CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

THE UNIVERSITY OF MICHIGAN

VOL. 30, NO. 6, PP. 191-198 December 15, 1999

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THE UNIVERSITY OF MICHIGAN
ANN ARBOR

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FIRST CARPALS OF THE EOCENE PRIMATE FAMILY OMOMYIDAE

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MARK W. HAMRICK[1]

Abstract — Two hamates and one pisiform from middle Eocene deposits of the Bridger Basin, Wyoming, are attributable to the early Cenozoic primate family Omomyidae. Comparative evidence and information on the distribution of omomyid primates at localities where the specimens were found, taken together, suggest that these carpals are best assigned to the omomyine *Omomys carteri*. The new carpals are similar to those of the middle Eocene adapiform primate *Smilodectes gracilis* in virtually all respects but are significantly smaller. *Omomys carteri* and North American adapiforms exhibit similar patterns of hamate and pisiform morphology, which are inferred to represent ancestral conditions for the order Primates. Comparative functional analysis of the new carpals suggests that *O. carteri* resembled extant small-bodied, pronograde arboreal primates in several features related to midcarpal ulnar deviation, pronation, and powerful manual grasping.

INTRODUCTION

The tarsiiform primate family Omomyidae is known from a large sample of dental and gnathic remains from the Eocene of North America and Europe. These fossil materials have proven useful for reconstructing both phylogenetic relationships (Szalay, 1976; Gingerich, 1981; Bown and Rose, 1987) and dietary adaptations (Covert, 1986; Covert and Hamrick, 1991). A thorough understanding of omomyid evolutionary biology has, however, been limited by a paucity of postcranial specimens attributed to this group. Our knowledge of omomyid skeletal morphology comes primarily from the tarsus (Covert and Hamrick, 1991; Gebo, 1988; Godinot and Dagosto, 1983), tibia (Covert and Hamrick, 1991; Dagosto, 1985), and femur (Dagosto and Schmid, 1996). The only forelimb elements described for omomyids are proximal and distal humeri (Dagosto, 1993). This paper describes three carpals of Omomyidae from the middle Eocene Bridger Basin of western North America. These are compared to carpals of extant primates as well as those of several early Tertiary adapiforms in order to infer patterns of evolutionary change in primate carpal morphology and function.

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TABLE 1 — Mean species carpal dimensions (in mm; standard deviations in parentheses) for extant primates included for comparison with carpal dimensions for the three fossil specimens. Species symbols used in Figure 1 follow species names in parentheses.

Species (symbol)	Pisiform ulnar facet breadth	Hamate distal breadth	N
Microcebus murinus (m)	0.99 (0.20)	1.26 (0.15)	13
Lepilemur mustelinus (l)	2.98 (0.52)	3.31 (0.54)	19
Hapalemur griseus (h)	3.28 (0.46)	3.97 (0.35)	21
Cheirogaleus major (c)	2.68 (0.63)	2.92 (0.41)	5
Indri indri (i)	7.36 (1.32)	8.51 (0.68)	17
Varecia variegata (v)	6.42 (1.19)	7.60 (0.53)	19
Propithecus verreauxi (p)	4.74 (0.80)	5.63 (0.51)	15
Avahi laniger (a)	3.65 (0.65)	4.29 (0.32)	12
Lemur fulvus (f)	4.55 (0.75)	5.52 (0.59)	19
Cheirogaleus medius (e)	1.49 (0.49)	1.95 (0.22)	4
Tarsius syrichta (t)	1.89 (0.15)	2.28 (0.14)	3
Otolemur crassicaudatus (o)	2.40 (0.49)	4.20 (0.40)	15
Galagoides demidovii (d)	1.14 (0.10)	1.31 (0.06)	5
Galago senegalensis (s)	1.72 (0.26)	2.03 (0.43)	9
Euoticus elegantulus (u)	2.49 (0.20)	2.29 (0.42)	9
Omomys carteri (UM 32319a)	1.63	—	1
Omomys carteri (UM 32319b)	—	2.79	1
Omomys carteri (UM 32306)	—	2.86	1

INSTITUTIONAL ABBREVIATIONS

AMNH — American Museum of Natural History, New York
UM — University of Michigan Museum of Paleontology, Ann Arbor
USNM — United States National Museum of Natural History, Washington

DESCRIPTIVE PALEONTOLOGY

The carpals described here are from the Bridger Basin, Wyoming, and reside in the University of Michigan Museum of Paleontology collections. UM 32306 is a right hamate from UM locality BRW-42 in the Bridger 2 horizon (Br-2), also referred to as Bridger B (Gingerich, 1981). UM 32319a is a right hamate from UM locality BRW-14, also in Br-2. UM 32319b is a right pisiform from UM locality BRW-14 (Br-2).

The pisiform is attributed to the order Primates based on its radioulnarly broad dorsal surface which forms a "beak" pointing radially. This morphology is also observed in pisiforms of the early Tertiary adapiforms *Smilodectes*, *Notharctus*, and *Adapis* as well as those of extant prosimian primates such as *Tarsius*, *Microcebus*, *Cheirogaleus*, and *Galago*. The dorsal pisiform surface of extant anthropoids is not so expanded radioulnarly as that of prosimians. Pisiforms of living and extinct prosimian primates differ from those of rodents, insectivores, carnivores, marsupials, and tree shrews in having a radioulnarly broad dorsal surface, a pisiform body that is not markedly expanded dorsopalmarly, and a palmar pisiform surface that slopes radially and is not expanded proximodistally.

The two hamates are attributed to the order Primates based on the presence of a well-developed "spiral" facet for the triquetrum and a clearly distinguishable hamulus on each hamate. The hamates

of rodents, insectivores, carnivores, and tree shews differ from those of primates in lacking both a well-developed spiral facet and a prominent hamulus (Hamrick, 1997). Marsupials possess a moderately developed hamate "spiral" facet and a very well developed hamate hamulus; however, marsupial hamates differ from those of primates in being more elongate proximodistally, narrow radioulnarly, and having a very bulbous articular surface on the proximal hamate surface (Lewis, 1985; pers. obs.).

The primate carpals described here are similar to those of *Smilodectes gracilis* in virtually all respects aside from being significantly smaller. Thus, these specimens are attributed to Omomyidae rather than Adapidae solely on the basis of size. The most common omomyid primate found at UM localities BRW-14 and BRW-42 is *Omomys carteri*. *Washakius insignis* is less common at BRW-14 and very rare at locality BRW-42, whereas both *Trogolemur myodes* and *Hemiacodon gracilis* are very rare at each of these two localities.

The natural log of (1) radioulnar breadth of the pisiform's articular facet for the ulna and (2) radioulnar breadth of the distal hamate were regressed on the lower first molar area (Smith, 1996) in a large sample of extant prosimian primates (Table 1) in order to assign the isolated carpals to specific taxa. The correlation coefficient was $r = 0.96$, $p < 0.001$ in the case of ulnar facet breadth, and $r = 0.98$, $p < 0.001$ in the case of distal hamate breadth. Bivariate plots of these data are shown in Figure 1.

Metric dimensions of the fossil specimens were then plotted against mean lower first molar areas for *Trogolemur myodes*, *Washakius insignis*, *Omomys carteri*, and *Hemiacodon gracilis*. Results demonstrate that the pisiform (UM 32319b) lies closest to the regression line when matched with the first lower molar area of *Omomys carteri* (Fig. 1a). This specimen could also be attributed to *Washakius insignis* based on its lower first molar area (Fig. 1a). However, given that *Omomys* is most common at the locality, the specimen is provisionally attributed to *O. carteri*.

The hamates (UM 32319a and 32306) lie closest to the regression line when matched with the first lower molar area of *Hemiacodon gracilis* (Fig. 1b). The hamates of early Tertiary primates do, however, differ from those of extant primates in being much broader distally (Hamrick and Alexander, 1996). The strong positive residual values for distal hamate breadth relative to tooth size in the early adapiforms *Notharctus tenebrosus* and *Smilodectes gracilis* are shown in Fig. 1b. The two omomyid hamates, like the pisiform, are therefore also provisionally attributed to *Omomys carteri*. This assignment is reasonable given the fact that dental remains of *H. gracilis* are very rare at the two localities where the hamates were found.

COMPARATIVE AND FUNCTIONAL MORPHOLOGY

The omomyid pisiform resembles that of modern pronograde, small-bodied prosimians such as *Cheirogaleus* and *Microcebus* in being approximately as wide (radioulnarly) on its dorsal surface as is it is high dorsopalmarly (Fig. 2). The omomyid pisiform is not reduced in its dorsopalmar dimension like that of either slow-climbing lorises or certain vertical clingers, indicating that omomyids possessed a relatively well-developed lever arm for the flexor carpi ulnaris muscle (Hamrick, 1996a). The overall shape of this element in omomyids is similar to that of the North American adapiforms *Smilodectes* and *Notharctus*, however the omomyid pisiform differs from that of adapiforms in being significantly smaller in size. The omomyid pisiform resembles that of tarsiers, anthropoids, and North American adapiforms in having an articular facet for the triquetrum that is larger than the articular facet for the ulna (Fig. 3). Living strepsirhines and the European adapiform *Adapis* show the derived condition of having an articular facet for the ulna on the pisiform that is larger than the articular facet for the triquetrum (Beard and Godinot, 1988; but see also Schwartz and Yamada, 1998).

The omomyid hamates possess a well-developed "spiral" facet (Fig. 2) for conjunct ulnar deviation and pronation at the midcarpal joint during arboreal, quadrupedal locomotion (Hamrick, 1996a,b). Morphology of this articular facet resembles that of pronograde active arboreal quadrupeds such as *Cheirogaleus* in being somewhat radioulnarly directed (Fig. 4). The omomyid specimens

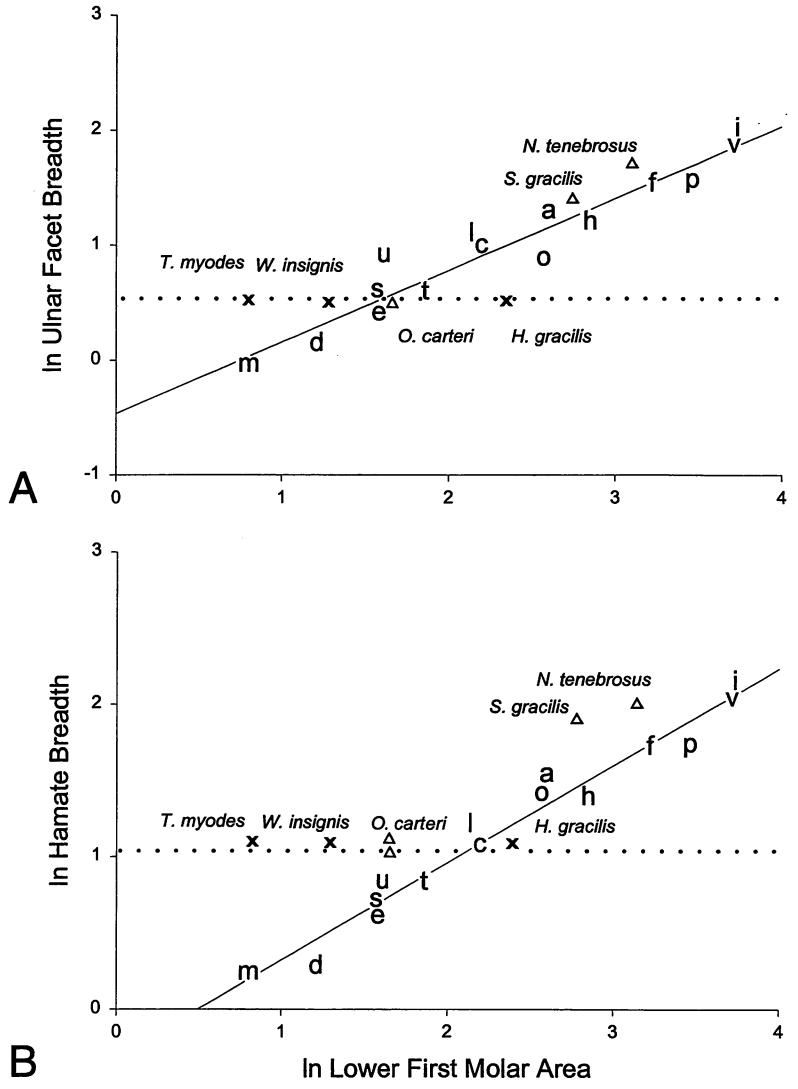

FIG. 1 — Bivariate plots of carpal dimensions and lower first molar areas for extant and fossil prosimian primates. Symbols, measurements, and samples sizes for the extant taxa are shown in Table 1. Mean lower first molar areas for the extant taxa are from Smith (1996), whereas molar dimensions for the fossil taxa are from Gingerich (1981) and Conroy (1987). Dimensions of the omomyid carpals are plotted against lower first molar areas of four different omomyid taxa: *Trogolemur myodes*, *Washakius insignis*, *Omomys carteri*, and *Hemiacodon gracilis*. A, plot of natural log radioulnar diameter of the pisiform's ulnar facet against natural log lower first molar area. Solid line is ordinary least-squares regression line (slope = 0.62, Y-intercept = -0.46, $p < 0.001$) for the extant sample. Pisiform articular diameter for *Smilodectes gracilis* is measured from USNM 256745 and for *Notharctus tenebrosus* from AMNH 127167. The horizontal dotted line represents the pisiform breadth value for the omomyid fossil specimen (UM 32319a). B, plot of natural log maximum radioulnar breadth of the hamate against natural log lower first molar area. The solid line is an ordinary least-squares regression line (slope = 0.63, Y-intercept = -0.30, $p < 0.001$) for the extant sample. Distal hamate breadth for *Smilodectes gracilis* is measured from USNM 21815 and for *Notharctus tenebrosus* from AMNH 127167. The horizontal dotted line represents the hamate breadth value for one of the omomyid fossil specimens (UM 32319b), although measurements for both specimens are shown on the plot.

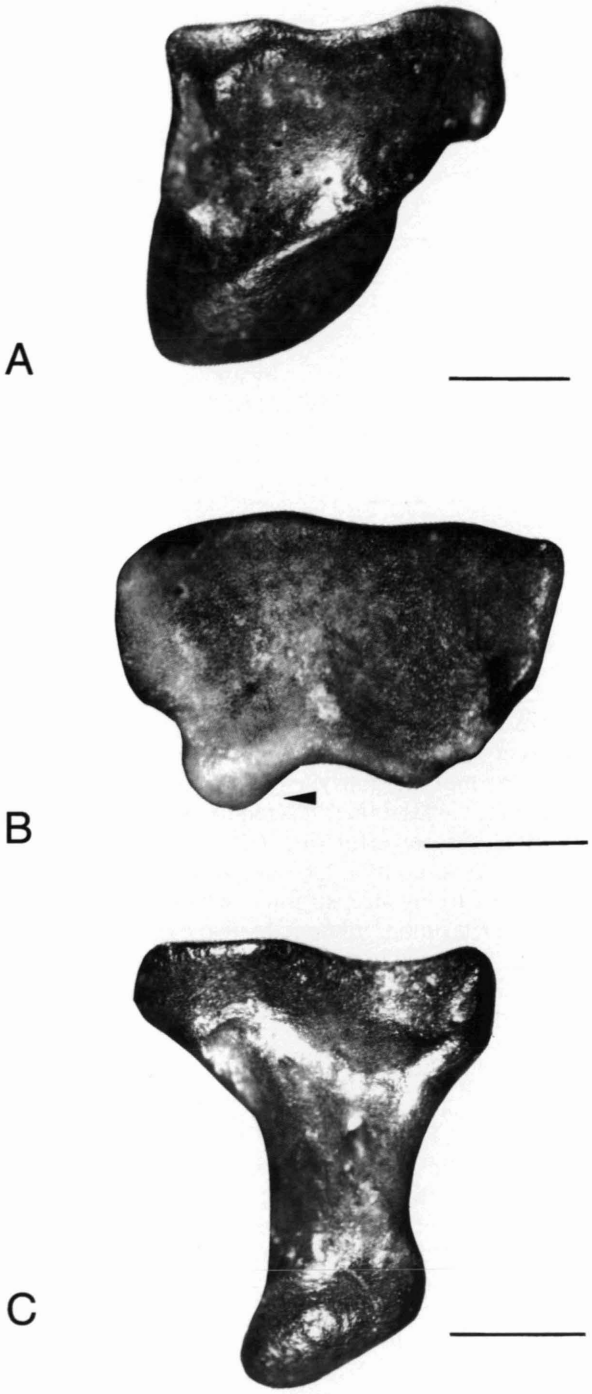

FIG. 2 — Omomyid carpals from the Bridger Basin, Wyoming. A, dorsal view of UM 32319b, right hamate. B, distal view of UM 32319b, right hamate (arrow points to the hamulus). C, proximal view of UM 32319a, right pisiform. Scale bars = 1 mm.

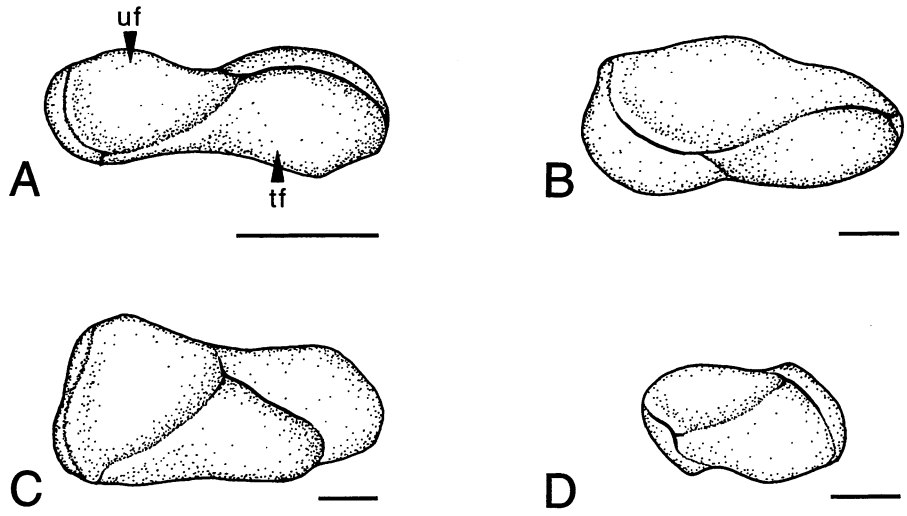

FIG. 3 — Right pisiforms (dorsal view) of A, cf. *Omomys carteri* (UM 32319a); B, *Lemur catta*; C, *Smilodectes gracilis* (USNM 256745); and D, *Saimiri sciureus*. Scale bars = 1 mm. Abbreviations: *uf* = articular facet for ulna, *tf* = articular facet for triquetrum. Pisiforms of *Lemur*, *Smilodectes*, and *Saimiri* redrawn from Beard and Godinot (1988).

therefore differ from those of more orthograde forms such as *Tarsius*, which have a more proximodistally directed facet (Fig. 4). The hamate hamulus of omomyids is also moderately developed (Fig. 2) for attachment of the transverse carpal ligament. The presence of a hamulus in these specimens indicates that the carpal tunnel was relatively deep for the passage of well-developed long digital flexors, important for powerful finger flexion and manual grasping in an arboreal environment. Relative size of the omomyid hamulus resembles that of tarsiers, anthropoids, and adapiforms more so than that of living strepsirhines, which is quite large (Hamrick, 1997). The proximal articular surface of each omomyid hamate also exhibits an articular facet for the lunate but none for the centrale. The omomyid hamates therefore resemble those of tarsiers, anthropoids, and adapids in this respect but differ from those of living strepsirhines, which possess centrale-hamate contact (Beard and Godinot, 1988).

CONCLUSIONS

Primate carpals from the middle Eocene Bridger Basin of North America attributed to the omomyid *Omomys carteri* suggest that this taxon resembled extant small-bodied, pronograde arboreal primates in having a well-developed and ulnarly directed spiral facet on the hamate for conjunct pronation and ulnar deviation at the midcarpal joint. These omomyid hamates resemble those of modern monkeys, tarsiers, and early Tertiary adapiforms in possessing a hamate hamulus, but the hamulus of omomyids is not so well-developed as that of extant strepsirhines. The omomyid pisiform resembles that of modern monkeys, tarsiers, and the North American adapiforms *Smilodectes* and *Notharctus* in having an articular facet for the triquetrum that is larger than the articular facet for the ulna. In contrast, extant lemuriforms and the European adapiform *Adapis* possess pisiforms that differ from the omomyid pisiform in having an articular facet for the triquetrum that is smaller than the articular facet for the ulna. These comparative observations indicate that both a hamate "spiral" facet and a hamate hamulus are morphotypic euprimate features related to midcarpal ulnar deviation, pronation, and powerful manual grasping during arboreal locomotor and postural behaviors. The North American omomyids and adapiforms exhibit similar patterns

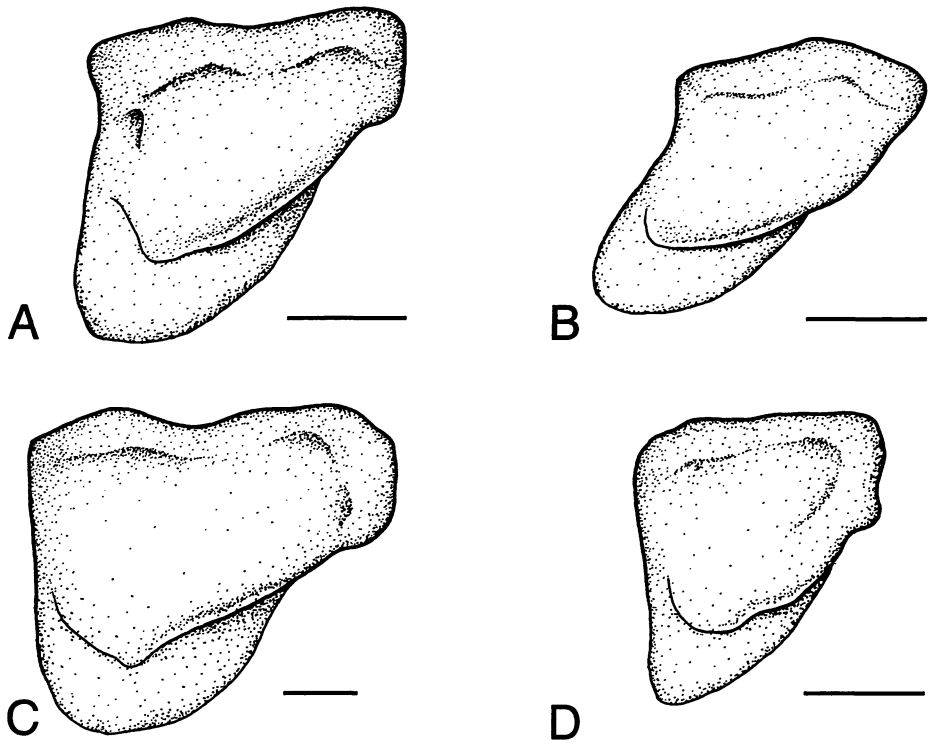

FIG. 4 — Right hamates (dorsal view) of A, cf. *Omomys carteri* (UM 32319b); B, *Tarsius syrichta*; C, *Smilodectes gracilis* (USNM 21815); and D, *Cheirogaleus medius*. Scale bars = 1 mm.

of hamate and pisiform morphology, which are inferred to represent ancestral conditions for the order Primates.

ACKNOWLEDGMENTS

I thank Drs. G. F. Gunnell and P. D. Gingerich for permitting me to study the omomyid carpals described here from the University of Michigan Bridger Basin collections. The specimens were first brought to my attention by Dr. H. H. Covert. Drs. K. C. Beard, H. H. Covert, P. D. Gingerich, and G. F. Gunnell provided helpful comments that improved the quality of the manuscript. Funding for this research was provided by the L. S .B. Leakey Foundation and National Science Foundation grant SBR-932037.

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