Transformation from Plantigrady to Digitigrady: Functional Morphology of Locomotion in *Hesperocyon* (Canidae: Carnivora)

XIAOMING WANG[1]

ABSTRACT

The most primitive canid *Hesperocyon* from the late Eocene to early Oligocene (Duchesnean to Whitneyan) of North America possesses a combination of both cursorial and noncursorial limb characteristics. Compared to the archaic miacoid carnivorans, *Hesperocyon* has a number of advanced features suggestive of running adaptations, such as absence of a large teres major process on the scapula, a relatively reduced deltoid crest on the humerus, elongated and adjoined metapodials, and laterally oriented fovea capitis femoris. On the other hand, *Hesperocyon* retains some primitive, arboreal characteristics such as a short, broad scapula with long acromion, a stout humerus with a deep bicipital groove and a thin-bladed brachioradialis crest, an anteriorly bowed ulna, a sharply angled pelvic floor, a relatively large muscle scar for flexor digitorum longus and caudal tibialis on the tibia, and a short, deep, and hooked distal phalanx suggestive of a retractile claw.

This combination of cursorial and noncursorial characters shows that *Hesperocyon* represents a transitional stage from its arboreal plantigrade ancestors to its cursorial digitigrade descendants. Examination of a series of miacoids and primitive canids (*Vulpavus*, *Miacis*, *Hesperocyon*, *Cormocyon*, *Leptocyon*, and *Tomarctus*) reveals that the canid metatarsus did not become erect until the Arikareean *Cormocyon* and *Leptocyon*. Increased extension angle of the tibioastragalar joint was achieved through realignment of the plantar tendon groove to be continuous with the astragalar trochlea and elimination of the astragalar foramen. By combining anatomical characters with results of a morphometric analysis, I have concluded that *Hesperocyon* was plantigrade in posture and probably scansorial in life.

[1] Frick Postdoctoral Fellow, Department of Vertebrate Paleontology, American Museum of Natural History.

INTRODUCTION

Two major categories of standing postures are commonly recognized among carnivorans: plantigrady and digitigrady. In plantigrady the entire palm or sole is placed flat on the ground (such as the human foot), in contrast to a digitigrady in which animals stand and walk on the distal ends of metapodials and middle phalanges, creating the appearance of standing on fingers and toes. By changing from a plantigrade to a digitigrade posture, the limbs gain the entire length of the metapodials. This strategy of increasing the stride has two advantages: (1) it utilizes existing appendages without having to elongate or add new bones; and (2) the metapodial regions are relatively free of musculature, thus minimizing weight gain in the distal segment of limbs and keeping the angular inertia to a minimum. This kind of limb modification has attained its most extreme expression in ungulates, the hoofed mammals, who are literally standing on the very tip of their toes—the unguligrade posture.

Within the living terrestrial carnivorans, nearly all fast-running members, such as felids, canids, and hyaenids, have long limbs and are digitigrade, adapted for pursuit of prey at high speed. Many other taxa are either arboreal or capable of climbing trees for escape (scansorial), such as felids, procyonids, some herpestids, some viverrids, and some ursids. A significant number of these are also plantigrade (ursids, procyonids, some mustelids, some herpestids, and some viverrids).

Living canids (Family Canidae) have acquired highly cursorial adaptations that enable them to run fast and maneuver quickly on flat ground. In contrast to the mostly ambush-hunting large felids, large canids are pursuit predators, i.e., running at high speed for sustained periods of time. All living canids are obligatory digitigrades and entirely terrestrial with the exception of the occasionally scansorial gray fox, *Urocyon cinereoargenteus* (Fritzell and Haroldson, 1982), fennec fox *Fennecus* (Hildebrand, 1954), and domestic dogs trained to climb trees.

Whether or not arboreality is the primitive state for mammals has been a longstanding subject of debate (Huxley, 1880; Lull, 1904; Matthew, 1904; Ginsburg, 1961; Haines,

1958; Martin, 1989). Nobody seems to doubt, however, that mammals were initially plantigrade (nonmammalian tetrapods are certainly plantigrade). By common consensus, the closest ancestors of canids can probably be found within the miacoids, a group of archaic carnivorans in the Eocene-Oligocene time (Matthew, 1930; Clark, 1939; Tedford, 1976; Flynn and Galiano, 1982; Flynn et al., 1988; Wang, 1990). The miacoids were almost certainly plantigrade, as reflected in the primitive configuration of their ankle joints: shallow and short astragalar trochlea, and deep plantar tendinal groove on the proximal end of and at an angle with the astragalar trochlea, allowing very limited rotation of the tibioastragalar joint. Many miacoids were probably arboreal as evidenced by their overhung acromion of the scapula, curved limbs, flexible wrist and ankle joints, steep angled pelvic floor, and strong development of the clavicles, presumably adaptations to the predominantly forest environment in the Eocene (Webb, 1981; Martin, 1989). Although plantigrady and arboreality are not necessarily linked (e.g., cats are digitigrade but capable of arboreality), these two categories do coexist extensively among carnivorans. Plantigrade posture allows a firm grasp on tree trunks and lowers the center of gravity for horizontal movements along branches (Cartmill, 1974).

In contrast to the primitive plan of miacoids, all living carnivorans, plantigrade or digitigrade, have restructured their limb bones to different degrees, shedding some of the archaic characters (e.g., high deltoid crest and deep plantar tendinal groove proximal to astragalar trochlea). The earliest canid, *Hesperocyon* Scott, from the late Eocene to early Oligocene (Duchesnean to Whitneyan) of North America, exhibits a combination of advanced features and primitive conditions. For example, its hands and feet have closely compressed metapodials, and had thus been assumed to be digitigrade (Tedford, 1978). On the other hand, *Hesperocyon* retains a large number of primitive limb characters and is a long way from the slender, trimmed limbs of its living relatives. Early vertebrate paleontologists at the turn of this century had long

noticed this mixture of characteristics in *Hesperocyon* limb morphology. Scott (1898: 399) compared postcranial skeletons of *Hesperocyon* with those of living civets (*Viverra*, Viverridae) and concluded that ". . . from the resemblance of the limb and foot bones of *Cynodictis* [*Hesperocyon*] to those of the civets, it seems very probable that the former had a similar semiplantigrade gait." Matthew (1901: 381) was equally puzzled by this resemblance of *Hesperocyon* to viverrids, and to him, the only character that separated the two groups was the presence of a lower third molar in *Hesperocyon*.

The early canids would thus seem to stand in a transitional stage between the archaic plantigrade, arboreal miacoids and the later, fully digitigrade terrestrial canids. Phylogenetically, the small *Hesperocyon* played a central role in the early diversification of the Canidae (Matthew, 1930; Tedford, 1978; Wang, 1990). Not only did it give rise to the first major canid radiation (contained in the subfamily Hesperocyoninae), but from this stock arose the subsequent radiations of the Borophaginae, dominant in the Mio-Pliocene, and of the Caninae, the living canids and their recent fossil relatives. *Hesperocyon* is therefore a focal point of the present paper, which examines its standing posture and locomotor adaptations in relation to later canids.

A survey of the distribution of limb characters in living carnivorans was first provided by Ginsburg (1961), who contrasted typical living digitigrade representatives of felids, canids, and hyaenids with typical plantigrade members of ursids, mustelids, and procyonids. Twenty-seven osteological characters were found to correlate in different degrees to limb postures. However, the majority of what Ginsburg considered "digitigrade" characters are related to cursorial adaptations instead of standing postures. Similarly, most of his "plantigrade" characters may represent arboreal or fossorial adaptations. Ginsburg's empirical approach also encounters difficulties when one is trying to project the modern morphology onto fossils; early carnivorans often had to make do with existing primitive, noncursorial structures to accomplish many of the same tasks that can be accomplished

much more efficiently by living carnivorans possessing highly modified limbs.

Other related studies are far less comprehensive in regard to the standing postures of carnivorans. Taylor (1971, 1974, 1976, 1989) suggested using metapodial/propodial ratios as indicators of standing posture. However, no particular number was proposed to cut through what appears to be a continuum. Munthe (1989) listed three criteria for distinguishing digitigrady: tightness of contact between astragalus and calcaneum, orientation of the astragalar trochlea, and morphology of the distal articular surfaces of the metatarsus. However, she did not elaborate further as to how these criteria should be applied.

Because the most fundamental difference between plantigrady and digitigrady is the extent of ankle extension, the astragalar trochlea on which the distal tibia rotates thus plays a central role in the transformation between these two postures. The present study intends to show that trochlear configuration does indeed closely reflect maximally allowable ankle extension, and offers a direct osteological criterion for determination of limb postures. It examines the transformation from the archaic arboreal miacoids to the initiation of cursorial adaptations in early canids. *Hesperocyon* is the focus of this investigation; not only is it the earliest canid, but it also represents the beginning of the transition from plantigrady to digitigrady.

INSTITUTIONAL ABBREVIATIONS

AMNH   Department of Vertebrate Paleontology, American Museum of Natural History, New York, New York

AM:CA   Comparative Anatomy Collection, American Museum of Natural History

AM:MA   Department of Mammalogy, American Museum of Natural History

F:AM   Frick Collection, American Museum of Natural History

FMNH   Field Museum of Natural History, Chicago, Illinois

KUMA   Division of Mammalogy, Museum of Natural History, University of Kansas, Lawrence, Kansas

KUVP   Division of Vertebrate Paleontology, Museum of Natural History, University of Kansas

UCMP   Museum of Paleontology, University of

California at Berkeley, Berkeley, California

UNSM Nebraska State Museum, University of Nebraska, Lincoln, Nebraska

USNM United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.

MATERIALS AND METHODS

Hesperocyon is abundantly preserved, especially in the White River Group of northern Great Plains, and postcranial skeletons are readily available. Several skeletons of *Hesperocyon* were studied in the collections of various museums. Together they constitute the most complete picture of a genus of small carnivorans of its time. The following *Hesperocyon* postcranial specimens have been examined: AMNH 1408, 1487, 8774, 9318, 39096; F:AM 50264, 50265, 50278, 50321, 50333, 63997, 63998, 72517, 76158, 76187, 128064; FMNH UC495, P12224; UCMP 126095; USNM 69, 18911, 16892. All are partial postcranial skeletons associated with cranial and dental materials (except AMNH 9318, F:AM 50264 and 50333, FMNH P12224), and are from the White River Group of North American late Eocene to early Oligocene (Chadronian–Whitneyan).

Selected representatives of primitive canids were also compared. Advanced hesperocyonines were not included because of the paucity of postcranial specimens known for these forms. *Cormocyon* and *Tomarctus* were used as representatives of primitive Borophaginae [for large, more derived borophagines, I relied on Munthe (1979, 1989)]. Our knowledge of *Cormocyon* is incomplete. For the present study, three partial skeletons with associated cranial materials were examined: F:AM 49031, 49060, and 50299, all associated with cranial and dental materials, from Whitneyan to Early Arikareean of eastern Wyoming. Eight postcranial skeletons of primitive *Tomarctus* (mainly *T. thomsoni*) are available: AMNH 12874; F:AM 49017, 49067, 49096A, 49096B, 49097; KUVP 27672, 27673; all are associated with cranial and dental materials, and from Hemingfordian of western Nebraska and eastern Wyoming. Fossil records for primitive canines are rather sparse, and only a few intermediate forms can provide sketchy information about

the limb transformation toward the living canines. The following fossil canine specimens were examined: *Leptocyon gregorii*, F:AM 67994, right humerus from Dunlap Camel Quarry, Dawes County, Nebraska, Middle Hemingfordian; *Leptocyon vulpinus*: AMNH 12883, partial skeleton with associated upper and lower dentition, from Pine Ridge area, South Dakota, Late Arikareean; *Leptocyon vafer*: F:AM 62780, partial left and right tibii, nearly complete right foot, from Teseque Formation, Santa Fe County, New Mexico, Early Barstovian; F:AM 72674, right tibia, from Echo Quarry, Olcott Formation, Sioux County, Nebraska, Early Barstovian; F:AM 72701, right humerus, Burge Member of Valentine Formation, Early Clarendonian of Nebraska. No attempt was made to survey every genus of living canids, which are relatively uniform (e.g., Hildebrand, 1954; Stains, 1975). Instead, selected representatives were examined: *Canis*, *Otocyon*, *Urocyon*, and *Vulpes*.

Where character polarities are discussed, they are determined through outgroup comparisons. A phylogenetic appraisal of primitive canid and precanid miacoids, the traditional outgroup of caniform carnivorans, is the subject of a separate study by Wang and Tedford (MS), which suggests that *Miacis* and *Vulpavus* form successively more primitive outgroups within the caniform clade. Within the miacoids my analysis was primarily based on *Vulpavus ovatus* (AMNH 11497 and 11498 of partial skeletons, both associated with cranial materials, from Bridgerian of Wyoming), and *Vulpavus protectus* (AMNH 12626, partial skeleton associated with cranial material, from Level B of Bridger Formation, Wyoming, Bridgerian). They are represented by the most complete postcranial skeletons available and are supplemented in this study by two specimens of *Miacis parvivorus* (AMNH 11496, isolated limb bones associated with left ramus; USNM 214706, isolated limb bones associated with partial cranium; both from Bridgerian of Wyoming).

Postcranial descriptions of living African herpestids and viverrids are mainly based on Taylor (1974, 1976), and his observations are checked for accuracy in the AMNH specimens (e.g., Taylor listed *Herpestes ichneumon* as digitigrade; there is, however, a clear

presence of hypothenar and thenar pads according to Haines (1958: fig. 1). My own observation is in support of Taylor, i.e., no thenar or hypothenar pad is found). The following living caniform carnivorans have been examined: Procyonidae: *Potos, Ailurus, Nasua, Procyon*; Mustelidae: *Meles, Mephitis, Mustela, Taxidea*; Ursidae: *Ursus, Tremarctos*.

Van Valkenburgh's (1985, 1987) seven morphometric indices are adopted (body size excluded) for statistical comparisons. The average values of corresponding indices from four fossil taxa (*Vulpavus, Hesperocyon, Cormocyon*, and *Tomarctus*) are combined with Van Valkenburgh's (1985) published data on living carnivorans. Discriminant function analysis is applied to the combined data set. The fossil taxa are then classified on the basis of their morphological distances to living carnivorans.

COMPARATIVE OSTEOLOGY OF FORELIMBS

SCAPULA: The scapula of *Hesperocyon* is relatively shorter than that of living cursorial carnivorans, and is characterized by a proximodistally short blade much like certain arboreal viverrids such as the African palm civet (*Nandinia*) and genet (*Genetta*). Retaining the primitive structure of miacoids, e.g., *Miacis gracilis* (illustrated in Clark, 1939), the cranial border of the *Hesperocyon* scapula is greatly arched due to a larger distal area for the supraspinous fossa, in contrast to the straighter borders in Recent canids. Like the living canids, *Hesperocyon* has a well-developed supraglenoid tubercle that projects beyond the coracoid process, unlike that of the procyonids in which the tubercle is much less extensive. There is in *Hesperocyon* a large metacromion and a long acromion that overhangs the glenoid fossa.

Discussion: Of the African herpestids and viverrids that Taylor (1974) examined, only the arboreal *Nandinia* has an overhung acromion. The long acromion may indicate a strong acromiodeltoid muscle for abduction (Taylor, 1974) and was suggested to indicate the presence of a clavicle (Scott and Jepsen, 1936), before its occurrence was known for *Hesperocyon*. Perhaps of phylogenetic sig-

nificance, the scapula of canids does not have a large teres major process possessed by most living arctoid carnivorans (Tedford, 1976; but also see Flynn and Galiano, 1982).

CLAVICLE: Matthew (1901) published a reconstruction of *Hesperocyon* based on a partially articulated skeleton embedded in matrix (AMNH 8774). The illustration, based on photographs of a living genet (*Genetta*), shows no existence of a clavicle. A reexamination of AMNH 8774 shows a slender clavicle lying on the surface of the left humerus in the lower neck region. The clavicle is slightly curved and is approximately 1 mm thick and 15 mm long. Matthew (1909) similarly overlooked the presence of a clavicle in a specimen of *Vulpavus ovatus* (AMNH 11498), even though he inferred that a clavicle should be well developed on the basis of an overhanging acromion process. The clavicle in *Hesperocyon* is more reduced than in *Vulpavus ovatus* (AMNH 11498), whose acromion process is also larger. The previously undescribed clavicle in AMNH 11498 is 41 mm long and has an oval cross section (with a long and short axis of 4.7 and 2.2 mm near its middle section) along most of its length. No clavicle was found in borophagine canids (Munthe, 1989), suggesting absence or reduction of this bone similar to the situation in living canids (Hildebrand, 1954). Loss of a functional clavicle has been suggested to indicate increased freedom of rotation of the scapula in the sagittal plane (Hildebrand, 1985) and decreased mobility of lateral deflection (Jenkins, 1974).

HUMERUS: Proximally, the humeri of *Hesperocyon, Cormocyon*, and early *Leptocyon* (*L. vulpinus* in Late Arikareean and *L. gregorii* in Hemingfordian) are similar to those of the African palm civet *Nandinia* in having a deep, clearly defined bicipital groove, suggesting a large m. biceps brachii (Taylor, 1974). As in the procyonids, the humeral head in *Hesperocyon*, and to a lesser extent *Cormocyon*, is more convex along the mediolateral axis than those of *Tomarctus* and advanced borophagines. Living canids are similar to borophagines in having relatively flat humeral heads.

The greater tubercle is almost at the same level or below the top of the humeral head in *Vulpavus, Nandinia, Hesperocyon* (fig. 1A),
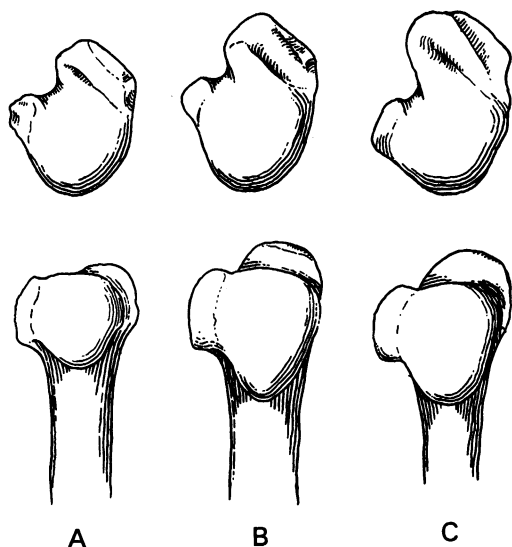
Fig. 1. Proximal (upper) and anterior (lower) views of proximal halves of right humeri in different canids. A. *Hesperocyon gregarius* (FMNH P12224); B. *Cormocyon* sp. (F:AM 49031); C. *Leptocyon vafer* (F:AM 72701). All drawn to approximately the same size.

and *Procyon*. In *Cormocyon* (fig. 1B) and *Leptocyon* (fig. 1C), it is more elevated above the humeral head and enlarged relative to the head, and, in advanced borophagines it is raised significantly above the head (Munthe, 1989). The top of the greater tubercle is flat in miacoids and *Hesperocyon*, in contrast to the convex surface in more advanced canids.

The situation in the lesser tubercle is almost the reverse of that of the greater tubercle. *Hesperocyon* has a relatively large and medially protruding lesser tubercle, as also occurs in arboreal procyonids. This primitive condition is retained in the borophagines but lost in canines. In the latter, the tubercle is medially flattened.

Miacoids (and primitive mammals in general) have a very high and prominent deltoid crest trailing distally from the deltoid tuberosity; most living carnivorans, on the other hand, have lost the deltoid crest. A large deltoid crest is still retained in fossorial taxa such as *Taxidea*. In *Hesperocyon*, the crest reaches to the mid-shaft of the humerus or further distally. The deltoid crest becomes progressively shorter and less distinct in the more advanced canids and is almost confined to

the upper third of the humeral shaft in living *Vulpes*.

As in arborealists such as *Nandinia*, *Procyon*, and *Ailurus*, the lateral brachioradialis crest in *Hesperocyon* and *Cormocyon* is a very sharp and thin blade, in contrast to a lower and more gentle crest found in advanced canids. Although deeper than that of *Vulpavus*, the olecranon fossa in *Hesperocyon* is relatively shallow like that of living procyonids, mustelids, herpestids, and viverrids. More derived canids, e.g., *Tomarctus* and *Vulpes*, have much deeper olecranon fossae and, correspondingly, wider medial epicondyles.

Associated with the shallow trochlea in *Hesperocyon* is a pit on the posterior surface of the medial epicondyle just below the olecranon fossa and medial to the trochlea (also reported to be present as a "medial pit" in the primitive eutherian *Protungulatum* by Szalay and Dagosto, 1980). In domestic dogs, this pit is very shallow and serves as an attachment for the olecranon ligament (Evans and Christensen, 1979). The ligament inserts on the saddlelike area between anconeal and coronoid processes above and to the medial side of the semilunar notch of the ulna. The olecranon ligament serves to anchor the semilunar notch to the humeral condyle. In advanced canids (e.g., most borophagines and canines), the increase in depth of the medial epicondyle of the humerus fills much of the space originally occupied by the pit for the olecranon ligament.

An entepicondylar foramen is present in most small primitive canids (*Hesperocyon*, *Cormocyon*, *Tomarctus*, and *Leptocyon*). It is independently lost in *Borophagus*, a highly derived member of the borophagines, in Hemphillian *Vulpes*, and all later canines. The marked protrusion of the medial epicondyle in the early canids seems to be related to the presence of the entepicondylar foramen. In later canines, where the foramen is lost, the medial epicondyle is far less prominent.

Discussion: The size of the deltoid area has been suggested to correlate with the degree of plantigrady (Ginsburg, 1961), i.e., the larger the area, the less digitigrade the posture. The depth of the olecranon fossa is a direct reflection of how much lateral rotation of the ulna is allowed or how restricted the forearm is within the parasagittal plane. An increased

depth of the olecranon fossa is a direct consequence of a wide (craniocaudally), medial epicondyle. The epicondyle tends to grow posteriorly in cursorial animals, thus increasing the depth of the trochlea.

The size and depth of scars for the olecranon ligament are inversely correlated with the depth of the olecranon fossa. Carnivorans with shallow trochleas tend to have large areas of ligamentous attachments, suggesting more flexible elbow joints. A striking example is seen in *Enhydrocyon crassidens* (AMNH 12886), a large, hypercarnivorous member of Hesperocyoninae, in which the pit for the olecranon ligament sinks in deeply alongside the medial border of the trochlear surface.

ULNA: The ulna of *Hesperocyon* (fig. 2A) is robust and has about the same thickness as the radius, as in *Cormocyon* and *Tomarctus* (fig. 2B); that of the canines are considerably more elongated and slender (fig. 2C). The lateral outline of the *Hesperocyon* ulna is posteriorly bowed, close to that of *Genetta*; those of *Cormocyon* and *Leptocyon* are straightened slightly in comparison. Early canids do not have an enlarged process at the posteroproximal corner of the olecranon; this cone-shaped structure is present in living *Canis* and *Vulpes*, and is for attachment of the triceps brachii and anconeus muscles. Instead, *Hesperocyon* and *Cormocyon* have a large, flat posterior area on the olecranon; this flat condition is also present in *Vulpavus* and *Miacis*.

In miacoids, primitive canids (*Hesperocyon* and *Cormocyon*), and living plantigrade carnivorans, the groove on top of the olecranon is shallow and the two tubercles on each side are asymmetrical, i.e., the medial one is larger than the lateral one. In *Leptocyon*, the groove is deepened but the tubercles remain asymmetrical.

Discussion: As is the case in many cursorial mammals, the overall thickness of the ulnar shaft, in relation to that of the radius, tends to be reduced in taxa that are capable of fast running; this is especially true in the distal part of the ulna. Taylor (1974) observed that arboreal *Nandinia* and *Genetta* have a posteriorly bowed ulna shaft, in contrast to the anteriorly arched posterior border in more terrestrially adapted *Herpestes* and *Ichneu-*
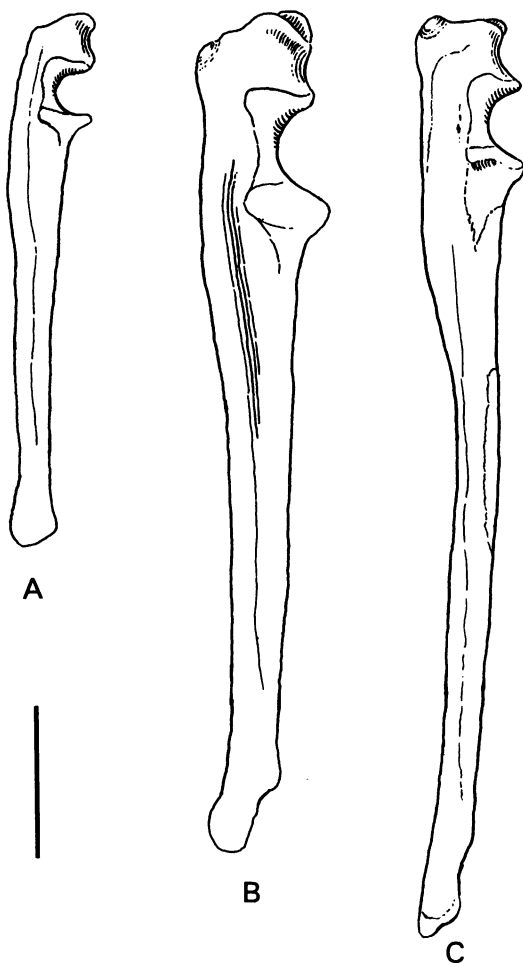

Fig. 2. Lateral view of ulna. **A.** *Hesperocyon gregarius* (FMNH P12224); **B.** *Tomarctus thomsoni* (F:AM 49097); **C.** *Otocyon* (AM:CA 2852). Scale = 20 mm.

mia. In caniforms, *Hesperocyon* and procyonids retain a posteriorly bowed ulna.

Ginsburg (1961) pointed out that digitigrade carnivorans have on top of the olecranon a deep groove bordered on each side by two tubercles of equal height. The tendon of the triceps brachii glides in the groove and the two tubercles serve as guides to prevent slip on either side. The tubercles of *Hesperocyon* are far smaller than those of *Cormocyon*, *Leptocyon*, and living canines to serve the above function well.

RADIUS: The radii of canids are little changed during their entire history. In miacoids, the anterior surface of the distal radius
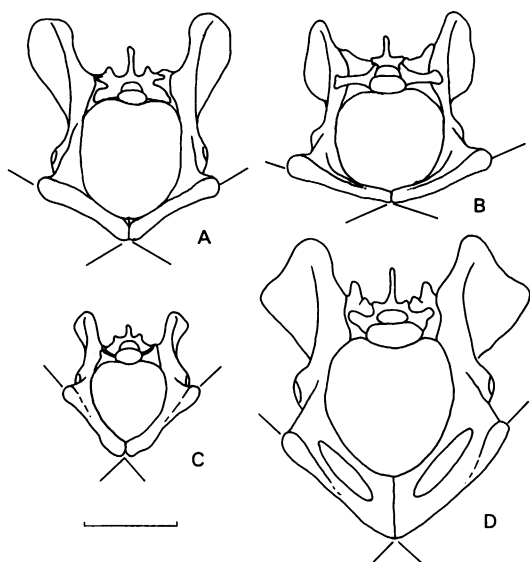
Fig. 3. Posterior view of pelvis showing the angles of pelvic floor. **A.** *Tomarctus* sp., UNSM 26664; **B.** *Vulpes vulpes*, KUMA 81751; **C.** *Hesperocyon gregarius*, FMNH P12224; **D.** *Procyon lotor*, KUMA 12212. Scale = 30 mm.

has a prominent process which separates two grooves on either side—the groove for m. extensor digitalis communis laterally, and the groove for m. extensor carpi radialis medially. This process is also well defined in *Hesperocyon*, *Cormocyon*, and primitive *Tomarctus*, but is nearly lost in living canids. The posterior border of the distal radius has a similar process that has undergone comparable change; this posterior process is best developed in *Hesperocyon* and *Cormocyon*, and is reduced in later canids.

COMPARATIVE OSTEOLOGY OF HIND LIMBS

PELVIC GIRDLE: Jenkins and Camazine (1977) observed that living canids have the flattest pelvic floor and most downwardly oriented acetabulum among the families analyzed; the posterior border of the ischium of Recent canids is oriented nearly horizontally (fig. 3). Jenkins and Camazine (1977; see Femur section below) examined the femur of *Hesperocyon*, and found, in the femoral head, cursorial features similar to those of domestic cats. Pelvic girdles of *Hesperocyon*, however, show just the opposite of what

would be predicted on the basis of femoral morphology examined by Jenkins and Camazine. The left and right ischial borders form a steep angle of approximately 90° (fig. 3). In a partial right pelvis of *Leptocyon vulpinus* (AMNH 12883), the posterior border of the ischium is as horizontally flat as in living canids. This specimen provides by far the earliest record (Harrison Formation, Late Arikareean) of a canine pelvis, and forms a sharp contrast to the far more primitive constructions of primitive hesperocyonines and borophagines.

Discussion: Using cineradiographic imaging techniques, Jenkins and Camazine (1977) demonstrated that pelvic and hind-limb movements of living carnivorans have discrete locomotor patterns during walking. Four taxa in three families were included in their analysis: ambulatory raccoon (Procyonidae); arboreal domestic cat (Felidae); and cursorial fox and domestic dog (Canidae). Among the three families, canids showed the most restricted hind-limb abduction, as contrasted with procyonids at the other extreme, which are capable of wide degrees of abduction, presumably suited for climbing.

These differences in locomotor patterns were found to be associated with the orientation of the ischium and acetabulum (Jenkins and Camazine, 1977). The angled pelvic floor in *Hesperocyon* is apparently primitive as it also occurs in *Vulpavus*, *Cormocyon*, and living raccoons and bears; it suggests far less restricted movements (within the sagittal plane) than in *Leptocyon* and more derived canines.

FEMUR: Two muscle scars are visible on the greater trochanter of canids. The facet on the proximal part of the trochanter marks the insertion of the middle gluteal muscle. Anterior to this facet and extending laterally and distally is the elongated facet for the deep gluteal muscle (Munthe, 1989). These two facets are more or less continuous in *Hesperocyon*, only slightly separated by a narrow space in *Cormocyon*, and progressively more widely separated by a shallow groove in *Tomarctus* and living canids.

In *Vulpavus*, primitive small canids, and living raccoons, the surface area lateral and distal to the greater trochanter is relatively flat and smooth. This area has become more

pointed and more rugose in advanced canids such as *Tomarctus*, *Canis*, and *Vulpes*. The third trochanter, where the gluteus maximus muscle is inserted, is distinct in miacoids. This trochanter has become much smaller in *Hesperocyon* and *Cormocyon*, and has almost disappeared in living canids.

Ginsburg (1961) observed that most plantigrade carnivorans (bears, raccoons, pandas, etc.) have a very flat, wide patellar surface (femoral trochlea) on the distal femur. *Vulpavus* also has a flat trochlea. *Hesperocyon* and later fossil canids, however, are quite modern in this respect in having a long, deep, and narrow patellar surface. The only difference is that the two ridges bordering the patellar surface are asymmetrical in advanced borophagines and living canids, whereas *Hesperocyon* and, to a lesser extent, *Cormocyon* have symmetrical ridges. Most living canids have a well-developed lateral supracondylar tuberosity (lateral epicondylar tuberosity) and a less prominent medial supracondylar tuberosity. These two tuberosities are for originations of the lateral and medial heads of the gastrocnemius muscle. The tubercles are either not present or very weak in all of the primitive fossil canids up to *Tomarctus*. The m. gastrocnemius, which inserts on the tuber of the calcaneum through a strong tendon in living canids, is one of the most important muscles responsible for pulling the tibiotarsal joint up from the ground into a digitigrade posture. Although absence of muscle scars on bones does not always correspond to absence of a muscle (Bryant and Seymour, 1990), the relatively weak development of a supracondylar tubercle seems to correlate with a weak gastrocnemius muscle in primitive fossil dogs.

Discussion: Jenkins and Camazine (1977: 366) contended that the femoral head of *Hesperocyon* has the configuration of a cat femur, "possessing distinctly cursorial features"; the position of the fovea capitis femoris and the orientation of the femoral head suggest that the femoral shaft of *Hesperocyon* has adopted an upright posture. They concluded (p. 369): "Certain features among Eocene miacoids appear to represent cursorial specializations, but only in the Oligocene canid *Hesperocyon gregarius* are all the hip adaptations of a modern cursor developed."

However, the pelvis of *Hesperocyon* is the opposite of what Jenkins and Camazine (1977) regarded as the cursorial type of hip structure. The orientation of the ischium is such that would allow a considerable degree of lateral abduction of the femur. These differences of pelvic versus femoral morphology in *Hesperocyon* may indicate the actual evolutionary transformations which canids had gone through to achieve progressively more cursorial adaptations. Thus, the femoral shaft first became upright without a flat pelvic floor to physically limit the abduction; the pelvis was later reoriented to further secure the movement of the femur within a sagittal plane.

TIBIA: The proximal articular surfaces of the tibia, the medial and lateral condyles, are relatively stable in morphology throughout the evolution of canids. One noticeable change occurs in the position and depth of the muscular groove (sulcus muscularis, Evans and Christensen, 1979) for the tendon of m. extensor digitorum longus. In living canids (*Canis*, *Vulpes*, and *Urocyon*) this groove forms a deep notch located immediately in front of the lateral condyle, isolating a small process between the lateral condyle and the tibial tuberosity (fig. 4D). At the other extreme, *Hesperocyon*, *Cormocyon*, and to a lesser extent *Tomarctus* have very poorly developed muscular grooves (fig. 4A, B, C). The groove first appears in some individuals of *Leptocyon vafer*, a derived species of the genus.

Recent canids also differ from their primitive ancestors in having a high cnemial crest (tibial crest), which develops a second tuberosity distal to the prominent tibial tuberosity (fig. 4D); attached to this lower tubercle is the biceps femoris muscle. In *Hesperocyon*, *Cormocyon*, and *Leptocyon*, the cnemial crest is far less anteriorly extended and the lower tubercle blends smoothly with the crest. The situation in *Tomarctus* is somewhat intermediate between the two extremes. In *Hesperocyon* and *Cormocyon*, the popliteal notch posterior to the medial and lateral condyles is very deep in contrast to more shallow notches in *Tomarctus* and living canids (fig. 4).

Four muscles are located on the rather flat caudal surface of the tibial shaft in *Canis* (Evans and Christensen, 1979). On the me-
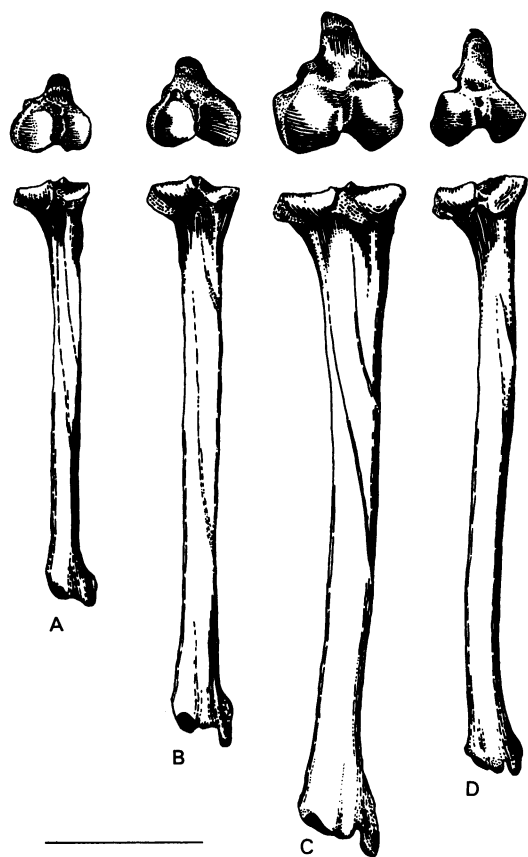
A

B

C

D

Fig. 4. Posterior (below) and proximal (above) views of left tibii of different canids. Muscle attachments are marked by two solid or dashed lines that form a slight angle with the lateral borders of the tibial shafts. The line on the left divides flexor hallucis longus (left) from caudal tibialis and flexor digitorum longus (middle); that on the right divides the former two from the popliteus muscle (right). Note the reduction of the middle muscle scar in the digitigrade fox. **A.** *Hesperocyon gregarius* (FMNH UC495); **B.** *Cormocyon* sp. (AMNH 49060); **C.** *Tomarctus* sp. (KUVP 27672); **D.** *Vulpes velox* (KUMA 121601). Scale = 30 mm.

dial side is the popliteus muscle which usually spreads around to the medial surface of the shaft. On the lateral side of the tibia and spreading to part of the fibula is m. flexor hallucis longus, which flexes the proximal phalanges. Between these two muscle scars is a narrow zone where the caudal tibial and flexor digitorum longus muscles originate. On most specimens of canids, there are two distinct ridges on the posterior surface of the

tibial shaft marking the borders among these three groups of muscles (fig. 4); the caudal tibial and flexor digitorum longus muscles often leave a single scar on the tibia surface.

With the combined flexor digitorum longus and caudal tibialis muscles occupying most of the proximal half of the shaft, the tibii of *Hesperocyon* and *Cormocyon* (fig. 4A, B) are definitely of plantigrade type according to Ginsburg's (1961) criterion (see discussion below). Living canids, on the other hand, have a greatly enlarged area of insertion for flexor hallucis longus at the expense of the caudal tibialis and flexor digitorum longus (fig. 4D). In *Tomarctus*, however, these two muscles share about the same amount of insertion area, a condition more advanced toward a digitigrade posture (fig. 4C), although there seems to be more variation at this stage of transition. In *Leptocyon*, the area for flexor digitorum longus and caudal tibialis is still large, even though its astragalus is clearly of digitigrade type (see below).

It is interesting that the living gray fox *Urocyon*, the only living canid that occasionally climbs trees (Fritzell and Haroldson, 1982; Yeager, 1938), has a tibial muscle attachment pattern that is intermediate between typical plantigrade and digitigrade, i.e., the areas for the combined caudal tibialis/flexor digitorum longus, and the flexor hallucis longus muscles scars are about the same. However, the gray fox is a true digitigrade as are all extant canids.

The distal tibia is similar throughout Canidae. Starting from *Hesperocyon*, it already has a rather deep trochlea on the distal articular surface. Later canids have progressively deeper articular surfaces, indicating a trend toward increasingly secure articulation with the astragalus.

Discussion: Ginsburg (1961) claimed that the relative size of the muscle scars on the posterior surface of tibial shaft offers the best criterion for differentiating between plantigrade and digitigrade carnivorans. According to him, all digitigrade carnivorans have a relatively larger (wider) area for the flexor hallucis longus in contrast to the smaller area of the combined caudal tibialis and flexor digitorum longus (Ginsburg did not mention the latter muscle); the reverse is true for plantigrade carnivorans. A similar pattern has been
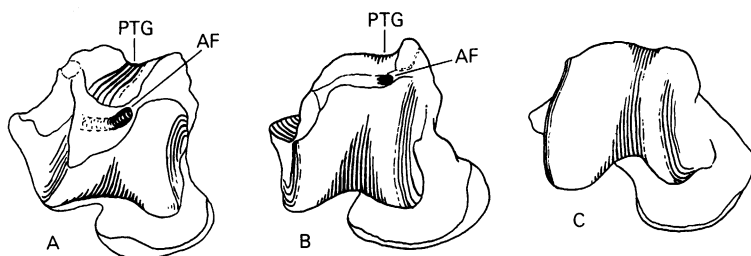
Fig. 5. Posteroproximal aspects of three caniform right astragali to show possible morphological steps in the evolution of an elongated astragalar trochlea. The transformation involves: 1) the reorientations of the plantar tendinal groove (PTG) and the trochlea into a common pathway for the tibia; 2) the stretching of the proximal end of the trochlea at the expense of the plantar tendinal groove; 3) the reduction and eventual elimination of the astragalar foramen (AF). **A.** *Vulpavus ovatus*, AMNH 11497 (reversed from right side), Miacoidea, Bridgerian, middle Eocene; **B.** *Hesperocyon gregarius*, FMNH P12224, Canidae, Orellan, middle Oligocene; **C.** *Vulpes vulpes*, KUMA 81751, Canidae, Recent. All drawn to approximately the same size.

recorded in African herpestids and viverrids (Taylor, 1976), although my own observations indicate that *Civettictis civetta*, listed as digitigrade by Taylor (1974, 1976), has long and wide areas of insertion for m. caudal tibialis and m. flexor digitorum longus.

The present observation of fossil canids indicates more variation of the muscle scars than Ginsburg (1961) had accounted for, and my conclusion of a plantigrade *Hesperocyon* contradicts Ginsburg's tibial criterion of plantigrady vs. digitigrady.

ASTRAGALUS: Mammalian astragali are strong and highly compact; they are readily preserved and known for many fossil carnivorans. The plantigrade nature of the miacoid astragalus is apparent because of its restricted extension of the tibioastragalar joint (fig. 5). Its trochlea is terminated proximally by a diagonal (relative to the long axis of the trochlea) line that marks the posterior extent of tibial rotation. The trochlea is so short and oriented in such a way that the tibia cannot extend beyond 90° from the long axis of tarsometatarsus. In *Vulpavus*, there is a prominent nutrient foramen (astragalar foramen) immediately behind the posterior margin of the astragalar trochlea (Matthew, 1909). The astragalar foramen opens slightly towards the lateral side, where there is a triangular, rough area dropping below the polished surface of the trochlea. Posterior to the astragalar foramen is the plantar tendinal groove (sensu Matthew, 1909), which is deeper than, and at an angle with, the astragalar trochlea. The

plantar tendinal groove continues onto the calcaneum on the posterior surface of the sustentaculum tali. In dogs, the tendons of flexor hallucis longus and flexor digitorum profundus are bound on the posterior surface of the sustentaculum tali by a flexor retinaculum—the fascia that spans the medial edge of the sustentaculum tali and the body of the calcaneum (Evans and Christensen, 1979). The plantar tendinal groove in miacoids is obviously not part of the astragalar trochlea because of its different depth and orientation (approximately 15–20°) from the trochlea. The presence of a large astragalar foramen between the trochlea and the plantar tendinal groove further suggests that the posterior edge of the distal tibia does not rotate beyond the foramen.

Some small arboreal or scansorial carnivorans (e.g., *Viverricula*, *Viverra*, *Genetta*, *Meles*, *Ailurus*, and *Potos*) still retain the astragalar foramen as well as the narrow grooves on either side of the foramen across the trochlea. In some individuals, the astragalar foramen clearly penetrates the trochlea to emerge on the other side of the astragalus. In some living ursids, the proximal end of the astragalar trochlea develops a lip that effectively stops the tibia from further rotation.

The overall construction of the astragalus of *Hesperocyon* is similar to that of living raccoons with a relatively shallow trochlea. A small astragalar foramen is present (see more discussion below). In *Cormocyon*, the astragalus is closer to that of a true digiti-
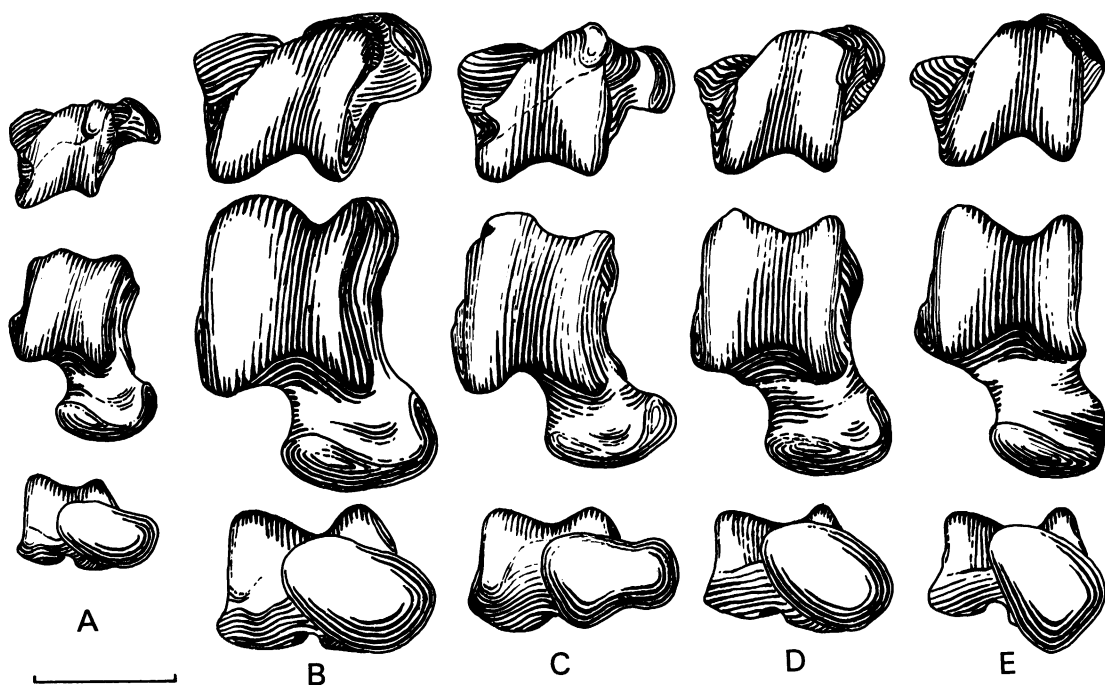
Fig. 6. Proximal (top), anterior (middle), and distal (bottom) views of right astragali of **A**. *Hesperocyon gregarius*, FMNH P12224; **B**. *Tomarctus thomsoni*, AMNH 49096; **C**. *Procyon lotor*, KUMA 3625; **D**. *Urocyon cinereoargenteus*, KUMA 87737; **E**. *Vulpes vulpes*, KUMA 81751. See text for explanations. Scale = 10 mm.

grade. The transverse line on the trochlea that usually marks the end of tibial rotation is completely obliterated (see discussion below). The astragalar foramen is considerably reduced and may not have been functional. The tibia can rotate through the entire length of the trochlea plus the "plantar tendinal groove"; the tendon for flexor hallucis longus and flexor digitorum profundus presumably no longer glides inside this groove when the animal is standing fully upright because the groove is now occupied by the distal tibial trochlea. The astragalus of *Tomarctus* has achieved a high degree of trochlea depth and slightly increased degree of rotation at the tibioastragalar joint; its astragalar foramen is lost. However, *Tomarctus* still retains a few primitive characters shared with *Hesperocyon* and raccoons, a narrow neck constricted at the base (fig. 6A, B, C); a deep fossa on the lateral side of the trochlea toward the proximal end; and long axis of the head perpendicular to the trochlear groove on distal view. The last character is also seen in the scansorial gray fox *Urocyon* (fig. 6D).

Discussion: The astragalus is one of the most important hind-limb elements in the transformation from plantigrade to digitigrade, because changes of postures directly affect construction of the tibioastragalar joint. Since the main difference between plantigrady and digitigrady is the degree of plantar extension between the tibia and astragalus, the rotational arc of the astragalar trochlea serves as a direct measurement of ankle extension.

Transformation of the astragalus from plantigrade miacoids to digitigrade canids involves a reorientation of the plantar tendinal groove to align itself with the trochlea, so that the groove becomes part of the trochlea. This additional segment of the trochlea allows farther extension of the ankle joint and clears the way for the elongation of the trochlea toward the proximal end. The initial stage of this transformation is seen in *Hesperocyon*. The plantar tendinal groove of *Hesperocyon* is in the same direction and has similar depth as the trochlea. However, this groove does not yet function as the end segment of the trochlea for two reasons. Firstly, like the mia-

coids, most *Hesperocyon* specimens have an astragalar foramen of variable size. The trochlea ends just distal to the foramen marked by a transverse line identical to that in *Vulpavus*, which closely corresponds to the contour of the posterior edge of the distal tibia. Beyond (proximal to) this line, the "trochlear" surface is less polished, indicating that the area was not used (at least not frequently) for articulation with the tibia. Further tibial extension beyond the astragalar foramen would also compress the soft tissue outside the foramen. Secondly, there is in *Hesperocyon* (and also in plantigrade *Procyon*) a small tubercle near the proximal end of the medial trochlear rim, at the same transverse level as that of the astragalar foramen. This tubercle is slightly higher than the trochlear rim and blocks the posterior (proximal) edge of the tibia from further extending on the astragalus (fig. 5). The astragalus of *Hesperocyon* thus suggests a plantigrade posture.

Living canids (and also fossil canines, even *Leptocyon vulpinus*, from Late Arikareean) have lost the astragalar foramen on the trochlear surface of the astragalus. The foramen on the other (plantar) side of the astragalus may still be present. The tibia can rotate on the astragalus along the entire trochlear course (including the segment converted from the plantar tendinal groove), until the tibial shaft touches the calcaneum. Thus, living digitigrade canids enjoy a much greater range of rotation along the astragalar trochlea that allows the tibioastragalar joint to be much more fully extended. The axis of the tarsometatarsus can be closely in line with the tibial axis (more than 150° between the two) in resting position—a desirable posture in terms of energy efficiency (see fig. 9). The tibia of *Hesperocyon*, by comparison, forms an approximately 110° angle with the tarsometatarsal axis even when fully extended.

CALCANEUM: Stains (1975) compared calcanea of 25 species of living canids and concluded that they do not vary significantly. There are, however, some differences among the fossil taxa in this study. In contrast to the relatively robust calcanea of most plantigrade carnivorans, the slender proportions of the calcaneum of *Hesperocyon* are more similar to those of more derived canids. *Hesperocyon* still retains the primitively large peroneal tu-

bercle on the lateral edge at the base of the calcaneum. This tubercle was also present in *Vulpavus*, *Cormocyon*, some large borophagine canids (Munthe, 1989), and some living plantigrade carnivorans (e.g., *Meles*, *Martes*, *Taxidea*, *Mustela*, *Ailurus*, *Nasua*, *Procyon*, and most viverrids), but is greatly reduced in living canids. In lateral view, the posterior edges of all calcanea of primitive fossil canids are more curved than those of living canids.

In *Vulpavus*, the medial articular facet on the sustentaculum tali is greatly expanded toward the medial side and is almost completely below the lowest level of the lateral articular facet. The calcaneum of *Hesperocyon* (and also *Cormocyon*) is advanced in this regard. It has brought the medial facet up close to the same level as the lateral articular facet and has very limited medial extension, a condition that indicates an irreversible hind foot (Jenkins and McClearn, 1984). If *Hesperocyon* did climb trees, it probably could not descend head-down.

METAPODIALS: Scott (1898) and Scott and Jepsen (1936) recognized that there are five metatarsals in *Hesperocyon*, even though only the proximal halves of metatarsals I–IV were preserved in the materials they examined. All of the early canids in this study remain pentadactyl, i.e., a functional first metapodial is present on the fore and hind feet. The extremely reduced first digits in living canids are thus a derived condition within the subfamily Caninae.

Among all individuals of *Hesperocyon* with articulated metapodials, the shafts are more compressed than is illustrated in Scott (1898, pl. XX, figs. 23, 24) and Scott and Jepsen (1936, pl. XIII, figs. 3, 4); the metapodials are nearly parallel with one another. The reduction of metatarsus I and metacarpus I, lost in living canids (Ginsburg, 1961), has already become apparent in *Hesperocyon*, although the length of these digits is still more than half that of the metapodials III or IV (except F:AM 50333, which has a metatarsus I slightly shorter than half the length of its metatarsals III–IV).

In a well-preserved hind foot of *Leptocyon vafer* (F:AM 62780, from the Tesuque Formation of New Mexico, Early Barstovian), the metatarsals are more elongated and tightly compressed than in *Hesperocyon*. The first
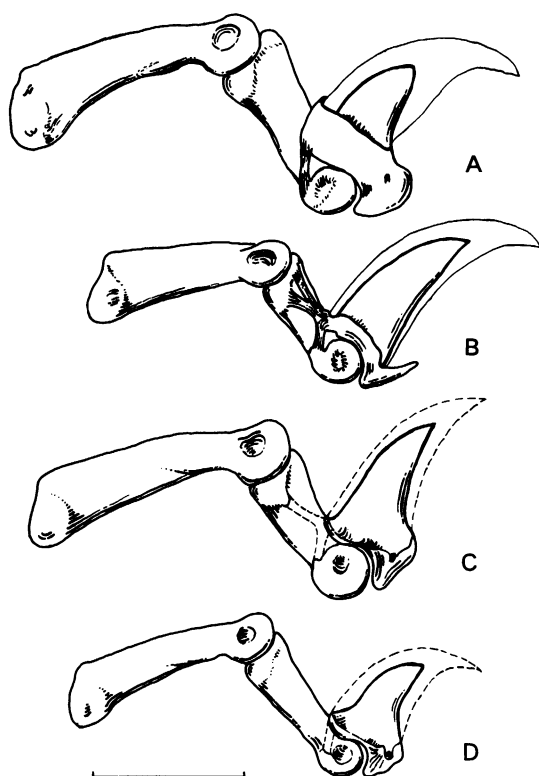
Fig. 7. Lateral view of proximal-distal phalanges showing shapes of claw sheath and retraction of claws by the elastic lateral dorsal ligament(s). Dashed lines in the fossil taxa (C and D) are the author's interpretations of the horny sheath and elastic ligaments. A. Domestic cat, ligament attachments after Gonyea and Ashworth (1977); B. *Vulpes fulva*, KUMA 14414, prepared skeleton, ligament still intact on bones; C. *Tomarctus*, n. sp., KUVP 27672; D. *Hesperocyon gregarius*, USNM 67, digit III. Exact digits are mostly not determinable due to disarticulation. Scale = 10 mm.

metatarsus is reduced to less than half the length of metatarsus III and is more slender than the rest of the digits.

Discussion: Tightly compressed metapodials and reduction of digits have long been identified with cursoriality (e.g., Lull, 1904; Brown and Yalden, 1973; Taylor, 1974, 1976) or digitigrady (Ginsburg, 1961; Tedford, 1978). Whereas adjoined metapodials are generally correlated with cursoriality, the correspondence breaks down with regard to digitigrady. Among small herpestids and viverrids, compressed metapodials are not always

associated with digitigrady; this is especially true in animals that are diverse in their locomotor behaviors. Thus, genets (*Genetta*) have tightly compressed metapodials but are plantigrade, and mongooses (*Mungos*) are digitigrade (Taylor, 1974, 1976), but have more separated fingers and toes.

PHALANGES: On the middle phalanx of typical retractile cats, the trochlea is transversely elongate toward the lateral sides resulting in an asymmetrical configuration. There is correspondingly a broad depression proximal to this extension, so that the phalanx body is asymmetrical in both dorsal view and cross section (Gonyea and Ashworth, 1977). This concave middle phalanx allows the distal phalanx to rotate beyond the physical constraint of the bony body of the middle phalanx. The asymmetry of the middle phalanx is often absent or ill-defined in nonretractile carnivorans, e.g., *Canis*. The actual retraction of claws is passively accomplished by the elastic "lateral dorsal ligament" inserted on the dorsal tip of the distal phalanx. The ligament originates from a small tubercle on the palmar side of the lateral epicondyle of the head of the middle phalanx (Gonyea and Ashworth, 1977; this study, fig. 7A). In the nonretractile domestic dogs this ligament originates from the proximodorsal end of the middle phalanx (Evans and Christensen, 1979), a condition that has no downward component to fully retract the claws.

The situation of tendon attachment in canids is more complex than suggested by Gonyea and Ashworth (1977). The living red fox (*Vulpes vulpes*) has as many as three branches of the elastic ligaments all converging toward the top of the distal phalanx: one branch originates in the catlike position on the lateral epicondyle, a second branch in the doglike position on the dorsal side of phalanx body, and a third in an intermediate position that originates from a proximoventral tubercle of the middle phalanx (fig. 7B). One specimen of gray fox (*Urocyon*, KUMA 11907) has lost the catlike component, the "lateral dorsal ligament."

The middle phalanx of *Hesperocyon* is fundamentally canidlike in its lack of a laterally elongated distal epicondyle (fig. 7A). The relatively long and deep (in cross section) shaft in *Hesperocyon*, however, remains somewhat

catlike. *Tomarctus*, on the other hand, has a short middle phalanx with a dorsoventrally flattened cross section more similar to that of the red fox (fig. 7B). The scars for ligamentous attachments in *Tomarctus* are well developed, and suggest a ligament of two rami; one from the lateral epicondyle and another from the posterolateral wall (fig. 7C).

The outlines of the claws of *Hesperocyon* (figs. 7D, 8A) are somewhat close to those of the trunk-climbing squirrel (*Sciurus*), illustrated by Yalden (1985), which has an inwardly curving hook (or "needle-like point" in Yalden's terminology) on the horny sheath like those of tree-climbing mammals and birds. In addition, part of the upper articular surface in *Hesperocyon* is at a slight angle with its axis of rotation so that it fits with the middle depression on the middle phalanx. The claw of *Tomarctus*, however, is more elongated than that of *Hesperocyon* and is relatively thick mediolaterally in cross section (figs. 7C, 8B). Its overall shape is similar to that of living foxes (figs. 7B, 8C). No canid, fossil or Recent, has a bony hood surrounding the horny sheath, in contrast to cats, which have a deep hood within which the claw sheath is firmly embedded.

Discussion: The shape of the middle and distal phalanges is important in the inference of locomotor behavior. Although the presence of retractile claws alone is not sufficient evidence for arboreal life (large cats use them to bring down prey rather than climb trees), it is nevertheless a necessary condition for climbing large trees.

Carnivorans who cannot fully retract their claws tend to quickly wear out their claw sheath (Ewer, 1973). Arboreal animals that use claws for climbing always have sharply curved, thin-bladed horny sheaths for grasping, and they keep the claw fully retracted when not in use. In the bony distal phalanx, retractibility is correlated with a relatively short, deep, laterally compressed, and sharply edged bony claw, a condition also displayed in some herpestids and viverrids (Taylor, 1974). The contrary is commonly true for nonretractile carnivorans.

The overall phalangeal morphology of *Hesperocyon* indicates that it probably had sharply curved claw sheaths which may have functioned as climbing devices, as predicted
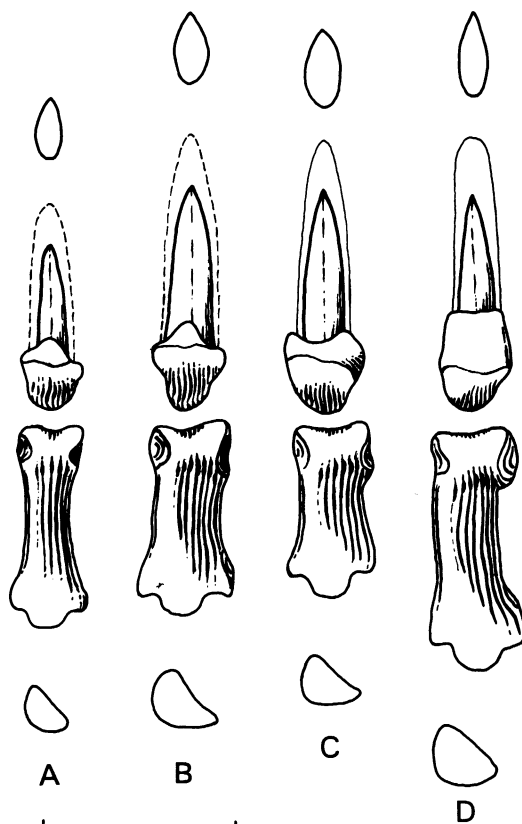

Fig. 8. Dorsal view of right middle and distal phalanges and their cross sections. Cross sections of the distal phalanges (top) are at the basal part of the claws and those of middle phalanges (bottom) are at the level of minimal mediolateral width, usually in the middle part of the body. Dashed lines are the author's interpretation of the horny sheath. **A**. *Hesperocyon gregarius*, USNM 67; **B**. *Tomarctus* sp., KUVP 27672; **C**. *Vulpes fulva*, KUMA 14414; **D**. Domestic cat. Scales = 10 mm.

by Matthew (1930). Hildebrand (1954: 447) found evidence of arboreal adaptations (increased rotation of forearms) in the gray fox, the only tree-climbing canid, but noted that the "claws of the gray fox are not sharper than those of foxes which do not climb," and "neuromuscular and psychological factors probably are at least as important as morphological specialization in determining the climbing ability of these foxes."

QUANTITATIVE ANALYSIS

In a digitigrade posture, the moment arm by body weight, W, exerted on the trochlea

TABLE 1

**Measurements of the Humerus and Ulna of Three Primitive Canids: *Hesperocyon*,
Cormocyon, and *Tomarctus***

GL, greatest length; BP, greatest breadth at the proximal end; BD, greatest breadth at the distal end; SD, smallest breadth of diaphysis; BL, body length of ulna; LO, length of the olecranon. For the metacarpus and metatarsus, all measurements are greatest lengths of respective digits. See Von den Driesch (1976) for definitions of measurements.

	Hesperocyon			*Cormocyon*	*Tomarctus*		
	N	Mean	Range	N = 1	N	Mean	Range
Humerus							
GL	9	73.32	58.7–83.8	82.1	4	111.05	106.2–116.0
BD	9	16.26	13.4–18.5	18.5	4	25.13	23.5–27.5
SD	9	5.26	4.1–6.3	6.4	4	8.73	8.2–9.5
Ulna							
GL	2	73.75	71.4–76.1	84.8	4	107.75	101.4–117.0
LB	2	57.90	56.7–59.1	67.2	5	85.48	77.9–95.7
LO	3	9.30	8.7–10.3	11.8	5	14.30	8.4–17.7
Femur							
GL	3	81.43	73.0–88.2	101.7	4	127.25	113.8–140.3
BD	3	14.33	12.5–15.6	17.3	3	24.10	20.8–27.5
Tibia							
GL	5	87.84	80.7–92.6	109.5	5	118.02	110.1–127.4
BP	5	14.84	13.8–16.4	18.4	4	25.95	22.0–29.1
Metatarsus							
I	3	18.10	14.0–20.2	21.8	2	23.50	23.4–23.6
II	5	28.42	26.7–29.7	35.5	3	39.67	38.8–40.5
III	5	33.60	30.8–35.7	40.6	3	45.53	43.8–46.5
IV	6	35.28	32.2–37.9	42.5	3	47.17	44.8–48.5
V	3	30.47	27.6–33.3	39.9	3	43.77	42.0–45.0
Metacarpus							
I	1	10.70		12.5	2	17.75	15.5–20.0
II	1	16.40		20.9	4	28.83	27.5–30.5
III	1	19.40		25.3	3	34.00	32.7–34.8
IV	1	19.40		25.0	3	34.27	32.9–35.5
V				20.4	3	27.07	25.8–27.8

of the astragalus, is $W \cdot R$ or $W \cdot \cos(\alpha) \cdot TM$, where α is the angle between the axis of tarsometatarsus and the ground, and TM is the length of tarsometatarsus (fig. 9A), ignoring the weight of the foot bones themselves. This is counteracted by the moment arm generated by gastrocnemius muscle (F), i.e.,

$$W \cdot \cos(\alpha) \cdot TM = F \cdot \cos(\beta) \cdot (TM + C).$$

Where β is the small deviation of F from the perpendicular line with the TM axis ($\cos[\beta]$ is thus close to one). The maximum load on F (when α is near zero, and thus $\cos[\alpha]$ is close to one), may be approximated as:

$$F = W \cdot TM/(TM + C).$$

Therefore, given a fixed body weight, the force, F, needed to raise the feet is proportional to the ratio $TM/(TM + C)$. For most carnivorans, elongation of the calcaneum is rather limited compared to lengthening of the metatarsus. The increased demand for F due to the lengthening of the metatarsus thus approaches an upper limit of $W \cdot TM/(TM + C)$. In digitigrade canids, the ratios of TM/C ranges from 3.8 in *Cormocyon* to 4.2 in
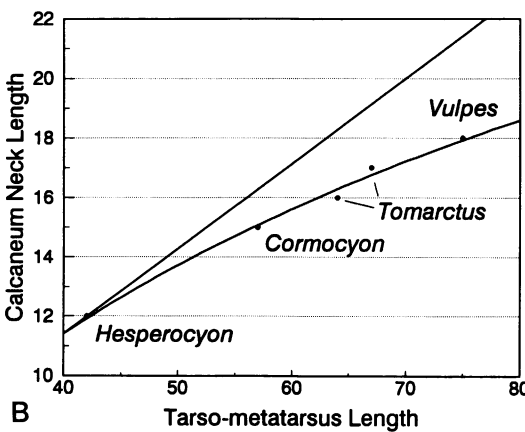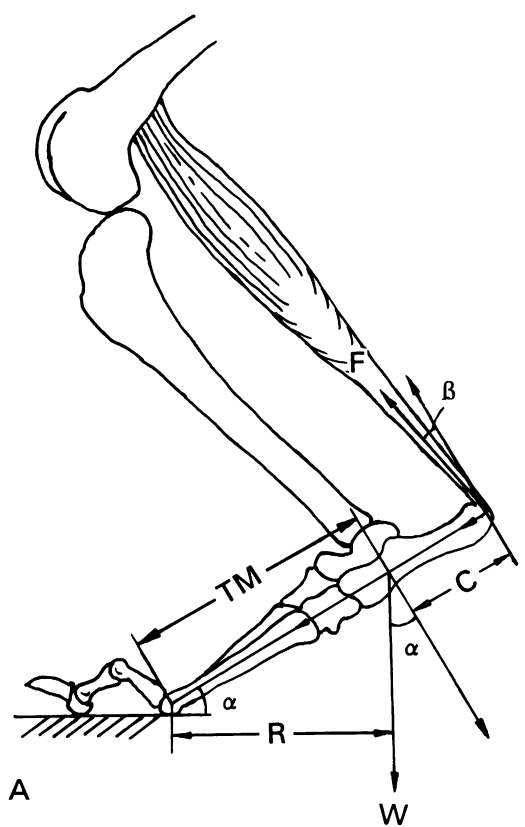
A

B

Fig. 9. **A.** Simplified relationship between the muscle force (F) pulling foot up and the body weight (W) pushing it down. It is assumed that the articulations along the calcaneum-tarsus-metatarsus line are structurally rigid. Abbreviations: C, length of calcaneum neck; TM, length of distal calcaneum through tarsus-metatarsus. **B.** Bivariate diagram showing the increasing length of tarsometatarsus

TABLE 2

List of Ratios of Greatest Length of Femur over that of Tibia (F/T), and Greatest Length of Metatarsus III over that of Femur (MT/F)

Ratios for living taxa are species means from data in Clutton-Brock et al. (1976).

Taxa	F/T	MT/F
Miacoids		
Vulpavus	1.08[a]	0.26[a]
Fossil canids		
Hesperocyon	0.93	0.41
Cormocyon	0.93	0.40
Tomarctus	1.08	0.37
Recent canids		
Vulpes	0.89	0.49
Otocyon	0.94	0.46
Alopex	0.89	0.49
Dusicyon	0.94	0.46
Nyctereutes	0.95	0.43
Speothos	1.08	0.37
Chrysocyon	0.95	0.49
Canis	0.98	0.43
Cuon	1.04	0.42
Lycaon	0.97	0.41

[a] Femur measurement is estimated from the composite of AMNH 11497 and 19198.

Vulpes; F thus ranges from 0.79W to 0.81W given the above conditions. Changes in length proportions among these bones do not seem to significantly increase the load of m. gastrocnemius. In fact, the length increase of the calcaneum lags behind that of the tarsometatarsus in the history of canids (fig. 9B).

It has been well recognized that living cursorial canids (and also mammals in general) tend to elongate the distal segments of the limb bones (e.g., Hildebrand, 1952; Ginsburg, 1961). In particular, the metatarsus/femur ratio of canids is greatly increased in contrast to the much smaller ratio in miacoids (tables 1, 2). The primitive canids in the present study have already reached the lower range of living canids. The relative length between femur and tibia, however, does not seem to change very much in the history of canids. In fact, some living canids, e.g.,

←

(x axis) and the slower increase of calcaneum neck length (y axis) in selected canid taxa. Scales in mm.
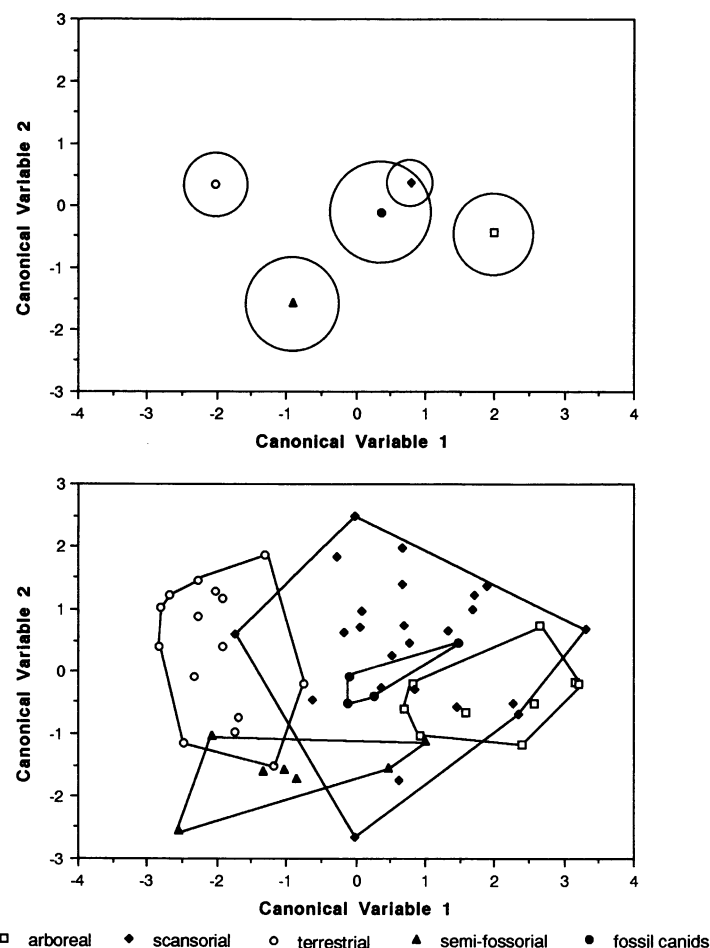
Fig. 10.   Scatter diagrams for living carnivorans and fossil canids on the first and second canonical variables. **Top**: distribution of group centroids surrounded by 95% confidence interval (circles) for group means. The radius of the circles is inversely related to the sample size of the group. Thus, the larger the sample size, the more precise the location of the group mean would be. **Bottom**: distribution of individual taxa surrounded by the maximum ranges of the groups (polygons). See table 3 and Van Valkenburgh (1985) for original data. Designations of locomotory categories of living carnivorans follow those of Van Valkenburgh (1985).

Speothos and *Cuon*, have the same femur/tibia proportion as the miacoid *Vulpavus* (tables 1, 2).

One interesting point derived from table 2 is that, in living canids, the fox-sized genera (*Alopex* and *Vulpes*) have a relatively longer metatarsus than those of wolf-sized genera (*Canis* and *Lycaon*). Fossil canids seem to be equally diverse in their limb bone proportions. The ratio difference between *Hesperocyon* and *Tomarctus* is particularly striking since the latter is several million years younger than the former.

Van Valkenburgh (1985, 1987) proposed several limb measurements as morphometric indices for four locomotor categories in living carnivorans: arboreal, scansorial, terrestrial, and semifossorial. Using these indices, she made further inferences based on multivariate statistics of the locomotor behavior of large Oligocene carnivorans. Combined with Van Valkenburgh's (1985) data, measurements of four fossil carnivorans (*Vulpavus*, *Hesperocyon*, *Cormocyon*, and *Tomarctus*; see table 3) were subjected to discriminant function analysis. Except *Hesperocyon*, which

TABLE 3
Morphometric Indices of Limb Bones Used in Discriminant Analysis
The abbreviations for measurements are: LBW, log body weight (kg); UD, ungual phalanx depth; ARCH, ungual phalanx curvature; MCP, metacarpal-phalanx ratio; OLA, olecranon orientation; OLL, olecranon length; FMT, femur-metatarsal ratio; ASD, astragalar trochlear depth. If more than one specimen was available for a particular measurement, averages were taken of the total number. See Van Valkenburgh (1987) for definitions of the variables and estimations of the log body weight on fossil taxa.

Taxa	LBW	UD	ARCH	MCP	OLA	OLL	FMT	ASD
Vulpavus	0.546	1.95	0.243	1.833	20	0.25	2.441	0.077
Hesperocyon	0.557	1.65	0.199	1.750	15	0.17	2.441	0.200
Cormocyon	0.577	1.66[a]	0.165[a]	1.917	5	0.20	2.405	0.198
Tomarctus	0.602	1.71	0.140	2.074	17	0.20	2.727	0.282

[a] Estimated from the means between those of *Hesperocyon* and *Tomarctus*.

is marginally classified in the arboreal category, the rest of the taxa, although close to the arboreal group range, are all classified in the scansorial category (all living canids are classified as terrestrial) (fig. 10).

The statistical predictions that primitive canids were scansorial is generally confirmed by their anatomical characteristics noted above. However, the statistical analysis cannot differentiate the phylogenetic components in the limb morphology that may play a significant role in placing the fossil taxa into the "primitive" categories (arboreal and scansorial). Limb morphology of Oligocene carnivorans as a whole tends to have a primitive configuration. This is also reflected in Van Valkenburgh's (1987) study which placed most of the large Oligocene carnivorans into the scansorial category, because her morphometric indices are designed to emphasize the derived conditions in living carnivorans.

DISCUSSION

Before proceeding to the discussion of the transformation from plantigrady and digitigrady, I will briefly outline the phylogeny of fossil canids in order to provide some paleontological perspective (fig. 11). A tripartite division of the Canidae was formulated by Tedford (1978) and had since gained wide acceptance: subfamilies Hesperocyoninae, Borophaginae, and Caninae. The earliest and most primitive canids were represented by the initial radiation of hesperocyonines (including *Hesperocyon*) in the Eocene to early Miocene (38–15 million years ago) (Wang,

MS). This archaic group of canids was gradually replaced by borophagines in Mio–Pliocene, which was in turn replaced by canines (including all living canids) mainly in the Pliocene to Present (Primitive canines such as *Leptocyon* can be traced back to late Oligocene of Arikareean age: Tedford, 1978; Tedford and Taylor, MS).

For purpose of clarity, the present discussion of plantigrady vs. digitigrady assumes a static posture. Most plantigrade mammals become digitigrade when running fast. As observed by Brown and Yalden (1973), some carnivorans traditionally regarded as plantigrade, such as bears, actually have digitigrade forelimbs. Determinations of posture are then based on hind limbs (ursids are thus plantigrade). Brown and Yalden (1973: 124) also attempted to define, on morphological grounds, a digitigrady in which "the weight is borne on the digital and interdigital pads; the thenar and hypothenar pads are reduced or lost." In other words, presence of the thenar and hypothenar pads is the only permissible evidence that the heel actually touches the ground. Such a narrow criterion, however, tends to include a large number of carnivorans into the digitigrade category, even though many still place their feet almost flat on the ground and are practically plantigrade (in some plantigrade viverrid, e.g., *Genetta*, no thenar or hypothenar pads are present; instead, a large area of bare skin is present on the heel presumably because of a relatively light touch on the ground). Moreover, foot pads are rarely preserved in fossils (fossil trackways, on the other hand, often cannot be positively linked to any particular taxon)
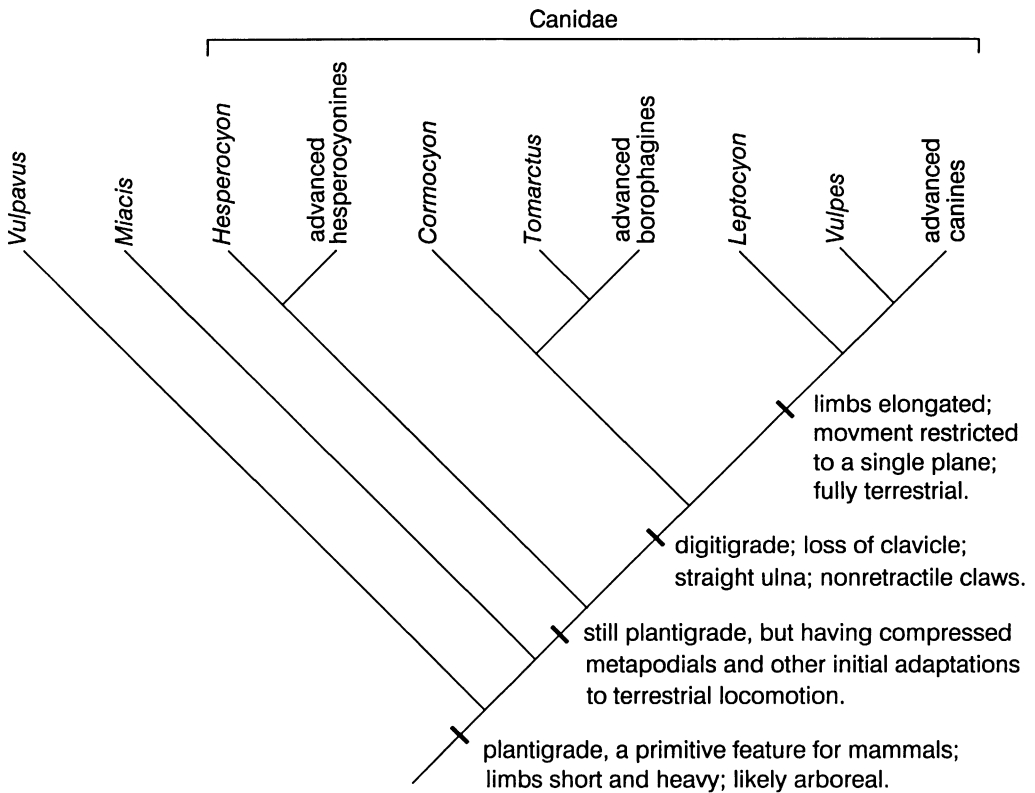
Canidae

Vulpavus

Miacis

Hesperocyon

advanced hesperocyonines

Cormocyon

Tomarctus

advanced borophagines

Leptocyon

Vulpes

advanced canines

X limbs elongated; movment restricted to a single plane; fully terrestrial.

X digitigrade; loss of clavicle; straight ulna; nonretractile claws.

X still plantigrade, but having compressed metapodials and other initial adaptations to terrestrial locomotion.

X plantigrade, a primitive feature for mammals; limbs short and heavy; likely arboreal.

Fig. 11. Phylogeny of Canidae and precanid miacoids showing postulated limb transformations leading to the fully digitigrade and highly terrestrial limbs in living canids. Only the most primitive members of each subfamily are shown. The phylogeny of canids is based on Tedford (1978) and that of miacoids based on Wang and Tedford (MS).

and cannot be used as a criterion for the present study.

Scott (1898; also Scott and Jepsen, 1936) had long called attention to the similarities of the postcranial skeletons of *Hesperocyon* and viverrids. This primitiveness of the *Hesperocyon* limb bones has been the basis for regarding *Hesperocyon* as having a "semi-plantigrade gait [posture]" (ibid). Matthew's (1901) reconstruction of *Hesperocyon* featured a genetlike body with its hind feet nearly touching the ground. On the other hand, *Hesperocyon* possesses some characteristically canid (among caniform carnivorans) limb features, e.g., elongated and adjoined metapodials, that have been suggested to signify digitigrady (Tedford, 1978).

A different criterion is suggested in the present study to differentiate plantigrady and digitigrady, i.e., estimating the degree of ankle extension, as reflected on the astragalar

trochlea. *Hesperocyon* is thus determined to have been plantigrade. Its astragalus displays a limited angle of rotation for tibial extension. Its lengthened and compressed digits are here interpreted as adaptations toward increased cursoriality rather than indicators of standing postures.

The reoriented plantar tendinal groove in *Hesperocyon*, aligned with the astragalar trochlea, may seem to be part of the trochlea. However, the presence of a transverse tibial stop line on the trochlea and astragalar foramen along this line suggests that the tibia does not go further beyond this line. Perhaps it indicates the tibial position when the animal is standing still; in fast running, however, the tibia may go beyond this line. The reorientation of the plantar tendinal groove may be a result of a more abducted position of the hind limbs. As the tibia becomes more abducted and the medial rim of the astragalar

trochlea more raised, the originally more medially directed groove begins to be parasagittally oriented. This reoriented plantar tendinal groove may thus prove to be a preadaptation as an additional segment of the astragalar trochlea enabling greater posterior tibial excursion.

Dublin (1903) recognized that most arboreal carnivorans were capable of terrestrial locomotion and found little anatomical difference between what he called "partially arboreal" animals and typical terrestrial types. Although more detailed studies (e.g., Jenkins and Camazine, 1977; Taylor, 1974) increased our appreciation of their anatomical differences, a nonobligatory arboreality continues to be difficult to demonstrate on the basis of osteology alone because of the mechanical compromises required for an intermediate locomotor type. Similar problems are encountered with regard to the primitive fossil canids. The overall evidence seems to be consistent with the classification derived from discriminant analysis—*Hesperocyon* may be marginally placed within the arboreal category and close to the scansorial animals.

Morphological features that support the conclusion that *Hesperocyon* was capable of climbing trees include: long, overhung scapular acromion; shallow olecranon fossa of the humerus; posteriorly bowed ulna, angled pelvic floor; large area of muscle attachment on the tibia for flexor digitorum longus and caudal tibialis; and deep terminal phalanx, although some of these characters may be retentions of primitive conditions rather than indicators of locomotor types. On the other hand, *Hesperocyon* possesses a significantly modernized skeleton, as compared to the miacoids, that suggests increased cursoriality: lack of a large teres major process on the scapula; reduced deltoid crest on the humerus; laterally oriented fovea capitis femoris; reoriented plantar tendinal groove aligned with the astragalar trochlea; and elongated and compressed metapodials.

The astragalar structure of *Cormocyon* suggests that it is probably capable of a large degree of extension and therefore likely to be digitigrade. The primitive *Tomarctus* species are more advanced toward digitigrady, but retain relatively short distal limbs. Based on the earliest available evidence, *Leptocyon* is also digitigrade (e.g., *L. vulpinus*, Late Arikareean). The present sketchy data do not allow sufficient resolution to clarify the question of whether digitigrady was independently acquired in *Cormocyon* (a representative of primitive borophagines) and *Leptocyon* (a representative of primitive canines). It seems that canines are diverged from borophagines in their slender and elongated appearances of limbs (fig. 11).

Primitive canids started to shed the archaic limb structure inherited from miacoids at the beginning of their appearance (*Hesperocyon*), probably in response to the more open savanna habitats of the early Oligocene of the North American continent (Webb, 1981; Martin, 1989). However, canids probably did not become fully erect in their limb posture until several million years later.

ACKNOWLEDGMENTS

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