

POSTCRANIAL MORPHOLOGY AND LOCOMOTOR BEHAVIOUR OF TWO EARLY EOCENE MIACOID CARNIVORANS, *VULPAVUS* AND *DIDYMICTIS*

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ABSTRACT. The postcranial skeletons of two contemporaneous early Eocene carnivorans, the miacid *Vulpavus* and the viverravid *Didymictis*, are described and compared with behaviourally diverse small and medium-bodied extant carnivorans. Body mass estimates based on the cross sectional geometry of humeri and femora indicate that these two taxa were similar in size, estimates for both genera ranging from about 3.5 to 7.5 kg. It is argued that *Vulpavus* was well adapted for climbing and was possibly arboreal, with locomotor behaviours comparable to those of the coatimundi (*Nasua*). *Didymictis*, on the other hand, was primarily terrestrial and probably incipiently cursorial. No modern taxon is similar to *Didymictis* in all aspects of the postcranial skeleton, but the Oriental civet (*Viverra*) is probably a reasonable modern analogue.

LIVING members of the order Carnivora possess an array of postcranial specializations that enable particular taxa to exploit habitats ranging from marine, in the case of pinnipeds, to arboreal, exemplified by the prehensile-tailed kinkajou (*Potos*) and binturong (*Arctictis*). This morphological diversity and associated locomotor behaviours, probably derive from both of the early Tertiary carnivoran families, Miacidae and Viverravidae (Wortman and Matthew 1899; Flynn and Galiano 1982; Hunt and Tedford 1993), collectively termed miacoids. Although separate miacid and viverravid lineages extend back into the late Cretaceous (MacIntyre 1966; Fox and Youzwyshyn 1994), most of what has been known about miacoid postcrania is based on material no older than mid Eocene (Matthew 1909; Clark 1939; Springhorn 1980, 1982, 1985). Exceptions to this are a discussion of a fragmentary innominate and proximal femur belonging to the Palaeocene viverravid *Protictis haydenianus* (MacIntyre 1966), and very brief descriptions of *Vassacyon promicrodon* (Matthew 1915), and two species of *Didymictis*, *D. altidens* (Scott 1888; Matthew 1915) and *D. protenus* (Matthew 1901). More recently, however, and owing to fieldwork conducted over the past 15 years in the Willwood Formation of the Bighorn Basin, north-western Wyoming (Bown *et al.* 1994), the amount of early Eocene miacoid postcranial material has increased significantly (Rose 1990; Heinrich 1995; Heinrich and Rose 1995).

Two genera are particularly well represented in these new collections, the miacid *Vulpavus* and the viverravid *Didymictis*. *Didymictis* is known from both North America and Europe (Savage and Russell 1983). It first appears in the latest Paleocene (Clarkforkian North American Land Mammal Age, NALMA) and its temporal range extends through the early Eocene (Gingerich and Winkler 1985). *Vulpavus* on the other hand is an exclusively North American taxon known from both early (Wasatchian NALMA) and mid (Bridgerian NALMA) Eocene sediments (Gingerich 1983). It is the postcranial anatomy and locomotor behaviour of these two genera that is the focus of the present analysis. We describe their appendicular postcrania, comparing and contrasting their morphologies with one another and with an array of modern small- and medium-bodied carnivorans.

MATERIALS

Most of the fossil postcrania analysed and described in this study are from the early Eocene Willwood Formation, and are housed at the following institutions: the US Geological Survey

(USGS), now housed at the Department of Paleobiology, National Museum of Natural History, Smithsonian Institution; the American Museum of Natural History (AMNH), New York; and the University of Michigan (UM), Ann Arbor. This material was supplemented, however, by several North American mid Eocene miacids from the collections of the AMNH and the National Museum of Natural History (USNM), Washington. Extant carnivores from the mammalogy departments of the AMNH and USNM as well as from the personal collections of the authors were used for comparative purposes. Among the 34 extant taxa analysed were representatives of each of the carnivore families Mustelidae, Procyonidae, Canidae, Viverridae, Herpestidae and Felidae.

Although *Vulpavus* and *Didymictis* are in need of taxonomic revision, the only species presently recognized in the Willwood Formation are *V. australis*, *V. canavus* and *D. protenus*, and we tentatively assign all of the early Eocene material described here to these three taxa. *Vulpavus canavus* may, on average, be slightly larger than *V. australis*, but otherwise there appear to be no specific differences in postcranial morphology. Several of the postcranial elements of early Eocene *Vulpavus*, however, are known only from poorly preserved and/or incomplete specimens and, therefore, in several instances we have figured bones of two other Wasatchian miacids, *Miacis petilus* (USGS 7161, distal tibia and fibula) and *Uitacyon massetericus* (USGS 21910, distal humerus), and two Bridgerian miacids, *Miacis parvivorus* (AMNH 11496, lunar) and a specimen attributed to *Vulpavus* sp. (USNM 362847, scapula, proximal tibia, and astragalus). Although this latter specimen lacks an associated cranium and dentition, the appendicular skeleton is well preserved and nearly complete and its overall similarities to other Bridgerian *Vulpavus* specimens leave little doubt that USNM 362847 belongs to this genus.

Abbreviations of osteological features shown in Text-figures 1–8 are given in the Appendix.

BODY MASS ESTIMATES

The importance of reliable estimates of body mass for inferring locomotor behaviour and life history parameters of fossil taxa has been discussed at length (Damuth and MacFadden 1990, and references cited therein). Although these estimates have generally been calculated from regressions derived for dental dimensions (Gingerich *et al.* 1982; Legendre and Roth 1988; Van Valkenburgh 1990), it is intuitively obvious that a strong correlation exists between the size of a terrestrial mammal and the magnitude of mechanical loads that act on its limb bones. Body mass estimates for fossil taxa, therefore, have increasingly relied on extant mammal regressions of body mass on cross sectional parameters of various limb elements (Ruff *et al.* 1989; Anyonge 1993; Biknevicius *et al.* 1993; Runestad 1994; Heinrich and Rose 1995).

Methods for obtaining cross sectional data used to derive the regressions employed here have been described in detail elsewhere (Heinrich 1995; Heinrich and Rose 1995). Briefly, cortical bone area and several measures of the distribution of cortical bone in cross section (i.e. second and polar moments of area) were collected at femoral midshaft and just below humeral midshaft for 24 extant caniform taxa (Table 1). Three methods were used to obtain these data: physical sectioning of bones, computer tomographic (CT) images, and biplanar X-rays. For the first of these, the cross section of a transversely sectioned bone was photographed and the endosteal and periosteal outlines digitized using a modified version of the computer program SLICE (Nagurka and Hayes 1980; Ruff and Hayes 1983) which calculates automatically the cross sectional parameters of interest. CT scans were digitized in the same way. Where bones could not be sectioned physically or subjected to CT scanning, the humerus and femur were modelled as hollow beams with a concentrically positioned medullary cavity, and biplanar X-rays were used to obtain medullary diameters (measured to the nearest 0.1 mm) in the anteroposterior and mediolateral planes. Section properties could then be estimated using standard geometrical formulae for an ellipse (Timoshenko and Gere 1972), a method which has been shown to provide accurate estimates of diaphyseal cross sectional properties (Runestad *et al.* 1993; Heinrich 1995).

Least squares regressions of body mass on cortical area and polar moment of area using log-transformed species mean values for the 24 extant taxa analysed are given in Table 2. As a means

TABLE 1. Extant carnivoran taxa for which cross sectional data of the humerus and femur were collected. *N*, sample size per species; Technique, method of obtaining cross sectional data.

Taxon	Common name	<i>N</i>	Technique
Family Mustelidae			
<i>Spilogale putorius</i>	Spotted skunk	10	X-ray
<i>Martes americana</i>	Pine marten	20	Physical section
<i>Mustela vison</i>	American mink	10	X-ray
<i>Ictonyx striatus</i>	Zorilla	5	X-ray
<i>Mephitis mephitis</i>	Striped skunk	9	X-ray
<i>Melogale personata</i>	Ferret badger	5	X-ray
<i>Galictis vittata</i>	Greater grison	5	X-ray
<i>Martes pennanti</i>	Fisher	20	Physical section
<i>Conepatus mesoleucus</i>	Hog-nosed skunk	10	X-ray
<i>Eira eira</i>	Tayra	10	X-ray
<i>Taxidea taxidea</i>	North American badger	11	X-ray
<i>Meles meles</i>	European badger	5	X-ray
<i>Gulo gulo</i>	Wolverine	20	Physical section
Family Procyonidae			
<i>Bassariscus astutus</i>	Ringtail	10	X-ray
<i>Bassaricyon gabbi</i>	Olingo	5	X-ray
<i>Potos flavus</i>	Kinkajou	5	X-ray
<i>Ailurus fulgens</i>	Lesser panda	6	X-ray
<i>Procyon lotor</i>	Raccoon	8	X-ray
Family Canidae			
<i>Fennecus zerda</i>	Fennec fox	6	CT scan
<i>Alopex lagopus</i>	Arctic fox	10	Physical section
<i>Urocyon cinereoargenteus</i>	Gray fox	10	CT scan
<i>Vulpes vulpes</i>	Red fox	10	Physical section
<i>Cerdocyon thous</i>	Crab-eating fox	10	X-ray
<i>Canis latrans</i>	Coyote	10	CT scan

TABLE 2. Regressions of log-transformed body mass on log-transformed cross sectional properties of the humerus and femur based on taxa given in Table 1. *r*, correlation coefficient; SE, standard error of regression; % SEE, percentage standard error of estimate.

Cross sectional property	Slope	Intercept	<i>r</i>	SE	% SEE
Humerus					
Cortical area	1.259	-1.270	0.980	0.080	20.2
Polar moment of area	0.633	-0.987	0.986	0.067	16.7
Femur					
Cortical area	1.326	-1.308	0.968	0.101	26.2
Polar moment of area	0.663	-1.019	0.963	0.110	28.8

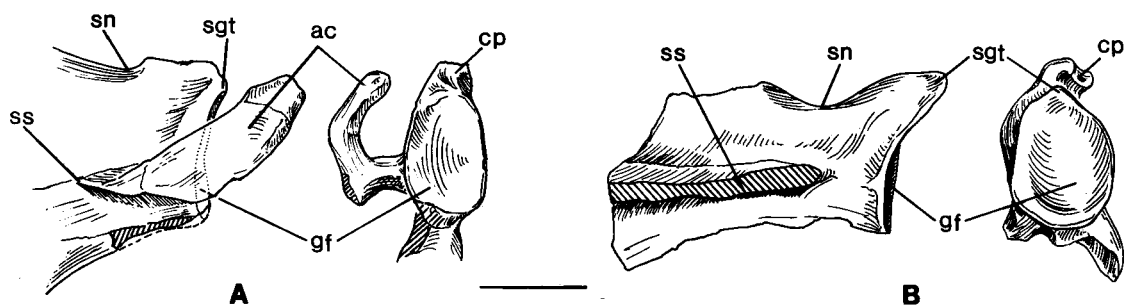
of assessing each equation's ability to estimate accurately the dependent variable, the percentage standard error of estimate (percent SEE) was calculated for each regression where the percent SEE = $\text{antilog}(2 + \text{the standard error of the regression}) - 100$ (Smith 1984; Van Valkenburgh 1990). For both sectional properties the percentage SEE is less for the humeral than for the comparable

femoral regression (Table 2) suggesting that among carnivorans sectional properties of the humerus provide a better estimate of body mass than do those of the femur. Body mass estimates based on the four regressions given in Table 2 range from 3.4 kg to 6.6 kg (average 4.5 kg) for four specimens of *Vulpavus* (includes three specimens of *V. canavus* and one of *V. australis*) and from 3.9 kg to 8.3 kg (average 5.5 kg) for eight specimens of *Didymictis protenus* (Heinrich 1995). If only humeral regressions are considered, the range of body masses calculated for the eight specimens of *D. protenus* is 3.9 kg to 7.2 kg (average 5.0 kg), whilst the range for *Vulpavus* remains the same. Skeletal material of early Eocene Willwood Formation *Vulpavus* and *Didymictis*, therefore, suggests that these two fossil carnivorans were comparable in size to the living carnivorans *Nasua nasua* (coatimundi) and *Vulpes vulpes* (red fox) respectively.

FORELIMB MORPHOLOGY

Description and comparisons

Scapula. Only fragmentary scapulae of Wasatchian *Vulpavus* and *Didymictis* are known, and descriptions here are limited to the glenoid region of that bone, the surface that articulates with the humeral head. In *Vulpavus*, the glenoid fossa is shallow and elliptical to pyriform-shaped, being wider posteriorly (i.e. at the axillary border) than anteriorly (Text-fig. 1A). In contrast, the glenoid



TEXT-FIG. 1. Right scapulae of *Vulpavus* (A, USNM 362847) and *Didymictis* (B, USGS 5024, reversed) in lateral (left) and proximal (right) views. See Appendix for abbreviations. Scale bar represents 10 mm.

fossa of *Didymictis* is rounder in outline (medial margin is expanded) and the supraglenoid tubercle (an attachment site for *m. biceps brachii*) extends well beyond the posteriormost aspect of the glenoid fossa. As a result of the supraglenoid morphology, the fossa of *Didymictis* is notably more concave anteroposteriorly than that of *Vulpavus* (Text-fig. 1B). Taylor (1974) noted an association among viverrids and herpestids of a deep glenoid with terrestrial adaptation, and a shallow glenoid fossa with arboreality.

The suprascapular notch of *Vulpavus* is weakly developed so that scapular neck width (i.e. the shortest distance between axillary and anterior borders dorsal to the glenoid) is greater than the maximum length of the glenoid fossa (Text-fig. 1A). This contrasts with *Didymictis* where the suprascapular notch is deeper and neck width noticeably less than glenoid fossa length (Text-fig. 1B). Among modern carnivorans studied, neck width is always greater than glenoid length, but neck width tends to be greater in arboreal than in terrestrial taxa (Heinrich 1995). In *Didymictis* the base of the scapular spine is relatively farther from the glenoid margin than in *Vulpavus*, but in both the spine is closer to the axillary than to the anterior border (Text-fig. 1A–B).

More complete scapulae that include the acromion process are known for several Bridgerian specimens of *Vulpavus* (e.g. AMNH 11498 and USNM 362847). In these animals the acromion

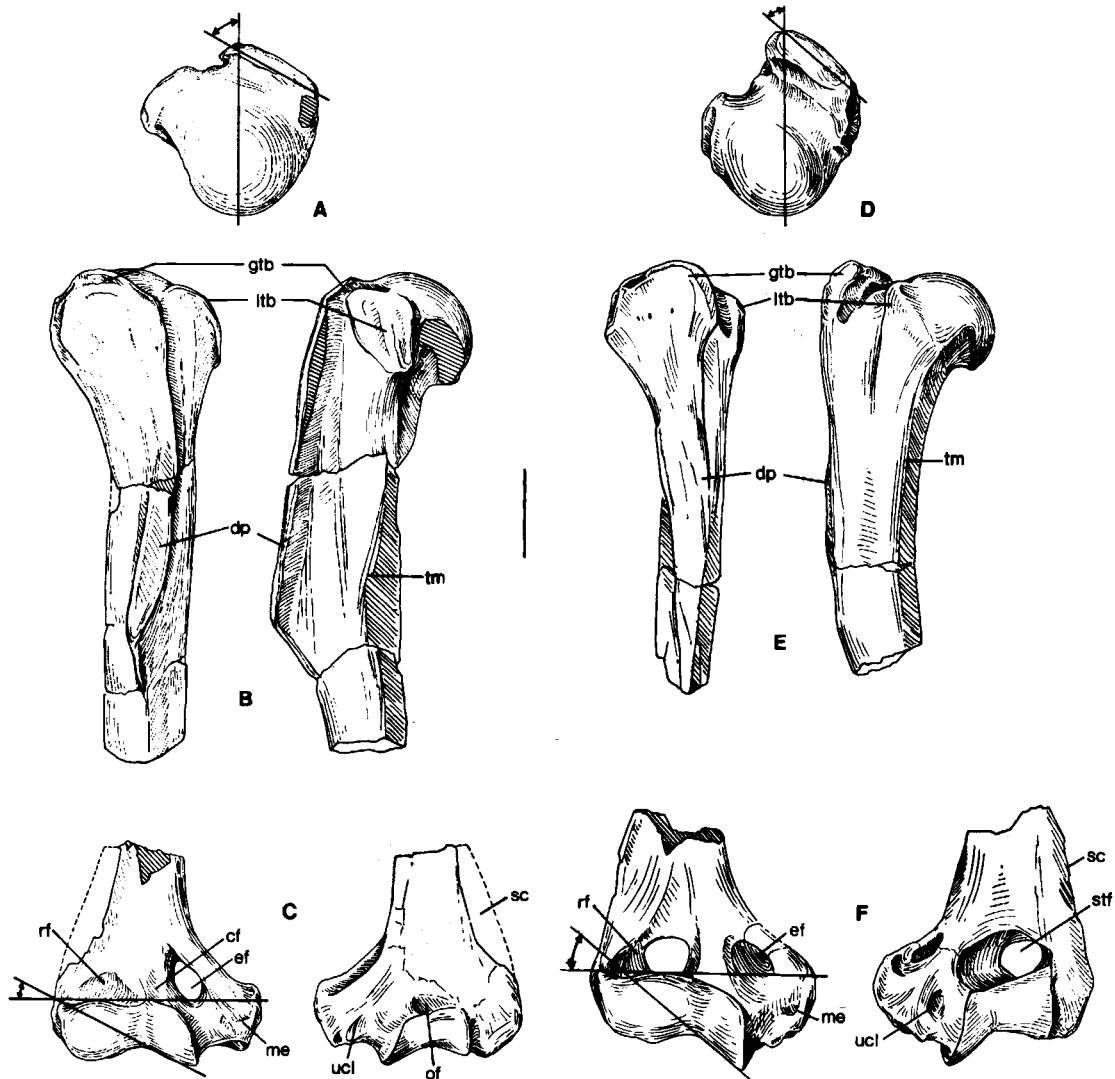
extends well beyond the glenoid fossa as in *Procyon* suggesting a well-developed m. acromiodeltoid and strong abduction (i.e. movement of the forelimb away from the midline of the body as opposed to adduction or movement towards the midline) capability. Wang (1993) also has described a relatively well developed clavicle (in AMNH 11498), a bone that is vestigial or absent in all modern Carnivora (Davis 1964). Unfortunately, the scapular spine is not well enough preserved in any specimen of *Didymictis* to discern the morphology of the acromion and no clavicle has yet been described.

Humerus. Humeral head shape is similar for *Vulpavus* and *Didymictis*, but the size and orientation of the greater and lesser tuberosities differ markedly. In proximal view, the greater tuberosity of *Vulpavus* is narrow and forms a relatively wide angle with the sagittal plane of the diaphysis or humeral shaft, while the greater tuberosity of *Didymictis* is wider and oriented more anteroposteriorly (note superimposed lines in Text-fig. 2A, D). Unlike *Vulpavus* which is similar to extant arboreal (Text-fig. 3A) and most scansorial carnivorans in that neither tuberosity projects above the humeral head (Taylor 1974; Leach 1977; Laborde 1986, 1987), the greater tuberosity of the *Didymictis* humerus is well-developed, extending farther both anteriorly and proximally than in the miacid (Text-fig. 2B, D), and being quite similar in this respect to the morphology found in *Canis* (Text-fig. 3B) and *Felis*. The bicipital groove, for the tendon of m. biceps brachii, is better defined in *Vulpavus* than in *Didymictis*, a characteristic *Vulpavus* shares also with extant arboreal taxa such as *Nandinia* (Taylor 1974).

Along the posteromedial aspect of the humerus of *Vulpavus*, just distal to the lesser tuberosity, is a relatively rugose insertion site probably for the muscles teres major and latissimus dorsi (Text-fig. 2B, D), large muscles involved in medial (i.e. internal) rotation of the shoulder joint and retraction of the forelimb (i.e. decreasing the distance between humeral shaft and axillary border of the scapula). The size and posteromedial flaring of this muscle attachment site gives the proximal diaphysis of *Vulpavus* a more markedly triangular cross sectional shape than the mediolaterally compressed humerus of *Didymictis*. Anteriorly, the deltopectoral crest of *Vulpavus* (on which insert important abductor, adductor, protractor and medial rotators of the forelimb) extends distally as a raised crest of bone that flares laterally just before ending abruptly at about midshaft (Text-fig. 2B, D). This morphology is not found among modern carnivorans but is very similar to that of the opossum *Didelphis* and the arboreal early Tertiary arctocyonid *Chriacus* (Rose 1987). In *Didymictis* the deltoid (i.e. lateral) margin of the deltopectoral crest is sharper and more distinct than the pectoral (i.e. medial) margin, and the deltopectoral crest is only slightly raised above the humeral shaft. Relatively wider proximally and occupying more of the anterior surface of the humerus than that of *Vulpavus*, the deltopectoral crest of *Didymictis* tapers distally and merges into the diaphysis well proximal to the midshaft (Text-fig. 2D), as occurs in extant cursorial carnivorans (Text-fig. 3B).

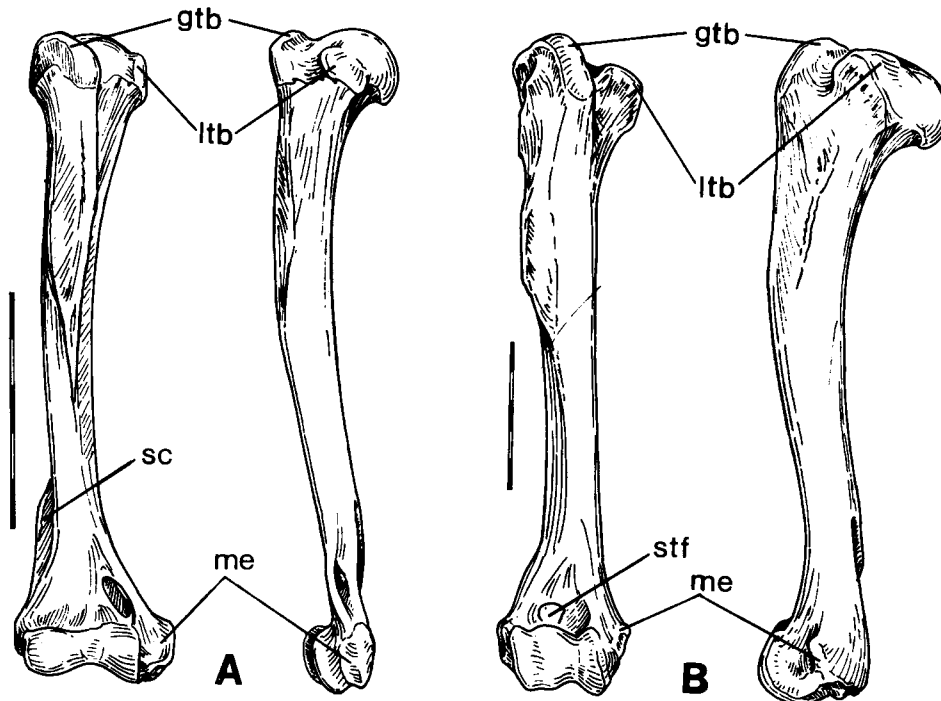
The distal humerus of miacoids has a large entepicondylar foramen and is transversely broad with a well-developed medial epicondyle (better developed in miacids than in *Didymictis*), the origin of m. pronator teres and the forearm and digital flexors (Text-fig. 2C, F). Large medial epicondyles are characteristic of carnivorans that climb and dig (Taylor 1974), are present but less well developed in *Felis* and *Viverra*, and are all but lost, along with the entepicondylar foramen, in cursorially specialized taxa like *Vulpes* and *Canis* (Text-fig. 3B). The lateral supinator crest of *Vulpavus* and *Didymictis* humeri are relatively wide and extend approximately one-half and one-third the length of the humerus respectively (Matthew 1901, 1915), providing a large attachment site for the flexor m. brachioradialis and the forearm and digital extensors. The size of the supinator crest in these miacoids is more similar to those of extant arboreal and scansorial taxa than to those of cursorial specialists (Text-fig. 3).

The capitulum (for articulation with the radial head) is relatively wide and cylindrical in miacoids (Text-fig. 2C, F), but the trochlea (for articulation with the ulna) of at least some early Eocene miacids such as *Uintacyon*, and all of the known Bridgerian *Vulpavus* (Matthew 1909, figs 26, 36) differs from that of *Didymictis* in having a medial trochlear rim that extends only minimally beyond, and at a relatively shallow angle to the capitulum (note difference in angles formed by the



TEXT-FIG. 2. Right proximal and distal humerus. Proximal humeri of *Vulpavus* (A–B, USGS 25219) and *Didymictis* (D–E, USGS 5024) in proximal (A and D), anterior (B and E left) and medial (B and E right) views. Angles formed by greater tuberosity and sagittal plane of the humerus (i.e. superimposed lines in A and D) are approximately 60° for USGS 25219 and 40° for USGS 5024. Distal humeri of *Uintacyon* (C, USGS 21910, supinator crest reconstructed from *Vulpavus* USGS 16488) and *Didymictis* (F, USGS 27585) in anterior (left) and posterior (right) views. Note steeper medial trochlear rim relative to the long axis of the capitulum (i.e. superimposed lines) in the viverrauid than the miacid. See Appendix for abbreviations. Scale bar represents c. 10 mm.

superimposed lines in Text-fig. 2C, F). This is similar to the morphology found in arboreal carnivorans (Text-fig. 3A). Other early Eocene miacids, however, including *Miacis petilus* (Heinrich and Rose 1995), *Vassacyon promicrodon* and possibly Wasatchian *Vulpavus*, possess a trochlear rim morphology more similar to those of *Didymictis* and the scansorial carnivorans *Martes* and *Nasua*. All miacids are similar to the arborealists *Nandinia* and *Potos* in having a well delineated coronoid

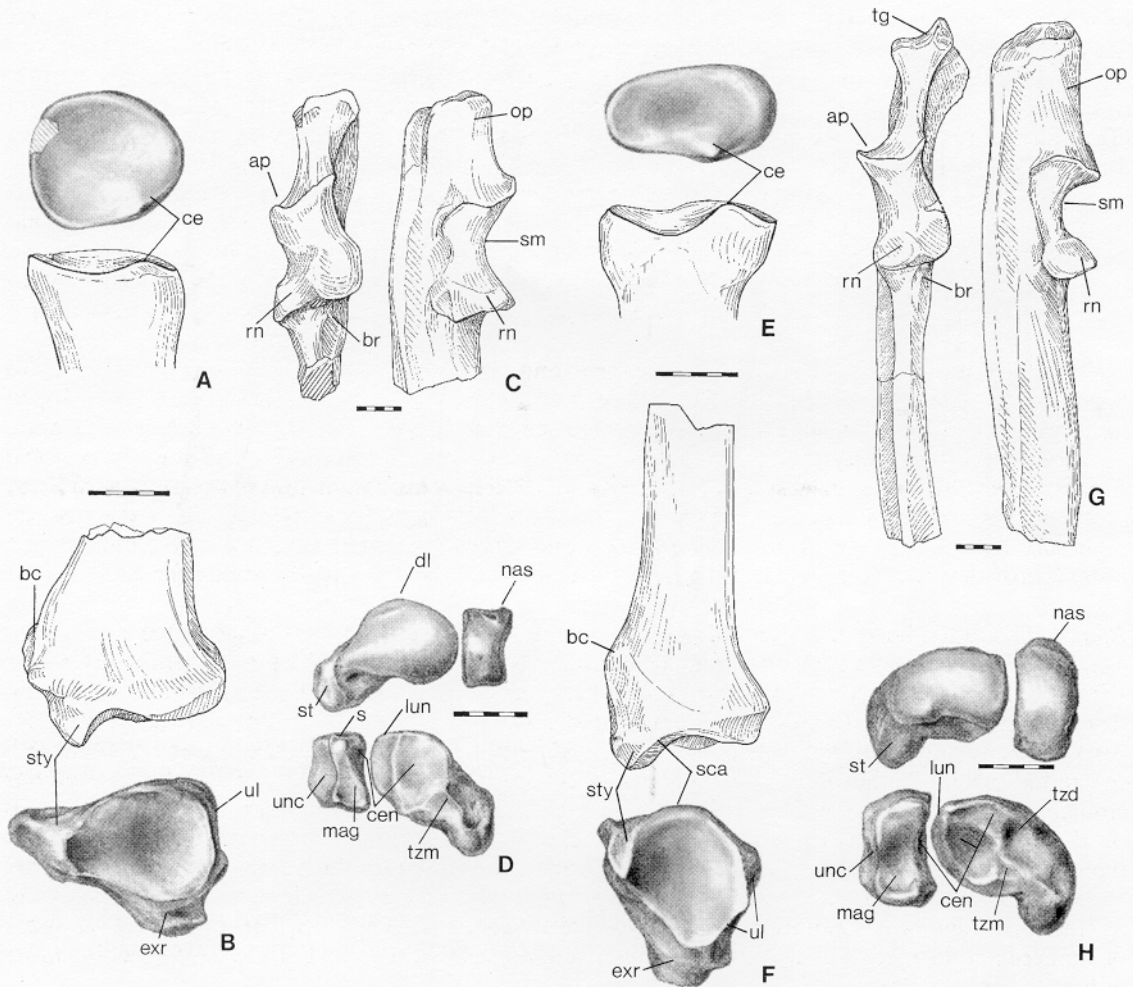


TEXT-FIG. 3. Anterior (left) and medial (right) views of humeri belonging to the extant carnivorans *Arctictis binturong* (A, USNM 49642) and *Canis lupus* (B, USNM 324994). See Appendix for abbreviations. Scale bars represent 50 mm.

fossa (Text-figs 2C, 3A) proximal to the trochlea proper, suggesting habitual use of highly flexed forelimb postures. The coronoid fossa is absent in *Didymictis* and modern carnivorans like *Canis* (Text-fig. 3B).

The extremely shallow olecranon fossa of miacids is similar to that of the extant *Potos*, and is in striking contrast to the perforate supratrochlear foramen of *Didymictis* (Text-fig. 2F). The combination of perforate foramen and deeply grooved and angled (rather than proximodistally aligned trochlea as in canids; Text-fig. 3B) posterior trochlea in the viverravid is similar to the morphology found in badgers such as *Mellivora*, and indicates a significantly greater range of extension at the elbow and an enhanced stability of the humeroulnar articulation relative to *Vulpavus*. Between the medial epicondyle and the trochlear rim posteriorly, is a pit for attachment of the ulnar collateral ligament, a structure which anchors the semilunar notch of the ulna to the humerus (Evans and Christensen 1979). This pit is considerably larger and deeper in *Didymictis* than in miacids (Text-fig. 2C, F).

Ulna. The ulnae of *Vulpavus* and *Didymictis* are mediolaterally compressed along their entire length with posterior diaphyseal borders that are slightly convex proximally (opposite the semilunar notch) and, at least in *Didymictis*, concave more distally (Text-fig. 4c, G). The olecranon process is nearly straight in both taxa but relatively longer in *Didymictis* than in *Vulpavus* (and most extant carnivorans), providing the viverravid with increased leverage for the forearm extensor, m. triceps. Bridgerian specimens of *Vulpavus* differ from those of the lower Eocene in that the olecranon process proximal to the semilunar notch is inclined anteriorly (Matthew 1915) as in the most



TEXT-FIG. 4. Right proximal and distal radius, proximal ulna, and carpal bones. Proximal radii of *Vulpavus* (A, USGS 5025) and *Didymictis* (E, USGS 21836, reversed) in proximal (top) and anterior (bottom) views. Distal radii of *Vulpavus* (B, USGS 25219) and *Didymictis* (F, USGS 25039) in posterior (top, forearm pronated) and distal (bottom) views. Ulnae of *Vulpavus* (C, USGS 25219) and *Didymictis* (G, USGS 5024) in anterior (left) and lateral (right) views. Scaphoid and lunar bones (D and H) in proximal (top) and distal (bottom) orientations, the dorsal margin of the bones is towards the top of the page. Scaphoids of *Vulpavus* (USGS 5025) and *Didymictis* (USGS 25039), lunars of *Miacis* (AMNH 11496) and *Didymictis* (USGS 25038). See Appendix for abbreviations. Scale bars represent 5 mm.

arboreal of extant carnivores (Taylor 1974; Van Valkenburgh 1987). The proximalmost aspect of the olecranon process is higher medially than laterally in both miacoids, but in *Didymictis* this proximal projection is enhanced and a distinct groove for the tendon of *m. triceps brachii* is present (Text-fig. 4G). A well-developed *m. triceps* tendinal groove is found in extant carnivorans where rapid and complete extension of the forearm are important during locomotion.

The anconeal process of *Didymictis*, and particularly the lateral margin, projects farther anteriorly than that of *Vulpavus*, producing a deeper, more concave semilunar notch than in the miacid (Text-fig. 4C, G). This smaller radius of curvature results in a more congruent articulation between ulna and the humeral trochlea of *Didymictis* throughout the range of flexion and extension.

More specifically, a strong contact is created between the lateral margin of the anconeal process and the posteriorly projecting medial trochlear margin which effectively locks the anconeal process in the trochlea during extension. By contrast, in *Vulpavus* and the arboreal *Potos*, the semilunar notch is less well defined and the lateral anconeal margin is distal and posterior to the medial margin (Text-fig. 4C) resulting in a smaller area of articular contact between ulna and the humeral trochlea during extension.

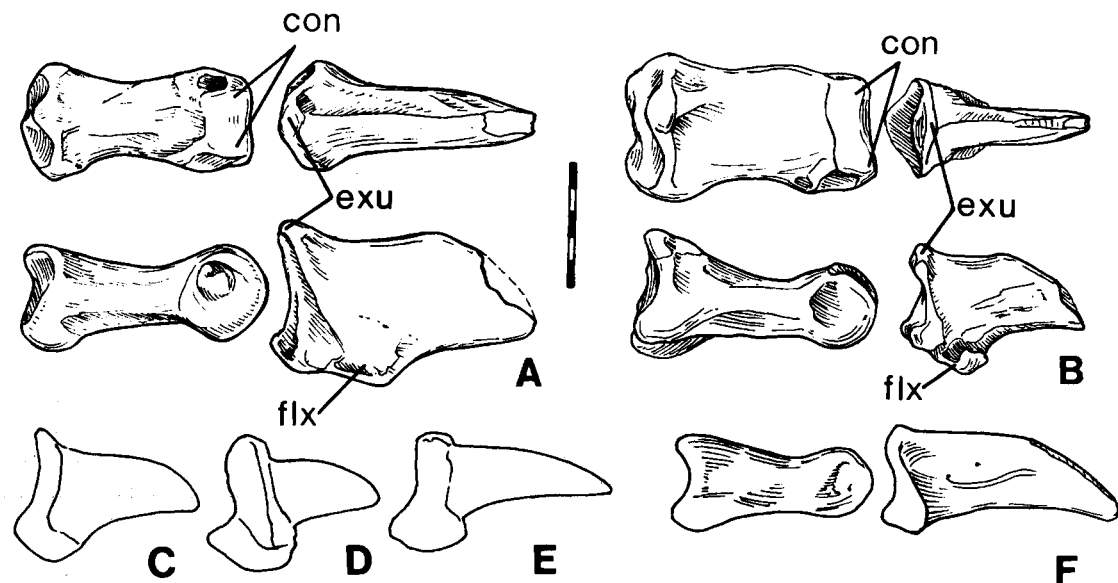
The radial notch (i.e. articular surface for radial head) of both *Vulpavus* and *Didymictis* is relatively flat. *Vulpavus* differs, however, in having a long and narrow anterolaterally facing radial notch whilst that of *Didymictis* is nearly as wide proximodistally, as long anteroposteriorly and somewhat more anteriorly directed (Text-fig. 4C, G). A long and narrow muscle scar just distal to the coronoid process (Text-fig. 4C, G) of both miacoids is probably the insertion site of the forearm flexor m. brachialis.

Distally, the anterior ulna of both *Vulpavus* and *Didymictis* flattens and widens, both sides bordered by sharp bony flanges. This large surface area implies a relatively well developed m. pronator quadratus in both taxa, a muscle that helps to pronate the forearm such that the palm of the forefoot is on the ground during locomotion. As in other miacids (Heinrich and Rose 1995), *Vulpavus* and *Didymictis* possess a flattened articular facet for the radius that is well separated from a second hemispherical facet at the end of the short, robust styloid process. The only obvious difference between the distal ulnae of *Vulpavus* and *Didymictis* is the presence in the miacid of a bony flange that projects posteriorly from the carpal articular facet of the styloid process.

Radius. The radial head of *Vulpavus* is remarkably round with a small capitular eminence (Text-fig. 4A), and the proximal surface is oriented obliquely to the long axis of the radial shaft (Matthew 1915, fig. 28), with the posterolateral margin being notably higher than the anteromedial margin (forearm in pronation). In contrast, the proximal surface of the radial head of *Didymictis* is nearly perpendicular to the diaphysis, its outline is strongly elliptical, with the margin for articulation with the radial notch of the ulna being much less convex than that of *Vulpavus*, and the capitular eminence is much better developed (Text-fig. 4E). Analysis of radial head outline shape demonstrates similarities between *Vulpavus* and extant arboreal mammals capable of considerable supination on the one hand, and *Didymictis* and cursorial and fossorial forms on the other (MacLeod and Rose 1993). Proximally, the radial diaphysis of *Vulpavus* is relatively circular in cross section compared to the mediolaterally compressed diaphysis of *Didymictis*. The bicipital tuberosity is more prominent and located farther from the radial head in *Vulpavus* than in *Didymictis*, suggesting more powerful forearm flexion in the miacid.

The distal radius of *Vulpavus* is wide and flat posteriorly and convex anteriorly, giving it a semilunar shape in cross section (Text-fig. 4B). In contrast, the distal diaphysis of *Didymictis* is almost triangular in cross section, with a considerably wider lateral (i.e. ulnar) margin than *Vulpavus* (Text-fig. 4F), and in this respect closely resembles radii of herpestids and *Viverra*. The facet for articulation with the ulna is somewhat larger and more concave in *Didymictis* than *Vulpavus*. Unlike *Vulpavus*, the radiocarpal surface of *Didymictis* possesses an expanded scaphoid articular surface that extends over the posteromedial lip as a convex facet (Text-fig. 4F). In modern carnivorans such as canids and felids, this expanded articular surface is even more prominent and functions to increase the range of flexion possible at the radiocarpal joint (Yalden 1970).

Carpus. The carpus of early Eocene miacoids is poorly known, and descriptions and comparisons of carpal morphology are limited here to the scaphoid and lunar. Although fusion of these two bones along with the centrale into a single scapholunar bone is common to all living Carnivora (Flower 1871), among Wasatchian and Bridgerian miacids a fused scapholunar has been described only for *Vassacyon promicrodon* (Matthew 1915) and *Vulpavus profectus* (Matthew 1909), although fusion of the centrale and scaphoid has also been noted for *Palaearctonyx meadi* (Matthew 1909). The scaphoid and lunar are not fused in the single *Vulpavus* specimen known from the Willwood Formation, and Scott (1888) had previously noted that none of the three bones is fused in



TEXT-FIG. 5. Middle (left) and ungual (right) phalanges of *Vulpavus* (A, USNM 362847 and USGS 5025 respectively) and *Didymictis protenus* (B, USGS 27585 reconstructed in part from AMNH 2855) in dorsal (top) and lateral (bottom) views, and *Didymictis altidens* (C, AMNH 14781 after Matthew 1915, text-fig. 19) in lateral view. Unguals of extant carnivorans *Martes pennanti* (C, USNM 188226), *Viverra zibetha* (D, USNM 240208), and *Canis latrans* (E, USNM 49889). See Appendix for abbreviations. Scale bar represents 5 mm; C-F not drawn to scale.

Didymictis. The sporadic occurrence of a fused scapholunar among miacoids led Flynn *et al.* (1988) to conclude that the scapholunar was acquired independently in various carnivoran lineages.

1. Scaphoid. The proximal scaphoid of *Vulpavus* (for articulation with the radius) is not uniformly convex, as in *Didymictis*, but relatively flatter dorsally than ventrally. The dorsalmost aspect possesses a slight lip (Text-fig. 4D) which would have come into contact with the radius during maximal extension at the radiocarpal joint. Laterally, the proximal scaphoid articular surface of *Vulpavus* is wide and convex but it narrows medially, pinching off at the base of the medially projecting scaphoid tubercle (Text-fig. 4D). In contrast, the proximal scaphoid of *Didymictis* is nearly rectangular in outline and lacks a lip along the dorsal margin (Text-fig. 4H). The prominent scaphoid tubercle extends more ventrally than laterally, and there is some slight expansion of the articular surface onto the base of the tubercle (Text-fig. 4H). This latter expansion is not as well developed as in canids and felids, where a distinct concave articular surface between tubercle and proximal scaphoid (Yalden 1970; Gonyea 1978) comes into contact with the posterior margin of the radiocarpal surface during hyperflexion at this joint (Yalden 1970), but the expanded articular surface found on the *Didymictis* scaphoid probably functioned in a similar manner.

The lunar facet of the scaphoid is relatively larger in *Vulpavus* than in *Didymictis*, but in both it is flat and oriented distolaterally (Text-fig. 4D, H). Medial to the lunar facet is the centrale facet which in *Vulpavus* extends as a slightly concave articular surface from the dorsal to the ventral margins of the scaphoid. In *Didymictis* the centrale facet is divided by a small ridge into a larger, oval, ventral facet and a smaller, more elongate, dorsal facet (Text-fig. 4D, H). Medial to the ventral aspect of the centrale facet in both miacoids is the small, rounded trapezium facet (Text-fig. 4D, H). The trapezoid of *Vulpavus* probably articulated only with the centrale, while in *Didymictis* the trapezoid may also have articulated with the scaphoid (Text-fig. 4D, H).

2. Lunar. Whilst the proximal articular surface of the miacid lunar is relatively narrow along its entire dorsoventral curvature, it is further restricted to the medial margin dorsally by a non-articular shelf of bone (Text-fig. 4D). This non-articular shelf, much reduced in *Didymictis* (Text-fig. 4H), probably served as a ligamentous attachment site. In both miacoids the lateral margin of the lunar has two articular facets, a relatively narrow, flat facet for the cuneiform (not well preserved for the available *Didymictis* specimen, USGS 25038), and a more distally oriented, concave articular surface for the unciform. In miacids, the unciform facet is wider dorsally than ventrally (Text-fig. 4D).

The lunar of miacoids has two additional articular surfaces, a large, distally oriented magnum facet and a small, more medially oriented facet for articulation with the centrale (Text-fig. 4D). In miacids the magnum facet is triangular, being wider ventrally than dorsally, and moderately concave except for its dorsalmost aspect which is nearly flat (Text-fig. 4D). This flat articular surface, set at an angle to the remainder of the magnum facet, is reminiscent of the morphology found in modern carnivorans in which a stop mechanism between magnum and lunar exists to prevent hyperextension at the midcarpal row (Yalden 1970). The magnum facet of *Didymictis* is rectangular rather than triangular, and more concave than that of miacids (Text-fig. 4H). No stop mechanism is apparent but this may be due to incomplete preservation of the bone. The centrale facet of the lunar is relatively larger and more nearly perpendicular to the magnum facet in *Didymictis* than in miacids (Text-fig. 4H).

Metacarpals and phalanges. Metacarpals and phalanges are poorly preserved for the miacoids of the Willwood Formation, preventing comparisons of their relative proportions both with one another and with other forelimb elements. In general, metacarpal (and metatarsal) diaphyses of *Didymictis* are dorsoventrally flatter than those of *Vulpavus*, and the proximal phalanges appear to differ only in that the distal articular surface is more deeply grooved in *Didymictis* than in *Vulpavus*. There are, however, several notable differences in the middle and ungual phalanges of these two fossil carnivorans.

In addition to having a less prominent dorsoventral median ridge on the proximal articular surface, the middle phalanges of *Didymictis* differ from those of *Vulpavus* in having a more noticeable articular condyle asymmetry and a distinct flattening of the dorsal surface proximal to the articular head (Text-fig. 5A–B). This asymmetry and dorsal flattening of the middle phalanges of *Didymictis* resembles, superficially, that of the phalanges of felids and viverrids, carnivorans that possess retractile claws (Gonyea and Ashworth 1975). The middle phalanges of *Didymictis* differ from those of these modern carnivorans, however, in lacking the excavated lateral margin of the phalanx past which the ungual is retracted.

The ungual or terminal phalanges of *Vulpavus* and *Didymictis protenus* are similar in being strongly compressed mediolaterally, in having a strongly curved dorsal margin (particularly near the tip of the bone), in possessing relatively well developed dorsal extensor and ventral flexor tubercles, and in lacking the dorsal fissure characteristics of extant fossorial mammals (Hildebrand 1985) and many creodonts (Denison 1938). They differ, however, in that the unguals of *Didymictis protenus* have a relatively wider proximal articular surface and the body of the phalanx is dorsoventrally narrower/shallower (Text-fig. 5A–B). Interestingly, the unguals of *D. protenus* are quite unlike those of the later early Eocene species *Didymictis altidens* (Text-fig. 5F), a morphological difference that does not appear to be expressed in other parts of the skeleton. The terminal phalanges of this younger taxon are relatively longer and less curved, and lack the well-developed flexor tubercle characteristic of *D. protenus* (Text-fig. 5B, F). These differences in ungual morphology may relate to fore- and hindlimb phalangeal comparisons (all unguals known for *D. altidens* are from the hindlimb while those attributed to *D. protenus* are indeterminate), but given that there is a number of unguals known for *D. protenus*, all with the same general morphology, this explanation for the morphological variation seems unlikely.

Comparisons of lateral ungual outline shape between miacoids and modern taxa indicate that the unguals of *Vulpavus* are most similar to those of mammals classified as arboreal, while those of

D. protenus and *D. altidens* are generally similar to scansorial and terrestrial mammals respectively (MacLeod and Rose 1993). There is, however, considerable overlap between ungual morphologies and some types of locomotor behaviour, and although *D. protenus* shares many ungual attributes with scansorial taxa such as *Martes* (Text-fig. 5C), its unguals are not unlike those of the more strictly terrestrial and moderately cursorial *Viverra* (Text-fig. 5D). The unguals of *D. altidens*, on the other hand, resemble those of cursorial carnivorans like *Canis* (Text-fig. 5E) and, probably to an even greater extent, the terminal phalanges of semifossorial badgers like *Meles* (MacLeod and Rose 1993).

Functional morphology of the forelimb

Glenohumeral joint and brachium. The shoulder morphology of *Vulpavus* differs from that of *Didymictis* in ways that indicate a greater range of motion at the glenohumeral joint and increased leverage of extrinsic shoulder musculature acting on the arm. Relatively greater mobility at this joint is inferred for *Vulpavus* from the shallow glenoid fossa and the low and angled greater and lesser tuberosities, both of which are indicative of habitually employed medial and lateral rotation at the shoulder. Reduced mobility at the glenohumeral joint of *Didymictis* is suggested by the deep, rounded glenoid fossa, and the proximally projecting and anteroposteriorly aligned greater tuberosity. Morphology of the greater tuberosity in particular, indicates restricted abduction of the humeral head and at the same time increased leverage of *m. supraspinatus*, a muscle that helps stabilize the shoulder joint during terrestrial locomotion (Taylor 1974; Jenkins and Weijs 1979; Larson and Stern 1989, 1992).

The insertion sites for flexor, protractor and abductor-adductor musculature are more prominent and positioned farther distally in *Vulpavus* than in *Didymictis*, indicating that the miacid generated relatively larger forces with many of the muscles that cross the shoulder joint than did the viverravid. Specifically, *Vulpavus* possesses a high deltopectoral crest that extends to midshaft, a character that has been equated with enhanced climbing abilities in small carnivorans (Taylor 1974), and a prominent posteriorly projecting crest of bone for insertion of *mm. latissimus dorsi* and *teres major*. Insertion sites for these same muscles in *Didymictis* are much less well defined and their more proximal position suggests that muscular force was compromised in favour of speed of contraction (Hildebrand 1988).

Humeroulnar and radioulnar joints. The large medial epicondyle, moderately well developed supinator crest, wide trochlea and capitulum, and angled olecranon fossa of the distal humerus characteristic of both *Vulpavus* and *Didymictis* are traits common to carnivorans that habitually climb or dig. In addition, however, *Vulpavus* possesses a distinct coronoid fossa, only moderately grooved posterior trochlea, and a shallow olecranon fossa, all of which are indicative of an emphasis on flexed rather than extended forelimb postures, implying that the animal was adapted for climbing. In contrast, the humeroulnar joint of *Didymictis*, with its perforate supratrochlear foramen, deeply grooved trochlea, long olecranon process, and trochlear rim that extends well distal to, and at a relatively sharp angle to the capitulum, possesses characters which serve to maximize forearm extension and increase stability of the humeroulnar joint by 'locking' the semilunar notch in the trochlea. The humeroulnar joint of *Didymictis*, therefore, is most similar in morphology to that of semifossorial carnivorans such as badgers which produce large forces across this joint.

At the proximal radioulnar joint, the nearly round radial head of *Vulpavus* suggests that this animal was capable of substantial supination (perhaps up to 180°), whereas the ovoid radial head and anterolaterally facing radial notch in *Didymictis* indicate significantly less motion at this joint in the viverravid. The relatively large capitular eminence in *Didymictis* may also have restricted rotation of the radial head (Davis 1964), although an alternative function of this structure may be to stabilize the elbow in flexion, with the capitular eminence coming into contact with the medial

capitular wall and preventing lateral movement of the ulna on the trochlea. In either case the well-developed eminence of *Didymictis* is also indicative of increased stability in the elbow relative to *Vulpavus*.

Radiocarpal joints and manus. Several characters of the proximal carpal row indicate that the radiocarpal joint of *Didymictis* was modified primarily for flexion and extension while no such specializations are found in the wrist of *Vulpavus*. The proximal scaphoid of the miacid has a larger radius of curvature than that of *Didymictis*, and a dorsal lip that probably served to limit rather than increase extension as the scaphoid came into contact with dorsal margin of the radiocarpal articular surface of the radius. Flexion at the radiocarpal joint of *Didymictis* was enhanced by expansion of the scaphoid articular surface on to the base of the scaphoid tubercle. This results in an articulation between the scaphoid and distal radius that is comparable to that found in extant carnivorans, but which is particularly well developed in cats and dogs where it allows for a range of flexion sufficient to prevent contact between the foot and opposite forelimb as the foot swings forward to initiate the next step in the gait cycle (Yalden 1970).

The morphology of the middle and distal phalanges of *Vulpavus* (specifically the well-developed median ridge of the proximal articular surface and lack of asymmetry in the distal articular condyles of the middle phalanx, and the strong flexor tubercle and deep body of the unguals), indicates strong symmetrical flexion of the phalanges, probably an adaptation for digging the claws into tree-trunks and limbs during climbing. The unguals of *D. protenus* and *D. altidens* display two very different morphologies. *D. protenus*, the smaller and older of the two taxa, has relatively short, curved unguals that are more similar to those of *Vulpavus* than those of *D. altidens* and suggest that *D. protenus* may have done some climbing. The longer and less curved unguals of *D. altidens* more closely resemble those of strictly terrestrial extant carnivorans, particularly semifossorial taxa, suggesting that this species was a more proficient scratch digger than *D. protenus*.

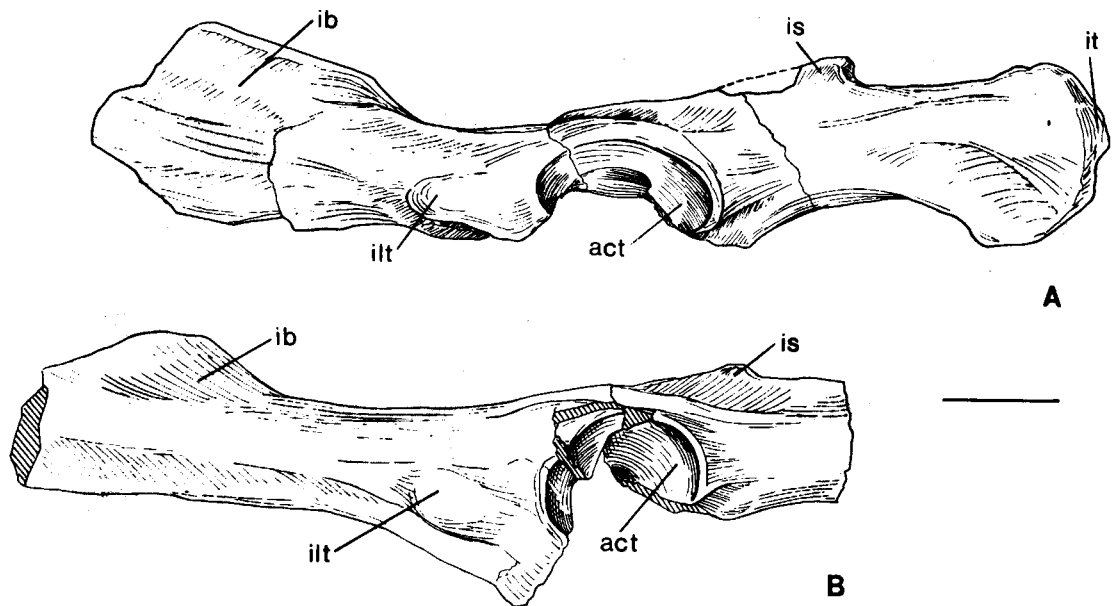
The dorsally flattened middle phalanx and slight asymmetry of the condyles, common to both *D. protenus* and *D. altidens* (but not found in *Vulpavus*), suggest that these animals could partially retract the unguals into a position on the dorsum of the middle phalanx. They were not, however, capable of fully retracting the unguals alongside the diaphysis of the middle phalanx as occurs in modern felids and viverrids. Retractable claws are considered to be important for manipulating prey during killing (Gonyea and Ashworth 1975). Given that fully retractile claws are not found in either miacid or viverravid carnivorans, claw retractibility is unlikely to have been the primitive condition for Carnivora as argued by Flynn *et al.* (1988).

HINDLIMB MORPHOLOGY

Description and comparisons

Innominate. The acetabulum or hip socket of both *Vulpavus* and *Didymictis* is buttressed anterodorsally, and a prominent tubercle for origin of the thigh flexor and leg extensor m. rectus femoris, lies just in front of the acetabulum (Text-fig. 6A-B). Among modern carnivorans this tubercle is better developed in scansorial than terrestrial taxa (Laborde 1986). The ventral margin of the ilium is quite wide in both miacoids, providing a large surface for the origin of a second important thigh flexor, m. iliacus. The lateral aspect of the iliac blade, however, appears wider and more concave in *Vulpavus* than in *Didymictis* (Text-fig. 6A-B), suggesting a relatively greater adductor muscle mass in the miacid.

Posterior and dorsal to the acetabulum is the ischial spine, a partial origin for the gemelli muscles which abduct and laterally rotate the thigh. This spine is significantly more robust and situated farther from the acetabulum in *Vulpavus* than *Didymictis*. Among modern carnivorans the ischial spine is particularly well developed and positioned further posteriorly in the arboreal taxa *Potos* and *Arctictis*. In contrast, cursorial carnivorans such as *Vulpes* and *Canis* which have much less mobility at the hip joint (Jenkins and Camazine 1977), have poorly developed ischial spines. A greater distance between ischial spine and hip joint increases the mechanical advantage of the gemelli

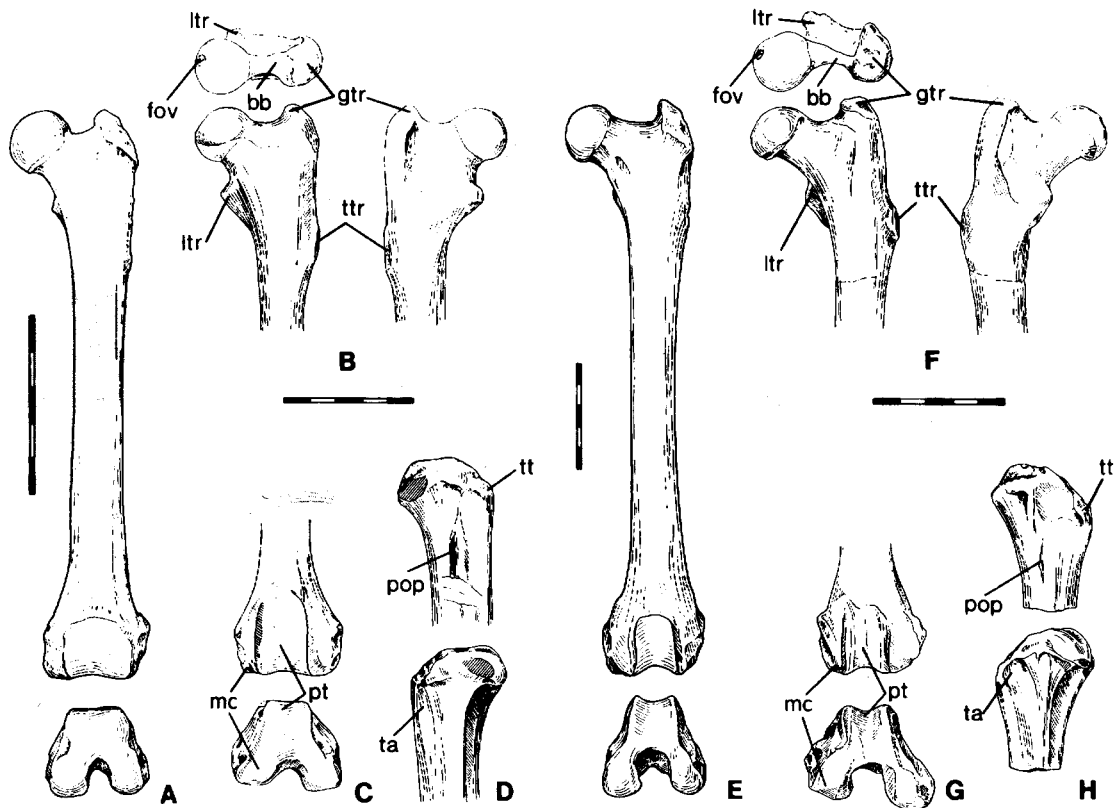


TEXT-FIG. 6. Left innominate of *Vulpavus* (A, USGS 16488, reversed) and *Didymictis* (B, reconstructed from USGS 21835 and 6087) in lateral views. See Appendix for abbreviations. Scale bar represents 10 mm.

musculature, hence abduction and particularly lateral rotation of the thigh was probably stronger in *Vulpavus* than in *Didymictis*. The ischial tuberosity, preserved only for *Vulpavus* (Text-fig. 6A), is relatively broad and heavily scarred along its margin, indicating strong muscle attachments for the extensors of the thigh.

Femur. The femoral head of *Vulpavus* is quite round, the articular surface extends well onto the femoral neck, and the femoral neck is relatively short (Text-fig. 7B), characters shared with modern arboreal (Text-fig. 7A) and scansorial carnivorans. In contrast, the femoral head of *Didymictis*, and terrestrial taxa generally, has a greater radius of curvature (i.e. forms a less complete sphere than that of *Vulpavus*), the articular surface is restricted to the margin of the head or is minimally expanded onto the femoral neck, and the femoral neck is elongate (Text-fig. 7E-F). The greater trochanter of *Didymictis* projects above the femoral head, and the ridge of bone joining the head and greater trochanter is much narrower anteroposteriorly (particularly notable just medial to the greater trochanter) than that of the miacid (Text-fig. 7B, F). A greater trochanter that projects above the femoral head is common to cursorial and saltatorial mammals (Howell 1944), where it enables *m. gluteus medius* to act as a powerful extensor particularly in the later stages of retraction (Taylor 1976; Evans and Christensen 1979). Among modern carnivorans, the only taxa found to have the distinct anteroposterior narrowing of bone between femoral head and greater trochanter are canids, which also possess a less spherical femoral head and long femoral neck as in *Didymictis*.

The lesser trochanter, for insertion of *m. iliopsoas*, projects more posteriorly than medially in *Didymictis*, canids, herpestids and terrestrial viverrids, while in *Vulpavus* and extant arboreal and scansorial taxa the lesser trochanter is oriented medially (Text-fig. 7B, F). Taylor (1976) has suggested that a more medially directed lesser trochanter provides for increased mobility and specifically enhanced lateral rotation at the hip. The proximal femoral diaphysis of early Eocene miacoids, and particularly *Didymictis*, is bowed or medially inflected (Text-fig. 7B, F) as in creodonts (Denison 1938; Gebo and Rose 1993), and is quite unlike the straight femoral diaphysis of most modern taxa (Text-fig. 7B, F). This morphology is made more prominent by an enlarged third trochanter, the insertion site of the superficial gluteal muscle. The superficial gluteal muscle is of

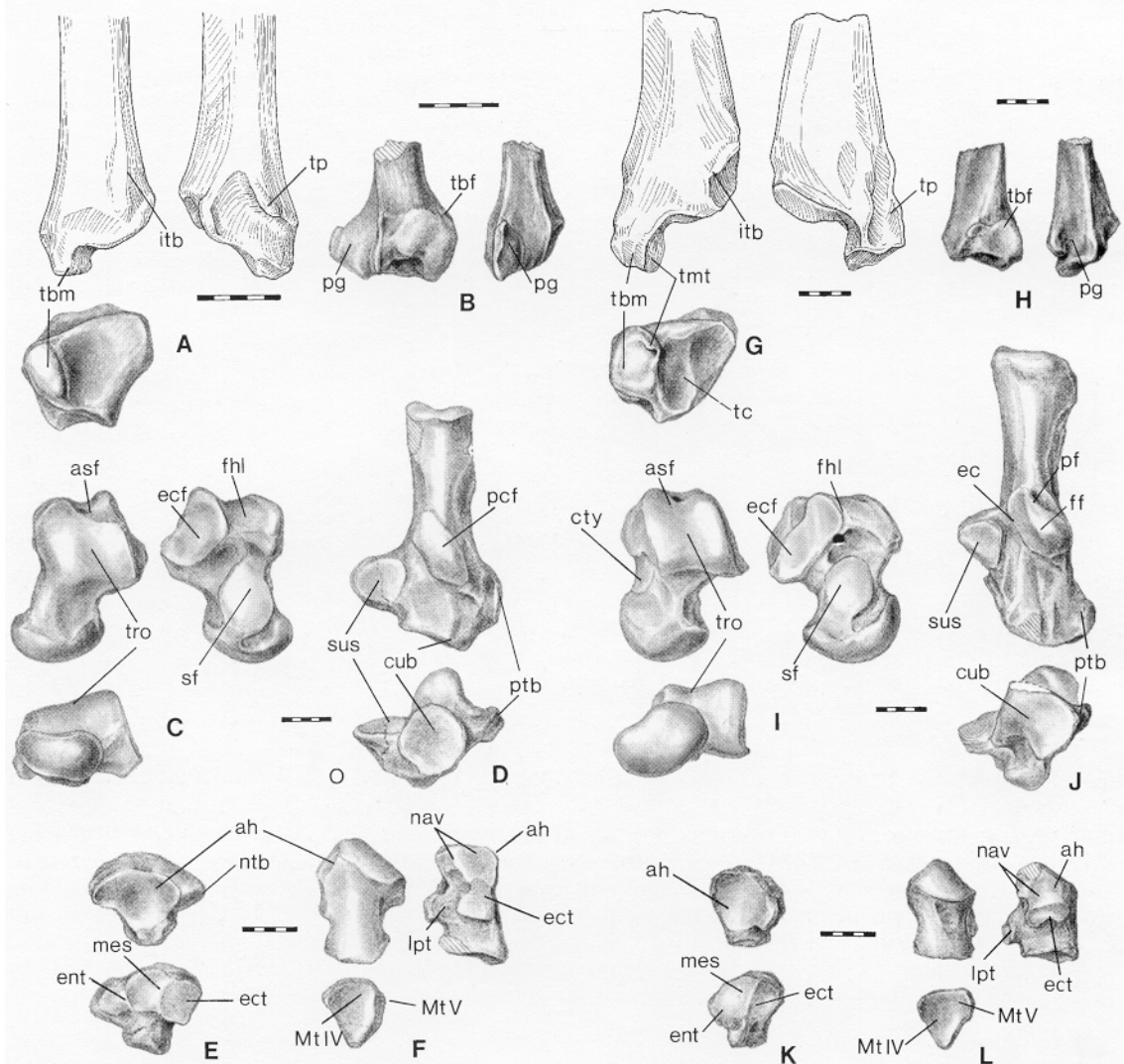


TEXT-FIG. 7. Left femur and proximal tibia. Femora of *Paradoxurus hermaphroditus* (A, USNM 49868) and *Viverra zibetha* (E, USNM 256673, greater trochanter restored from the right side), arboreal and terrestrial extant carnivorans respectively. Proximal femora of *Vulpavus* (B, USGS 7143, reversed) and *Didymictis* (F, USGS 6087, reversed) in proximal (top), anterior (left), and posterior (right) views. Distal femora of *Vulpavus* (C, USGS 7143, reversed) and *Didymictis* (G, USGS 25040, reversed) in anterior (top) and distal (bottom) views. Proximal tibiae of *Vulpavus* (D, USNM 362847, reversed) and *Didymictis* (H, USGS 5024) in medial (top) and lateral (bottom) views. See Appendix for abbreviations. Scale bars represent 25 mm.

variable size and function among modern carnivorans, acting as a flexor and medial rotator of the thigh in *Ailuropoda* (Davis 1964), primarily an extensor of the thigh in *Canis* (Evans and Christensen 1979), and an abductor of the thigh in *Felis* (Gilbert 1968). The position and orientation of the third trochanter of *Vulpavus* and *Didymictis* suggests that the superficial gluteal muscle acted primarily as a flexor and medial rotator much as in bears.

Distally, the femur of miacoids is characterized by having medial and lateral condyles of similar width and a rugose medial epicondyle, for attachment of the medial collateral ligament. The distal femur of *Didymictis* from patellar trochlea to posteriormost aspect of the femoral condyles is deeper anteroposteriorly than that of *Vulpavus*, and the trochlea of *Didymictis* is more deeply grooved (Text-fig. 7C, G), closely resembling the morphology found in canids, felids, herpestids and *Viverra* (Text-fig. 7E). The wide and relatively flat patellar trochlea of *Vulpavus* is similar to that of extant scansorial and arboreal taxa such as *Bassariscus* and *Paradoxurus* (Text-fig. 7A), as well as the arboreal early Eocene arctocyonid *Chriacus* (Rose 1987).

Tibia. The proximal tibiae of *Vulpavus* and *Didymictis* are similar in having a saddle-shaped medial condyle (convex anteroposteriorly and concave mediolaterally) that is higher than the nearly flat



TEXT-FIG. 8. All elements from left side. Distal tibiae of *Miacis* (A, USGS 7161) and *Didymictis* (G, USGS 27585) in anterior (left), posterior (right), and distal (bottom) views. Distal fibulae of *Miacis* (B, USGS 7161) and *Didymictis* (H, USGS 16472) in medial (left) and posterior (right) views. Astragali of *Vulpavus* (C, USNM 362847) and *Didymictis* (I, USGS 27585) in dorsal (left), ventral (right), and distal (bottom) views. Calcanei of *Vulpavus* (D, USGS 7143, partly reconstructed from a second *Vulpavus* specimen, USGS 25186) and *Didymictis* (J, USGS 27585) in dorsal (top) and distal (bottom) views. Naviculars of *Vulpavus* (E, USGS 5025) and *Didymictis* (K, AMNH 2855) in proximal (top) and distal (bottom) views. Cuboids of *Vulpavus* (F, USGS 5025, reversed and partially reconstructed from *Vulpavus*, USGS 25186) and *Didymictis* (L, AMNH 2855, reversed) in dorsal (left), medial (right), and distal (bottom) views. See Appendix for abbreviations. Scale bars represent 5 mm.

lateral condyle, and in having a sharp ridge that extends distally from the posterior border of the medial condyle, probably separating the m. tibialis posterior laterally from the knee flexor m. popliteus medially. The tibial tuberosity of *Didymictis* is narrower and projects farther anteriorly than that of *Vulpavus*, and the m. tibialis anterior fossa lateral to the tuberosity, is more deeply

excavated in the viverrid (Text-fig. 7D, H). In both of these respects *Didymictis* is similar to modern cursorial carnivorans. On the anteromedial surface of the tibial shaft is a large raised tubercle (probably the insertion site of m. popliteus) that is better developed and more distally situated in *Vulpavus* than *Didymictis* (Text-fig. 7D, G), suggesting more powerful flexion and medial rotation of the crus in the miacid. The tibial diaphysis of both *Vulpavus* and *Didymictis* is compressed mediolaterally along most of its length.

The distal tibia of miacoids bears a raised tubercle that runs from the lateral margin of the bone obliquely to the anterior surface. This interosseous tubercle (Text-fig. 8A, G) is more prominent in *Didymictis* than in *Vulpavus*, and was probably an attachment site for a strong interosseous membrane or syndesmosis between tibia and fibula. The tubercle is reduced in those modern carnivorans in which it can be discerned at all (e.g. *Potos*). On the posterior and medial aspect of the tibia is a second, well-defined tubercle, lateral to which passed the m. tibialis posterior tendon. In *Vulpavus* and other miacids (Text-fig. 8A, G), as in modern scansorial and arboreal carnivorans, this tibialis posterior tubercle angles anteriorly well proximal to the tibial malleolus, whilst in *Didymictis* and cursorially adapted modern taxa, the tubercle continues distally as a straight ridge of bone until it reaches or nearly reaches the distal margin of the malleolus. We interpret this difference in morphology as effectively positioning the m. tibialis posterior tendon to act primarily as an inverter of the foot in *Vulpavus* (and extant taxa that habitually climb) and as a plantarflexor of the foot in *Didymictis* (and terrestrial extant taxa). The anterior and distalmost aspect of the tibial malleolus of *Didymictis* projects laterally as a small malleolar tubercle for articulation with the cotylar fossa of the astragalus (Text-fig. 8G, I), a morphology not developed in miacids. It is found, however, among extant carnivorans such as canids in which the tibioastragalar articulation is restricted to flexion and extension.

In all miacoids the distal tibia for articulation with the astragalar trochlea is set at an angle to the long axis of the tibia, rather than being nearly perpendicular to it as is more typical of modern carnivores. In *Didymictis* this sloping articular surface is divided into a small, horizontal, medial facet and a wider (albeit anteroposteriorly shorter) and strongly angled lateral facet, whereas in miacids these two facets are more equal in width and of similar slope (Text-fig. 8A, G). Dividing these medial and lateral facets is a ridge of bone (tibial crest of Jenkins and McClearn 1984) that articulates in the groove of the astragalar trochlea. This tibial crest is prominent in *Didymictis* but almost undetectable in miacids (Text-fig. 8A, G). Among living carnivorans, the tibial crest is best developed in cursors where it stabilizes the tibioastragalar joint, and restricts rotation to flexion and extension, while in arboreal taxa such as *Nandinia* the ridge is poorly developed allowing for some adduction and abduction at this joint in addition to flexion and extension (Taylor 1976).

Fibula. Distal fibular morphology of *Vulpavus* and most other miacids differs from that of *Didymictis* in that the posterior aspect of the fibula has a shallow, medially oriented peroneal groove (rather than a deeper laterally oriented groove), and lacks an articular facet for the calcaneum (Text-fig. 8B, H). Proximal to the astragalar facet is a variably developed articulation for the tibia. This tibial facet (Text-fig. 8B, H) is present but small in some specimens of *Vulpavus* (e.g. USGS 7143) and *Didymictis* (USGS 16472, AMNH 2855), while in others it is absent (e.g. USGS 5025, *Vulpavus*). In another specimen of *Didymictis* (USGS 27585) the distal tibia and fibula are nearly fused and the articular facets obliterated. The combination of a relatively small distal tibiofibular articulation (where present at all) and large interosseous tubercle (Text-fig. 8A, G), suggests that a distal tibiofibular synovial joint was not as well developed in early Eocene miacoids as in living felids, viverrids, ursids, and most mustelids (Barnett and Napier 1953; Taylor 1976; pers. obs.). Instead, support at the tibiofibular joint of miacoids was probably maintained by a strong fibrous syndesmosis, a morphology considered by Barnett and Napier (1953) to be primitive for placental mammals.

Tarsus. The miacid tarsus, like that of extant carnivorans, includes seven bones: astragalus, calcaneum, navicular, cuboid and three cuneiforms – ecto, meso and entocuneiform. Of these the

astragalus and calcaneum have received considerably more attention than any of the other tarsal bones, and both have been used to address questions of functional morphology and phylogenetic relationships among carnivorans (Matthew 1909, 1915; Szalay 1977; Flynn and Galiano 1982; Gingerich 1983; Flynn *et al.* 1988; Wang 1993). In addition to the astragalus and calcaneum, we describe the navicular and cuboid.

1. Astragalus. The astragalar trochlea of *Vulpavus*, for articulation with the distal tibia, differs from that of *Didymictis* in being less well grooved, in that the lateral aspect of the trochlea does not expand as far posteriorly (Text-fig. 8C, i), and in the medial and lateral trochlear crests having very different rather than comparable radii of curvature (the medial crest being smaller). In *Vulpavus* the trochlear articular surface expands onto the lateral aspect of the lateral trochlear crest (Text-fig. 8C, i), a morphology which probably relates to a greater range of abduction and possibly inversion of the foot during plantarflexion as discussed further below. Unlike modern carnivorans in which the astragalar foramen is oriented posteriorly or is absent (Wang 1993), the astragalar foramen of miacoids is large and more dorsally positioned, particularly in *Vulpavus* (Text-fig. 8C, i). Soft tissue structures passing through this foramen (e.g. nerves or vessels) may well have limited the range of motion possible between astragalus and tibia as suggested by Wang (1993), but the degree to which plantarflexion was restricted by this structure is difficult to determine given the remainder of the tibioastragalar joint morphology. Specifically, the medial aspect of the trochlear articular surface expands posteriorly well beyond the astragalar foramen in all miacoids (Text-fig. 8A, G) as noted by Szalay (1977) and others. This enabled the anteroposteriorly longer medial facet of the distal tibia (Text-fig. 8A, G) to maintain contact through a substantial range of rotation before the shorter, lateral facet of the distal tibia came into contact with the astragalar foramen. We estimate that *Vulpavus* was capable of rotating the astragalus to a position of about 115° from the long axis of the tibia, while the angle between tibial diaphysis and the long axis of the astragalus probably exceeded 140° in *Didymictis* during maximum plantarflexion.

On the medial aspect of the astragalus of *Didymictis* is a distinct, concave facet (the cotylar fossa) for articulation with the lateral aspect of the tibial malleolus (Text-fig. 8G, i). This fossa, not present in miacids, is associated with a short, narrow, and dorsally directed groove occupied by the posterior margin of the tibial malleolus when the two bones are articulated. This combination of cotylar fossa and groove has also been noted for the early Eocene arctocyonid *Anacodon* (Rose 1990) and at least some species of the mesonychid *Pachyaena* (O'Leary and Rose 1995), and a well-developed malleolus-cotylar fossa articulation characterizes many extant cursorial mammals, including canids.

The sustentacular and ectal facets on the ventral surface of the astragalus articulate with the sustentaculum and posterior calcaneal facet of the calcaneum respectively, collectively forming the subtalar joints. The sustentacular facet of *Vulpavus* is more convex than that of *Didymictis* (which is nearly flat) while the ectal facet of miacids is strongly concave and helical in morphology (Text-fig. 8C), the posterior aspect facing more laterad and the anterior aspect distoventrad. In contrast, the ectal facet of *Didymictis* has a greater radius of curvature and lacks the helical orientation (Text-fig. 8i). The ectal and sustentacular facets are relatively farther apart in *Vulpavus* than in *Didymictis*, and the sustentacular facet of miacids is more distinctly anterior, there being little overlap between the posterior aspect of the sustentacular facet and the anterior aspect of the ectal facet. Sustentacular and ectal facet morphology of *Vulpavus* is similar to that found in the extant carnivoran *Potos* where it enhances inversion and eversion at the subtalar joints (Jenkins and McClearn 1984). Posterior and lateral to the ectal facet is the groove for the tendons of the plantarflexor mm. flexor hallucis longus and flexor digitorum longus. This groove is conspicuously deeper on the astragalus of *Vulpavus* than on that of *Didymictis* (Text-fig. 8C, i), but in both taxa it is oriented at an angle oblique to, rather than aligned with the long axis of the astragalar trochlea as occurs in extant canids (Wang 1993).

The astragalar head of *Vulpavus* is flattened dorsoventrally and smoothly convex, with the articular surface for the navicular expanding farther onto the lateral aspect of the head than in

Didymictis (Text-fig. 8C). The astragalar head of *Didymictis* is rotated so that its long axis is more closely aligned to the parasagittal plane (Text-fig. 8I), a character common to modern cursorial carnivorans. The astragalar head of *Didymictis* also possesses a distinct articular surface, absent or very reduced in *Vulpavus*, for contact with the calcaneum, as is also found in canids.

2. Navicular. The navicular of *Vulpavus* is notably wider than that of *Didymictis*, in large part due to the presence of a tubercle projecting from the dorsal and medial corner of the bone (Text-fig. 8E) probably for the insertion of m. tibialis posterior. A second tubercle is present ventrally, probably for insertion of the calcaneonavicular (spring) ligament. This latter tubercle is quite round in *Vulpavus* but anteroposteriorly elongate in *Didymictis*, extending anteriorly beyond the articular surface for the cuneiforms.

Along the lateral margin of the navicular is a slightly concave articular surface for the cuboid. This facet is longer anteroposteriorly and more rectangular in *Didymictis* than in *Vulpavus*, resulting in a strong contact with very little movement between navicular and cuboid in the viverravid. The same facet in *Vulpavus* is helical in shape, the dorsal part facing directly laterally and the ventral part oriented somewhat more posterolaterally, and the articular surface narrows considerably between the dorsal and ventral aspects of the facet. Articulation of the cuboid and navicular indicates considerably more motion between these two bones in *Vulpavus* than was possible in *Didymictis*.

The distal aspect of the navicular has three well-defined articular facets for the cuneiforms, the lateral or ectocuneiform facet being the largest in both miacoids (Text-fig. 8E, K). The cuneiform facets of *Didymictis* tend to be wider dorsally than ventrally, whilst in *Vulpavus* the same facets are more nearly square. The ento- and mesocuneiform facets are slightly convex dorsoventrally in both *Vulpavus* and *Didymictis* but unlike the convex curvature of the lateral cuneiform facet of *Vulpavus*, the ectocuneiform of *Didymictis* is nearly flat.

3. Calcaneum. Like the astragalus and navicular, the calcaneum of *Vulpavus* differs from that of *Didymictis* in several notable ways. The sustentaculum is relatively larger, more dorsally oriented, and located farther from the posterior calcaneal facet than that of *Didymictis* (Text-fig. 8D, J). Unlike *Vulpavus*, in which the posterior calcaneal articular surface comes into contact only with the ectal facet of the astragalus, in *Didymictis* the posterior calcaneal articular surface is divided by a distinct ridge into a medially oriented ectal facet and a dorsally oriented fibular facet (Text-fig. 8J). Just posterior to the fibular facet is a small pit where the posterior and distalmost aspect of the fibula contacts the calcaneum, providing the ultimate limiting factor in the range of plantarflexion possible at the tibioastragalar joint of *Didymictis*, as noted by Hunt and Tedford (1993).

The calcaneum of *Didymictis*, unlike that of *Vulpavus*, is elongated both proximal and distal to the subtalar joints (Text-fig. 8D, J), a morphology characteristic of cursorial and saltatorial mammals generally (Howell 1944; Hildebrand 1988). The peroneal tubercle of *Didymictis*, like that of canids, is small and situated distally (i.e. just lateral to the cuboid facet), and is in contrast to the much better developed and more proximally positioned peroneal tubercle of *Vulpavus* (Text-fig. 8D, J). This latter morphology is found among modern carnivorans well adapted for climbing, such as *Potos*, *Nasua* and *Nandina*, where the peroneal musculature, and particularly m. peroneus longus, functions to evert and abduct as well as plantarflex the foot. In dogs, the peroneal musculature acts primarily to plantarflex the pes (Evans and Christensen 1979).

The cuboid facet of the calcaneum is at an acute angle to the long axis of the calcaneum in both *Vulpavus* and *Didymictis* but this angle is more acute and the cuboid facet flatter (rather than concave) in the viverravid than in the miacid (Text-fig. 8D, J). In both of these respects the calcaneum of *Didymictis* is more similar to those of herpestids and canids while the calcaneum of *Vulpavus* closely resembles that of some living scansorial and arboreal carnivorans. The calcaneum of *Vulpavus* also differs from that of *Didymictis* in (1) lacking a well-developed articular surface for the astragalar head along the dorsomedial aspect of the cuboid facet (Text-fig. 8D, J), (2) having a less

well defined groove for the flexor hallucis longus tendon along the ventral aspect of the sustentaculum tali, and (3) having a smaller plantar tubercle positioned at the margin of the cuboid facet rather than well proximal to it. Szalay (1977) argued that a plantar tubercle set well back from the cuboid facet, as in *Didymictis*, is a synapomorphic character of Creodonta and early carnivorans, but in fact the morphology cited by Szalay (1977) does not even characterize viverravids (pers. obs.) let alone miacoids.

4. Cuboid. Whereas the cuboid of *Didymictis* is relatively rectangular, that of *Vulpavus* is distinctly wider proximally than distally owing to a more laterally expanded proximal facet for articulation with the calcaneum (Text-fig. 8F, L). This, along with its more uniform convex morphology, allowed for a substantially greater degree of abduction at the transverse tarsal joint in *Vulpavus* than in *Didymictis*. On the medial aspect of the cuboid are facets for the astragalar head, navicular and ectocuneiform (Text-fig. 8F, L). The flat ectocuneiform facet of *Didymictis* is clearly demarcated from the navicular facet by an approximately 30° change in orientation. In *Vulpavus* the ectocuneiform facet is saddle-shaped (i.e. slightly concave proximodistally and convex dorsoventrally) and the change in orientation between navicular and ectocuneiform facets is closer to 45°.

The distal cuboid of miacoids articulated with the fourth and fifth metatarsals with the facet for the fourth being much larger than that for the fifth (Text-fig. 8F, L). In *Didymictis* both of these facets face distally whereas in *Vulpavus* the facet for the smaller fifth metatarsal faces more laterally than distally, indicating that the fifth digit of *Vulpavus* was capable of being abducted considerably farther than that of *Didymictis*. Ventrolaterally, and oriented more or less perpendicular to the long axis of the cuboid, is a well-developed tubercle, probably for insertion of the long plantar ligament (Text-fig. 8F, L). In *Didymictis* this tubercle is well separated from both the calcaneal and metatarsal facets, but in *Vulpavus* the tubercle is expanded laterally and nearly continuous with the lateral expansion of the proximal calcaneal facet.

Functional interpretation of the hindlimb

Hip and knee joints. Innominate and proximal femoral morphology indicate that the hip joints of *Vulpavus* and *Didymictis* were heavily muscled. The well-developed anterior iliac tubercle, wide ventral ilium, and distally positioned and laterally oriented third trochanter, suggest powerful flexion of the thigh in both taxa. Several characters indicate that *Vulpavus*, unlike *Didymictis*, regularly employed abducted and laterally rotated hip postures, as do extant scansorial taxa such as *Procyon* (Jenkins and Camazine 1977) as well as arboreal taxa. These include a well-developed and posteriorly positioned ischial spine, a more spherical femoral head, expansion of the femoral head articular surface onto the femoral neck, and a medially projecting lesser trochanter. In contrast, the smaller, more cranial ischial spine, reduced ilium, posteriorly directed lesser trochanter, and less spherical femoral head with a more restricted articular surface, indicate that the hip joint of *Didymictis* had a more limited range of motion and was probably involved in more strictly parasagittal gaits.

The knee joint of *Didymictis* is characterized by anteroposteriorly deep femoral condyles, deeply grooved patellar trochlea, deep m. tibialis anterior fossa, and a mediolaterally compressed and anteriorly projecting tibial tuberosity. Although not as well developed as in canids, these characters are indicative of an emphasis on rapid flexion and extension of the knee. The knee morphology of *Vulpavus* on the other hand, with its mediolaterally wide and anteroposteriorly narrow femoral condyles, shallowly grooved patellar trochlea, and well-developed m. popliteus insertion site, is indicative of an emphasis on powerful flexion and more plantigrade and ambulatory locomotion (Ginsburg 1961).

Ankle, subtalar and transverse tarsal joints. The pes of *Vulpavus* was adapted for mobility, specifically abduction-adduction and inversion-eversion, while the ankle and intertarsal joints of *Didymictis* suggest that motion was largely restricted to flexion and extension. The shallow trochlea

(and related flat articular surface of the distal tibia) and unequal curvatures of the medial and lateral trochlear crests of the *Vulpavus* astragalus indicate simultaneous inversion and abduction at the tibioastragalar joint during plantarflexion, as described for *Potos* by Jenkins and McClearn (1984). The range of flexion and extension possible in the ankle of *Didymictis* was greater than that of *Vulpavus*, characters indicative of an emphasis on plantarflexion at the tibioastragalar joint in the viverravid including (1) a more distally positioned astragalar foramen, (2) the increased length of the astragalar trochlea resulting from elongation of the trochlea laterally, (3) the presence of small, comparably developed radii of curvature of the medial and lateral trochlear crests, and (4) the more salient astragalar trochlear groove, associated with a well-developed tibial crest.

Anterior translation or sliding of the astragalus on the calcaneum produced inversion at the subtalar joint of *Vulpavus* as the helically shaped ectal facet rotated from the anterolateral to posteromedially oriented aspects of the posterior calcaneal facet. In *Potos* this motion accompanies plantarflexion and, along with the abduction and inversion at the tibioastragalar joint, enables this animal to reverse its hindfoot completely when hanging from branches or descending vertical supports (Jenkins and McClearn 1984). Although there was substantial capacity for hindfoot inversion and abduction in early Eocene *Vulpavus*, it was probably incapable of complete hindfoot reversal for two reasons: (1) the restricted range of plantarflexion at the tibioastragalar joint due to the dorsal position of the astragalar foramen (the trochlea of *Potos* forms an almost 180° arc), and (2) the relatively short posterior calcaneal facet (the posterior aspect of this facet is notably longer in *Potos*). This latter character would have functioned to limit the extent of posterior translation and subsequent conjunct rotation in *Vulpavus*. In *Didymictis* the large fibular-calcaneal articulation prevented the ectal facet from articulating with the dorsally oriented and more anterior aspect of the posterior calcaneal surface, thereby reducing, if not effectively eliminating, inversion at the subtalar joint. Motion of the astragalus on the calcaneum, therefore, was limited to fore-and-aft translation on the medially facing ectal facet.

The transverse tarsal joint of *Vulpavus* was also capable of a greater degree of inversion–eversion and abduction–adduction than that of *Didymictis*. Szalay and Decker (1974) argued that a lateral and dorsally expanded articular surface on a dorsoventrally flattened astragalar head as is characteristic of *Vulpavus* is indicative of habitual eversion, while the well-developed peroneal tubercle of this animal indicates enhanced eversion and abduction by increasing the mechanical advantage of the peroneal musculature. Conversely, the dorsoventrally rotated astragalar head of *Didymictis* reflects an emphasis on flexion and extension at the astragalonavicular articulation, and the similarity of peroneal tubercle morphology among *Didymictis*, herpestids, and canids suggests that the peroneal musculature in the viverravid may have functioned predominantly as a plantarflexor.

Inversion at the transverse tarsal joint of *Didymictis*, as in the subtalar joints, also appears to have been restricted. Transverse tarsal inversion requires that the calcaneum, cuboid and navicular rotate as a unit about the astragalar head (Jenkins and McClearn 1984), an action limited in *Didymictis* by the combination of the cuboid–calcaneum articular morphology, and an interlocking tarsal organization, involving the astragalar head, calcaneum and cuboid, similar to that described for the hyaenodontid *Gazinocyon* (Polly 1996). Increased mobility at the transverse tarsal joint of *Vulpavus* is indicated by the mediolaterally wider and more concave facet of the proximal navicular, lack of a well-developed astragalar head–calcaneum articulation, and the more concave and better defined articulation between the calcaneum and cuboid.

Although Hildebrand (1988, p. 478) stated that tarsal bones lengthen only in jumping mammals (although see the cheetah calcaneum; Hildebrand 1988, text-fig. 24-15), the clearly elongate calcaneum of *Didymictis* relative to that of *Vulpavus* is similar to the differences found between the calcanei of the cursorial *Alopex* and the arboreal *Potos*. The elongate tuber calcaneum of extant cursors increases the lever arm of the main plantarflexor musculature (i.e. mm. gastrocnemius, plantaris and soleus), indicating selection for power over speed of contraction at the tibioastragalar joint. This is contrary to what is more often the case in mammals adapted for speed: maximization of the velocity of rotation about distal joints. There are at least two reasons why cursors may

increase the lever arm of the main plantarflexors of the ankle: (1) to increase the force generated by the relatively reduced plantarflexor muscle mass associated with weight reduction of distal limb segments; and (2) to increase the mechanical advantage of these muscles during a prolonged digitigrade stance. This latter possibility raises the question of whether *Didymictis* was digitigrade, subdigitigrade or plantigrade. In a resting position, living digitigrade canids form an angle of about 150° between tibia and long axis of the tarsometatarsus (Wang 1993). Although *Didymictis* was probably incapable of creating an angle between tibia and tarsometatarsus of more than 150° during maximal plantarflexion, the significant increase in the amount of plantarflexion possible relative to miacids and the substantial elongation of the tuber calcaneum strongly indicate that this animal employed at least a semidigitigrade stance, as proposed by Matthew (1909).

SUMMARY

The appendicular skeleton of Wasatchian *Vulpavus* indicates that this animal possessed a considerable range of motion at most joints of the fore- and hindlimb, a degree of mobility that is similar to that found in modern carnivorans adapted for exploiting arboreal habitats (Text-fig. 9).



Drawing by Jay H. Matternes © 1989

TEXT-FIG. 9. Reconstruction of the Bridgerian NALMA (middle Eocene) miacid *Vulpavus ovatus*.

The postcranial skeleton of *Didymictis*, on the other hand, is suggestive of more restricted parasagittal motion (particularly in the hindlimb) and increased joint stability, as characterizes extant carnivorans adapted primarily for speed. There are, however, several characters in the forelimb that imply that *Didymictis* also employed substantial digging in its behavioural repertoire.

The forelimb of *Vulpavus* is characterized by: a shallow glenoid fossa, low greater tuberosity, narrow and laterally flared deltopectoral crest, large supinator crest, large projecting medial epicondyle, a medial trochlear rim extending only minimally beyond the capitulum, shallow olecranon fossa, wide semilunar notch with a poorly defined lateral wall, flat and laterally facing radial notch, wide anterior ulna distally, round radial head, strong extensor tubercles and relatively shallow articular surface on the distal radius, and deep, laterally compressed, dorsally curved ungual phalanges with well-developed flexor and extensor tubercles. These characters imply the capability for powerful protraction–retraction, abduction–adduction, and medial–lateral rotation

about the glenohumeral joint and flexion–extension about the humeroulnar and radiocarpal joints, an extreme range of pronation–supination at the proximal and distal radioulnar joints, and strong, sharp claws, all of which are essential for climbing.

Similarly, characters of the *Vulpavus* hindlimb are suggestive of considerable rotation at the hip joint and extensive abduction–adduction and inversion–eversion at the tibioastragalar and subtalar joints. These characters include: a large ischial spine, rounded femoral head with posteriorly expanded articular surface, medially directed lesser trochanter, relatively wide and shallow patellar trochlea, flat and inclined distal tibial articular surface, proximal and anteriorly oriented malleolar tubercle, medial and lateral astragalar trochlear crests with differing radii of curvature, laterally and dorsally expanded articular surface of the astragalar head, absence of a fibular–calcaneal articulation, large and laterally projecting peroneal tubercle, and helical morphology of the articulation between ectal and posterior calcaneal facets.

Behavioural interpretations based on the forelimb and hindlimb of *Didymictis*, unlike those for *Vulpavus*, are not completely congruous. The forelimb possesses a deeper, more rounded glenoid fossa, increased articular congruence at the glenohumeral joint, a proximally projecting greater tuberosity, reduced deltopectoral crest, relatively well developed supinator crest (although less well developed than in *Vulpavus*), wide medial epicondyle, deep and perforate olecranon fossa, steeply inclined humeral trochlear rim, large olecranon process having a well-defined triceps tendinal groove proximally, a deep semilunar notch, anterolaterally facing radioulnar notch and very oval radial head with prominent capitular eminence, a very concave distal radial articular surface expanded over the posterior margin as a convex articular surface for the scaphoid, and a scaphoid and lunar with small radii of curvature along their proximal articular surfaces. Relative to *Vulpavus*, all of these are indicative of reduced mobility at the glenohumeral, elbow and radiocarpal joints, where rotation and supination are sacrificed for stability during powerful flexion and extension. Although most of these characters resemble those found in extant cursors, the morphology of the distal humerus and the outline shape of the unguals of *D. altidens* are decidedly more similar to those of modern semifossorial taxa.

The hindlimb of *Didymictis* is indicative of incipient cursoriality. The reduced ischial spine and ilium, less spherical femoral head with reduced articular surface, posteriorly directed lesser trochanter, and narrow ridge of bone between head and greater trochanter, all suggest reduced capacity for employing rotated and abducted hip postures. Restriction of hindlimb motion to a parasagittal gait is further enhanced by the narrow and deep patellar trochlea, more vertically oriented malleolar tubercle, medially projecting tibial malleolus, better defined tibial crest on the distal tibia articular surface, deep and posterolaterally facing peroneal groove, dorsoventrally oriented astragalar head, well-developed calcaneo–fibular articulation, reduction of the peroneal tubercle, and elongate calcaneum. All of these characters suggest an emphasis on flexion and extension at the expense of eversion–inversion and abduction–adduction. It seems likely, therefore, that *Didymictis* was a relatively specialized terrestrial carnivore capable of hunting either with speed or by pursuing its quarry by means of digging.

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APPENDIX

Abbreviations used for morphological characters discussed in text.

ac	acromion	Met IV	fourth metatarsal facet
act	acetabulum	Met V	fifth metatarsal facet
ah	facet for astragalar head	nas	non-articular shelf
ap	anconeal process	nav	navicular facet
asf	astragalar foramen	ntb	tubercle of navicular
bb	bone bridge	of	olecranon fossa
bc	brachioradialis crest	op	olecranon process
br	m. brachialis insertion site	pcf	posterior calcaneal facet
ce	capitular eminence	pf	pit for fibula
cen	centrale facet	pg	groove for peroneal tendons
cf	coronoid fossa	pop	m. popliteus insertion site
con	phalangeal condyles	pt	patellar trochlea
cp	coracoid process	ptb	peroneal tubercle (process)
cty	cotyler fossa	rf	radial fossa
cub	cuboid facet	rn	radia notch
dl	dorsal lip	s	stop facet for magnum

dp	deltpectoral crest	sc	supinator crest
ec	articular surface for ectal facet	sca	expanded articular surface for scaphoid
ecf	ectal facet	sf	sustentacular facet
ect	ectocuneiform facet	sgt	supraglenoid tubercle
ef	entepicondylar foramen	sm	semilunar notch
ent	entocuneiform facet	sn	scapular notch
exr	extensor tubercle of radius	ss	scapular spine
exu	extensor tubercle of unguis	st	scaphoid tubercle
ff	fibular facet	stf	supratrochlear foramen
fhl	groove for flexor hallucis longus tend.	sty	styloid process
flx	flexor tubercle	sus	sustentaculum talus
fov	articular fovea	ta	m. tibialis anterior fossa
gf	glenoid fossa	tbf	tibial facet
gtb	greater tuberosity	tbm	tibial malleolus
gtr	greater trochanter	tc	tibial crest
ib	iliac blade	tg	m. triceps brachii tendinal groove
ilt	iliac tubercle	tm	m. teres major insertion site
itb	tubercle for interosseous membrane	tmt	tibial malleolar tubercle
it	ischial tuberosity	tpt	m. tibialis posterior tubercle
is	ischial spine	tro	astragalar trochlea
lpt	long plantar tubercle	tt	tibial tuberosity
ltb	lesser tuberosity	ttr	third trochanter
ltr	lesser trochanter	tzd	trapezoid facet
lun	lunar facet	tzm	trapezium facet
mag	magnum facet	unc	unciform facet
mc	medial condyle	ucl	ulnar collateral ligament insertion site
me	medial epicondyle	ul	ulnar facet
mes	mesocuneiform facet		