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Phylogeny of the Caninae (Carnivora: Canidae): the Living Taxa

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ABSTRACT

Fifty-seven characters of the skull, mandible, dentition, and postcranium distributed among 122 character states obtained from specimens representing 15 living genera of the canid subfamily Caninae (67% of which are monotypic) were subjected to cladistic analysis assisted by a maximum-parsimony computer program (HENNIG86). The program found a single tree, 90 steps in length with a consistency index of 65 and retention index of 78. The reconstruction delineates two sister taxa: the foxlike tribe Vulpini, and the wolflike and South American taxa, tribe Canini. This division is also supported by karyological and biomolecular studies although the composition of each group varies with the evidence used. The osteological evidence leads to a more fully resolved relationship than presently available from other systems. Problem taxa include the foxes *Urocyon* and *Otocyon*, considered sister taxa and members of the Vulpini clade osteologically, but either as members of the

Canini clade (with *Fennecus*) on chromosome morphology or in a basal unresolved multichotomy with other canines on allozyme evidence. More contentious is the position of the Asian raccoon-dog *Nyctereutes*, placed as a sister taxon of the South American crab-eating "fox" *Cerdocyon* in our analysis but allied with *Vulpes* on karyological evidence or a part of the basal canine multichotomy with regard to the allozyme results. The South American bush-dog *Speothos*, a hypercarnivore, is placed on osteological grounds in a clade with the rest of the South American genera in agreement with chromosome evidence although allozymes relate it to the *Canis* group. Despite these individual cases there is reasonable concordance in the conclusions drawn from the three lines of phyletic inference. Previous neontological and paleontological studies of canines have not clarified relationships within this group.

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INTRODUCTION

Some years ago the first and second authors of the present contribution undertook a phylogenetic analysis of the living wild canids as a step toward an analysis that would include the fossil record of New World species. Although that work is in advanced stages of completion, the present authors thought that the analysis of the living taxa was of sufficient interest that its results should not be delayed further. Interest in the phylogeny of living canids has intensified in recent years, especially as molecular techniques of analysis have become available (Wayne et al., 1989).

In previous studies, beginning with a preliminary account by Tedford in 1976, two of us have explored the basis for the monophyly of the family Canidae (Wang and Tedford, 1994) and the larger phylogenetic framework (Wang and Tedford, in press) which substantiates the recognition of a three-taxon system as characteristic of canid phylogeny (fig. 1). The present work focuses on analysis of the Caninae using the other clades (Hesperocyoninae and Borophaginae) as outgroups. Species of the paraphyletic fossil canine *Lepdocyon*, stem group for the Caninae, serve as a third outgroup in this analysis.

Another convention is adopted in presenting our analysis concerning the level of the operational taxonomic units employed. Data-gathering was at the specific level (see appendix 1); our analysis is at the generic level. This is justified because nearly 70 percent of living genera are monotypic and the remainder (*Vulpes*, *Urocyon*, "*Pseudalopex*," and *Canis*) are not markedly heteromorphic. *Vulpes zerda* and *V. lagopus*, are commonly separated as monotypic subgenera but they are contained within the range of interspecific variation shown by this diverse genus. They also possess a defining synapomorphy (short nasals, character 19, table 1) that groups them. Furthermore, mitochondrial DNA analyses (Geffen et al., 1992) confirm the monophyly of *Vulpes* species including the fennec and arctic fox. "*Pseudalopex*" species (e.g., "*P.*" *gymnocercus*, "*P.*" *griseus*, "*P.*" *sechurae*) are a group not consistently differentiated from either *Pseudalopex culpaeus* or, more commonly, from *Dusicyon australis* in previous analyses. We group these small paraphyletic

"zorros" of South America together, although they lack a uniting synapomorphy except for those characterizing the South American canines as a whole. Likewise *Canis* lacks a synapomorphy but contains a suite of species that are closely similar morphologically and lack hypercarnivorous specializations seen in its sister group *Cuon* + *Lycaon*. Such conventions may be perceived as weaknesses in the analysis as they affect 61 percent of the species on which the analysis is based. Nevertheless they are not a priori groupings as we believe there is sufficient morphological coherence among the species in such groups to justify treating them as units in the analysis. Some karyological and biochemical evidence, discussed below, also confirms their relationship.

In the cladistic analysis of the Caninae which follows, we have employed dental, cranial, and postcranial characters. Some of these characters were resolved into several character states and some of the latter seemed to form morphocline series. We used a total of 57 characters representing 122 character states in our analysis. The emphasis on dental characters reflects the relative uniformity of the skull and skeleton within the Caninae and the practical necessity of eventually bringing the evidence from fossil and living taxa into a common framework. Table 1 lists the characters used in this analysis, numbered in the order in which they appear at branching points on the cladogram (fig. 2), which is constructed from the character matrix in table 2. The 57 numbered characters used in the analysis are treated by osteological regions to facilitate comparison.

Institutional abbreviations used are: AMNH(M), American Museum of Natural History, Department of Mammalogy; ANSP, Academy of Natural Science, Philadelphia; F:AM, Frick Collection, American Museum of Natural History; UCMP, University of California, Museum of Paleontology.

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CHARACTER ANALYSIS

The synapomorphies discovered in comparative study of the Caninae are examined by osteological region in an effort to examine their possible functional significance and the morphocline relationships between character states. We comment on cases of apparent parallelism implied by the most parsimonious cladogram consonant with all these data. In the following paragraphs boldface numbers in parentheses refer to the characters/states (assuming the derived state "1" for the character numbers alone) as listed in table 1 and to their postulated occurrence on the cladogram (fig. 2). This provides a useful cross reference for this discussion and related material.

SKULL: The gross morphology of the canid skull is stereotyped and primitive on the whole when compared to other Carnivora. Most canids have mesocephalic skulls where the antorbital part of the skull constitutes about 40 percent of the total skull length. Although domestic breeds of *Canis lupus familiaris* show the extremes of antorbital skull length possible while still maintaining a functional system, wild canid species rarely show such adaptations under natural selection. Lengthening of the antorbital portion of the skull results in a narrow muzzle, and an increase in the diastemata between the premolars. This is an autapomorphy known only in three living species, a vulpine (*Vulpes ferriata*), and two canines (*Chrysocyon brachyurus* and *Canis simensis*). Shortening of the antorbital part of the skull is part of a functional complex including widening of the palate (41) (especially the anterior region which may range up to 20% of skull length), premolar crowding, and loss of posterior molars (51). This complex has characterized the most hypercarnivorous of living canines (*Speothos venaticus*, *Cuon alpinus*, and *Lycan pictus*) in addition to some Neotropical fossil species (Berta, 1988).

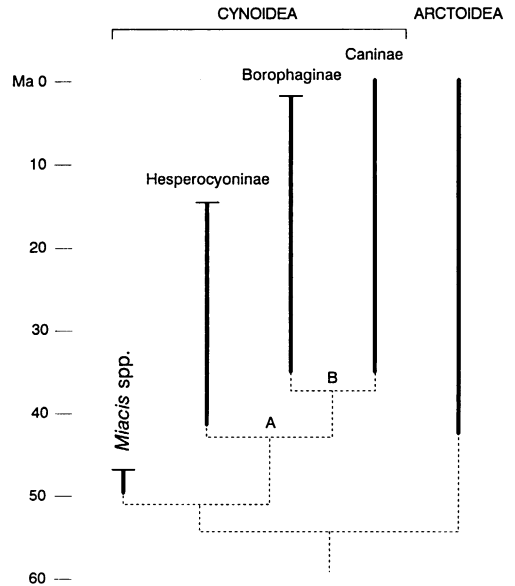


Fig. 1. Cladogram indicating the phyletic relationships of the major divisions of the Canidae and their temporal ranges. Relationships with other Caniformia as developed in Wang and Tedford (1994: fig. 9). Letters identify branch points in fig. 2.

In the majority of Caninae the nasal bones (19) reach posteriorly to or beyond the most posterior extent of the maxillary-frontal suture. Short nasals, ending in front of the maxillary-frontal suture, are a synapomorphy found in all species of *Vulpes* (fig. 3A). This character occurs only in *Atelocynus* (fig. 3F) and *Speothos* among the Canini where, along with their very small frontal sinuses, it constitutes a synapomorphy phyletically linking these genera.

Huxley's (1880) study of the frontal sinus (32) in living Canidae and his selection of it as the key character in subdivision of that family has been widely criticized (most completely by Matthew, 1924) mainly on the grounds that its presence and volume is basically linked to increasing body size. Huxley anticipated this criticism and tried to demonstrate that such a correlation did not exactly hold. We have reinvestigated this character in some depth in living and especially fossil Canidae and confirm that enlargement of the frontal sinus (sensu Miller et al., 1964) occurs as a derived state in all subfamilies

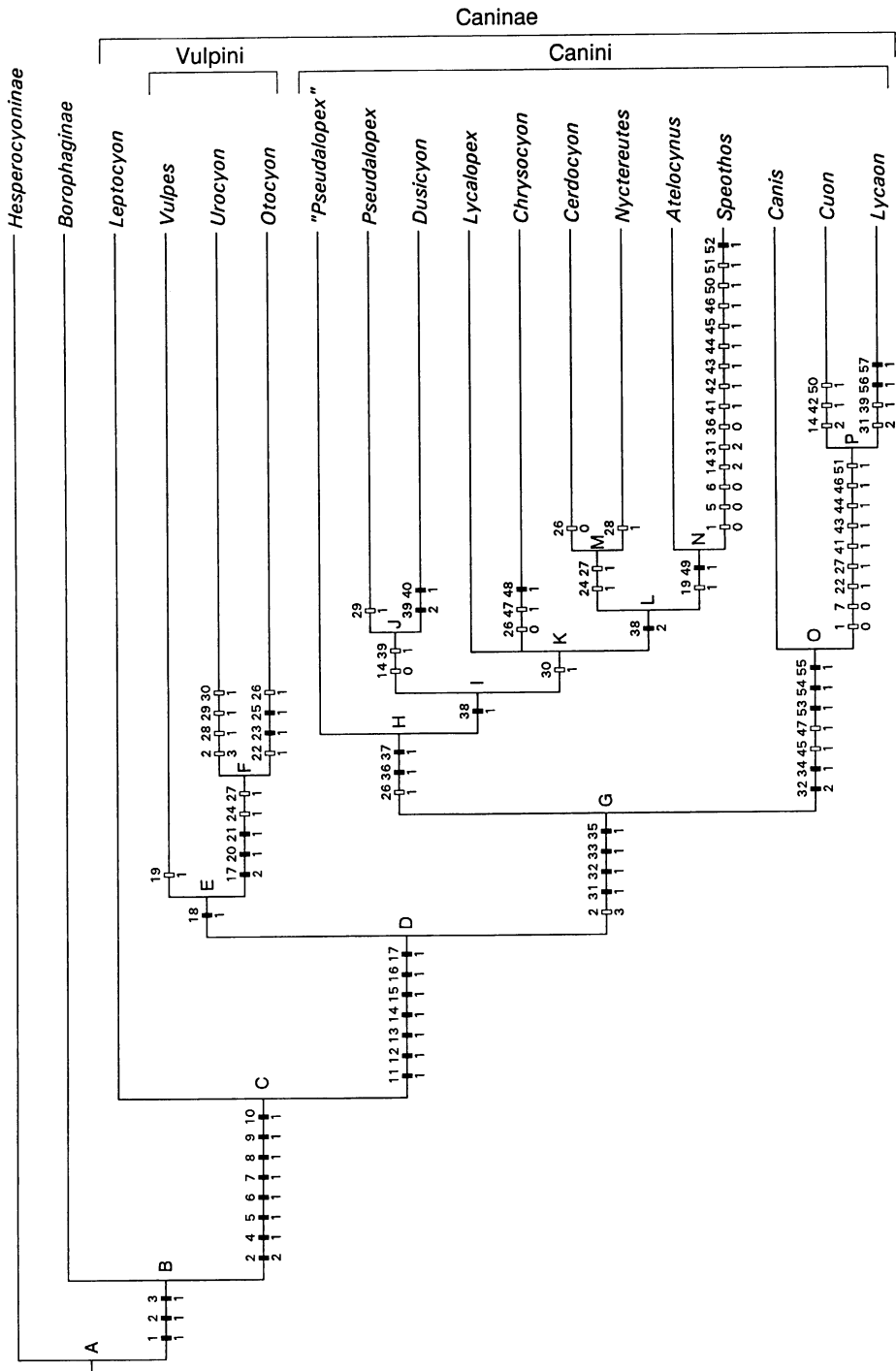


Fig. 2. Cladogram of the Canidae showing phylogenetic relationships of genera within the subfamily Caninae. Characters considered synapomorphies and autapomorphies are indicated at branching points and terminations by number (left) and state (right) in reference to the list in table 1. Characters indicated by closed bars are synapomorphies or autapomorphies. Those indicated by open bars are found at two or three points on the cladogram and are considered to represent parallelisms or reversals (state 0). Lettered branching points represent important cladogenetic events discussed in the text.

within the Canidae and is not related to body size. Figure 3 illustrates the development of the sinus in living Caninae. The primitive state (lack of the sinus) is manifested externally by a shallow depression or groove creasing the dorsal surface of the postorbital process. The primitive condition is common to all the living foxes (tribe Vulpini, fig. 3A, B). Enlargement of the frontal sinus that occurs within members of the tribe Canini includes lateral expansion into the base of the postorbital process, inflation of this process and posterior and ventral expansion of the sinus along the anterior surface of the braincase [32(1), fig. 3A, B]. Inflation of the base of the postorbital process usually removes the depression on its dorsal surface except in *Chrysocyon*. In the more derived state [32(2), fig. 3G, H], shown by *Canis* and related genera, the sinus penetrates the postorbital process to its tip and the sinus is expanded posteriorly along the anterodorsal surface of the braincase ultimately to the frontoparietal suture. This inflation of the frontal region gives a markedly convex outline to the dorsal surface of the cranium above the orbits and it widens the postorbital constriction. In some members of the Canini, including *Nyctereutes*, *Atelocynus*, and *Speothos*, the frontal sinus is small and little expanded (fig. 3F). This is indicated by the lack of a depression on the dorsal surface of the postorbital process despite the superficially foxlike appearance of the process. Hence this feature is not scored as a reversal in table 2. *Cerdocyon*, sister group of *Nyctereutes*, retains a very large and laterally inflated sinus (fig. 3D), which, as in other South American Canini, does not penetrate the relatively small postorbital process. The sinus in *Cerdocyon* is not markedly expanded posteriorly nor is it markedly inflated dorsally, but the cavity is extended lateral to the ethmoturbinates.

In the hesperocyonines and borophagines, a postparietal foramen (11) is primitively present on the dorsolateral aspect of the temporal region at the parietal/supraoccipital suture. In canines except *Leptocyon* this suture (corresponding to the tentorium on the inner side of the brain cavity) is pushed posteriorly due to enlargement of the cerebrum and the postparietal foramen becomes extremely reduced or lost.

Primitively the form of the supraoccipital bones in canids are rectangular or fan-shaped when the skull is viewed from the rear and the inion usually fails to overhang the occipital condyles to any degree in lateral view (fig. 4A–D). In *Canis* and sister taxa the supraoccipital shield is triangular in shape, the inion is usually pointed and consistently overhangs the occipital condyles [(55), fig. 4E, F]. The posterior production of the inion and establishment of the triangular form of the supraoccipital shield is correlated with the relative size of the interparietal part of the sagittal crest. This feature is thus not simply correlated with large size since the smaller jackal species show this condition and they clearly overlap in size the *Pseudalopex* species which have the primitive form of the supraoccipital shield (compare fig. 4C and E). These differences were recognized by Pocock (1913) in his comparison of *Dusicyon australis* and *Canis latrans*. This character shows no homoplasy in the Caninae and hence appears to be of significance in phyletic analysis.

In most canids the palatine bones extend to or just anterior to the end of the tooth row. Two exceptions are the South American canines and the closely related *Nyctereutes* which have long palatines that extend the palate to and behind the tooth row (26). In *Cerdocyon*, however, the cladogram suggests that the palatine is secondarily shortened. The palatine of *Chrysocyon* is also short, probably owing to the relatively elongated upper toothrow, as seen in other dolichocephalic taxa such as *Canis simensis* and *Vulpes ferrilata*. The highly autapomorphous *Otocyon*, alone among the vulpines, has a posteriorly extended palate. *Otocyon* is largely an insectivorous canid and hence shares that feature with other mammals in which termites are an important food (Ewer, 1973).

In lateral view, canids primitively have a moderately arched or nearly flat zygoma. In dorsal view the jugal flares markedly from the side of the skull; the orbital border of this bone is everted and shelflike. The squamosal process of the zygoma is relatively deep throughout its length. In the Caninae the zygoma is rather strongly arched dorsoventrally (4), the jugal lacks the degree of lateral flare from the side of the skull, and its orbital border is not everted (35) as in the Vulpini. In

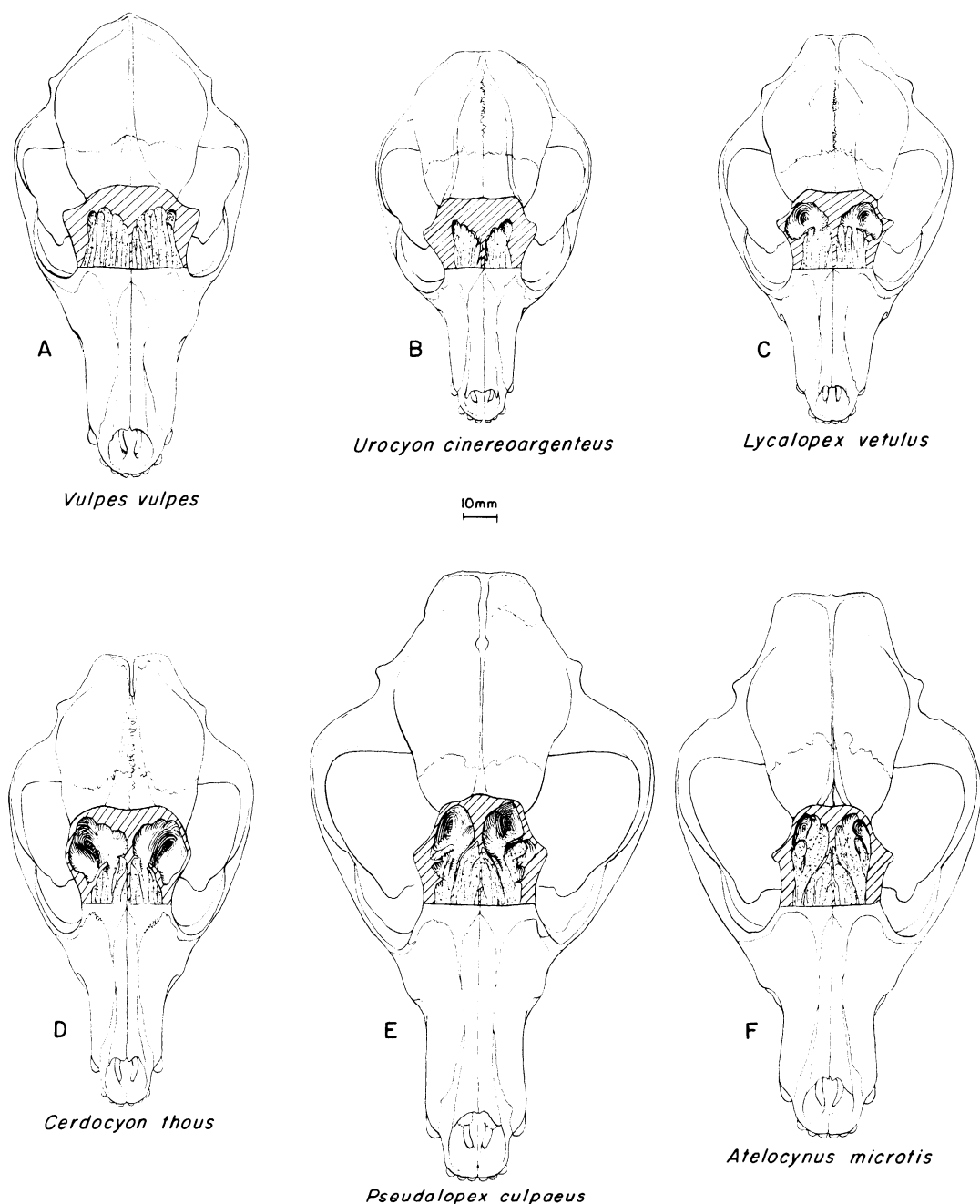
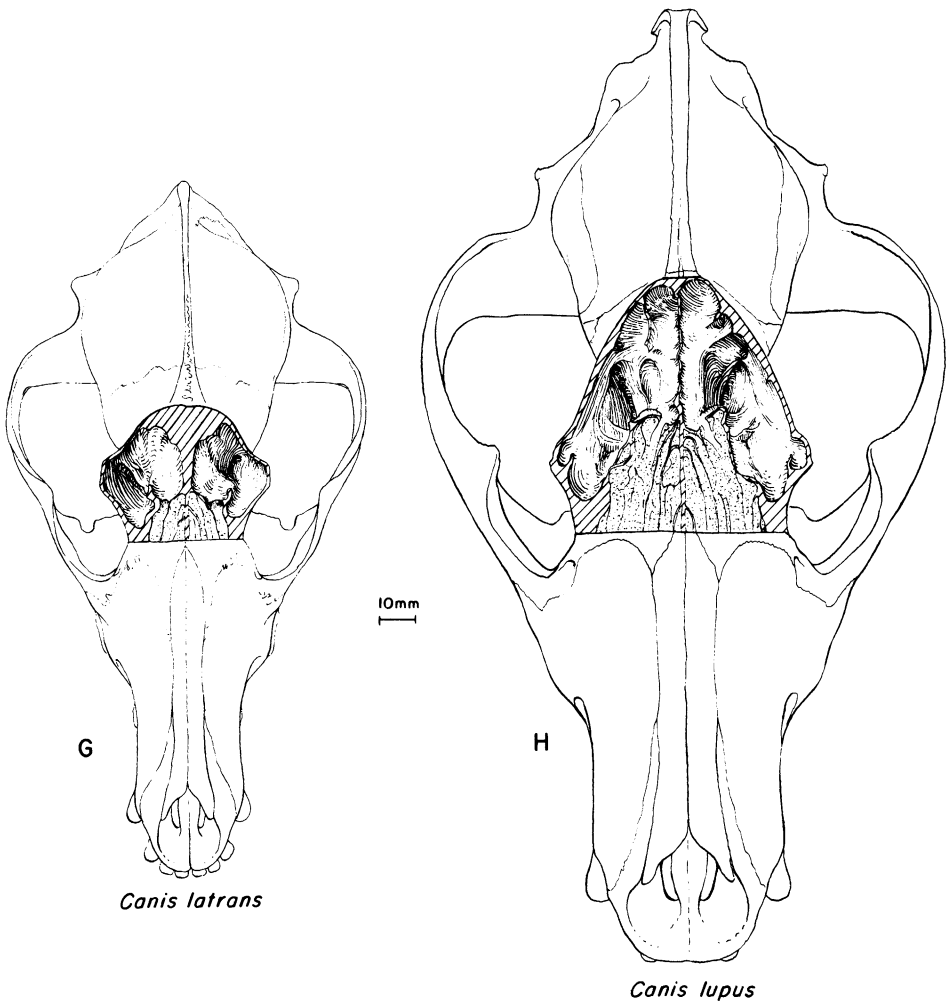


Fig. 3. Comparative dorsal views of the skulls of living canid species sectioned to show the extent and form of the frontal sinus (character 32, table 1); frontal turbinates stippled, frontal sinus shaded. **A**, *Vulpes vulpes*, AMNH(M) 60C. **B**, *Urocyon cinereoargenteus*, AMNH(M) 536 (partly restored after AMNH(M) 121276) which shows the primitive lack of a frontal sinus common to the Vulpini; **C**, *Lycalopex vetulus*, AMNH(M) 391, a form similar in size to the vulpines in A and B, showing a large frontal sinus that does not penetrate the postorbital processes (character state 32(1), table 1); **D**, *Cerdocyon thous*, AMNH(M) 36503, and **E**, *Pseudalopex culpaeus*, AMNH(M) 66737, also show character state 32(1) typical of most South American Canini; **F**, *Atelocynus microtis*, AMNH(M) 100095, shows prim-



itively small frontal sinuses (character state 32(1), table 1) confined to the lateral walls of braincase. G, *Canis latrans*, F:AM uncataloged, and H, *Canis lupus*, F:AM uncataloged, showing the large frontal sinus especially its posterior extension to the frontal-parietal suture in *C. lupus* (character state 32(2), table 1).

the South American canine clade, as first noted by Berta (1988: 26), the long scar for the origination of the medial masseter muscle on the ventrolateral surface of the zygoma becomes uniquely enlarged (36), particularly in the anterior segment. In these taxa the insertion of the medial masseter is correspondingly enlarged, forming a triangular scar below the masseteric fossa and anterolateral to the angular process of the mandible.

Characters in the auditory region that define the Canidae include: large entotympanic that ossifies from at least two centers (large

caudal and small rostral elements); a partial septum formed from the entotympanic; and an internal carotid artery that lies in a groove on the medial side of the caudal entotympanic (see Hunt, 1974; Wang and Tedford, 1994 for further discussion and figures). The auditory region undergoes little change during the history of the Canidae except for the development of the external auditory meatus which is produced laterally as a short tube from the porus acousticus, especially in the living genera of vulpines and canines. Only some South American canines and the allied

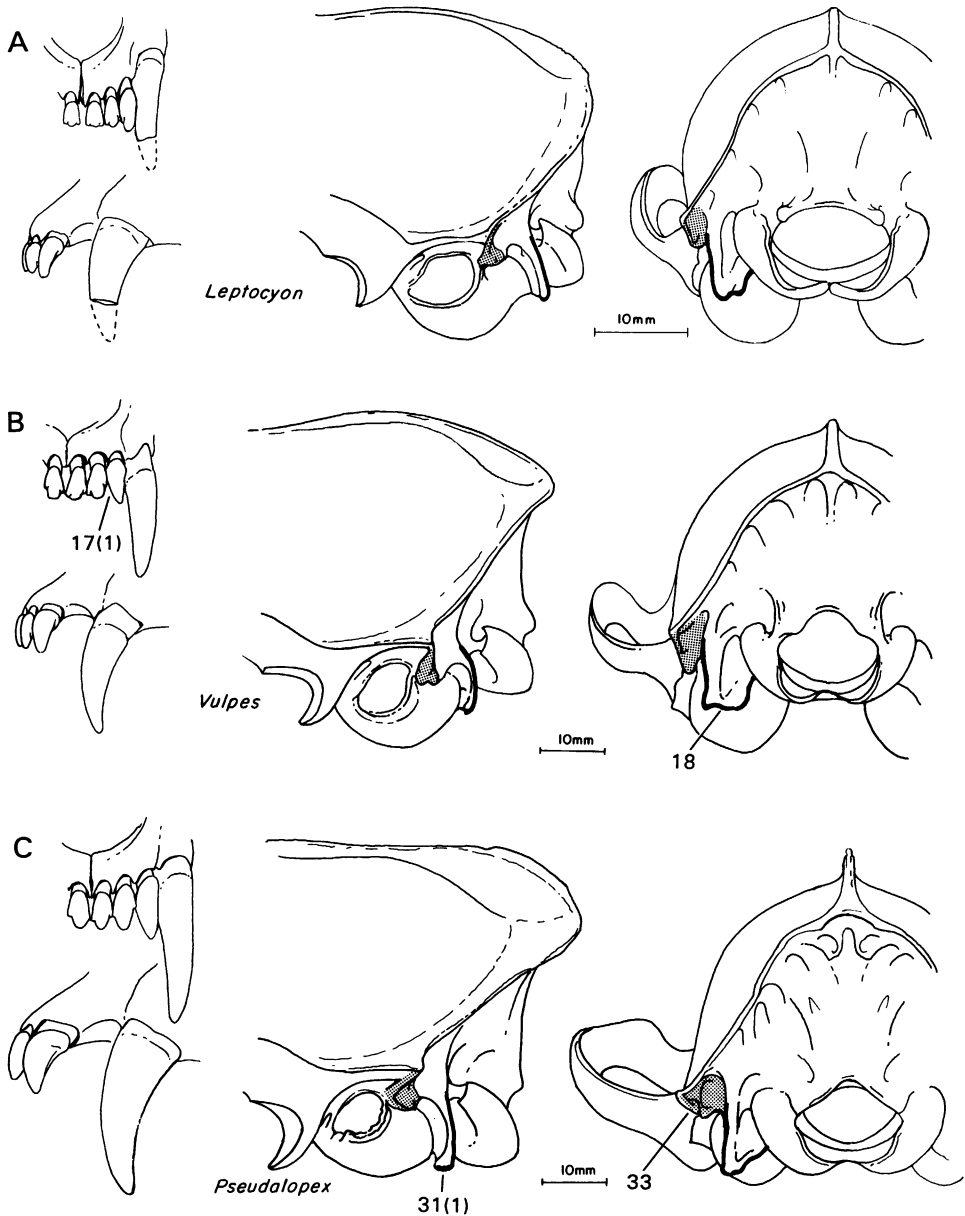
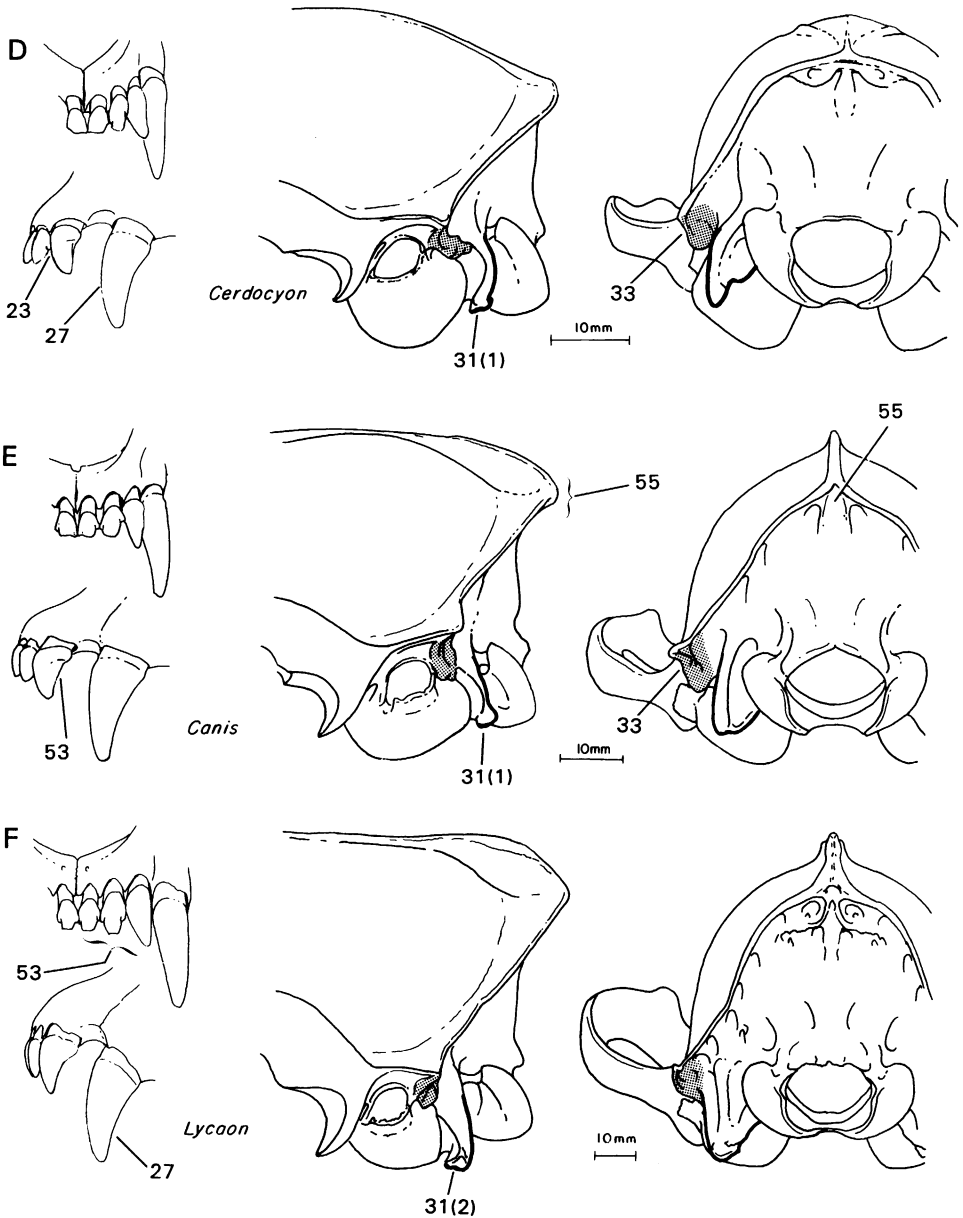


Fig. 4. Comparative views of the left upper incisors and canine (anterior view above lateral view) and the left side of the braincase (lateral view to the left of posterior view, mastoid process stippled, paroccipital process accentuated to show several features used in phyletic analysis (character states numbered to correspond to table 1). A, *Leptocyon vafer*, incisors, F:AM 27412, cranium, UCMF 77703, show the primitive condition in incisor and canine form and relative size plus supraoccipital, mastoid and paroccipital form and relative size; B, *Vulpes vulpes*, AMNH(M) 29055, I3 lacks median cuspule [character state 17(1)], paroccipital process broad, closely appressed to bulla, (character 18); C, *Pseudalopex culpaeus*, AMNH(M) 66737, showing large mastoid process (character 33) among character states common to Canini in this member of the South American clade; D, *Cerdocyon thous*, AMNH(M) 30628, I2-3 separated by diastema (character state 23), upper canine short and slender (character 27), primitive narrow and salient paroccipital process and derived large mastoid (character 33) in this small canine; E, *Canis aureus*, AMNH(M) 88712, I3 enlarged with posterior cingulum (character state 53).



Supraoccipital shield triangular in shape, inion overhangs condyles (character 55); F, *Lycaon pictus*, AMNH(M) 164162, shares characters with *Canis*. All drawings to a common size for ease of comparison, specimens selected to conform to a median size to minimize allometric relationships imposed by individuals of markedly differing relative size.

Nyctereutes show a significant departure in this general trend by possessing a short metatus surrounding a relatively small diameter porus.

Primitively the base of the paroccipital

process in canids is closely associated with the posterodorsal surface of the large bulla with the process usually having a considerable portion of its length free from the bulla. This free tip is directed posteriorly in prim-

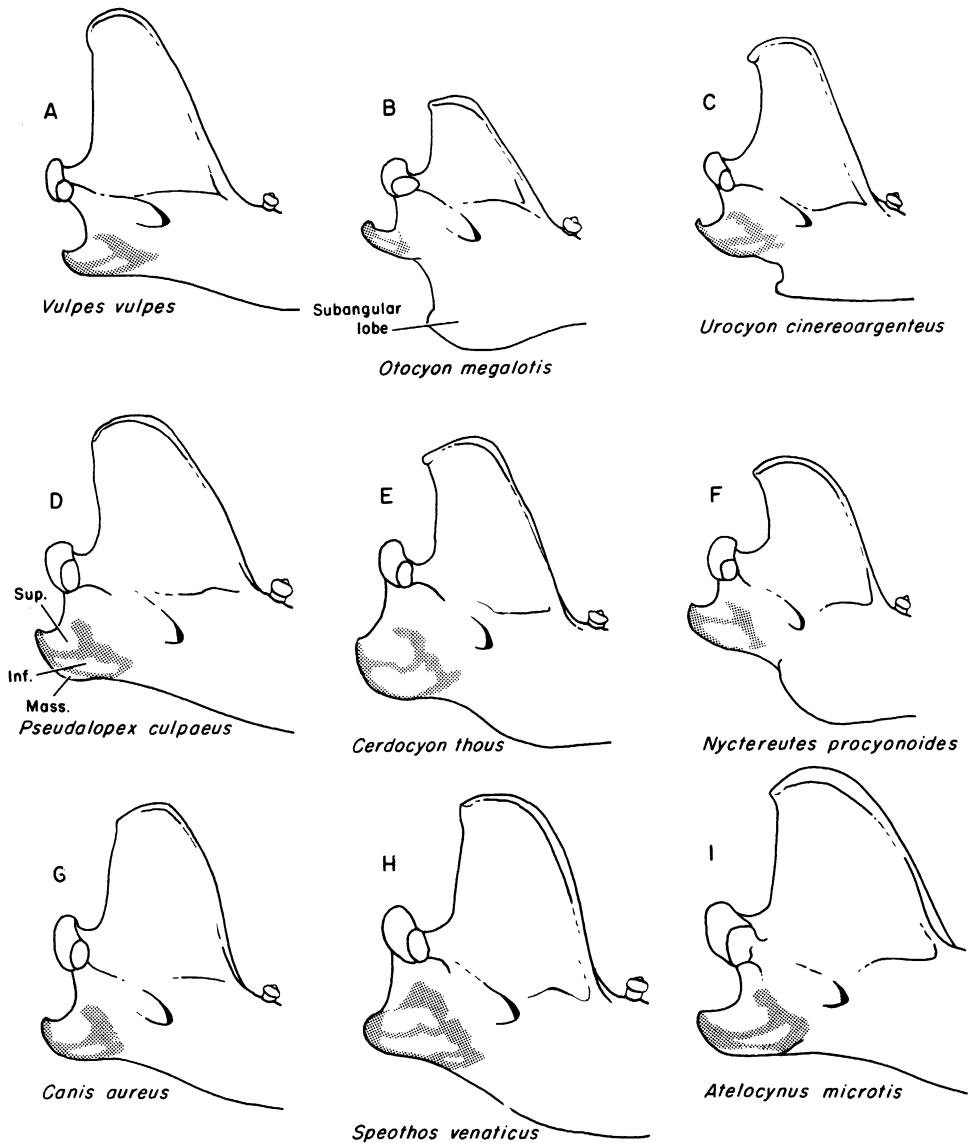


Fig. 5. Comparative internal views of the left ascending ramus of the mandible of representative canids to show the subangular lobe (character 24, table 1), form of the angular process, and distribution of rami of the median pterygoid muscle. Muscular insertions represented by roughened areas on the angular process, symbolized in stippled pattern. Inf., fossa for inferior ramus, median pterygoid; Mass., process for pars reflexa external masseter; Sup., fossa for superior ramus, median pterygoid (character states 38(1)–(2), table 1), and the form of the coronoid process (character 37, table 1). A, *Vulpes vulpes*, AMNH(M) 185649, primitive state of characters 24, 37 and 38; B, *Otocyon megalotis*, AMNH(M) 161153, showing subangular lobe but primitive angular process ("Type A" of Gaspard, 1964); C, *Urocyon cinereoargenteus*, AMNH(M) 4270, showing subangular lobe and "Type A" angular process with expanded base; D, *Pseudalopex culpaeus*, AMNH(M) 67088, derived angular process ("Type B" of Gaspard 1964) and coronoid process; E, *Cerdocyon thous*, AMNH(M) 14627, derived angular process ("Type D" of Gaspard, 1964) and low subangular lobe; F, *Nyctereutes procyonoides*, AMNH(M) 57113, derived angular process ("Type D" of Gaspard, 1964) and large subangular lobe, and low coronoid; G, *Canis aureus*, AMNH(M) 81041, derived angular process ("Type C" of Gaspard, 1964) with primitive short coronoid relative to height; H, *Speothos venaticus*, AMNH(M) 98560, and I, *Atelocynus microtis*, AMNH(M) 76579 show the derived angular process ("Type D" of Gaspard, 1964) and long coronoid.

itive hesperocyonines and borophagines, and turned ventrally in canines (10), a feature also independently acquired in some hesperocyonines and borophagines. Later canines usually show increasing union between the bulla and paroccipital process, especially in forms in which the bulla is relatively inflated, with the base of process hollowed out for reception of the bulla, and the free tip consequently shorter in length (fig. 4). A further modification is seen in all the Vulpini in which the base of the process is laterally expanded to cover most of the posterior surface of the bulla. The free tip of the process is very short and turned laterally, not extending markedly below the body of the process contacting the bulla [(18), fig. 4B]. A broad paroccipital process is also found in two species of jackals, *Canis adustus* and *C. simensis*, but the free tip is longer and directed ventrally as in other Canini. According to this analysis the state of this character in the Vulpini appears to be a unique feature separating the foxes and their allies from all other Caninae. A posteriorly expanded paroccipital process [31(1)] tends to characterize the Canini; such an expansion is carried to an extreme condition to produce a longitudinal plate [31(2)] in the hypercarnivorous *Speothos* and *Lycan*.

The Canini show enlargement of the mastoid process (33) that is evident even in small species similar in size to those in the Vulpini (fig. 4C, D). Important axial muscles that extend and control the lateral movement of the head insert on the mastoid process. The enlargement of this insertion may imply correspondingly more powerful movement of the head.

MANDIBLE: Most canids have relatively deep and thick horizontal rami of the lower jaw, but the Caninae are typified by possessing shallow and thin jaws (5) that support the extended and relatively delicate premolar series. In a few taxa of the Caninae there are unique enlargements of the digastric insertion on the horizontal ramus into a distinct process called the "subangular lobe" (24) by Huxley (1880: 251). This is markedly developed in vulpines with complex molars, specifically *Urocyon* and *Otocyon* (fig. 5B, C). A subangular lobe is also present among Canini in *Cerdocyon* (fig. 5E), and is especially marked in *Nyctereutes* (fig. 5F). The angular process in these canines differs from the del-

icate attenuated process in the vulpines in being rounded in form and more robust even though the species of all of these genera are closely similar in size. Accompanying the development of the subangular lobe is the anteriorly converging superior and inferior margins of the horizontal ramus of the mandible.

The Canidae primitively show an angular process of the mandible which is expanded medially to form a broad shelf for the insertion of the branches of the median pterygoid muscle. This shelf separates the insertion of the superior branch from the smaller fossa for the inferior branch which lies on the ventral surface of the shelf adjacent to the insertion of the pars reflexa of the external masseter. In the primitive Caninae a shelf for insertion of the superior branch of the median pterygoid is lacking and the whole process is slender, attenuated and often terminates in a dorsal hook.

A conspicuous and unique expansion of the angular process is characteristic of the South American Canini and the allied *Nyctereutes*, excluding the stem taxon "*Pseudalopex*" ("*P.*" *gymnocercus*, etc.). In this group the primitive slender angular process with its dorsal hook and small pterygoid fossae ("Type A" of Gaspard, 1964: fig. 24; fig. 5A-C of this paper) is modified by dorsoventral expansion, reduction of the dorsal hook, and conspicuous enlargement of the fossa for the inferior ramus of the medial pterygoid muscle [38(1), "Type B" of Gaspard, 1964: fig. 24; fig. 5D of this paper]. Associated with these features is a coronoid process that is anteroposteriorly long at its base relative to its height (37) rather than the shorter based and high coronoid found widely distributed within the Canidae (compare figs. 5D and G). In the *Cerdocyon*, *Nyctereutes*, *Atelocynus*, *Speothos* clade, both fossae for the medial pterygoid muscle are expanded on the internal side of the large angular process [38(2), "Type D" of Gaspard 1964: fig. 24; fig. 5E, F, H, I of this paper]. A large angular process in which the fossa for the superior branch of the medial pterygoid is expanded [(54), "Type C" of Gaspard 1964: fig. 24] characterizes the genus *Canis* and its sister taxa (fig. 5G). This type of process seems merely a modification of the primitive "Type A", and therefore is

coded as a separate character (54) instead of one state of character 38.

The above references to Gaspard (1964) refer to her recognition of four functional groups of mandibular structure in the living canids, based on the pattern of insertion of the two rami of the medial pterygoid and the pars reflexa of the external masseter. We illustrate these four types from actual specimens (fig. 5) and contend that the patterns have phylogenetic significance in that canines with "Type A" angular processes are relatively plesiomorphic, while types B through D have more limited distribution within the Caninae as discussed above.

CANINES AND INCISORS: Although in the Canidae sexual dimorphism is manifested in relative canine size there are some clades characterized by relatively small canines in both sexes. Canines of small diameter and short crowns (27), are present in *Cerdocyon* and *Nyctereutes* (fig. 4D) on the one hand and *Cuon* and *Lycaon* (fig. 4F) on the other. Relatively small canines are also possessed by the Vulpini that have mandibles bearing the subangular lobe (*Urocyon* and *Otocyon*). This condition is thus associated with dental and mandibular features indicating both greater omnivory and carnivory.

Primitively the incisors of canids show a gradual increase in size from I1 to I3 but the I3 is usually enlarged disproportionately in most forms. The Caninae show even greater enlargement of the I3 relative to I1-2. The I1-2 are primitively flattened conical teeth with medial and lateral cusplets, without posterobasal cingula. The I3 is primitively a high cone with a medial cusplet (fig. 4A) and a posteromedial cingular cusplet. The upper incisors in the Caninae are simplified, the medial cusplet on I3 is absent [17(1), fig. 4B] and in the *Urocyon-Otocyon* clade the cusplets on I1-2 are very weak or absent [17(2)]. These teeth maintain an apically interlocking occlusion with the lower incisors. In *Otocyon* an unusual short diastema occurs between I2 and I3 (23), that arises because the I1-2 have a more anterior position than the I3. An approach to this condition is also present as individual variation in *Nyctereutes* and *Cerdocyon* (fig. 4D) but the diastemata are shorter so that the crown of I2 is still not completely seen in front of I3 in lateral view as

it is in *Otocyon*. In *Canis* and sister taxa the I3 is enlarged [(53), fig. 4E, F], the posteromedial cingulum is enlarged, and a sharp crest appears on the medial side of the tooth that passes from the crown apex to merge with the medial cingulum. In addition, a shelflike posterior cingulum is developed on I1-2 which includes the bases of the enlarged lateral and medial cusplets to form a yokelike crest encircling the posterior part of the incisor crown. These modifications of the upper incisive battery are mirrored to a lesser extent by the lowers and together they represent a functional complex paralleled by some of the Borophaginae.

PREMOLARS: The Caninae are characterized by the presence of narrow and elongate premolars (6) with weak or absent posterior cusplets on P3 and p2-3 (7) set in a shallow ramus (5) and separated by short diastemata [(8), fig. 6]. The primitive condition, retained by the Borophaginae (fig. 6), includes broad and short premolars with strong cusplets forming a nearly closed tooth row and a relatively deep jaw. In some Caninae the premolar row is further modified by changes in the form of the premolar teeth. They become short and relatively high-crowned [(20), fig. 7B, C] and the p2 is isolated by longer diastemata (21) in some of the Vulpini (*Urocyon* and *Otocyon*). Anterior cusplets derived from the cingulum on the premolars are primitively retained in some Caninae (*Leptocyon*) but the vulpines and all canines lack these stylar cusplets. In the *Canis*-group in general, a second posterior cusplet on p4 [(34), fig. 7G-I] is present. In the canine genera *Lycaon* and *Cuon*, the p4 has an anterior cusplet [(22), fig. 7H, I] and in *Lycaon*, the p2-3 have strong anterior cusplets (57). These cusplets have differentiated from the anterior crest of the premolars rather than from the cingulum. They are not homologous with the stylar cusplets possessed by other canids.

CARNASSIALS: In canids the carnassials have changed very little from the primitive form common to most Caniformia. The upper carnassial in the Caninae is more elongate and narrower across the paracone (9) than in the Borophaginae where the primitive robust form is retained and accentuated by increasing the width to length ratio. The protocone is relatively reduced in the Caninae; the an-

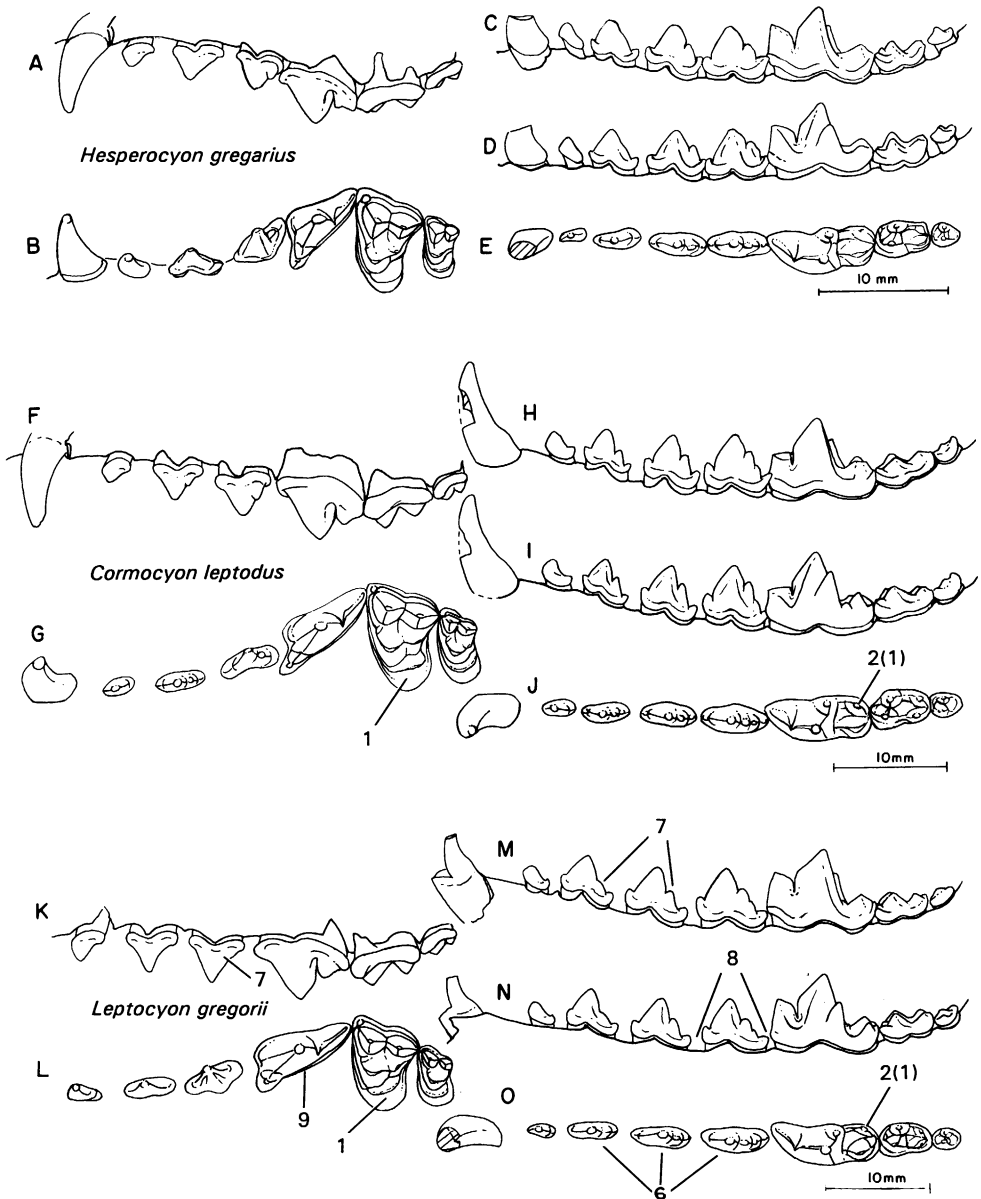


Fig. 6. Comparative views of the cheek teeth of the three major groups within the Canidae. A-E, Hesperocyoninae: *Hesperocyon gregarius* (F:AM 76177, Orellan, early Oligocene); A, lateral and B, occlusal views of the left upper cheek teeth; C, lateral, D, medial and E, occlusal views of the left lower cheek teeth. F-J, Borophaginae: *Cormocyon leptodus* (F:AM 49045, Arikareean, medial Oligocene); F, lateral and G, occlusal views of the left upper cheek teeth; H, lateral, I, medial and J, occlusal views of the left lower cheek teeth. K-O, Caninae: *Leptocyon gregorii* (F:AM 49063, Arikareean medial Oligocene); K, lateral and L, occlusal views of the left upper cheek teeth; M, lateral, N, medial and O, occlusal views of the left lower cheek teeth. Drawn to the same size as dentitions in fig. 7. Numbers refer to characters listed in table 1 and indicate features that distinguish these very similar forms.

terior cingulum is correspondingly reduced, often leaving a strong notch between the anterior base of the paracone and protocone. Only in *Otocyon* among the Caninae do we see molarization of the P4, involving expansion of the buccal cingulum and the protocone, and reduction in size of the metacone blade. More common in the Caninae is a condition in which the upper carnassials are relatively small as compared to the size of the molars that succeed them. Huxley (1880: 248) recognized this relationship but measured it with reference to the basicranial axis and applied the term "microdont" to the condition in which the P4 was proportionally small (25%) relative to this axis. We have found it more practical, especially in working with fossils, to express the relationship of the length of P4 to the sum of the lengths of M1 and M2. The term "small" here refers to upper carnassials less than 80 percent the combined length of the upper molars. Such dentitions, useful at the specific level diagnosis, are highly homoplastic in the higher level phylogeny of the Canidae where they are associated with complex molar structure and other features that may be related to increased omnivory.

The form of the lower carnassial (m1) is especially instructive in phyletic analysis. Certain changes in its structure can be resolved as steps in morphocline trends toward talonid enlargement and complexity (hypocarnivory) on the one hand, and talonid reduction and simplification (hypercarnivory) on the other. Beginning with the bicuspid talonid [2(1)], synapomorphic for the sister-taxa Borophaginae and Caninae, the entoconid is a discrete cusp or crest and a nearly complete buccal cingulum is present (fig. 6). In the Caninae the entoconid enlarges, the base of which may become large enough to coalesce with that of the hypoconid to block the talonid basin [2(2)]; the buccal cingulum is reduced. Most Vulpini have achieved the latter condition and populations of *Vulpes* and *Urocyon* species may include a sizable proportion of individuals in which the entoconid and hypoconid are joined by cristids from these cusps to form a transverse crest [2(3), fig. 7B]. This transverse crest is the final step in the morphocline leading to the carnassial talonid structure typical of living Canini. Associated with the increasing size of the

entoconid is the enlargement of the posterior cingulum (or hypoconulid shelf) which often encloses a small posterior basin behind the talonid cusps and may bear a hypoconulid (13). A hypoconulid shelf appears as an individual variation in *Leptocyon* species, but it otherwise occurs consistently only the Vulpini and Canini. Among the more hypocarnivorous vulpines the talonid is conspicuously wider than the trigonid (fig. 7B, C) and a protostylid may occur on the trigonid. A protostylid (29) also occurs on the carnassials of *Urocyon* (fig. 7B) and some South American canines (fig. 7D), sometimes accompanied by a mesoconid on the cristid obliqua.

Two independent adaptations for hypercarnivory are seen in *Speothos* and in the sister genera *Lycaon* and *Cuon*. These groups increase the sectorial function of the carnassials by reduction or loss of the entoconid [(42), (43), fig. 7H, I] and often the metaconid as well. *Speothos venaticus* has lost the M2 and m3 (51), but the late Pleistocene *S. pacivorous* retains a small double-rooted M2 (Berta, 1988). Fossil taxa otherwise closely resembling *Cuon* suggest the path of talonid reduction as having evolved from a taxon with a bicuspid talonid.

Since the carnassials form a vital functional unit in carnivores and canids achieve a complexity of carnassial structure unique in many ways, their importance is often emphasized in phyletic analyses (e.g., Matthew, 1924, 1930). However, as discussed above, the functional requirements of hyper- or hypocarnivory, constrained by the primitive form of the canid carnassial, place limits on the directions of morphological transformation. Such orienting influences force similar solutions to these specialized feeding modes resulting in considerable homoplasy in dental form.

UPPER MOLARS: The primitive canid upper molar is transversely elongate with a well-developed labial cingulum bearing a prominent parastyle connected to the paracone by a crista; a lingual cingulum with a hypocone usually posterolingual to the protocone; and subequal para- and metacones and small para- and metaconules borne on well developed cristae that link the protocone with the principal labial cusps. Changes in this fundamental form include: increase in size of the

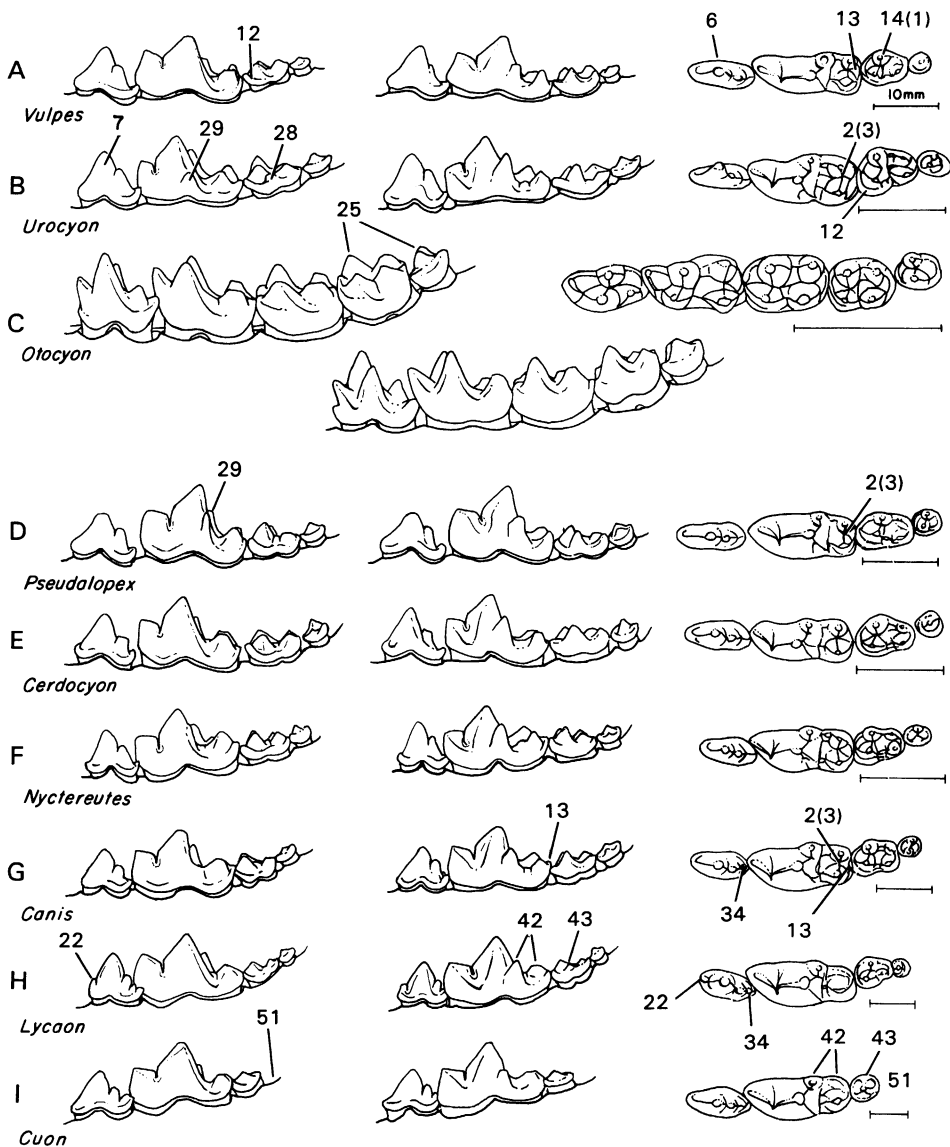


Fig. 7. Comparative views of part of the lower dentition (p4 m1-3) of representative Caninae showing in sequence from left to right in each row, the lateral view of the left side, medial view of the right side and occlusal view of the left side of the cheek teeth. Numbers refer to characters and character states listed in table 1. A, *Vulpes vulpes*, AMNH(M) 29055; B, *Urocyon cinereoargenteus*, AMNH(M) 100224; C, *Otocyon megalotis*, AMNH(M) 161153; D, *Pseudalopex culpaeus*, AMNH(M) 66737; E, *Cerdocyon thous*, AMNH(M) 30628; F, *Nyctereutes procyonoides*, AMNH(M) 57113; G, *Canis aureus*, AMNH(M) 88712; H, *Lycaon pictus*, AMNH(M) 164162; I, *Cuon alpinus*, AMNH(M) 54842. All drawn to the same scale as *Vulpes vulpes*, bar equals 10 mm.

hypocone [(1), fig. 6]; reduction in size of the conules, especially the paraconule; great reduction in size of the parastyle [(3), it is usually very weak to absent in living Canini];

decrease in transverse diameter so that the teeth are very narrow for their length [(30), as seen in the more hypocarnivorous South American taxa and *Nyctereutes*]; increase in

height of the labial cusps; disproportionate enlargement of the paracone until it becomes conspicuously larger than the metacone [(45), in *Canis* and its close relatives] often accompanied by reduction in the buccal cingulum (46). In hypercarnivorous taxa the hypocone becomes very reduced (44), even lost; and finally the M2 is also lost (50).

LOWER MOLARS: Primitively the canid m2 (fig. 6) possesses a complete buccal cingulum; a small, but discrete, paraconid; a metaconid equal to or slightly smaller than the protoconid; and a talonid with a hypoconid and an entoconid crest. The Caninae have reduced buccal cingula in which only the anterobuccal segment is retained (fig. 6M, O). Enlargement of the anterobuccal cingulum (12) is a universal trend among all Caninae (fig. 7). In certain Vulpini and among the South American Canini and *Nyctereutes* the buccal cingulum is extended posteriorly to the hypoconid (fig. 7). In addition, *Urocyon* has a protostylid [(28), fig. 7B] developed from the buccal cingulum at the base of the protoconid. Enlargement of the metaconid (14) occurs early in the history of the Caninae at about the same stage as expansion of the anterobuccal cingulum. The metaconid may be equal to or larger than the protoconid and its swollen base gives a decidedly convex outline to the lingual border of the tooth (fig. 7). *Otocyon* is also unique in having both a completely molariform m3 and a small oval m4 (25) (fig. 7C).

POSTCRANIAL SKELETON AND SOFT PARTS: Most canids, including all vulpines and some canines, have epipodials that are shorter in the front limbs than in the hind. This is indicated by the ratio of the radius to the tibia which is less than 90 percent in those forms. In derived canids (*Chrysocyon*, *Canis* and allies), the radius equals or exceeds 90 percent of the length of the tibia (47). Values between 80 and 90 percent are seen in several species of *Vulpes* (e.g., *V. vulpes*, *V. macrotis*, *V. lagopus*) and *Otocyon* among the vulpines and nearly all other Canini. The South American Canini are relatively short-legged, and among them, *Speothos* and *Atelocynus* show exceptionally short limbs (49) with respect to length of the spinal column from cervicals to lumbers (Hildebrand, 1952: fig. 6; Langguth, 1969). These same genera, along with *Cer-*

docyon and *Nyctereutes*, are also typified by having relatively short ears. On the other hand, *Chrysocyon* has a conspicuously elongated limb (48). *Cerdocyon*, *Nyctereutes*, and *Speothos* also have a straight or nearly straight caecum, a character shared with *Chrysocyon*. The distribution of this latter character is not fully determined from the data at hand, but its polarity can be established by reference to other Carnivora (Ewer, 1973). In a comparative study of the calcanea of canids, Stains (1975) found that the most distinctive taxa were *Nyctereutes*, *Atelocynus*, *Speothos*, and *Chrysocyon*. Of these four genera only *Nyctereutes* and *Atelocynus* showed a clear resemblance to one another. *Speothos* was unique and *Chrysocyon* was most similar to *Canis*. From the fossil record we were able to determine that the metatarsal (MT) I is reduced to a proximal rudiment (15) in Caninae above the level or organization of *Leptocyon* (although *Vulpes* and domestic dogs occasionally have a MT I as an atavistic variant). *Lycaon* is unique among canids in reduction of the metacarpal I to a rudiment (56). The entepicondylar foramen of the humerus is lacking (16) in all canines above *Leptocyon* (although this primitive state may also occur as a variant in other Caninae).

PHYLOGENY RECONSTRUCTION

Table 1 lists the morphological characters discussed above; character numbers and character state numbers in parentheses correspond to those cited. Character polarities are determined by using *Hesperocyon* and *Cormocyon* as successive outgroups. Not only are these two genera known by nearly complete cranial, dental, and postcranial materials, but they are probably the closest representatives of the primitive morphotype of their respective subfamilies, Hesperocyoninae and Borophaginae (Tedford, 1976; Wang, 1994; Wang and Tedford, 1994, in press).

A single shortest tree is found by HENNIG86 (Version 1.5; Farris, 1988) on the 18 taxon character matrix (table 2). All characters are nonadditive and unweighted. The tree is calculated using the option of "implicit enumeration" (i.e., a search algorithm designed to find trees of minimal length). Aided by CLADOS (Version 1.2; Nixon,

TABLE 1
List of Characters in Phylogenetic Analysis
 Character numbers and state numbers in parentheses correspond to those in the character matrix in table 2 and figure 2

Character	Primitive		Derived
	Primitive	Derived	
1. M1 hypocone	(0) small, barely differentiated from lingual cingulum	(1) enlarged	
2. m1 entoconid	(0) entoconid is a low crest on the lingual border of talonid	(1) conical or crestlike, as discrete cusp (2) conical, enlarged, may coalesce with base of hypoconid to block talonid basin (3) joining with hypoconid by cristids to form transverse crest (1) weak or absent (1) strongly arched dorsoventrally	
3. M1-2 parastyles	(0) strong	(1) shallow and thin	
4. zygomatic arch	(0) nearly flat or moderately arched in lateral view	(1) narrow and elongated (1) weak or absent (1) separated by diastemata	
5. horizontal ramus	(0) deep and thick	(1) slender, protocone small, anterior cingulum reduced or absent, particularly across the paracone	
6. shape of premolars	(0) broad and short	(1) directed ventrally and fused with bulla, no or little free tip, attachment area on bulla narrow	
7. P3 and p2-3 posterior cusplets	(0) present	(1) absent	
8. posterior premolars	(0) closed tooth row	(1) large	
9. P4 shape	(0) broad, protocone large, anterior cingulum strong	(1) present (1) enlarged, taller than protoconid (2) greatly reduced or lost (1) reduced to proximal rudiment (1) absent	
10. paraoccipital process orientation	(0) posteriorly directed, not fused with bulla, entire process is a free tip	(2) cusplet in I3 absent (2) cusplet in I1-2 weak or absent (1) broad, closely appressed to bulla, short free tip turned laterally, rarely extends below body of process	
11. postparietal foramen	(0) present	(1) short, rarely extend to level of most posterior position of maxillary-frontal suture (1) high-crowned	
12. m2 anterobuccal cingulum	(0) small		
13. m1 hypoconulid shelf	(0) absent		
14. m2 metaconid	(0) equal to or lower than protoconid		
15. metatarsal I	(0) unreduced		
16. entepicondylar foramen of humerus	(0) present		
17. I1-3 medial cusplets	(0) present		
18. paroccipital process width	(0) narrow mediolaterally		
19. nasal length	(0) long, usually extending posteriorly beyond maxillary-frontal suture		
20. crown height of premolars	(0) low-crowned		

TABLE 1—(Continued)

Character	Primitive	Derived
21. p2 position	(0) not isolated	(1) isolated by relatively larger diastemata than other premolars
22. p4 anterior cusplet	(0) weak or absent	(1) strong
23. I2-3 diastema	(0) I3 close to I2	(1) I3 separated from I2 by short diastema visible in lateral view
24. subangular lobe of mandible	(0) absent	(1) present
25. supernumerary cheek teeth	(0) no	(1) yes: presence of "M3" and "m4"
26. palatine length	(0) extends posteriorly to or just anterior to end of tooth row	(1) extends beyond end of tooth row
27. canine shape	(0) long, slender with recurved crown	(1) short and slender, crown not recurved
28. m2 protostylid	(0) absent	(1) buccal cingulum bears protostylid
29. m1 protostylid	(0) absent	(1) present
30. M1-2 shape	(0) transversely wide for their labial length	(1) narrow for their labial length
31. paroccipital process posterior expansion	(0) no or little expansion	(1) expanded posteriorly from bulla, usually with prominent free tip
32. frontal sinus	(0) absent; presence of a depression on dorsal surface of postorbital process	(2) large, greater posterolateral expansion (1) present; lacks a depression on dorsal surface of postorbital process (2) present, large; penetrates postorbital process and expands posteriorly toward the frontal-parietal suture
33. mastoid process	(0) small, crestlike	(1) enlarged, knob- or ridgelike
34. p4 second posterior cusplet	(0) absent	(1) present
35. zygoma, orbital part	(0) presence of a lateral flare and eversion of dorsal border	(1) lack of lateral flare and dorsal border thickened
36. scars of medial masseteric muscle	(0) narrow and uniform width on zygomatic arch and on lateral surface of angular process	(1) wide on zygomatic arch and enlarged on mandible
37. coronoid process	(0) short at base relative to dorsoventral height	(1) long at base relative to dorsoventral height
38. angular process	(0) slender, attenuated, with dorsal hook; inferior pterygoid fossa not expanded	(1) large, usually blunt without dorsal hook; fossa for inferior branch of medial pterygoid muscle expanded

TABLE 1—(Continued)

Character	Primitive	Derived
39. P4 protocone	(0) salient, located medial to anterior border of paracone	(2) deep, short process; fossae for the pterygoid muscle are expanded (1) reduced
40. p3-4 crown	(0) upright, short, blunt	(2) further reduced or absent, located posterior to anterior border of paracone
41. palate width	(0) not widened	(1) tilted backward, slender, sharp
42. m1 metaconid and entoconid	(0) not reduced	(1) widened
43. m2 metaconid and entoconid	(0) not reduced	(1) greatly reduced or absent
44. M1-2 hypocones	(0) not reduced	(1) greatly reduced or absent
45. M1-2 paracones	(0) not enlarged	(1) enlarged relative to metacone
46. M1-2 buccal cingulum	(0) not reduced	(1) reduced or lost
47. relative length of fore- to hindlimbs	(0) short, radius/tibia ratio <90%	(1) long, radius/tibia ratio >90%
48. forelimb (humerus + radius) elongation	(0) no: considerably shorter than 50% of head-body length	(1) yes: more than 50% of head-body length
49. forelimb (humerus + radius) shortening	(0) no: longer than 30% of head-body length	(1) yes: less than 30% of head-body length
50. M2	(0) triple-rooted	(1) double-rooted, or M2 absent
51. m3	(0) present	(1) absent
52. orbital process of jugal	(0) extends anterior of orbital rim, in broad contact with lacrimal	(1) lack of extension to antorbital rim, no contact with lacrimal
53. I3	(0) small crown extending to or just below level of I1-2; postero-medial cingulum weak or absent	(1) large crown extending markedly below level of I1-2; cingulum enlarged, medial crest of I1-2 present merges with cingulum
54. angular process, superior fossa	(0) not expanded	(1) expanded with large fossa for superior branch of medial pterygoid muscle
55. supraoccipital shield	(0) rectangular or fan-shaped in posterior view;inion may not overhang condyles	(1) triangular in shape; inion usually pointed and overhangs condyles
56. first digit of front foot	(0) present	(1) vestigial or absent
57. p2-3 anterior cusplets	(0) absent	(1) present

1992), the character distribution of this single tree was further explored and plotted as shown in figure 2. The tree statistics (not counting the autapomorphies) are: tree length = 90, consistency index = 65, and retention index = 78.

Nodes A and B represent the fundamental cladistic relationships of the Canidae. The characters shown at Node C are those common to all members of the monophyletic subfamily Caninae. Primitive states of these characters are present in the extinct sister taxon, the Borophaginae. *Leptocyon* includes a group of species completely plesiomorphous with respect to the rest of the Caninae. Later occurring species of the genus show some derived character states within dental morphoclines that suggest closer phyletic relationship to the Caninae represented by Node D, such as: lengthening and increasing height of crown of the premolars, enlargement of the m1 entoconid and presence of a weak hypoconulid shelf, and a short m2 relative to m1 with enlargement of the metaconid and anterobuccal cingulum. The suggestion of a specific patristic relationship of *Leptocyon* species with later vulpines is thus a permissible conclusion in developing the genealogy of the phyletic tree. In cladistic analysis, however, our knowledge of *Leptocyon* is not sufficient to recognize any of the species as sister taxa of the more derived species of canines. Thus the genus *Leptocyon* remains a paraphyletic group awaiting further analysis.

Node D represents a fundamental split within the Caninae into foxlike (tribe Vulpini) and wolflike (tribe Canini) sister taxa. The derived characters possessed by both of these groups and presumably uniquely typifying their common ancestor, include only a few, seemingly minor, characters of the lower molars and the loss of the postparietal foramen, the hallux and the entepicondylar foramen of the humerus. The dental characters involve increasing molarization of the m1 and m2 through enlargement of the m1 posterior cingulum (hypoconulid shelf) and the variable presence of a hypoconulid closing the talonid basin posteriorly. Enlargement of the m2 metaconid to a size equal to or exceeding the protoconid, thus markedly increasing the convexity of the lingual border of the tooth. Enlargement of the anterobuccal

cingulum of m2, also increased the breadth of this tooth across the trigonid.

Apparently, the Vulpini developed a distinctive paroccipital process early in their history which appears at Node E. The breadth of the process, cupping the posterior surface of the bulla, and the very weak development of the horn of the process, stand in noteworthy contrast to those of all other canids. *Vulpes* is plesiomorphous in most of its dental characters. However, living species of this genus show a high frequency of development of a transverse crest on m1 through the coalescence of cristids from the hypoconid and entoconid, thus dividing the talonid basin into larger anterior and smaller posterior sub-basins. This development seems to represent the ultimate level of elaboration of the m1 talonid, a condition also achieved by most Canini (Node G) as well as the Borophaginae.

A group of omnivorous foxes, here termed the *Urocyon* group, represents a clade (Node F) in which the dentition is modified for increasing hypocarnivory. These taxa show characteristically short upper carnassials, quadrate upper molars, and relatively wide lower molar talonids. Node F represents the vicariance of a stock characterized by having simple incisors lacking cusplets, short, tall crowned premolars isolated by diastemata (especially around p2), and an m1 talonid wider than its trigonid. The New World representative, the living *Urocyon*, has a highly distinctive mandible bearing a subangular lobe and high condyle, a transverse crest on the m1 talonid, and relatively small canines. This same combination of characters occurs in the highly apomorphic *Otocyon* that represents the Old World vicar. *Otocyon* is uniquely distinguished by a diastema between I2 and I3, the presence of M3, a submolariform P4, and a posteriorly extended palate, as well as the mandibular characters mentioned above.

In addition to the presence of a frontal sinus, the common ancestor of all Canini (Node G), is hypothesized to have modified the primitive zygoma. The jugal has lost its lateral flare; its lateral surface has come into line with the sides of the muzzle when viewed dorsally and the zygomatic process of the squamosal is reduced in depth anteriorly. The angular process of the mandible is also en-

larged in different ways for insertion of the increasingly important medial pterygoid muscle. Consistent dental modifications present at this point are the transverse crest between hypoconid and entoconid on m1 and the elimination or great reduction of the M1-2 parastyles.

The sister taxa that emerge at Node G represent on the one hand a mainly Neotropical group of small to medium-sized forms (Node H), and on the other the large wolflike species (Node O). Synapomorphies uniting members of the former group include unique features of the ascending ramus, i.e., a wide and low coronoid process, enlarged muscle attachments for the medial masseter on the zygoma and on the anterolateral face of the angular process, a palate that extends to or behind the tooth row, post-orbital processes not invaded by the frontal sinus. Also uniting members of clade H are a suite of less consistent dental features (hence not coded in this analysis) particularly in the m2 in which the buccal cingulum is extended to the hypoconid, a mesoconid is present, and the paracristid forms a strong blade although the paraconid is lacking or nearly so.

Within the South American canids, species of "*Pseudalopex*" ("*P.*" *gymnocercus*, "*P.*" *griseus*, and "*P.*" *sechurae*) are left at the base of the clade due to their plesiomorphous nature. Clade I is slightly more derived owing to an enlarged angular process bearing a relatively large fossa for the inferior branch of the medial pterygoid. Beginning in *Pseudalopex culpaeus*, the more primitive species of Clade J, the metaconid of m2 becomes lower than the protoconid, and the P4 protocone is reduced. This trend continues in *Dusicyon australis* and more derived fossil taxa in which the P4 protocone is nearly lost and the p3-4 have developed a posterior tilt (Berta, 1988).

The remaining South American canines plus *Nyctereutes* (Node K) are weakly held together by their narrow (relative to labial length) upper molars. This clade contains a diverse group of taxa ranging from moderately hypocarnivorous *Nyctereutes*, *Cerdocyon*, and *Lycalopex*, to more or less mesocarnivorous *Chrysocyon*, and *Atelocynus*, to completely hypercarnivorous *Speothos*. The range of their postcranial morphology is equally broad, as this group contains the lon-

gest-legged canid, *Chrysocyon*, and the shortest-legged canids *Atelocynus* and *Speothos*. An unresolved trichotomy occurs at Node K: the *Lycalopex*, *Chrysocyon*, and the *Cerdocyon-Speothos* clade. Except its slight tendency toward hypocarnivory, *Lycalopex vetulus* is perhaps closest to the primitive morphotype of the taxa in Clade K. *Chrysocyon*, on the other hand, is highly autapomorphous with its very elongate skull, with a short palatine relative to an elongated tooth-row, and extremely elongated limbs. Beside such autapomorphies, *Chrysocyon* possesses an intriguing combination of characters that make its phylogenetic position difficult to assess. The frontal shield still has a depression on top of the postorbital process even though the frontal sinus may be extended into the base of the process (on one side of AMNH(M) 36962) and its caecum is straight like the other Canini grouped at Node L. In addition, its elongated legs also hint at membership with the *Canis-Cuon-Lycaon* clade. In fact, such a hypothesis would require only two more steps than in the shortest tree of figure 2.

The apomorphous sister group signaled by Node L demonstrates an interesting trend toward frontal sinus reduction, further enlargement of the angular process, the presence of short pinnae (and correspondingly short and small-caliber external auditory meati), and short legs. In those taxa investigated anatomically, the caecum is straight or nearly so in contrast to the convoluted state primitive in the Canidae. These taxa can be resolved into two sister groups showing contrasting dental adaptations. Hypocarnivorous taxa (*Cerdocyon* and *Nyctereutes* at Node M) possess short diastemata between I2 and I3, a short P4 compared to the length of the molars, relatively small canines, and a mandible with the subangular lobe also seen in *Urocyon* and *Otocyon*. *Cerdocyon* is plesiomorphic in retaining a large frontal sinus, but it is autapomorphic in having lost the cusplules on I1-2. The recognition that *Nyctereutes*, a form restricted to the Palearctic, is the sister genus of *Cerdocyon* was an interesting conclusion from this analysis. It shows reduction in the size of the frontal sinus although fossil species of *Nyctereutes* have a slightly larger sinus than the living form. The other sister group united at Node N represents a hypercarnivorous ad-

aptation culminating in the unique loss of M2 and m3 in *Speothos*. Its plesiomorphous sister taxon *Atelocynus* likewise nearly lacks a frontal sinus, and both have short nasals that rarely extend to the level of the most posterior position of the maxillary-frontal suture.

All the large wolflike Canini are united by possession of very large frontal sinuses that are extended laterally into the postorbital processes and posteriorly to the parietal suture (Node O). They too have enlarged angular processes of the mandible, but they emphasize differential development of the superior branch of the medial pterygoid rather than the inferior branch as in the South American forms. In addition the front limbs are elongated relative to the hind limbs, particularly the epipodials (expressed as a radius/tibia ratio of greater than 90%). *Canis* and its hypercarnivorous sister taxa *Cuon* and *Lycaon* also possess a number of dental synapomorphies including enlargement of I3 (relative to I1–2), enlargement of its cingulum, and development of a medial crest; enlargement of the paracone of M1–2 relative to the metacone; reduction of the buccal cingulum on the upper molars; presence of a second posterior cusplet on p4; and lack of the paraconid plus presence of a weak paracristid on m2. In addition the sagittal crest becomes more important, the interparietal portion especially so, such that the supraoccipital shield assumes a triangular shape and the pointedinion markedly overhangs the condyles. The latter characters are usually more pronounced in old males, but they constitute an obvious difference in form even when comparing some of the smaller jackal species with plesiomorphous forms of similar size, such as *Dusicyon australis* or *Pseudalopex culpaeus*.

Cuon and *Lycaon* are closely related to *Canis*, but diverge (Node P) in aspects of adaptation to a more predatory way of life. Their molars emphasize shearing functions by reducing the lingual cusps, the hypocone on M1–2, and the metaconid and entoconid on m1–2. Their canines are also small relative to the size of their cheek teeth. *Lycaon* shows the most derived state of hypercarnivory with its large multicuspid premolars, unusually wide palate, and unique reduction of the plex to a vestige as befits a pack-hunting, cur-

sorial carnivore of open grassland and savanna. The dental modifications in this genus parallel those of some of the more derived Borophaginae and also converge on the type of dentition possessed by primitive Hyaenidae.

PREVIOUS PHYLOGENETIC HYPOTHESES

NEONTOLOGY

Despite the voluminous literature on the living canids (the Caninae of this review) there have been few neontological studies of the phyletic relationships of these taxa. Historical proposals to group species into genera constitute attempts at limited phyletic analysis and these will be specially noted in the paragraphs that follow. Huxley's (1880) division of the canines into foxlike (alopecoid) and jackal-like (thooid) groups, primarily based on the presence or absence of a frontal sinus, was an attempt to group the species of *Canis* as that genus was used in the last century. However, Huxley's conclusions were not used as a basis for classification by subsequent workers, including the first monographic review of the Canidae by Mivart (1890). Mivart relegated the foxes and dogs to the genus *Canis* but accorded separate generic rank to *Cuon*, *Lycaon*, *Otocyon* and *Speothos*. The simple key used to characterize these genera was based on digital count and dental formula.

Recognition of the foxes as a genus *Vulpes*, distinct from *Canis*, gained almost universal favor in the 20th century although debate continued as to the generic status of the more distinctive forms: the fennec (*Fennecus zerdai*), arctic fox (*Alopex lagopus*), and gray fox (*Urocyon cinereoargenteus*). Likewise the South American canids, generally separated from *Canis* in the 19th century, were later united under *Canis* (except *Speothos*) by Mivart (1890), and again separated generically in the early 20th century. Thomas (1914), Kraglievich (1930), Cabrera (1931) and Osgood (1934) were among the principal revisors. An early test of the classical grouping of the South American forms with *Canis* was a comparison of *C. antarcticus* and *C. latrans* by Pocock in 1913. Pocock concluded that

the affinities of *C. antarcticus* (the type species of *Dusicyon* H. Smith, 1839) lay with the South American forms whereas the coyote was related to the wolf and jackal. Thomas (1914), and later Cabrera (1931), developed morphological keys for identification of the South American species. They recognized several genera (*Lycalopex*, *Dusicyon*, *Cerdocyon* and *Pseudalopex*), the first two of which were considered monotypic and *Cerdocyon* became so by transfer of *C. microtis* to a new genus *Atelocynus* Cabrera, 1940. The peculiar *Chrysocyon* was also accorded generic rank and *Speothos* was still placed in a separate subfamily Simocyoninae by such recent authors as Simpson (1945). Some (e.g., Osgood, 1934) believed that *Urocyon* had a special affinity with the other South American forms rather than with *Vulpes*. Among the attempts to group these genera were the studies of living and fossil taxa by Kraglievich (1930) who recognized three genera: *Lycalopex* (for *L. vetulus* only), *Canis* with four subgenera (*Cerdocyon*, *Chrysocyon*, *Pseudalopex*, and *Dusicyon*), and *Speothos* (as a simocyonine). *Lycalopex vetulus* was regarded as a basal taxon. Osgood (1934) likewise chose to recognize the South American forms as a group, but he concurred with Thomas and Cabrera in recognizing their generic distinction from *Canis*. He advocated the use of the subgenus as a means of showing the affinities of these forms among themselves. Thus he recognized two genera (apart from *Urocyon* and *Speothos*): *Chrysocyon* and *Dusicyon*, the latter with three subgenera, *Cerdocyon*, *Lycalopex* and *Dusicyon*. The first two subgenera were monotypic, following Osgood's transfer of *microtis* from *Cerdocyon* to *Dusicyon*. Simpson (1945) adopted Osgood's classification.

There have been few changes in the nomenclature until the group was reviewed by Langguth (1969, 1970, 1975). Langguth comprehensively compared the biology of the South American canids as a whole and with special reference to *Chrysocyon*. He concluded in 1969 and 1970 that there were four generic groups: (1) "zorros de campo," placed in the genus *Dusicyon* with *Dusicyon* and *Pseudalopex* as subgenera; (2) "zorros de monte," using the genus *Cerdocyon* and placing *Cerdocyon*, *Atelocynus* and *Speothos* as

subgenera; (3) *Chrysocyon*; and (4) *Lycalopex*. Later (1975) he relegated the "zorros de campo" to the genus *Canis* with *Dusicyon* and *Pseudalopex* as subgenera concluding that these taxa represented "generalized dogs" in the same way as other species attributed to *Canis*. The "zorros de monte," on the other hand, represent "differentiated dogs" that Langguth intimates form a monophyletic group that originated in the Brazilian highlands. These forms were united morphologically using some of the characters we use to support the same grouping. *Chrysocyon* and *Lycalopex* were too specialized in their own ways for Langguth to clearly discern their phyletic relationships.

In a dissertation study of large Quaternary South American canids, published in 1988, Berta was the first to employ cladistic methods as a main tool for phylogenetic reconstruction. Her cladistic framework of the living South American canids was influenced by an earlier manuscript of this project, and has reached somewhat the same conclusions. Many of the same characters have been used in support of her phylogeny as well as ours. Our conclusion, however, differs from those of Berta's in two aspects: (1) placement of *Chrysocyon* and *Lycalopex* in the same clade as *Cerdocyon* group; (2) separation of several species of "*Pseudalopex*" (e.g., "*P.*" *gymnocercus*) from the genotypic species *P. culpaeus* and their placement at the base of the South American canid clade.

Clutton-Brock et al. (1976) undertook a phenetic study of 35 of the 39 living species by numerical methods. These workers scored 90 characters in their analysis, including morphological features of skull (13 characters), teeth (13), pelage of head and body (17), pelage of extremities (plus other external features, 17), postcranial skeleton and internal anatomy (14), and behavior (16). Only about 10 percent of the same characters were used in our analysis. The phenetic analysis was presented as two-dimensioned plots of the principal coordinates algorithm for all characters and for the skull and teeth only. A list of "near-neighbor" similarity figures for the same combinations of data was used in assessing the details of species relationships. The principal results illustrated the isolated positions of the monotypic living genera *Ly-*

caon, *Cuon*, *Speothos*, *Otocyon*, *Nyctereutes*, *Chrysocyon*, and more weakly *Alopex* (from *Vulpes*). *Urocyon* and *Fennecus* had high similarity to other *Vulpes* species (this comparison showed *V. vulpes* to be atypical), and *Cerdocyon* and *Atelocynus* were closely similar to species of *Dusicyon* (sensu Simpson, 1945). In addition to the monotypic genera, three larger genera were recognized: *Canis*, *Vulpes*, and *Dusicyon*, although these were found to be closely related. In a sense their conclusions represent a return to the scheme used by Mivart (1890), and at one point Clutton-Brock et al. (1976: 140) remarked that "no objective analysis of the results of this study would produce these three genera as presently composed but nor would it produce any other clear-cut grouping of species"!

Van Gelder's (1978) review of the canid classifications of Langguth (1975) and Clutton-Brock et al. (1976) attempted to reconcile these schemes in light of his contention that the genus can be defined as a collection of species capable of interbreeding and producing hybrids. Applying this rule of thumb to the few data regarding canid hybrids (usefully summarized in Gray, 1971), Van Gelder (1978) concluded that all living species currently assigned to *Canis*, *Dusicyon* and *Vulpes* should be included within the genus *Canis*, thus advocating the taxonomic suggestion made by Clutton-Brock et al. (1976) and quoted above. The monotypic *Nyctereutes*, *Chrysocyon*, *Speothos*, *Cuon*, *Lycaon* and *Otocyon* were retained as distinct genera although no interbreeding tests of these species were cited to substantiate this view. Van Gelder (1978) used the subgenus to group the species of his *Canis* into presumably phyletic units and the resulting classification differs very little from that of Clutton-Brock et al. (1976) or, for that matter, from that of Mivart (1890). The ability to hybridize can be viewed as a symplesiomorphy, a primitive feature, for the ability to interbreed between two species must reflect the retention of much of the genome of their common ancestral stock. This view explains the lack of resolution of phyletic affinities to be gained from interbreeding studies, a point elaborated by Rosen (1979: 275–278) in discussing the relevance of hybridization data in cladistic analysis. Thus, in Van Gelder's (1978) classification the spe-

cies of *Canis*, *Dusicyon*, and *Vulpes* form an unresolved multichotomy under *Canis*. *Canis* in turn has an unspecified relationship to the six monotypic genera that follow it in his classification. In contrast to these phenetic analyses, cladistic analysis is able to offer hypotheses about the phyletic relationships of these groups as well as illuminate the possible phylogenetic relationships of the more apomorphic forms that appear so distinctive on phenetic analysis.

PALEONTOLOGY

There have been few paleontological contributions to the phylogeny of the living canids based on first hand studies other than those of Matthew (1924, 1930). His views have been very widely accepted and are now well entrenched in textbooks. Matthew was one of the principal proponents of the concept of the unicuspid talonid "dogs" or Simocyoninae as a monophyletic group. Simpson (1945: 109–110, 223–224) retained this group with reservations, and listed the genera attributed to it. Only 7 (*Enhydrocyon*, *Philotrox*, *Euoplocyon*, *Protocyon*, *Speothos*, *Cuon*, and *Lycaon*) out of a total of 15 genera assigned by Simpson to this group belong to the Canidae as we have defined it. The remainder, including the fossil *Simocyon* itself, belong to arctoid families. A growing dissatisfaction with the phyletic basis for this view has been indicated by others (e.g. Clutton-Brock et al., 1976) and the superficial basis for grouping the canids in this manner has been rather strongly refuted by the data presented herein. Matthew also believed that species of the genus *Tomarctus* lay at the root of the phylogeny of *Vulpes* and *Canis*. He indicated that "*Nothocyon*" (now *Cormocyon*, and partly including species referred to *Leptocyon*) was in turn ancestral to *Tomarctus*. Although we could agree that some species placed in "*Nothocyon*" by Matthew have a phylogenetic relationship with *Vulpes*, we deny any close phylogenetic relationship of *Tomarctus* with *Vulpes* or *Canis*. *Tomarctus* is a typical borophagine with an overlay of apomorphic features typical of later members of that group (complex incisors and premolars, massive molars, strong premaxillary-frontal union, etc.). An unprecedented amount of evolutionary reversal would have

to accompany the origin of any living canines from that source. The evidence seems clear that the Caninae have a phyletic relationship with the vulpines and, along with *Leptocyon*, constitute a monophyletic group. The fossil record of the Caninae, to be discussed elsewhere, does not alter this view and fossil genera inserted into the cladogram based on Recent forms amplify some groups but does not change the branching pattern indicated in figure 2. However, canid fossils do serve three important functions. First is the correct interpretation of homoplasies. Apparent synapomorphies inferred from living taxa alone can turn out to be independently derived when fossil taxa are included in the analysis. The second function of fossil canids is their transitional positions in phylogeny, which breaks up seemingly long lists of synapomorphies into smaller components or intermediate states. Although this latter function has the appearance of weakening the support for each node (diluting the synapomorphies), it actually strengthens the overall phylogeny by displaying evidence of the actual sequence of character acquisition, thus further corroborating hypotheses of character transformations. The third function is that the direct historical record provided by fossils yields data on the temporal succession of taxa, their zoogeographic relationships, and predictions regarding the history of the group.

KARYOLOGY

In recent years, increasingly comprehensive karyological data have become available for the Canidae. Chiarelli (1975) summarized these data and used the aspects of chromosome morphology to advance phylogenetic conclusions. His conclusions were dependent on the acceptance of a particular hypothesis of chromosome evolution. Chiarelli (1975) posited a Robertsonian or centric-fusion mechanism and hence regards higher chromosome number as representative of the primitive state. In his view, *Canis* has the more generalized karyotype ($2n = 78$), *Vulpes* (*V. vulpes* $2n = 34-38$; *V. bengalensis* $2n = 60$) the more specialized one. In another contribution using the same data base, Todd (1970), in an innovative view of canid chromosome evolution, postulated a karyotypic

fission mechanism that he held to be a rare centric misdivision leading to an increase in diploid number. Thus, low diploid number would be primitive in his view. Todd deduced that the primitive diploid number for the Carnivora is $2n = 38$ from inspection of the distribution of diploid numbers among karyotyped Carnivora.

Comparing the karyotypes among the canid genera led Chiarelli (1975) to the following general conclusions:

(1) *Canis* (including *C. aureus*, *C. familiaris*, *C. latrans*, *C. lupus*, *C. mesomelas*, *C. rufus*), *Lycaon*, *Chrysocyon*, *Atelocynus*, *Lycalopex* (*L. vetulus*), "*Pseudalopex*" *griseus* (Gallardo and Formas, 1975), "*P.*" *gymnocercus* (Brum-Zorilla and Langguth, 1980) and *Speothos* all have only acrocentric autosomes, a high diploid number (74-78), share morphologically identical X chromosomes, and some show similar autosome morphologies.

(2) *Vulpes* species (*V. bengalensis*, *V. pallida*, *V. ruppelli*, *V. vulpes*) have a range of diploid numbers (34-60) but the same fundamental number of autosomes (72). The extremes, *V. vulpes* (34-40) and *V. bengalensis* (60; the "basic-fox" of Clutton-Brock et al., 1976), may hypothetically be differentiated by centric fusion mutations in Chiarelli's view.

(3) *Urocyon* and *Fennecus* (*Vulpes zerda*) differ slightly in diploid number (66 and 64 respectively) but have an identical fundamental number (70) and have two morphologically similar chromosomes marked by an achromatic region near the centromere.

(4) *Alopex* (*Vulpes lagopus*), *Otocyon*, *Cerdocyon*, and *Nyctereutes* have karyotypes not completely comparable with other canids in terms of chromosome morphology. *Alopex* shows chromosome polymorphism with diploid numbers 48, 49, 50, and 52 having been observed, but the fundamental number is 88 due to the large number of meta- or submetacentric chromosomes. Nevertheless, close karyological relationship exists with *Vulpes vulpes* as shown by comparative chromosome studies (Mäkinen and Gustavsson, 1892; Yoshida et al., 1983) and reciprocal crosses of these species in which the hybrids show reduced fertility (Gray, 1971). *Otocyon* shows a high diploid number (72) and large fundamental number (80). Although the

karyotype seems to be dominated by acrocentric chromosomes, the number of metacentrics or submetacentrics appeared to differ in different animals studied. Todd (1970) suggested, without discussion, a relationship to the karyotype of *Vulpes bengalensis*. *Cerdocyon*, karyotyped by Wurster-Hill in 1973, was found to have a unique chromosome complement with diploid number of 74, but a fundamental number of 110 due to a nearly equal number of submetacentric and metacentric chromosomes (36) and acrocentrics (38). This is the highest fundamental number known within the Carnivora. Partial genetic compatibility with *Canis* is shown by production of sterile hybrids in crosses with the domestic dog (Gray, 1971). *Nyctereutes* races show considerable karyotypic variability. *Nyctereutes procyonoides viverrinus* (the Japanese race) has a low diploid number (42) and fundamental number of 68 and morphologically unique chromosomes (X is the largest acrocentric and Y is a small, satellited acrocentric). Todd (1970) deduced that the chromosome complement of *Nyctereutes* corresponds to that required to yield the New World canine array through the fissioning mechanism, and hence that genus is a survivor of an early stage in the differentiation of the Canini. However, recent studies by Mäkinen and Fredga (1980), Ward et al. (1987) and Wurster-Hill et al. (1986, 1988) indicate that the mainland nominate race, *N. p. procyonoides*, has a more typical Canini karyotype ($2n = 56$, NF 68) with an X chromosome, a medium-sized metacentric and a small Y metacentric with satellites. The autosomes consist of 10 metacentrics to submetacentrics and 44 acrocentrics.

In a more recent summary, Wayne et al. (1987a, 1987b) used the Giemsa-banding patterns of chromosomes to more closely compare their morphology in a selected group of canids. These studies delineated two major groupings based on diploid number. Those species having a high diploid number ($2n > 64$) and largely acrocentric chromosomes correspond to the first group discussed by Chiarelli (1975) plus *Cerdocyon*, *Otocyon* and Chiarelli's third group (*Urocyon* and *Fennecus*). Similarities in chromosome morphology revealed by G-banding techniques allowed Wayne et al. (1987a) to recognize con-

siderable similarity in chromosome morphology despite the variation expressed by missing chromosomes and unique additions and rearrangements. The gray wolf served as a basis of comparison in reconstruction of the phylogenetic relationships of the taxa investigated. A three-taxon statement resulted in which the gray wolf had the South American canids (*Speothos*, *Cerdocyon* and *Chrysocyon*) as a sister taxon and they in turn were the sister group to a clade including *Urocyon*, *Fennecus* and *Otocyon*. Four lower diploid canids ($2n < 64$), in which metacentric chromosomes predominate, were compared by G-banding techniques. Wayne et al. (1987b) found that *Alopex* and *Vulpes macrotis* have identical G-banding patterns and chromosome morphology. The red fox, *V. vulpes*, has only two chromosomes in common with *Alopex* and *V. macrotis* but shows extensive chromosome arm similarity with these foxes justifying a postulated close phyletic relationship between these species. The raccoon-dog, *Nyctereutes procyonoides* ($2n = 42$) was found to share some chromosomes with these foxes and also with *Canis lupus*. In fact Wayne et al. (1987b) reported that approximately three-fourths of the gray wolf chromosomes ($2n = 78$), or about 85 percent of the length of the wolf karyotype, have similarity to a chromosome arm or entire chromosome of the raccoon-dog. About three-fourths of the chromosome arms of *Nyctereutes* are also morphologically similar to those of the red and arctic foxes but there is less correspondence in terms of the total length of the karyotype than the case of the wolf.

Despite the uncertainty about the precise relationship of *Nyctereutes*, Wayne et al. (1987b) placed the raccoon-dog as a sister taxon to the foxes and joined the low and high diploid trees at the base in the "most parsimonious" arrangement. *Nyctereutes* was compared with representative feline chromosomes and found to contain a number of morphologically similar features resulting in their assessment that that genus possessed the most primitive canid karyotype. Wayne et al. agree with Todd (1970) that the low diploid number of the raccoon-dog implies that fission mechanisms must be involved to yield higher diploid numbers. In addition, fusion, translocation and terminal addition mecha-

nisms must also be involved to yield the phylogenetic pattern discerned from the karyotypic data.

Comparing the cladistic relationships of the investigated taxa deduced from the karyological data with those deduced from the morphological evidence advanced in this paper (fig. 8), we see three major areas of agreement: (1) the *Canis* and *Vulpes* groups of species represent the primary sister taxa; (2) that the South American taxa examined constitute a monophyletic group allied to *Canis* and have the same branching pattern; and (3) that the *Vulpes* species, including *Alopex* are a monophyletic group. Areas of disagreement are also threefold: (1) in the Wayne et al. analysis *Nyctereutes* is a member of the vulpine clade; (2) *Otocyon* and *Urocyon* are in a clade associated with the South American canids and *Canis*; and (3) *Fennecus* is associated with the gray and bat-eared foxes rather than *Vulpes*. Despite these details it is encouraging to see that both sets of data group most canids into vulpine and canine clades and that the South American taxa are allied to the canines.

BIOCHEMICAL SYSTEMATICS

Wayne and O'Brien (1987) used electrophoretic methods to examine the protein products of 51 genetic loci from blood and tissue preparations. Eleven of 15 canid genera (*Cuon*, *Dusicyon*, *Atelocynus*, and *Pseudalopex* omitted) were examined. The electrophoretic data were analyzed quantitatively using several methods for calculating genetic distance and illustrated by two methods of tree construction (UPGMA and distance Wagner). These phenograms reflect overall and specific similarity which may or may not represent phylogeny. The data have the same significance in phylogeny reconstruction as the karyological data discussed above. They summarized their results in a strict consensus tree which depicted phenetic relationships less resolved than the chromosome data (fig. 9). The tree is rooted using *Ursus arctos* as the outgroup, but the canid relationships form a pentachotomy with the relationships of *Urocyon*, *Otocyon* and *Nyctereutes* completely unresolved. The South American canids (less *Speothos*) are, however, grouped and that

group placed as a sister taxon to *Canis* and *Lycaon*. *Speothos* is separated from the South American taxa and allied with *Canis* and *Lycaon*, an association that would require five additional steps in our morphological analysis. This result also demands significantly greater karyotypic resemblance of *Speothos* and *Canis* than shown by the chromosome evidence.

The phylogenetic position of *Nyctereutes* also remains unresolved in the allozyme comparisons although it now becomes a monotypic element in the pentachotomy rather than a part of the vulpine group as in the karyotype phenogram. Likewise the allozyme data do not clarify the relationships of *Otocyon* or *Urocyon* to each other or other canids, but *Fennecus* is grouped with the other *Vulpes* species as in the morphological results.

In 1989 Wayne et al. reported the results of DNA hybridization among the same canid taxa and found it yielded limited information beyond confirming the grouping of the wolf-like canids (wolf and jackals) and the foxlike canids (red fox, arctic fox and fennec). Other taxa could not be resolved because the standard error of the measurements (melting temperatures) is too large to permit clear discrimination of further groupings of taxa.

A DNA sequence study by Geffen et al. (1992) used mitochondrial DNA restriction fragment and restriction site data plus the sequence variation among 402 base pairs of cytochrome b to resolve the relationships of the foxlike canids. The results confirmed the monophyly of *Alopex*, *Vulpes* and *Fennecus* and some details of relationship among these and other species of *Vulpes*, but it left the relationships of *Otocyon* and *Urocyon* to one another or to other foxes unresolved.

CONCLUSIONS

In the preceding pages, features of the osteology of the Recent canine carnivores have been used to generate a phylogenetic synthesis based on 57 characters distributed among 122 character states. Polarity was established from examination of three extinct outgroups that represent successive sister taxa of the living Caninae. Fifteen canine taxa were chosen as the basis for the analysis, ten of which

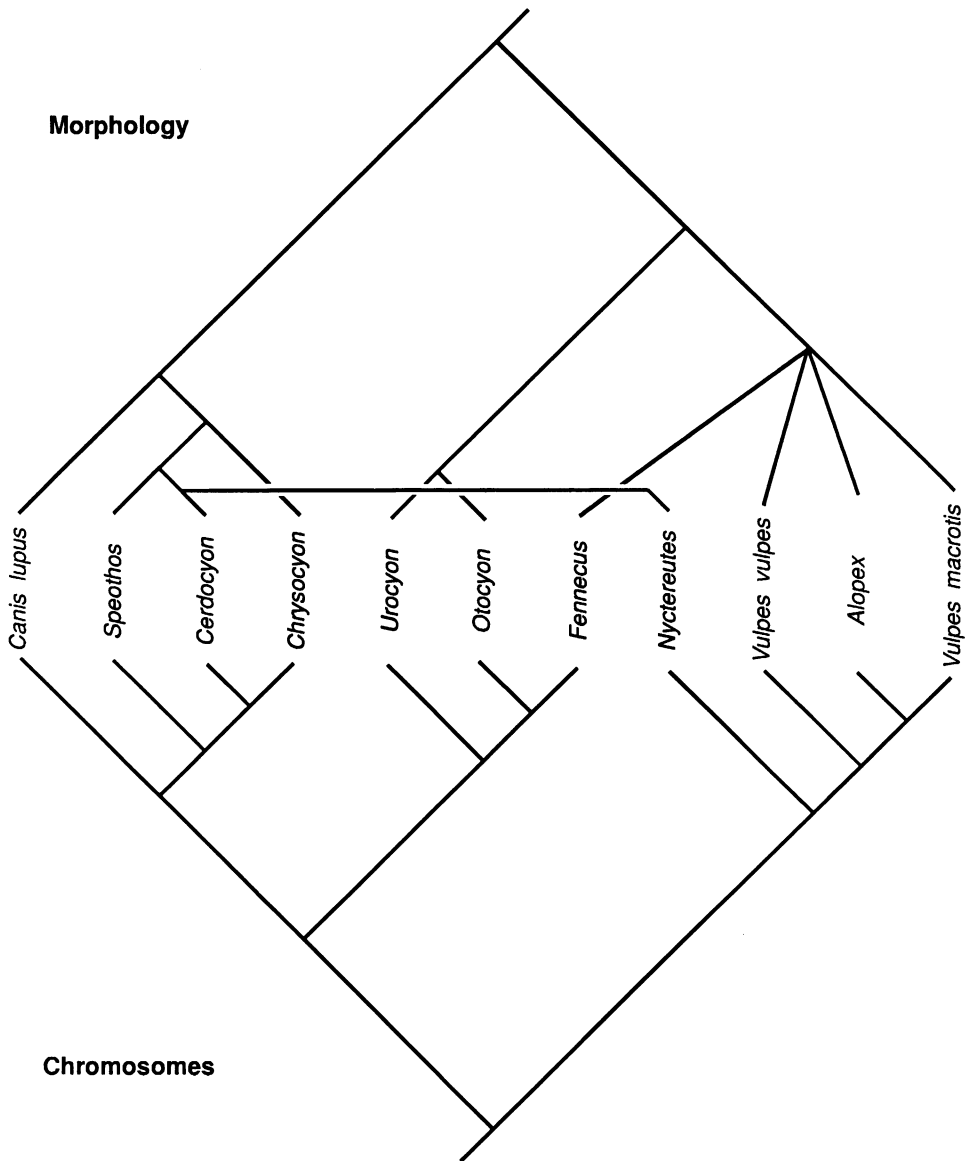


Fig. 8. Cladograms depicting canine relationships based on Wayne et al. (1987b) chromosomal data compared with the morphological data provided by the present study. Array of taxa limited to comparable forms.

were monotypic genera and four polytypic taxa were considered monophyletic because of close morphologic resemblance of their species, bolstered in the case of *Canis* and *Vulpes* by chromosomal and molecular evidence of propinquity. Character analysis was however based on the array of specimens listed in Appendix 1.

Phylogenetic reconstruction by a maximum parsimony program (HENNIG86, Version 1.5, Farris, 1988) was analyzed using CLADOS, Version 1.2, Nixon, 1992). A single tree was found with length = 90 (excluding autapomorphies), consistency index = 65 and retention index = 78 (fig. 2). The reconstruction delineates two sister taxa (fig. 2, Node

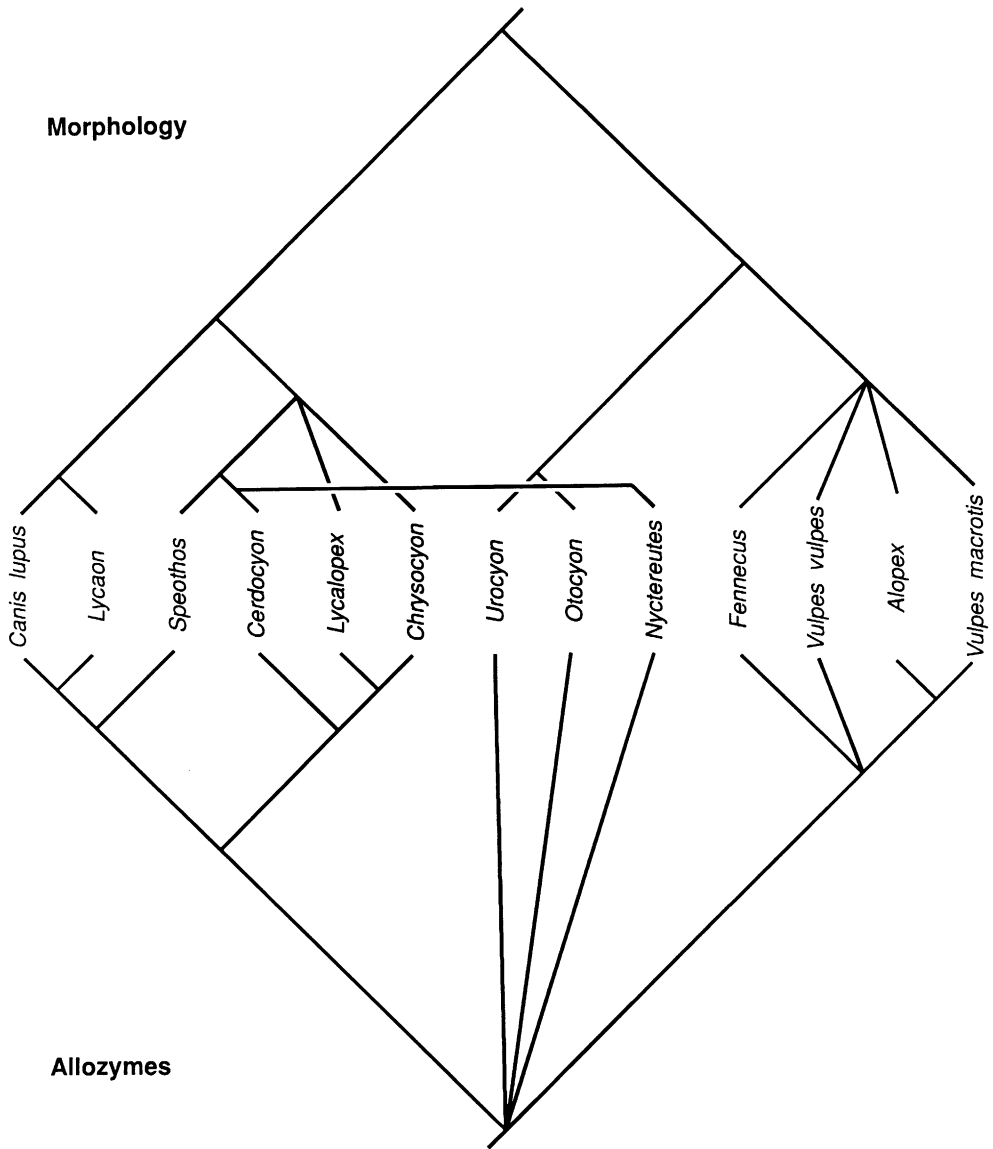


Fig. 9. Cladograms depicting canine relationships based on Wayne and O'Brien's (1987) allozyme data compared with the morphological data provided by the present study. Array of taxa limited to comparable forms.

D): the foxlike Caninae, tribe Vulpini, and the wolflike and South American taxa plus the raccoon-dog, tribe Canini. This fundamental subdivision is supported by karyological and biomolecular studies although the precise composition of each group varies with the evidence used. In all cases the morphological evidence leads to more fully resolved relationships than presently available from

any other system (figs. 8, 9). The position of the foxes *Urocyon* and *Otocyon* are variously portrayed in the phenetic analyses of chromosome morphology (a sister taxon of the fennec and of the Canini clade) or of allozyme alleles (as part of the basal pentachotomy of canine relationships). Even more contentious is the position of the Asian raccoon-dog, *Nyctereutes*, which is firmly included within the

South American clade as a sister taxon of the crab-eating "fox," *Cerdocyon*, in our analysis, but is allied with *Vulpes* based on karyology or joins *Otocyon* and *Urocyon* in the basal canine pentachotomy in the allozyme results. The position of the South American bush-dog, *Speothos*, also has different relationships in the chromosome analysis versus the allozyme data. Chromosome morphology and osteology agree in placing *Speothos* within the South American clade, but allozymes ally it with the wolf group as a sister taxon of *Canis lupus* plus the hunting-dog, *Lycaon pictus*. In an earlier version of the osteological synthesis (Berta, 1988) the maned-wolf, *Chrysocyon*, was held to be a sister taxon of the wolf group, but the present results place

it in a trichotomy (fig. 2, Node K) with members of the South American clade in agreement with both chromosome and allozyme evidence.

There is thus reasonable concordance of results with the three methods of phyletic inference as to the basic framework of canine phylogeny. Chromosomal and molecular methods have not been applied to the whole array of Recent species so the analysis is more comprehensive in the case of the osteological investigation. It is hoped that further biomolecular data will eventually allow as comprehensive a sample and that sequencing studies may provide additional insights into the phylogenetic relationships of the Recent Canidae.

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APPENDIX 1

List of Specimens of Living Canids Examined

The sample was chosen such that interspecific variations were evaluated in genera with multiple species. Specimens listed below constitute the total sample from which morphological observations, illustrations, or measurements were made. The classification follows that by Wozencraft (1993) except as noted below. The arctic fox *Alopex lagopus* is here considered a species of *Vulpes*. We restrict the usage of *Pseudalopex* to its genotypic species *P. culpaeus*. The small South American "zorros" placed under the genus *Pseudalopex* by Wozencraft (1993) are a paraphyletic group in our analysis. Three of these species are thus without a proper generic name, here indicated by quotation marks: "*Pseudalopex*" *gymnocercus*, "*P.*" *sechurae*, and "*P.*" *griseus*. *Lycalopex* is available for *L. vetulus* as a monotypic genus.

We were not able to examine the following species: *Urocyon littoralis*, *Vulpes cana*, *V. ferrilata*, and *V. rueppelli*. An asterisk following the catalog number indicates specimens whose frontal bone is cut open to expose the frontal sinus area or whose frontal sinus (or the lack of it) can be observed from natural breakages.

Number	Sex	Locality
<i>Vulpes bengalensis</i> :		
AMNH(M) 54517	M	Kheri Forest, Uttar Pradesh, India
AMNH(M) 54526	F	Kheri Forest, Uttar Pradesh, India
<i>Vulpes chama</i> :		
AMNH(M) 81760	—	Orange Free State, South Africa
<i>Vulpes corsac</i> :		
AMNH(M) 85021	—	Gobi Desert, Mongolia
<i>Vulpes (Alopex) lagopus</i> :		
AMNH(M) 15637	—	Northwest Territory, Canada
AMNH(M) 40979	M	Melville Bay, Greenland
<i>Vulpes macrotis</i> :		
AMNH(M) 589	M	Arizona, United States
<i>Vulpes pallida</i> :		
AMNH(M) 82198	M	Jobelein, Sudan
<i>Vulpes velox</i> :		
AMNH(M) 15871	M	Alberta, Canada
AMNH(M) 100190	M	New York Zoo, United States
<i>Vulpes vulpes</i> :		
AMNH(M) 60C*	—	No data
AMNH(M) 295*	—	No data
AMNH(M) 29055	M	Northwest Territory, Canada
AMNH(M) 88713	M	Turkomen Desert, Iran
AMNH(M) 98223	F	Alberta, Canada
AMNH(M) 141148	M	New Jersey, United States
AMNH(M) 166938	F	New Jersey, United States
AMNH(M) 185649	M	Georgia, United States
AMNH(M) 243093*	M	Florida, United States
AMNH(M) 253187	M	Florida, United States
<i>Vulpes (Fennecus) zerda</i> :		
AMNH(M) 70126	M	Egypt
AMNH(M) 80019	M	New York Zoo, United States
<i>Urocyon cinereoargenteus</i> :		
AMNH(M) 536*	M	California, United States
AMNH(M) 4270	—	Chihuahua, Mexico
AMNH(M) 5366	F	Florida, United States
AMNH(M) 26016	M	Jalisco, Mexico

APPENDIX 1—(Continued)

Number	Sex	Locality
AMNH(M) 29488*	—	San Rafael del Norte, Nicaragua
AMNH(M) 100224	—	Florida, United States
AMNH(M) 121276*	F	California, United States
AMNH(M) 243095	F	Florida, United States
<i>Otocyon megalotis</i> :		
AMNH(M) 111*	—	no locality
AMNH(M) 114270	M	Masi Sand River, Kenya
AMNH(M) 161153	—	Kondoa, Tanzania
"Pseudalopex" <i>gymnocercus</i> :		
AMNH(M) 205778	M	Soriano, Uruguay
AMNH(M) 205783	M	Treintay Tres, Uruguay
AMNH(M) 205786	F	Treintay Tres, Uruguay
AMNH(M) 205787	F	Treintay Tres, Uruguay
AMNH(M) 205792	M	Treintay Tres, Uruguay
"Pseudalopex" <i>sechurae</i> :		
AMNH(M) 46525	M	Portoviejo, Ecuador
AMNH(M) 46528*	M	Portoviejo, Ecuador
"Pseudalopex" <i>griseus</i> :		
AMNH(M) 14081	F	Patagonia, Argentina
AMNH(M) 33292*	M	Temuco, Maguehue, Chile
AMNH(M) 41510*	F	Lavalle, Santiago del Estero, Argentina
AMNH(M) 90050	F	New York Zoo (from Chile)
<i>Pseudalopex culpaeus</i> :		
AMNH(M) 66737*	—	Upper Rio Pila, Ecuador
AMNH(M) 67088	F	Sincha, Ecuador
AMNH(M) 147547	M	New York Zoo, United States
AMNH(M) 262663	M	Oruro, Bolivia
<i>Dusicyon australis</i> :		
ANSP 588 (cast)	—	Falkland Islands
<i>Lycalopex vetulus</i> :		
AMNH(M) 391*	—	Chapada, Brazil
AMNH(M) 100100	F	New York Zoo, United States
<i>Chrysocyon brachyurus</i> :		
AMNH(M) 36962*	M	Urucum, Mato Grosso do Sul, Brazil
AMNH(M) 120999	—	Alegrete, Rio Grande de Sul, Brazil
AMNH(M) 133940	F	Mato Grosso, Brazil
AMNH(M) 133941	M	Mato Grosso, Brazil
<i>Cerdocyon thous</i> :		
AMNH(M) 14623	—	Bonda, Colombia
AMNH(M) 14627	—	Cacaqualito, Colombia
AMNH(M) 14636	—	Onaca, Colombia
AMNH(M) 30628	F	La Bomba, Venezuela
AMNH(M) 36503*	M	Trinidad, Paraguay
AMNH(M) 63942*	—	Caqueta, Colombia
AMNH(M) 133934	M	Mato Grosso, Brazil
AMNH(M) 133935	M	Mato Grosso, Brazil
AMNH(M) 209122	M	Beni, Bolivia
AMNH(M) 209124	F	Beni, Bolivia
AMNH(M) 234221	M	Misiones, Paraguay

APPENDIX 1—(Continued)

Number	Sex	Locality
<i>Nyctereutes procyonoides:</i>		
AMNH(M) 22792*	F	New York Zoo, United States
AMNH(M) 43139	F	Fujian, China
AMNH(M) 45333	F	Zhejiang, China
AMNH(M) 57113	M	Sichuan, China
AMNH(M) 59323	M	Fujian, China
AMNH(M) 249766	F	Honshu Island, Japan
AMNH(M) 249767	F	Honshu Island, Japan
<i>Atelocynus microtis:</i>		
AMNH(M) 76031	—	Urubamba, Peru
AMNH(M) 76579	M	Lagarto, Loreto, Pará, Peru
AMNH(M) 95284	M	Rio Tapajoz, Pará, Brazil
AMNH(M) 95285	F	Rio Tapajoz, Pará, Brazil
AMNH(M) 98639	F	Iquitos, Loreto, Peru
AMNH(M) 100095*	F	New York Zoo, United States
<i>Speothos venaticus:</i>		
AMNH(M) 98558	M	Iquitos, Loreto, Peru
AMNH(M) 98560*	F	Iquitos, Loreto, Peru
AMNH(M) 167846	M	New York Zoo, United States
AMNH(M) 184668	—	New York Zoo, United States
<i>Canis adustus:</i>		
AMNH(M) 83767	M	Tabora, Tanzania
<i>Canis aureus:</i>		
AMNH(M) 54033	—	Ethiopia
AMNH(M) 54515	F	Hardwar, India
AMNH(M) 81041	M	Billata River, Ethiopia
AMNH(M) 88712	M	Dar Koleh, Iran
<i>Canis latrans:</i>		
AMNH(M) 21269*	—	Durango, Mexico
AMNH(M) 24860	M	Sinaloa, Mexico
<i>Canis lupus:</i>		
AMNH(M) 69452	—	no locality
<i>Canis mesomelas:</i>		
AMNH(M) 34732*	M	Uasin Gishu, Kenya
AMNH(M) 180109*	F	Lotome, Karamoja, Uganda
AMNH(M) 233009	M	Windhoek, Otjikundua, Namibia
<i>Canis rufus:</i>		
AMNH(M) 4609	M	Illinois, United States
<i>Canis simensis:</i>		
AMNH(M) 81001	F	Kordofan Plateau, Sudan
AMNH(M) 81025	F	Kordofan Plateau, Sudan
AMNH(M) 81034*	F	Kordofan Plateau, Sudan
AMNH(M) 214798*	F	Africa
AMNH(M) 214799	—	Africa
<i>Cuon alpinus:</i>		
AMNH(M) 54842	M	Dharwar, India
AMNH(M) 99636*	—	New York Zoo, United States
AMNH(M) 101882	M	Het Zang Plateau, Java

APPENDIX 1—(Continued)

Number	Sex	Locality
<i>Lycaon pictus</i> :		
AMNH(M) 114248	M	Masi Sand River, Kenya
AMNH(M) 114254*	F	Masi Sand River, Kenya
AMNH(M) 164162	M	Mourage, Chad

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