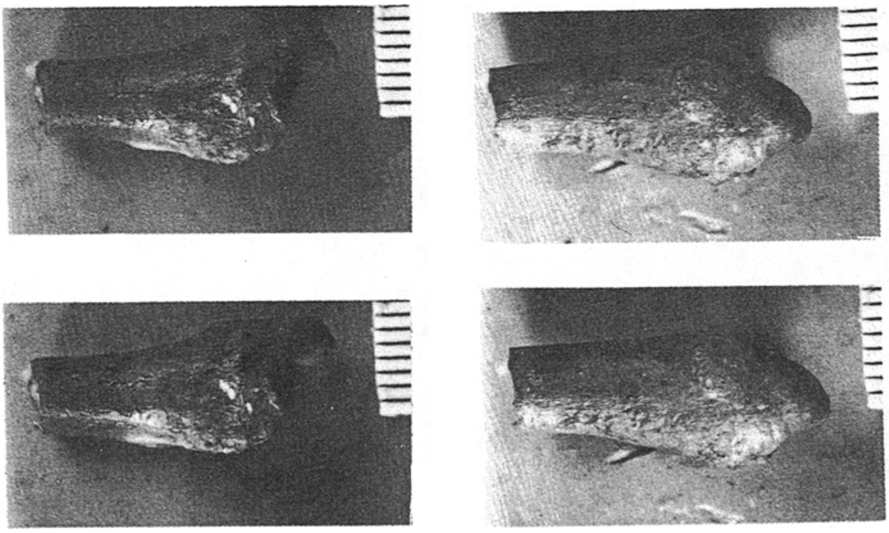
The remains attributed to primates in this paper were carefully compared with their homologs in Eocene mammals of similar size. Most Eocene fossil "insectivores" (erinaceids, adapisoricids, nyctitheriids, palaeoryctids, and apatemyids) are not represented by postcranial remains, but the distal tibia of those that are (pantolestids, Oligocene leptictids) is quite similar to that of living insectivorans (except *Erinaceus*) and differs from the eutherian morphotype mainly in the marked depth of the grooves for the

Table II. Distribution of Features of the Distal Tibia Discussed in this Paper in Some Mammalian Taxa[a]

Feature	Primitive eutherian condition	Strepsirhini	Tarsiiformes	Anthropoidea	Rodentia	Insectivora	Creodonta, Carnivora
Inferior tibial facet	Flat	Moderate grooving	Moderate grooving	Moderate grooving	Marked grooving	Variable grooving	Variable grooving
ATiL(Ti)	ML exceeds AP	AP exceeds ML	AP exceeds ML	AP equals or exceeds ML	Variable, AP exceeds ML	ML usually exceeds AP	ML exceeds AP
	Anterior and posterior edges converge laterally	Ant. and post. edges diverge laterally	Ant. and post. are parallel	Ant. and post. are parallel	Ant. and post. are parallel	Ant. and post. are parallel	Ant. and post. converge laterally
Medial malleolus	Short inferiorly	Long inferiorly	Long	Long	Short or absent	Short or absent	Short
	Aligned on a parasagittal axis	Marked medial rotation	Moderate medial rotation	Moderate medial rotation	Parasagittal	Parasagittal	Parasagittal
	Flat ATiM(Ti)	Convex ATiM(Ti)	Convex anteriorly, flat posteriorly	Convex anteriorly, flat posteriorly	Flat	Flat	Flat
Groove for tibialis posterior	Runs on the medial side of the malleolus	Runs on the inferior edge of the malleolus	Medial or inferior	Mixed	Medial	Medial	Medial
Posterior process	Absent	Absent (except indriids)	Absent	Absent	Present	Usually present	Variable
Anterior process	Absent	Present	Present	Present	Present	Usually present	Present
Distal tibio-fibular joint	Syndesmosis	Synovial	Synostosis or syndesmosis	Synovial or syndesmosis	Syndesmosis or synostosis	Syndesmosis or synostosis	All types

[a] See also Figs. 3, 4, and 5 and Table III. Some data are from Ford (1980), Carleton (1941), and Barnett and Napier (1953).





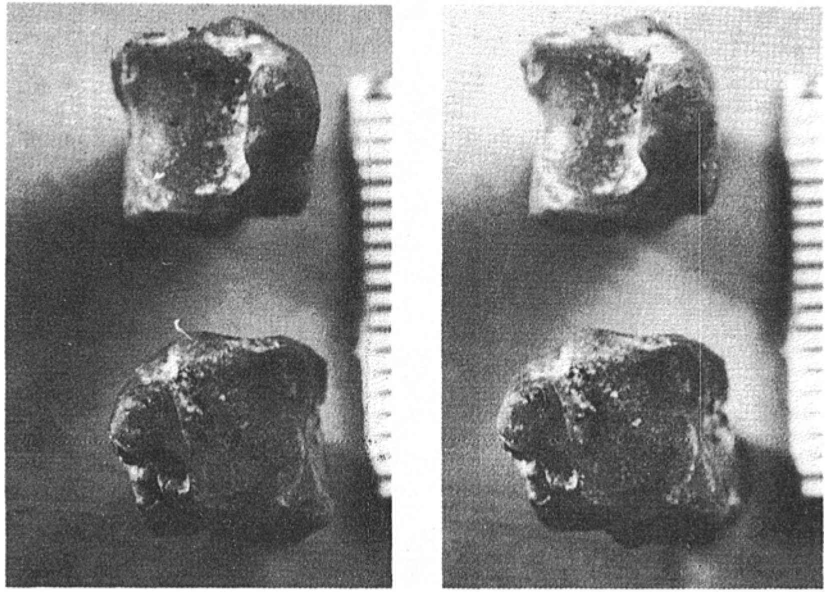


Fig. 4. Omomyid right distal tibiae from Grizzly Buttes, Middle Eocene, North America, USNM 336190. Top row from left to right, anterior and posterior views; middle row, medial and lateral views; bottom row, inferior view of USNM 336190 (top) and USNM 336189 (bottom). All stereopairs, scale in millimeters.

Table III. Index of Relative Length and Width of ATiL(Ti) (AP/ML) and Degree of Malleolar Rotation Measured in Degrees for Some Primates and Other Mammals[a]

Taxon	*N*	AP/ML	Range	*SD*	Malleolar rotation	Range	*SD*
Lemur fulvus	5	128.94	124.29-128.21	3.1	38	35-40	2.7
Propithecus verreauxi	3	128.55	125.26-133.33	4.2	36	22-45	12.1
Galago demidoviii	5	114.34	100.00-120.00	8.3	26	20-30	5.1
Perodicticus potto	3	151.34	147.62-150.00	4.2	41	37-45	5.6
Smilodectes gracilis AMNH 11478	1	125.71	–	–	35	–	–
Pelycodus AMNH 4717	1	142.65	–	–	30	–	–
Tarsius	5	111.96	105.5-120.69	5.5	13	10-15	2.4
Necrolemur (Montauban)	1	129.17	–	–	20	–	–
North American omomyids							
USNM 336190		131.25	–	–	12	–	–
USNM 336189		126.47	–	–	15	–	–
AMNH 21589		120.58	–	–	–	–	–
UWA 36483		118.18	–	–	21	–	–
Saimiri sp.	6	117.00[b]	106.00-123.00	–	23	17-30	5.4
Cebus apella	6	112.55	108.43-117.72	3.3	26	25-30	2.2
Cercopithecus aethiops	6	106.73	96.55-118.99	8.1	34	30-40	4.7
Presbytis	4	106.92	100.74-118.52	8.1	27	20-35	6.4
Pan troglodytes	6	105.59	96.31-115.59	6.8	34	30-40	3.8
Plesiadapis gidleyi AMNH 17379	1	99.99	–	–	0	–	–
Tupaia glis	2	90.54	88.23-93.75	–	12	10-14	–
Arctocyon ferox AMNH 16542	1	91.25	–	–	0	–	–
Loxolophus hyattianus AMNH 16343	1	92.86	–	–	0	–	–
Miacis parvivorus AMNH 11496	1	96.49	–	–	0	–	–
Vulpavus sp.	2	85.55	83.33-87.77	–	10	10-10	–
Paramys delicatus AMNH 11592	1	137.45[c]	–	–	0	–	–

[a] AP/ML is the anterior-posterior length of the ATiL(Ti) × 100 divided by the mediolateral width of the ATiL(Ti). See Figs. 3C and D. After Ford (1980). In Ford's work the AP dimension was called width (FW) and the ML dimension was called length (FL). The terms are reversed here only to correspond to previous descriptions of the ATiL(A) as being "long" anterior-posteriorly and "narrow" mediolaterally (Szalay and Decker, 1974).

[b] Data from Ford (1980).

[c] Includes the large posterior process.

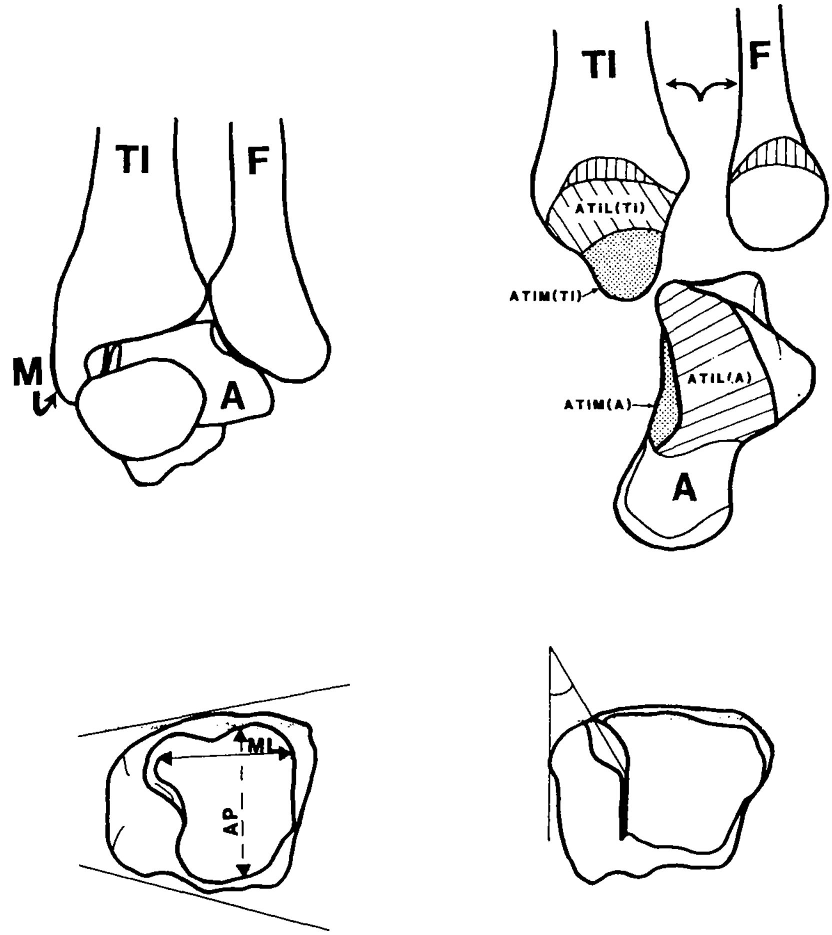


Fig. 5. Anatomical abbreviations used for features discussed in this paper (after Szalay, 1982). Top left, anterior view of left tibia (Ti), fibula (F), and astragalus (A), articulated in a position midway between full plantarflexion and dorsiflexion. M, medial malleolus. Top right, same as top left, but with the bones disarticulated. The tibia and fibula are rolled away from each other in the directions of the arrows and are also tilted anteriorly. The astragalus is plantarflexed from its previous position, so that its dorsal surface is visible. ATiL, lateral astragalotibial articulation (indicated by hatched surfaces on the tibia and astragalus); ATiL(A), articular surface on the dorsal surface of the astragalus for the ATiL; ATiL(Ti), articular surface on the inferior surface of the tibia for the ATiL; ATiM, medial astragalotibial articulation (indicated by stippled surfaces on the tibia and astragalus); ATiM(A), articular surface on the astragalus for the ATiM (on the medial side of the astragalus); ATiM(Ti), articular surface on the tibia for the ATiM joint (on the lateral face of the medial malleolus). The vertically lined surfaces on the tibia and fibula indicate the facets for the inferior tibiofibular joint. Bottom left, inferior view of the distal tibia of *Lemur*, illustrating AP and ML measurements of the ATiL(Ti) and divergence of the anterior and posterior edges. Bottom right, inferior view of the distal tibia of *Saimiri*, illustrating how malleolar rotation was measured.

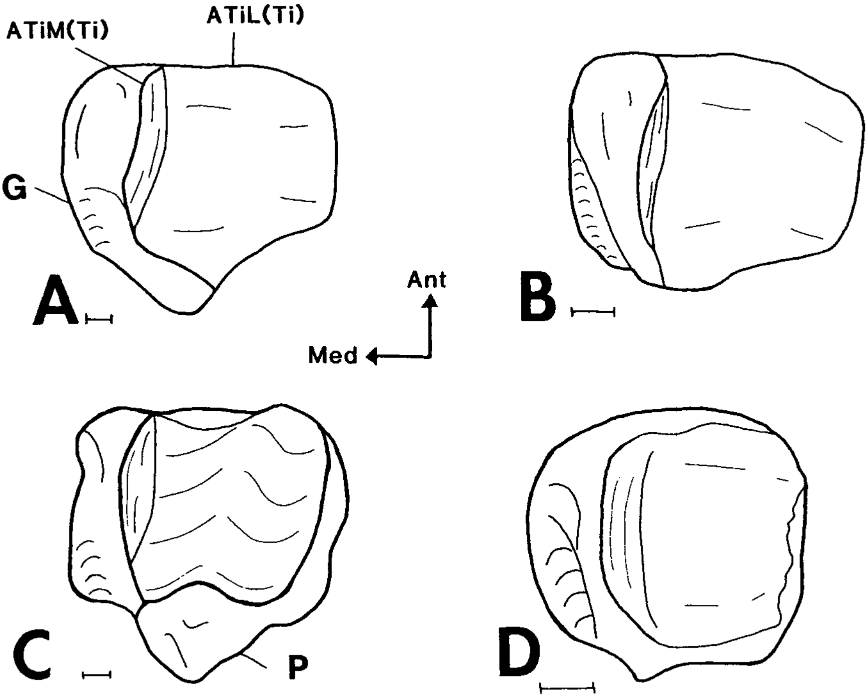


Fig. 6. Inferior view of the left distal tibiae of various mammals. Scales represent 1 mm. (A) The condylarthran *Loxolophus hyattanius,* AMNH 16343 (Puercan); (B) the carnivoran *Miacis parvivorus,* AMNH 11496 (Bridgerian); (C) the rodent *Thisbemys,* AMNH 94062 (Bridgerian); (D) the primate *Plesiadapis gidleyi,* AMNH 17379 (Tiffanian). G, groove for tibialis posterior; Med, medial; Ant, anterior; P, posterior process.

high and sharp medial and lateral crests of the astragalar trochlea, the reduction or loss of the medial malleolus, and the presence of a prominent posterior process. These conditions are derived compared to a eutherian morphotype and are not commonly exhibited by any primate. Rodents are similar to insectivores, differing from primates in the same ways (Fig. 6C). Most creodonts and carnivorans examined have a distal tibia which is very like a primitive eutherian one. Advanced features, such as the degree of grooving of the inferior surface and the presence of a posterior process, are variable.

Other taxa compared with the fossil remains attributed to primates in this paper include extant and fossil marsupials, *Metachiromys, Hyopsodus,* and Eocene artiodactyls and perissodactyls, none of which resembles fossil or extant primates very closely. It is beyond the scope of this paper to detail tibial morphology of all mammalian groups. For descriptions and illustrations of tibiae and astragali of many of the taxa discussed above, the reader

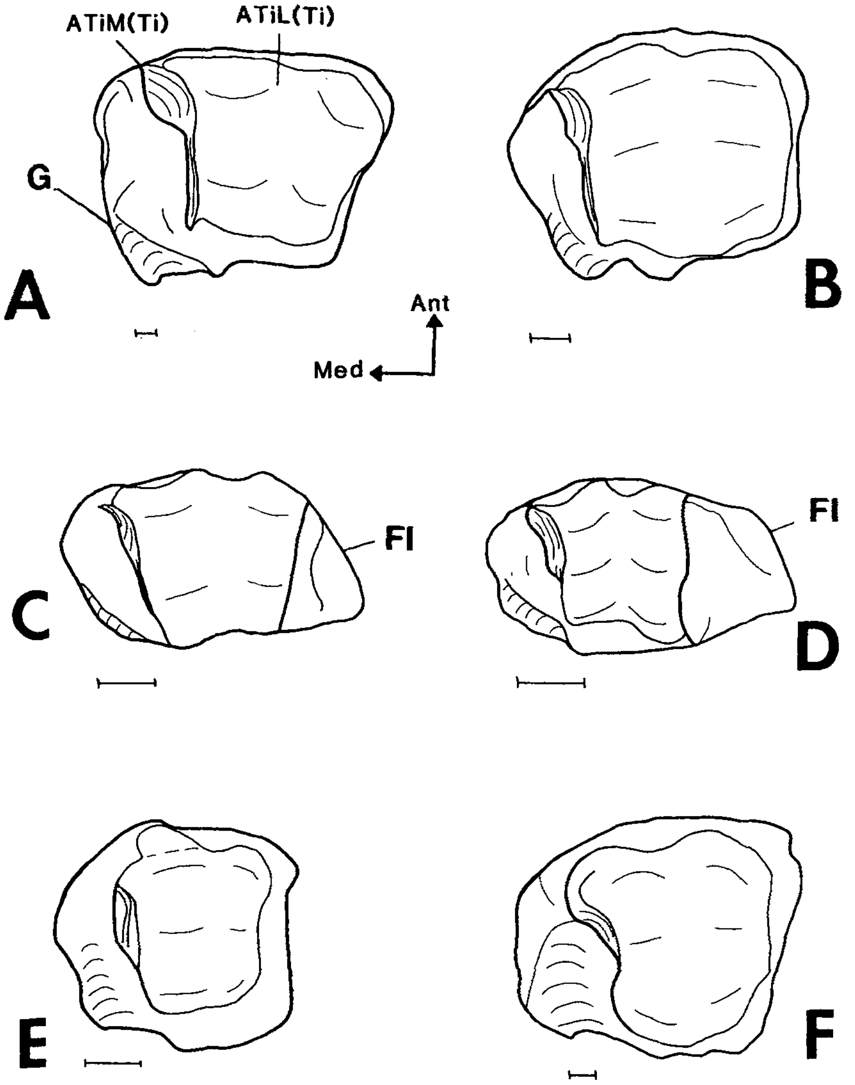


Fig. 7. Inferior view of left distal tibiae of some primates. Scales represent 1 mm. (A) *Cercopithecus aethiops*; (B) *Saimiri*; (C) *Tarsius*; (D) *Necrolemur* (unnumbered, Montauban); (E) Grizzly Buttes omomyid (USNM 336189); (F) *Lemur*. Abbreviations as in Fig. 4; Fl, fibula.

is referred to Gazin (1968), Matthew (1909, 1937), Schaeffer (1947), Szalay (1977), and Wood (1962). Szalay (1984) has discussed in detail the morphology, origin, and function of the upper ankle joint in metatherians and eutherians and also stresses the derived nature of the primate upper ankle joint.

THE TIBIOASTRAGALAR JOINT OF PRIMATES: MORPHOLOGY AND FUNCTION

The distal tibia of strepsirhine primates is quite different from that of any nonprimate eutherian. The entire articular surface of the medial malleolus [the ATiM(Ti)] of strepsirhine primates (including *Pelycodus, Notharctus, Smilodectes, Adapis,* and *Leptadapis*) is quite markedly medially rotated from its primitive laterally facing position; it faces approximately 30–40° from the sagittal plane (Fig. 7, Table III). The malleolus is concave proximally to accept the rounded border of the medial rim of the dorsal astragalus but then becomes convex in its distal part to articulate with the concave ATiM(A), which ends in a marked cup on the posterior aspect of the astragalar neck. The anterior and posterior edges of the distal end of the tibia diverge from each other, producing a triangle-shaped surface in which the anteroposterior dimension exceeds the mediolateral (Figs. 5 and 7, Table III).

In *Tarsius, Necrolemur,* and the Bridger omomyids, the "rotation" of the malleolus is less pronounced than in strepsirhines; its articular surface deviates only 10–15° from a parasagittal plane (Fig. 7, Table III). Although the anterior part of the ATiM(Ti) maintains a convex shape (in its most distal aspect) and exhibits medial rotation, the posterior part of the facet is flat and faces directly laterally. (The flat part of the facet is larger in *Tarsius* than in *Necrolemur, Hemiacodon,* or the lower Bridger omomyids.) This is associated with an ATiM(A) less concave than in most strepsirhines and with less exaggerated cupping on the astragalar neck. The anterior and posterior edges of the inferior tibial surface are nearly parallel.

Though variable, anthropoids are more like tarsiiforms than like strepsirhines (Fig. 7). Most anthropoid species exhibit a convex medial malleolus with only moderate rotation of the anterior part (20–30°); the posterior part is flat and faces laterally.

This survey of mammalian and primate distal tibiae suggests that there are several features which are present in most euprimates but are not commonly found in other eutherians and are thus considered to be derived for euprimates. These are a prominent, inferiorly long, pyramid-shaped medial malleolus with a distally convex, anterolaterally facing articular surface; an inferior joint surface which is as long (anteroposteriorly) as, or longer than, it is wide (mediolaterally) and which has laterally divergent or parallel anterior and posterior borders; and a distal tibiofibular joint with a synovial articular surface. In addition to these derived traits, the euprimate morphotype retains some primitive traits (grooving of the inferior tibial surface only moderate, lack of a posterior process, retention of a medial malleolus) which are usually modified in other mammalian orders.

Some archontans approach the conditions observed in euprimates. *Tupaia,* but not *Ptilocercus, Lyonogale,* or *Urogale,* also has a long, triangular medial malleolus which is distally convex and slightly rotated. In contrast to euprimates, however, the ATiL(Ti) is longer than wide (Table III). The ATiL(Ti) of *Galeopithecus,* like that of euprimates, is as wide as it is long but can be distinguished from that of euprimates by its virtually featureless surface; it lacks even the moderate degree of undulation found in euprimates. This reflects the low, rounded dorsal surface of the astragalus in living and fossil demopterans (Szalay and Drawhorn, 1980). The malleolus of *Galeopithecus* does not appear to be rotated, but it is difficult to judge given the torsion of the tibia in this genus. The ATiM(Ti) is not convex.

Associated postcrania of microsyopids are rare in the fossil record; however, Szalay and Drawhorn (1980) have described some tarsals which may be those of microsyopids. The morphology of the astragalus in these specimens suggests a dermopteran-like distal tibia.

The only plesiadapiform primate which preserves the distal tibia is *Plesiadapis gidleyi* (AMNH 17379). In describing this specimen, Simpson (1935) found that the medial malleolus was smaller than in *Lemur* and lacked the characteristic "hooklike" shape seen in other primates. The malleolus is indeed shorter inferiorly than is usual for euprimates and exhibits almost no convexity of its articular surface [indeed, the surface is mildly concave (Fig. 6D)]. The ATiM(Ti) faces wholly laterally, exhibiting no rotation. *P. gidleyi* does approach euprimates in one respect: its inferior tibial surface is nearly as long as it is wide (Table III). Astragali of *Plesiadapis* and *Phenacolemur* lack the curved, concave medial edge and cup-like medial malleolar stop of euprimates, so it is not surprising that they lack the correlated unique features of the medial malleolus listed above. Thus, despite the presence of some euprimate-like features in *Tupaia, Galeopithecus,* and *P. gidleyi,* it appears that the features listed above are euprimate, rather than archontan or primate specializations.

The derived euprimate features of the distal tibia are related to derived euprimate features of the astragalus. The longer-than-wide inferior tibial joint surface of euprimates reflects their relatively long and narrow trochlea [the ATiL(Ti)] (Szalay and Decker, 1974). In euprimates, the anterior and posterior borders of the inferior tibia are either parallel or diverge laterally, respectively, reflecting a trochlea which either has medial and lateral edges of equal length or has a longer lateral edge (due to the curvature of the medial edge). In most eutherians (and in the eutherian morphotype) the edges of the inferior tibia converge laterally. This morphology is associated with an astragalus in which the medial edge is generally longer than the lateral.

In euprimates, the path of travel of the tibia along the trochlea of the astragalus does not describe a straight line but curves medially as it progresses distally. The ATiM(A) facet is also curved medially and ends in a cup on the posterior aspect of the astragalar neck. These curvatures dictate that, as the astragalus moves from a plantarflexed to a dorsiflexed position, it also abducts relative to the tibia[3] (Hafferl, 1932; Lewis, 1980). The "rotation" and distal convexity of the tibial malleolus are, of course, other reflections of this curvilinear astragalotibial movement, allowing the medial side of the astragalus to rotate around the medial malleolus. In the dorsiflexed, abducted position, which is the close-packed position of the upper ankle joint in most primate taxa, the medial malleolus fits into the cup-like depression on the astragalar neck (Clark and Leakey, 1951; Lewis, 1980). Lewis (1980) has related this suite of features and their mechanical consequences to the biological role of grasping arboreal supports.

In the majority of other mammals and in the eutherian morphotype, the medial surface of the astragalar body is virtually flat (or may even be convex, as in *Protungulatum*) and so is the corresponding malleolar surface. The trochlea does not twist medially and the cup-like tibioastragalar stop is usually absent, so the ATiM(Ti) surface faces strictly laterally. The astragalus simply slides backwards on the tibia during dorsiflexion; the amount of conjunct rotation accompanying this movement is limited.

The differences in distal tibial morphology between strepsirhines and haplorhines likewise imply differences in the amount of conjunct rotation associated with dorsi- and plantarflexion at the upper ankle joint. The lesser

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[3] Lewis (1980) claims that the foot is also inverted when dorsiflexed, although it is not entirely clear whether he relates the inversion of the foot to a conjunct rotation accompanying tibioastragalar dorsiflexion. From manipulations of disarticulated bones and ligamentous preparations of *Lemur*, it appears that, as in humans, the astragalus rotates medially about its own long axis during movement from a plantarflexed to a dorsiflexed position. Thus if the foot is considered as a passive appendage to the astragalus, it must evert (or at least become less inverted) during dorsiflexion. Of course, any conjunct eversion that occurs during dorsiflexion can be compensated for by movements at the subtalar and transverse tarsal joints. It is not clear if movements at the upper ankle joint can occur independently of movements at these other two joints; for example, all muscles capable of dorsiflexing the foot at the ankle also work on more distal tarsal joints capable of pronating or supinating the foot.

degree of malleolar rotation in haplorhines (especially in *Tarsius* and omomyids) is no doubt related to the less exaggerated twisting of the astragalar trochlea, the less pronounced concavity of the medial tibioastragalar facet, and the shallowness of the cup-like tibioastragalar stop. This suggests that the amount of abduction (and any inversion or eversion) accompanying dorsiflexion due to these particular morphological factors[4] is less in haplorhines than in strepsirhines. Two additional lines of evidence support this hypothesis. The obliquity of the upper ankle joint axis (relative to the ground) of the Fayum primates as determined by Conroy (1976) appears to be less than that determined for *Notharctus* and *Propithecus* by Decker and Szalay (1974), suggesting that less movement out of a sagittal plane would accompany dorsiflexion in the Fayum forms. The second line of evidence is a functional argument from Hafferl (1932). Only the medial edge of the astragalus curves medially; the lateral edge is straight or flares laterally, therefore, some movement between the tibia and the fibula must accompany dorsiflexion, because during dorsiflexion the tibia rotates medially about its long axis (in relation to a stationary astragalus) while the fibula rotates laterally about its long axis (Barnett and Napier, 1952, 1953; Lewis, 1980; but see Reimann and Anderhuber, 1980). Obviously, in forms where movement between the tibia and the fibula is impossible because of fusion, or limited because of a syndesmosis, compensational displacement of the fibula is not possible. Therefore, the medial swing and rotation of the tibia during dorsiflexion must necessarily be limited (barring adjustments in the astragalofibular joint). Although there is variation in the degree of tibiofibular joint mobility within both strepsirhines and haplorhines, all strepsirhines exhibit a large, synovial distal tibiofibular articulation allowing rotatory or sliding movements between the two bones, while some haplorhines (*Tarsius*, omomyids, many small platyrrhines) exhibit a restricted syndesmosis or synostosis at this joint (Barnett and Napier, 1953; Carleton, 1941; Fleagle and Simons, 1983).

Insight into the probable adaptive significance of the differences in upper ankle joint structure between strepsirhines and haplorhines is gained by looking at the variation present within each group. Within strepsirhines it is the galagines (especially *G. senegalensis* and *G. demidovii*) that mimic the typical haplorhine conditions. Among haplorhines it is the larger monkeys and hominoids that generally have more marked malleolar rotation, medial curvature of the astragalus, and astragalar cupping. It appears

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[4] Displacements out of a sagittal plane could be produced by other means, for example, by the obliquity of the trochlea to the long axis of the foot (Barnett, 1955). However, this does not seem to be an important factor in primates.

that a morphological complex involving a minimal amount of rotation of the medial malleolar articular surface, less exaggerated medial curvature of the astragalar trochlea and medial tibioastragalar joint, and a relatively rigid inferior tibiofibular articulation, all of which limit dorsi- and plantarflexion to a sagittal plane, is found in small-bodied saltatorial primates. This combination of features is seen, in various degrees of expression, in *Galago, Tarsius, Necrolemur,* omomyids, *Saimiri,* and *Apidium.* The fact that this morphology is present in all known tarsiiforms, some platyrrhines, and some early anthropoids suggests that it is primitive for haplorhines and that the more strepsirhine-like conditions seen in other haplorhines (hominoids, for example) are modifications of this morphology, not primitive retentions from a strepsirhine ancestor.

However, the question of which condition (strepsirhine or haplorhine), if either, is primitive for euprimates is difficult to answer. Assuming that most other character states known for tarsiiform and anthropoid crania and postcrania are derived compared with the conditions seen in strepsirhines (Szalay and Delson, 1979), it seems likely that the upper ankle joint features of haplorhines are derived compared to a euprimate morphotype as well and that the features of the distal tibia shared by *Tarsius,* omomyids, and anthropoids are haplorhine synapomorphies. However, it is equally possible that the haplorhine condition is primitive for euprimates and that the strepsirhine conditions are derived, strepsirhine synapomorphies. This hypothesis is supported by the fact that the haplorhines differ less from the probable primitive eutherian condition (and the conditions seen in *Tupaia* and *Plesiadapis*) than do the strepsirhines. For example, it is difficult to imagine a transformation from no rotation of the medial malleolus (primitive) to a condition where the whole malleolus is strongly rotated (strepsirhines), without going through a stage where rotation was moderate (haplorhines). The partially flat ATiM(Ti) of haplorhines and the low AP/ML ratios of many anthropoids are additional features in which these groups are more like primitive eutherians than strepsirhines are. One would have to allow evolutionary reversals in all of these features if the hypothesis of a strepsirhine-like primitive euprimate condition were accepted. We know, however, that such transitions are possible since they have happened once before—in the galagines. From other postcranial remains, we know that all omomyids and some early anthropoids were, indeed, small, saltatorial forms in which we would expect such conditions to arise (Conroy, 1976; Fleagle and Simons, 1983; Szalay, 1976). Recourse to the fossil record does not help to resolve this issue, as both the earliest strepsirhines (*Pelycodus,* AMNH 4717) and the earliest omomyids (*Teilhardina,* the earliest omomyid for which an astragalus is known) already exhibit the conditions typical of their respective suborders.

OMOMYID DISTAL TIBIAE

The delineation of euprimate and haplorhine morphotypes for the distal tibia permits the secure identification of unassociated material in the fossil record.[5] The distal tibia is known in several omomyid genera. *Nannopithex* (Weigelt, 1933) was not examined in this study; the material is probably lost (Szalay, 1976). Savage and Waters (1978) attributed a distal tibia fragment to *Arapahovius gazini* but did not figure it or discuss its morphology. *Necrolemur* tibiofibulae were reported by Schlosser (1907), Schmid (1979), and Godinot and Dagosto (1983). Examination of the specimen published by Schlosser and the Montauban specimen confirms the allocation to primates (large, medially rotated distally convex medial malleolus, inferior surface longer than wide) and, in particular, to a haplorhine primate [moderate rotation of the malleolus, presence of a flat posterior part to the ATiM(Ti) facet, parallel anterior and posterior inferior tibial borders]. In addition to the features of the upper ankle joint discussed above (and those of the inferior tibiofibular joint, discussed below), the following characters can be noted. As in the majority of other primates, the anterior edge of the distal tibia extends more inferiorly than the posterior, and there is a pointed anterior process (Ford, 1980). There is, however, no articular facet on the anterior surface of this process in *Necrolemur*. It is also absent in *Tarsius* but present in the majority of primates (Ford, 1980). The shaft of the tibia just above the distal end is anteroposteriorly compressed, as in *Tarsius* [and atelines (Ford, 1980)]. This contrasts with the rounded shaft seen in the majority of primates. As in *Tarsius*, Fayum anthropoids, some platyrrhines, and most nonstrepsirhine mammals (Ford, 1980), the groove for the tendon of tibialis posterior is shallow and curves around the medial edge of the malleolus. *Necrolemur* differs from *Tarsius* (and most other primates) in the pronounced grooving of its inferior tibial surface, reflecting its high and sharp astragalar borders (Godinot and Dagosto, 1983). The AP/ML index (Table III) of 129 is typical for euprimates but is higher than in *Tarsius*, reflecting the longer, narrower trochlea of *Necrolemur* (Godinot and Dagosto, 1983). The proximal end and shaft of this tibia were described by Schlosser (1907).

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[5] This assumes the haplorhine condition to be derived. If the alternate hypothesis is accepted—i.e., that haplorhine morphology is persistently primitive euprimate morphology—then allocation of tibiae to dentally haplorhine taxa is less certain. In the case of *Necrolemur*, one could argue that the remains might be equally well attributed to a similar-sized dental adapid (e.g., *Huerzeleris*) that happened to preserve primitive euprimate tibial form (except for tibiofibular fusion). This hypothesis is made unlikely by the association of fused tibiofibulae identical to the ones under discussion at a site (La Bouffie) where only *Necrolemur antiquus* is known. In the case of the North American omomyids, no non-omomyid taxon of such small size is known in the Bridger.

The material attributed to the Grizzly Buttes omomyid is identified as primate on the basis of a prominent medial malleolus (exhibiting some medial rotation of its articular surface) and an inferior tibial surface which is longer than wide. In addition, the moderate degree of malleolar rotation, the presence of a flat, laterally facing posterior part of the ATiM(Ti) facet, and the parallel anterior and posterior borders of the inferior tibial surface mark these bones as haplorhine rather than strepsirhine. In this omomyid, as in the majority of euprimates (Ford, 1980), the anterior edge of the distal tibia projects further inferiorly than the posterior. The anterior process is present and bears a small articular facet medially. The shaft of the tibia just above the distal end is very rounded in cross section—a morphology not typical of *Tarsius* or *Necrolemur* but common in other primates (Ford, 1980). The groove for the tendon of tibialis posterior is fairly deep and passes directly over the inferior end of the medial malleolus. This is again in contrast to *Tarsius* and *Necrolemur* but agrees with the condition seen in most strepsirhines. The length/width index in this specimen is 128, a value typical for euprimates (Ford, 1980) but higher than in *Tarsius*.

Although the medial malleolus is not preserved, AMNH 21958 (attributed to *Hemiacodon gracilis*) may be allocated to an omomyid primate on the basis of its similarity in other features to the Grizzly Buttes omomyid, its AP/ML index of 120, and its parallel anterior and posterior borders. In other features this omomyid is almost identical to the Grizzly Buttes omomyid, differing only in having a shallower groove for tibialis posterior. The Crooked Canyon specimen (UWA 36483) is considered to be an omomyid on the basis of its medial malleolar morphology. It is very similar to the AMNH specimen and, like the latter, differs from the USNM specimen solely in the shallower tibialis posterior groove.

THE INFERIOR TIBIOFIBULAR JOINT

In contrast to the majority of eutherians, almost all euprimates[6] have a distal tibiofibular joint characterized by a semilunar-shaped, flat-to-concave facet on the lateral side of the tibia which articulates with a mildly convex facet on the fibula (Fig. 8). The tibial facet is covered in articular cartilage which is continuous with that of the upper ankle joint (Carleton, 1941; Barnett and Napier, 1953). Aside from this articulation, the leg bones are not in contact but are united by the anterior and posterior inferior

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[6] This region is damaged in *Plesiadapis gidleyi*, so the nature of the articulation here cannot be determined. *Galeopithecus* and *Ptilocercus* share with euprimates a small synovial facet (Carleton, 1941), but *Tupaia*, *Lynogale*, and *Urogale* have a syndesmosis.

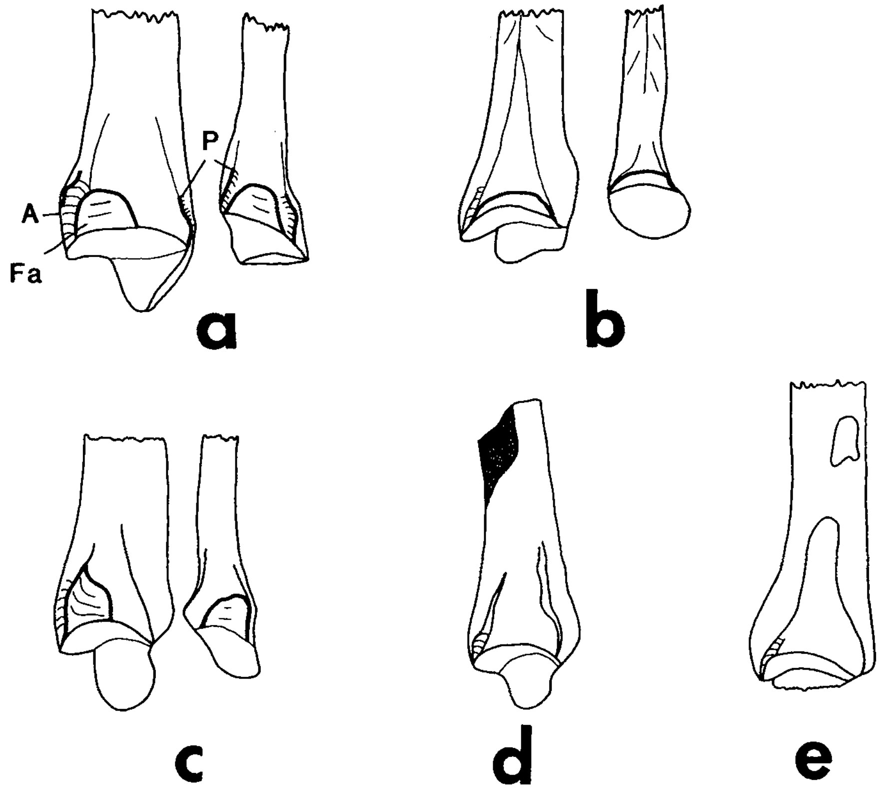

Fig. 8. Schematic representation of the left inferior tibiofibular joint (opened anteriorly) of (a) *Lemur*; (b) *Saimiri*; (c) *Galago demidovii*; (d) Grizzly Buttes omomyid; (e) *Hemiacodon* AMNH 21589. A, groove for anterior inferior tibiofibular ligament; P, groove for posterior inferior tibiofibular ligament; Fa, facet for articulation with the fibula (heavy outline on tibia and fibula). Not to scale. Hatching indicates breakage. Cf. omomyids (Figs. 3 and 4).

tibiofibular ligaments, the transverse tibiofibular ligament, the interosseous ligament, and the interosseous membrane. This type of joint allows a small amount of movement between the two bones (Barnett and Napier, 1953).

Among lower primates, *Tarsius*, the galagines, *Microcebus*, and the known omomyids are exceptions to this general scheme. *Tarsius* is the only extant primate with a synostosis between the distal tibia and the fibula. The bones are synostosed for nearly 60% of the tibia's length, with almost no visible suture line in adults (Fig. 2). Galagos, especially the smaller forms *G. senegalensis* and *G. demidovii*, differ from other strepsirhines in that the distal ends of the two bones are more tightly appressed, although there is no evidence of synostosis and the semilunar articular facet is retained. Two strongly marked crests extend from the anterior and posterior lateral margins of the tibia in these galagos, forming a triangular depression into which a small, reciprocally shaped protuberance on the fibula fits snugly (Fig. 8c). The crests are the sites of origin of the anterior and posterior inferior tibiofibular ligaments distally, and more proximally of the interosseous ligament, which is continuous proximally with the interosseous membrane. Judging from the robusticity of these crests, these ligaments, especially the interosseous ligament, appear to be more robust in *Galago* than in other strepsirhines. This arrangement limits movement between the distal tibia and the fibula.

Microcebus closely resembles the galagines in the conformation of the distal part of this joint but differs from other primates in that the tibia and fibula are in close contact, but not fused, for approximately 25-30% of the tibia's length. A similar condition is observed in *Apidium* (Fleagle and Simons, 1983).

The known omomyids differ from each other in the construction of this joint. The morphology of *Nannopithex* is in question; Weigelt (1933) originally reported that the tibia and fibula were fused, but Simons (1961) found that they were not. The tibia and fibula of *Necrolemur* are definitely fused, as reported by Schlosser (1907). The bones are synostosed for 37% of the tibia's length in the only specimen which permits this measurement (Fig. 1). This is less extensive fusion than is usual in *Tarsius,* and a groove representing the suture line between the two bones is sometimes clearly visible even in fully adult individuals. The fibula is stouter and more laterally flared than in *Tarsius* or *Apidium.* All of these features are indicative of a more primitive stage of tibiofibular fusion in *Necrolemur* than in *Tarsius* (Schlosser, 1907).

In the omomyid from Grizzly Buttes there is no evidence of tibiofibular synostosis. The tibiofibular articulation recalls the condition seen in *G. demidovii,* with well-developed anterior and posterior crests for the inferior tibiofibular ligaments surrounding a shallow triangular depression. The crests are more rugose in this specimen than in any other primate, but their smooth, rounded surface does not indicate any ossification of ligaments or interdigitation of bone between the tibia and the fibula. A synovial facet is not discernible on these specimens, which probably indicates a completely syndesmotic articulation; however, the facet is often difficult to detect on the tibiae of the smaller galagos, although the corresponding fibular facet is usually easily visible. Although only a small part of the shaft is preserved in the Grizzly Buttes specimens, there is no evidence (in the form of a scar on the tibial shaft) of tibiofibular contact above the point defined by the most proximal extent of the inferior tibiofibular ligament crests. Such scars are apparent in *Apidium* and sometimes in *Microcebus* (Fleagle and Simons, 1983).

The tibiofibular articulation of *Hemiacodon* differs slightly from that of the Grizzly Buttes omomyid. In *Hemiacodon,* the crests for the interosseous ligaments are not as rugose and they join proximally to form a closed triangular space, as in *Saimiri* but unlike the open-topped space in *Galago* or the Grizzly Buttes omomyid. A few millimeters above the top of this triangular space, there is a roughened protuberance indicating another (?ligamentous) contact point between the tibia and the fibula. This area of the shaft is preserved in USNM 336189, but no such protuberance exists. These differences are greater than I observed within a single species of extant primates, suggesting that the Grizzly Buttes omomyid is a taxon other than *Hemiacodon gracilis.* It also indicates that *Hemiacodon* exhibits a degree of tibiofibular approximation greater than that of the Grizzly Buttes taxon.

UWA 36483 presents the only evidence for possible tibiofibular fusion in nonmicrochoerine omomyids. In this specimen, a flange of bone extends proximally from 1 mm above the distal edge of the tibia for about 1 cm. Part of this flange appears to incorporate the fibular shaft. If this represents a natural synostosis, the nature of this fusion is quite different from that of *Tarsius* or *Necrolemur* or even from the near-fusion of *Apidium* or *Microcebus.* The attached flange of bone is very broad and the fibula does not appear to be incorporated into the shaft of the tibia. If the total width of the flange is all fibular shaft, the fibula is rather massive, even compared to those primates with unfused tibiae and fibulae. If, however, the total width of the flange is not all fibula, but incorporates an ossified interosseous ligament, fusion is again unlike that seen in other primates (or even rodents, insectivores, or carnivores), all of which fuse the bones by approximating and ultimately incorporating the fibular shaft into the tibia, not by ossifying a broad part of the interosseous membrane.

The nature of the bone itself, however, suggests that the fusion is not "natural" (in the sense of being part of normal ontogenetic development in this species). The color and texture of the fossilized bone lateral to the tibia differ from those of the shaft of the tibia (Fig. 3), and this bone can clearly be seen to have overgrown the tibial shaft. In addition, there are two sites of union, separated by a 1- to 2-mm gap, in which the true, smooth lateral surface of the tibia is clearly visible. The morphology seen here is strongly reminiscient of woven bone growth and callus formation which follows a fracture. Thus, the "fusion" in this specimen does not provide evidence of tibiofibular union in omomyids, as it is almost certainly pathological in origin.

CONCLUSIONS

A euprimate tibia can be distinguished from the tibia of other eutherians by a set of several unique features which are derived compared to the probable eutherian morphotype. The functional significance of these features is related to the production of conjunct rotations (especially abduction) during dorsiflexion at the upper ankle joint. Within euprimates, strepsirhines and haplorhines can be distinguished by some subtle differences in upper ankle joint structure which function to limit the conjunct rotation accompanying dorsiflexion in haplorhines. Two alternate polarity hypotheses can be constructed for the evolution of distal tibial morphology in euprimates. If the conditions of the distal tibia exhibited by strepsirhines are also primitive for euprimates, then *Tarsius*, omomyids, and anthropoids share several derived features of the upper ankle joint. This hypothesis supports haplorhine monophyly but requires several evolutionary reversals. If haplorhine upper ankle joint morphology is primitive for euprimates, then Adapiformes and Lemuriformes share derived upper ankle joint features, providing some previously lacking evidence for a monophyletic Strepsirhini (Cartmill and Kay, 1978). Both hypotheses require some parallelisms—between galagines and tarsiiforms, for example, or between strepsirhines and large anthropoids. At present, there seems to be no clear reason to prefer one hypothesis over the other.

The distal tibial morphology of *Necrolemur* and North American omomyids is significantly different. *Necrolemur* shares many, probably derived, tibial features with *Tarsius*, including tibiofibular fusion, an anteriorly-posteriorly compressed distal tibial shaft, and a shallow, medially directed tibialis posterior groove. These features may phylogenetically link *Tarsius* and *Necrolemur* (Schlosser, 1907), but the lack of any supporting evidence from the skull or dentition (Szalay, 1976; Schmid, 1980) and some contradictory evidence from other postcranial remains (Godinot and Dagosto, 1983) imply an independent history for the two genera and, thus, the convergent attainment of these features. Tibiofibular fusion in *Necrolemur*, along with its tarsal morphology (Godinot and Dagosto, 1983), strongly implies that this genus commonly used leaping as its primary mode of locomotion.

The tibia of North American omomyids exhibits more primitive character states than does that of *Necrolemur*. *Hemiacodon* and unallocated lower Bridger omomyids have a rounded distal tibial shaft, a large, inferiorly directed tibialis posterior groove, and a syndesmotic or perhaps synovial inferior tibiofibular joint. This demonstrates that a range of postcranial morphology and locomotor modes is likely to have characterized the Omomyidae. Not all of them are as derived postcranially as is *Tarsius*.

Tibiofibular fusion is *not* characteristic of all tarsiiform primates, nor was it likely to have been the primitive condition in tarsiiforms. Therefore, its presence in *one* omomyid does not preclude a tarsiiform ancestor for the anthropoids, as has been implied (e.g., Gingerich, 1981). The ancestral omomyid may have differed from the ancestral euprimate in some aspects of this joint; for example, the well-developed inferior tibiofibular ligament crests and tight tibiofibular articulation (judging by the similarities to *Galago*) indicate less freedom of movement at this joint than in notharctine or lemuriform strepsirhines. This is true of some early catarrhines and many platyrrhines as well (Fleagle and Simons, 1983) and, thus, may be an ancestral haplorhine character.

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REFERENCES

Barnett, C. H. (1955). Some factors influencing angulation of the neck of the mammalian talus. *J. Anat.* (Lond.) 89: 225-230.

Barnett, C. H., and Napier, J. R. (1952). The axis of rotation at the ankle joint in man. Its influence upon the form of the talus and the mobility of the fibula. *J. Anat.* (Lond.) 86: 1-9.

Barnett, C. H., and Napier, J. R. (1953). The rotatory mobility of the fibula in eutherian mammals. *J. Anat.* (Lond.) 87: 11-21.

Carleton, A. (1941). A comparative study of the inferior tibio-fibular joint. *J. Anat.* (Lond.) 76: 45-55.

Cartmill, M., and Kay, R. F. (1978). Cranio-dental morphology, tarsier affinities, and primate sub-orders. In Chivers, D. J., and Joysey, K. A. (eds.), *Recent Advances in Primatology, Vol. 3,* Academic Press, New York, pp. 205-213.

Clark, W. E. L., and Leakey, L. S. B. (1951). The Miocene Hominoidea of East Africa. *Fossil Mammals of Africa,* No. 1, British Museum, Natural History, London, pp. 1-117.

Conroy, G. C. (1976). Primate postcranial remains from the Oligocene of Egypt. *Contributions to Primatology,* Vol. 8, Karger, New York.

Crochet, J.-Y., Hartenberger, J.-L., Rage, J.-C., Rémy, J. A., Sigé, B., Sudre, J., and Vianey-Liaud, M. (1981). Les nouvelles faunes de vértebrés antérieures à la "grand Coupure" decouvertes dans les Phosphorites du Quercy. *Bull. Mus. Nat. Hist. Nat.* 3: 245-266.

Decker, R. L., and Szalay, F. S. (1974). Origins and function of the pes in the Eocene Adapidae (Lemuriformes, Primates). In Jenkins, F. A. (ed.), *Primate Locomotion,* Academic Press, New York, pp. 261-291.

Fleagle, J. G., and Simons, E. L. (1983). The tibio-fibular articulation in *Apidium phiomense,* an Oligocene anthropoid. *Nature* 301: 238-239.

Ford, S. M. (1980). *A Systematic Revision of the Platyrrhini Based on Features of the Postcranium,* Ph.D. thesis, University of Pittsburgh, Pittsburgh.

Gazin, C. L. (1968). A study of the Eocene condylarthran mammal *Hyopsodus. Smithson. Misc. Coll.* 153: iv-90.

Gingerich, P. D. (1981). Early Cenozoic Omomyidae and the evolutionary history of tarsiiform primates. *J. Hum. Evol.* 10: 345-374.

Godinot, M., and Dagosto, M. (1983). The astragalus of *Necrolemur* (Primates, Microchoerinae). *J. Paleontol.* 57: 1321-1324.

Hafferl, A. (1932). Bau und Funktion des Affenfusses. Ein Beitrag zur Gelenk- und Muskelmechanik. II. Die Prosimier. *Z. Anat. Ent.-geschichte.* 99: 63-112.

Lewis, O. J. (1980). The joints of the evolving foot. I. The ankle joint. *J. Anat. (Lond.)* 130: 527-543.

Matthew, W. D. (1909). The Carnivora and Insectivora of the Bridger Basin, middle Eocene. *Mem. Am. Mus. Nat. Hist.* 9: 289-567.

Matthew, W. D. (1937). Paleocene faunas of the San Juan Basin, New Mexico. *Trans. Am. Phil. Soc.* 30: iii-510.

Reimann, R., and Anderhuber, F. (1980). Kompensationsbewegungen der Fibula, die durch die Keilform der Trochlea Tali erzwungen werden. *Acta Anat.* 108: 60-67.

Savage, D. E., and Waters, B. T. (1978). A new omomyid primate from the Wasatch Formation of southern Wyoming. *Folia primatol.* 30: 1-29.

Schaeffer, B. (1947). Notes on the origin and function of the artiodactyl tarsus. *Am. Mus. Nov.* 1356: 1-24.

Schlosser, M. (1907). Beitrag zur Osteologie und systematischen Stellung der Gattung *Necrolemur,* sowie zur Stammesgeschichte der Primaten überhaupt. Separat *N. Jb. für Min. Geol. und Paläontol.,* pp. 197-226.

Schmid, P. (1979). Evidence of microchoerine evolution from Dielsdorf (Zurich region, Switzerland)—a preliminary report. *Folia primatol.* 31: 301-311.

Schmid, P. (1980). Comparison of Eocene nonadapids and *Tarsius.* In Chiarelli, A. B., and Corrucini, R. S. (eds.), *Primate Evolutionary Biology,* Springer-Verlag, New York, pp. 6-13.

Simons, E. L. (1961). Notes on Eocene tarsioids and a revision of some Necrolemurinae. *Bull. Br. Mus. (Nat. Hist.) Geol.* 5: 43-69.

Simpson, G. G. (1935). The Tiffany fauna, Upper Paleocene. II. Structure and relationships of *Plesiadapis. Am. Mus. Nov.* 816: 1-30.

Simpson, G. G. (1940). Studies on the earliest primates. *Bull. Am. Mus. Nat. Hist.* 77: 185-212.

Szalay, F. S. (1976). Systematics of the Omomyidae (Tarsiiformes, Primates): Taxonomy, phylogeny, and adaptations. *Bull. Am. Mus. Nat. Hist.* 156: 157-450.

Szalay, F. S. (1977). Phylogenetic relationships and a classification of the eutherian Mammalia. In Hecht, M. K., and Goody, P. (eds.), *Major Patterns in Vertebrate Evolution,* Plenum Press, New York, pp. 315-374.

Szalay, F. S. (1982). A new appraisal of marsupial phylogeny and classification. In Archer, M. (ed.), *Carnivorous Marsupials,* Royal Zoological Society of New South Wales, Sydney, pp. 621-640.

Szalay, F. S. (1984). Arboreality: Is it homologous in metatherian and eutherian mammals? In Hecht, M. K. (ed.), *Evolutionary Biology.* Plenum Press, New York.

Szalay, F. S., and Dagosto, M. (1980). Locomotor adaptations as reflected on the humerus of Paleogene primates. *Folia primatol.* 34: 1-45.

Szalay, F. S., and Decker, R. L. (1974). Origins, evolution, and function of the tarsus in Late Cretaceous Eutheria and Paleocene primates. In Jenkins, F. A. (ed.), *Primate Locomotion,* Academic Press, New York, pp. 223-259.

Szalay, F. S., and Delson, E. (1979). *Evolutionary History of the Primates,* Academic Press, New York.

Szalay, F. S., and Drawhorn, G. (1980). Evolution and diversification of the Archonta in an arboreal milieu. In Luckett, W. P. (ed.), *Comparative Biology and Evolutionary Relationships of Tree Shrews,* Plenum Press, New York, pp. 133-169.

Teilhard de Chardin, P. (1927). Les mammifères de l'Éocene inferieur de la Belgique. *Mem. Mus. Roy. Hist. Nat. Belg.* 36: 1-33

Weigelt, J. (1933). Neue Primaten aus dem mitteleozänen (oberlutetischen) Braunkohle des Geiseltals. *Nova Acta Leopold.* 1: 97-156.

West, R. M. (1976). Paleontology and geology of the Bridger formation, southern Green River basin, Southwestern Wyoming. Part 1. History of field work and geological setting. *Contrib. Biol. Geol. Milwaukee Publ. Mus.* 7: 1-12.

Wood, A. E. (1962). The early Tertiary rodents of the family Paramyidae. *Trans. Am. Phil. Soc.* 52: 1-261.

Wortman, J. L. (1903). Studies of the Eocene Mammalia in the Marsh collections. Primates. *Am. J. Sci.* 15: 12-250.