To the Graduate Council:

I am submitting herewith a dissertation written by Darcy F. Morey entitled "Cranial Allometry and the Evolution of the Domestic Dog." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Anthropology.

Walter E. Klippel, Major Professor

We have read this dissertation and recommend its acceptance:

Accepted for the Council:

Vice Provost
and Dean of the Graduate School

CRANIAL ALLOMETRY AND THE EVOLUTION OF THE DOMESTIC DOG

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Darcy F. Morey

August 1990

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ABSTRACT

Domestication is usually defined as a process involving human subjugation of other animal or plant species. From this perspective, it is often presumed that morphological changes in domestic animals are the product of conscious or unconscious human selection. A broader evolutionary perspective does not make this presumption.

The origin of the domestic dog (Canis familiaris) is best understood as a consequence of human adoption of wolf pups (Canis lupus) some 12,000 years ago. Young wolf pups growing up in human society formed their primary social bonds with humans. The radically altered circumstances experienced by these early domestic canids placed them in a new role as ecological colonizers. Selection under these circumstances favored precocious maturation, resulting in evolutionary progenesis, a form of heterochrony. Concurrently, an abrupt shift in diet resulted in rapid size reduction in the new evolving species.

Craniometric data are analyzed from modern wild Canis and prehistoric domestic dogs from North America and northern Europe, all predating 3,000 B.P. The goal is to assess whether or not morphological changes in dogs are allometric consequences of size reduction, brought about by heterochronic alterations. Previous investigations of canid allometry involving wild canids and modern dog breeds serve as a frame of reference.

Bivariate analysis of static data reveals that the dogs exhibit uniquely wide cranial vaults and palates, and are distinct from allometric trends seen among other groups. Anterior cranial length variables are tightly scaled among all groups, with proportional variation a consequence of allometric scaling. Dogs also tend to have proportionally longer teeth than similar sized wild canids. Bivariate analysis of ontogenetic data reveals that wide vaults and palates in dogs are associated with a greater correspondence to wolf ontogenetic regression lines relative to other groups. On anterior cranial length variables all groups exhibit evidence of ontogenetic scaling. Multivariate analysis indicates that dogs are morphologically more similar to juvenile wolves than to any adult group.

Juvenilized morphology in dogs is a consequence of rapid size change with morphology constrained to developmental pathways. Invariance in gestation period in Canis may pose a fundamental morphological constraint on dog morphology. Confinement of morphology to developmental boundaries may be indicative of rapid evolutionary change in general. Heterochronic mechanisms responsible for this mode of change may be important in the evolution of domestic animals other than the dog.

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CHAPTER I

INTRODUCTION AND PROBLEM DEFINITION

This is a study of evolutionary process. It is an effort to better understand evolutionary changes seen in a particular episode of speciation involving wolves (Canis lupus) and their descendents, domestic dogs (Canis familiaris). From a beginning presumed to lie about 12,000 years ago, wolves associated with humans radiated geographically and evolved into a new species, the domestic dog. Because this process of speciation occurred in the context of a social, ecological relationship with humans, it cannot be understood independent of that relationship.

Questions relating to the origins and evolution of the dog have been dealt with repeatedly by western science for well over a century (e.g., Galton 1865; Darwin 1868; Allen 1920; Dahr 1942; Werth 1944; Degerbøl 1961; Scott 1968; Clutton-Brock 1984; S. Olsen 1985). In fact, it has been remarked that this animal generates more interest than any other domestic species (Bökönyi 1974:313; S. Olsen 1979:188; Benecke 1987:31). Considering the attention bestowed on the dog, it is remarkable how little is actually known about its origins and early evolution. For example, it is not known where the dog originated, or whether its domestication occurred once or several times independently. Nor is it clear just when its domestication

took place, though this can be reliably pushed back to about nine thousand years ago, less reliably to about 12,000 years or more (see Chapter II).

Even identification of the basic ancestry of dogs cannot be considered fully settled, though there is a broad modern concensus that one or more varieties of the wolf (C. lupus) represents the progenitor of modern dogs (e.g., Scott and Fuller 1965; Scott 1967; Reed 1969; Bökönyi 1974; Clutton-Brock et al. 1976; Olsen and Olsen 1977; Aaris-Sørensen 1977a; Clutton-Brock 1981, 1984; S. Olsen 1985). This concensus is based on structural, physiological, and behavioral similarities between the two species. Although it is assumed here that the wolf was indeed the ancestor of the dog, it must be acknowledged that the issue is not fully closed (see Chapter II). As Clutton-Brock (1984:202) has observed, it is surprising how little our knowledge on this topic has advanced since Darwin (1868) argued over a century ago for a multiple ancestry for dogs involving both wolves and jackals (Canis aureus).

This study deals with morphological divergence of dogs from wolves. Analysis and discussion in the ensuing chapters focus on three interrelated questions: (1) What morphological changes occurred in the evolution of dog from wolf dog?, (2) How are these changes structurally or physiologically interrelated?, and (3) Why did these

changes occur? With the exception of the first question, these can be counted among those frequently addressed basic issues that have not been resolved. In this study quantitative analysis of craniometric data from recent and subfossil canids, including wolves and prehistoric domestic dogs, provide the basis for attacking these questions. This study builds on a substantial body of literature that deals with these very questions and spans more than a century of investigations.

Because this study focuses on morphological divergence from wolves, the data base emphasizes early prehistoric dog remains. All specimens are from North America or northern Europe. It is considered desirable to focus on early, morphologically generalized dogs associated with peoples whose lifeway still consisted largely of broad spectrum hunting and gathering. With reference to archaeological taxonomy, this refers to "Mesolithic" (or earlier) materials in Europe while in North America "Archaic" (or earlier) remains are most appropriate. Thus, emphasis is placed on materials that predate roughly 3,000 B.P.

The reason for this emphasis is that sedentary agricultural or urban life among humans is correlated with the widespread emergence of morphologically specialized breeds of dogs (cf. Bökönyi 1974:313-334; Clutton-Brock 1984:207-208). The development and geneaology of modern dog breeds has been dealt with by other investigators

(e.g., Hilzheimer 1932; Lumer 1940; Epstein 1971; Bökönyi 1974; Clutton-Brock 1984) but is beyond the scope of this study. Discussions of modern or recent dogs are employed at various junctures, but only when they help shed light on questions concerning the early evolution of dogs from wolves. Questions concerning the emergence of modern, specialized breeds are not unimportant or uninteresting--they simply are not the questions under investigation here.

Numerically, wolves comprise the greatest portion of the data base used in this study, all coming from several North American varieties (including the red wolf, Canis rufus). Use of North American specimens does not reflect theoretical concerns, but only the fact that these materials were most readily available to this author. Although North American wolves may have participated in the ancestry of some dogs (cf. Olsen and Olsen 1977:533; Clutton-Brock 1984:199), their predominance in the data base should not be construed as an argument in support of this possibility. It is simply assumed that North American wolves provide a generally valid model of static variation and growth in the species that gave rise to the dog. In addition to wolves the data base includes a series of golden jackals (Canis aureus) and North American coyotes (Canis latrans).

The rationale for undertaking yet another study of the origins and early evolution of the domestic dog is multi-

faceted. For anthroplogists, this topic is important because the evolution of the dog apparently signifies the first domestic relationship between man and another animal species. Early domestication had far reaching consequences, for subsequent human evolution was inextricably linked with domestic relationships.

For biologists the riddle of early dog evolution poses a fascinating problem concerning mechanisms of evolutionary change. A principal challenge is to determine the genetic and developmental factors that control the expression of morphological variability in dogs. This task cannot be meaningfully undertaken without reference to the evolutionary divergence of dogs from wolves. Identification of the mechanisms that have produced different morphologies in polymorphic species poses an important problem for evolutionary biology, with application beyond the specific taxa dealt with here (e.g., Stockhaus 1965; Wayne 1986a, 1986b).

Finally, at a broader level, it is this author's hope to contribute to a better understanding of domestication as an evolutionary process.

Domestication as Evolution

Domestication is commonly viewed as a condition imposed by humans on other animals (or plants--this study deals only with domestic relationships involving humans and

other animals). Consider the following examples:

> I would define the essence of domestication as: the capture and taming by man of animals of a species with particular behavioral characteristics, their removal from their natural living area and the breeding community, and their maintainance under controlled breeding conditions for profit [Bökönyi 1969:219].

> It seems reasonable to accept the fact that the events leading from animals that were wild to those that were finally domesticated would follow the process of capture, taming, and controlled breeding (but not necessarily conducted as a well-organzed procedure) [S. Olsen 1979:175].

> A domestic animal is one that has been bred in captivity for purposes of economic profit to a human community that maintains complete mastery over its breeding, organization of territory, and food supply [Clutton-Brock 1981:21].

> . . . domestication can be said to exist when living animals are integrated as objects into the socioeconomic organization of the human group, in the sense that, while living, those animals are objects for ownership, inheritance, exchange, trade, etc., as are the other objects (or persons) with which human groups have something to do [Ducos 1978:54].

Understandably, these definitions focus on the implications of domestic relationships for humans. It is certainly legitimate for investigators linked with anthropology to exhibit primary concern for the role of a process or relationship in human existence. Among the above definitions some (Bökönyi, Olsen) contain assumptions about the mechanisms by which humans impose this condition on other animals (e.g., "capture", "taming"), while others (Clutton-Brock, Ducos) avoid statements of mechanism and stress instead the characteristics or roles of domestic

animals in human society (e.g., "economic profit", "objects of ownership"). More recent discussions mirror these perspectives (Bökönyi 1989; Clutton-Brock 1989; Ducos 1989).

When domestication is viewed as human subjugation of another species, it is natural to characterize it in terms of the purposes behind it or the processes by which humans accomplished it. The economic impact on human society of animals like cows, pigs, or sheep is so obvious that this approach is intuitively appropriate. However, as Bökönyi (1974:313) has suggested, dogs are not economically important now and probably never were (for a different view see Clutton-Brock 1984:204). Because of this perception, it has been suggested that dogs basically domesticated themselves (cf. Haag 1948:257-258; Bökönyi 1974:313), or that at least they were less a product of human subjugation for economic reasons than other animals (e.g., Epstein 1955:137). Even so, morphological changes associated with domestication in dogs are often presumed to be direct products of human selection, conscious or unconscious (e.g., Davis and Valla 1978:608; Fox 1978a:89; Clutton-Brock 1984:38; Casinos et al. 1986:73). Thus, humanly directed morphological evolution is believed to be operative from the very onset of a domestic relationship.

Its intuitive appeal notwithstanding, it is legitimate to seek a broader understanding of domestic relationships

than is afforded by an anthropocentric perspective. Some investigators, for example Reed (1959, 1984), Scott (1968), Zeuner (1963), and Herre (1970), have focused on domestication as a symbiotic ecological relationship between two species that potentially entails evolutionary consequences for both (see also Rindos 1984). This approach has by no means yielded a uniform outlook. Reed (1959:1636) spoke of domestication in terms of "beneficial mutualism" at about the same time Zeuner (1963:36) was using the term "slavery" as a virtual synonym for "domestication". Nevertheless, both viewed domestication in terms of ecological relationships with evolutionary outcomes, however broad the spectrum of those relationships might be.

This evolutionary perspective entails much more than a difference in descriptive terms. It lends the concept of domestication greater latitude than is possible when it is viewed anthropocentrically. First, and probably most obvious, domestic relationships are not restricted to humans, though this implication itself sometimes generates discomfort even when it is accepted (e.g., Herre 1970:259). Domestic relationships occur among nonhuman animals (Zeuner 1963:36-64) and between plants and nonhuman animals (Rindos 1984:99-112).

Second, an evolutionary perspective forcibly draws attention to the fact that domestic relationships involve

two species, not just one. When viewed anthropocentrically, it is easy to forget that the consequences of human-animal domestic relationships are not restricted to humans. The evolutionary stakes for participating animals are high indeed. One need look no farther than dogs for a dramatic illustration. Dogs now abundantly populate virtually the entire world while their ancestors, wolves, have been extirpated from all but a few remote places. From a Darwinian point of view, taking up residence with humans a few thousand years ago was an awfully smart thing for wolves to do.

Finally, and most importantly for this study, an evolutionary perspective discourages the assumption that early morphological changes associated with domestic relationships must be the direct products of conscious or unconscious human selection for different traits. Every morphological change in an evolving domestic animal does not necessarily occur because it serves some end for humans (cf. Berry 1969). The animals have their own Darwinian ends to serve. It is even possible, as Chaplin (1969:231) pointed out, that some changes may be purely coincidental with the evolution of a domestic relationship.

The foregoing discussion should not be construed as a general indictment of an anthropocentric view of domestication. The relatively recent emergence of human-animal domestic relationships had tremendous impact on

human cultural evolution. The broader view of domestication afforded by an evolutionary perspective does not lessen that impact or call into question the legitimacy of focusing on the human side of the domestication equation. Nor does it negate the obvious fact that most human-animal domestic relationships have resulted in the literal subjugation of the nonhuman participant. A cow, for example, has little input into its own existence.

Nevertheless, it is appropriate to be critical of the frequently employed assumption that morphological changes in a domestic animal must be the product of human selection. Human selection is something to be demonstrated, not assumed. In addition to this criticism, an anthropocentric view is rejected here simply because it is inappropriate given the objectives of this study. This study poses questions about the evolution of dogs, not humans. A broader evolutionary perspective is better suited for dealing with these questions because it fosters greater flexibility in seeking answers without ignoring the fact that dogs are indeed a direct product of a domestic relationship with humans. Domestication is evolution (Rindos 1984:1); it will be investigated as such here.

Evolution, Genes, and Culture

Evolutionary theory is a framework for understanding change as differential persistence of variation (Dunnell

1980:38). Most variation in nonhuman organisms is the product of genetic information, whereas most variation in humans is the product of cultural information. Culture is regarded here as phenotypic information transmitted between organisms behaviorally rather than genetically. In this view culture is not the exclusive domain of humans, but may be found in other social animals (Bonner 1980), albeit in much more limited form. However, there is little question that humans are the only animal in which cultural information has superceded genetic information as the primary agent of evolutionary change.

In genetic systems information encoded in DNA is physically transferred from parents to offspring. Rates of evolutionary change are directly limited by the rate of generational turnover in a species. In cultural systems information flow is not restricted to parents and offspring. It may potentially be passed among any individuals, though there is undoubtedly patterning in the kinds and quantities of information most likely transmitted between different categories of individuals (e.g., parents, siblings, unrelated conspecifics, etc.--see Cavalli-Sforza et al. 1982; Richerson and Boyd 1987). Evolutionary change mediated by cultural information need not be dependent on generational turnover and may take place at an explosive pace relative to genetically mediated evolution.

Variability in genetic systems is affected by

replication and recombination of genetic material. Occasionally a mistake occurs in replication, resulting in a mutation. New variants for any particular trait are produced by mutations. In cultural systems information can be recombined and transmitted throughout an organism's life, and new variation is not dependent on occasional mistakes in genetic replication. In addition, inheritance of cultural information is much less precise than inheritance of genetic information. Culturally transmitted aspects of individual phenotypes are highly malleable. Yet, in spite of the tremendous variability in cultural systems, and the potential for rapid change during a cultural being's lifetime, there is a large degree of heritability in cultural information systems. Expression of culturally derived traits is not simply random, as any anthropologist well knows.

In spite of the distinctive features of cultural information systems, they are in principle subject to Darwinian processes. There is nothing in the basic structure of Darwinian theory to exclude mechanisms of inheritance other than genes (Blute 1979; Dunnell 1980:62). If variation exists, if that variation is heritable, and if different expressions of that variation affect an organisms's capacity to live, thrive, and reproduce successfully, evolution will occur following the Darwinian model (Lewontin 1970:1; Pyke et al. 1977:138;

Dunnell 1980:63; Richerson and Boyd 1987:31).

Wolves entering into a domestic association with humans cannot be simplistically viewed as genetically controlled robots, blindly executing programmed behaviors. Wolves are intelligent social animals whose survival depends not only on genetic endowment, but also on a repertoire of learned skills and behaviors. Sharp (1978) has strongly implied that wolves should be regarded as cultural organisms, while Sullivan (1978:31) refers to ". . . social and cultural traditions of individual packs." In attempting to understand evolutionary changes in animals like wolves, the effects of alterations in behaviorally transmitted information should be considered. If adoption of wolf pups by humans initiated this domestic relationship, as seems likely (see Chapter II), these pups were subject to profound alterations in behaviorally transmitted information. They experienced a very different learning environment than their wild counterparts. The implications of this situation are relevant for understanding the evolutionary divergence of dogs from wolves.

CHAPTER II

BACKGROUND TO THE STUDY OF DOG DOMESTICATION

The previous chapter presented three questions that provide the analytical framework for this study. Several other basic issues were also identified that are addressed more fully in this chapter. These issues include determination of what species was (or were) involved in the ancestry of dogs, when dog domestication occurred, where it occurred, and how it occurred. No attempt is made to be exhaustive in dealing with these issues; rather, the intent is to present an overview that provides a frame of reference for subsequent analysis.

Finally, based on the current state of knowledge regarding these issues, the second portion of this chapter develops some expectations about the nature of morphological changes in the evolution of wolf to dog. These expectations then serve as the point of departure for attacking the central questions posed in Chapter I.

The Ancestry of the Dog

The Wolf as Projenitor

As noted in Chapter I, modern concensus holds that one or more varieties of the wolf, *C. lupus*, gave rise to modern dogs. This is not a simple assertion; over the last century several other members of the genus *Canis* have

been suggested as playing the sole or at least a significant role in the ancestry of the dog. At the head of this list is the golden jackal, Canis aureus, believed by Darwin (1868) to share ancestry with the wolf, and later by Lorenz (1954), who eventually recanted this view (Lorenz 1975). In addition, the problematical Australian dingo, Canis dingo (cf. Macintosh 1975; Newsome et al. 1980), has been implicated (Dahr 1942), as well as the North American coyote (Skaggs 1946). Finally, Fox (1978a:248) has made the suggestion that dogs and wolves share a common ancestor prior to domestication and ". . . the dog was a dog before it was domesticated." This is unsupported paleontologically.

The strong case for the wolf as projenitor is based on several considerations. First, genetic affinity between wolves and dogs is beyond dispute since they are fully capable of interbreeding (Iljin 1941). They are nevertheless legitimately regarded as distinct biological species (cf. Williams 1966:252; Wilson 1975:9; Mayr 1982:270-275) since ecological barriers minimize the occurrence of hybridization unless it is encouraged by humans (cf. Clutton-Brock 1984:203). In any case interfertility between dogs and wolves is insufficient by itself to establish the wolf as projenitor. Jackals apparently are also capable of interbreeding with dogs (Gray 1972:45-46), and coyotes certainly are (Mengel 1971;

Gipson et al. 1974). Interfertility among members of the genus Canis is the rule rather than the exception (cf. Gray 1972:45-51; Evans and Cristensen 1979; Schmitz and Kolenosky 1985). However, additional support for wolf ancestry is provided by biochemical analysis of genetic affinities among canids through utilization of electrophoretic techniques (Simonsen 1976; Wayne and O'Brien 1987; Wayne et al. 1989). These studies consistently demonstrate that at a molecular level the dog is more similar to the wolf than to other members of Canis.

In addition to clear genetic affinity the case for the wolf as ancestor of the dog is built on structural and behavioral grounds. Because large, morphologically generalized dogs are osteologically so similar to wolves, powerful multivariate analytical techniques are sometimes employed in an effort to make taxonomic distinctions, particularly with archaeological materials (e.g., Walker and Frison 1982; Morey 1986; Benecke 1987). Osteological similarities and differences between dogs and wolves, as well as other canids, are treated much more extensively in subsequent chapters.

The social behavior and communication systems of wolves and dogs are so similar that Scott (1950:1019) was led to comment that ". . . the patterns of behavior of dogs in human society are the same as those of wolves in wolf society" (see also Bekoff et al. 1975). Although wolves

exhibit a wide range of variability, they are in general highly social animals (cf. Mech 1970; Peterson 1977), more so than jackals or coyotes (Fox 1971, 1975; Bueler 1973; Clutton-Brock 1981:34). Wolf society is intricately structured in heirarchical fashion, with social relations established and maintained primarily by the vocal, facial, and postural communication of dominance and submission (Schenkel 1967; Mech 1970; Zimen 1975). In fact, the patterns of social behavior in wolf and man are remarkable for their mutual intelligibility (Scott 1950:1019, 1968:257; Clutton-Brock 1977, 1981:34), another factor placing the wolf in the most favorable position for ancestry in terms of compatibility with human society. In addition, the vocalizations of wolves and dogs are similar, while those of jackals are quite different (Lorenz 1975; Clutton-Brock 1984:206). Thus, the case for the wolf as projenitor of the dog is convincing but unverified (Clutton-Brock 1984; S. Davis 1987:132). It is the strongest working hypothesis presently available and is employed as a basic assumption in this study.

Where did Domestication Occur?

While much attention has been bestowed on identification of the ancestral species, widespread agreement that the wolf holds this role has prompted considerable attention to identification of the geographic variant(s) of *C. lupus* responsible. It is widely held that

most dogs are too small to have been derived from the larger, northern varieties of C. lupus. This has led many investigators to advance a case for small Indian or Arabian wolves, Canis lupus pallipes or Canis lupus arabs, as prime candidates for projenitor of the dog (Werth 1944; Zeuner 1963; Lawrence 1967; Epstein 1971; Hemmer 1976; Clutton-Brock 1984). However, the case for these wolves is not advanced to the exclusion of other varieties. S. Olsen (1974, 1985; Olsen and Olsen 1977) argues that the small Chinese wolf, Canis lupus chanco, gave rise to most Asian and North American dogs, the latter arriving in North America with humans by way of the Bering Strait. Bökönyi (1975) presents a case for local in situ domestication of wolves in southeastern Europe at about 8,000 B.P. Clutton-Brock (1984:199, Fig.22.1) graphically illustrates the probability that several subspecies of C. lupus were involved in the ancestry of dogs in different parts of the world.

It is agreed here that a single variant of C. lupus is unlikely to be wholly responsible for the ancestry of domestic dogs. Many dogs may have originated from smaller Eurasian varieties such as C.l. chanco and C.l. pallipes. This author is not convinced, however, that larger northern varieties must be excluded by virtue of their size. Since size reduction is a conspicuous feature of canid domestication this reasoning may be faulty. Even

proponents of the small southern wolves as primary ancestors do not exclude large northern varieties from a role in the ancestry of some dogs (Olsen and Olsen 1977; Clutton-Brock 1984:199).

The point is as follows: it is not clear where canid domestication occurred. It is entirely possible--probable in this author's view--that several variants of C. lupus were involved in different places.

When did Domestication Occur?

Canid remains that predate about 9,000 B.P. and are believed to be domestic dog have been reported from several parts of the world. The most dubious of these claims have been reviewed by S. Olsen (1985) and are not repeated here. However, even some of the more plausible identifications must be regarded with uncertainty.

The specimen most frequently cited as the earliest known trace of a domestic dog is a partial mandible from Palegawra Cave in Iraq, and was reported by Turnbull and Reed (1974). The specimen is associated with deposits that date to about 12,000 B.P. Turnbull and Reed's identification is based primarily on the relatively close spacing of the teeth and its overall small size compared to modern wolves of the region. S. Olsen (1985:72-73) has cautioned that this specimen could come from an atypical wild wolf.

Prior to the discovery of the Palegawra Cave specimen,

North American materials from Jaguar Cave in Idaho were regarded as the oldest known domestic dog remains in the world (Lawrence 1967, 1968). Lawrence (1967:44) originally reported a date of just over 10,000 B.P. associated with these dogs. However, reanalysis of these specimens suggests they are much younger, no more than about 2,000-3,000 years old (cf. Gowlett et al. 1987:145-146). Elsewhere in North America Grayson (1988:23) has reported a skull fragment and two mandibles of domestic dog from Danger Cave in Utah that date between 10,000 and 9,000 B.P. These are presently the oldest known remains of domestic dog in North America.

Davis and Valla (1978) have reported canid remains from Natufian contexts in Israel that date between 11,000 and 12,000 B.P. The lengths of two lower first molars were compared to corresponding lengths from a variety of recent wolves. The Natufian specimens are small compared to recent wolves and, based on this, they are identified as domestic dogs (Davis and Valla 1978:610). However, the Natufian specimens fall close to the lower limits of the wolf groups with the smallest teeth (Davis and Valla 1978:610, Table 1). One specimen (Ein Mallaha) clearly falls within the range of the smallest wolf group (Arabian peninsula wolves). Although Davis and Valla's analysis is strengthened by consideration of Pleistocene-Holocene trends in size reduction among wild <u>Canis</u> in the region,

the identification remains subject to uncertainty.

From Europe, a fragmented cranium from Starr Carr in England, dated at about 9,500 B.P., was identified as domestic dog by Degerbøl (1961). Degerbøl's identification is based primarily on large, overlapping teeth in a very short jaw. The specimen is from an immature individual. S. Olsen (1985:71) insists that at best it should only be tentatively identified as C. familiaris. He goes on to suggest that it might in fact be a tamed wolf pup. Benecke's (1987) recent analysis also casts doubt on the identification of this specimen as domestic dog.

Other early (pre-9,000 B.P.) specimens from Europe identified as dog are reported from Senckenberg (Mertens 1936) and Bonn-Oberkassel (Nobis 1979, 1986) in Germany, and from Döbritz-Kniegrotte in Czechoslovakia (Musil 1974, 1984). Musil's identification of the Czechoslovakian material as domestic dog is explicitly tentative (Musil 1974:47). Nobis (1986) presents a case for domestication with the Bonn-Oberkassel specimens (see also Benecke 1987) based primarily on a short jaw (with several missing premolars) relative to wolves. The specimens, excavated over 70 years ago, are dated at about 14,000 years old. It must be borne in mind that absence of teeth that apparently never erupted (Nobis 1986:370-371) could simply signify an aberrant wild wolf. The Senckenberg specimen from Germany, a complete cranium, is clearly a domestic dog. While its

dating must be viewed with caution (Degerbøl 1961; Bökönyi 1975:167), it is believed to be 9,000-10,000 years old. The Senckenberg dog is used in this study.

It is important to stress that even the tentative identifications reviewed above are based on thorough analyses. The identifications are clearly reasonable. The problem is with the materials themselves in the context of inherent taxonomic difficulties. Fragments of jaws and isolated teeth from 12,000 years ago do not lend themselves to certain identification. Indeed, at 12,000 years ago one must wonder whether a truly valid morphological distinction between dogs and wolves exists. It is agreed here that the evolutionary divergence of dogs from wolves was surely underway by 12,000 years ago. Presently, however, specimens of this purported age remain subject to taxonomic uncertainty. After about 9,000 B.P. morphologically distinct dogs were indisputably in existence (Degerbøl 1961; Grayson 1988); they are increasingly encountered archaeologically after this time. (e.g., Haag 1948; Lawrence 1967:56-57; McMillan 1971; Hill 1972; Harcourt 1974; Brothwell et al. 1979; Higham et al. 1980; J. Olsen 1985).

How did Domestication Occur?

It has been emphasized that the overlapping ecological niches of wolves and human hunter-gatherers during the late Pleistocene ensured contact between the two species (Zeuner

1963; Scott 1968; Clutton-Brock 1980, 1981; S. Olsen 1985). Both were social species that hunted for many of the same prey items. Wolves, as opportunistic scavengers, may have learned to be aware of human hunting activities and to scavenge from human kills. Perhaps humans even learned to do the same with wolves. Wolves and humans were ecological competitors but may also have benefitted each other in some situations.

In western culture wolves are often symbols of evil and as such are highly feared (Lopez 1978). Our folklore and fairly tales abound with evil wolf figures (Fiennes 1976:175-190; Zimen 1978:302-315). This is not necessarily true of hunter-gatherers many thousands of years ago (Fox 1978b:25). Alaskan Eskimos, an example of people who were recently hunter-gatherers and who presently live in the same environment as wolves, express not irrational fear of wolves, but admiration--admiration for their intelligence, their sociality, their prowess as hunters, and the purposiveness and individuality of their behavior (Aghook and Stephenson 1975; Lopez 1978).

The most reasonable scenario for the origins of canid domestication follows the two premises introduced above. First, human hunter-gatherers and wolves had overlapping niches and were accustomed to contact with each other. Second, at least some groups of ancient hunter-gatherers did not share the culturally reinforced aversion to wolves

that characterizes many western industrial societies. Given these premises, we need merely to posit that somewhere, someplace (perhaps more than once), some young wolf pups were found and adopted by humans. Why a given incident of wolf pup adoption occurred many thousands of years ago is a matter of speculation. A reasonable suggestion is frequently made that pet keeping (cf. Serpell 1989) was the motivation behind adoption (e.g., Zeuner 1963:39; Reed 1969, 1984:5; Clutton-Brock 1984:204). However, this question can never be answered empirically and is not pursued further here.

More to the point for this study are the consequences of adoption. Numerous studies have shown that wolf pups taken at an early age and reared by humans are easily tamed and socialized (Fentress 1967; Pulliainen 1967; Woolpy and Ginsburg 1967). According to Scott and Fuller (1965) the most crucial social bonds of a dog or wolf's life are formed when the animal is three to eight weeks old (see also Woolpy and Ginsburg 1967). Wolf pups adopted and socialized by humans during this period will form their primary social bonds with humans. The animals are progressively more difficult to socialize with advancing age, though even adults can be socialized with considerable difficulty. Thus, wolf pups taken very young and reared by humans will form their primary social bonds with members of their human "pack".

This characteristic of social development among wolves provides an efficient mechanism for the integration of wolves into human society. It need not be posited that captured animals had to be tamed as adults or confined to prevent their escape. Remarkable compatability in overall social organization and communication systems, above and beyond other highly social carnivores, made wolves especially well suited for domestic life with humans. Of course, some individuals would not possess the necessary temperment to fit into a social setting with dominant humans. Certainly individual wolves exhibit a wide range of variability in temperment and behavior (Murie 1944:25; Aghook and Stephenson 1975; Sullivan 1978; MacDonald 1987). Only animals predisposed to a submissive temperment or capable of learning a subordinate role to humans would have been tolerated in human society (Clutton-Brock 1981; see also Belyaev and Trut 1975).

In terms of evolutionary implications an adopted wolf's options for achieving genetic representation in future generations were limited. Individuals whose temperment prohibited their successful integration into human society would likely have been disposed of. If an occasional wolf left the human group as an adult, to "return to the wild", it could probably survive but its chances of reproducing successfully would be slim. Wild wolves are unlikely to accept unrelated outsiders into

their pack (cf. Mech 1970:51-56), and breeding opportunities are limited by social regulations within a pack (Peterson 1977:80-85; Jenks and Ginsburg 1987; Schotté and Ginsburg 1987). Thus, for an adopted wolf to contribute to future generations it had to fit into human society and, having been raised by humans, remain there.

With that, the domestic relationship that produced dogs from wolves was underway, However, adoption and rearing of tame wolves does not in and of itself define a new species. The evolutionary implications of this domestic relationship, whose outcome was a new species, Canis familiaris, are explored in the discussion below.

Consequences of the Early Domestic Relationship

Young domestic wolves growing up with humans experienced a dramatic change in lifeway relative to their wild counterparts. It is reasonable to expect that this change entailed immediate developmental consequences for individual wolves, as well as long term evolutionary (genetic) consequences for domestic wolves as a whole. Between developmental and evolutionary processes, the result was morphological changes that allow us to confidently pinpoint the presence of domestic dogs from the archaeological record by early Holocene times. The following discussion emphasizes the consequences of the radically altered learning environment experienced by a

domestic wolf, and explores the roles of individual development and genetic selection.

The Altered Ecological Niche of Early Domestic Wolves

Wild wolves are carnivorous. In most regions presently inhabited by wolves one or two large ungulate species constitute the principal prey items, for example deer in many temperate environments or caribou and moose in arctic or subarctic regions. However, a variety of smaller animals is also occasionally consumed, including mice, rabbits, birds, and so on (Mech 1970; Pulliainen 1975). Wild juvenile wolves also grow up on a diet of animal products. As pups are weaned their diet shifts to regurgitated stomach contents provided by one or both parents (Mech 1970). Eventually the juveniles are taken to kill locations or rendevous sites and eat unprocessed meat. As they mature they begin to accompany adults on hunts and learn the hunting skills necessary for survival.

The early domestic wolf grew up quite differently. Humans, the source of their food, are omnivorous. Human hunter-gatherers were unlikely to provide a young wolf with an optimal diet. Rather, these wolves were probably subject to a diverse array of human food refuse, dominated by plant products and meat scraps, much of which may have been spoiled or simply undesirable to humans. A "finicky" wolf probably stood little chance of survival. It is thus

reasonable to expect that young domestic wolves experienced nutritional stress during their early months.

The survival skills learned by a maturing domestic animal would be fundamentally different from those learned by a wild one. For a domestic wolf, there were no experiences available from which to learn the group hunting skills of wild wolves. Humans simply could not provide that environment. Although some captive wolves learn to kill animals like deer (Mech 1970:138), survival skills reinforced through learning experiences by the early domestic wolf more likely involved scavenging and solicitation of food from humans. These activities would be supplemented by hunting of small animals (e.g. rabbits, rodents, etc.) whose capture did not require the more refined and usually group oriented tactics employed in dispatching a deer or caribou. In short, their altered (omnivorous) diet continued into adulthood. Only individuals who learned to survive under these circumstances could contribute to future generations.

These altered circumstances might leave their mark on a domestic wolf, especially during early months of normally rapid growth. Captive wolves provide a crude model for the consequences of this situation (cf. Epstein 1971:83-86; Stockhaus 1965; Clutton-Brock 1970:305). Domestic wolves might exhibit smaller adult sizes and shortening of the facial region of the cranium, with their large teeth

consequently crowded into shorter jaws. The reader who is familiar with the subject of morphological changes associated with canid domestication will recognize that these traits are widely held as the most conspicuous and consistent general differences between dogs and wolves (Zeuner 1963; Lawrence 1967; Clutton-Brock 1970, 1981; Epstein 1971; Bökönyi 1975; S. Olsen 1985). As Clutton-Brock (1984) and Bökönyi (1975) have noted, the large teeth apparently became reduced in size as dog evolution proceeded during the Holocene.

It would thus appear that basic morphological divergence between dogs and wolves is efficiently explained on purely developmental grounds. The problem is that the basic traits involved--head shape, tooth size, body size--are clearly inherited in modern dogs (Degerbøl 1961:41; Stockhaus 1965; Lawrence 1967; Epstein 1971:86; see also the breeding experiments of Stockard 1944). This is not to suggest that early domestic wolves did not experience altered development or that the changes in question did not manifest themselves in such animals. It is simply argued that nongenetically altered development is insufficient to explain evolutionary divergence of dogs from wolves.

While individually altered development might result in reduced adult body size, there are sound reasons for expecting smaller body size to have been a target of selection under conditions of abrupt and dramatic dietary

change. No single aspect of structure and physiology is more important than sheer body size in shaping an organism's niche (Peters 1983; Calder 1984; Werner and Gilliam 1984; LaBarbera 1986). In carnivores as a group there is a clear positive correlation between adult body size and prey size (Rosenweig 1966; Gittleman 1985). Radinsky (1982) suggests that variation in body size, reflecting partitioning of prey resources, was an important factor in the late Eocene radiation of modern carnivore families. Among modern wolves geographic variations in body size have been correlated with variation in primary prey size (Kolenosky and Standfield 1975). Schmitz and Lavigne (1987) have explicitly related recent changes in body size among Canis in Ontario with shifts in modal prey size.

The parallel being advanced here may seem sloppy. Early domestic wolves experienced a dietary shift from carnivory to omnivory. Nevertheless, this shift undoubtedly entailed a dramatic decrease in "package" size (Rosenweig 1966:603) of foods to be competed for, probably coupled with an overall decrease of bulk available. Smaller animals, with reduced caloric requirements, would have been at a distinct advantage under competition for such resources. In turn, morphological changes may simply be allometric consequences of size reduction (Lumer 1940; Epstein 1971; Wayne 1986a). This issue is explored in

detail in this study.

Beyond the pressure to learn a different set of surivial skills related to subsistence, early domestic wolves had to fit into human society. Domestic animals could not violate a subordinate position to humans in this new social heirarchy. Selection for animals compatible with human society may have had significant physiological ramifications. For example, in a study of captive silver foxes (Vulpes fulvus) Belyaev and Trut (1975) found that selection for submissiveness and docility was correlated with significant alterations in seasonal periodicity of breeding cycles within a few generations. Overall, there are sound reasons for expecting selection for major alterations in reproductive strategy under conditions of domestication, a topic explored below.

Dogs as Colonizers: Evolutionary Implications

Lewontin (1965:78) defined colonization as ". . . the establishment of a population of a species in a geographical or ecological space not occupied by that species." This definition clearly applies to early domestic dogs. As Scott (1968) pointed out, dogs may be viewed as a species that entered a new habitat, rapidly spreading to fill a new ecological niche. They were colonizers, ecologically poised for rapid population growth.

Discussions of ecological colonization and population

growth are often linked in recent literature with the concepts of r and K selection. As originally formulated by MacArthur and Wilson (1967), r referred to selection for high population growth under uncrowded conditions while K referred to selection for competetive ability in crowded populations. However, as Parry (1981) has noted, the concept was rapidly expanded (Gadgil and Bossert 1970; Pianka 1970; Gadgil and Solbrig 1972; Wilbur et al. 1974; Southwood et al. 1974). In its expanded form the r/K dichotomy predicts an association of life history traits into two groups: "r-selected" organisms will be characterized by early maturity, large numbers of offspring, semelparity, little or no parental care, and large reproductive effort. On the other hand, "K-selected" organisms will have delayed reproduction, small numbers of young, iteroparity, parental care, and small reproductive effort (Parry 1981:260). The utility of this expanded concept has been intensively scrutinized and many criticisms have been raised (Stearns 1976, 1977; Parry 1981).

This author has little interest in debating the overall merits or liabilities of the expanded concept of r and K. The goal here is simply to provide the basis for linking some important life history traits with general ecological parameters, an endeavor that cannot reasonably be uncoupled from the literature on r and K. The reader

familiar with this literature will have no trouble grasping the contrast that is portrayed, with wild wolves as K-selected organisms, evolving as r-strategists when associated domestically with humans. The development offered below is expanded and modified from a previous discussion (Morey 1987).

Wolf populations are regulated primarily through adjustments in rate of reproduction and by juvenile mortality (Pimlott 1975:284). Fall is a crucial time for young wolves and mortality is often related to malnutrition, particularly in juveniles (Van Ballenberghe and Mech 1975:57; Mech 1977). According to Rausch (1969:119) in Alaska pups may make up as much as 60 per cent of a wolf population at any given time. Wolf mortality (excluding human "predation") is often closely linked to the availability of primary food resources and may thus be characterized as density dependent, especially since predation (again excluding humans) is insignificant (cf. Parry 1981). Wolves generally exist in a close balance with their primary resources.

The hallmark of a colonizing episode is the absence of density dependent mortality (Lewontin 1965:78). Colonization entails rapid population growth. Well before MacArthur and Wilson (1967) developed the r/K dichotomy it was pointed out that selection in rapidly growing populations will lower the age at first reproduction (Cole

1954; Lewontin 1965), a point that has been reasserted several times (Meats 1971; Giesel 1976; Stearns 1976; Gould 1977:326). As Lewontin (1965) put it, small absolute alterations in developmental rates function approximately the same as large increases in fertility.

Gould's (1977) influential work, Ontogeny and Phylogeny, presents an extended argument for heterochrony (evolutionary changes in developmental timing) as a major force in affecting evolutionary change (see also Alberch et al. 1979; McKinney 1988a; McNamara 1988). The point summarized in the preceding paragraph is a primary building block in the foundation of an important hypothesis put forward by Gould (1977:293): progenesis, the accelerated onset of sexual maturity, will be associated with r-selected regimes, while neoteny, the general retardation of somatic growth, will be associated with K-selected regimes (see McNamara 1986 for a recent detailed presentation of the terminology of heterochrony). Gould detailed several examples in support of this hypothesis and, in spite of recent unpopularity of the r/K dichotomy, cautiously advanced empirical support can still be found (e.g., McKinney 1986). This hypothesis leads directly to the prediction of progenesis in the early evolution of the dog. It should be noted that the concept of progenesis has recently been expanded in a manner that will be important later in this study. For the present discussion, however,

it is used as outlined by Gould in 1977: truncation of growth period through accelerated onset of maturity.

Wild wolves reach maturity at about two years of age (Murie 1944; Young and Goldman 1944; Novikov 1962; Mech 1970; Pulliainen 1975). In contrast, modern dogs may breed at six months to a year (Scott and Fuller 1965; Fox 1978a; Clutton-Brock 1984). It would thus appear that modern dogs are progenetic with respect to wolves. Two considerations compromise the apparently neat correspondence of prediction and result with this progenesis hypothesis. First, the timing of onset of puberty in dogs is more complicated than portrayed above. Six to twelve months or slightly later brackets the onset of puberty in most dogs, but in large breeds particularly this may not occur until well into the second year (Hancock and Rowlands 1949; Andersen and Wooten 1959; Johnston et al. 1982). Second, even if one accepts that modern dogs are progenetic with respect to wolves, this does not establish the same for early dogs, several thousand years ago (Price 1984:22). Rapid generational turnover could be an artifact of modern selective breeding.

Thus, the morphological consequences of progenesis provide a more useful avenue of investigation for this study. As outlined by Gould (1977) the basis of progenetically caused morphological change is the association between onset of maturity and truncation of

somatic growth. Progenesis is expected to result in size reduction and paedomorphosis, the latter referring to juvenilized morphology in the adult stage of an organism with respect to its ancestors (Gould 1977:255). Size reduction has already been noted as a frequently observed correlate of canid domestication. Moreover, it has been observed that adult morphology in many modern dogs, especially in the cranium, appears to reflect arrested development or juvenilization (Hilzheimer 1932; Zeuner 1963; Epstein 1971; Clutton-Brock 1984). In descriptive terms at least, shortening of the rostrum in particular appears to represent a juvenilized feature.

If progenesis alone underlies size reduction and juvenilized morphology in dogs, there should be a tight correlation between adult body size and age at onset of puberty. Houpt and Wolski (1982:133) note that there is no strict correlation between adult size and age at puberty, but smaller breeds generally attain puberty earlier than larger breeds (see also Christiansen 1984:5). In addition, large breeds tend to grow for a longer period than small breeds (Kirkwood 1985:102; Wayne 1986a, 1986b).

Despite the complications noted above it is clear that heterochrony, and progenesis in particular, warrants investigation as an evolutionary process with morphological consequences in canid domestication. There are additional complications in the analysis of heterochrony and these

will be dealt with at appropriate points during analysis. Recent studies of growth and allometry in dogs, also dealt with later, will yield additional insights into the evolution of the dog.

To sum, early domestic wolves experienced a radically altered environment relative to their wild counterparts. Some individuals had the necessary genetic endowment for integration into human society and a capability of learning vastly different survival skills. Only these individuals had an opportunity to reproduce and pass those genes and learned behaviors to subsequent generations. Individual development was undoubtedly impacted under these circumstances, but it cannot explain evolutionary divergence of dogs from wolves. The radically new niche being filled by early domestic wolves would have placed a selective premium on reduced body size and altered reproductive strategy. This study seeks to determine if these processes could account for morphological changes seen in the evolution of the dog.

CHAPTER III

OBJECTIVES AND METHODS

To address questions concerning the morphological evolution of dogs, both bivariate and multivariate analyses are employed. Bivariate analyses explore craniometric scaling relationships among different groups of canids. The objective is to document relationships between variation in size and variation in morphology among the species, and to determine the degree to which the prehistoric dogs are consistent with those relationships. Adult static variation in size is analyzed separately from variation due to growth. By beginning with a bivariate approach, specific components of morphological variation can be isolated and assessed (Wayne 1986a). To allow detailed analysis a small set of cranial and dental measurements is used (see Chapter IV). Multivariate analysis is then used to assess overall structural similarity between adults of different species and juvenile wolves. The ultimate objective is to determine if heterochronic processes can account for morphological variation in early dogs.

This study faces methodological and theoretical problems, exacerbated by the fact that ontogenetic data are unavailable for the dog groups used here. The remainder of this chapter presents description of the techniques of

analysis, explanation of their use, discussion of problems of interpretation, and a selective summary of relevant previous allometric investigations involving osteometric data from domestic dogs or wild canids.

Bivariate Analysis

This study deals with questions about allometry, the study of size and its consequences (Gould 1966). The most common approach to bivariate allometry follows the pioneering work of Huxley (1932), particularly his development of the equation

$$Y = bX^a$$

where Y and X are biological growth variables and b and a are constants. This power curve, the equation of allometry (Laird 1965; Gould 1966), has been applied to a broad range of biological growth phenomena (e.g., Cock 1966; Gould 1966, 1975a, 1975b; Peters 1983; LaBarbera 1986, and references therein). In practice, the X and Y variables are usually logarithmically transformed to facilitate data manipulation and interpretation, allowing a linear equation of the form:

$$\text{Log}Y = a(\text{Log}X) + \text{Log}b$$

Here, a is the slope coefficient and b is the Y-intercept of the regression equation.

Although the widespread and often uncritical use of the power curve has occasioned criticism (e.g., Smith 1980), it has several things to recommend it for this study. Gould (1966) pointed out that the power curve may not be the best or even the simplest model for describing scaling relationships in any specific context. Rather, the advantage of the power curve is its interpretability and broad applicability to a wide range of biological phenomena. In this study selection of a single form of equation is essential because the objective is comparison of scaling relationships between groups. Thus, the power curve is used here with variables transformed to base 10 logarithms.

Kinds of Data

Cock (1966:135-137) identifies three basic kinds of data for allometric studies: longitudinal, cross-sectional, and static. Longitudinal data are comprised of multiple observations on single individuals at different stages during their ontogeny. Longitudinal data are the best and the most difficult to obtain. They are unavailable for this study.

Cross-sectional data consist of single observations on individuals of different stages of growth in a population sample. Hence, the investigator cannot truly follow ontogeny of individuals, but ontogenetic development can reasonably be approximated. In this study limited cross-

sectional data are available from two species of wild canids, C. lupus and C. rufus.

Static data consist of observations on individuals at a single stage of development, usually adults. From necessity much of this study treats static data. At certain points in analysis comparisons involve adult and juvenile series.

Comparison of Regression Coefficients

For a given bivariate analysis with two or more groups, the first question to be asked is whether or not the regression slopes are equal. If the null hypothesis of homogeneity of slopes cannot be rejected, one may then ask if the regression lines fall at the same elevation. When least squares regression is used (see below) these two analytical steps comprise analysis of covariance (Tatsuoka 1971:40-50; Sokal and Rohlf 1981:509-530). Comparison of slopes and elevations, whether accomplished formally or subjectively, is the core of all studies of bivariate allometry.

Several situations that may result when two groups are compared are illustrated on Figure 1 (see Tatsuoka 1971:41 and Sokal and Rohlf 1981:523 for similar illustrations and discussion). Let it be assumed that the plots on Figure 1 represent static data from two closely related species. Variables X and Y are two measurements, perhaps skull length (X) and palate length (Y).

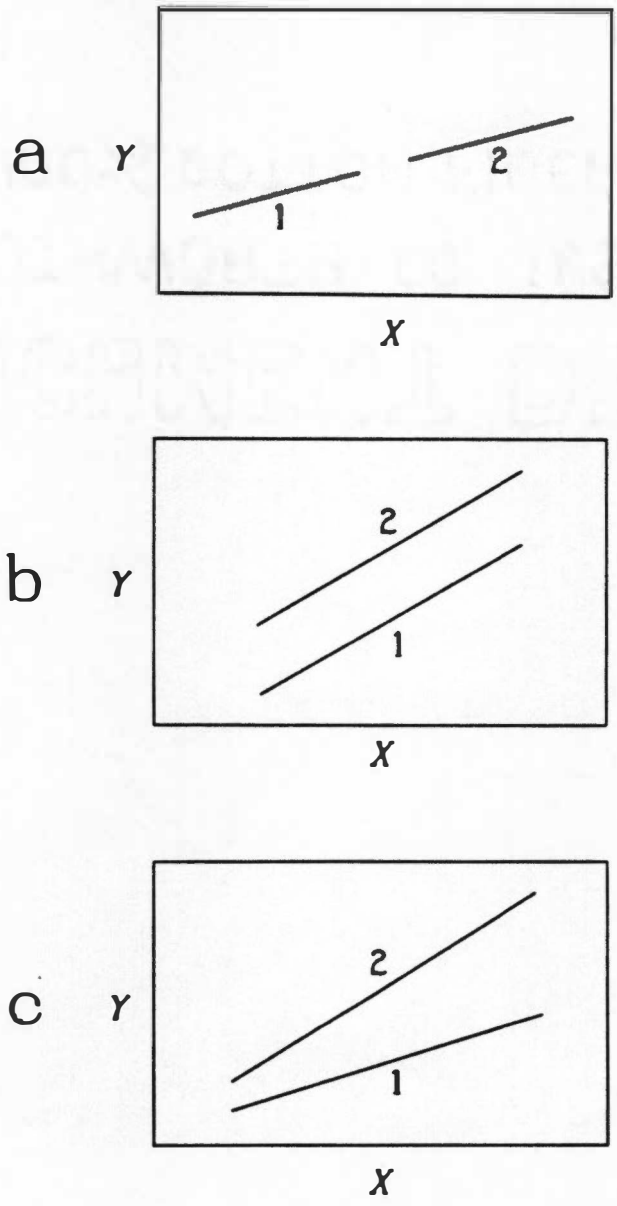


Figure 1. Hypothetical bivariate plots showing different relationships between regression lines. 3a: equal slopes and elevations; 3b: equal slopes, unequal elevations; 3c: unequal slopes, unequal elevations.

On Figure 1a the slopes of the two regressions are equal and they share the same elevation. If the slope is isometric (equal to 1) the two variables are geometrically proportional at all sizes, across both species. If the slope is allometric (unequal to 1), the two species will exhibit proportional differences at different sizes. The nature of these differences will depend on whether the scaling relationship is positively allometric (slope coefficient greater than 1) or negatively allometric (slope coefficient less than 1). Statistically, a single regression line may be used to characterize both groups.

The situation in Figure 1b is referred to as transposition (White and Gould 1965). The slopes of the regressions are equal but the lines exhibit different elevations. Transpositions without slope differences can neatly describe shape differences where ranges on the X variable overlap. At a common skull length (X), species 1 has a longer palate (Y) than species 2. Within each species the scaling relationship is the same, but at different elevations.

In Figure 1c the slopes are unequal, a circumstance that confounds assessment of transposition. At the smallest sizes both species exhibit a similar relationship between the two variables. At larger sizes species 2 probably has a significantly longer palate (Y) than species 1, in relation to skull length (X). Evaluation of

transposition in situations involving unequal slopes must often employ subjective judgement and can only be done on a case by case basis.

Solving the Allometric Equation

The basic equation of allometry may be solved by one of several criteria, each producing different results. Because considerable debate exists over the optimal form of solution, discussion of this problem is warranted.

Model I, or least squares, regressions assume error only with respect to the Y variable. Minimized deviations from the regression line are measured as squared vertical distances. Model II regressions assume error with respect to both variables. The minimization criterion solves for perpindicular deviations from the regression line (major axis), or areas of triangles bounded by the regression line and lines projected from data points to the regression line, parallel to the X and Y axes (reduced major axis). Discussions and illustrations of the differences between these two basic approaches can be found in J. Davis (1973:200-204), Sokal and Rohlf (1981), Harvey and Mace (1982) and Rayner (1985).

It has been argued that least squares regression is poorly suited for allometric analysis if both variables are measured with error and there is no reason to assign causal priority (i.e. "dependent" versus "independent" status) to one over the other (Gould 1966, 1975a; Jungers 1979;

Harvey and Mace 1982; Rayner 1985; LaBarbera 1986; McKinney 1988b). Because the least squares solution treats variation only in one variable, slope estimates are shallower than Model II solutions. Thus, least squares may be inappropriate for determining structural relationships between variables or comparing coefficients to theoretically or empirically expected scaling coefficients.

Many investigators have continued to use least squares regression in allometric analyses (e.g., Wolpoff 1982; Leigh 1986; Wayne 1986a, 1986b; Shea and Gomez 1988). Wayne (1986a) explicitly defined independent and dependent variables for his canid craniometric study, thereby justifying a least squares approach (see also Wayne 1986b). Shea and Gomez (1988:120) argue that use of least squares regression is justifiable when one is not attempting to assess congruence between obtained and theoretically predicted slope values. Wolpoff (1982) found that least squares solutions consistently predicted canine size from molar size among African apes more accurately than reduced major axis solutions. At a theoretical level Lande (1979, 1985) argues, based on a genetic model for static allometry, that the least squares solution is more informative, especially in situations where phenotypic correlations are low. Wolpoff (1985:295) has asserted that Lande's model is a powerful argument for preferring least squares regression over other approaches.

One reason least squares regression is commonly employed is that the model II approaches have their own problems (Sokal and Rohlf 1981:547-551). For example, when the reduced major axis approach is used slopes are meaningless if correlations are low (Jolicoeur 1975a; Gould 1975b; Seim and Sæther 1983; Rayner 1985). In general, the least squares approach is appropriate when causal relationships between variables are known, when correlations may be low, when prediction is the analytical goal, or when relative patterns of scaling between groups are emphasized. When correlations between variables approach unity the choice of approach is largely inconsequential (Seim and Sæther 1983; Rayner 1985; LaBarbera 1986).

In this study reduced major axis slopes are reported alongside least squares slopes, as suggested by LaBarbera (1986). However, all tests of significance and comparisons between groups are based on least squares coefficients. This study does not seek to evaluate obtained coefficients against theoretical expectations (cf. Shea and Gomez 1988). Rather, relative patterns of scaling are emphasized (cf. Wayne 1986a). Following Wayne (1986a), a skull length dimension, condylobasal length (CL--see Chapter IV),) is used as the independent variable in all analyses. This measurement provides the best single characterization of skull size, and other cranial dimensions are modeled to

vary around this dimension. CL cannot be considered an absolute substitute for body size (Stockhaus 1965). However, there is no question that animals with larger skulls (e.g., wolves) have larger bodies than animals with smaller skulls (e.g., dogs or jackals--cf. Wayne 1986a:261, 1986c:399). Radinsky (1984) suggests that a total skull length measure is an appropriate standard for comparison when the goal of analysis is to explore overall differences in skull shape.

Interpretive Problems in Bivariate Allometry

Historically, much work in bivariate allometry has assumed that patterns of static allometry among adults of a species will mirror relative growth, or patterns of ontogenetic allometry, in the same species (see Shea 1981 and Cheverud 1982, and examples cited therein). Unfortunately, there is no theoretical justification for this assumption (Cock 1966; Shea 1981; Cheverud 1982). Static allometry will mirror growth only when there is low variation in individual ontogenetic slopes and intercepts relative to the length of ontogenetic vectors (Cheverud 1982:140); or, in simpler English, when ". . . there is very little individual variation in growth patterns . . . and smaller adults resemble arrested ontogenetic stages of larger adults" (Shea 1981:192). Correspondence between static and ontogenetic allometry has been documented in some contexts (e.g., Freedman 1962), but found lacking in

other empirical studies (e.g., Shea 1981; Cheverud 1982). Thus, this assumption can only be used when empirically justified.

The fallacy of making such an assumption is illustrated on Figure 2. Figure 2a depicts hypothetical adult static regression lines from a bivariate plot of two linear measurements in two closely related species. The slopes and elevations of the regression lines are the same. Assuming equivalence of static and ontogenetic allometry, one would argue that the species exhibit ontogenetic scaling. In other words, species 2 has a longer growth trajectory than species 1, but the slope of the trajectory is the same for both species (see Shea 1981, 1983, and 1985a for discussions of ontogenetic scaling).

Hypothetical individual ontogenetic vectors for each species show how such an inference can be grossly incorrect. There is no overlap in the ontogenetic trajectories for individuals of different species. Hence, the ontogenetic regressions will have different slopes. A single regression line is adequate for predicting values of $\underline{Y}$ from $\underline{X}$ with adults, but the growth trajectories producing those adult values cannot be inferred from static data.

Figure 2b illustrates a different situation. The adult static regression lines exhibit different slopes and elevations. Under the assumption of equivalence of static and ontogenetic allometry, one would infer that the two

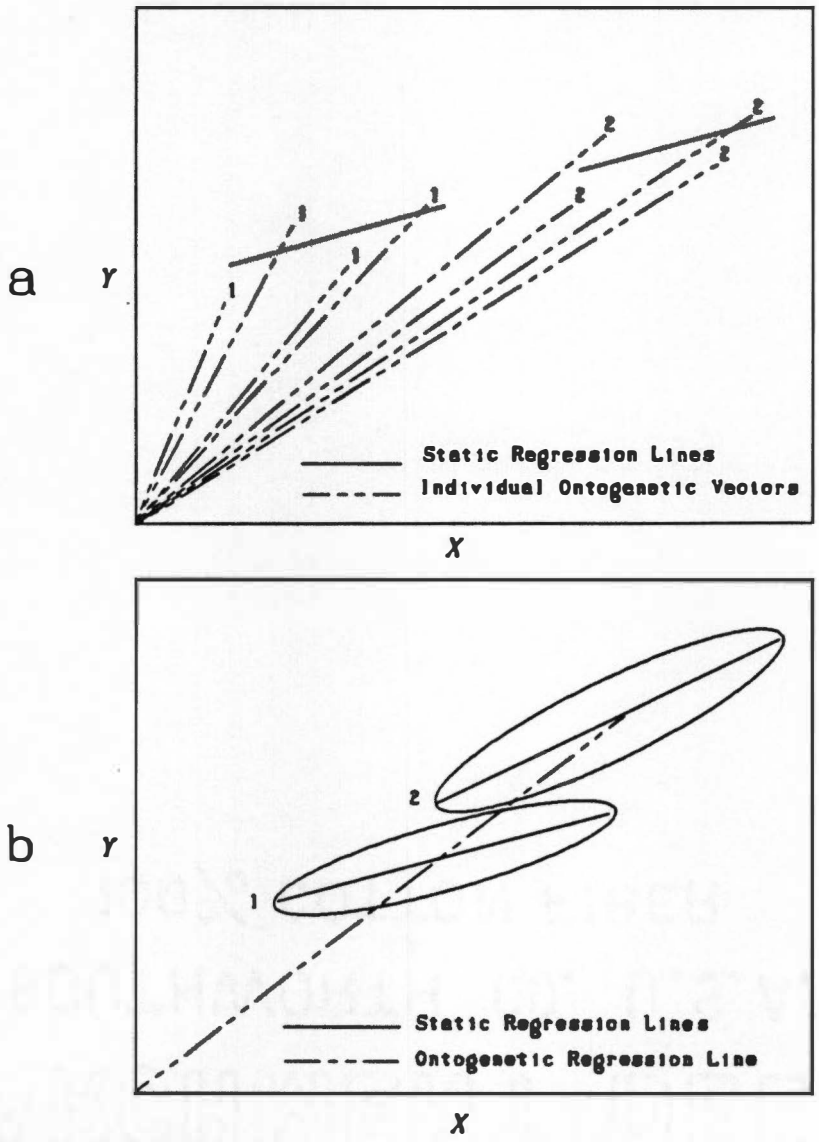


Figure 2. Hypothetical regressions showing possible relationships between ontogenetic and static allometry of two groups. X and Y are linear measurements. 4a: Individual ontogenetic vectors termininating in adult data points (numbers). Despite equal static slopes and elevations the groups are not ontogenetically scaled. 4b: Shared ontogenetic regression line for two groups (numbers) reaching different adult sizes and patterns of static variation (ellipses). The groups are ontogenetically scaled.

species do not exhibit the same growth trajectory. However, a single ontogenetic regression line describes the growth trajectory of both groups. They are ontogenetically scaled. Because static allometry does not necessarily mirror ontogenetic allometry, two groups with divergent patterns of static variation may share the same general growth trajectory.

Continuing with Figure 2b, if species 1 is known to be an evolutionary descendent of species 2, it can be described as progenetic (Gould 1977; MaNamara 1986; McKinney 1988b). Species 1 exhibits truncated development relative to species 2. This, in turn, brings up another interpretive problem. It is no accident that Figure 2b (as well as Figure 2a) does not express or imply a time variable. It is unknown what the growth rates of the two species are. Growth rates cannot be inferred from such allometric plots, and size cannot be assumed to be a valid proxy for time (Shea 1983, 1988; Jones 1988; McKinney 1988b).

If growth rates between the two species are known to be the same, one could infer "time progenesis" (cf. McKinney 1988b), or "time hypomorphosis" (Shea 1983). Species 1 reaches maturity sooner than species 2, but growth rates are unchanged. This corresponds to progenesis as outlined by Gould (1977). Alternatively, if species 1 exhibits a slower growth rate than species 2, one could

infer "rate progenesis" (McKinney 1988b) or "rate hypomorphisis" (Shea 1983). Both species may mature in approximately the same length of time, but species 1 grows more slowly. In the absence of growth rate information, McKinney (1988b) has suggested that heterochronic inferences drawn from allometric plots be labeled as just that. Thus, in the present example, species 1 exhibits "allometric progenesis".

The vexing problem of generating heterochronic inferences from allometric data without knowledge of growth rates is a central concern in the study of heterchrony, and will likely remain so for some time (cf. Gould 1988:4).

An Interpretive Framework for Bivariate Allometry

With problems associated with bivariate allometry in mind, a simplistic interpretive framework for this study is presented below. This framework is intended only as a starting point to guide analysis and interpretation, and to focus discussion.

Shea (1981:180-181) argues that any assertion that a shape difference between two species is an allometric consequence of size differences can be vacuous (see also Gould 1966). An analytical distinction must be drawn between kinds of size-correlated change. Size-related changes involve ". . . interspecific shape differences that mirror those between young and adults of the larger

species" (Shea 1981:181). Size-required changes are those that ". . . simply obey biomechanical laws of size required shape alteration" (Shea 1981:181).

Accordingly, morphological patterning resulting from broad, consistent allometric trends between related taxa of differing size suggest size-required changes. Although such patterning cannot be used to argue that only size selection is involved (Cheverud 1982), it is consistent with an hypothesis that morphological patterning is closely linked with size differentiation. Deviations from such a trend may imply size-related changes via ontogenetic scaling (cf. Shea 1981, 1985a, 1988; Gould 1975b), or selection for functionally altered "novel" morphology, presumably requiring greater genetic alterations (cf. Gould 1977; Shea 1985a, 1988). These two basic alternatives--size-required versus size-related change--provide a logical starting point for examining the morphological divergence of dogs from wolves. The following discussions revolve around Figure 3.

Static Allometry

Figure 3a is relevant to the analysis of static allometry presented in Chapter V. In Figure 3a hypothetical regressions from adult static data from five groups are presented. X is a linear dimension that best summarizes size, perhaps skull length, while Y is another cranial dimension, perhaps palatal length.

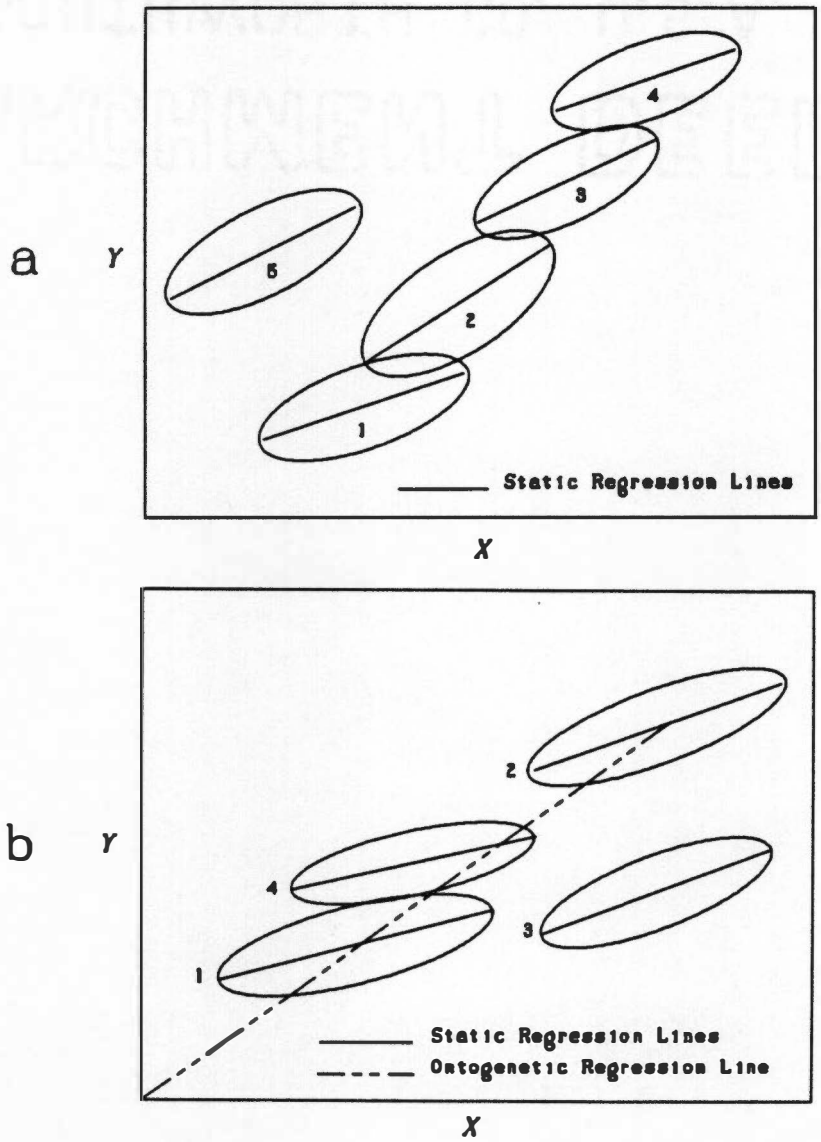


Figure 3. Hypothetical regressions for different groups (numbers) on two linear measurements (X and Y). Ellipses are range of variation around static regression lines. 5a: Static regressions for five groups. Group 5 deviates from a size correlated trend shown by groups 1 through 4. 5b: Static regressions for four groups, and ontogenetic regression for group 2. Group 1 is ontogenetically scaled with group 2, group 4 probably is not, and group 3 definitely is not.

Groups 1 through 4 exhibit a discernable statistical pattern of variation correlated with size differentiation. Group two is transposed above group 1, group 3 above group 2, and group 4 above group 3. This pattern is cause for suspicion that morphological variability between these groups is "size-required". If the pattern holds for other bivariate relationships, this hypothesis is strengthened.

Group 5 is not consistent with the pattern discussed above. Given the pattern among groups 1 through 4, one would expect the regression line describing group 5 to be transposed below group 1. Instead, its elevation is nearest groups 2 and 3. This causes suspicion that some factor other than simple allometric scaling has been most important in creating the morphology of this group, especially if its divergent location is consistent on other bivariate plots.

Several methodological precautions are in order. First, relative locations of regression line elevations are not necessarily an accurate guide to morphology, except where individuals from different groups share a common value of X. Consider Figure 3a again. From the pattern of downward transposition at smaller sizes it is tempting to interpret proportionally shorter palates (Y) at smaller sizes. However, an overall regression of groups 1 through 4 might yield a perfectly isometric slope of 1. This pooled regression, which would pass close to the mean value

of $\underline{X}$ for each group, would accurately reflect an overall morphological trend of isometric change. The morphological relationship between two individuals of any group will always depend on the slope of the line connecting them. Thus, average sized individuals from different groups will exhibit similar proportions.

This characteristic of the individual group scaling patterns does not diminish the utility of exploring patterns of static variation. Accurate identification of deviations from broad allometric trends is a primary goal of this phase of analysis. Pooled regressions describe basic morphological trends, while intergroup patterning in static variation allows identification of deviations from those trends.

As a second precaution, it should be noted that the regression approach used can effect the results of analysis. A pattern of downward transposition between groups generated from least squares coefficients could appear as identical elevations or even transposition in the opposite direction using a model II regression (Harvey and Mace 1982:357). However, this analysis emphasizes relative rather than absolute patterns of scaling. Since all regression coefficients are generated by the same criterion, relative patterning can be assessed.

Finally, it must be emphasized that analysis of static allometry does not concern growth. Again assuming

homogeneity of slopes, both statistical transposition and morphological differences are easily documented between groups like 1 and 5 on Figure 3a. They exhibit a widely overlapping range of variation on X (skull length), and group five clearly has higher values on Y (longer palates).

Groups with non-overlapping ranges of variation on X (like 1 and 4) are trickier. In this situation what is statistically meaningful may not be meaningful in terms of biological growth. When analysis of covariance is used to test for elevation differences, the covariate variable, X, is adjusted to a common mean value for both groups (cf. Tatsuoka 1971:40-48). The resulting predicted values of Y, which form the basis for this test, are generated by utilizing the common slope from both groups. The effect is to move both groups to a common point on the the X axis, with positions on the Y axis shifted according to the slope gradient defined by the pattern of static variation. Group 1 gets "bigger", while group 4 "shrinks". Biologically, size can only be changed in individuals through growth. The true effect of increased or decreased size cannot be gauged by the static allometry coefficient, but only by an appropriate ontogenetic allometry coefficient.

A conclusion of transposition with groups like 1 and 4 is not incorrect; it is simply not a meaningful conclusion about growth unless static and ontogenetic allometry are the same. Rather, it is a meaningful conclusion about

relative locations of regression lines generated from static data. Thus, analysis of static allometry focuses on patterns of variation rather than unwarranted inferences about the hypothetical consequences of growth.

Ontogenetic Allometry

The objective of ontogenetic analysis presented in Chapter VI is to determine whether or not patterns of static variation in domestic dogs are consistent with a hypothesis of ontogenetic scaling with wolves. Ideally, ontogenetic data from both groups would be utilized. In the absence of ontogenetic data from one group (the dogs in this study), it is imperative that ontogenetic data be available from one species (Shea 1981:181).

Figure 3b corresponds to the analysis of ontogenetic allometry in this study. Here, hypothetical adult static regressions from four groups are illustrated, along with the ontogenetic regression for group 2. The variables X and Y are the same as those for Figure 3a. Note that the slope of the static regression for group 2 does not correspond to the slope of its ontogenetic regression (though it could). This ontogenetic regression passes squarely through the range of static variation exhibited by group 1. If group 1 is known on other grounds to be an evolutionary descendent of group 2, this pattern could be construed as support for the hypothesis of progenetic heterochrony (cf. Gould 1977; McKinney 1988b). Groups 1

and 2 may exhibit ontogenetic scaling, with smaller size and altered morphology in group 1 a consequence of truncated development. If other bivariate plots exhibit a similar pattern, the hypothesis is strengthened.

Groups 3 and 4 exhibit a different situation. Let it be assumed that these species are also known to be evolutionary descendents of group 2. Group 3 is well removed from the group 2 ontogenetic regression. It is unlikely to be ontogenetically scaled with group 2. Morphological change in this group is probably the result of some other factor.

Group 4 is more problematical. The group 2 ontogenetic regression passes through its range of variation, but not centrally. It is tempting to read similarity into this pattern, but caution is in order. If the data are well controlled an hypothesis of ontogenetic scaling is strongly supported only when an ontogenetic regression line passes squarely through the range of static variation of another group. In practice, determining how close an ontogenetic regression line comes to the central portion of another groups's range of static variation is subjective, unless the static and ontogentic regression slopes are the same. If the two slopes are the same, analysis of covariance can be used to test for elevation differences. If elevations do not differ the hypothesis of ontogenetic scaling is strengthened.

If the slopes are not the same, subjective evaluation is used. In any case, a consistent pattern involving several bivariate relationships must obtain before the hypothesis can be considered strengthened or weakened. If group 1 exhibits the relationship to group 2 shown on Figure 3b (page 53) but shows a different pattern on other bivariate plots, perhaps like group 3, the hypothesis is not strongly supported.

Multivariate Analysis

The advantage of multivariate techniques in morphometric studies is that information from several variables can be analyzed simultaneously (Oxnard 1978; Shea 1985b:369). The disadvantage is that specific components of variation become more difficult to isolate (Wayne 1986a). For this reason, bivariate analysis precedes multivariate analysis in this study. With specific components of variation among dogs and wild canids isolated and assessed, multivariate analysis is used to augment these results by assessing overall patterns of morphological variability.

Following Jolicoeur's (1963) development of a multivariate generalization of bivariate allometry, principal components analysis is commonly employed in allometric studies (e.g., Davies and Brown 1972; Cheverud 1982; Shea 1985b; Tissot 1988). A closely related

technique, discriminant function analysis (cf. Tatsuoka 1971:157-216; Morrison 1974; Klecka 1980), can also be informative and is used here. It has, for example, been successfully employed in studies of canid taxonomy and geographic variation (e.g., Jolicoeur 1959; Lawrence and Bossert 1967; Nowak 1979; Morey 1986). In allometric studies Wayne (1986a, 1986b, 1986c) has utilized discriminant analysis to investigate morphological variation and evolutionary relationships among canids.

The advantage of discriminant analysis is that different groups are predefined by the investigator, and variation between groups rather than within groups is maximized (Wayne 1986a, 1986b). A series of linear functions is computed that maximally separates those groups in multivariate space. The discriminant functions can then be used to classify individuals into a group on the basis of their proximity to different group centroids. This, coupled with multivariate distances, allows the investigator to assess the success of the discriminant functions and to gauge intergroup distances. In general, distances between groups on discriminant axes should reflect evolutionary distances (Wayne 1986a).

In this study discriminant analysis is used to assess overall patterns of morphological variability between canid groups. First, exploratory analysis is conducted for adult groups utilizing raw values on all variables (i.e., not log

transformed). Logarithmic transformation does not improve results or enhance interpretability (Corruccini 1987:289-303). Discriminant analysis is then conducted on adult groups using indexed data. The measurement CL (see Chapter IV) is used as the standard, and remaining cranial variables are expressed as a proportion of this measurement. This is appropriate because other cranial variables are analyzed in terms of their relationship to CL in the bivariate analysis. Finally, indexed data are used to compare juveniles with adult groups. If dogs are progenetic, their morphology should be most similar to juvenile wolves.

Considerable debate has been generated concerning undesirable mathematical properties of ratios and their use for statistically partitioning "size" from "shape" in morphometric studies (e.g., Atchley et al. 1976; Dodson 1978; Thorington and Heaney 1981; Shea 1985b; Corruccini 1987). However, separation of "size" from "shape" is not the goal here; conceptually, they may not be separable (McKinney 1988b). Rather, the goal here is not to remove statistical effects of size but to analyze dimensions as proportions of size (Corruccini 1987:291).

Following Dodson (1978) and Shea (1985b), ratios are used carefully with results cross-checked against results already obtained from bivariate analysis. Expressing other cranial dimensions as a proportion of CL provides the

necessary conceptual link for this pragmatic approach. Use of ratios does not partition size from shape (whatever that is), but does ensure that intergroup discrimination will not be based on sheer differences in magnitude of dimensions in smaller versus larger canids.

Previous Investigations of Canid Allometry

The following discussion summarizes several previous allometric investigations that have dealt with questions or produced results of direct relevance to this study. This review is highly selective. First, an exhaustive review of morphometric studies that have included domestic dogs for one purpose or another could entail an entire monograph. Second, a substantial body of appropriate literature is in German, a language in which this author has limited skills. For an introduction to this extensive literature the reader may consult discussions and bibliographies in Lumer (1940), Weidenreich (1941), Epstein (1971), and Wayne (1986a, 1986b). In any case, review of several major allometric studies, including selected German works, provides an informative background for the analysis that follows.

An early investigation of allometry in domestic dogs was conducted by Lumer (1940). Lumer's goal was to clarify evolutionary and taxonomic relationships among dogs by studying cranial and post-cranial allometry. Data from a variety of modern adult domestic dogs and wolves yielded

various patterns of allometry. Based on analysis of static data, Lumer subjectively defined several "allometric tribes", which represented different groups of breeds thought to share similar bivariate scaling relationships.

Ontogenetic data from 30 German Shepherds revealed approximately the same slope as for the "terrier tribe", the group to which German Shepherds were assigned based on several bivariate plots. Lumer hypothesized equivalence of static and ontogenetic allometry, and suggested (1940:461) that ". . . within a tribe the larger breeds recapitulate in their development . . . the body porportions of the adult stages of smaller breeds." Juvenilization was argued to be a consequence of decrease in adult body size with no significant changes in the course of relative growth.

Though Lumer's subjective methodology has been soundly criticized (Cock 1966), his study is important for its emphasis on allometry as a mechanism of morphological change with changing body size. His general observation of juvenilized morphology in smaller breeds was consistent with both earlier (e.g., Hilzheimer 1932) and later studies (e.g., Wayne 1986a, 1986b). In Lumer's formulation, juvenilized morphology is simply an inevitable consequence of size reduction, and only size selection need be invoked to explain it.

Another early allometric investigation was conducted by Dahr (1942). Dahr analyzed allometry of the braincase

in wild canids and modern domestic dogs, hoping to arrive at inferences concerning the ancestry of dogs. Several species of wild canids were used and treated as one group, while "normally-shaped" domestic dogs were used for comparison. He argues that when size changes are correlated with form changes they must be regarded as independent of human intention. Breeds not conforming to this criterion, such as bulldogs and greyhounds, were eliminated.

Dahr's summary of difficulties in assembling samples of modern dogs that accurately approximate "primitive" dogs is so well presented that it casts doubt on any conclusions he draws. He notes that once evolutionary transitions between "normal" forms and "aberrations" are underway, all possible gradations exist between them. Further, frequencies of different forms are highly irregular, being time and space specific and subject to change with shifting human economic needs or even "fashion trends" (Dahr 1942:29).

In the end, Dahr derived evolutionary inferences from his data. First, he documented a pattern of negative allometry involving breadth and length of the cranial vault in wild canids. Cephalic index (breadth/length x 100) declines with increasing size. His sample of "primitive" modern dogs exhibited even more pronounced negative allometry. Hence, the two groups have intersecting

regression lines with different slopes.

Dahr concluded that the difference in slopes indicates different directions of deviation between dogs and wild canids. Actually, the direction is the same in both (negative allometry), with only a difference in magnitude. Nonetheless, Dahr suggested that an ancestor of dogs must be sought in the size range represented by the intersection of the two regression lines. Both jackals and wolves were rejected, the former being too small and the latter too large. Dahr argued that the Australian Dingo provides an appropriate ancestor based on his analysis. As Werth (1944) subsequently pointed out, similarity between dingos and medium sized dogs simply suggests that the dingo itself is basically a domestic dog. Thus, although Dahr recognized the fundamental importance of allometry in producing size-correlated form changes, his evolutionary inferences must be rejected.

Another extensive allometric investigation involving canids was conducted by Stockhaus (1965). Stockhaus assembled craniometric data from wild wolves, zoo wolves, modern "primitive" dogs, and modern dogs of specialized breeds. A principal goal of his investigation was to determine how zoo wolves and primitive dogs differ in allometric relations from wild wolves (this summary does not address his analysis of breed dogs). Most dimensions were scaled against cranial capacity, while some were

scaled against basal length of the skull.

Regressions were performed separately on the different groups and results compared. For wild wolves, Stockhaus found that most dimensions were positively allometric in relation to cranial capacity. Thus, larger skulls have smaller cranial volumes, a result consistent with the findings of Dahr (1942). Zoo wolves exhibited marked reductions in length measures but little change in breadth measures. Thus, most zoo wolves have relatively broader skulls than their wild counterparts.

For primitive dogs Stockhaus found that all linear measures were positively allometric with respect to cranial capacity. Many measures exhibited slopes similar to wolves, but transposed up or down. Overall, Stockhaus argued that allometric distinctions between zoo wolves and wild wolves are generally the same as those between primitive dogs and wild wolves. The similarity in scaling relationships between dogs and zoo wolves relative to wild wolves warrants attention. In zoo wolves, reduced size and altered morphology are presumably the consequences of environmentally induced developmental alterations. In dogs, reduced size and altered morphology presumably have a genetic basis. This suggests that genetically produced alterations in size and morphology in these animals are subject to constraints imposed by developmental pathways (see below). As Stockhaus (1965:186) himself observed,

genetic differences apparently have the same consequences as environmentally caused changes.

Limitations to the expression of morphological variability in dogs have been explored in a series of papers by R.K. Wayne (1986a, 1986b, 1986c; see also Wayne 1984). Wayne's general objective was to determine how shared developmental and genetic architecture limit morphological evolution. Although Wayne did not set out specifically to address questions about the causes of morphological change in the evolution of the dog from the wolf, his results have direct bearing on those questions and warrant careful consideration.

The first paper (Wayne 1986a) deals with cranial allometry. Dental and cranial measurements were recorded on adult domestic dogs of various breeds and adult wild canids of different species. Longitudinal data were recorded from four growing dogs of different breeds, ranging from a Lhasa Apso (smallest) to a Great Dane (largest). In all analyses total skull length was used as an independent variable in the computation of least squares regression coefficients.

Considering static data first, Wayne found that the scaling of cranial length components on total skull length was similar in wild canids and dogs. All slopes were close to isometry. However, the two groups exhibited different scaling patterns on cranial width and depth variables as

well as dental variables. In these cases, slopes from the dog regressions were shallower, with both groups exhibiting strong negative allometry. All small breeds were found to have wider skulls than wild species of comparable size, with regressions intersecting at largest sizes.

Thus, variability in scaling of skull length components is tightly constrained in all canids, and all dog breeds ". . . are exact allometric dwarfs with respect to measures of skull length" (Wayne 1986a:247). As a result of the dissimilar scaling of skull width and depth dimensions, dogs show overall morphological similarity only to their close relatives, the larger wolf-like canids. Discriminant analysis demonstrated that the dogs overlap only with the wolf-like genera (Canis, Cuon, Lycaon). Wayne argues that morphological change in dogs has not transcended phylogenetic boundaries, as evidenced by the separation of all dog breeds from smaller fox-like canids.

Turning to ontogenetic allometry, Wayne found that the scaling of juvenile dogs of different ages was similar to that of adult dogs of different sizes. Wild canids, adult dogs, and juvenile dogs all exhibit similar scaling of skull length measures. In width and depth measures, juvenile dogs are more similar to adult dogs than to wild canids. Thus, ontogenetic and static allometry of dogs are similar when the tremendous range of size and morphology present in modern dogs is represented. Wayne (1986a:256)

concludes that under conditions of rapid evolutionary change, especially involving size selection, ontogenetic scaling may constrain morphological diversity among adults.

In a closely related paper Wayne (1986b) investigated allometry in the limb bones of domestic dogs and wild canids. He utilized samples similar to those used in his study of cranial allometry and regressed various limb bone measurements against femur length. Considering static data, Wayne found that the scaling of long bone lengths with femur lengths was similar in dogs and wild canids. Slopes were isometric or only weakly allometric. Long bone widths, however, scaled differently. Dog slopes were shallower, resulting in wider bones relative to wild species of comparable femur length. Discriminant analysis clearly distnguished the dogs from all groups except their close relatives. Ontogenetic analysis revealed that adult dogs and juvenile dogs exhibit similarity in scaling patterns.

Wayne notes that given the evolutionary distance of dogs from some of the wild taxa, similarity in scaling between the groups is surprising. Subtle differences that exist, however, are taxonomically important and may relate to locomotor behavior. Nevertheless, he argues that the pervasive similarity suggests that size selection is sufficient for generating most of the diversity of limb proportions in canids.

Wayne deals most extensively with growth and development in a third paper (Wayne 1986c). Here, he notes that it is commonly expected that ontogenetic differences between breeds or species will appear late in ontogeny, while differences among higher taxa will appear early. Thus, because dogs differ markedly in limb size and proportion, these differences should be due to altered postnatal growth rates.

Wayne collected longitudinal data from four growing puppies representing breeds of vastly different size and morphology: Lhasa Apso, Cocker Spaniel, Labrador Retriever, and Great Dane. Radiographs taken at systematic intervals were used to generate measurements during a period from about 40 to 250 days post-partum, or about 75 percent of postnatal growth in limb bone length. Specific growth rates (basically absolute growth rate divided by size) were calculated to express proportionate increase in size with age.

Wayne found specific growth rates similar in all four breeds. Because of this, the four breeds must exhibit proportional differences in size as puppies that are similar to those among adults. Generalized growth curves were utilized to construct hypothetical dogs by shifting the initial 40 day sizes and projecting growth to 250 days. Discriminant analysis of hypothetical dogs and real dogs corresponded closely, supporting the assertion that

patterns of postnatal growth in most dogs are similar to that of the four measured for Wayne's study. However, large dogs deviated from the growth curve model, perhaps because they have an extended period of late postnatal growth relative to small dogs.

Wayne argues that similar growth rate patterns after 40 days indicate that differences in limb conformation among adults are due either to differences in initial birth size or in specific growth rate soon after birth. Birth weight differences account in part for size differences, but not fully. Thus, Wayne argues that small breeds must also have reduced perinatal (0 to 40 days) growth rates.

It is argued here that Wayne may be underestimating the effects of an extended growth period in larger dogs. Elsewhere (Wayne 1986b) he observes, for example, that the tiny Lhasa Apso grows for only about 10 months, while the enormous Great Dane grows for up to two years, albeit at a very slow rate in the second year. Growth rates in a medium-sized breed like the Beagle are slow at 300 days, and decline with increasing age (Anderson and Floyd 1963). Simple truncation or extension of development should not be ignored as a contributing factor (cf. Kirkwood 1985:102), though alone it is certainly incapable of explaining the vast size differences between breeds.

Wayne also utilized growth data from two species of wild canids, the bush dog (Speothus venaticus) and the

maned wolf (Chrysocyon brachyurus). Wayne notes that the three groups (including domestic dogs) represent almost the entire range of limb proportions in canids. Yet, remarkably, there are no significant differences in specific growth rates. Like the domestic dogs, differences in size and proportion among different canid species must be due either to differences in initial birth size or in perinatal growth rates.

Size differences at birth imply either different foetal growth rates or differences in gestation times. Wayne observes that in general there is a strong relationship between size at birth and gestation time among vertebrates. Foetal growth rates are similar and gestation lengths determine neonate size. Dogs, however, are a conspicuous exception to this generalization. As Wayne notes, their gestation time, 60-63 days, is invariant (Kirkwood 1985:104; Rivers and Burger 1989:84). Thus, smaller neonates of small breeds can only result from slower foetal growth rates. Contrary to the general expectation, breeds are characterized by variation in foetal and perinatal growth rates rather than variation in postnatal rates.

Small dog breeds differ morphologically from small wild canids in part because of different gestation lengths. Among wild canids differences in limb bone conformation are related to discrepancies is gestation time. Among domestic

dogs, differences are due to alterations in foetal specific growth rates and perinatal rates.

The implications of Wayne's research will be returned to when results of the present analysis have been presented. For the moment, several points should be emphasized. First, morphological variability in dogs is largely constrained to the range of variability expressed in ontogeny. Modern dogs, resulting from deliberate selection for all manner of sizes and forms, have not accomplished the genetic reorganization necessary to transcend the range of morphology represented by a basic phlylogenetic boundary. There is no reason to expect that earlier prehistoric dogs did either. Thus, morphology of early dogs should be confined to the ontogenetic pathway of their immediate ancestor, C. lupus. In a review of allometric relations between body weight and physiological parameters in modern dogs, Kirkwood (1985) argues that allometries of dogs in general are confined to developmental boundaries.

If size alteration must produce morphologies conforming to developmental pathways, it may be difficult to distinguish the results of size selection from selection on life history traits. Selection on developmental parameters may have been an important channel available for contributing to size reduction. Hence, the conceptual distinction gets fuzzy.

In his analyses of size-correlated changes, Wayne has utilized virtually the entire range of size and morphology represented in modern dogs. The following chapters attempt to determine the degree to which morphology in prehistoric dogs is a reflection of size-correlated changes. These dogs are of a generalized type, far more uniform in size and morphology than modern breeds. Despite their small size, they are legitimately regarded as true primitive dogs (see Chapter VIII). They represent what investigators like Dahr (1942) and Stockhaus (1965) hoped to approximate when they subjectively selected "primitive" dogs from among modern breeds.

CHAPTER IV

MEASUREMENTS, ASSOCIATED OBSERVATIONS, AND SAMPLES

Measurements and Associated Observations

The data base used in this study consists of measurements and associated observations from 349 skulls of recent wild canids and archaeologically recovered domestic dogs from the earliest time periods possible. All measurements and observations used in this study were recorded by the author. These data reside on a computer file stored at the Department of Anthropology, University of Tennessee. Appendix A presents raw data from all specimens used in this study.

In an earlier study (Morey 1986) the author relied on metric data published in William Haag's (1948) osteometric study of native North American dogs. Because of this, the initial suite of measurements defined for this research was taken directly from Haag (1948). As this research progressed, however, some measurements were eliminated and several new ones were defined to suit the purposes of this investigation. Thus, all specimens available for analysis do not have an identical suite of measurements. For this reason the number of specimens utilized in any given phase of analysis fluctuates slightly, depending on which measurements are under consideration.

The measurements used in this study are defined on

Table 1 and illustrated on Figures 4 and 5. Cranial dimensions (CL, PL, IM2, OI, PW, MCW)) were taken in whole millimeters with slide calipers. Dental measurements (CAN, P1, P2, P3, LC) were taken to the nearest .1 mm. with dial calipers. Measurements CL, PL, PW, OI, MCW, and IM2 correspond to Haag's (1948) measurements 3, 4, 5, 12, 17, 18, and 19, respectively. Identical or similar measurements are described and illustrated by von den Driesch (1976). These measurements were selected to include a variety of dimensions that had previously proven useful in analyzing differences between domestic dogs and wild canids (Morey 1986). In addition, use of these measurements minimized elimination of archaeological specimens with missing data.

Dental measurements require additional clarification. P4 is the only measurement taken as a crown length. Other dental measurements, involving the canine and premolar teeth (CAN, P1, P2, P3), were taken as alveolar lengths for a purely practical reason. Many archaeological specimens were lacking several if not most of these teeth. If crown lengths were utilized the number of analyzable archaeological specimens would have been significantly reduced. This is unfortunate in that alveolar lengths are not necessarily directly proportional to crown lengths, especially in subadult individuals with newly erupted dentition. In such individuals it can be observed that

Table 1. Measurements used in analysis of canid crania.

Measurement	Description
CL	condylobasal length
PL	palatal length
PW	palatal width at M1
OI	lateral face length (orbit to anterior alveolus of I1)
MCW	maximum cranial width
IM2	tooth row length (anterior alveolus of I1 to posterior alveolus of M2)
CAN	alveolar length of the canine tooth
P1	alveolar length of the first premolar
P2	alveolar length of the second premolar
P3	alveolar length of the third premolar
P4	crown length of the carnassial tooth

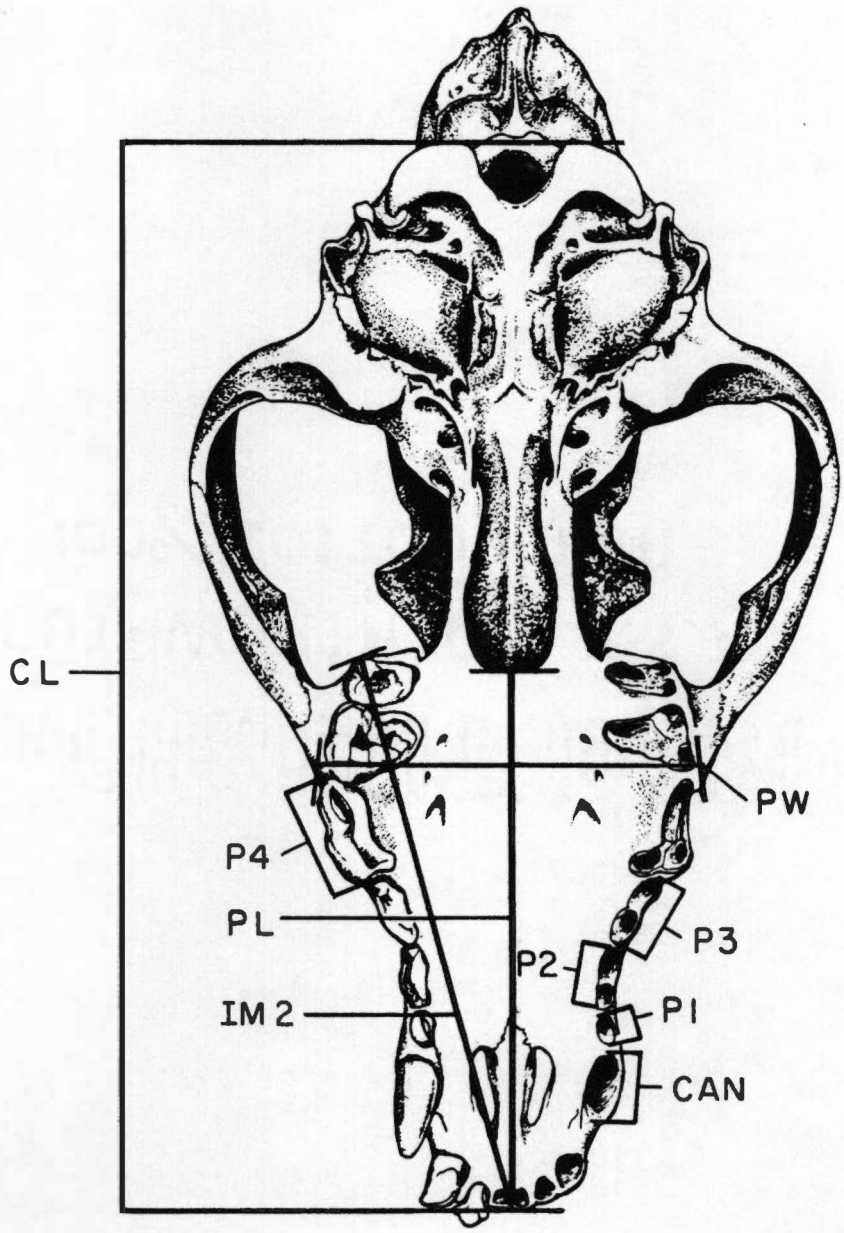


Figure 4. Palatal view of a canid skull, showing location of measurements CL, PL, IM2, PW, CAN, P1, P2, P3, and P4. Model is Canis lupus lycaon, about 70 percent actual size.

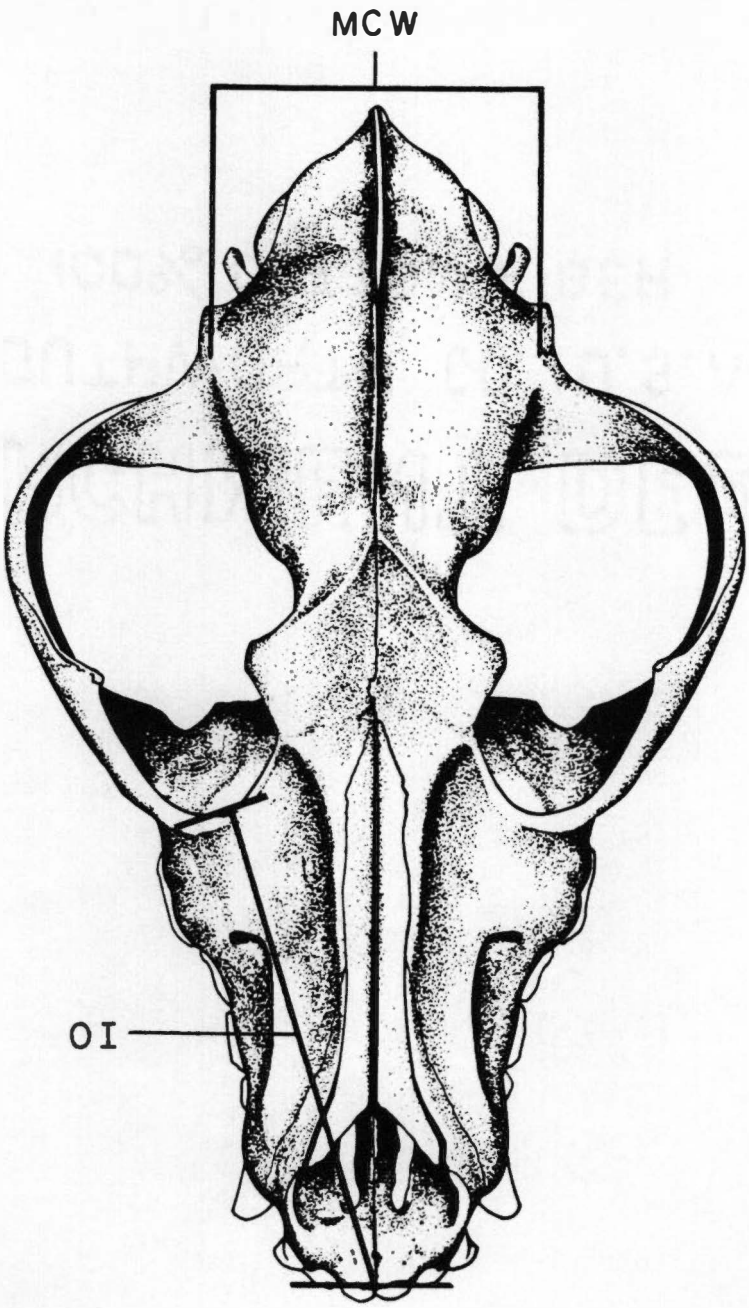


Figure 5. Sagittal view of a canid skull, showing location of measurements OI and MCW. Model is Canis lupus lycaon, about 70 percent actual size.

teeth are often not fully seated in their sockets, with the alveoli gradually filling in as the teeth are cemented into place. However, only adults are used in analyses involving these measurements.

In addition to metric data, information was recorded on several nominal or ordinal level variables. This includes organizational information (specimen number, institutional location), geographic location, and biological information such as sex and age. Because age will be an important variable in this study, it warrants clarification. Five age categories were defined, summarized on Table 2. The criteria described are not fully objective but they provide a reasonably accurate basis for distinguishing different general age groups. They were derived by examination of specimens of known age, coupled with published information on timing of dental eruption in wolves, C. lupus (Mech 1970:140). It should be stressed that the "corresponding age" shown on Table 2 is only an approximation, and pertains directly only to C. lupus. However, timing of dental eruption in modern dogs is similar to that in wolves (cf. Smythe 1970:43-45).

Sexes are not analyzed separately in this study. Although failing to control for sexual dimorphism is unfortunate it would serve little purpose here. There is no way to reliably distinguish males from females in the prehistoric dog samples (see below). Presumably both sexes

Table 2. Description of ontogenetic age categories defined for analysis of canid crania.

Age Category	Description	Corresponding Age
(1) puppy	deciduous dentition erupting or in place	45 days - 4 months
(2) juvenile	deciduous dentition being replaced	4-6 months
(3) advanced juvenile	permanent dentition erupted; cranial sutures not fully sealed; bone very porous	6 months - 1 year
(4) young adult	most sutures fully closed; most bone fully ossified; no visible wear on teeth;	1-2 years
(5) adult	all sutures fully closed; visible wear on teeth;	over 2 years

are represented. Thus, because this study hinges on comparisons of dogs and wild canids, sexes are pooled.

Wild Canid Samples

Four species of wild Canis are used in this study, including the gray wolf (C. lupus), red wolf (C. rufus.), coyote (C. latrans), and golden jackal (C. aureus). These taxa provide a substantial range of size variation, with C. lupus representing the largest and C. aureus the smallest. The domestic dogs used in this study (see below) are on average even smaller, but overlap considerably with the C. aureus specimens in condylobasal length.

Selection of specimens for analysis is complicated by the highly polymorphic nature of most species of Canis. With the species used here several or many subspecies are recognized which exhibit substantial variation in size and morphology. The adult wild canid specimens used in analysis are summarized on Table 3. Selection of these samples is explained below. For purposes of this study, individuals assigned to age categories 4 and 5 (see Table 2) are regarded as adults, and are pooled in all analyses.

Table 3. Summary of adult wild canid specimens (age categories 4 and 5) used in analysis (totals for different species in parentheses).

Species/Subspecies	Geographic Location	No. of Specimens
Canis lupus		(102)
C. lupus lycaon	Minnesota, Michigan, or Ontario	59
C. lupus baylei	southern Arizona, New Mexico, or northern Mexico	43
Canis rufus		
C. rufus rufus	Texas	29
Canis latrans		
C. latrans thamnos	Illinois	62
Canis aureus		(29)
C. aureus morrocanus	Morocco or Mauritania	6
C. aureus algirensis	Morocco	2
C. aureus spp.	Morocco	5
C. aureus lupaster	Egypt or Libya	6
C. aureus indicus	Nepal or India	4
C. aureus lanka	Sri Lanka	1
C. aureus anthus	Senegal	5
Total		222

Adult Wild Canids

As the presumed ancestor the dog, selection of appropriate samples of C. lupus presents an especially vexing problem. In addition to dramatic size variation, substantial morphological variation in the cranium is well documented among different subspecies (e.g., Jolicoeur 1959, 1975b). Ideally, the subspecies known to have been involved in domestication would be selected and analyzed. However, as explained in Chapter II, this information is presently beyond our grasp.

Two North American subspecies of C. lupus are utilized in this study. C.l. lycaon is the gray wolf of northeastern North America. Once ranging throughout the Great Lakes region, New England, Ontario, and Quebec (Young and Goldman 1944:437-441; Hall 1981:929-933), viable populations still survive in northern Minnesota, Isle Royale, and portions of the two Canadian provinces. Much of our current knowledge of behavior and lifeways of North American subarctic wolves comes from long term investigations of this subspecies (e.g., Mech 1970; Peterson 1977).

The other subspecies, C.l. baylei, is the desert wolf of the extreme southwestern United States and Mexico (Young and Goldman 1944:469-471; Hall 1981:929-933). It is the smallest of the North American subspecies. It is now extinct in the United States (and probably Mexico), a

situation encouraged by a government aided extermination program carried out in the first half of the twentieth century (Brown 1983).

The small red wolf, C. rufus, once ranged throughout the south-central and southeastern United States. It is now probably extinct in its former range, although a reintroduction program involving captives is underway in northeastern North Carolina (Phillips and Parker 1988). C. rufus is surrounded by taxonomic problems (e.g., Lawrence and Bossert 1967, 1975; Gipson et al. 1974; Nowak 1979). At different times it has been regarded as a variant of C. lupus or an intermediate form between C. lupus and C. latrans (cf. Nowak 1979:85-90). Nowak (1979) regards original populations of C. rufus as a separate species with three geographic subspecies (see also Young and Goldman 1944:483-486; Hall 1981:933-934) The smallest of the three subspecies, C. r. rufus, the Texas red wolf, is used in this study.

Because of the taxonomic problems surrounding C. rufus, compounded by recent hybridization with C. latrans, it is inadvisable to place too much weight on patterns of static variation in this species. Hence, a limited sample of 29 adult specimens was selected. Twenty-six of the 29 specimens are from southeast Texas, east of the Edwards Plateau region, one of the last strongholds of unmodified C. rufus in the twentieth century (Nowak 1979:45). The

majority predate 1920, and all but one predate 1950. The remaining three are from north-central Texas, where populations were strongly affected by hybridization with C. latrans. However, all three are relatively early (pre-1930). In any case, considerable similarity between the two species can be expected in this study.

The coyote, C. latrans, is represented by a single relatively large subspecies, C.l. thamnos (Hoffmeister 1989). When dealing with recent coyote populations the inevitable problem of coyote-dog hybridization surfaces (Mengel 1971; Gipson et al. 1974; Lawrence and Bossert 1975; Nowak 1979). Specimens used here are all from the collections of the Illinois State Museum in Springfield, and all are from Illinois. They were classified as "pure" coyote on the basis of a quantitative investigation which allowed their separation from specimens that appeared to reflect genetic mixing with domestic dogs. Unfortunately, this study was never published, though a published note makes brief reference to this work when it was in progress (Paul 1969; see also Hoffmeister 1989:271).

The single Old World wild canid represented in this study is the golden jackal, C. aureus. This species ranges from northern Africa through the Near East and into southern Asia (cf. Hufnagel 1971:36-37; Rosevear 1974:36-49; Stains 1975:19). This is a geographically heterogeneous sample, with at least six subspecies

represented, and five specimens of undetermined subspecific identity. Because of the small samples available, this diverse series is treated as a single sample in all analyses.

Subadult Wild Canids

This study includes data from 60 subadult wolves (age categories 1,2, or 3) of two species, C. lupus and C. rufus. Because of the small number of specimens available, the subadult samples incorporate data from several subspecies not included in the adult series. In both cases, however, the majority of the subadult specimens belong to the subspecies represented in the adult samples. The subadult samples are summarized on Table 4.

Twenty-six of the 38 C. lupus specimens are C.l. lycaon or C.l. baylei. The remaining 12 specimens are comprised of three additional North American subspecies, C. lupus youngi, C. lupus irremotus, and C. lupus nubilus (cf. Young and Goldman 1944). All specimens representing the latter three subspecies are from the continental United States.

Twenty-two subadult specimens of C. rufus are available for this study. Sixteen are C.r. rufus, the subspecies comprising the adult series. Most of these specimens (13) are from southeastern Texas. One, collected in 1929, is from from north-central Texas, while the remaining two, collected in 1905 and 1922, are from

Table 4. Summary of subadult wild canid specimens (age categories 1, 2, and 3) used in analysis (totals for different species in parentheses).

Species/Subspecies	Geographic Location	No. of Specimens
Canis lupus		(38)
C. lupus lycaon	Minnesota, Michigan, or Ontario	22
C. lupus baylei	southern New Mexico, Arizona, or northern Mexico	4
C. lupus youngi	New Mexico	7
C. lupus irremotus	Wyoming	4
C. lupus nubilus	Colorado	1
Canis rufus		(22)
C. rufus rufus	Texas or Oklahoma	16
C. rufus gregoryi	Arkansas, Louisiana, Texas, or Missouri	6
Total		60

southern Oklahoma. Six specimens of C. rufus gregoryi, the Mississippi Valley red wolf (Young and Goldman 1944:483-486; Nowak 1979) are included in the subadult C. rufus sample.

Several points concerning the utility of these subadult samples should be noted. First, the inclusion of subspecies not represented in the adult series introduces an element of inconsistency into analysis. However this should not be a major problem since the subadult samples are dominated by subspecies comprising the adult samples. Second, the subadult samples incorporate data from several individuals that were apparently members of the same birth litter. This is true, for example, of three C. r. gregoryi specimens from Missouri, and several C.l. youngi specimens from New Mexico. Thus, the degree of genetic similarity among some of the subadult specimens is surely much greater than in the adult series, which should more closely (though certainly not perfectly) approximate a random sample within a given region.

Finally, many of the measurement points (see Figures 4 and 5, pages 78 and 79), defined for adult specimens, are not directly applicable to subadults. This is most obvious with respect to dimensions that utilize tooth locations as measurement points. Subadults falling into age categories 1 and 2 have no permanent dentition; hence, the defining criteria for measurements like PW or IM2 are not directly

applicable. In the case of PW, the measurement was taken as the widest dimension of the palate, which corresponds approximately to the more precisely defined PW applied to adults. Similarly, IM2 for subadults was taken as maximum length of the lateral margin of the palate, where the teeth would eventually have erupted. This measurement was frequently unavailable from youngest specimens.

Domestic Dog Samples

Assembling appropriate samples of prehistoric domestic dogs presents some special problems. For reasons explained in the previous chapters, it is desirable to restrict analysis to relatively early specimens, predating about 3,000 B.P. Because of inevitable problems with preservation conditions or recovery techniques, many specimens are incomplete or badly fragmented. There is no escape from this frustrating situation when dealing with archaeological remains.

A minimum criterion for inclusion of archaeological specimens in this study was the availability of the measurement CL. Unfortunately, this necessary requirement eliminated many well preserved specimens that had small but crucial portions of the cranium missing. Some specimens, however, could be measured after reconstruction of broken skulls. Reconstructions were done as carefully as possible, and it must be assumed that any errors are small

and unbiased.

Sometimes a measurement not apparently available could be carefully estimated. For example, palatal width (PW) spans the distance across the palate between P3 and M1 on either side (see Figure 4, page 78). If one side of the palate was missing, bilateral symmetry allowed estimation of the measurement. The distance from the available P3-M1 location to the mid-sagittal line could be measured and then doubled to estimate palatal width. In other instances a specimen with C1 available might have one or more other measurements unavailable. Thus, the numbers of specimens used in each analysis fluctuates slightly.

Finally, preservation of juvenile specimens from the archaeological record is rare. In the collections examined for this study, only three measureable juvenile specimens were encountered. They are not included in analysis. Thus, all dogs used in this study are adults (age categories 4 and 5).

Two groups of prehistoric dogs are used in analysis, summarized below.

North American Dogs

The largest series of dogs, summarized on Table 5, is from the southeastern and midwestern United States. Most specimens are from Kentucky and Alabama; the remainder are from Tennessee and Illinois. Most of the Kentucky and Alabama specimens were included in Haag's (1948)

Table 5. Summary of North American Archaic Period archaeological dog crania used in analysis.

Site (Site Number)*	Date (B.P.)	No. of Specimens	References
Koster	8400	2	Houart 1971 Streuver & Holton 1978 Brown et al. 1983 Wiant et al. 1983
Modoc (11R5)	7000	1	Fowler 1959a, 1959b Styles et al. 1983
Indian Knoll (15OH2)	7000-3000	14	Webb 1946 Winters 1974
Chiggerville (15OH1)	7000-3000	1	Webb & Haag 1939
Carlson Annis (15BT5)	7000-3000	5	Webb 1950a Marquardt & Watson 1983 Watson 1985
Read (15BT10)	7000-3000	2	Webb 1950b
Ward (15McL11)	7000-3000	4	Webb & Haag 1940
Perry (1LU25)	7000-3000	7	Webb & DeJarnette 1942, 1948a
Flint River (1MA48)	7000-3000	2	Webb & DeJarnette 1948b
Whitesburg Bridge (1MA10)	7000-3000	1	Webb & DeJarnette 1948c
Little Bear Creek (1CT78)	7000-3000	2	Webb & DeJarnette 1948d
Mulberry Creek (1CT27)	7000-3000	3	Webb & DeJarnette 1942
Bailey (40GL26)	7000-3000	1	Bentz 1988

Table 5 (continued).

Site	Date (B.P.)	No. of Specimens	References
Cherry (40McL84)	7000-3000	2	MaGennis 1977
Eva (40McL6)	7000-3000	2	Lewis & Lewis 1961
Total		49	

*Site numbers beginning with 11 are in Illinois. Those beginning with 1, 15, and 40 are in Alabama, Kentucky, and Tennessee, respectively.

descriptive analysis of aboriginal North American dogs. Although Haag's data from these specimens have been used repeatedly by other investigators (e.g., Potter and Baby 1964; Colton 1970; Olsen 1970; Walker 1980; Walker and Frison 1982; Morey 1986), to this author's knowledge this is the first study in which the specimens were reexamined and measured since Haag's original work in the 1940s.

Most of the North American specimens are the product of excavations in aboriginal shell middens, conducted during the first half of the twentieth century. As a consequence, it is impossible to assign firm dates to most of them beyond their general association with Middle or Late Archaic occupations. This is the reason for the general time span of 3,000-7,000 B.P. indicated on Table 5. The earlier specimens, from Koster and Modoc in Illinois, are securely dated as indicated.

Overall, these may be classified as "small" dogs (cf. Allen 1920; Colton 1970; Emslie 1978); they are, on average, slightly smaller than most of the golden jackals (C. aureus) used in this study (see Chapter IV). On subjective grounds they exhibit a consistent generalized morphology. The earliest specimens, from Koster and Modoc, are significantly larger than most of the southeastern dogs from Kentucky, Tennessee, and Alabama (see Chapter IV). Many of the southeastern specimens represent deliberate interments, often associated with human interments (Webb

1946; Lewis and Lewis 1961). The Koster specimens, although not associated with human burials, are also deliberate interments (Morey and Wiant 1989).

On figures and tables in subsequent chapters the North American series is referred to as "C. familiaris NA".

European Dogs

A smaller series of dogs, summarized on Table 6, comes from northern Europe. With one exception, they are all from Denmark. The exception, Senckenberg, is from northern Germany. It should be noted that the Senckenberg specimen is a plaster cast; the original was lost or destroyed during World War II.

Because of the small samples available, this series includes specimens from early Neolithic contexts, rather than being restricted to earlier time periods. However, these Neolithic contexts (Bundsø, Spodsbjerg, Lidsø) correspond with the later Archaic time period in North America (ca. 5,000-4,000 B.P.). Excavations yielding the European specimens span the past century, and the reliability of associated dates is variable. Uncertain dates are indicated with a question mark on Table 6.

Like the North American dogs, these animals are relatively small, though they are on average slightly larger than many of the North American dogs. The more recent Neolithic specimens tend to be the smallest. Many of these specimens have been used in previous studies

Table 6. Summary of European archaeological dog crania used in analysis.

Site	Date (B.P.)	No. of Specimens	References
Senckenberg	10000-9000?	1	Mertens 1936 Benecke 1987 Degerbøl 1961
Vedbæk Boldbaner	7300-6500	1	Degerbøl 1946 Aaris-Sørensen 1977b
Saltpetersmosen	6600-5100	2	unpublished*
Ringkloster	5700-5000?	2	Andersen 1974
Ertebølle	5800-5000	1	Madsen et al. 1900 Andersen & Johansen 1986
Bundsø	4700-4200	7	Degerbøl 1939, 1961
Spodsbjerg	ca. 4300	1	Aaris-Sørensen 1985 Nyegaarde 1985
Lidsø	4400-4200	3	Hatting 1978
Total		18	

*Information obtained through personal communication with Kim Aaris-Sørensen at the Zoological Museum, University of Copenhagen, Denmark, August, 1988.

(e.g., Degerbøl 1927, 1961). It has been suggested that the prehistoric dogs of Denmark were used as hunting aids or even as an occasional food source (Aaris-Sørensen 1988:157-162).

On figures and tables in subsequent chapters this series is referred to as "C. familiaris EU".

CHAPTER V

BIVARIATE ALLOMETRY: ANALYSIS OF STATIC DATA

This chapter presents analyses of bivariate allometry of adult canid groups. For organizational purposes, analyses of cranial variables (PL, IM2, OI, PW, MCW) is presented separately from analyses of dental variables (CAN, P1, P2, P3, P4). As explained in Chapter III condylobasal length, CL, is used as the independent variable in all analyses.

Regressions were calculated using the simple regression model in the SAS GLM (General Linear Models) procedure (SAS Institute 1985). To minimize the risk of generating spurious slopes and elevations from weakly correlated variables, regressions were performed only when correlations (Pearson's R) were significant at the .01 level. Goodness of fit and homoscedasticity were evaluated by inspection of residuals (Zar 1984:288-289).

First, interspecific regressions for all groups were calculated for each variable. Slopes from these regressions can indicate basic allometric trends across all species. A second set of interspecific regressions was then calculated for wild canids only. If slopes from the two interspecific regressions differ, the dogs probably deviate from the basic allometric trend, and may distort it.

When intragroup correlations were significant, assessment of conformity to basic allometric trends was accomplished through analysis of covariance on intragroup regressions. Slopes of different groups were compared using the GLM homogeneity of slopes model. When differences between slopes were found to be insignificant, elevations were compared utilizing the the GLM analysis of covariance model. A general cutoff value for tests of homogeneity of slopes was 0.1. This unusually high cutoff value was employed to minimize error in comparisons of elevations. However, when slope tests yield significance values less than but approaching 0.1 (e.g. > 0.09), results of elevation tests are reported. Thus, the reader may reach his own determination.

With some wild canids separate group regressions were not performed due to insignificant correlations. In these cases conformity of a group to a basic allometric trend can be roughly gauged by referring to Appendix B. This appendix contains a compilation of bivariate plots of each variable against CL with interspecific regression lines illustrated.

Analysis of Cranial Variables

Summary statistics on cranial variables from the different canid groups are presented on Table 7. As a preliminary step, groups belonging to the same species

Table 7. Means, standard deviations (SD), and sample sizes (n) from cranial measurements of adult canids.

Group	Measurement (mm)					
	CL	PL	IM2	OI	PW	MCW
C.l. lycaon						
Mean	229.0	120.5	122.1	107.1	76.0	72.5
SD	11.84	6.37	5.86	6.18	4.53	2.82
n	59	59	59	59	59	59
C.l. baylei						
Mean	217.5	112.8	116.3	102.6	72.8	71.5
SD	8.11	4.36	4.22	4.34	2.40	2.46
n	43	43	43	43	43	43
C. rufus						
Mean	202.1	105.0	108.5	94.5	60.0	61.2
SD	7.59	3.37	3.45	3.33	2.46	1.75
n	29	29	29	27	29	29
C. latrans						
Mean	183.6	94.9	99.9	88.6	56.2	58.8
SD	8.05	4.77	4.54	4.72	2.75	2.27
n	62	62	62	62	62	62
C. aureus						
Mean	158.2	81.7	85.6	71.1	50.7	53.3
SD	11.13	5.62	5.41	5.77	3.75	2.61
n	29	29	27	29	29	29
C. familiaris EU						
Mean	156.1	80.8	84.4	70.6	56.1	57.0
SD	11.81	5.93	6.45	5.56	3.94	2.59
n	18	18	18	17	18	18
C. familiaris NA						
Mean	149.2	78.0	82.4	67.6	54.5	54.2
SD	9.35	4.74	4.59	5.42	3.07	3.48
n	49	48	49	47	48	48

(C.l. lycaon and baylei, C. familiaris EU and NA) were tested among themselves for homogeneity of slopes and elevations for regressions of each variable. The objective was to pool these groups when justifiable to simplify subsequent analysis. For the two dog groups differences in slopes and elevations were insignificant on PL and PW ($p>0.10$). For the C. lupus groups differences were insignificant on IM2, OI, and PW. Table 8 presents summary statistics for regressions calculated for all cranial variables. A regression was not calculated for C. rufus on the variable PW due to an insignificant correlation with CL. All other correlations among every group are significant ($p<.01$). Table 9 presents analysis of covariance results for comparisons of all separate groups. To help construct a general picture of static cranial allometry in these canid groups, the regressions of each variable against CL are discussed sequentially.

Palatal Length (PL)

The pooled regression of PL against CL for all groups yields a slope (1.008) that reflects virtually perfect isometry (Table 8). Removal of the domestic dogs to create a wild canid regression has only a minor effect on that slope (1.037), suggesting that the dogs are consistent with this broad allometric trend. Approximate isometry of palate length with skull length in canids has been found in other studies (e.g., Lumer 1940; Stockhaus 1965; Wayne

Table 8. Least squares slopes (LS) and associated standard errors (SE), least squares Y-intercepts (Y-INT), correlations (R), and reduced major axis slopes (RMA) from regressions of cranial variables against CL for adult canids (all variables log transformed).

Dependent Variable	Group	Slope* (LS)	SE	Y-INT	R	Slope (RMA)
PL	All Groups	1.008	.007	-0.301	>.99	1.015
PL	Wild Canids	1.037	.010	-0.369	.99	1.047
PL	C.l. lycaon	0.944	.054	-0.146	.92	1.026
PL	C.l. baylei	0.936	.070	-0.136	.90	1.040
PL	C. rufus	0.752	.080	0.286	.86	0.874
PL	C. latrans	1.083	.049	-0.474	.94	1.148
PL	C. aureus	0.932	.054	-0.137	.96	0.971
PL	C. familiaris EU/NA	0.905	.037	-0.076	.95	0.953
IM2	All Groups	0.927	.007	-0.101	>.99	0.934
IM2	Wild Canids	0.937	.009	-0.124	.99	0.946
IM2	C.l. lycaon/baylei	0.884	.033	0.001	.94	0.940
IM2	C. rufus	0.774	.070	0.252	.90	0.860
IM2	C. latrans	0.994	.046	-0.250	.94	1.055
IM2	C. aureus	0.835	.061	0.096	.94	0.888
IM2	C. familiaris EU	0.944	.075	-0.145	.95	0.994
IM2	C. familiaris NA	0.851	.040	0.066	.95	0.896
OI	All Groups	1.094	.009	-0.549	>.99	1.104
OI	Wild Canids	1.093	.012	-0.545	.99	1.107
OI	C.l. lycaon/baylei	0.954	.046	-0.219	.90	1.060
OI	C. rufus	0.886	.138	-0.066	.79	1.122
OI	C. latrans	1.192	.053	-0.766	.95	1.261
OI	C. aureus	1.099	.060	-0.565	.96	1.145
OI	C. familiaris EU	0.978	.086	-0.294	.95	1.029
OI	C. familiaris NA	1.199	.065	-0.776	.94	1.276
PW	All Groups	0.828	.025	-0.093	.89	0.929
PW	Wild Canids	1.144	.027	-0.828	.94	1.217
PW	C.l. lycaon/baylei	0.815	.062	-0.043	.80	1.019
PW	C. rufus	insignificant correlation				
PW	C. latrans	0.827	.095	-0.123	.75	1.106
PW	C. aureus	0.918	.110	-0.316	.85	1.080
PW	C. familiaris EU/NA	0.715	.065	0.182	.81	0.883

Table 8 (continued).

Dependent Variable	Group	Slope (LS)	SE	Y-INT	R	Slope (RMA)
MCW	All Groups	0.704	.016	0.193	.93	0.755
MCW	Wild Canids	0.861	.019	-0.175	.95	0.907
MCW	C.l. lycaon	0.568	.067	0.520	.75	0.757
MCW	C.l. baylei	0.669	.102	0.291	.71	0.937
MCW	C. rufus	0.574	.099	0.463	.75	0.765
MCW	C. latrans	0.659	.073	0.278	.76	0.867
MCW	C. aureus	0.637	.066	0.326	.88	0.724
MCW	C. familiaris EU	0.459	.099	0.748	.76	0.604
MCW	C. familiaris NA	0.783	.093	0.032	.78	1.001

*All least square slopes are significantly different from zero ($p<.001$).

Table 9. Analysis of covariance results from paired comparisons of adult canid cranial measurements, with CL as a covariate (all variables log transformed). Included are F-ratios (F) and associated probabilities from tests of homogeneity of slopes (PS), F-ratios and associated probabilities from tests of equality of adjusted group means (PAGM), and adjusted group means (AGMEAN) with associated standard error (SE)*.

Dependent Variable/ Comparison	PS (F)	PAGM (F)	AGMEAN (SE)
PL			
C.l. lycaon	.937 (<0.1)	<.001 (15.6)	2.0717 (.0012)
C.l. baylei			2.0640 (.0014)
C.l. lycaon	.094 (2.1)	<.001 (11.3)	2.0644 (.0014)
C. rufus			2.0537 (.0023)
C.l. lycaon	.062 (3.6)		
C. latrans			
C.l. lycaon	.878 (<0.1)	.007 (7.7)	2.0307 (.0023)
C. aureus			2.0127 (.0045)
C.l. lycaon	.554 (0.4)	.002 (10.5)	1.9925 (.0031)
C. familiaris EU/NA			1.9739 (.0028)
C.l. baylei	.101 (2.8)	.161 (2.0)	2.0409 (.0013)
C. rufus			2.0374 (.0017)
C.l. baylei	.091 (2.9)	.788 (<0.1)	2.0069 (.0021)
C. latrans			2.0078 (.0015)
C.l. baylei	.959 (<0.1)	.071 (3.4)	1.9998 (.0026)
C. aureus			1.9888 (.0037)
C.l. baylei	.722 (0.1)	.029 (4.9)	1.9642 (.0033)
C. familiaris EU/NA			1.9525 (.0022)
C. rufus	.001 (11.2)		
C. latrans			
C. rufus	.090 (3.0)	.008 (7.6)	1.9734 (.0028)
C. aureus			1.9590 (.0028)
C. rufus	.151 (2.1)	.009 (7.2)	1.9422 (.0033)
C. familiaris EU/NA			1.9299 (.0017)
C. latrans	.037 (4.5)		
C. aureus			
C. latrans	.007 (7.6)		
C. familiaris EU/NA			
C. aureus	.695 (0.2)	.201 (1.7)	1.8984 (.0017)
C. familiaris EU/NA			1.9010 (.0011)

Table 9 (continued).

Dependent Variable/ Comparison	PS (F)	PAGM (F)	AGMEAN (SE)
IM2			
C.l. lycaon/baylei	.231 (1.5)	.143 (2.2)	2.0687 (.0008)
C. rufus			2.0657 (.0017)
C.l. lycaon/baylei	.060 (3.6)		
C. latrans			
C.l. lycaon/baylei	.439 (0.6)	.002 (9.7)	2.0499 (.0012)
C. aureus			2.0353 (.0038)
C.l. lycaon/baylei	.378 (0.8)	.054 (3.8)	2.0559 (.0011)
C. familiaris EU			2.0459 (.0044)
C.l. lycaon/baylei	.534 (0.4)	.104 (2.7)	2.0273 (.0016)
C. familiaris NA			2.0196 (.0032)
C. rufus	.015 (6.1)		
C. latrans			
C. rufus	.562 (0.3)	.002 (10.5)	1.9935 (.0028)
C. aureus			1.9769 (.0028)
C. rufus	.123 (2.5)	.160 (2.0)	1.9966 (.0026)
C. familiaris EU			1.9879 (.0039)
C. rufus	.398 (0.7)	.066 (3.5)	1.9657 (.0019)
C. familiaris NA			1.9568 (.0031)
C. latrans	.029 (4.9)		
C. aureus			
C. latrans	.519 (0.4)	.179 (1.8)	1.9836 (.0011)
C. familiaris EU			1.9790 (.0028)
C. latrans	.021 (5.5)		
C. familiaris NA			
C. aureus	.258 (1.3)	.938 (<0.1)	1.9291 (.0023)
C. familiaris EU			1.9294 (.0019)
C. aureus	.812 (0.1)	.007 (7.7)	1.9174 (.0018)
C. familiaris NA			1.9234 (.0012)
C. familiaris EU	.223 (1.5)	.004 (8.9)	1.9129 (.0020)
C. familiaris NA			1.9201 (.0012)
OI			
C.l. lycaon/baylei	.671 (0.2)	.383 (0.8)	2.0123 (.0011)
C. rufus			2.0096 (.0026)
C.l. lycaon/baylei	.002 (9.5)		
C. latrans			
C.l. lycaon/baylei	.076 (3.2)		
C. aureus			
C.l. lycaon/baylei	.797 (0.1)	.004 (8.4)	1.9996 (.0014)
C. familiaris EU			1.9791 (.0061)

Table 9 (continued)

Dependent Variable/ Comparison	PS (F)	PAGM (F)	AGMEAN (SE)
OI (continued)			
C.l. lycaon/baylei	.002 (10.3)		
C. familiaris (NA)			
C. rufus	.025 (5.2)		
C. latrans			
C. rufus	.158 (2.1)	.056 (3.8)	1.9171 (.0036)
C. aureus			1.9044 (.0034)
C. rufus	.585 (0.3)	.033 (4.5)	1.9331 (.0036)
C. familiaris EU			1.9145 (.0054)
C. rufus	.075 (3.3)		
C. familiaris NA			
C. latrans	.238 (1.4)	.038 (4.4)	1.9078 (.0013)
C. aureus			1.9011 (.0023)
C. latrans	.018 (5.9)		
C. familiaris EU			
C. latrans	.932 (<0.1)	.168 (1.9)	1.8845 (.0021)
C. familiaris NA			1.8904 (.0026)
C. aureus	.236 (1.5)	.067 (3.5)	1.8473 (.0019)
C. familiaris EU			1.8531 (.0025)
C. aureus	.290 (1.1)	.006 (8.0)	1.8317 (.0022)
C. familiaris NA			1.8399 (.0017)
C. familiaris EU	.051 (4.0)		
C. familiaris NA			
PW			
C.l. lycaon/baylei	.913 (<0.1)	<.001 (108)	1.8454 (.0022)
C. latrans			1.7932 (.0033)
C.l. lycaon/baylei	.298 (1.1)	<.001 (21.4)	1.8438 (.0023)
C. aureus			1.8035 (.0069)
C.l. lycaon/baylei	.262 (1.3)	.779 (295)	1.8207 (.0033)
C. familiaris EU/NA			1.8184 (.0050)
C. latrans	.519 (0.4)	.052 (3.9)	1.7311 (.0024)
C. aureus			1.7422 (.0042)
C. latrans	.342 (0.9)	<.001 (105)	1.7162 (.0030)
C. familiaris EU/NA			1.7698 (.0029)
C. aureus	.104 (2.7)	<.001 (181)	1.6925 (.0031)
C. familiaris EU/NA			1.7437 (.0020)

Table 9 (continued).

Dependent Variable/ Comparison	PS (F)	PAGM (F)	AGMEAN (SE)
MCW			
C.l. lycaon	.420 (0.7)	.004 (8.6)	1.8545 (.0015)
C.l. baylei			1.8619 (.0018)
C.l. lycaon	.965 (<0.1)	<.001 (126)	1.8499 (.0017)
C. rufus			1.8075 (.0028)
C.l. lycaon	.361 (0.8)	<.001 (41.8)	1.8302 (.0028)
C. latrans			1.7972 (.0027)
C.l. lycaon	.474 (0.5)	<.001 (21.6)	1.8283 (.0029)
C. aureus			1.7909 (.0055)
C.l. lycaon	.333 (0.9)	.085 (3.1)	1.8395 (.0026)
C. familiaris EU			1.8227 (.0075)
C.l. lycaon	.062 (3.6)		
C. familiaris NA			
C.l. baylei	.528 (0.4)	<.001 (206)	1.8462 (.0018)
C. rufus			1.7989 (.0023)
C.l. baylei	.937 (<0.1)	<.001 (57.7)	1.8255 (.0030)
C. latrans			1.7887 (.0022)
C.l. baylei	.794 (0.1)	<.001 (22.0)	1.8181 (.0035)
C. aureus			1.7799 (.0050)
C.l. baylei	.138 (2.3)	.048 (4.1)	1.8313 (.0034)
C. familiaris EU			1.8103 (.0075)
C.l. baylei	.478 (0.5)	.757 (0.1)	1.7885 (.0063)
C. familiaris NA			1.7921 (.0057)
C. rufus	.541 (0.4)	.012 (6.5)	1.7687 (.0025)
C. latrans			1.7773 (.0015)
C. rufus	.616 (0.2)	.330 (1.0)	1.7536 (.0033)
C. aureus			1.7596 (.0033)
C. rufus	.438 (0.6)	.005 (9.0)	1.7656 (.0034)
C. familiaris EU			1.7897 (.0052)
C. rufus	.327 (1.2)	<.001 (20.5)	1.7248 (.0065)
C. familiaris NA			1.7707 (.0041)
C. latrans	.941 (<0.1)	.827 (<0.1)	1.7553 (.0017)
C. aureus			1.7550 (.0029)
C. latrans	.085 (3.0)		
C. familiaris EU			
C. latrans	.304 (1.1)	<.001 (27.4)	1.7395 (.0029)
C. familiaris NA			1.7709 (.0036)
C. aureus	.122 (2.5)	<.001 (85.7)	1.7250 (.0022)
C. familiaris EU			1.7575 (.0028)

Table 9 (continued).

Dependent Variable/ Comparison	PS (F)	PAGM (F)	AGMEAN (SE)
MCW (continued)			
C. aureus	.255 (1.3)	<.001 (42.7)	1.7145 (.0030)
C. familiaris NA			1.7403 (.0023)
C. familiaris EU	.035 (4.7)		
C. familiaris NA			

*PAGM and AGMEAN are reported when slopes are assumed to be equal based on PS, i.e. when p>.1. PAGM and AGMEAN are also reported in several instances where PS yields a probability less than but very near .1. See text for explanation.

1986a). Thus, these two variables remain approximately proportional throughout the size range represented. Separate regression slopes for each group tend to be shallower, with the exception of C. latrans.

Regression lines for each group are shown on Figure 6. The regression lines here and on all figures in this chapter were derived by solving the appropriate regression equation for the two extreme values of X (CL) from each group. On Figure 6 the regression lines are all grouped tightly with no apparent major deviations from the overall trend. Quantitative comparisons (Table 9) reveal that C.l. baylei and C. rufus are indistinguishable, and both are transposed below C.l. lycaon. Because of its steeper slope, placement of the C. latrans regression is difficult to compare to other groups, though it is apparently similar to C.l. baylei. At the smaller end of the spectrum, the C. familiaris groups are indistinguishable from C. aureus. Both groups are transposed weakly below C.l. baylei, more strongly below C.l. lycaon, and apparently also below C. rufus.

The basic statistical pattern is slight downward transposition at smaller sizes. The largest wolf group is transposed above every other group, while all of the wolf groups are transposed above the dogs and jackals. The effect of the steeper slope exhibited by C. latrans is to connect the upwardly transposed wolf group regression lines

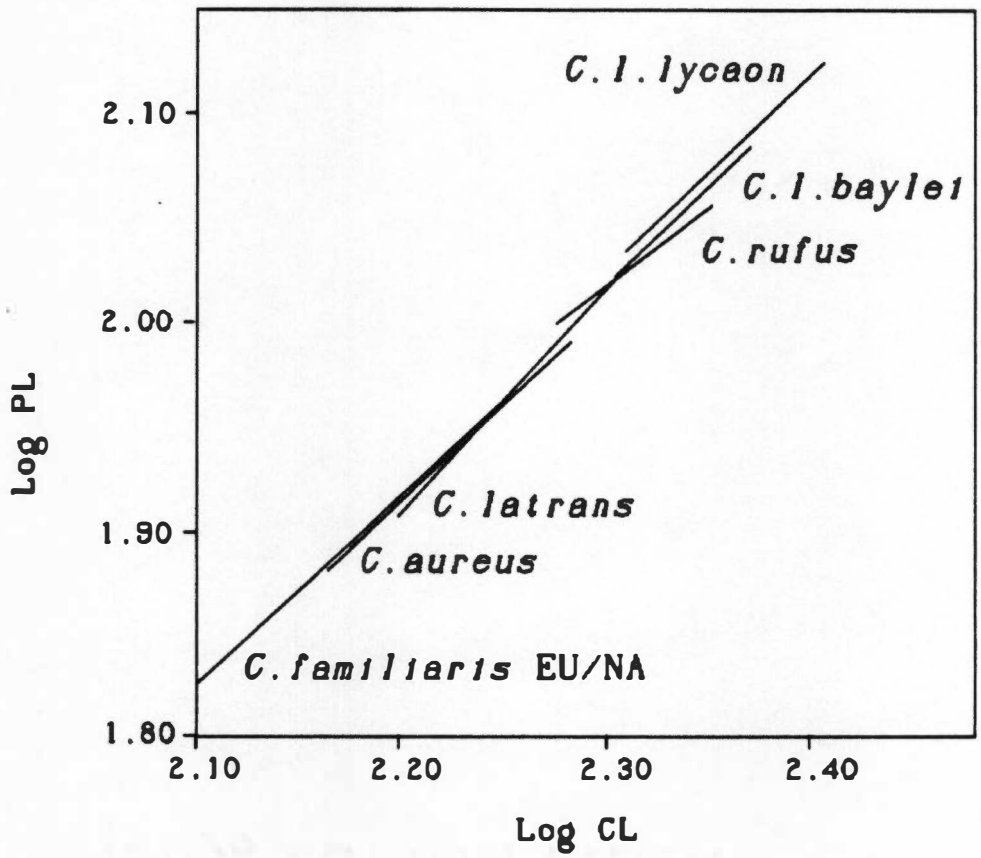


Figure 6. Static regression lines from analysis of PL x CL for adult canid groups.

with the downwardly transposed dog and jackal regression lines. None of the statistical differences are of great magnitude. The dogs fit comfortably within the general pattern, indicating that they are consistent with the broad allometric trend of isometry between these variables.

Tooth Row Length (IM2)

For this regression the slope coefficient of all the groups combined (0.927) suggests weak negative allometry (Table 8). Thus, larger groups like wolves exhibit proportionally shorter tooth rows than smaller groups. Removal of the dogs from this pooled regression has virtually no effect on the slope (0.937). Separate regression lines for each group vary around these interspecific slopes, with C. latrans the steepest (0.994) and C. rufus the shallowest (0.774).

Separate regression lines are illustrated on Figure 7. C.l. lycaon and baylei, pooled during preliminary analysis, are indistinguishable from C. rufus (Table 9). The situation with the smaller canids is more complicated than that for PL, partly because the two dog groups could not be pooled. The European dogs are indistinguishable from C. aureus, and both are transposed below the North American dogs. The C. lupus groups cannot be securely distinguished from the North American dogs, and are only weakly transposed above the European dogs. C. latrans is indistinguishable from the European dogs.

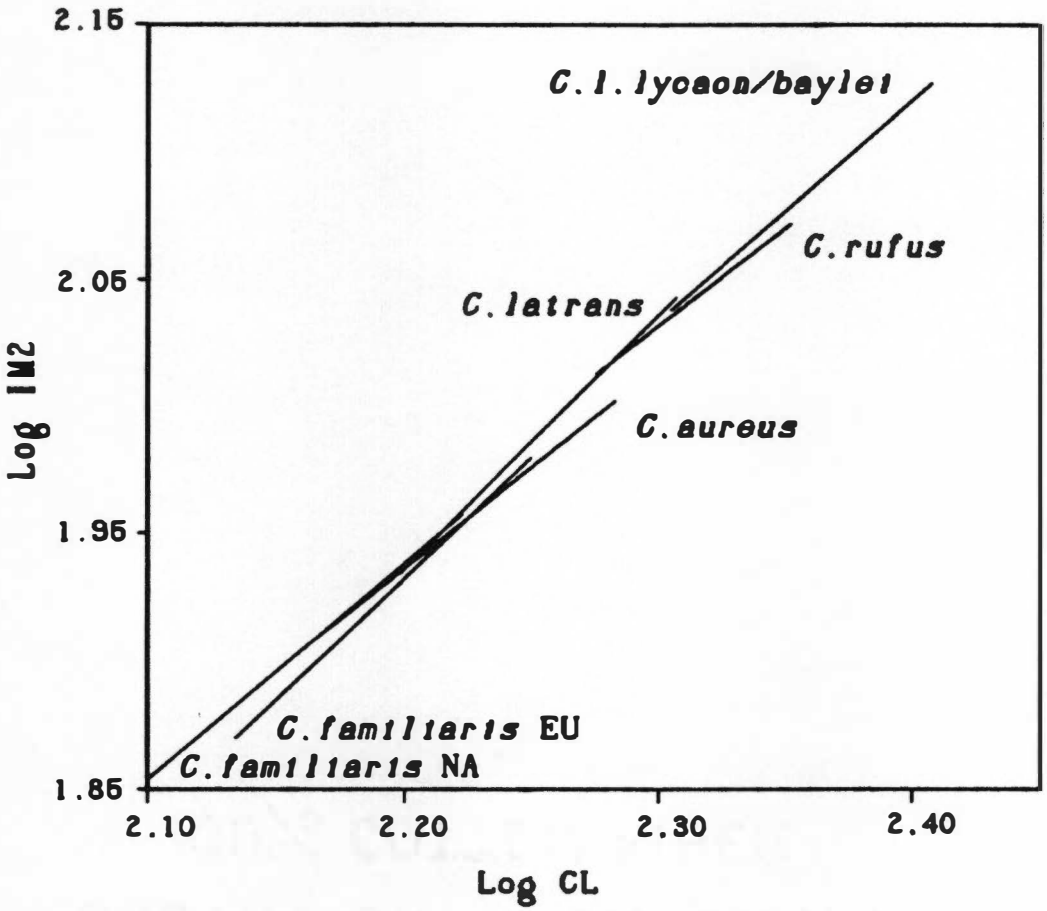


Figure 7. Static regression lines from analysis of IM2 x CL for adult canid groups.

The pattern yielded by the regression of this variable is best interpreted as follows. There are slight, statistically significant differences in slopes or elevations between groups. However, the pattern of transposition is discernable only at the broadest scale. C. lupus tends to be weakly transposed above smaller dogs and jackals, though in one instance (North American dogs) the transposition is probably insignificant (p=.104). At a finer scale, the smaller North American dogs are transposed above the slightly larger European dogs and jackals. In any case, differences are slight and the dogs fit within the general allometric trend. There are no major deviations from the general trend among any groups.

Lateral Face Length (OI)

The interspecific regression slope for all groups on this variable (1.094) reflects weak positive allometry (Table 8). Thus, larger groups have lateral face lengths that are proportionally slightly longer than smaller groups. Removal of the dogs from the pooled regression has no appreciable impact on the slope (1.093). Separate group regression slopes vary around these similar interspecific slopes. Lumer (1940) found that a measure of "snout length" exhibited strong positive allometry among different breeds of dogs, and that this pattern seemed to be reflected in ontogenetic growth.

Separate group regrssion lines are illustrated on

Figure 8. Like PL and IM2, OI reflects a tight pattern of scaling among the groups. The two C. lupus groups, pooled in preliminary analysis, are not significantly different from C. rufus (Table 9). At the other end of the size range, the two dog groups have different slopes, but the intersection of their regression lines reflects similarity in placement. The wolf groups are all transposed above the European dog group and, by subjective inference, the North American dog group. Because C. rufus is transposed above C. aureus, it is inferred that the C. lupus groups are as well.

Analysis of OI reveals a basic pattern of slight downward transposition at smaller sizes, at least on a broad scale. Largest wolf groups are transposed above the smaller dogs and jackals. C. latrans forms an intermediate group that connects them. However, C. aureus is transposed slightly below the smaller dog group. In all cases, differences in elevations are slight, as indicated by the frequent occurrence of probabilities associated with these tests that approach insignificance (see Table 9). There are no major deviaitons from the trend of weak positive allometry, and the dogs fit squarely within this trend.

Palatal Width (PW)

On this variable the interspecific regression slope of all groups combined (0.828) indicates marked negative allometry (Table 8). However, reduced correlations

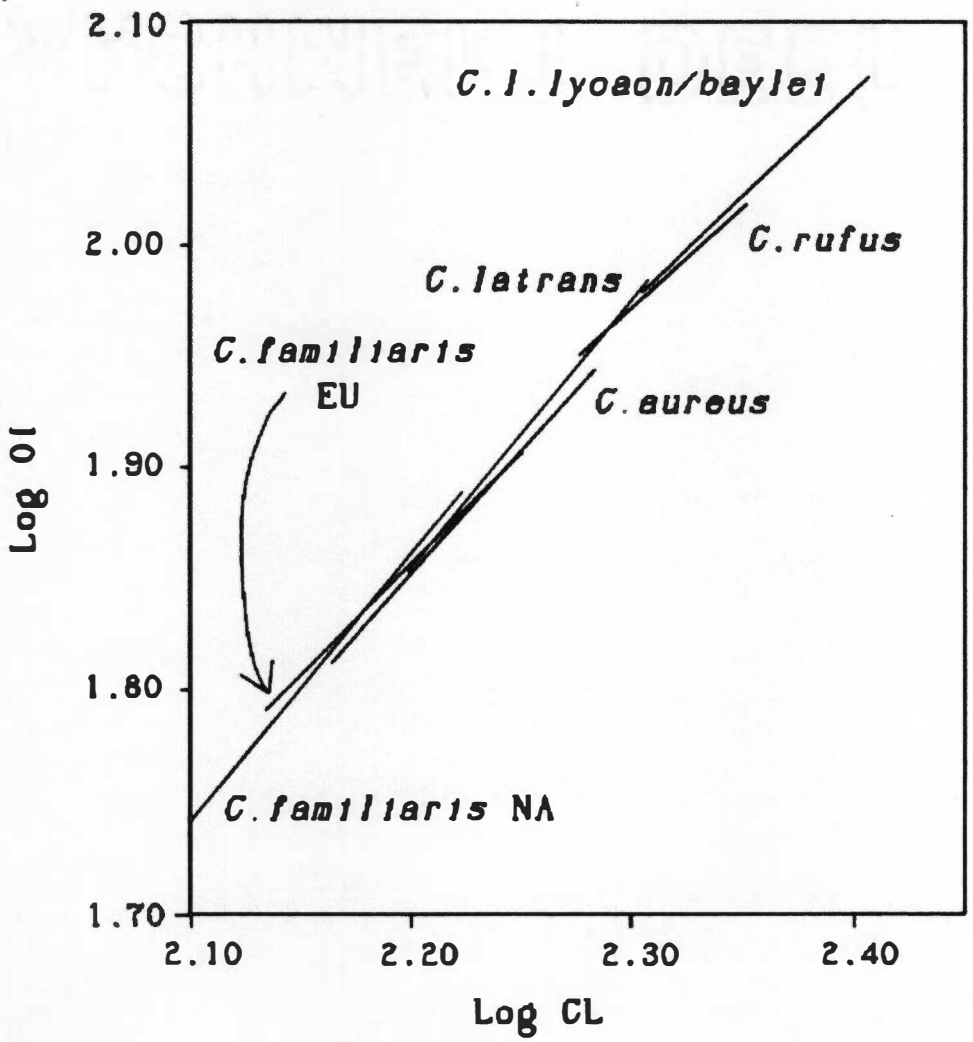


Figure 8. Static regression lines from analysis of OI x CL for adult canid groups.

relative to anterior cranial length variables portend greater variability in scaling relationships. When dogs are removed from the interspecific regression, the resulting slope of 1.144 is much steeper, indicating positive allometry. Wayne (1986a) found an approximately isometric relationship for this variable based on a broader range of wild canids.

Separate regression lines for this analysis are shown on Figure 9. It will be recalled that C. rufus was eliminated due to an insignificant correlation. Because interspecific regressions suggested deviation of this group from an overall trend, its location is shown by the placement of actual data points. The two C. lupus groups are transposed strongly above C. latrans and C. aureus (Table 9). By subjective inference, they are transposed above C. rufus as well. C. aureus is weakly transposed above C. latrans. Thus, they are similar, and both are probably similar to C. rufus. Among the wild canids a broad pattern separates the largest wolves from smaller and medium sized canids by strong transposition. However, C. rufus may be transposed farther down than would be expected given its size. Alternatively, the C. lupus groups may be regarded as deviant from a trend exhibited by the other wild canids.

Regardless of how the pattern among wild canids is interpreted, the dogs are distinct. They are transposed

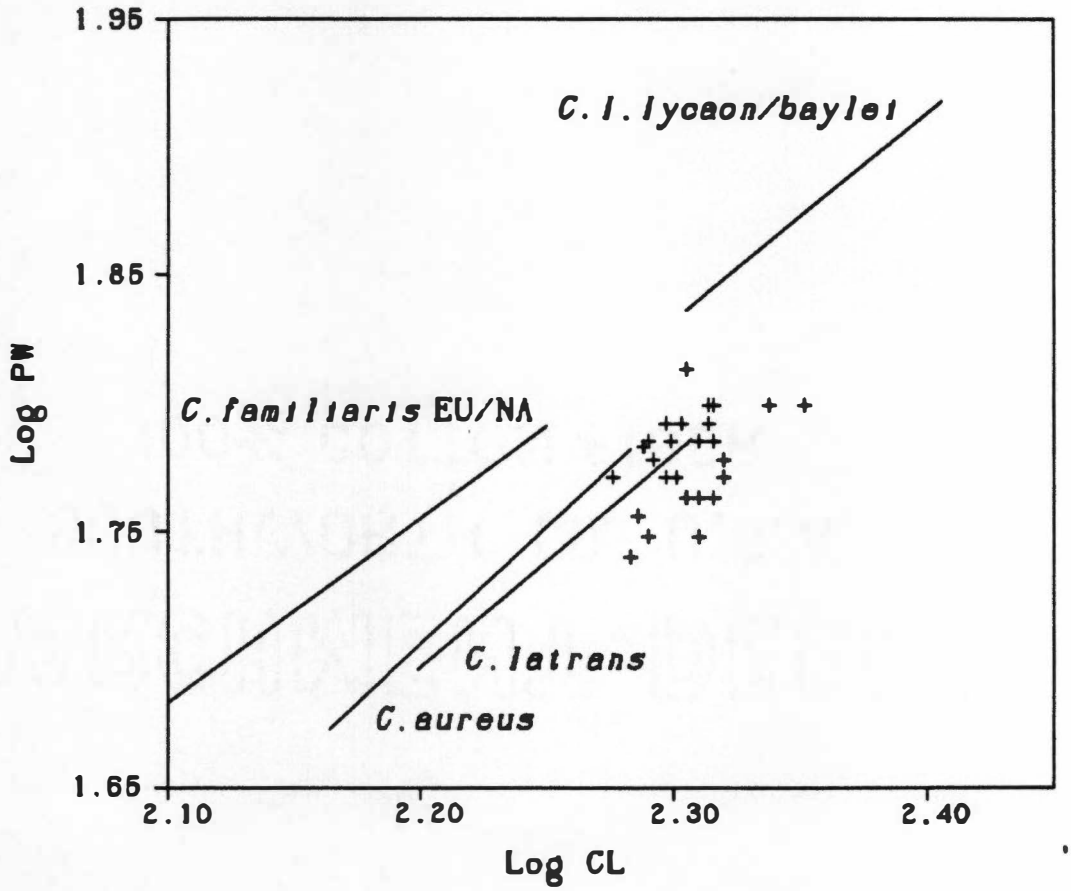


Figure 9. Static regression lines from analysis of PW x CL for adult canid groups. Crosses are data points for C. rufus.

strongly above both C. aureus and C. latrans. From inspection of Figure 9 it can be seen that the dogs have proportionally wider palates than either of these groups. The dogs are not significantly different from C. lupus in slope or elevation. They have proportionally wider palates than C. lupus as a consequence of a common negatively allometric regression slope. However, the disparity between the dogs and C. lupus is not as pronounced as that between the dogs and other wild canids. For example, the average ratio of PW/MCW among the dogs is .365, while for C. aureus it is .320 and for C. lupus it is .332. In short, the dogs have proportionally wider palates than any wild canid group. This morphological pattern does not relate to any trend seen among wild canids.

Maximum Cranial Width (MCW)

On this variable the interspecific regression slope of all groups combined is 0.704, indicating strong negative allometry (Table 8, page 102). Removal of the dogs from the regression elevates the slope (0.861), but negative allometry is maintained in the wild canids. Thus, smaller groups have proportionally wider cranial vaults compared to larger groups. Wayne (1986a) also found negative allometry with this variable in wild canids and domestic dog breeds.

Separate regression lines for the groups are shown on Figure 10. C.l. baylei is transposed slightly above C.l. lycaon, and both are transposed strongly above C. rufus, C.

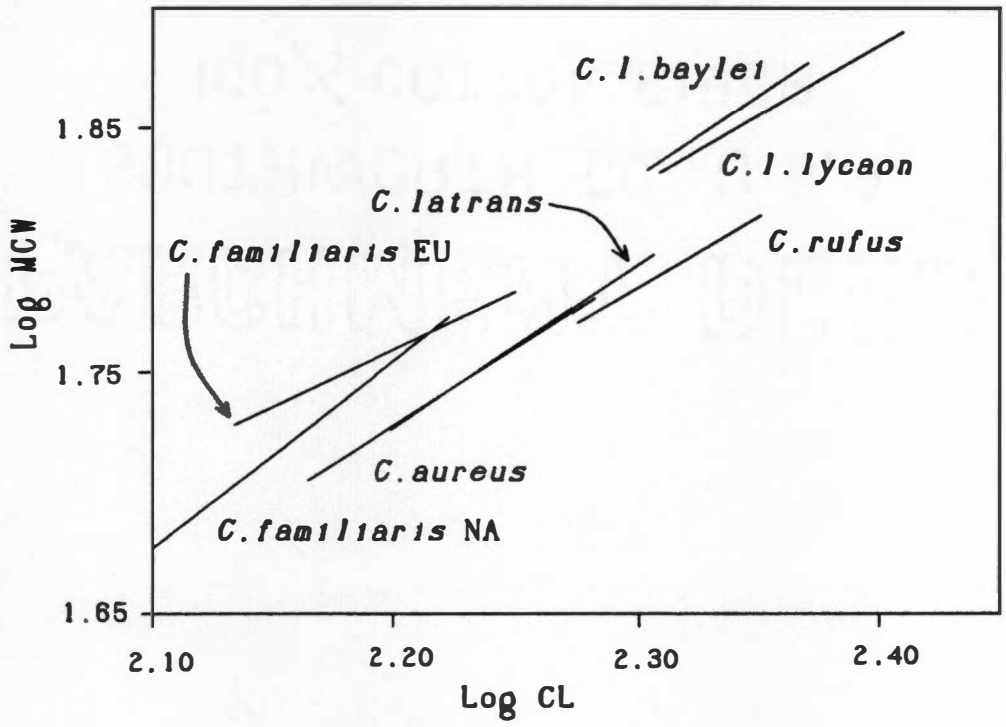


Figure 10. Static regression lines from analysis of MCW x CL for adult canid groups.

latrans, and C. aureus (Table 9, page 104). The latter three groups form a cluster; C. rufus is transposed below C. latrans, but neither is significantly different from C. aureus. Thus, the basic pattern is significant downward transposition separating largest wolves (C. lupus) from smaller wolves (C. rufus) and the other smaller wild canids. Within these groups, there are minor reversals in this transpositional trend. Only C. rufus provides a case for significant deviation from this trend. Given its size, one might expect its elevation to be higher. However, the magnitude of this deviation is not great.

The dogs deviate from the basic trend. Their sharp upward transposition relative to similar sized wild canids and C. rufus (Table 9, page 104) signifies cranial vaults that are considerably wider than the basic allometric trend would predict. Their average ratio of MCW/CL is .363. The most similar group is C. aureus, which exhibits a corresponding ratio of .334. The magnitude of this difference is greater than that seen among similar sized wild canid groups.

Unlike PW, the dog regression lines are not always statistically indistiguishable from the C. lupus regressions. However, the differences are slight. The European dogs are weakly transposed below C.l. lycaon ($p=.085$) and C.l. baylei ($p=.048$), while the North American dogs are indistinguishable from C.l. baylei and cannot be

directly compared to C.l. lycaon due to inequality of slopes (see Table 9, page 104). The dogs have proportionally wider vaults than the much larger C. lupus groups due to similarity in negatively allometric slopes of their regression lines. Overall, the dogs are morphologically distinct. They have cranial vault widths that are substantially greater than would be expected from the basic allometric trend seen among wild canids.

Analysis of Dental Variables

Analysis of dental variables is conducted according to the same format as the analysis of cranial variables. Summary statistics on dental variables from the different canid groups are presented on Table 10. Table 11 presents correlations between these variables and CL for each group. Five of the seven groups exhibit insignificant correlations for P1. Thus, separate regressions are not calculated and analyzed for this variable. At a taxonomic level, C. rufus exhibits insignificant correlations on four of the five variables. This undoubtedly reflects the small sample and the limited range of size variation within that sample. Separate regressions are not performed for C. rufus. However, this sample is included in the interspecific regressions.

C.l. baylei is eliminated from analysis on P2 due to an insignificant correlation. Like C. rufus it is included

Table 10. Means, standard deviations (SD), and sample sizes (n) on dental measurements from adult canids.

Group	Measurement (mm)				
	CAN	P1	P2	P3	LC
C.l. lycaon					
Mean	14.40	7.49	13.74	15.54	23.88
SD	1.178	0.585	0.903	0.842	1.203
n	58	58	58	58	58
C.l. baylei					
Mean	13.03	6.43	13.18	14.54	23.44
SD	1.014	0.468	0.968	0.874	0.852
n	30	29	30	29	42
C. rufus					
Mean	11.24	5.69	11.43	12.71	20.83
SD	0.786	0.575	0.774	0.502	0.949
n	24	24	24	24	29
C. latrans					
Mean	10.32	5.37	10.72	12.29	19.87
SD	0.930	0.467	0.886	0.803	0.986
n	61	62	62	62	62
C. aureus					
Mean	8.77	4.72	8.79	10.10	17.24
SD	0.818	0.386	0.720	0.677	0.955
n	29	29	29	29	28
C. familiaris EU					
Mean	9.99	4.37	9.12	10.49	16.80
SD	1.220	0.600	1.209	0.990	1.415
n	18	18	18	18	18
C. familiaris NA					
Mean	9.43	4.27	9.09	10.56	16.71
SD	0.958	0.421	0.773	0.791	0.980
n	47	42	47	49	49

Table 11. Correlations (Pearson's R) between dental variables and CL, and associated probabilities (in parentheses) for each group of adult canids.

Group	Variable				
	CAN	P1	P2	P3	LC
C.l. lycaon	.606 (.0001)	.569 (.0001)	.609 (.0001)	.481 (.0001)	.663 (.0001)
C.l. baylei	.604 (.0004)	.274* (.1508)	.450* (.0126)	.622 (.0003)	.616 (.0001)
C. rufus	.512* (.0106)	.134* (.5161)	.476* (.0186)	.536 (.0070)	.412* (.0261)
C. latrans	.690 (.0001)	.316* (.0125)	.545 (.0001)	.485 (.0001)	.567 (.0001)
C. aureus	.549 (.0021)	.433* (.0188)	.567 (.0013)	.542 (.0024)	.504 (.0021)
C. familiaris EU	.759 (.0003)	.548* (.0186)	.718 (.0008)	.717 (.0008)	.751 (.0003)
C. familiaris NA	.716 (.0001)	.465 (.0019)	.432 (.0024)	.506 (.0002)	.546 (.0001)

*Denotes insignificant correlation (p>.01).

in the interspecific regression for this variable. Because interspecific regressions did not suggest major deviations among groups with insignificant correlations (see Appendix B), data points for eliminated groups are not indicated on illustrations. Like analysis of cranial variables, groups belonging to the same species were tested for homogeneity of slopes and elevations in order to pool the samples where appropriate. As a result the dogs were pooled on CAN, while the two C. lupus groups were pooled on P2.

Table 12 presents summary statistics for regressions calculated for all dental variables. Table 13 presents analysis of covariance results for comparisons of all separate groups. Like analysis of cranial variables, regressions of each variable against CL are discussed sequentially.

Canine Alveolar Length (CAN)

Interspecific regression of this variable for all groups yields an approximately isometric slope of 1.017 (Table 11). However, removal of the dogs steepens the slope to 1.309, resulting in strong positive allometry among wild canids. Thus, among wild canids the largest groups have proportionally longer canine alveoli than smaller canids. Separate group regressions yield substantial variability in slopes, ranging from 0.754 in C. aureus to 1.412 in C latrans. However, because of low correlations (Table 12) and wide scatter around the

Table 12. Least squares slopes (LS) and associated standard errors (SE), least squares Y-intercepts (Y-INT), correlations (R), and reduced major axis slopes (RMA) from regressions of dental variables against CL for adult canids (all variables log transformed).

Dependent Variable	Group	Slope* (LS)	SE	Y-INT	R	Slope (RMA)
CAN	All Groups	1.017	.032	-1.265	.89	1.140
CAN	Wild Canids	1.309	.037	-1.946	.93	1.408
CAN	C.l. lycaon	0.987	.173	-1.172	.66	1.495
CAN	C.l. baylei	1.190	.297	-1.670	.60	1.971
CAN	C. latrans	1.412	.193	-2.181	.69	2.045
CAN	C. aureus	0.754	.221	-0.716	.55	1.372
CAN	C. familiaris EU/NA	1.143	.128	-1.511	.75	1.530
P1	All Groups	1.177	.033	-1.929	.91	1.293
P1	Wild Canids	1.167	.045	-1.905	.87	1.341
P2	All Groups	1.011	.027	-1.255	.92	1.104
P2	Wild Canids	1.144	.034	-1.564	.92	1.239
P2	C.l. lycaon	0.783	.136	-0.711	.61	1.286
P2	C. latrans	1.048	.208	-1.342	.55	1.923
P2	C. aureus	0.704	.197	-0.606	.57	1.242
P2	C. familiaris EU	1.306	.317	1.306	.72	1.821
P2	C. familiaris NA	0.572	.178	-0.285	.43	1.323
P3	All Groups	0.917	.023	-0.985	.92	0.993
P3	Wild Canids	1.051	.031	-1.297	.92	1.142
P3	C.l. lycaon	0.516	.126	-0.027	.48	1.073
P3	C.l. baylei	1.015	.245	-1.211	.62	1.630
P3	C. latrans	0.716	.167	-0.531	.48	1.477
P3	C. aureus	0.543	.162	-0.190	.54	1.002
P3	C. familiaris EU	0.899	.219	-0.951	.72	1.255
P3	C. familiaris NA	0.592	.147	-0.264	.51	1.169
P4	All Groups	0.844	.017	-0.614	.95	0.890
P4	Wild Canids	0.851	.023	-0.630	.93	0.915
P4	C.l. lycaon	0.644	.097	-0.142	.66	0.971
P4	C.l. baylei	0.604	.122	-0.042	.62	0.981
P4	C. latrans	0.638	.120	-0.145	.57	1.125
P4	C. aureus	0.422	.142	0.309	.50	0.836
P4	C. familiaris EU	0.853	.188	-0.646	.75	1.136
P4	C. familiaris NA	0.506	.113	0.123	.55	0.926

*All least squares slopes are significantly different from zero ($p<.01$).

Table 13. Analysis of covariance results from paired comparisons of adult canid cranial measurements, with CL as a covariate (all variables log transformed). Included are F-ratios (F) and associated probabilities from tests of homogeneity of slopes (PS), F-ratios and associated probabilities from tests of equality of least square means (PLSM), and least square means (LSMEAN) with associated standard errors (SE)*.

Dependent Variable/ Comparison	PS (F)	PAGM (F)	AGMEAN (SE)
CAN			
C.l. lycaon	.565 (0.3)	.002 (10.2)	1.1497 (.0038)
C.l. baylei			1.1274 (.0055)
C.l. lycaon	.105 (2.7)	.024 (5.2)	1.0985 (.0075)
C. latrans			1.0674 (.0072)
C.l. lycaon	.392 (0.7)	.002 (10.4)	1.1095 (.0083)
C. aureus			1.0357 (.0156)
C.l. lycaon	.477 (0.5)	.295 (1.1)	1.0523 (.0105)
C. familiaris EU/NA			1.0725 (.0094)
C.l. baylei	.544 (0.4)	.909 (<0.1)	1.0444 (.0097)
C. latrans			1.0460 (.0054)
C.l. baylei	.268 (1.3)	.057 (3.8)	1.0532 (.0132)
C. aureus			1.0034 (.0136)
C.l. baylei	.823 (<0.1)	.012 (6.6)	0.9871 (.0138)
C. familiaris EU/NA			1.0376 (.0069)
C. latrans	.024 (5.3)		
C. aureus			
C. latrans	.258 (1.3)	<.001 (45.3)	0.9590 (.0060)
C. familiaris EU/NA			1.0290 (.0057)
C. aureus	.117 (2.5)	<.001 (60.2)	0.9271 (.0062)
C. familiaris EU/NA			0.9854 (.0041)
P2			
C.l. lycaon	.285 (1.2)	.102 (2.7)	1.0922 (.0071)
C. latrans			1.0709 (.0067)
C.l. lycaon	.727 (0.1)	<.001 (15.4)	1.0970 (.0069)
C. aureus			1.0228 (.0129)
C.l. lycaon	.057 (3.7)		
C. familiaris EU			
C.l. lycaon	.350 (0.9)	.011 (6.8)	1.0817 (.0100)
C. familiaris NA			1.0257 (.0122)
C. latrans	.237 (1.4)	.013 (6.5)	1.0108 (.0050)
C. aureus			0.9810 (.0086)

Table 13 (continued).

Dependent Variable/ Comparison	PS (F)	PAGM (F)	AGMEAN (SE)
P2 (continued)			
C. latrans	.447 (0.6)	.496 (0.5)	1.0102 (.0051)
C. familiaris EU			1.0205 (.0122)
C. latrans	.086 (3.0)		
C. familiaris NA			
C. aureus	.092 (3.0)	.077 (3.3)	0.9401 (.0068)
C. familiaris EU			0.9600 (.0086)
C. aureus	.627 (0.2)	<.001 (13.5)	0.9326 (.0063)
C. familiaris NA			0.9633 (.0049)
C. familiaris EU	.030 (5.0)		
C. familiaris NA			
P3			
C.l. lycaon	.072 (3.3)		
C.l. baylei			
C.l. lycaon	.338 (0.9)	<.001 (16.2)	1.1606 (.0060)
C. latrans			1.1170 (.0056)
C.l. lycaon	.892 (<0.1)	<.001 (37.8)	1.1623 (.0060)
C. aureus			1.0603 (.0113)
C.l. lycaon	.086 (3.0)		
C. familiaris EU			
C.l. lycaon	.698 (0.2)	<.001 (11.7)	1.1429 (.0088)
C. familiaris NA			1.0793 (.0104)
C.l. baylei	.353 (0.9)	.248 (1.4)	1.1212 (.0083)
C. latrans			1.1076 (.0045)
C.l. baylei	.131 (2.3)	.001 (11.4)	1.1157 (.0103)
C. aureus			1.0494 (.0103)
C.l. baylei	.734 (0.1)	.794 (0.1)	1.1095 (.0097)
C. familiaris EU			1.1033 (.0149)
C.l. baylei	.203 (1.6)	.175 (1.9)	1.0927 (.0137)
C. familiaris NA			1.0634 (.0085)
C. latrans	.460 (0.6)	<.001 (22.4)	1.0757 (.0040)
C. aureus			1.0312 (.0069)
C. latrans	.482 (0.5)	.268 (1.2)	1.0759 (.0039)
C. familiaris EU			1.0631 (.0094)
C. latrans	.582 (0.3)	.453 (0.6)	1.0632 (.0055)
C. familiaris NA			1.0549 (.0067)
C. aureus	.184 (1.8)	.018 (6.0)	1.0017 (.0050)
C. familiaris EU			1.0217 (.0064)
C. aureus	.828 (0.1)	<.001 (24.0)	0.9942 (.0053)
C. familiaris NA			1.0280 (.0040)

Table 13 (continued).

Dependent Variable/ Comparison	PS (F)	PAGM (F)	AGMEAN (SE)
P3 (continued)			
C. familiaris EU	.239 (1.4)	.049 (4.2)	1.0093 (.0070)
C. familiaris NA			1.0261 (.0041)
LC			
C.l. lycaon	.814 (<0.1)	.057 (3.7)	1.3714 (.0021)
C.l. baylei			1.3781 (.0025)
C.l. lycaon	.967 (<0.1)	.025 (5.2)	1.3456 (.0044)
C. latrans			1.3275 (.0041)
C.l. lycaon	.171 (1.9)	<.001 (15.9)	1.3490 (.0048)
C. aureus			1.2948 (.0094)
C.l. lycaon	.224 (1.4)	.040 (4.38)	1.3487 (.0042)
C. familiaris EU			1.3164 (.0120)
C.l. lycaon	.359 (0.8)	<.001 (11.9)	1.3290 (.0068)
C. familiaris NA			1.2795 (.0080)
C.l. baylei	.859 (<0.1)	<.001 (13.1)	1.3423 (.0046)
C. latrans			1.3163 (.0033)
C.l. baylei	.354 (0.9)	<.001 (26.6)	1.3367 (.0052)
C. aureus			1.2755 (.0081)
C.l. baylei	.241 (1.4)	.024 (5.4)	1.3367 (.0052)
C. familiaris EU			1.3008 (.0111)
C.l. baylei	.623 (0.2)	<.001 (18.7)	1.3231 (.0078)
C. familiaris NA			1.2621 (.0068)
C. latrans	.231 (1.5)	<.001 (15.0)	1.2872 (.0030)
C. aureus			1.2592 (.0054)
C. latrans	.277 (1.2)	.016 (6.1)	1.2860 (.0030)
C. familiaris EU			1.2643 (.0071)
C. latrans	.431 (0.6)	.003 (9.4)	1.2755 (.0041)
C. familiaris NA			1.2503 (.0050)
C. aureus	.066 (3.6)		
C. familiaris EU			
C. aureus	.644 (0.2)	.826 (<.1)	1.2279 (.0043)
C. familiaris NA			1.2267 (.0032)
C. familiaris EU	.096 (2.9)	.122 (2.5)	1.2150 (.0056)
C. familiaris NA			1.2254 (.0033)

*PAGM and AGMEAN are reported when slopes are assumed to be equal based on PS, i.e. when p>0.1. PAGM and AGMEAN are also reported in several instances where PS yields a probability less than but very near 0.1.

regression lines, the only significant slope difference is that between C. aureus and C. latrans (Table 13).

Separate group regression lines are shown on Figure 11. C.l. lycaon is transposed above all other wild canids. C.l. baylei is not significantly different from C. latrans, but is transposed weakly above C. aureus. The dogs are transposed strongly above C. latrans and C. aureus, less strongly above C.l. baylei. Thus, among wild canids smaller groups tend to be transposed below larger groups.

The dogs deviate from the overall allometric trend shown by wild canids. They are transposed strongly above C. latrans, less strongly above C.l. baylei. They are statistically indistinguishable from C.l. lycaon. The dogs have proportionally longer canine alveoli than similar sized coyotes or jackals.

First Premolar Alveolar Length (P1)

Interspecific regressions for all groups on this small tooth yield a positively allometric slope coefficient of 1.177 (Table 12). Removal of the dogs from this regression has virtually no effect on the slope (1.167). As explained above, separarate regressions were not performed due to numerous insignificant correlations. Inspection of bivariate plots (Appendix B, Figure 34) suggested no significant deviations from the overall trend among the wild canids.

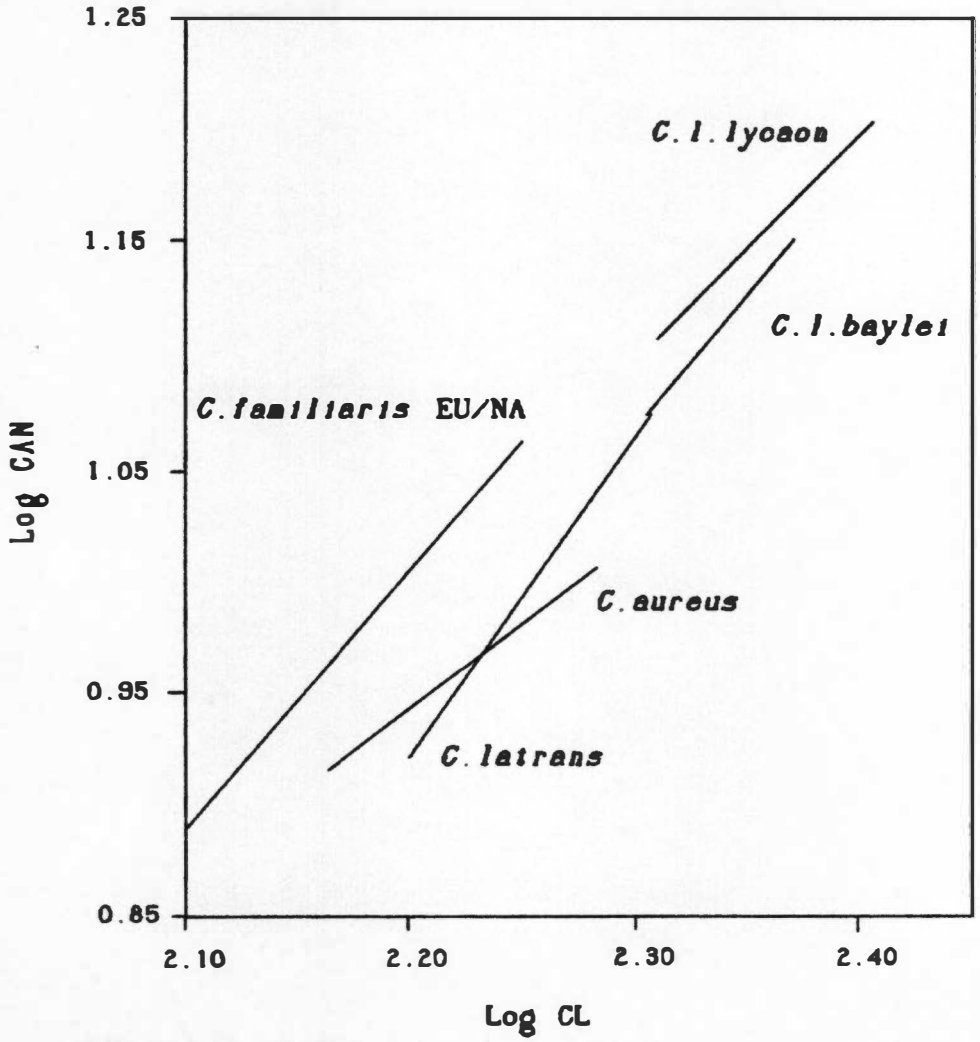


Figure 11. Static regression lines from analysis of CAN x CL for adult canid groups.

Second Premolar Alveolar Length (P2)

The interspecific regression of all groups for this variable yields an approximately isometric slope coefficient of 1.011 (Table 12). Removal of the dogs steepens the interspecific slope appreciably (1.144). Thus, among wild canids, this variable shows marked positive allometry.

Separate group regression lines are shown on Figure 12. C.l. lycaon may be slightly transposed above C. latrans, but the probability value associated with the elevation test (.102) is borderline (Table 13). C.l. lycaon is clearly transposed above C. aureus and the North American dogs. Both C. latrans and the North American dogs are transposed above C. aureus. The extremely steep slope yielded by the European dogs complicates comparisons. The European dogs are probably transposed above C. aureus, though the slope test is ambiguous (p=.092), shaking confidence in an almost equally ambiguous elevation test (p=.077).

The wild canids exhibit a general pattern of downward transposition at smaller sizes. The dogs deviate from this trend, exhibiting elevations apparently most similar to larger C. latrans. In turn, both dog groups are apparently transposed above C. aureus, though divergent slopes complicate these comparisons. Dogs tend to have proportionally longer P2 alveoli than comparably sized wild

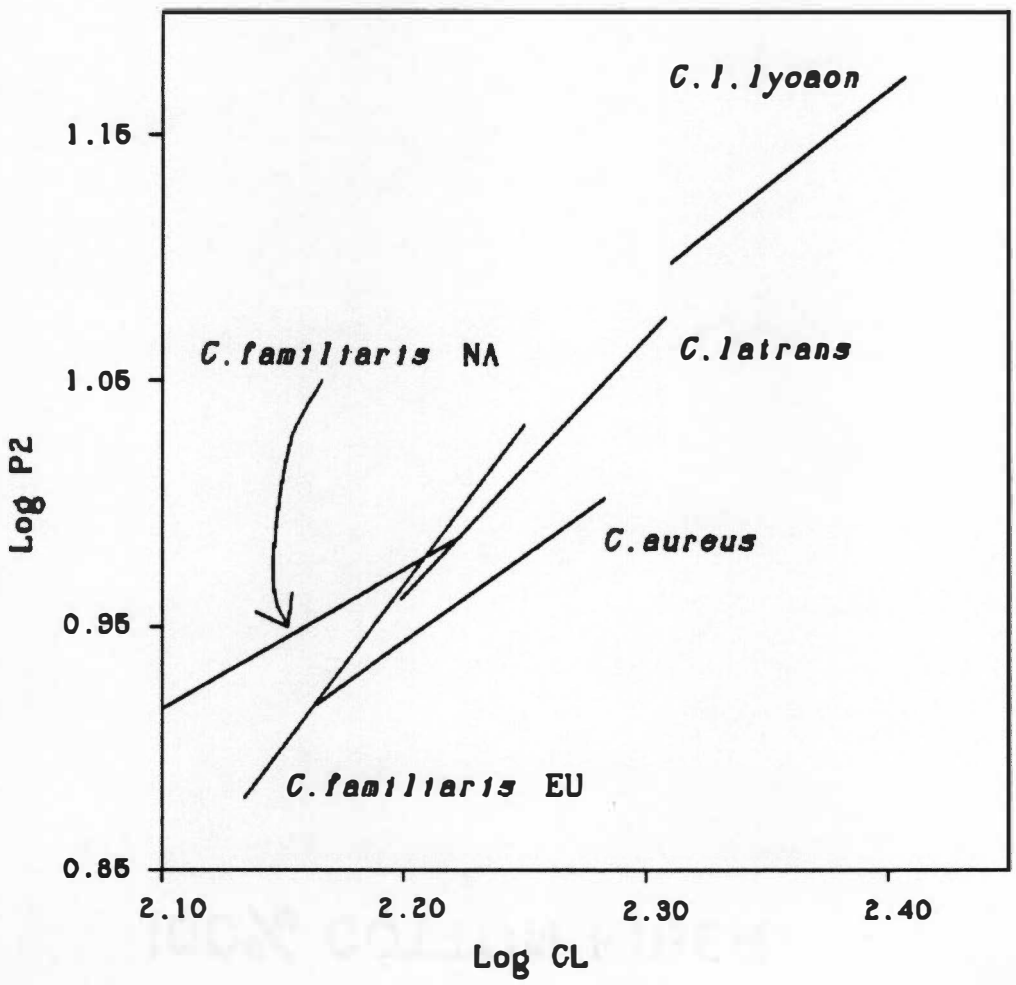


Figure 12. Static regression lines from analysis of P2 x CL for adult canid groups.

canids.

Third Premolar Alveolar Length (P3)

The interspecific regression of all groups on this variable yields a slightly negatively allometric slope coefficient of 0.917 (Table 12). However, an interspecific regression of wild canids yields a steeper slope of 1.051. Thus, among wild canids this bivariate relationship is approximately isometric, tending towards weak positive allometry. Wayne (1986a) found weak positive allometry for P3 crown length with a larger series of wild canids, and negative allometry for dog breeds.

Separate group regression lines are shown on Figure 13. C.l. lycaon is strongly transposed above C. latrans, while C. latrans is, in turn, strongly transposed above C. aureus (Table 13). C.l. baylei exhibits a different slope from C.l. lycaon, but is not significantly different from C. latrans, and is transposed above C aureus. Neither C.l. baylei nor C. latrans are distinguishable from either of the dog groups. Both dog groups are transposed above C. aureus. The two dog groups exhibit elevations that are only weakly separated (p=.049).

The pattern is similar to that for P2. Among wild canids smaller groups tend to be transposed down from larger groups, though C.l. baylei is apparently similar to C. latrans. The dog groups are clearly different, with elevations most similar to C. latrans and C.l. baylei. One

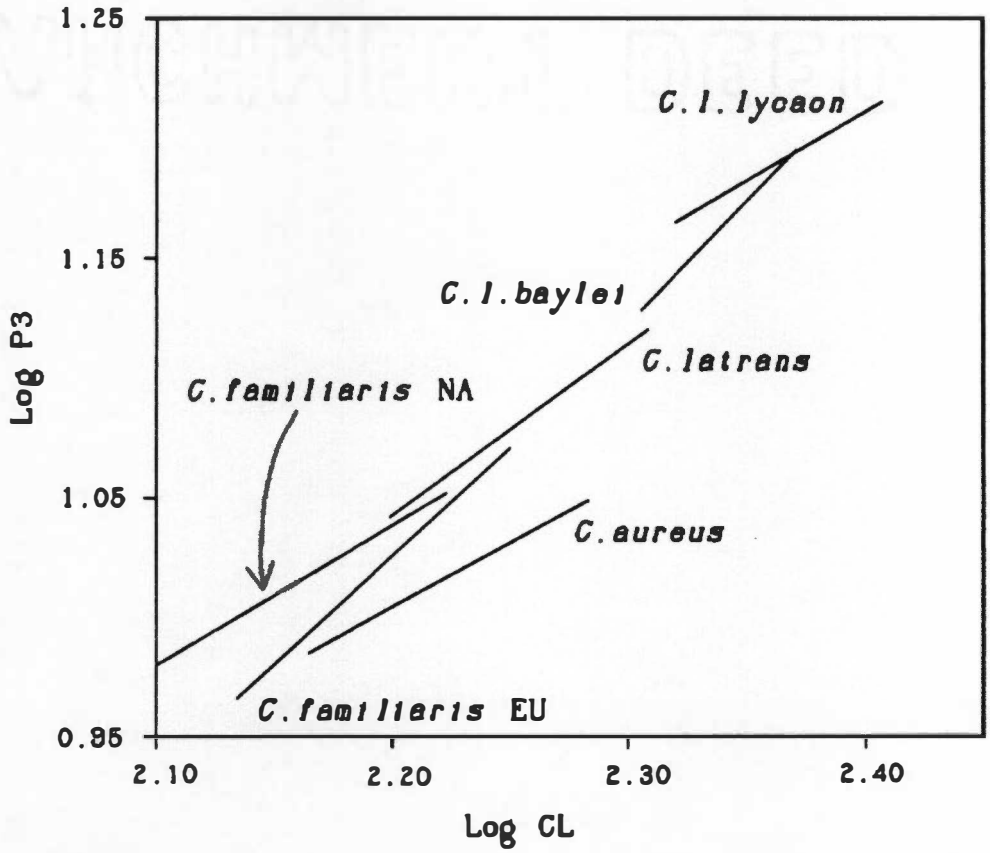


Figure 13. Static regression lines from analysis of P3 x CL for adult canid groups.

would expect them to be located near C. aureus; instead, they are transposed above. Thus, the dogs are not consistent with the broad allometric trend seen in wild Canis. They exhibit proportionally longer P3 alveoli than comparably sized wild canids.

Carnassial Crown Length (P4)

The interspecific regression for all groups on LC yields a negatively allometric slope coefficient of 0.844 (Table 12). Unlike previous dental variables, removal of the dogs has no significant impact on that slope. Thus, larger groups have proportionally shorter carnassials than smaller groups. Wayne (1986a) found positive allometry for this variable among wild canids but strong negative allometry among dog breeds.

Separate group regression lines are shown on Figure 14. C.l. baylei is slightly transposed above C.l. lycaon (p=.057--Table 13). Both are transposed above C. latrans which is, in turn, strongly transposed above C. aureus. Thus, the wild canids exhibit a general pattern of downward transposition at smaller sizes. The weak transposition of C.l. baylei above C.l. lycaon represents a minor deviation from that trend.

Unlike other dental variables, the dogs are consistent with this trend. Both dog groups are transposed below the C. lupus groups and C. latrans. The North American dogs are not significantly different from C. aureus, while the

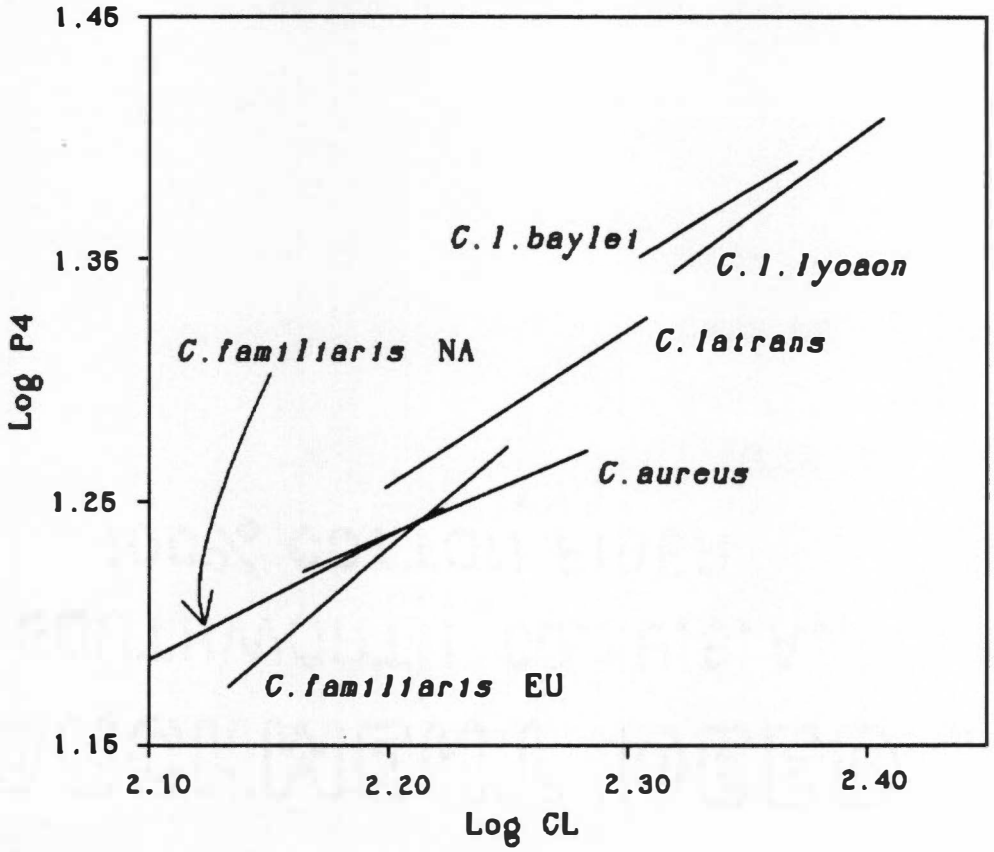


Figure 14. Static regression lines from analysis of P4 x CL for adult canid groups.

European dogs cannot be objectively compared due to inequality of slopes. However, it can be seen from the intersection of the European dog regression line with the C. aureus line that they are similar. The dogs are only slightly different from each other, as reflected by the borderline probabilities (.096 for slope, .122 for elevation) associated with significance tests (Table 13).

Evaluation of Static Allometry

Anterior cranial length measurements (PL, IM2, OI), all highly correlated with CL, are tightly scaled among all groups. There are no significant deviations from the overall allometric trend seen with each variable. In contrast, cranial width measurements (PW, MCW), exhibiting lower correlations with CL, are more variable. Broad allometric trends are evident but there are deviations from those trends. Among the wild canids deviations are relatively minor. Among the prehistoric dogs deviations are pronounced. The dogs are transposed far higher than would be expected given their size. They have proportionally wider cranial dimensions than any wild canids. On PW the disparity is greatest in comparison to similar sized jackals and coyotes. On MCW the disparity is pronounced relative to all groups, but especially wolves.

These results are consistent with the findings of Wayne (1986a). It will be recalled that Wayne found high

correspondence between static allometries of modern dog breeds and wild canids with the scaling of cranial length variables against skull length. In contrast, cranial width and depth variables showed divergent patterns. Small dog breeds always had wider cranial dimensions than similar sized foxlike canids. As a consequence, dogs were found to be morphologically similar only to closely related wolf-like genera.

Results here augment Wayne's observations. Taxa in this study are all from a single genus; they are all closely related and "wolf-like" (sensu Wayne 1986a). Yet, dogs are morphologically distinguishable from similar sized individuals of other taxa. Their divergent patterns of static variation are clearly discernable within a restricted range of "wolf-like" taxa. The nature of that divergence is identical to that found by Wayne at a more general taxonomic level.

With respect to anterior cranial length variables, Wayne (1986a) found high correspondence between static allometries of dog breeds, static allometries of wild canids, and ontogenetic allometries of dog breeds. Conversely, cranial width and depth variables differed. Static and ontogenetic allometries of dog breeds were similar, but both diverged from interspecific wild canid allometries. Thus, morphology of dogs is constrained to ontogenetic boundaries on all variables. In wild canids,

only anterior cranial length variables mirror dog ontogeny.

These findings, coupled with results here, provide the basis for predictions concerning analysis of ontogenetic allometry. Dogs should exhibit evidence of ontogenetic scaling with wolves on all cranial dimensions. Other wild canids should appear ontogenetically scaled with wolves on anterior cranial length dimensions only. However, C. rufus and C. latrans may correspond closely (see Chapter IV). In any case, major deviations from these predictions would suggest that causes other than simple allometric or ontogenetic scaling underly morphological evolution in these groups. These problems are dealt with in greater detail in the next chapter.

Analysis of dental allometry is characterized by consistently weaker intragroup correlations between tooth dimensions and condylobasal length, along with substantial variability in scaling relationships among groups. Only the carnassial (P4) exhibits a tight interspecific scaling pattern. This reduced variability is not surprising given the morphological complexity of carnassial teeth in canids (Pengilly 1984). Conversely, greater variability in other premolars and the canine is consistent with their simpler morphological or occlusal characteristics (Gingerich and Winkler 1979; Pengilly 1984).

Wayne (1986a) found that wolves had proportionally longer post-canine teeth than dogs of comparable size. He

suggested that such tooth dwarfism is a reflection of functional rather than developmental differences, presumably related to "artificial" versus "natural" selection (Wayne 1986a:247). Describing this phenomenon as "dwarfism" obscures the fact that it applies only to largest dogs. Small dogs have proportionally longer teeth. In any case, proportional tooth size reduction under domestication is apparently a delayed phenomenon, characteristic of recent dogs (Bökönyi 1975; Clutton-Brock 1984). Large, crowded teeth among early Holocene specimens are often taken as evidence of early domestication (e.g., Degerbøl 1961; Turnbull and Reed 1974). Observations of proportionally small teeth in dogs usually refer to large, recent dogs (e.g., Olsen 1974:343; Clutton-Brock 1984; Morey 1986; Wayne 1986a).

The prehistoric dogs used in this study, which date no later than about 3,000 B.P., do not exhibit proportional tooth size reduction relative to wolves, except with respect to the diminutive (and often absent) P1. Where scaling relationships among wild canids are positively allometric (CAN, P2, P3), the smaller dogs are transposed above similar sized wild canids, resulting in proportional similarity or even longer teeth. The dogs are consistent with an allometric trend only on P4, where the wild canids exhibit negative allometry. However, Wayne (1986a) found positive allometry for this variable among wild canids,

suggesting that negative allometry of P4 may be characteristic of Canis only. In any case, the dogs have proportionally longer carnassials than even C. lupus. These morphological inferences are easily verified. For example, the average ratio of P4 to CL among the two C. lupus groups is .1043, while among both dog groups it is .1109.

Summary

1. On anterior cranial length variables (PL, IM2, OI) all groups produce tight scaling patterns, and the domestic dogs are consistent with those patterns. Proportional differences in morphology are the result of nonisometric interspecific slopes.

2. On cranial width variables (PW, MCW) there is greater variability in scaling patterns, and the dogs are distinct from allometric trends seen among wild Canis. The dogs have proportionally wider palates and vaults than wild Canis.

3. The dogs tend to have proportionally longer teeth relative to wild Canis. With one exception, P4, this pattern does not relate to allometric trends seen among wild Canis.

4. Overall, relative scaling patterns exhibited by the domestic dogs are consistent with results from previous allometric studies involving modern dog breeds. Though

dogs show morphological similarity to wild Canis they are nonetheless distinct, suggesting that their morphological patterning involves more than simple allometric (biomechanical) scaling.

CHAPTER VI

BIVARIATE ALLOMETRY: ANALYSIS OF ONTOGENETIC DATA

This chapter presents analysis of ontogenetic data from wolves (C. rufus and C. lupus) in relation to static data from domestic dogs and the other wild canids (C. aureus, C. latrans). In accordance with an hypothesis of progenetic heterochrony in dogs (see Chapters II and III), the primary objective is to determine whether the dogs and wolves consistently exhibit ontogenetic scaling (Gould 1975b; Shea 1981, 1983, 1985b, 1988; McKinney 1988b). The interpretive framework for this analysis, outlined in Chapter III, is similar to that discussed by Shea (1981:181) for analysis of extended growth trajectories in ancestor-descendent relationships. Briefly, if an ontogenetic regression line from a larger species (wolf) passes through the range of static variation of a smaller species (dog, jackal, coyote), an hypothesis of ontogenetic scaling is supported. If this pattern is consistent across several bivariate relationships, the hypothesis is further strengthened. If this pattern is not found the hypothesis of ontogenetic scaling is not supported. Analysis excludes dental variables because young juveniles do not have permanent dentition.

C. rufus is included in this phase of analysis because of similarity in adult size with small Asiatic wolves like

C. lupus chanco or C. lupus pallipes, forms that have been implicated in the ancestry of dogs. The C. rufus adults in this study have a mean condylobasal length of 202 millimeters (Table 7, page 100). Three specimens of C.l. chanco examined by this author at the National Museum of Natural History, Washington, D.C. (age categories 4 or 5), ranged from 197 to 210 millimeters in this dimension. On qualitative grounds, this size similarity is accompanied by morphological similarity. Although similarity in adult size and form does not guarantee identical patterns of growth, similarity in growth is a reasonable assumption. In the absence of ontogenetic data from Asiatic wolves, C. rufus is used as a crude approximation.

Analysis of ontogenetic data is restricted to age categories 1, 2, and 3 (see Table 2, page 81). Consequently, the regression slopes are unaffected by static variation characteristic of age categories 4 and 5. Precise ages cannot be assigned to individuals in different age categories. However, from dental eruption criteria used to create age categories, it is reasonably certain that all individuals are approximately 45 days or older (Table 2, page 81). Accordingly, generated postnatal growth trajectories exclude the perinatal growth period of 0-40 days after birth (Wayne 1986c). It must be assumed that the schedule of dental eruption and other basic developmental events among recent wolves pertains to

prehistoric populations.

Several precautions regarding the quality of the subadult wolf samples must be emphasized. First, the samples are small: 22 C. rufus and 38 C. lupus. Second, unlike the corresponding static series they are subspecifically heterogeneous (Table 4, page 88). Finally, the actual age distribution of the samples is skewed, as shown on Table 14. Both series are numerically dominated by individuals from age category 3.

The problem of skewed age distributions is especially pronounced with C. rufus, for which only three age category 1 individuals are represented. There is a tremendous gap in size (i.e., growth data) between these three and the next individuals from age category 2. Hence, it must be assumed that they are roughly representative of C. rufus at that stage of development. If not, results are spurious. The location of these three cases with respect to other data points can be observed in Appendix C. This appendix presents bivariate plots of cranial variables against CL for both juvenile series of C. rufus and C. lupus, with calculated regression lines illustrated.

The C. lupus sample is a clear improvement over the C. rufus sample. Though it is also skewed, it reflects a more even distribution of individuals across the age categories. Consequently, greater confidence may be placed in the accuracy of calculated regression coefficients. The

Table 14. Summary data on *C. lupus* and *C. rufus* juveniles used in analysis of ontogenetic allometry.

Species/ Age Category	Parameter	Measurement CL	PL	IM2	OI	PW	MCW
C. lupus							
age cat. 1	minimum	74	42	41	28	42	43
	maximum	143	78	61	64	59	60
	n	12	12	5	12	12	12
age cat. 2	minimum	179	93	98	83	57	64
	maximum	194	103	109	93	73	67
	n	7	7	7	7	7	7
age cat. 3	minimum	182	98	101	83	63	65
	maximum	230	120	123	109	76	75
	n	19	19	19	19	19	19
C. rufus							
age cat. 1	minimum	78	44	--	31	38	46
	maximum	80	45	--	31	40	48
	n	3	3	0	3	3	3
age cat. 2	minimum	163	83	88	74	54	55
	maximum	175	92	100	81	62	61
	n	4	4	4	4	4	4
age cat. 3	minimum	170	88	92	78	53	56
	maximum	204	104	110	94	64	63
	n	15	15	15	15	15	15

general conformity of these data to the regression lines (Appendix C) encourages the assumption that the gap in the C. rufus data is also adequately described by a straight line connecting the separated groups of points.

The characteristics of these subadult samples require a broad interpretive framework. It would be unrealistic to demand precise, unequivocal evidence of ontogenetic scaling. Rather, general correspondence between ontogenetic and static patterns is sought across several different bivariate relationships. Increased subjectivity in interpretation is an unavoidable consequence of decreased control over sample composition.

Treatment of the adult samples differs from that presented in the previous chapter. The two C. lupus groups and the two dog groups are pooled on all variables, regardless of statistically significant differences in slopes or elevations. Differences within groups are never of great magnitude. Moreover, the objective of this chapter is to determine the relationship of wolf ontogenetic regressions to the overall range of static variation among different groups. Pooling all adults of the same species facilitates this task.

Ontogenetic Allometry of Wolves

Ontogenetic regressions from C. lupus and C. rufus for each cranial variable against CL are summarized on Table 15. This table also summarizes regressions from pooled adult C. lupus samples on PL and MCW, and pooled C. familiaris samples on IM2, OI, and MCW. Because these groups were analyzed separately on those variables in Chapter V, these regressions were not previously presented. Other adult regressions used in this chapter may be found on Table 8 (page 102).

From inspection of Table 15 it can be seen that slopes of the C. rufus and C. lupus ontogenetic regressions are similar on PL, OI, and PW. They differ substantially on MCW. A C. rufus regression was not calculated on IM2 because this measurement could not be recorded on the three age category 1 individuals. Adult regressions, from Table 15 and Table 8 (page 102) apparently differ considerably from the ontogenetic regressions.

Table 16 presents analysis of covariance results from comparisons of juvenile wolf regressions with each other, and juvenile wolves with their corresponding adult group. Obviously, the ontogenetic regressions for each group must intersect the range of variation of the corresponding adult group. From Table 16 it can be seen that of the eight juvenile-adult wolf comparisons possible, six exhibit different slopes. A seventh, C. rufus on PL, yields

Table 15. Least squares slopes (LS) and associated standard errors (SE), least squares Y-intercepts (Y-INT), correlations (R), and reduced major axis slopes (RMA) from regressions of cranial variables against CL for juvenile wolves (age categories 1,2, and 3) and pooled adult groups not previously reported (all variables log transformed).

Variable	Group	Slope* (LS)	SE	Y-INT	R	Slope (RMA)
PL	C. lupus (juvenile)	0.912	.016	-0.084	>.99	0.919
PL	C. rufus (juvenile)	0.899	.012	-0.057	>.99	0.908
PL	C.l. lycaon/baylei (adult)	1.025	.040	-0.334	.93	1.096
IM2	C. lupus (juvenile)	0.991	.017	-0.239	>.99	0.996
IM2	C. familiaris EU/NA	0.852	.036	0.063	.95	0.901
OI	C. lupus (juvenile)	1.176	.009	-0.735	>.99	1.178
OI	C. rufus (juvenile)	1.198	.012	-0.780	>.99	1.210
OI	C. familiaris EU/NA	1.124	.051	-0.612	.94	1.193
PW	C. lupus (juvenile)	0.498	.020	0.694	.97	0.513
PW	C. rufus (juvenile)	0.449	.033	0.744	.95	0.473
MCW	C. lupus (juvenile)	0.436	.014	0.829	.98	0.444
MCW	C. rufus (juvenile)	0.287	.021	1.124	.95	0.302
MCW	C.l. lycaon/baylei (adult)	0.517	.050	0.642	.72	0.721
MCW	C. familiaris EU/NA	0.712	.071	0.188	.78	0.912

*All least squares slopes are significantly different from zero ($p<.01$).

Table 16. Analysis of covariance results from paired comparisons of cranial measurements from adult wolves (age categories 4 and 5) and juvenile wolves (age categories 1,2 and 3), with with CL as a covariate (all variables log transformed). Included are F-ratios (F) and associated probabilities from tests of homogeneity of slopes (PS), F-ratios and associated probabilities from tests of equality of adjusted group means (PAGM), and adjusted group means (AGMEAN) with associated standard errors (SE)*.

Dependent Variable/ Comparison	PS (F)	PAGM (F)	AGMEAN (SE)
PL			
C. lupus (juvenile)	.015 (6.1)		
C. lupus (adult)**			
C. rufus (juvenile)	.095 (2.9)	.017 (6.2)	.9798 (.0017)
C. rufus (adult)			1.9857 (.0015)
C. lupus (juvenile)	.383 (0.7)	<.001 (17.3)	1.9433 (.0016)
C. rufus (juvenile)			1.9324 (.0021)
IM2			
C. lupus (juvenile)	.012 (6.5)		
C. lupus (adult)			
OI			
C. lupus (juvenile)	<.001 (23.7)		
C. lupus (adult)			
C. rufus (juvenile)	.016 (6.3)		
C. rufus (adult)			
C. lupus (juvenile)	.181 (1.8)	.191 (1.7)	1.8671 (.0013)
C. rufus (juvenile)			1.8700 (.0018)
PW			
C. lupus (adult)	<.001 (20.2)		
C. lupus (juvenile)			
C. lupus (juvenile)	.201 (1.7)	<.001 (128)	1.7963 (.0032)
C. rufus (juvenile)			1.7367 (.0042)

Table 16 (continued).

Dependent Variable/ Comparison	PS (F)	PAGM (F)	AGMEAN (SE)
MCW			
C. lupus (juvenile)	.135 (2.3)	.297 (1.1)	1.8382 (.0023)
C. lupus (adult)			1.8412 (.0013)
C. rufus (juvenile)	.023 (5.5)		
C. rufus (adult)			
C. lupus (juvenile)	<.001 (33.4)		
C. rufus (juvenile)			

*PAGM and AGMEAN are reported when slopes are assumed to be equal based on PS, i.e. when p>.1. PAGM and AGMEAN are also reported in instances where PS yields a probability less than but very near .1.

**The C. lupus adult group consists only of C.l. lycaon and C.l. baylei. The C. lupus juvenile group contains additional subspecies, as explained in the text.

ambiguous results. Only the C. lupus comparison on MCW suggests equivalence of static and ontogenetic allometry. Assuming static allometry to be representative of ontogenetic allometry for single species would have been a serious error.

Comparisons between the juvenile wolf groups (Table 16) yield inconsistent results. On PL and PW the two groups have similar slopes but different elevations, suggesting differences in growth patterns during the prenatal or perinatal periods. They are indistinguishable on OI, and exhibit divergent slopes on MCW. Though the small samples used to generate these comparisons must be borne in mind, these data suggest that different varieties of wolves may show significant variation in ontogenetic growth patterns.

Analysis of Ontogenetic Scaling

In the following analysis ontogenetic regressions from C. lupus and C. rufus are compared to patterns of static variation among C. latrans, C. aureus, and C. familiaris. All analysis of covariance comparisons are assembled on Table 17. Discussion of each analyzed group is presented sequentially.

Table 17. Analysis of covariance results from paired comparisons of cranial measurements from juvenile wolves (age categories 1, 2, and 3) and adult canids (age categories 4 and 5), with CL as a covariate (all variables log transformed). Included are F-ratios (F) and associated probabilities from tests of homogeneity of slopes (PS), F-ratios and associated probabilities from tests of equality of adjusted group means (PAGM), and adjusted group means (AGMEAN) with associated standard errors (SE)*.

Dependent Variable/ Comparison	PS (F)	PAGM (F)	AGMEAN (SE)
PL			
C. lupus (juv.)	.007 (7.7)		
C. latrans			
C. rufus (juv.)	<.001 (13.4)		
C. latrans			
C. lupus (juv.)	.809 (<0.1)	<.001 (57.9)	1.9373 (.0016)
C. aureus			1.9188 (.0018)
C. rufus (juv.)	.536 (0.4)	.001 (12.3)	1.9253 (.0017)
C. aureus			1.9175 (.0015)
C. lupus (juv.)	.797 (<0.1)	<.001 (62.3)	1.9227 (.0016)
C. familiaris EU/NA			1.9069 (.0012)
C. rufus (juv.)	.867 (<0.1)	.014 (6.3)	1.9088 (.0019)
C. familiaris EU/NA			1.9034 (.0011)
IM2			
C. lupus (juv.)	.969 (<0.1)	.011 (6.8)	1.9992 (.0017)
C. latrans			1.9937 (.0012)
C. lupus (juv.)	.053 (3.9)		
C. aureus			
C. lupus (juv.)	.003 (9.6)		
C. familiaris EU/NA			
OI			
C. lupus (juv.)	.773 (<0.1)	.004 (8.7)	1.9037 (.0014)
C. latrans			1.9088 (.0011)
C. rufus (juv.)	.915 (<0.1)	.565 (0.3)	1.9149 (.0017)
C. latrans			1.9160 (.0010)
C. lupus (juv.)	.196 (1.7)	.829 (<0.1)	1.8593 (.0015)
C. aureus			1.8598 (.0017)

Table 17 (continued).

Dependent Variable/ Comparison	PS (F)	PAGM (F)	AGMEAN (SE)
OI (continued)			
C. rufus (juv.)	.089 (3.0)	.381 (0.8)	1.8606 (.0018)
C. aureus			1.8584 (.0016)
C. lupus (juv.)	.275 (1.2)	<.001 (14.0)	1.8404 (.0018)
C. familiaris EU/NA			1.8490 (.0014)
C. rufus (juv.)	.146 (2.2)	.033 (4.7)	1.8386 (.0024)
C. familiaris EU/NA			1.8447 (.0014)
PW			
C. lupus (juv.)	.003 (9.0)		
C. latrans			
C. rufus (juv.)	<.001 (12.1)		
C. latrans			
C. lupus (juv.)	<.001 (12.2)		
C. aureus			
C. rufus (juv.)	<.001 (14.6)		
C. aureus			
C. lupus (juv.)	.003 (9.0)		
C. familiaris EU/NA			
C. rufus (juv.)	<.001 (12.8)		
C. familiaris EU/NA			
MCW			
C. lupus (juv.)	.007 (7.7)		
C. latrans			
C. rufus (juv.)	<.001 (23.0)		
C. latrans			
C. lupus (juv.)	.014 (6.3)		
C. aureus			
C. rufus (juv.)	<.001 (22.1)		
C. aureus			
C. lupus (juv.)	<.001 (16.5)		
C. familiaris EU/NA			
C. rufus (juv.)	<.001 (34.8)		
C. familiaris (EU/NA			

*PAGM and AGMEAN are reported when slopes are assumed to be equal based on PS, i.e. when p>.1. PAGM and AGMEAN are also reported in instances where PS yields a probability less than but very near .1.

Analysis of C. latrans

Plots illustrating the range of static variation of C. latrans in relation to ontogenetic regressions of wolves are shown on Figure 15. Figure 15a indicates that both ontogenetic regressions pass through the range of static variation, C. rufus more centrally than C. lupus. Divergent static and ontogenetic slopes prohibit statistical comparison of elevations (Table 17). On IM2 the C. lupus ontogenetic regression passes through the C. latrans data points, slightly above the central portion (Figure 15b). Weak transposition is statistically demonstrable (Table 17). On OI the C. lupus ontogenetic regression is transposed below the C. latrans static regression, while the C. rufus regression is indistinguishable (Table 17). On Figure 15c it can be seen that the C. rufus regression line passes squarely though the C. latrans static data points. The C. lupus regression also passes through the C. latrans data points, slightly below the central portion.

The patterns shown by PW and MCW are similar to each other and markedly different from anterior cranial length variables. In both cases static slopes are different from ontogenetic slopes. Further, in both cases the C. rufus ontogenetic regressions pass through the C. latrans data points, slightly above the central portion (Figure 15d and 15e). Finally, in both cases the C. lupus ontogenetic

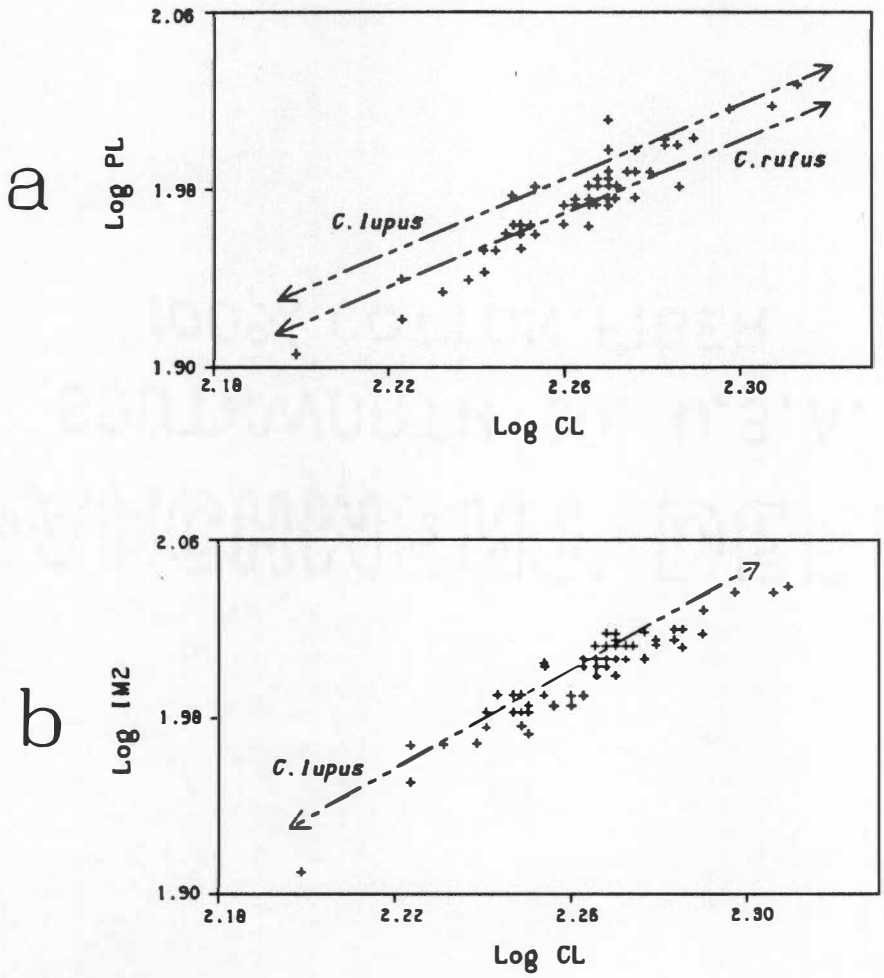
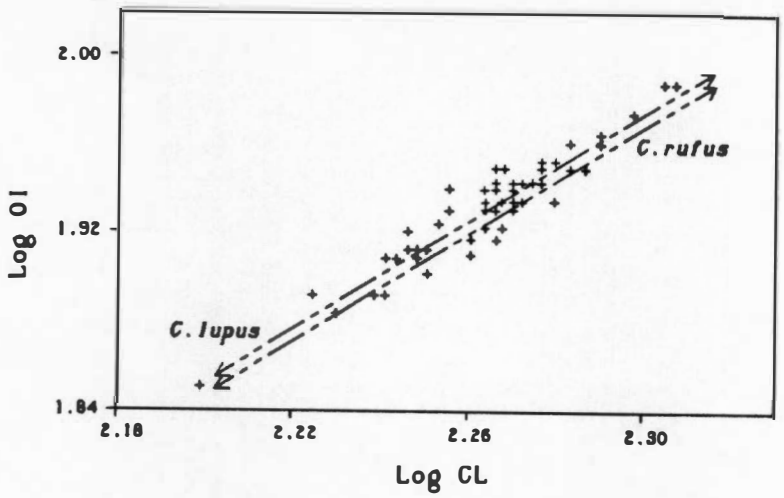
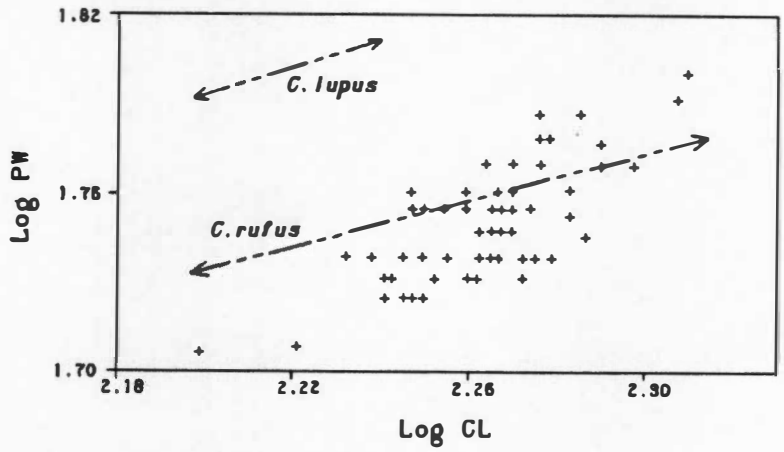


Figure 15. Bivariate plots showing relationship between C. latrans static data points (crosses) and wolf ontogenetic regression lines (broken lines) from analysis of cranial variables against CL. 15a: PL x CL; 15b: IM2 x CL; 15c: OI x CL; 15d: PW x CL; 15e: MCW x CL.

c



d



e

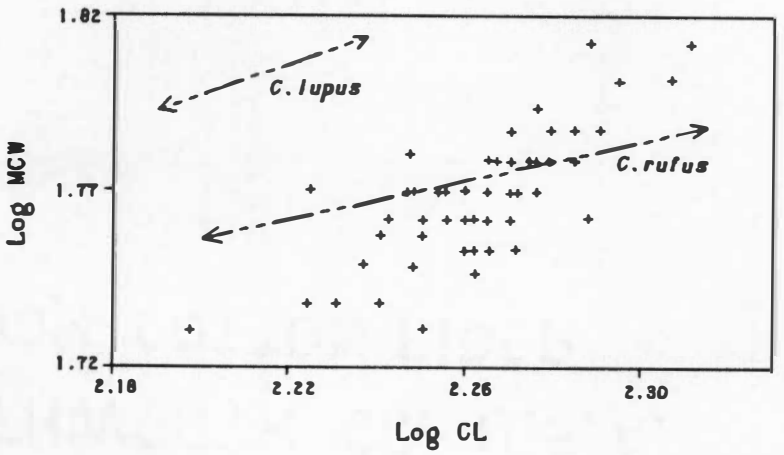


Figure 15 (continued).

regression is removed far above all of the C. latrans data points.

As expected, a reasonable case for ontogenetic scaling can be made with respect to the three anterior cranial length variables (PL, IM2, OI). In all three cases both wolf ontogenetic regressions pass through a large portion of the range of static variation of C. latrans. Statistical differences between static and ontogenetic regressions exist, but they are not of great magnitude. Conversely, on PW and MCW C. latrans adults are far removed from the C. lupus ontogenetic regression. However, considerable similarity is evident between C. rufus and C. latrans. Given the probability of genetic mixing between these species (see Chapter IV), this similarity is not surprising. In this case apparent ontogenetic scaling probably results not from evolutionary divergence constrained by developmental pathways (e.g., Wayne 1986a), but from secondary convergence producing similarities in development and final adult morphology.

Analysis of C. aureus

Figure 16 shows plots that illustrate the range of static variation of C. aureus in relation to the wolf ontogenetic regressions. On PL the wolf regressions pass through the C. aureus data points at their upper margin (Figure 16a). This apparent transposition is statistically demonstrable (Table 17). Similarly, on IM2 the C. lupus

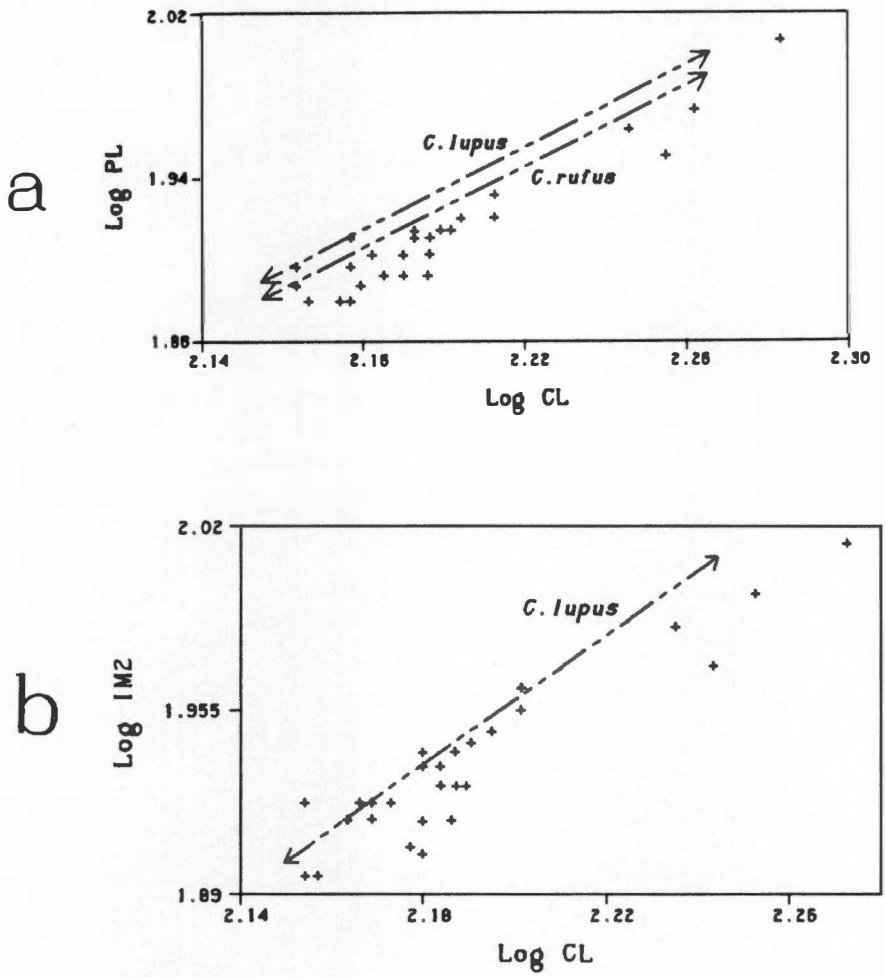


Figure 16. Bivariate plots showing relationship between C. aureus static data points (crosses) and wolf ontogenetic regression lines (broken lines) from analysis of cranial variables against CL. 15a: PL x CL; 15b: IM2 x CL; 15c: OI x CL; 15d: PW x CL; 15e: MCW x CL.

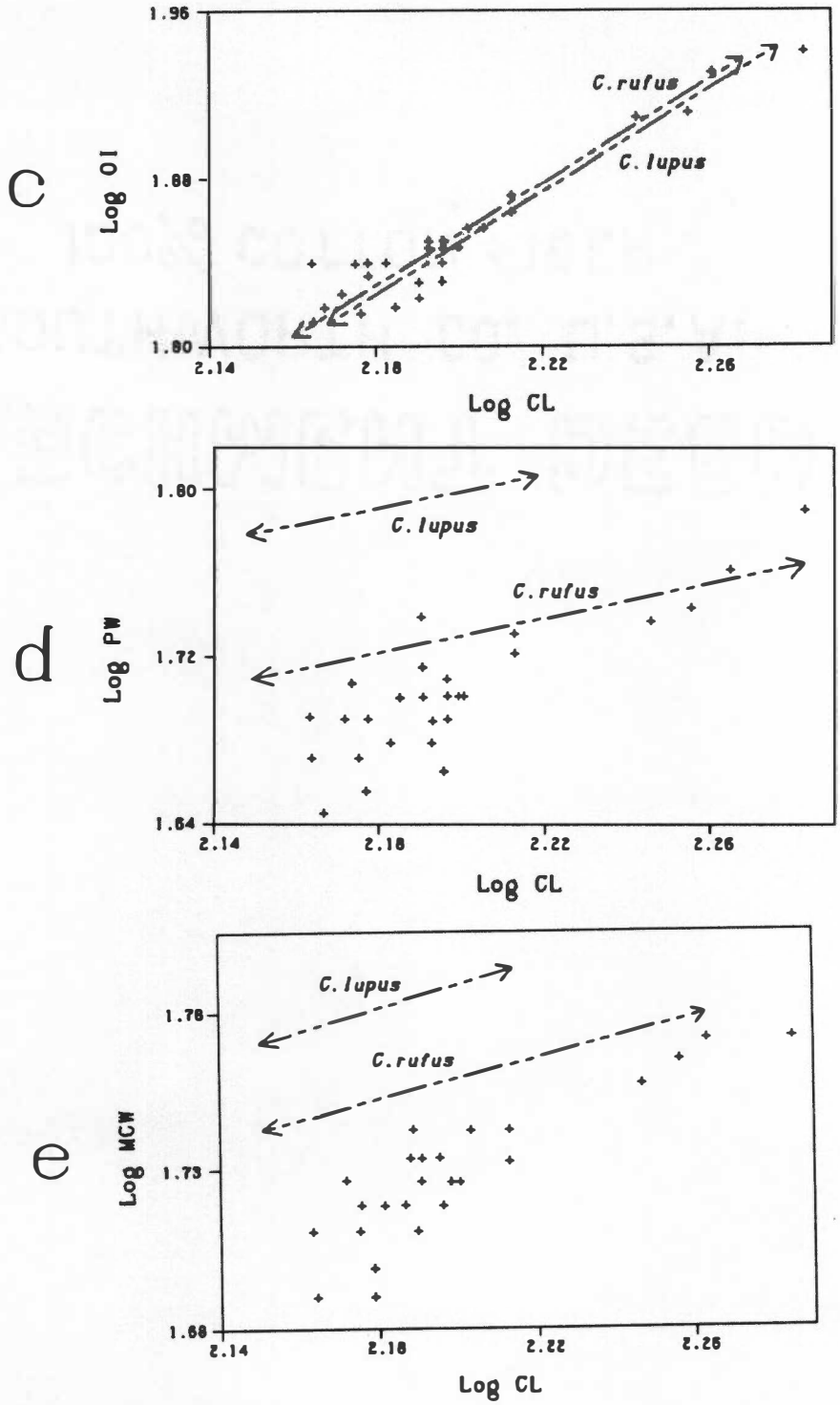


Figure 16 (continued).

ontogenetic regression passes through the upper portion of the C. aureus data points (Figure 16b). Divergent static and ontogenetic slopes prohibit evaluation of elevations. On OI both ontogenetic regressions pass squarely through the C. aureus range of static variation (Figure 16c). Slopes and elevations are statistically indistinguishable or similar (Table 17).

The variables PW and MCW exhibit greater disparity between static and ontogenetic patterns of variation. On PW the C. rufus ontogenetic regression barely crosses the range of C. aureus data points at its upper margin. The C. lupus ontogenetic regression is removed far above (Figure 16d). Although slope differences prevent formal comparison of elevations (Table 17), the differences are clearly substantial. MCW exhibits even greater differences. Again, ontogenetic and static slopes are different (Table 17). However, both ontogenetic regressions fall above the entire C. aureus range of static variation, with C. lupus the farthest removed.

Patterns of static variation in C. aureus are generally consistent with an hypothesis of ontogenetic scaling with wolves in anterior cranial length variables. Admittedly the evidence is problematical. Robust evidence of ontogenetic scaling is found only with OI. On PL and IM2 the wolf ontogenetic regressions fall higher than would be expected under conditions of ontogenetic scaling. In

both cases, however, they intersect the range of static variation of C. aureus.

As expected, the cranial width variables do not reflect ontogenetic scaling. C. lupus does not even approach the C. aureus range of static variation on either PW or MCW. C. rufus intersects the C. aureus range of data points only on PW, and only at its uppermost range of variation. Wolf ontogenetic regressions arguably conform to an hypothesis of ontogenetic scaling only on anterior cranial length variables.

Analysis of C. familiaris

Plots showing the range of static variation of the dogs in relation to wolf ontogenetic regressions are presented in Figure 17. Figure 17a indicates that both ontogenetic regressions pass through the range of variation of the dogs, with C. rufus approaching the central portion of that range. However, both ontogenetic regressions are transposed slightly above the dog static regression (Table 17). On IM2 the C. lupus ontogenetic regression exhibits a different slope from the C. familiaris static regression, preventing formal comparison of elevations. Figure 17b shows that the C. lupus regression passes squarely through the range of the C. familiaris data points, slightly above the central portion of that range. On OI the ontogenetic regressions are transposed below the C. familiaris static regression (Table 17). However, both ontogenetic

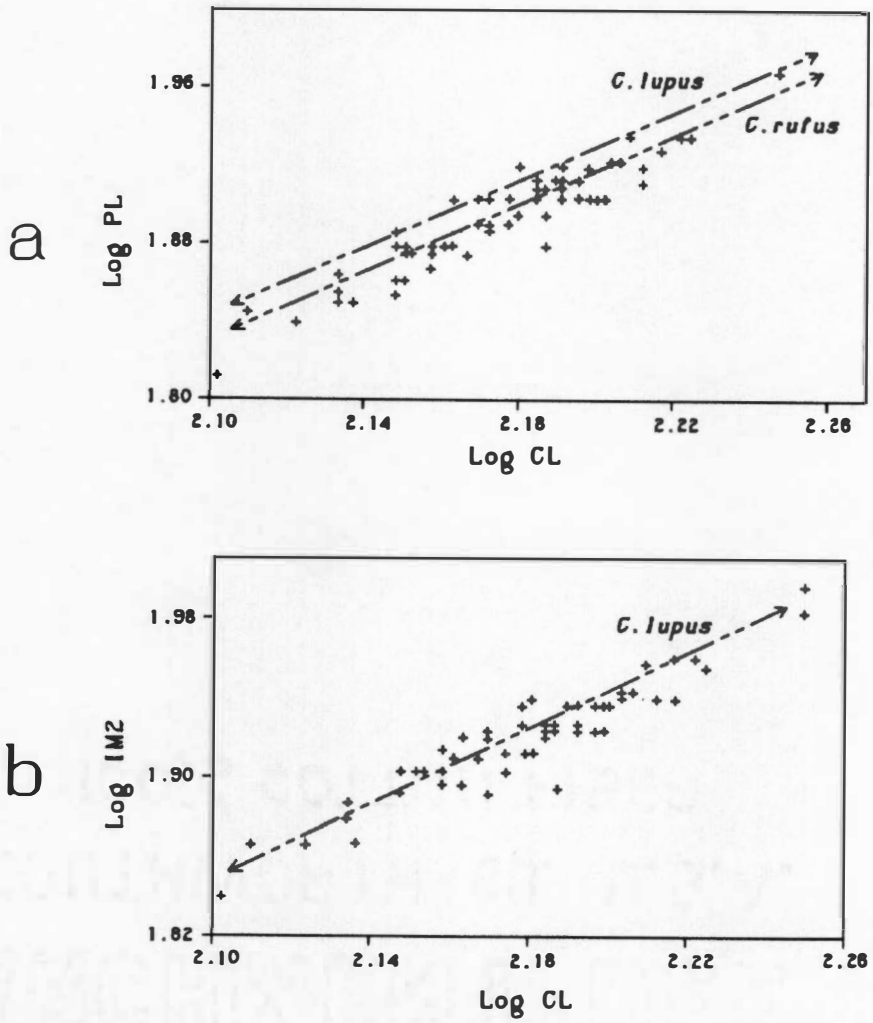
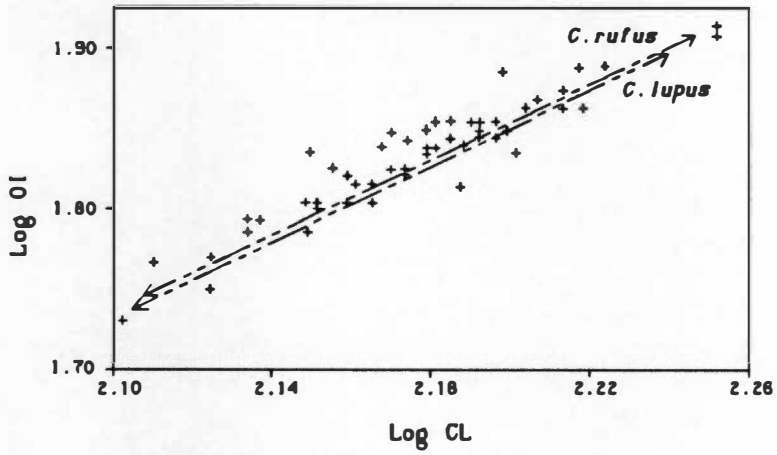
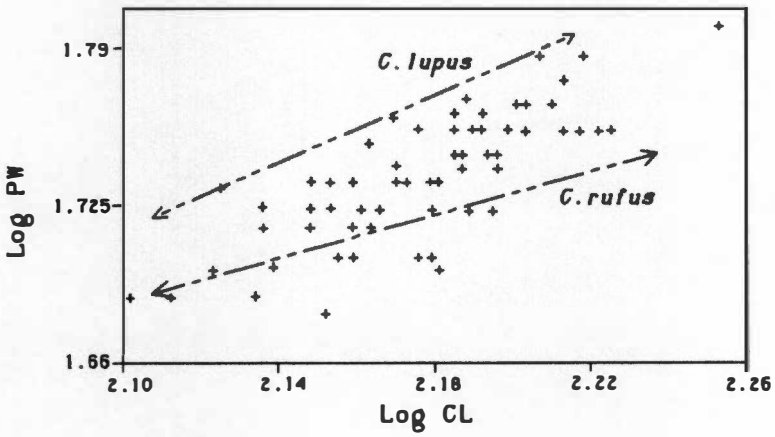


Figure 17. Bivariate plots showing relationship between C. familiaris static data points (crosses) and wolf ontogenetic regression lines (broken lines) from analysis of cranial variables against CL. 15a: PL x CL; 15b: IM2 x CL; 15c: OI x CL; 15d: PW x CL; 15e: MCW x CL.

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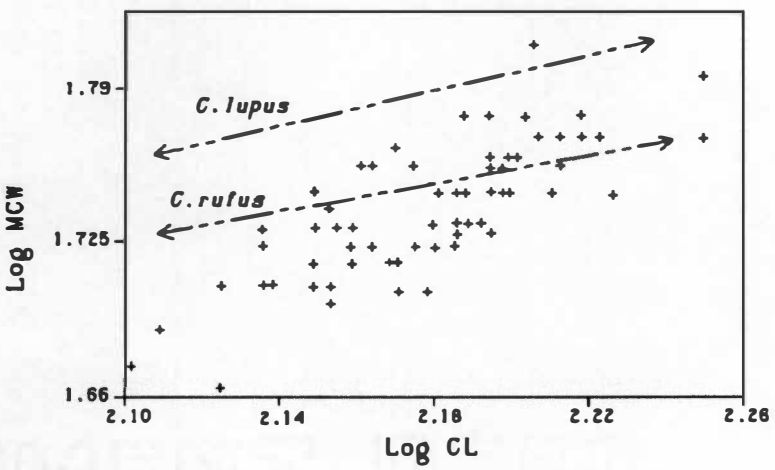


Figure 17 (continued).

regressions pass through a substantial portion of the range of C. familiaris data points (Figure 17c).

On PW and MCW ontogenetic slopes are different from the static regression slopes. On PW both ontogenetic regressions intersect the range of C. familiaris data points, C. lupus at the uppermost margin and C. rufus in the lower portion of that range (Figure 17d). Together, they almost bound the C. familiaris data points. On MCW the C. lupus ontogenetic regression passes through the range of C. familiaris data points at its uppermost margin, while the C. rufus ontogenetic regression passes through in close proximity to the central portion of that range (Figure 17e).

Overall, the patterning exhibited by dogs on anterior cranial length variables is similar to that exhibited by C. aureus and C. latrans. Wolf ontogenetic regressions always intersect the range of static data points, often close to the central portion of that range. On cranial width variables the dogs and other adult canids diverge. The C. lupus ontogenetic regressions for both PW and MCW are removed far above the ranges of static variation shown by C. aureus and C. latrans. The C. rufus ontogenetic regression is consistently similar only to C. latrans, an unsurprising pattern given the probability of hybridization. Conversely, both C. lupus and C. rufus ontogenetic regressions invariably intersect the range of

C. familiaris data points on both PW and MCW, if only marginally. Evidence for ontogenetic scaling with respect to these variables is stronger for the dogs than for the other adult canids.

Evaluation of Ontogenetic Allometry

Based on analysis and discussion in previous chapters it was proposed that dogs should exhibit ontogenetic scaling with wolves on all cranial variables. In contrast, other wild canids should exhibit ontogenetic scaling on anterior cranial length variables only. Results of analysis presented in this chapter are suggestive, though problematical. On anterior cranial length variables ontogenetic regressions from both C. lupus and C. rufus always pass through the range of variation exhibited by the adult canids. In some cases evidence for ontogenetic scaling is strong. Examples are the comparisons of both C. rufus and C. lupus to C. aureus on OI, and the C. lupus-C. familiaris comparison on IM2. In other cases the ontogenetic regression lines pass through the upper or lower portions of the range of static variation of a given group. It is argued here that the general correspondence between static variation and wolf ontogenetic trajectories provides tentative support for an hypothesis of ontogenetic scaling of all groups on anterior cranial length variables. Better samples, particularly of juveniles, will be required

before a more definitive conclusion can be reached.

Results from analysis of cranial width variables are also suggestive but problematical. As expected, wolf ontogenetic regressions are usually far removed from ranges of static variation exhibited by C. aureus and C. latrans. A conspicuous and unsurprising exception involves C. rufus-C. latrans comparisons. Conversely, and as expected, wolf ontogenetic regressions consistently intersect the range of static variation shown by the dogs. There is no question that the dogs exhibit better evidence of ontogenetic scaling on PW and MCW than C. latrans or C. rufus. However, wolf ontogenetic regressions do not pass through the central portion of C. familiaris data points. Hence, absolute evidence of ontogenetic scaling is ambiguous.

Nonetheless, greater relative correspondence between the locations of C. familiaris adults and the C. lupus ontogenetic regressions is striking. C. lupus ontogenetic regressions do not even approach the ranges of static variation of C. aureus or C. latrans on either cranial width variable. Greater correspondence between C. familiaris and C. lupus is symptomatic of the upward transposition of C. familiaris relative to C. aureus or C. latrans (see Chapter V). This upward transposition brings the C. familiaris adults into closer proximity to the ontogenetic regression line of C. lupus. Despite the relatively close correspondence of C. familiaris to the C.

lupus ontogenetic regressions, the *C. rufus* ontogenetic regressions consistently pass closer to the central portion of the *C. familiaris* data points on all variables. However, results of multivariate analysis in Chapter VII complicate the apparent similarity between *C. familiaris* adults and *C. rufus* juveniles.

The general correspondence of wolf ontogenetic allometries to patterns of static variation among anterior cranial length variables is consistent with the findings of Wayne (1986a). On cranial width variables the disparities between adult wild canids and wolf ontogenetic allometries, with concurrent similarity between adults dogs and wolf ontogenetic allometries, are also consistent with Wayne's findings. In Wayne's case the divergent patterns shown by cranial width and depth allometries were viewed as a consequence of developmental constraints on dogs. Wayne argued that dogs are morphologically confined to boundaries associated with their own developmental pathway. It is argued here that morphology in dogs is largely confined to the developmental boundaries of their wolf ancestors. These arguments are complementary, not contradictory. Both specify a fundamental developmental constraint on the morphology of dogs.

Summary

1. On anterior cranial length variables (PL, IM2, OI) the dogs, jackals, and coyotes exhibit reasonable evidence of ontogenetic scaling with wolves (C. rufus and C. lupus).

2. On cranial width variables (PW, MCW) the C. lupus ontogenetic regressions are far removed from the range of static variation of the jackals or coyotes. The C. rufus ontogenetic regressions are far removed from the static data points of the jackals, but centrally intersect the coyote static data points. Ontogenetic scaling between C. rufus and C. latrans is not surprising.

3. On cranial width variables the domestic dogs exhibit considerably stronger evidence of ontogenetic scaling with wolves than do other canids (excluding the C. rufus-C. latrans comparisons). Greater proximity of the dog static data points to C. lupus ontogenetic regressions reflects upward transposition of the dogs relative to other adult groups. Adult dogs have wide cranial vaults and palates, features associated with juvenile wolves.

4. These results are consistent with previous allometric investigations. Though evidence is subject to uncertainty, an hypothesis of ontogenetic scaling between wolves and dogs is supported.

CHAPTER VII

MULTIVARIATE ANALYSIS

This chapter presents results of canonical discriminant analyses on adult and juvenile canid groups. As explained in Chapter III, discriminant analysis is used to assess overall patterns of morphological variability between different groups. A primary objective is to determine the relative degree of morphological correspondence between adult dogs and juvenile wolves. Discriminant analysis is well suited to this task because it seeks to achieve maximum separation between groups (Wayne 1986a). Groups characterized by greatest morphological similarity can be expected to fall closest to each other on the canonical axes.

Sample Composition and Objectives

The North American and European dog groups are pooled into a single sample in all analyses. Though there is variability between these groups, the goal of this analysis is to assess overall differences between dogs and other groups. Similarly, it would be undesirable to analyze the adult *C. lupus* groups separately. Rather than pool them into a single sample, only the *C.l. lycaon* adults are used. This helps reduce disparity between different sample sizes without seriously impacting the accuracy of results.

Bivariate analysis revealed considerable similarity between the two subspecies, though they are by no means identical.

Ordinarily, analysis of juvenile wolves as if they represented a separate species would be unjustified. The kind of variabiity expressed in these samples is fundamentally different from variability in the adult series. Morphological variation in adult groups is static, while the juvenile groups reflect variation in growth. It must be borne in mind that these comparisons relate to a specific hypothesis. This hypothesis predicts that morphological similarity between dogs and wolves will depend on the developmental stage of wolves. This is best assessed by direct comparison of juveniles with adults of different taxa.

Ideally, a series of juvenile samples would be used, each representing a different age: for example, four months, six months, eight months, etc. Given the present data base this is impossible. Rather, individuals representing a range of ages must be assembled into a single sample. To control the range of age and morphological variability only individuals from age categories 2 and 3 are used. Thus, the ages represented span from roughly four months to one year (see Table 2, page 81), though the samples are skewed towards the latter end of that range. This age range represents stages of development appropriate to the hypothesis of progenetic

heterochrony in dogs. At four months the animals are developing into advanced juveniles, signified by the replacement of deciduous dentition. At one year they have virtually attained their final adult size (cf. Mech 1970:123-142). Summary statistics for the juvenile samples used here are presented in Table 18.

There are eight basic discriminant analyses in this chapter. The first three analyses explore multivariate patterning among adults. The next five analyses incorporate juvenile wolf samples for comparison to adult groups. The technical objectives of all analyses are to (1) extract a series of discriminant functions, (2) assess the robustness of those functions, (3) evaluate intergroup distances on canonical axes, (4) determine the relative contribution of different variables to intergroup discrimination, and (5) plot discriminant scores on significant axes to facilitate visual interpretation of results. Discriminant analysis statistics and coefficients were calculated using a combination of features in BMDP, Program 7M (Jennrich and Sampson 1985) and the SAS CANDISC Procedure (SAS Institute 1985). For each analysis both programs computed identical discriminant functions; thus, results are fully compatible. Explanation of different coefficients and statistics is best accomplished with reference to actual results. Accordingly, the first exploratory analysis serves as a useful vehicle for

Table 18. Means and standard deviations (SD) on cranial measurements from juvenile wolves, age categories 2 and 3.

	Measurement					
Group*	CL	PL	IM2	OI	PW	MCW
C. lupus						
Mean	203.2	107.5	112.0	95.2	69.9	68.4
SD	14.90	6.67	6.22	7.88	4.30	3.58
C. rufus						
Mean	184.0	95.3	101.3	85.6	57.6	59.5
SD	12.45	6.40	6.46	6.64	3.20	2.44

C. lupus n=26; *C. rufus* n=19.

explaining procedure and interpretation. Subsequent analyses are summarized more briefly.

Analysis of Adults

Analysis 1: Untransformed Data, Seven Variables

In this analysis all the adult groups are analyzed with respect to seven variables, all untransformed. This includes the six cranial variables used for bivariate analysis (CL, PL, IM2, OI, PW, MCW), and one dental variable, P4. The latter variable is included to assess the effect of variation in tooth length on intergroup discrimination. Tables 19-22 and Figure 18 summarize results. From the summary statistics presented in Table 19 it can be seen that the first two functions account for over 98 percent of the variability in the samples.

Magnitude of dispersion between groups can be gauged from Mahalonobis D^2 statistics on Table 20. D^2 is a generalized distance between group centroids (multivariate means) that is independent of sample size (Klecka 1980:55-56). Associated F-ratios allow one to determine if D^2 distances between groups are significant. All distances are highly significant in this analysis. Greatest separation is obtained between *C. familiaris* and *C. lupus* (D^2=8.59) while least separation occurs between *C. rufus* and *C. latrans* (D^2=2.09). The dogs are closest to *C. aureus* (D^2=3.47).

Table 19. Summary statistics from discriminant analysis 1.

Function	Eigenvalue	Percent Variation	Canonical Correlation
1	10.856	71.94	.957
2	3.986	26.41	.894
3	0.173	1.15	.384
4	0.076	0.50	.265

Table 20. Matrix of Mahalanobis D^2 distances between groups and associated F-ratios (in parentheses) from discriminant analysis 1.*

Group	*Canis lupus*	*Canis familiaris*	*Canis latrans*	*Canis rufus*
C. familiaris	8.59 (309.7)			
C. latrans	6.15 (158.0)	5.61 (137.0)		
C. rufus	5.43 (75.7)	7.18 (135.5)	2.09 (11.4)	
C. aureus	8.13 (165.2)	3.47 (30.9)	3.26 (27.0)	4.81 (42.6)

*All F-ratios have 7 and 225 degrees of freedom, and are significant at the .001 level.

Table 21. Standardized discriminant function coefficients from the first two functions from discriminant analysis 1.

Variable	Function 1	Function 2
CL	1.410	-4.709
PL	1.529	2.653
IM2	-0.128	-1.527
OI	-0.376	-0.558
PW	-0.751	3.687
MCW	0.501	1.746
P4	1.221	-0.770

Table 22. Matrix of classification results from discriminant analysis 1.

	Group Classified Into				
Actual Group	Canis lupus	Canis familiaris	Canis latrans	Canis rufus	Canis aureus
C. lupus	58	0	0	0	0
C. familiaris	0	59	0	0	4
C. latrans	0	0	55	6	1
C. rufus	0	0	2	25	0
C. aureus	0	1	1	1	23

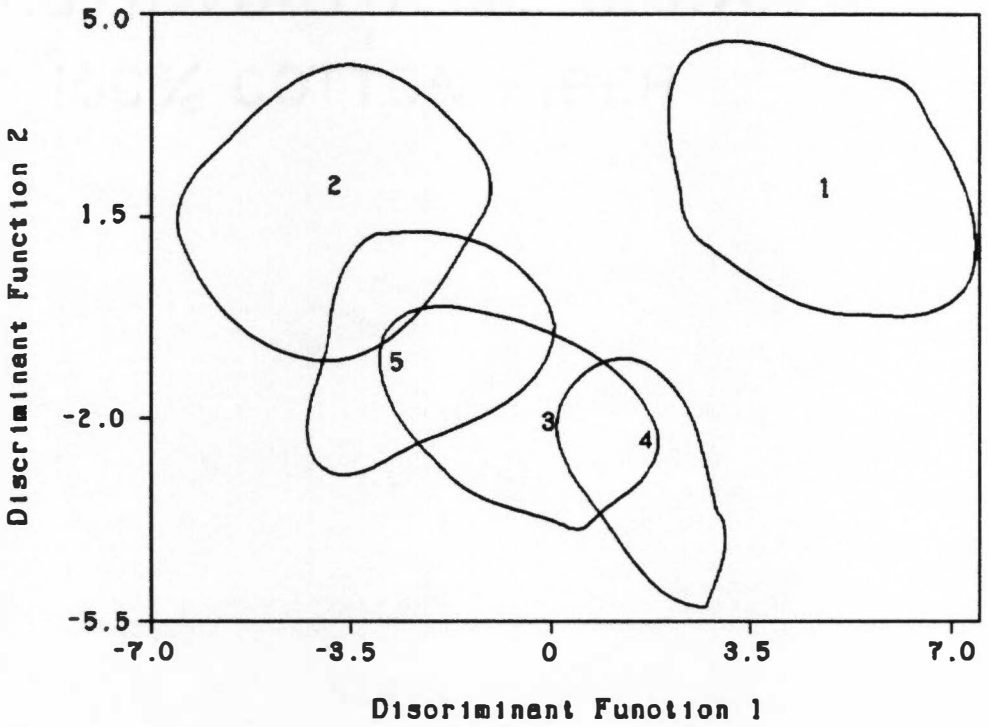


Figure 18. Discriminant analysis 1: plot of discriminant score ranges on two axes (contours) for each group, based on untransformed cranial variables and P4. Numbers are group centroids: 1=C.l. lycaon, 2=C. familiaris, 3=C. latrans, 4=C. rufus, 5=C. aureus. All groups are adults.

Relative locations between groups can be seen on Figure 18, which provides a plot of discriminant scores on the first two functions. Because two functions account for over 98 percent of the variability two dimensional plots are accurate. Function 1 orders the taxa by ascending size: smallest groups (dogs, jackals) have low discriminant scores while largest groups (wolves) have high discriminant scores. Size-related discriminant is a common phenomenon with untransformed data (e.g., Nowak 1979; Wayne 1986a; Morey 1986). The second function separates C. familiaris and C. lupus from the other groups, suggesting patterned morphological variability (see below).

Variables primarily responsible for intergroup discrimination on different axes can be identified by examining standardized discriminant function coefficients on Table 21. Ignoring the sign, variables with largest coefficients contribute the most to intergroup discrimination on the corresponding axis (Klecka 1980:29-30). On the first function coefficients for CL and PL have the highest values. It will be recalled that bivariate analysis revealed tight isometric scaling between these variables. Consequently, their importance on the first discrimant function supports the interpretation of size-related discrimination inferred from Figure 18. Once one or two variables have accounted for the basic size disparities between groups, other variables assume less

importance. However, P4 also apparently contributes significantly to size discrimination.

On the second function CL and PW are most important. Figure 18 indicates that this function separates C. familiaris and C. lupus from the other canid groups. Bivariate analysis revealed that C. familiaris and, to a lesser extent, C. lupus have proportionally wider palates in relation to other groups. Thus, the second discriminant function has keyed primarily on this morphological pattern.

Overall robustness of the discriminant functions can be gauged from classification results summarized on Table 22. Each individual is classified by its proximity to group centroids. If the discriminant functions are robust individuals are classified into the correct group. In this study the BMDP7M JACKKNIFE option is used. In the jackknife procedure the individual being classified is removed from the computation of the classification functions, and then returned when the next case is pulled out for classification. This approach to assessing classification error is less biased than the nonsubstitution routines found in many other software packages (cf. Lachenbruch and Mickey 1968).

In this analysis overall classification accuracy is 93.2 percent (Table 22). Not surprisingly, misclassifications occur primarily between C. rufus and C. latrans, and between C. familiaris and C. aureus. All C.

lupus individuals are correctly classified. Overall, a 93.2 percent success rate indicates relatively robust discriminant functions.

A final step taken in each analysis is a response to the fact that discriminant analysis can be influenced by substantial differences in sample sizes (Klecka 1980:63; Wayne 1986a). Because the goal is maximal overall separation, differences between groups with large sample sizes may be magnified relative to groups with smaller samples. For example, the apparent proximity of *C. familiaris* (n=63) to *C. aureus* (n=27) could result from discriminant functions designed primarily to maximize separation between *C. familiaris* and another large sample like *C. lupus* (n=58).

To check the accuracy of the primary discriminant analysis, a secondary analysis was performed using the same variables but with the dogs excluded from the computation of the discriminant functions. While this step eliminates sample size bias with respect to the dogs, it does not necessarily eliminate bias among the wild canids. However, subsequent analyses will resolve any interpretive ambiguities stemming from sample size disparities among wild canid groups.

In this secondary analysis the dogs were treated as if their species memberships are unknown. Accordingly, their classification is based on functions derived solely from

patterns of variability among wild canids. Primary analysis indicated that the dogs should fall closest to C. aureus. When secondary analysis was performed all 63 dogs were classfied with C. aureus. Thus, primary and secondary analyses yield consistent results.

To sum, this analysis of adults yields size discrimination on the first axis based primarily on the variables CL, PL, and, to a lesser extent, P4. The second axis separates groups with proportionally wide palates (C. familiaris and C. lupus) from groups with narrower palates (C. rufus, C. latrans, C. aureus). Overall, the dogs are closest to C. aureus.

Analysis 2: Indexed Data, Six Variables

This analysis uses the same groups as before, but with six indexed variables. PL, IM2, OI, PW, MCW, and P4 are all expressed as a ratio of CL. As explained in Chapter III, expressing each measurement as a proportion of CL focuses discrimination on morphological variability rather than sheer differences in the magnitude of dimensions. Because CL is the reference, results should be compatible with bivariate analyses in which the other measurements were scaled against CL.

Results of this analysis are summarized on Tables 23-26 and Figure 19. Table 23 indicates that the first two functions account for over 97 percent of the variability in

Table 23. Summary statistics from discriminant analysis 2.

Function	Eigenvalue	Percent Variation	Canonical Correlation
1	5.817	77.15	.924
2	1.534	20.34	.778
3	0.153	2.03	.365
4	0.036	0.47	.186

Table 24. Matrix of Mahalanobis D^2 distances between groups and associated F-ratios (in parenthesis) from discriminant analysis 2.*

Group	*Canis lupus*	*Canis familiaris*	*Canis latrans*	*Canis rufus*
C. familiaris	4.86 (116.4)			
C. latrans	3.43 (57.4)	5.66 (163.4)		
C. rufus	3.16 (30.1)	6.69 (138.0)	1.71 (9.0)	
C. aureus	3.34 (32.6)	4.21 (53.2)	2.13 (13.5)	3.23 (22.5)

*All F-ratios have 6 and 226 degrees of freedom and are significant at the .001 level.

Table 25. Standardized discriminant function coefficients from the first two functions from discriminant analysis 2.

Variable	Function 1	Function 2
PL/CL	-0.020	-0.583
IM2/CL	0.217	0.909
OI/CL	-0.182	-0.356
PW/CL	1.562	-1.598
MCW/CL	1.224	1.127
P4/CL	-0.479	0.191

Table 26. Matrix of classification results from discriminant analysis 2.

	Group Classified Into				
Actual Group	*Canis lupus*	*Canis familiaris*	*Canis latrans*	*Canis rufus*	*Canis aureus*
C. lupus	49	1	0	4	4
C. familiaris	0	59	1	0	3
C. latrans	2	0	46	9	5
C. rufus	2	0	1	24	0
C. aureus	2	1	2	1	20

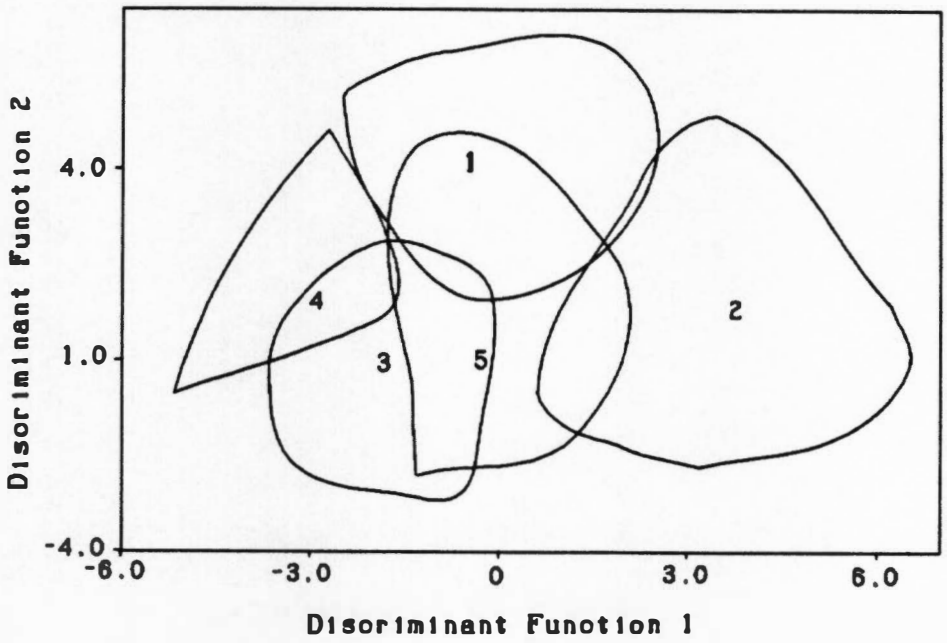


Figure 19. Discriminant analysis 2: plot of discriminant score ranges on two axes (contours) for each group, based on indexed cranial variables and indexed P4. Numbers are group centroids: 1=C.l. lycaon, 2=C. familiaris, 3=C. latrans, 4=C. rufus, 5=C. aureus. All groups are adults.

the samples. D^2 distances (Table 24) indicate greatest separation between C. familiaris and C. rufus, with weakest separation between C. latrans and C. rufus. Like the previous analysis, dogs are closest to C. aureus. The plot of discriminant scores (Figure 19) indicates that the first function separates the dogs from the wild canids while the second function primarily separates C. lupus from the other groups, especially the smaller wild canids.

Standardized discriminant function coefficients on Table 25 are especially noteworthy. Measurements important in the first analysis now assume a minor role. With indexed data, PW/CL and MCW/CL assume greatest importance on both of the first two functions, with IM2/CL also contributing significantly on Function 2. Thus, on the first function the dogs are conspicuously removed from other groups primarily as a consequence of proportionally wider palates and cranial vaults. Function 2 discriminates C. lupus, the only group exhibiting proportionally short tooth rows and narrow cranial vaults in combination with relatively wide palates.

Not surprisingly, classification results indicate weaker discrimination relative to the first analysis, with only 83.9 percent correct classification. Errors occur primarily between C. rufus and C. latrans, and between C. lupus and two of the wild canid groups. Clearly, indexing weakens taxonomic resolution. However, it provides a more

accurate assessment of morphological differences. The dogs remain relatively distinct, indicated by their correct classification in 59 of 63 cases, and by their position on the canonical axes (Figure 19).

Though the dogs are well separated from other groups, primary analysis has suggested they are closest to C. aureus, and not much further removed from C. lupus. Secondary analysis, in which dogs were removed from the computation of the discriminant functions, are consistent with primary analysis. Fifty-two of the dogs are classified with C. aureus, while the remaining eleven are classified with C. lupus.

Results of this analysis are consistent with bivariate analyses. C. familiaris and C. aureus are similar in length measurements as a consequence of similar size. While the dogs differ from C. aureus in width proportions, they are even more distinct from C. latrans or C. rufus. On the other hand, dogs exhibit greatest similarity in palate width to C. lupus (though they are still distinct). However, relative lengths of IM2 and OI are different as a consequence of allometric scaling. Thus, the kinds of patterning that relate dogs to C. lupus and C. aureus are different, but consistent with bivariate patterns. The overall morphological pattern analyzed here suggests greater proximity to C. aureus.

Analysis 3: Indexed Data, Five Variables

This analysis utilizes the same five groups with indexed data, but P4/CL is eliminated. This dental variable must be eliminated because it cannot be included in subsequent analyses involving juveniles. In any case, the previous analysis demonstrated that P4/CL was not an important discriminating variable. Patterns of discrimination among adults using only indexed cranial variables provide an appropropriate frame of reference for subsequent analysis of juveniles.

Results of this analysis, summarized on Tables 27-30 and Figure 20, parallel results from the previous analysis. Since P4/CL contibuted little to intergroup discrimination this is not surprising. In this analysis the first two functions account for 97.8 percent of the variability (Table 27). D^2 distances (Table 28) indicate greatest separation between C. familiaris and C. rufus, with weakest separation between C. latrans and C. rufus. The dogs are closest to C. aureus, followed by C. lupus. The plot of discriminant scores (Figure 20) is virtually identical to the plot from the previous analysis (Figure 19). Reversal of the axes is inconsequential. Standardized disciminant function coefficients (Table 29) exhibit the same pattern as the previous analysis. Classification results (Table 29) are also about the same. Finally, removal of the dogs from the analysis results in 55 specimens classifying as C.

Table 27. Summary statistics from discriminant analysis 3.

Function	Eigenvalue	Percent Variation	Canonical Correlation
1	5.029	74.89	.913
2	1.541	22.95	.779
3	0.143	2.12	.353
4	0.003	0.01	.050

Table 28. Matrix of Mahalanobis D^2 distances between groups and associated F-ratios (in parentheses) from discriminant analysis 3.*

Group	Canis lupus	Canis familiaris	Canis latrans	Canis rufus
C. familiaris	4.64 (128.9)			
C. latrans	3.34 (66.3)	5.19 (165.4)		
C. rufus	3.13 (35.7)	6.37 (150.9)	1.67 (10.4)	
C. aureus	3.36 (41.2)	3.73 (51.7)	2.11 (16.5)	3.28 (28.5)

*All F-ratios have 5 and 229 degrees of freedom and are significant at the .001 level.

Table 29. Standardized discriminant function coefficients from the first two functions from discriminant analysis 3.

Variable	Function 1	Function 2
PL/CL	-0.350	0.601
IM2/CL	-0.028	-1.017
OI/CL	-0.111	0.392
PW/CL	1.330	1.605
MCW/CL	1.219	-1.092

Table 30. Matrix of classification results from discriminant analysis 3.

	Group Classified Into				
Actual Group	Canis lupus	Canis familiaris	Canis latrans	Canis rufus	Canis aureus
C. lupus	52	1	1	1	4
C. familiaris	1	58	1	0	3
C. latrans	1	0	46	11	4
C. rufus	2	0	1	24	0
C. aureus	2	2	3	1	19

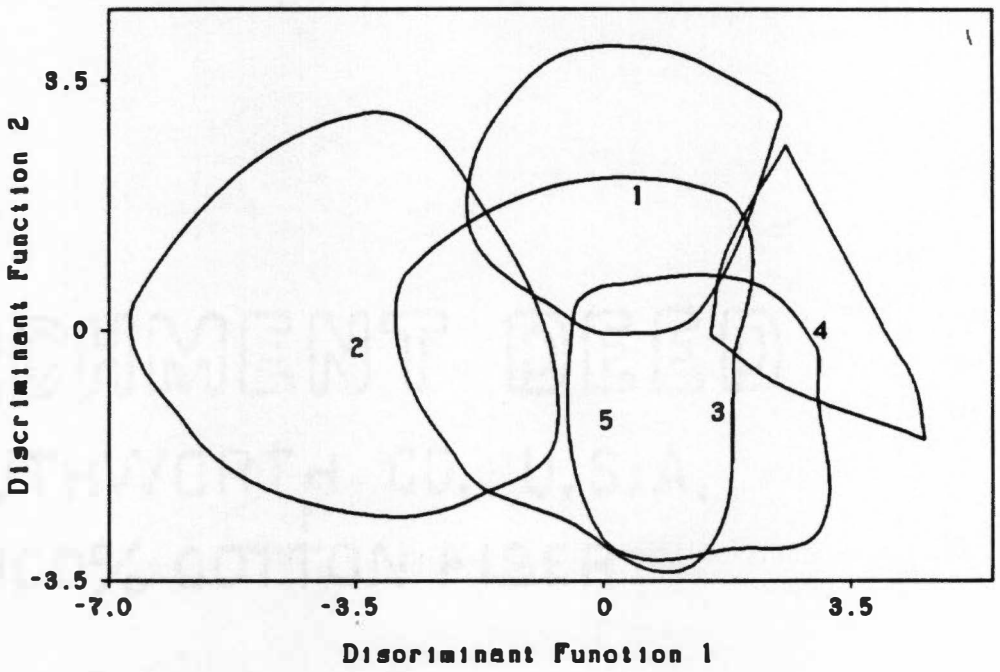


Figure 20. Discriminant analysis 3: plot of discriminant score ranges on two axes (contours) for each group, based on indexed cranial variables. Numbers are group centroids: 1=C.l. lycaon, 2=C. familiaris, 3=C. latrans, 4=C. rufus, 5=C. aureus. All groups are adults.

aureus, seven as C. lupus, and one as C. latrans.

Analysis of Adults and Juveniles

The remaining five analyses incorporate samples of juvenile C. lupus and C. rufus (See Table 18, page 173) with different combinations of the adult groups. Analyses 4 and 5 include all adult groups with one of the juvenile series. Then, to focus on specific groups, analyses 6, 7, and 8 use only combinations of the juvenile wolves, the dogs, and the jackals in three group analyses. All five analyses utilize the five cranial variables indexed against CL.

Analysis 4: All Adult Groups with Juvenile C. lupus

Results of this six group analysis are summarized on Tables 31-34 and Figure 21. The first two discriminant functions account for 96.2 percent of the variation (Table 31). D^2 distances between adult groups (Table 32) are consistent with previous analyses. The C. lupus juveniles are closest to the C. lupus adults, with both C. aureus and C. familiaris not much further removed. C. aureus is slightly closer to the juvenile group (D^2=2.64) than is C. familiaris (D^2=2.72). Though this result is surprising, it may be a consequence of disparate sample sizes. Subsequent analyses will focus on this problem. For the present, the most noteworthy result is that C. familiaris is closer to

Table 31. Summary statistics from discriminant analysis 4.

Function	Eigenvalue	Percent Variation	Canonical Correlation
1	4.306	72.54	.901
2	1.405	23.66	.764
3	0.195	3.29	.404
4	0.030	0.50	.170
5	0.000	0.00	.002

Table 32. Matrix of Mahalonobis D^2 distances between groups and associated F-ratios (in parentheses) from discriminant analysis 4.*

Group	*Canis lupus*	*Canis familiaris*	*Canis latrans*	*Canis rufus*	*Canis aureus*
C. familiaris	4.50 (121.6)				
C. latrans	3.31 (65.3)	5.01 (154.7)			
C. rufus	3.08 (34.6)	6.16 (141.3)	1.64 (9.96)		
C. aureus	3.37 (41.5)	3.62 (48.7)	2.09 (16.1)	3.22 (27.6)	
C. lupus (juveniles)	2.35 (19.7)	2.72 (26.8)	3.06 (33.9)	3.85 (38.7)	2.64 (18.2)

*All F-ratios have 5 and 254 degrees of freedom and are significant at the .001 level.

Table 33. Standardized discriminant function coefficients from the first two functions from discriminant analysis 4.

Variable	Function 1	Function 2
PL/CL	-0.040	0.625
IM2/CL	-0.140	-1.052
OI/CL	-0.030	0.444
PW/CL	1.237	1.572
MCW/CL	1.250	-1.051

Table 34. Matrix of classification results from discriminant analysis 4.

	Group Classified Into					
Actual Group	*Canis lupus*	*Canis familiaris*	*Canis latrans*	*Canis rufus*	*Canis aureus*	*Canis lupus* (juv)
C. lupus	48	0	1	1	2	7
C. familiaris	0	54	0	0	2	7
C. latrans	1	0	46	11	3	1
C. rufus	2	0	1	24	0	0
C. aureus	2	2	3	1	18	1
C. lupus (juveniles)	4	3	1	0	1	17

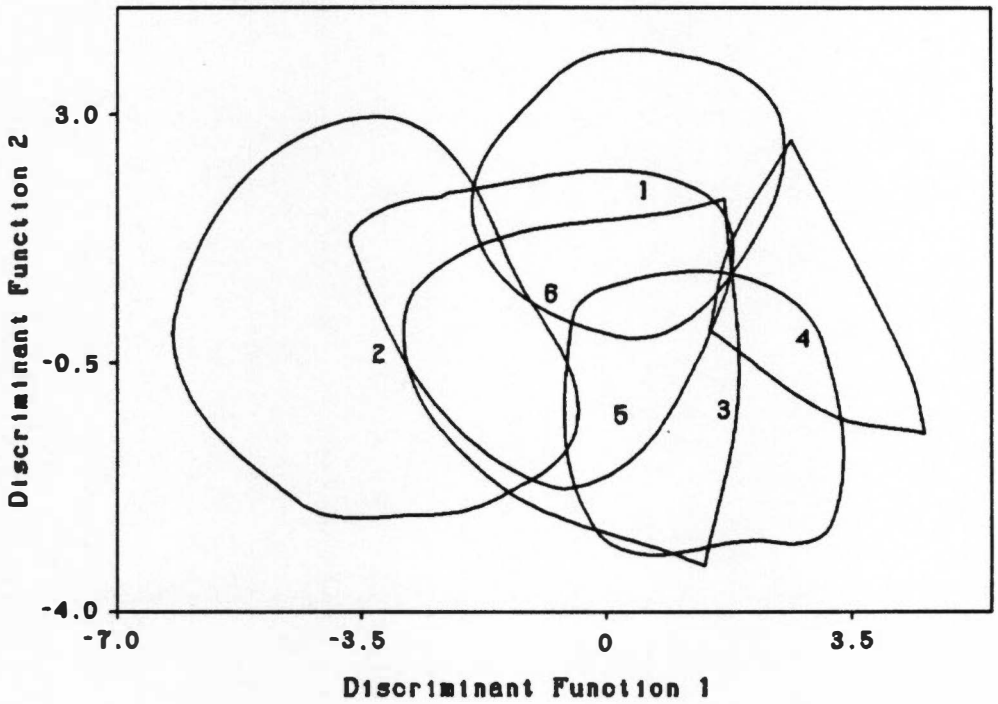


Figure 21. Discriminant analysis 4: plot of discriminant score ranges on two axes (contours) for each group, based on indexed cranial variables. Numbers are group centroids: 1=C.l. lycaon, 2=C. familiaris, 3=C. latrans, 4=C. rufus, 5=C. aureus, 6=C. lupus juveniles. Groups 1-5 are adults.

the juvenile wolves than to any adult group.

The discriminant score plot (Figure 21) illustrates the proximity between C. familiaris and the juvenile wolves. The basis for intergroup discrimination is not significantly altered by the addition of the juvenile wolves. Like analyses 2 and 3, the first function separates dogs from wild canids on the basis of differences in relative width of the palate and cranial vault (Table 33). The intermediate position of the juvenile wolves (Figure 21) reflects their wide palates and cranial vaults relative to adult wild canids. The second function again separates adult C. lupus on the basis of their unique combination of relatively wide palates with narrow cranial vaults and short tooth rows. The juvenile wolves were approaching similar proportions, evidenced by their relative proximity to adult C. lupus on the second axis (Figure 21).

Incorporation of the juvenile C. lupus groups results in a weak classification success rate of 78.4 percent (Table 34). About one third (9 of 26) of the juvenile wolves are misclassified, most with adult C. lupus (4) or C. familiaris (3). Because of their considerable range of variability, probably coupled with small sample size, the juvenile C. lupus group is not strongly separated. Nonetheless, they show greater morphological affinity with C. familiaris than does any other group. Secondary

analysis confirms this conclusion. When dogs are removed from the analysis, 52 of the 63 classify with the juvenile wolf group. The remaining 11 classify with C. aureus.

To sum, incorporation of juvenile C. lupus weakens overall discrimination. The basis for discrimination remains the same as in analyses 2 and 3, which included only adults. Most importantly, C. familiaris is more similar to juvenile C. lupus than to any other group.

Analysis 5: All Adult Groups with Juvenile C. rufus

Results of this analysis are summarized on Tables 35-38 and Figure 22. The first two functions account for 97.1 percent of the variation (Table 35). D^2 distances (Table 36) involving the C. rufus juveniles are markedly different from those involving C. lupus juveniles in the previous analysis (Table 32). While distances between juveniles and adults of the same species are similar, C. rufus juveniles are considerably closer to other adult groups, especially C. aureus and C. latrans. Remarkably, the D^2 distance between C. rufus juveniles and C. latrans is statistically insignificant. In terms of the few dimensions analyzed here, C. latrans is a perfectly juvenilized version of C. rufus.

The discriminant score plot (Figure 22) illustrates the proximity between C. rufus juveniles and C. latrans. The primary basis for overall discrimination remains the

Table 35. Summary statistics from discriminant analysis 5.

Function	Eigenvalue	Percent Variation	Canonical Correlation
1	4.245	70.94	.900
2	1.566	26.16	.781
3	0.156	2.67	.371
4	0.013	0.21	.113
5	0.001	0.00	.033

Table 36. Matrix of Mahalanobis D^2 distances between groups and associated F-ratios (in parentheses) from discriminant analysis 5.*

Group	*Canis lupus*	*Canis familiaris*	*Canis latrans*	*Canis rufus*	*Canis aureus*
C. familiaris	4.48 (120.6)				
C. latrans	3.30 (65.0)	4.89 (147.2)			
C. rufus	3.01 (33.1)	6.03 (135.2)	1.64 (10.0)		
C. aureus	3.40 (42.2)	3.56 (47.1)	2.05 (15.5)	3.17 (26.7)	
C. rufus (juveniles)	3.47 (34.1)	4.47 (57.5)	0.78 (1.76)	2.24 (11.0)	1.95 (8.4)

*All F-ratios have 5 and 247 degrees of freedom. With one exception, all are significant at the .001 level. *C. latrans* and *C. rufus* juveniles are not significantly different (p=.12).

Table 37. Standardized discriminant function coefficients from the first two functions from discriminant analysis 5.

Variable	Function 1	Function 2
PL/CL	-0.032	-0.605
IM2/CL	-0.070	1.034
OI/CL	-0.079	-0.377
PW/CL	1.227	-1.557
MCW/CL	1.171	1.099

Table 38. Matrix of classification results from discriminant analysis 5.

	Group Classified Into					
Actual Group	*Canis lupus*	*Canis familiaris*	*Canis latrans*	*Canis rufus*	*Canis aureus*	*Canis rufus* (juv)
C. lupus	52	1	1	1	4	0
C. familiaris	1	57	0	0	3	2
C. latrans	1	0	28	11	4	18
C. rufus	2	0	1	24	0	0
C. aureus	2	2	2	1	16	4
C. rufus (juveniles)	0	1	4	4	2	8

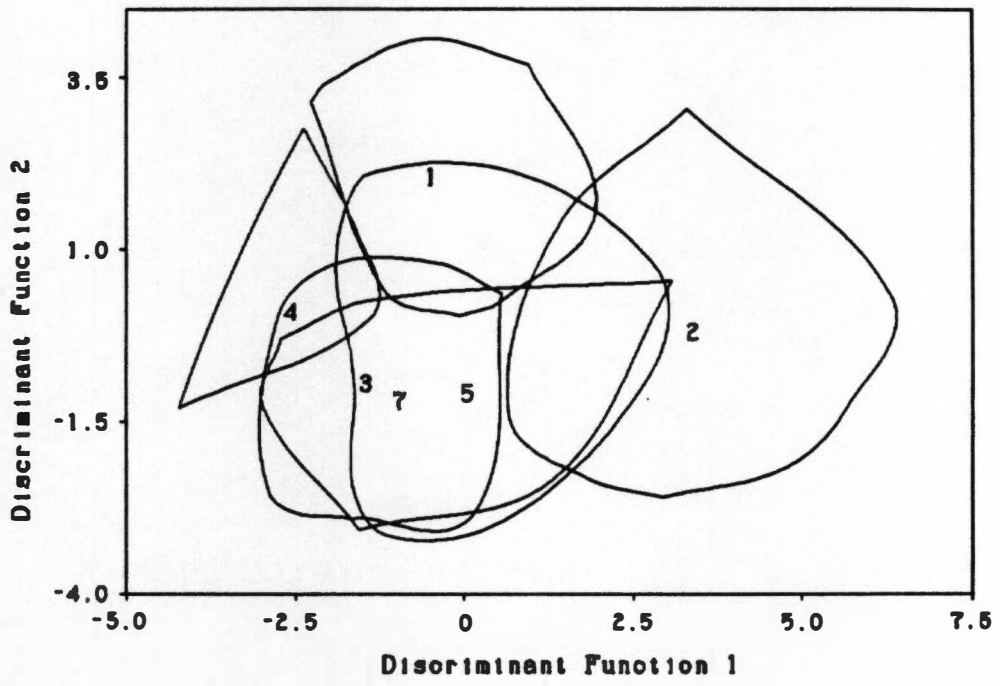


Figure 22. Discriminant analysis 5: plot of discriminant score ranges on two axes (contours) for each group, based on indexed cranial variables. Numbers are group centroids: 1=C.l. lycaon, 2=C. familiaris, 3=C. latrans, 4=C. rufus, 5=C. aureus, 7=C. rufus juveniles. Groups 1-5 are adults.

same as previous analyses. The dogs, with markedly wide palates and cranial vaults, are well demarcated by the first function. C. lupus, combining short tooth rows and narrow cranial vaults with wide palates, is discriminated by the second function (see Table 37). Overall classification success, at 72 percent, is the weakest thus far encountered (Table 38). Tremendous overlap between C. rufus juveniles and C. latrans is primarily responsible. Eighteen coyotes were incorrectly classified as C. rufus juveniles. Little confusion between C. familiaris and C. rufus juveniles is evident. When dogs are removed from the analysis, 54 of 63 are classified with C. aureus. Seven are classified with C. lupus and only two are classified with juvenile C. rufus. Clearly, the dogs are not similar to juvenile C. rufus.

Considering the proximity of C. rufus ontogenetic bivariate regressions to C. familiaris adult data points (Chapter VI), the distance between the two groups in this analysis seems surprising. Overall, C. familiaris exhibits much closer affinities to C. lupus juveniles. However, the apparent incongruity presented in this analysis is consistent with bivariate results. Explanation is best postponed until all multivariate analyses have been considered.

Analyses 1-5 have suggested several provocative patterns. First, among adult groups C. familiaris is most

similar to C. aureus. Second, C. familiaris is more similar to juvenile C. lupus than to any other group. Finally, C. familiaris is not similar to juvenile C. rufus. As noted earlier, however, a problem with multigroup analyses is that discrimination may be heavily biased towards groups with large sample sizes. Some of the trends just noted may be partially an artifact of this phenomenon, despite the measure taken to minimize this possibility (removal of dogs at the end of each analysis). To verify the basic accuracy of these trends, analyses 6-8 focus on morphological affinities only among dogs, jackals, and juvenile wolves.

Analysis 6: Dogs, Jackals, and C. lupus Juveniles

Results of analysis six are summarized on Tables 39-42 and Figure 23. Because three groups are involved, only two functions were extracted (Table 39). D^2 distances indicate that C. familiaris is closer to the C. lupus juveniles than to C. aureus (Table 40). Contrary to results of analysis 4, C. aureus is further removed from the C. lupus juveniles than is C. familiaris. The present result must be considered more accurate since this analysis keys on differences between only three groups.

The discriminant score plot (Figure 22) clearly shows that the first function separates the jackals and dogs, while the second function separates both the jackals and

Table 39. Summary statistics from discriminant analysis 6.

Function	Eigenvalue	Percent Variation	Canonical Correlation
1	1.872	74.8	.807
2	0.630	25.2	.622

Table 40. Matrix of Mahalanobis D^2 distances between groups and associated F-ratios (in parentheses) from discriminant analysis 6.*

Group	*Canis familiaris*	*Canis aureus*
C. aureus	3.30 (39.73)	
C. lupus (juveniles)	2.37 (19.97)	2.68 (18.34)

*All F-ratios have 5 and 109 degrees of freedom and are significant at the .001 level.

Table 41. Standardized discriminant function coefficients from discriminant analysis 6.

Variable	Function 1	Function 2
PL/CL	-0.225	0.321
IM2/CL	-0.232	-0.107
OI/CL	0.509	0.847
PW/CL	1.340	0.677
MCW/CL	0.652	-0.815

Table 42. Matrix of classification results from discriminant analysis 6.

	Group Classified Into		
Actual Group	*Canis familiaris*	*Canis aureus*	*Canis lupus* (juveniles)
C. familiaris	50	4	9
C. aureus	2	23	2
C. lupus (juveniles)	4	2	20

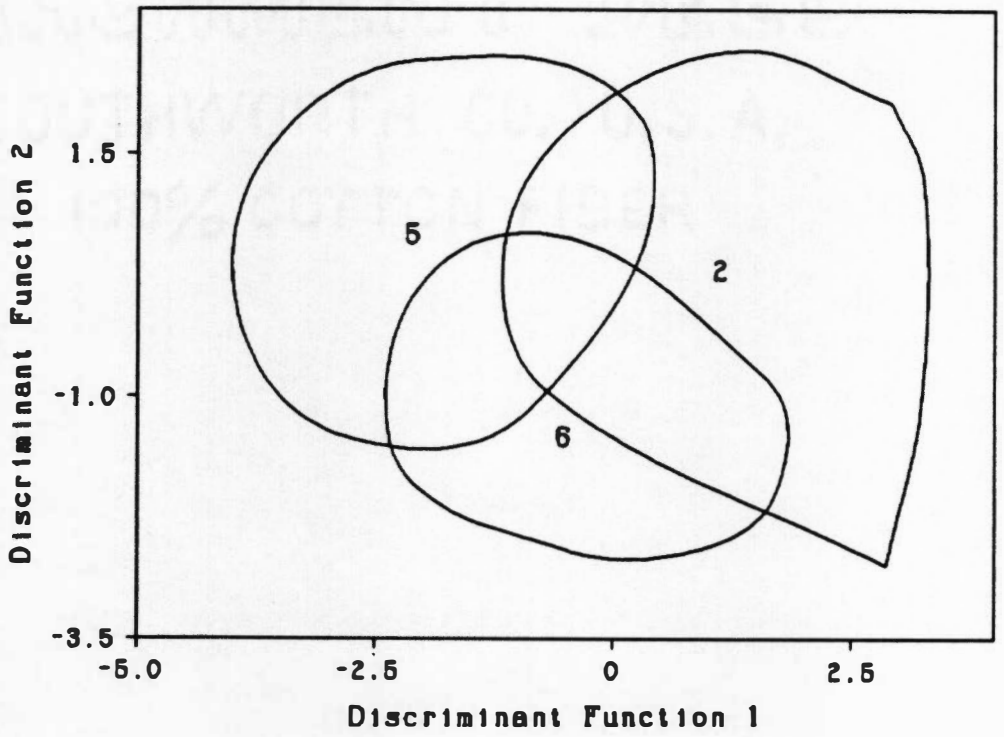


Figure 23. Discriminant analysis 6: plot of discriminant score ranges on two axes (contours) for each group, based on indexed cranial variables. Numbers are group centroids: 2=C. familiaris, 5=C. aureus, 6=C. lupus juveniles. Groups 2 and 5 are adults.

dogs from the C. lupus juveniles. Discrimination on the first function involves primarily differences in palate width (Table 41). Discrimination on the second function is based primarily on covariation between MCW and OI. In relation to their cranial vault widths, the C. lupus juveniles have longer faces than dogs. For example, the average ratio of MCW/CL is .337 for juvenile C. lupus and .365 for C. familiaris. Conversely, average ratio of OI/CL is .468 for juvenile C. lupus and .453 for C. familiaris.

Classification results indicate an overall success rate of 80.2 percent (Table 42). Similarity between the dogs and C. lupus juveniles is indicated by the misclassification of nine juveniles into the dog group. When dogs are removed from the analysis, 49 classify with the C. lupus juveniles and only 11 classify with C. aureus. Hence, basic results of previous analyses are confirmed. Dogs exhibit similarities to both C. aureus and C. lupus juveniles. However, they are most similar to the C. lupus juveniles.

Analysis 7: Dogs, Jackals, and C. rufus Juveniles

Results of this analysis are summarized on Tables 43-46 and Figure 24. The second function, accounting for 10.1 percent of the variability, shows reduced discriminating power relative to previous analyses (Table 43). D^2 distances (Table 44) indicate greatest proximity between C.

Table 43. Summary statistics from discriminant analysis 7.

Function	Eigenvalue	Percent Variation	Canonical Correlation
1	2.776	89.9	.857
2	0.313	10.1	.489

Table 44. Matrix of Mahalanobis D^2 distances between groups and associated F-ratios (in parentheses) from discriminant analysis 7.*

Group	*Canis familiaris*	*Canis aureus*
C. aureus	3.21 (37.4)	
C. rufus (juveniles)	3.72 (38.8)	1.79 (6.9)

*All F-ratios have 5 and 102 degrees of freedom and are significant at the .001 level.

Table 45. Standardized discriminant function coefficients from discriminant analysis 7.

Variable	Function 1	Function 2
PL/CL	-0.071	-0.553
IM2/CL	-0.249	0.612
OI/CL	0.334	0.924
PW/CL	1.575	0.610
MCW/CL	0.582	-0.480

Table 46. Matrix of classification results from discriminant analysis 7.

	Group Classified Into		
Actual Group	Canis familiaris	Canis aureus	Canis lupus (juveniles)
C. familiaris	58	4	1
C. aureus	2	20	5
C. lupus (juveniles)	1	2	16

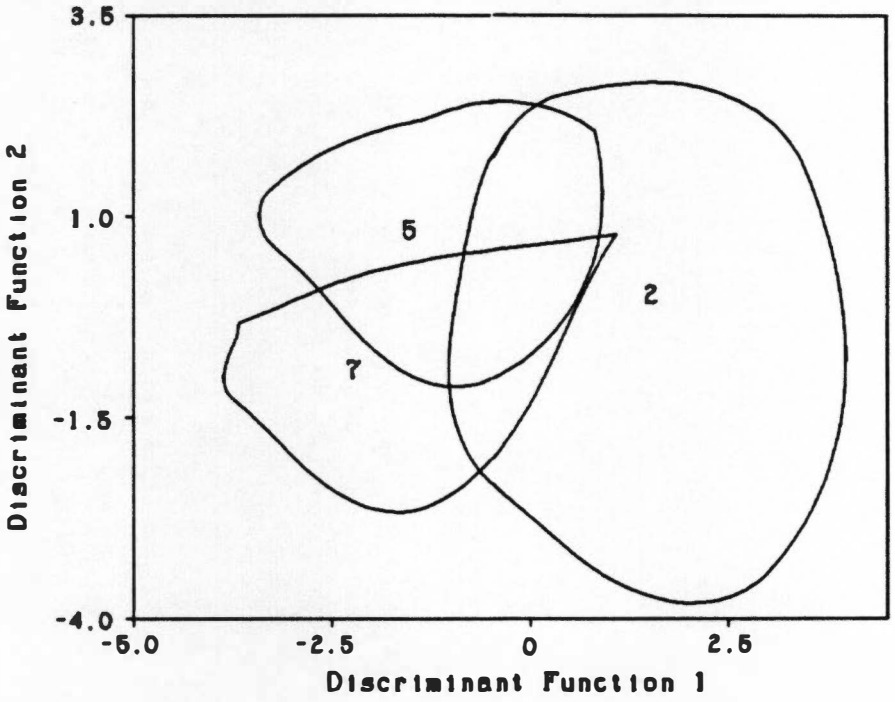


Figure 24. Discriminant analysis 7: plot of discriminant score ranges on two axes (contours) for each group, based on indexed cranial variables. Numbers are group centroids: 2=C. familiaris, 5=C. aureus, 7=C. rufus juveniles. Groups 2 and 5 are adults.

aureus and the C. rufus juveniles. C. familiaris is well removed from the C. rufus juveniles.

The discriminant score plot (Figure 24) indicates that the first function distinguishes the dogs from the other two groups. Not surprisingly, the primary basis for discrimination is variation in relative palate widths (Table 45). The weak second function contributes mostly to discrimination between C. aureus and the C. rufus juveniles. Variation in relative face lengths is primarily responsible (Table 45). Overall discrimination is good, evidenced by an 86.2 percent success rate (Table 46). Most misclassifications involve C. aureus and C. rufus juveniles. When dogs are removed from the analysis, 45 individuals classify with C. aureus and 18 classify with the C. rufus juveniles.

Basic results of earlier analyses are verified in this analysis. C. familiaris is not morphologically similar to the C. rufus juvenile group. Rather, C. familiaris is more similar to C. aureus. C. rufus juvenile morphology closely parallels that of adult C. latrans.

Analysis 8: Dogs, Juvenile C. lupus, Juvenile C. rufus

This final analysis seeks verification of the greater proximity of C. familiaris to C. lupus juveniles, relative to the C. rufus juveniles. Results are summarized on Tables 47-50 and Figure 25. D^2 distances (Table 48)

Table 47. Summary statistics from discriminant analysis 8.

Function	Eigenvalue	Percent Variation	Canonical Correlation
1	2.064	84.90	.821
2	0.367	15.10	.518

Table 48. Matrix of Mahalanobis D^2 distances between groups and associated F-ratios (in parentheses) from discriminant analysis 8.*

Group	*Canis familiaris*	*Canis lupus* (juveniles)
C. lupus (juveniles)	2.32 (19.0)	
C. rufus (juveniles)	3.66 (37.5)	2.38 (11.9)

*All F-ratios have 5 and 101 degrees of freedom and are significant at the .001 level.

Table 49. Standardized discriminant function coefficients from discriminant analysis 8.

Variable	Function 1	Function 2
PL/CL	-0.119	0.728
IM2/CL	-0.403	-0.629
OI/CL	0.043	0.665
PW/CL	1.048	1.162
MCW/CL	0.881	-0.778

Table 50. Matrix of classification results from discriminant analysis 8.

	Group Classified Into		
Actual Group	*Canis familiaris*	*Canis lupus* (juveniles)	*Canis rufus* (juveniles)
C. familiaris	52	8	3
C. lupus (juveniles)	4	20	2
C. rufus (juveniles)	1	2	16

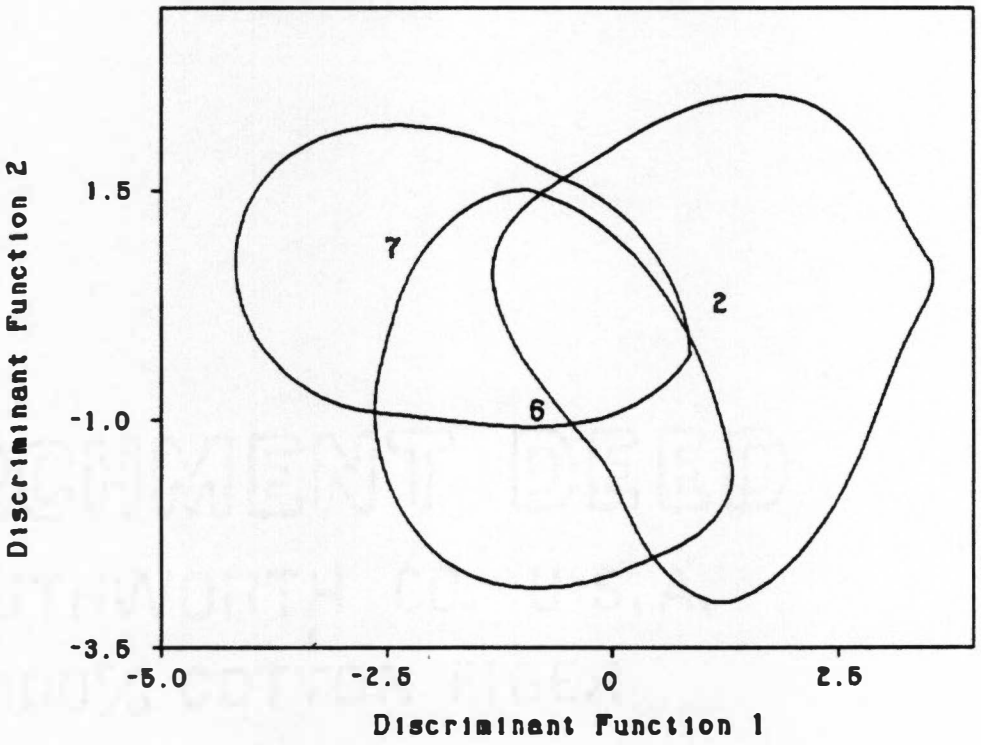


Figure 25. Discriminant analysis 8: plot of discriminant score ranges on two axes (contours) for each group, based on indexed cranial variables. Numbers are group centroids: 2=C. familiaris (adults), 6=C. lupus juveniles, 7=C. rufus juveniles.

clearly indicate that the dogs fall closest to the C. lupus juveniles. Greater proximity between these groups is evident on the discriminant score plot (Figure 25).

The first function distinguishes the groups on the basis of relative palate and cranial vault widths (Table 49). The groups are neatly ordered by increasing relative widths (Figure 24). The basis for discrimination on the weaker second function is less clear, but apparently involves different patterns of covariation between PW and other variables (Table 49). In any case, it does not effectively discriminate the dogs.

Classification produces an overall success rate of 81.5 percent (Table 50). The majority of misclassifications involve C. familiaris and the C. lupus juveniles. When dogs are removed from the analysis 51 individuals classify with the C. lupus juveniles, while 12 classify with the C. rufus juveniles.

Again, basic results of earlier analyses are confirmed. C. familiaris is morphologically more similar to C. lupus juveniles than to C. rufus juveniles. This result is consistently obtained regardless of different sample combinations.

Evaluation of Multivariate Results

Different combinations of groups have yielded consistent patterns of intergroup discrimination. Three

patterns are of primary significance. First, among adults the dogs are most similar to C. aureus. Second, among all groups dogs are most similar to C.l. lupus juveniles. Finally, the dogs are not similar to C. rufus juveniles. Instead, C. latrans is strikingly similar to--actually indistinguishable from--the C. rufus juveniles.

Given their similar size, relative similarity between C. familiaris and C. aureus is ensured from tight scaling of cranial length variables (PL, IM2, OI). Larger canids are divergent from dogs with respect to these dimensions as a consequence of allometric scaling. If C. familiaris and C. aureus exhibited similar scaling with respect to PW and MCW they might be indistinguishable. However, it is precisely these variables that allow discrimination between the dogs and jackals, and strengthen the separation of dogs from other adult groups. In bivariate analyses dogs are always transposed strongly above other groups on PW and MCW. In multivariate analyses using indexed data, the first function always serves primarily to separate dogs from other groups on the basis of wider palates and cranial vaults.

On the other hand, proximity of C. familiaris to C. lupus juveniles relative to C. rufus juveniles seems contrary to results of bivariate analysis. It will be recalled that ontogenetic regressions for both wolf groups suggsted ontogenetic scaling with dogs on PL, IM2, and OI.

On PW and MCW absolute evidence of ontogenetic scaling was less clear, but C. rufus ontogenetic regressions apparently provided stronger evidence than C. lupus ontogenetic regressions. Understanding why bivariate and multivariate results are consistent requires reconsideration of the bivariate ontogenetic analysis in relation to samples used for multivariate analysis.

On average, the juvenile wolves used in multivariate analysis are considerably larger than the adult dogs (see Table 18, page 173). The juvenile samples are biased towards advanced subadults. Consequently, the bivariate ontogenetic regressions in Chapter VI pass the static data points of the dogs (Figure 17, pages 163-164) at a condylobasal length considerably less than the average length of juveniles in the multivariate analysis. In fact, virtually no juvenile wolf specimens are represented in the size range of adult dogs. The proportional relationships exhibited by dogs and wolves at the size of dogs will remain constant at larger sizes only if all ontogenetic slopes are isometric. They are not.

Both C. lupus and C. rufus ontogenetic regressions for PL and OI are similar and apparently nonisometric. As growth in wolves produces increasing size disparity relative to dogs, their morphology will diverge accordingly. In these cases, however, both C. lupus and C. rufus will diverge in similar ways. Consequently, the

cause underlying morphological similarity between C. familiaris and the larger C. lupus juveniles must lie with the width variables, PW and MCW.

C. lupus and C. rufus ontogenetic regressions for PW and MCW are different. Their slopes are divergent (MCW) or the regressions are strongly transposed (PW--see Table 15, page 149). In both cases the C. lupus regressions fall at the upper margin of the C. familiaris data points, while the C. rufus regressions fall near the center or in the lower portion of those data points (Figure 17, page 164). Ontogenetic slopes for both juvenile series exhibit strong negative allometry. The morphological consequences at larger sizes are easily deduced. C. rufus, exhibiting similar or proportionally narrower palates and cranial vaults at the same size as dogs, diverge in morphology as growth proceeds. As advanced juveniles, they assume proportions like C. latrans.

The consequences for C. lupus in relation to C. familiaris are different. At the size of dogs the C. lupus juveniles have wider palates and vaults. Unlike C. rufus, negative allometry ensures that this disparity is reduced rather than magnified during subsequent growth. At some point on the ontogenetic trajectory the C. lupus juveniles must exhibit proportional similarity to dogs with respect to these dimensions, though that point is not necessarily the same for each dimension. Eventually, the C. lupus

juveniles attain adult proportions: narrower palates and vaults relative to dogs.

Thus, when examined closely the similarity between C. familiaris and C. lupus juveniles is consistent with bivariate analysis. In fact, it can be predicted that C. lupus samples with better age control would exhibit striking similarity to C. familiaris. Especially noteworthy is the fact that C. familiaris is more similar to the C. lupus juveniles than to C. aureus, despite being closer in overall size to C. aureus. Taking these patterns all into account, the evidence for juvenilized morphology in the dogs is strong. Their distinctively wider palates and vaults correspond to juvenile proportions in C. lupus. These proportions are not seen in other groups.

Summary

1. Discriminant analysis of untransformed data yields size related discrimination among adult groups. When indexed data are used multivariate analysis indicates that the dogs are most similar to jackals. Morphological similarity between these groups results from consistent allometric scaling of anterior cranial length variables.

2. Inclusion of juvenile wolf groups indicates that the dogs are morphologically more similar to juvenile C. lupus than to any adult groups. The dogs do not exhibit morphological similarity to juvenile C. rufus. C. rufus

juveniles and C. latrans adults are statistically indistinguishable.

3. When examined closely these results are consistent with results of bivariate analyses. Greater multivariate similarity between dogs and C. lupus juveniles relative to C. rufus juveniles stems from juvenile wolf samples skewed heavily towards advanced subadults. It can be deduced that juvenile C. lupus samples not as markedly skewed in this way would exhibit even greater similarity to the adult dogs.

4. The prehistoric dogs exhibit juvenilized morphology. Results of analysis are consistent with an hypothesis of ontogenetic scaling between dogs and wolves.

CHAPTER VIII

PATTERN AND PROCESS IN THE EVOLUTION OF THE DOG

The objective of this chapter is to integrate results of quantitative analysis with theoretical and methodological considerations outlined in the first three chapters. Ambiguities in results and associated interpretive problems are given primary consideration. The chapter culminates with a summary of the principal results and arguments presented in the dissertation.

Paedomorphosis and Heterochrony

Evidence for paedomorphosis (juvenilized morphology) in dogs has been a central target of investigation in this study. Paedomorphosis in general is a persistent theme in discussions of the origins and evolution of the domestic dog (e.g., Hilzheimer 1932; Lumer 1941; Weidenreich 1941; Zeuner 1963; Epstein 1971; Clutton-Brock 1981; Wayne 1986a). Therefore, it is necessary to assess the strength of this evidence and determine its interpretive significance.

Evidence for Paedomorphosis

Evidence for paedomorphosis in this study takes two primary forms. First, bivariate analysis revealed that uniquely wide cranial vaults and palates among adult dogs are associated with greater proximity to wolf ontogenetic

regressions relative to other groups. All groups exhibit reasonable evidence of ontogenetic scaling on anterior cranial length variables. Second, multivariate analysis revealed that the dogs exhibit greatest overall morphological similarity to juvenile C. lupus. Though compelling, these patterns are not free of potential complications.

The first potential complication is that absolute evidence of ontogenetic scaling between wolves and dogs is ambiguous. On cranial width variables wolf ontogenetic regressions consistently pass closer to the dog static data points than to data points of other adult groups (excluding the C. rufus-C. latrans comparisons). Wide vaults and palates are clearly a juvenilized feature, and they are exhibited by dogs. However, the wolf ontogenetic regressions do not consistently pass through the central portion of the dog static data points. This is especially true of the C. lupus regressions.

It is argued here that the greater similarity between dogs and juvenile wolves relative to other adult groups is far more compelling than lack of absolute correspondence. Wolves are polymorphic, exhibiting a wide range of size and morphology. The juvenile samples of C. lupus used here consist exclusively of a few North American subspecies, primarily C.l. lycaon. Without detailed knowledge of the ancestry of the dogs, to expect precise morphological

correspondence between dogs and the juvenile wolves is unreasonable. "Perfect" C. lupus ontogenetic regressions for different subspecies would undoubtedly yield a variety of similar but different trajectories. Presumably, some trajectories would pass closer to the central portion of the dog static data points while others would pass farther away, relative to the wolf ontogenetic regressions constructed here. Thus, the general correspondence between dogs and juvenile wolves is compelling.

Another complication is greater evidence of ontogenetic scaling between C. familiaris and C. rufus rather than C. lupus. At the size of dogs C. rufus is more similar to the dogs than is C. lupus. This, in and of itself, is not a problem. The problem is that C. rufus develops into adults shaped more like C. latrans than C. lupus. Consequently, multivariate analysis, focusing on advanced subadults, indicated little morphological correspondence between C. familiaris and C. rufus juveniles.

Even assuming the tiny C. rufus juvenile samples to be representative, this apparent dilemma is not serious. First, C. rufus and C. latrans are expected to be similar for historical reasons (see Chapter IV). Second, and most importantly, the coyote-like morphology of C. rufus is not dictated wholly by the elevation of cranial width ontogenetic regression lines. Numerous regression lines

can pass through the range of variation of the dogs, but their slope will influence adult morphology.

This point is illustrated on Figure 26. Note that several regressions pass centrally through the group 5 data points, but slight perturbations in slope produce different adult morphologies. The artificial scale necessary for constructing this diagram exaggerates the slope differences actually necessary to produce different adult morphologies. Without investigation of a more robust data base, it is reasonable to suggest that the coyote-like adult morphology of C. rufus is produced by unusually shallow ontogenetic regression slopes for cranial width variables. Slightly steeper slopes, which might characterize other small wolves, would produce slightly more "wolf-like" proportions. Clearly, additional studies are needed.

Overall, it is argued that evidence for juvenilized morphology in dogs is robust. Differing patterns of bivariate and multivariate similarity are associated with taxonomic and methodological problems. Thus, any argument concerning the ancestry of dogs among smaller versus larger wolves is unwarranted. For the present, it can safely be stated only that morphology of prehistoric dogs corresponds more closely to morphology of juvenile wolves than to adult wolves or adults of any other taxa. This similarity transcends size similarities.

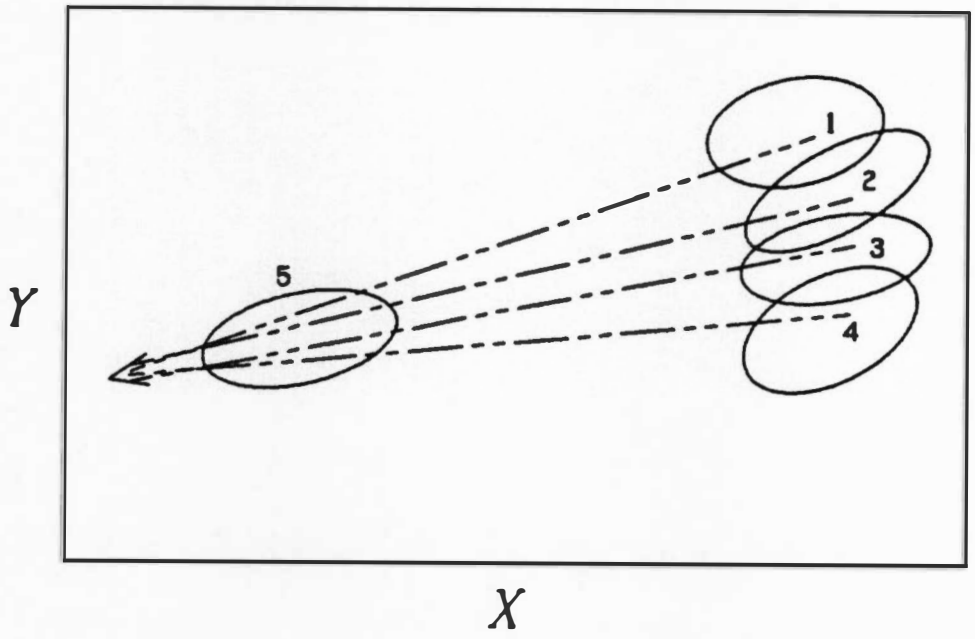


Figure 26. Hypothetical bivariate plot of two linear dimensions showing ranges of static variation (ellipses) for five groups in relation to ontogenetic regressions (broken lines) for groups 1 through 4.

The Cause of Paedomorphosis

Apparent paedomorphosis among modern dogs has prompted different ideas concerning its causes. Clutton-Brock (1981:37-38, 1984:205) suggests that among early dogs paedomorphic features, associated with submissive behavior, were more endearing to humans and were therefore selected for. While this notion has intuitive appeal, it is untestable. We do not know, and have no way of knowing, what features in dogs were "endearing" (Clutton-Brock 1981:38) to prehistoric human hunter-gatherers.

Other propositions concerning morphological change in dogs generally correspond to Shea's (1981) distinction between size-required and size-related changes (see Chapter III). Both are concerned with consequences of size reduction. A "size-related" perspective is associated especially with the work of German scholars in the early twentieth century (see discussion in Weidenreich 1941 and Epstein 1971). From this perspective juvenilized morphology itself is the key. The course of ontogenetic development is paralleled by the pattern of morphological change from small breeds to large breeds. Thus, skull forms among different sizes of adult dogs represent arrested developmental stages (Hilzheimer 1932:412). This view probably reflects the then current discussions of recapitulation in ontogeny--in this case reverse recapitulation--as an evolutionary force (see historical

review in Gould 1977).

A "size-required" perspective holds that paedomorphosis is a secondary consequence of biomechanical constraints associated with size reduction (e.g., Lumer 1940, Weidenreich 1941; Epstein 1971:83-106). For example, Epstein (1971:103-106) argued that juvenilization is an accurate morphological description, but indicates nothing about physiological mechanisms. Rather, size-correlated changes in cranial morphology are dictated by the fact that small animals must have relatively larger brains to maintain similar functions at different sizes (see also Weidenreich 1941; Stockhaus 1965:171-172; Radinsky 1981:383). Cranial morphology in small dogs appears paedomorphic in response to this biomechanical necessity.

Arguments advanced by Wayne (1986a, 1986b, 1986c) support a considerably refined version of the earlier recapitulation notions. Paedomorphosis is a consequence of size reduction, but this paedomorphosis itself is significant. Phylogenetic rather than purely biomechanical constraints are responsible for paedomorphic features in dogs. The existence of alternative morphologies among other canids of similar size seriously damages an argument of biomechanical necessity. Even if distinctive neurocranial proportions in dogs are necessitated by biomechanical constraints related to brain conformation,

this does not easily explain the distinctive palatal morphology of dogs. Moreover, brain development itself could be constrained by ontogenetic boundaries.

Results of this study are consistent with Wayne's findings. The prehistoric dogs are distinct from other adult groups in palate and cranial vault widths. It is precisely on those dimensions that the dogs correspond more closely than other groups to the ontogenetic regression lines of wolves. Where dogs scale similarly to other groups (anterior cranial length variables), all groups correspond generally to wolf ontogenetic regression lines. In general, dog morphology is juvenilized, evidenced by similarity to C. lupus juveniles in multivariate analysis.

Thus, as Wayne (1986a) argued, morphology of dogs is largely constrained to ontogenetic boundaries. Confinement of morphology to developmental pathways presumably reflects the genetically simplest means of accomodating rapid evolutionary size change (Wayne 1986a, 1986b). As Alberch et al. (1979:315) have stated, "Many elements of morphological evolution can be interpreted as minor reshuffling within a fundamental developmental program during phylogenesis." In general, developmental pathways may pose the single most powerful category of restrictions on evolutionary pathways (Gould and Lewontin 1979). Intensive selection for size change, channeled by ontogenetic boundaries, probably explains the generally

paedomorphic morphology of both prehistoric and recent dogs.

The Developmental Cause of Paedomorphosis: What Kind of Heterochrony?

As outlined by Gould (1977), classic progenesis entails truncation of development through accelerated sexual maturation. The consequence is reduced size and juvenilized morphology in descendents relative to their ancestors. Among modern dogs earlier sexual maturity relative to wolves, general correlation between adult size and age at maturity (see Chapter II), and general correlation between adult size and period of growth (cf. Kirkwood 1985:102) all suggest a role for this simple "time" progenesis in the evolution the dog.

Time progenesis alone is incapable of accounting for size diversity among modern dogs, or differences between dogs and wolves. Assuming an age at maturity of two years for C. lupus development could be truncated by a full year with little effect on size and morphology. Among living wolves yearlings are notoriously difficult to distinguish from mature adults (Mech 1970:141). Even at six months wolf pups strongly resemble adults (Mech 1970:141). In this study individuals judged to be about one year old were regarded as adults precisely because their cranial size and proportions are essentially adult.

Data in this study also verify the inadequacy of time

progenesis. At the size of dogs, with most condylobasal lengths falling in the 140-160 millimeter range, C. lupus juveniles are just beginning to lose their deciduous dentition (see Table 2, page 81 and Table 14, page 146). Clearly, alteration of developmental factors other than age at maturity are involved in size reduction of dogs.

Wayne's studies of growth and allometry in canids (1986a, 1986b, 1986c) strongly suggest that size and morphological diversity among dogs are largely a function of variability in foetal or perinatal specific growth rates. From Lhasa Apso to Great Dane, specific growth rates after 40 days post-partum are relatively invariant. The same is true of wild canids studied by Wayne. Wayne (1986c) argues that invariance in gestation period represents a fundamental morphological constraint on dogs. In fact, gestation lengths in Canis as a whole are similar (cf. Gittleman 1986:748). As a consequence, small dogs are distinct from similar sized canids of other genera, while showing similarity to their closest relatives in the genus Canis.

Stability of gestation periods may contribute to morphological similarity between dogs and similar sized wild Canis. Nonetheless, prehistoric dogs studied here are distinct from jackals or coyotes of similar size. Their distinctive morphology probably reflects developmental constraints that were not pronounced in the evolution of

other species of Canis. As Dahr (1942:35) observed almost 50 years ago, different patterns of allometry between domestic and wild canids may result from body size changes being brought about in different ways. This may apply as well to differences between domestic and wild canids in brain-body size allometries (cf. Weidenreich 1941; Dahr 1942; Clutton-Brock 1984:205-206).

The developmental mode of size change in dogs presumably reflects intensity of size selection. The consequences of early growth rate alterations caused early dogs to reduce dramatically and rapidly in size. One immediate consequence may have been disharmony between oversized teeth in undersized jaws (see below). This situation is frequently suggested among earliest dogs (Degerbøl 1961; Bökönyi 1975; Clutton-Brock 1984). Such anomalies may render this mode of size change unviable among more slowly evolving wild species. Among dogs, however, a radically altered niche dictated change of a major magnitude in a brief period of time.

Bonner and Horn (1982:268) note that a common problem in analysis of heterochrony is separating cases in which size/shape selection has produced accompanying changes in developmental timing, from cases in which selection on developmental timing has produced accompanying changes in size and shape. In the present case a solution to the Bonner and Horn dilemma can be advanced. As explained in

Chapter II, conditions associated with colonization of a new niche selected directly for precocious maturation among dogs. Consequently, dogs reach maturity sooner than wolves. However, this alteration had minor influence on size and morphology. As also outlined in Chapter II, body size was a primary target of selection among early dogs in abrubtly and radically altered circumstances. As a consequence, developmental rates were altered early in ontogeny. Thus, selection acted on both body size and developmental timing. Dogs exhibit both time and rate progenesis relative to their ancestors.

Time and Size Change

Size and Ancestry

As noted previously, many investigators seek ancestry for most dogs among small Eurasian wolf subspecies like C.l. pallipes or C.l. chanco (Zeuner 1963; Lawrence 1967; Epstein 1971; Olsen and Olsen 1977; Clutton-Brock 1984; S. Olsen 1985). Insistence on an important role for small subspecies stems in part from dramatic size disparities between wolves and early domestic dogs. Efforts to minimize the magnitude of size reduction in models of dog ancestry probably reflect a belief that evolutionary change, even under domestication, must occur relatively gradually. Thus, prevailing logic holds that relatively small early dogs were derived from small wolves (e.g.,

Lawrence 1967:57; Clutton-Brock 1970:307; Olsen and Olsen 1977; S. Olsen 1985:41-42).

It is argued here that intensive size selection, implemented through heterochrony, negates the necessity of deriving small dogs from small wolves. Because heterochrony involves relatively simple genetic alterations, evolutionary change can be rapid. From this perspective substantial size difference between early dogs and wolves is unsurprising. If a tiny toy dog like the Lhasa Apso can be produced from a wolf (of any size) in 12,000 years, the size differential between early dogs and wolves is no problem.

The objective of these comments is not to dogmatically assert that small Eurasian wolves played an unimportant role in dog ancestry. Rather, the point is that reduced size disparity between these wolves and early dogs is not convincing evidence of their ancestry. In this author's view the question of dog ancestry among smaller versus large wolves, or multiple ancestry involving wolves of different sizes, remains open.

Size reduction in early dogs indicates little about subspecific ancestry. However, it is an important clue regarding evolutionary process. The perspective advanced here is that size reduction was ubiquitous in the early evolution of the dog for ecological reasons already discussed. Because body size diversity at a given point in

time was initially constrained, morphological diversity was similarly constrained. The prehistoric dogs used in this study exhibit relatively limited size and morphological variation compared to more recent dogs. J. Olsen (1985:51) illustrates an early Neolithic dog cranium from Hemudu, China (6065±120 years B.P.), that is approximately the same size as many of the North American and European dogs used here. Clutton-Brock (1981:43-44) cautiously suggests that Neolithic dogs in Britain exhibited less variability than later populations. Scott (1968:249), citing a study in German by Dahr (1937), indicates that "Stone Age" dogs of Europe should be regarded as one general population, characterized by considerably less variation relative to modern dogs (see also Dahr 1942:32-33).

Size change through time is reflected in the limited data set analyzed here. Among the North American dogs the three earliest specimens have condylobasal lengths of 158 (estimated for Koster F2357), 165 (Koster F2256), and 162 millimeters (Modoc). These values are substantially higher than the mean of 149.2 for the North American series as a whole. Among the European dogs the earliest specimen, from Senckenberg, has a condylobasal length of 178 millimeters. The Mesolithic specimens, from Vedbæk Boldbaner, Saltpetersmosen, Ringkloster, and Ertebølle, have a condylobasal length range of 156-178 millimeters. The early Neolithic specimens, from Bundsø, Spodsbjerg, and

Lidsø, range in condylobasal length from 136-160 millimeters. Though samples are small and geographic variation may complicate comparisons, there is a clear tendency for early specimens to be larger than more recent specimens.

Figure 27 illustrates the general relationship between size change and time in the evolution of the dog. A single ancestry for dogs is implied only for clarity of illustration. For about 6,000 years dogs experienced rapid size reduction with limited morphological diversification. It is expected, of course, that these early populations exhibited variation, but the overall trend was towards decreasing size. Sometime between 6,000 and 3,000 B.P., depending on the region, increasing diversity in size and form is evident. For example, Clutton-Brock (1981:44) notes that in ancient Egypt considerable size and morphological diversity among dogs is evident by 4,000 B.P. In northern Europe and North America, sources of the dog samples used here, 3,000 B.P. is a useful time boundary for diversification of size and morphology in dog evolution.

To sum, early dog evolution was characterized by size reduction and limited morphological diversification. Because of the ubiquitous role of size reduction brought about by evolutionary alterations in development, it is impossible to specify the local variants of C. lupus involved in initial ancestry. Increased diversity in size

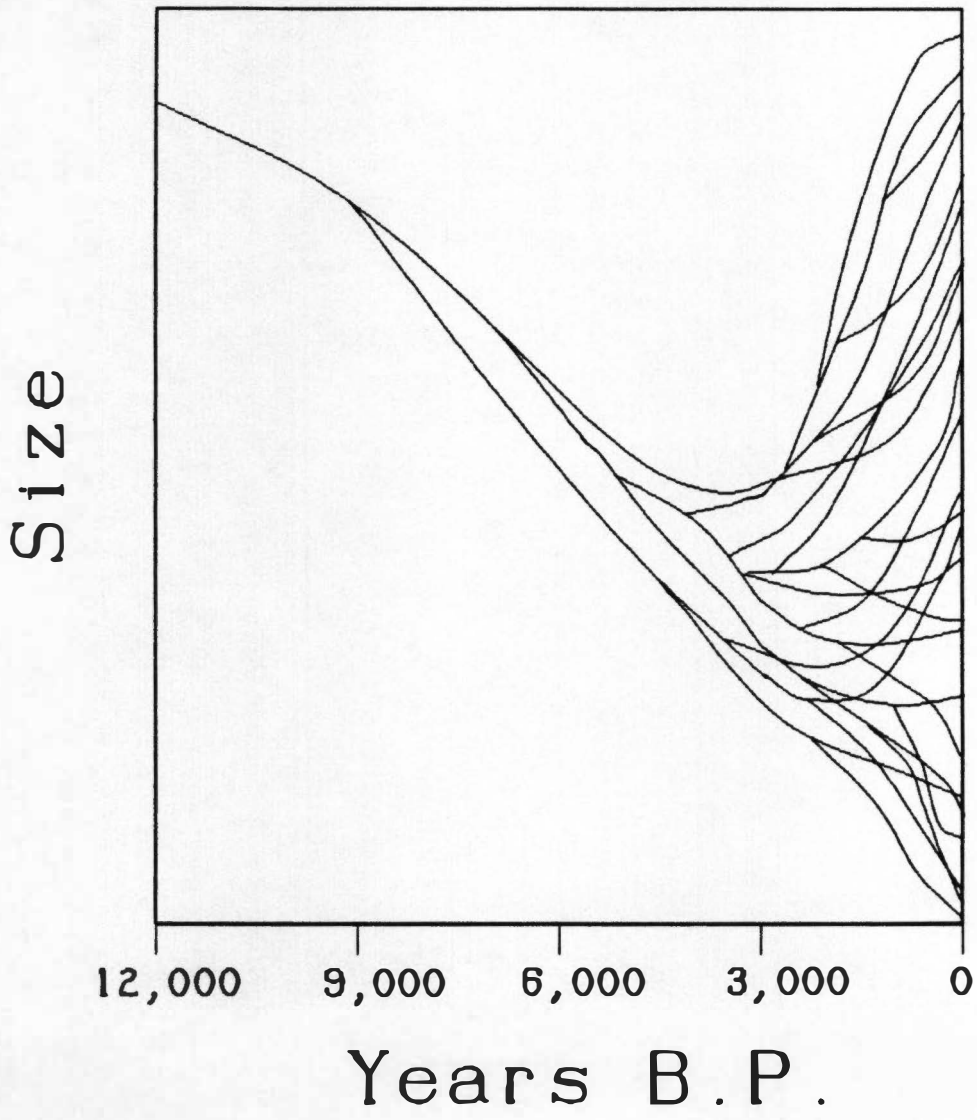


Figure 27. Inferred relationship between time and evolutionary changes in body size in the domestic dog. Different branches represent different varieties of dogs. The size axis is purely schematic and does not imply an absolute scale.

and morphology, presumably stemming from selective breeding by humans, appears at different times in different regions. Once underway the amazing range of sizes and forms, so familiar in modern times, was rapidly produced.

Size, Time, and "Primitiveness"

Not surprisingly, many investigators have sought to identify varieties of modern dogs that may be held as models of earliest dogs (Dahr 1942; Werth 1944; Stockhaus 1965; S. Olsen 1985). Large breeds that resemble wolves in many respects, for example northern Eskimo dogs, are usually regarded as primitive (e.g., Stockhaus 1965; Olsen 1985:x). Similarly, reduced size is taken as evidence of evolutionary distance from wolves. For example, S. Olsen (1985:35) refers to North American Archaic Period dogs from Kentucky and Alabama--i.e., some of the specimens used in this study--as "quite advanced."

It is argued here that similarities between a modern form and the wolf do not make that form primitive in an evolutionary sense. Size similarities will produce morpholological similarities through simple allometry. Most so-called primitive modern dogs are evolutionarily as far removed from wolves as are specialized breeds. In some morphological and behavioral traits they are certainly similar to wolves. Many other traits, however, are likely to represent 12,000 years of evolution. This is true even of varieties like Eskimo dogs that were probably subject to

occasional hybridization with wolves. As Haag (1948) argued many years ago, North American Eskimo dogs are no closer to their progenitor than any other recent native North American variety.

Under an assumption that size disparity can be a useful clue to evolutionary distance, most of the dogs used in this study are indeed "advanced". It is argued here that such an assumption is misleading. Rapid evolutionary size reduction is expected from the model advanced in this study. The dogs used here are primitive in the important sense that they are a more accurate reflection of early evolutionary divergence from wolves than living varieties. At a given point in time they may have varied more in size than wild populations, but their range of variation was considerably less than modern dogs. Their relatively consistent, generalized morphology suggests that deliberate selective breeding is unlikely. As Dahr (1942:29) cogently observed, once selective breeding was underway all possible gradations existed between generalized forms and derived specialized forms. Virtually all modern dogs are directly or indirectly a product of selective breeding. Early, morphologically generalized dogs, predating the relatively recent acceleration of morphological diversification, are true primitive dogs in an evolutionary sense.

Tooth Length Changes

Analysis in Chapter V revealed that the prehistoric dogs tend to have proportionally longer teeth than comparably sized wild canids or even C. lupus. Wayne's (1986a) analysis of dental allometry among modern dog breeds and wild canids revealed that tooth lengths among dogs showed pronounced negative allometry. In contrast, these dimensions were positively allometric in wild canids. Wayne, apparently impressed by proportionally small teeth among largest dogs, suggested that tooth dwarfism under domestication is a product of "artificial" versus "natural" selection. As noted previously, however, "dwarfism" is a misleading term; it applies only to largest dogs. An evolutionary basis for tooth length patterns in dogs is suggested below.

Gould (1975a) has observed that in rapidly dwarfed lineages dwarfed forms often exhibit relatively enlarged teeth. This could occur only if developmental factors controlling overall body growth are not tightly integrated with factors governing dental growth. Shea and Gomez (1988) found a developmental basis for this phenomenon in a study of tooth scaling in human pygmies. Small size in pygmies apparently relates to deficiencies in a specific postnatal growth hormone, insulin-like factor I. Shifts in growth hormone levels have virtually no effect on tooth size. Accordingly, body size is reduced while tooth size

is not (cf. Shea and Gomez 1988:126-127).

It would, of course, be inappropriate to equate dwarfism among canids with dwarfism among humans. However, this work provides one sound developmental basis for a case of relative tooth enlargement in a dwarfed lineage. Consistently weak intraspecific correlations between tooth lengths and condylobasal length in this study suggest relative independence of tooth size and skull size in canids. Robust correlations are obtained only with broad, interspecific regressions. Relative lack of integration between body growth and tooth growth may underlie patterns of dental allometry in dogs.

Early domestic dogs underwent rapid size reduction, a process accompanied by allometrically produced morphological changes. Evolutionarily, tooth size apparently lagged behind body size reduction due to different developmental pathways. This would account for the frequent observation that early dogs exhibit large, crowded teeth. These trends are also reflected in the present data set, though relatively subtly. A possible exception is the specialized carnassial teeth. In this study P4 is consistent with an interspecific allometric trend. However, the product of that consistency is proportionally longer carnassials relative to wolves.

During the early and middle Holocene dogs in many parts of the world evolved to a relatively small body size,

exemplified by the present samples from both North America and Europe. Later, as humans subjected the animals to intensive size selection in both directions, size and morphological diversification accelerated. Tooth size apparently lagged behind again, with the result evident in modern or recent breeds. Small dogs are well known for dental anomalies stemming from teeth that are crowded into undersized jaws (cf. Weidenreich 1941; Smythe 1970; Epstein 1971; McKeown 1975). Largest dogs, approaching or exceeding the size of wolves, commonly exhibit conspicuously small teeth, including carnassials (e.g., Clutton-Brock 1984:200; Morey 1986; Wayne 1986a).

From this perspective it is not surprising that Wayne (1986a) found strong negative allometry of tooth lengths with skull lengths among modern breeds. Smallest breeds have proportionally larger teeth than largest breeds. The range of variation in tooth size among dogs is less than the range of variation in skull and body size (McKeown 1975). Teeth have lagged behind rapid changes in body size. Consequently, a corollary can be suggested to the phenomenon of relative tooth enlargement in rapidly dwarfed lineages described by Gould (1975a). In rapidly enlarged lineages the enlarged forms will show relatively smaller teeth.

Changes in tooth size and morphology in the domestic dog are an important but poorly understood aspect of their

evolutionary divergence from wolves. Absolute reduction in body size is, of course, accompanied by absolute reductions in tooth size. However, absolute reductions at small sizes are associated with frequent loss of specific teeth and greater simplicity of tooth morphology relative to larger dogs or wolves (see detailed discussion in Weidenreich 1941). Clearly, efforts to understand evolutionary changes in teeth among dogs will require considerably more knowledge of the developmental bases underlying growth of different structures (e.g., Van Valen 1970).

Future Research

This study deliberately employed a strategy of analyzing of a small set of cranial and dental varibles. The advantages of this approach were twofold. First, variation in specific dimensions could be explored in detail. Second, fluctuations in sample composition among the archaeological specimens were minimized. The disadvantage is that important components of morphological variation were undoubtedly overlooked by the use of a small set of dimensions. Results were consistent with studies involving larger sets of measurements (e.g., Wayne 1986a), but complete consistency can only be presumed. Thus, future investigations should expand the suite of analyzed measurements. This expansion should minimally include additional neurocranial dimensions, including cranial

capacity. In addition, more detailed approximations of tooth size and morphology would be helpful.

There is no escape from a plea for better ontogenetic data for analyses of the kind presented here. The juvenile wolf samples used here are small and taxonomically heterogeneous. Though this author believes useful results were obtained, larger samples with better control would certainly be more convincing. They might also lead to altered conclusions.

This study has advanced a model in which dog evolution produced consistent, ubiquitous changes for several thousand years. Available data suggest the model is reasonable. It cannot be fully evaluated, however, until early specimens from a variety of geographic regions have been analyzed. Not surprisingly, appropriate specimens are scattered among collections in many different countries. Some may never have been formally reported. Among those reported measurements and other data are inconsistent. Even when measurements are consistent one must be concerned with interobserver error (cf. Olsen 1985:93). Interobserver error was eliminated in this study by using only measurements taken by the author. In any case, expansion of the data base of prehistoric dogs is clearly important. Because of the scattered locations of specimens, it may be necessary to combine data from different sources.

Finally, heterochrony has been advanced here as a major force in the evolution of the dog. Because R.K. Wayne's research (1986a, 1986b, 1986c) dealt specifically with growth and morphology in modern canids, it provided crucial results despite the fact that he was not specifically addressing questions about the origins of the dog. Continuation of this line of research is needed. Detailed studies of growth and development, keyed to isolating heterochronic processes are most important. Brain development in modern canids should also be analyzed from the same perspective.

Wayne (1986a) notes that developmental boundaries may constrain morphology in other domestic animals as well. For example, in cats and horses shape change during ontogeny is minimal. Similarly, morphological diversity among adults of modern breeds representing these taxa is minimal. On the other hand pigs (like dogs) exhibit a relatively wide range of cranial morphology as adults. Not surprisingly, they undergo considerable changes in cranial proportions during ontogeny. These patterns may be characteristic of domestic animals simply because they have undergone rapid evolutionary change. Under conditions of rapid change ontogenetic pathways may define the limits to morphological change, among both domestic and nondomestic taxa. Clearly, the role of heterochrony in producing changes associated with domestication warrants intensive

investigation in taxa other than Canis, and in nondomestic taxa as well.

Dissertation Summary

1. Domestication is often viewed as human subjugation of another species. Consequently, morphological changes in domestic animals are often presumed to be the results of human selection, conscious or unconscious. A broader evolutionary perspective focuses on other selective mechanisms without disregarding the crucial association with human society. An evolutionary perspective also encourages consideration of nongenetically mediated evolution.

2. Domestication of the dog began sometime near the close of the Pleistocene, probably through the adoption of wolf pups by humans. This may have taken place more than once and in more than one place. Adoption occurred for reasons that can only be speculated, and some growing pups were tolerated in the human group. Young wolves passed their critical first weeks of socialization in human society and were from that time on bonded with their human "pack".

3. The wolf, evolutionarily engineered for life as an apex predator with heirarchical social structural, elaborate communication, cooperative hunting of large game, and a capacity for learned behaviors, was abruptly

transplanted into radically altered circumstances among humans. Similarities in social structure and mutual intelligibility of portions of their respective communication systems provided necessary compatibility. Early domestic wolves had no opportunities to learn the hunting and related subsistence skills of the wild wolf pack. As members of a human "pack" they survived by learning different skills involving solicitation of food from humans, scavenging of human food refuse, and greater emphasis on hunting of small prey species. Some individuals exhibited the behavioral plasticity to successfully learn new survival skills without violating their inflexibly subordinate position in the social heirarchy. They were the founders of a new species, Canis familiaris.

4. The domestic niche with humans was fundamentally new. The evolutionary opportunity to fill it placed early domestic animals in the role of colonizers. Selection strongly targeted precocious maturation in this new environment, largely free of density dependent mortality. Concurrently, the diet of early domestic wolves was abruptly altered relative to their wild counterparts. Rather than keying on one or two large ungulate species, domestic wolves fed on a diverse variety of smaller food items. As a result, reduced body size was strongly targeted by selection. These two aspects of the selective

regime experienced by early domestic populations led to morphological changes that allow the identification of C. familiaris from prehistoric contexts.

5. Craniometric data from modern canids (C. lupus, C. rufus, C. latrans, and C. aureus) and prehistoric domestic dogs from North America and northern Europe, the latter all predating 3,000 B.P., were analyzed to determine if morphological changes exhibited by early dogs are allometrically linked with size reduction. Bivariate analysis of static data revealed that dogs have uniquely wide cranial vaults and palates, patterns not referrable to allometries seen among wild Canis. Face length proportions in dogs are referrable to broad interspecific allometries. The dogs also tend to have proportionally longer teeth than wild canids. Bivariate analysis of ontogenetic data revealed that unique morphological features in dogs are associated with greater proximity to wolf ontogenetic regressions relative to other adult canids. Multivariate analysis confirmed that dogs exhibit paedomorphosis; adult dogs are more similar to juvenile C. lupus than to any adult group. Dogs are ontogenetically scaled with wolves.

6. Unique morphology among dogs is allometrically produced, but not biomechanically necessitated. Morphology in dogs is largely constrained to developmental pathways, with juvenilized morphology a consequence. This pattern probably reflects the genetically simplest means of

accomodating rapid evolutionary size change, and may be unviable among more slowly evolving taxa.

7. The evolutionary mode of size change in dogs was progenetic heterochrony. Studies of modern dog breeds indicate that simple truncation of growth period (time progenesis), while probably characteristic of early dog evolution, cannot account for size disparity between early dogs and wolves. Because postnatal specific growth rates in modern dogs and other canids are similar, dogs must exhibit reduced prenatal of perinatal growth rates (rate progenesis). Invariance in gestation length may be a fundamental morphological constraint in Canis.

8. Proportionally longer teeth in early dogs may reflect lack of tight integration between dental development and overall somatic growth. Under conditions of rapid size change, tooth size changes lag behind. Consequently, modern dogs exhibit strong negative allometry of tooth size in relation to skull size.

9. Modern breeds like northern Eskimo dogs cannot serve as accurate structural models for earliest domestic dogs. Early dog evolution is ubiquitously characterized by size reduction. Large, modern breeds are a product of 12,000 years of evolution. Prehistoric dogs, though small, are a more accurate reflection of early divergence from wolves than are modern breeds.

10. Because heterochrony involves simple genetic

alterations, size disparity between early dogs and large northern wolves does not exclude the latter from a primary role in the ancestry of dogs. Similarly, reduced size disparity between small Eurasian wolves relative to early dogs is not convincing evidence of their ancestry. The question of ancestry of dogs among smaller versus larger wolves remains open.

11. Although early dogs underwent rapid evolutionary size reduction, deliberate selective breeding eventually produced great diversity in size and form. The point in time at which selective breeding can be inferred varies from region to region.

12. Future research should focus on larger suites of measurements, better ontogenetic data, and greater variety in the samples analyzed, of both prehistoric dogs and modern canids. Emphasis on heterochrony as a primary mechanism of evolutionary change in domestic animals should continue.

Conclusion

It is a tactical and theoretical error to assume that morphological changes in domestic animals must be products of human selection. This study has sought to demonstrate that general principles derived from evolutionary ecology more parsimoniously account for basic morphological changes during the early evolution of the domestic dog. When

humans are viewed as the primary component of the ecological niche of a colonizing organism, rather than as evolutionary engineers, anthropocentric assumptions become unnecessary.

To be sure, when research questions focus on implications of domestic relationships for humans an anthropocentric perspective is appropriate. However, when research questions deal with implications of domestication for nonhuman organisms a broader evolutionary perspective is more appropriate. Heterochrony may be a common underlying force associated with size and morphological changes during early evolution of many domestic animals. Ultimately, gaining a more complete understanding of domestic relationships will require recognition that evolutionary forces not under human control do not necessarily cease simply because a domestic relationship is underway. It is hoped that this study is a small step towards a more complete understanding of domestic relationships.

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APPENDIXES

APPENDIX A

RAW DATA AND CODING INFORMATION ON ALL CANID SPECIMENS USED IN ANALYSIS

Table 51 presents raw data on all canid crania used in this study. For each specimen this includes all measurements, age category (code numbers from Table 2, page 81), sex, and subspecies or geographic region. Each specimen is identified by a three letter acronym indicating its institutional location, followed by its institutional catalog number. Table 52 presents a key to institutional acronyms and code values for sex and subspecies or geographic region.

Table 51. Raw data on all canid specimens used in analysis.

Group/ Case	Specimen*	Measurements (mm) CL	PL	PW	OI	MCW	IM2	P4	CAR	P1	P2	P3	Observations** A	S	SG
Canis lupus lycaon adults															
1	JFB 001360	228	120	73	108	72	121	23.0	13.7	6.9	13.7	15.2	5	2	2
2	JFB 001872	250	130	80	116	77	130	24.4	15.8	8.5	13.9	15.9	5	1	2
3	JFB 012295	252	133	80	118	77	131	24.5	15.3	8.3	15.1	15.7	5	1	2
4	JFB 013259	230	121	77	109	75	123	22.9	14.0	7.9	14.8	16.0	5	1	2
5	JFB 005689	213	111	70	097	67	113	22.7	12.5	7.8	12.8	15.3	4	3	2
6	JFB 012290	226	123	76	110	73	123	23.6	15.3	7.6	13.9	15.7	5	2	2
7	JFB 001219	225	116	78	100	73	119	23.6	13.9	6.9	12.2	14.9	5	1	2
8	JFB 012252	230	122	73	106	72	120	24.0	13.2	8.4	13.1	15.7	5	1	2
9	JFB 001221	240	126	81	111	74	127	26.8	15.6	8.1	15.9	17.5	5	1	2
10	JFB 013243	224	118	74	103	76	121	23.9	14.9	7.4	13.4	15.3	5	1	2
11	JFB 012299	223	118	74	101	72	122	23.2	15.1	7.9	15.0	15.0	5	1	2
12	JFB 010634	240	125	79	112	79	126	25.1	15.4	7.5	14.2	15.7	4	1	2
13	JFB 012296	244	129	84	115	74	129	26.3	14.4	7.9	13.2	14.7	5	1	2
14	JFB 010633	236	122	75	107	74	125	24.6	15.8	8.0	15.4	16.7	5	1	2
15	JFB 013260	237	123	77	108	72	126	23.7	14.3	7.7	13.7	15.6	5	1	2
16	JFB 012301	228	123	76	107	71	123	24.0	13.2	7.0	13.7	16.2	5	1	2
17	JFB 001930	229	122	73	115	71	126	24.6	15.0	7.8	13.6	16.3	4	2	2
18	JFB 003850	230	120	77	106	74	121	23.2	14.3	7.5	13.3	15.6	5	1	2
19	JFB 001856	235	124	74	107	73	126	25.0	14.3	7.7	13.5	14.6	5	2	2
20	JFB 012303	223	124	73	107	72	123	24.3	14.5	7.2	13.8	15.0	5	2	2
21	JFB 001220	227	115	71	104	72	119	22.4	13.8	6.6	13.5	15.0	4	1	2
22	JFB 013265	249	126	83	120	76	132	26.8	15.8	8.1	15.4	16.8	5	1	2
23	JFB 013252	226	119	75	105	74	118	23.7	13.4	6.8	12.7	15.2	5	2	2
24	JFB 013266	209	110	73	96	73	111	21.4					5	2	2
25	JFB 013255	219	116	68	103	71	117	23.1	12.6	6.8	12.9	14.7	5	2	2
26	JFB 013256	237	129	81	112	74	127	24.5	14.4	7.6	13.0	15.8	5	2	2
27	JFB 012308	243	129	82	113	78	128	25.0	15.3	7.9	13.0	15.5	5	1	2
28	JFB 012309	255	135	81	122	75	135	26.0	16.7	9.0	16.2	16.7	5	1	2
29	JFB 013262	227	115	75	108	73	118	23.3	13.7	8.0	13.6	14.6	5	1	2
30	JFB 013261	239	128	79	111	74	127	24.8	14.1	7.5	14.4	15.6	5	1	2
31	JFB 013257	238	127	82	106	73	129	25.3	14.6	7.3	14.6	16.3	5	1	2
32	JFB 010631	233	123	78	110	69	126	23.4	14.5	8.6	14.6	16.0	5	2	2
33	JFB 013264	247	129	80	119	73	132	23.9	15.4	7.6	14.1	14.9	5	1	2
34	JFB 013250	218	117	74	99	70	116	22.2	14.0	7.1	12.8	14.8	5	2	2
35	JFB 010637	246	126	91	113	76	131	24.2	17.1	7.8	13.0	16.0	5	1	2
36	JFB 012313	244	125	84	111	78	127	24.3	14.2	8.0	14.7	15.8	5	2	2
37	JFB 012312	231	123	81	112	72	127	25.4	16.6	6.2	14.2	17.2	5	1	2
38	JFB 001350	228	119	79	109	74	122	23.9	14.3	7.3	14.2	16.3	4	1	2
39	JFB 012289	227	117	76	104	72	120	23.6	13.1	7.6	13.6	15.6	5	2	2
40	JFB 012293	212	114	72	104	65	116	22.8	14.3	7.5	13.3	15.4	4	2	2
41	JFB 012304	214	115	75	102	70	119	24.6	15.9	7.6	13.2	15.4	4	1	2
42	JFB 012306	219	117	75	99	70	120	23.8	15.1	7.2	13.6	15.9	4	1	2
43	JFB 013253	220	123	79	104	72	122		15.1	8.3	14.4	16.8	4	1	2
44	JFB 012292	214	113	72	110	67	116	22.6	13.6	7.5	13.3	15.3	4	2	2
45	SNM 289995	249	132	78	118	75	129	24.4	14.6	7.8	14.1	16.5	5	2	2
46	SNM 265071	223	120	79	110	73	123	25.6	16.0	7.3	13.8	16.1	5	1	2
47	SNM 258637	216	112	69	100	68	111	20.9	11.8	6.3	12.9	13.5	5	2	2
48	SNM 243973	224	120	70	107	73	120	23.0	12.9	6.7	12.7	13.9	4	2	2
49	SNM 243395	224	115	74	104	69	119	24.9	14.2	6.7	13.2	15.4	5	1	2
50	SNM 242290	216	117	69	102	68	115	22.6	12.6	6.6	13.3	14.2	5	2	2
51	SNM 170692	230	118	73	103	72	115	22.8	14.4	7.8	13.6	14.9	5	1	2
52	SNM 530436	204	106	69	095	68	109	22.4	12.9	6.6	11.7	14.1	4	2	2
53	SNM 530435	216	113	72	100	72	117	24.6	13.2	7.1	13.7	15.4	4	2	2

Table 51 (continued).

Group/ Case	Specimen	Measurements (mm) CL	PL	PW	OI	MCW	IM2	P4	CAN	P1	P2	P3	Observations A	S	SG
Canis lupus lycaon adults (continued)															
54	SNM 513676	215	111	73	100	71	114	23.2	13.0	7.0	12.8	14.6	4	2	2
55	SNM 529877	212	110	70	99	70	114	22.3	12.0	7.1	12.4	14.7	4	2	2
56	SNM 512026	233	124	74	109	72	124	23.7	15.5	7.6	14.3	16.7	4	3	2
57	SNM 512009	231	120	77	105	72	122	23.6	14.4	7.7	14.7	17.2	4	3	2
58	SNM 512007	233	122	73	109	74	122	23.3	15.9	7.0	14.6	14.9	4	3	2
59	SNM 347921	220	111	72	101	72	117	23.2	13.6	7.1	12.8	15.0	4	2	2
Canis lupus baylei adults															
60	SNM 224484	231	117	76	110	73	123	22.9	13.1	6.0	14.0	15.0	5	1	3
61	SNM 224485	212	106	73	99	72	114	23.1	12.8	6.4	12.2	13.9	4	2	3
62	SNM 225394	210	111	71	101	72	113	22.9	13.2	6.7	14.4	14.8	5	3	3
63	SNM 228269	220	114	72	104	73	117	24.6	12.6	6.1	13.6	13.9	5	1	3
64	SNM 231320	217	115	73	101	73	113	24.1	12.7	6.8	13.4	14.1	5	1	3
65	SNM 231322	224	114	76	103	72	117	22.7	12.6	6.2	13.1	14.6	5	1	3
66	SNM 231323	217	111	74	105	74	116	22.9	12.1	6.6	12.3	13.8	4	2	3
67	SNM 231324	225	117	74	107	72	123	24.4	13.8	6.0	13.2	15.1	5	1	3
68	SNM 231532	218	115	74	102	73	115	23.0	13.9		13.8	14.5	5	1	3
69	SNM 231533	217	112	75	101	73	117	23.4	13.9	6.8	14.7	15.8	4	1	3
70	SNM 231534	216	111	74	99	69	114	22.6	13.0	6.0	13.6	14.5	4	1	3
71	SNM 231536	210	107	73	101	70	113	22.3	12.1	6.0	12.3	14.4	5	2	3
72	SNM 232446	235	124	78	111	73	124	24.8	15.4	6.8	12.9		5	1	3
73	SNM 002193	203	104	69	96	66	109	21.7	11.6	5.5	10.8	12.5	5	3	3
74	SNM 285754	233	119	76	111	74	124	24.3	14.2	7.3	14.0	15.5	5	1	3
75	SNM 094728	210	110	73	102	67	118	24.5	13.6	7.4	14.8	15.9	5	2	3
76	SNM 003335	220	114	73	106	74	119	24.3	14.2	6.7	13.6	14.5	5	3	3
77	SNM 167989	208	111	71	96	68	111	22.9	13.0	6.2	12.9	13.9	4	2	3
78	SNM 095752	202	105	67	94	69	110	21.2	11.1	6.1	11.8	12.5	4	3	3
79	SNM 098307	222	114	69	105	70	117	23.9	12.6	6.6	13.1	13.9	5	1	3
80	SNM 098311	216	116	70	104	72	118	22.8	11.7	6.5	12.5	14.0	5	2	3
81	SNM 098313	225	116	72	107	74	122	23.6	13.2	6.8	13.3	15.1	5	1	3
82	SNM 099668	209	108	69	99	73	113	24.0	13.0	6.5	13.0	14.7	4	3	3
83	SNM 117059	232	121	77	108	77	123	24.5	13.9	6.5	14.5	16.0	5	1	3
84	SNM 117060	224	117	74	105	75	118		12.2	6.0	12.1	13.8	5	1	3
85	SNM 117061	214	113	73	100	73	116	23.0	12.2	6.0	11.3	14.1	4	2	3
86	SNM 117062	222	113	72	105	74	120	23.8	12.2	6.0	13.0	14.9	5	2	3
87	SNM 117542	219	112	70	105	72	119	22.6	11.8	5.9	13.4	14.9	4	2	3
88	SNM 170556	228	115	75	107	72	120	24.7	14.5	7.2	13.9	15.7	5	1	3
89	SNM 235089	225	116	74	109	71	122	24.5	14.6	7.0	14.0	15.3	4	1	3
90	UIM 001048	218	113	71	101	70	114	23.8					5	2	3
91	UIM 001153	227	116	77	104	73	119	24.0					5	1	3
92	UIM 001156	221	115	74	106	73	117	23.5					5	1	3
93	UIM 001160	221	120	73	107	74	120	24.5					5	1	3
94	UIM 001161	215	114	73	102	72	115	23.8					5	3	3
95	UIM 001163	210	109	74	99	69	113	22.5					5	3	3
96	UIM 001165	215	111	73	100	72	112	23.5					5	3	3
97	UIM 001164	207	108	70	93	66	108	23.7					5	1	3
98	UIM	211	109	72	98	70	111	24.0					5	2	3
99	UIM 001149	206	106	70	99	67	112	23.0					5	2	3
100	UIM 004105	209	108	73	100	69	112	22.6					5	2	3
101	UIM 004106	213	110	71	99	71	115	22.6					5	2	3
102	KUM 076473	214	113	71	101	70	114	23.1					5	2	3

Table 51 (continued).

Group/ Case	Specimen	Measurements (mm)											Observations		
		CL	PL	PW	OI	MCW	IM2	P4	CAN	P1	P2	P3	A	S	SG
Canis rufus adults															
103	SNM 266506	193	102	57	91	61	105	19.6	10.9	6.1	11.6	12.8	4	2	21
104	SNM 266173	189	97	59	86	58	101	19.9	10.5	5.7	11.0	12.0	5	3	21
105	SNM 265645	206	108	63	96	64	109	20.2	11.6	5.8	11.0	12.6	5	1	21
106	SNM 265599	192	99	55	89	59	103	19.9	11.1	5.8	9.1	12.3	4	1	21
107	SNM 224531	209	107	60	98	64	112	22.3	11.6	5.8	11.4	12.6	4	1	21
108	SNM 224972	204	106	61	96	63	108	21.2	11.1	5.0	11.8	13.7	5	1	21
109	SNM 224973	195	103	56	91	60	106	20.0	12.0	5.4	11.0	12.5	5	1	21
110	SNM 224974	198	103	59	94	62	106	21.1	12.5	5.4	11.7	13.0	4	1	21
111	SNM 225366	196	103	60	95	59	108	20.4	11.0	4.9	11.0	11.8	5	1	21
112	SNM 225367	204	107	58	96	61	109	20.3	11.3	5.2	10.7	12.3	5	1	21
113	SNM 227899	202	108	58	96	61	111	19.3	10.4	5.2	11.0	12.2	5	1	21
114	SNM 227900	199	103	61		60	106	21.4	10.8	5.9	11.7	13.0	5	1	21
115	SNM 228069	202	108	58	95	61	110	21.6	10.6	5.9	12.1	13.2	5	1	21
116	SNM 228089	195	100	61	93	62	105	20.5	10.0	5.5	11.5	12.3	4	2	21
117	SNM 228239	207	108	58	101	61	113	21.8	10.7	6.4	11.8	12.4	5	1	21
118	SNM 228517	198	103	62	93	60	108	21.3	10.7	6.3	11.5	12.7	5	1	21
119	SNM 251084	218	110	63	100	63	114	21.4	12.7	6.1	13.2	13.9	5	1	21
120	SNM 251085	225	113	63		65	118	22.0	12.9	7.1	11.9	13.0	5	1	21
121	SNM 251086	206	105	62	93	64	109	21.6	12.3	6.8	12.1	13.3	5	2	21
122	SNM 261609	204	106	56	96	60	111	22.4	11.1	5.6	12.4	12.8	4	1	21
123	SNM 261753	201	104	62	96	61	109	20.7	12.0	5.6	12.0	12.5	5	1	21
124	SNM 262105	207	106	61	93	61	107	19.7	10.7	4.9	11.4	13.1	5	2	21
125	SNM 262106	200	103	59	90	60	107	19.1	10.7	5.3	10.7	12.4	4	2	21
126	SNM 265458	209	108	59	98	62	110	19.4	10.6	5.0	10.8	12.7	5	2	21
127	KUM 024879	198	103	59	92	61	106	21.0					5	1	21
128	KUM 060148	201	105	62	95	62	109	21.4					5	2	21
129	KUM 024878	202	105	65	98	62	110	21.9					5	1	21
130	KUM 060149	194	107	61	94	58	106	20.9					5	2	21
131	KUM 054820	207	106	63	96	61	112	21.8					5	1	21
Canis latrans adults															
132	ISM 686535	180	96	57	87	58	100	20.7	10.6	5.3	11.3	12.8	5	1	36
133	ISM 001651	182	94	58	83	58	98	19.0	10.3	4.7	9.2	11.7	5	3	36
134	ISM 614755	174	88	53	78	57	95	19.6	8.6	4.6	9.3	11.8	5	2	36
135	ISM 683716	158	81	51	71	54	82	17.2	7.9	5.2	9.6	11.7	5	2	36
136	ISM 614240	170	86	55	77	55	93	20.6	9.8	5.7	11.1	11.9	5	2	36
137	ISM 687981	187	95	54	86	59	102	19.3	11.0	4.9	11.3	11.9	5	2	36
138	ISM 614378	183	95	54	87	58	100	19.0	9.2	5.1	11.1	11.9	5	2	36
139	ISM 614204	179	92	54	84	59	98	18.7	9.0	4.9	11.1	11.9	5	3	36
140	ISM 614754	189	98	61	90	62	101	21.2	11.2	5.3	12.3	14.1	5	1	36
141	ISM 688233	186	102	57	88	59	103	19.0	9.2	5.4	10.5	11.2	5	3	36
142	ISM 614569	180	91	55	85	59	97	18.7	9.4	5.3	10.8	11.9	5	2	36
143	ISM 614472	185	97	57	86	60	101	20.3	10.5	5.2	9.3	11.6	5	2	36
144	ISM 614379	203	106	63	97	65	109	19.3	11.3	5.2	11.7	12.9	5	1	36
145	ISM 683778	188	98	57	88	60	102	20.6	10.6	5.4	10.4	11.9	5	1	36
146	ISM 687966	195	101	59	91	58	106	21.2	10.8	5.6	11.4	12.5	5	1	36
147	ISM 614705	190	98	55	90	60	103	19.3	10.5	4.8	10.5	12.2	5	3	36
148	ISM 687968	183	94	53	84	56	98	20.0	10.3	5.0	10.9	11.3	5	1	36
149	ISM 614674	184	96	57	87	58	102	20.9	10.9	5.4	11.2	12.7	5	1	36

Table 51 (continued).

Group/ Case	Specimen	Measurements (mm) CL	PL	PW	OI	MCW	IM2	P4	CAN	P1	P2	P3	Observations A	S	SG
Canis latrans adulta (continued)															
150	ISM 687748	195	101	60	92	65	104	20.0	11.5	5.9	10.8	12.3	5	1	36
151	ISM 690935	193	100	61	89	61	105	22.1	11.7	5.9	12.1	13.1	5	3	36
152	ISM 614658	184	96	56	89	60	101	20.5	9.9	5.3	10.0	12.5	5	3	36
153	ISM 614390	178	91	55	80	57	96	18.4	9.3	5.2	11.2	11.7	5	3	36
154	ISM 614666	185	97	58	89	60	104	19.4	11.1	5.0	9.9	11.7	5	3	36
155	ISM 688235	186	98	59	88	61	104	21.1	10.4	6.1	10.5	11.5	5	3	36
156	ISM 614262	186	96	59	87	59	103	21.5	10.5	5.9	12.0	13.7	5	1	36
157	ISM 614254	192	100	57	89	61	104	20.1	10.5	6.1	10.4	12.3	5	1	36
158	ISM 614382	202	105	62	97	63	108	20.2	11.5	5.2	11.7	13.8	5	1	36
159	ISM 614731	167	87	49	78	55	93	17.8	8.5	5.3	9.5	10.0	5	2	36
160	ISM 614213	176	91	55	82	59	98	18.5	9.2	5.4	10.3	12.4	5	3	36
161	ISM 614562	183	95	53	85	57	100	20.6	10.4	5.6	10.4	12.3	5	1	36
162	ISM 614463	189	95	55	89	59	104	19.5	10.5	4.7	11.1	12.7	5	1	36
163	ISM 687983	177	92	58	82	59	96	19.8	10.2	5.2	10.1	11.5	5	3	36
164	ISM 614675	184	96	56	83	57	100	20.0	10.4	5.1	11.7	13.1	5	1	36
165	ISM 614398	182	92	54	82	59	97	19.5	10.0	4.6	10.7	12.3	5	3	36
166	ISM 614242	189	99	60	88	60	104	19.9	10.6	5.9	11.6	13.3	5	1	36
167	ISM 614241	178	92	57	82	58	97	19.8	9.1	4.9	10.1	12.6	5	2	36
168	ISM 614263	184	92	59	88	58	100	19.3	9.6	4.9	10.8	12.1	5	2	36
169	ISM 687967	184	94	55	85	59	99	20.0	10.6	5.0	10.8	11.7	5	1	36
170	ISM 614628	187	96	55	88	57	101	20.0	10.3	5.7	11.8	12.6	5	1	36
171	ISM 001364	183	95	55	86	57	100	19.6	10.4	5.3	8.3	11.8	4	3	36
172	ISM 001356	198	104	59	94	63	108	21.3	11.5	6.0	12.8	13.6	4	2	36
173	ISM 001665	167	84	51	78	59	90	18.6	9.7	4.9	8.2	11.0	4	3	36
174	ISM 001600	189	98	59	89	59	104	21.8	12.1	6.2	11.5	14.3	4	3	36
175	ISM 001631	186	99	58	88	59	102	21.5	12.3	6.7	10.1	12.4	4	3	36
176	ISM 000549	185	96	55	89	60	102	19.5	9.4	5.3	10.6	12.0	4	1	36
177	ISM 001357	193	96	56	89	61	102	19.7	11.4	5.3	10.5	11.8	4	1	36
178	ISM 614565	175	90	54	81	58	98	20.4	10.7	5.3	10.1	12.5	4	2	36
179	ISM 614265	173	87	55	78	56	93	19.3	9.6	4.9	9.7	11.3	4	2	36
180	ISM 614625	176	91	53	83	60	96	18.3	9.8	5.0	9.8	11.9	4	3	36
181	ISM 614277	192	101	58	91	60	105	21.3	12.4	5.8	10.9	13.3	4	1	36
182	ISM 614623	186	94	57	88	60	101	19.5	10.3	6.1	11.8	13.2	4	2	36
183	ISM 685944	174	90	54	81	55	96	19.5	11.6	5.4	11.1	13.2	4	2	36
184	ISM 684394	183	94	56	86	58	101	20.8	10.6	6.1	10.3	12.3	4	2	36
185	ISM 614474	177	95	53	82	56	95	19.2	10.3	5.2	11.2	11.9	4	2	36
186	ISM 614729	178	90	53	80	54	94	19.6	10.0	5.2	10.7	12.8	4	3	36
187	ISM 614261	190	98	60	86	61	102	20.2	9.8	5.7	11.6	12.7	4	2	36
188	ISM 614750	185	94	56	84	60	100	21.1	10.4	5.5	10.6	10.8	4	1	36
189	ISM 614532	186	97	53	85	58	103	20.2	11.3	5.0	10.8	12.0	4	1	36
190	ISM 686003	182	94	57	83	57	97	19.2	9.6	5.3	10.6	11.7	4	1	36
191	ISM 614389	186	95	56	86	59	99	20.3		5.4	11.3	12.6	4	1	36
192	ISM 614627	184	95	56	85	58	100	19.5	10.4	6.6	11.3	12.8	4	2	36
193	ISM 689929	177	92	57	81	56	98	19.1	9.1	4.9	10.6	13.1	4	1	36

Table 51 (continued).

Group/ Case	Specimen	Measurements (mm) CL	PL	PW	OI	MCW	IM2	P4	CAN	P1	P2	P3	Observations A	S	SG
Canis aureus adults															
194	SNM 290135	149	76	51	67	53	82		8.7	4.2	7.2	9.2	5	1	23
195	SNM 173280	150	76	47	66	52		16.0	8.0	4.1	7.5	8.6	5	2	23
196	SNM 173283	157	78	50	68	54	82	16.7	7.9	4.3	8.1	9.5	5	2	23
197	SNM 173284	153	78	50	66	52	81	16.5	8.5	4.7	9.1	10.3	4	2	23
198	SNM 256727	155	78	55	67	55	80	18.2	8.9	4.4	8.5	10.3	5	2	24
199	SNM 321958	192	101	61	88	59	101	18.8	10.8	5.5	10.1	11.4	5	1	25
200	SNM 321956	180	90	56	82	58	92	17.3	9.1	5.2	9.3	10.0	5	1	25
201	SNM 321954	176	91	55	81	57	95	16.9	9.8	5.5	9.0	10.6	5	2	25
202	SNM 322834	150	79	49	69	51	83	17.1	9.6	4.5	8.7	10.5	5	1	25
203	SNM 399436	155	80	52	68	54	86	17.8	8.5	4.6	10.0	10.4	4	3	1
204	SNM 322833	159	82	50	72	53	87	18.1	10.0	4.6	9.7	10.4	4	1	25
205	SNM 410915	157	80	47	70	52	86	16.8	8.0	5.0	8.8	9.6	5	2	1
206	SNM 399432	163	83	54	74	54	89	17.5	9.1	4.6	9.2	9.8	5	1	1
207	SNM 410910	151	77	49	68	50	83	16.1	7.7	5.2	8.1	9.6	5	2	26
208	SNM 410911	151	81	45	69	49	82	14.9	7.8	4.5	8.0	9.1	4	2	26
209	SNM 476031	157	81	49	71	54		16.7	8.2	4.3	8.3	9.7	5	2	26
210	SNM 486165	146	79	49	69	51	83	18.0	9.7	4.7	9.1	10.6	5	2	26
211	SNM 486167	152	80	48	69	52	83	17.1	8.4	4.7	8.2	9.6	5	2	26
212	SNM 476030	146	77	47	65	51	79	16.2	8.0	4.3	8.6	10.0	5	1	26
213	SNM 378686	147	76	44	66	49	79	15.6	9.1	4.4	7.9	9.5	4	2	27
214	SNM 476034	163	85	53	73	55	90	18.5	9.5	4.3	9.3	9.8	4	1	28
215	SNM 378688	158	82	50	70	53	84	17.1	9.0	5.3	9.2	10.6	5	1	27
216	SNM 378685	157	81	51	69	52	84	18.6	9.5	4.9	9.7	10.6	5	1	27
217	SNM 378684	155	80	50	68	51	82	17.6	8.0	5.1	8.2	10.8	5	2	27
218	SNM 378683	156	81	48	70	53	84	17.5	8.2	4.8	8.6	9.8	5	2	27
219	SNM 476856	155	80	50	68	54	85	17.4	7.8	5.0	8.5	9.7	5	2	28
220	SNM 399435	160	83	52	72	55	88	18.1	9.1	4.5	9.4	11.0	5	1	1
221	SNM 321951	183	93	58	85	59	97	18.5	9.6	4.9	9.4	11.6	5	1	25
222	SNM 399434	156	82	49	71	54	85	17.1	7.7	4.9	9.1	10.3	4	2	1
Canis lupus juveniles															
223	JFB 012302	207	110	68	99	67	115	24.6	14.8	8.2	14.4	16.0	3	3	2
224	JFB 012305	194	104	68	89	65	111	22.4	12.5	6.6	13.3	13.9	3	2	2
225	JFB 010632	182	98	69	83	66	101	22.6	14.1	7.0	12.6		3	2	2
226	JFB 013254	187	100	73	87	65	109						2	1	2
227	JFB 000091	217	115	74	104	72	118	23.1	13.4	7.8	12.7	15.3	3	2	2
228	JFB 012307	188	103	71	88	64	107						2	2	2
229	JFB 005019	216	114	72	101	71	115	24.0	13.8	7.7	15.2	15.8	3	2	2
230	JFB 013249	187	103	70	86	62	109						2	2	2
231	JFB 013258	184	98	70	83	63	107						2	1	2
232	JFB 012726	203	113	71	95	66	116	22.9	16.5	7.0	13.3	15.8	3	2	2
233	SNM 529878	194	103	64	93	66	108	22.5					2	2	2
234	SNM 347920	196	104	65	91	69	108	21.5	12.6	6.7	12.6	14.4	3	2	2
235	SNM 347919	198	103	67	93	68	107	22.2	12.8	6.4	12.6	14.3	3	1	2
236	SNM 347916	208	111	72	96	72	112	22.5	13.7	6.8	13.0	13.8	3	1	2
237	SNM 243394	191	102	67	90	67	106						2	2	2
238	SNM 243393	194	107	63	92	67	108	22.1	13.5	7.2	13.9	15.0	3	2	2
239	SNM 242291	217	114	68	103	70	119	23.8	15.1	7.5	13.4	15.8	3	2	2
240	SNM 170138	179	93	57	83	64	98						2	2	2
241	SNM 022371	206	110	72	95	69	112	24.3	13.2	6.8	12.7	13.5	3	2	2
242	SNM 156838	230	115	74	106	70	118	22.7	13.7	6.4	14.4	14.8	3	3	2
243	SNM 512021	218	113	72	100	71	115	21.8	12.2	6.4	12.7	14.5	3	1	2

Table 51 (continued).

Group/ Case	Specimen	Measurements (mm) CL	PL	PW	OI	MCW	IM2	P4	CAN	P1	P2	P3	Observations A	S	SG
Canis lupus juveniles (continued)															
244	SNM 170567	223	116	74	109	73	123	24.7	15.8	7.2	14.6	16.9	3	1	2
245	SNM 224172	212	109	76	99	73	116	24.4	15.3	6.8	14.3	15.6	3	1	3
246	SNM 224187	203	105	70	96	70	113	24.3	14.2	7.3	13.1	14.8	3	2	3
247	SNM 098328	223	112	74	104	75	119	24.8	13.1	7.1	13.3	15.1	3	1	3
248	SNM 117064	226	120	75	109	74	123	24.9	14.5	6.9	14.6	15.6	3	3	3
249	SNM 147203	75	42	42	28	43	41						1	1	16
250	SNM 147204	75	44	43	30	45	43						1	3	16
251	SNM 147195	74	43	43	29	43	41						1	3	16
252	SNM 147205	101	58	49	43	49	53						1	2	16
253	SNM 168427	113	63	54	49	54	61						1	1	15
254	SNM 232440	143	78	59	64	60							1	1	20
255	SNM 232439	139	73	55	62	57							1	1	20
256	SNM 232442	138	72	57	59	58							1	1	20
257	SNM 232441	135	70	57	60	56							1	2	20
258	SNM 231338	93	54	45	38	53							1	1	20
259	SNM 231340	89	49	46	36	47							1	1	20
260	SNM 231341	86	49	47	34	49							1	1	20
Canis rufus juveniles															
261	SNM 253474	170	88	53	78	58	92	20.6	9.7	5.3	10.5	11.7	3	2	21
262	SNM 243318	199	101	62	93	62	109	21.1	12.2	5.2	11.8	13.6	3	2	21
263	SNM 136879	185	97	60	89	62	105	22.7	14.1	5.4	10.0	12.3	3	2	21
264	SNM 289222	204	102	64	93	62	110	22.1	12.8	6.6	12.6	14.4	3	2	21
265	SNM 289221	202	103	60	94	61	108	22.8	12.8	7.3	12.4	13.9	3	1	21
266	SNM 271862	191	100	55	91	59	105	19.8	11.6	6.6	12.6	13.7	3	1	21
267	SNM 266156	190	99	57	89	60	102	20.7	12.9	5.5	12.5	13.2	3	1	21
268	SNM 266090	177	91	54	82	57	100	20.2	12.6	6.2	12.0	12.2	3	2	21
269	SNM 266101	185	96	56	88	58	102		11.5	5.4	11.8	13.3	3	1	21
270	SNM 266102	173	88	55	79	56	95	19.6	10.8	5.5	11.1	12.7	3	2	21
271	SNM 261758	163	84	54	75	55	88						2	1	21
272	SNM 224967	195	104	60	93	63	106	21.6	10.4	5.4	11.5	13.0	3	1	21
273	SNM 227892	186	96	55	86	60	102	20.1					3	2	21
274	SNM 227895	192	101	57	90	62	108	20.3	12.0	6.4	11.5	13.9	3	1	21
275	SNM 265735	163	83	56	74	56	92						2	1	21
276	SNM 266154	190	97	55	88	59	102	20.5	12.0	6.0	10.7	12.4	3	1	21
277	SNM 271885	186	98	60	87	62	105	20.0	12.9	6.4	12.3	12.7	3	2	22
278	SNM 265135	175	92	59	81	58	100						2	1	22
279	SNM 348042	170	90	62	76	61	93						2	1	22
280	SNM 244494	80	45	38	31	48							1	2	22
281	SNM 244495	78	44	40	31	47							1	1	22
282	SNM 244493	79	45	40	31	46							1	1	22

Table 51 (continued).

Group/ Case	Specimen		Measurements (mm) CL	PL	PW	OI	MCW	IM2	P4	CAN	P1	P2	P3	Observations A	S	SG
Canis familiaris North America																
Indian Knoll (15OH2)																
283	UKL	1-4	156	80	56	70	54	85	16.7	9.2	4.1	9.4	10.7	5	3	10
284	UKL	1-10	147	75	53	69	52	81	16.4	9.1		9.2	10.5	5	3	10
285	UKL	1-24	142	76	54	63	55	80	16.5		4.3	8.2	10.5	4	3	10
286	UKL	1-26	136	73	49	62	51	77	16.8	8.2	4.0	8.9	11.0	5	3	10
287	UKL	1-30	126	65	49	54	47	69	15.6	8.3	4.1	8.5	9.8	5	3	10
288	UKL	1-35	144	76	52	66	52	82	18.1	10.0	5.0	9.9	11.3	4	3	10
289	UKL	1-55	133	69	54	56	51	73	16.8	8.1	4.7	8.3	10.5	5	3	10
290	UKL	1-56	154	81	56	65	55	84	17.4	9.9	4.4	10.0	11.0	5	3	10
291	UKL	1-60	136	71	53	61	53	77	16.5	8.5	4.1	9.1	10.0	4	3	10
292	UKL	1-117	144	75	54	64	54	80	16.4	9.2		10.2	11.0	5	3	10
293	UKL	1-129	153	80	57	70	56	84	16.6	8.8	4.4	9.7	10.9	5	3	10
294	UKL	1-130	153	81	56	70	53	85	16.3	10.1	4.8	7.8	11.2	5	3	10
295	UKL	1-132	142	75	48	64	51	80	16.1	8.1	3.3	8.9	9.7	5	3	10
296	UKL	1-134	165	85	57	73	59	87	17.0	10.3	4.2	8.9	10.5	4	3	10
Carlson Annis (15BT5)																
297	UKL	1-146	143	75	51	67	54	80	15.6	8.6	3.8	8.4	10.1	5	3	10
298	UKL	1-148	152	83	54	72	56	87	16.6	9.2		9.5	10.5	5	3	10
299	UKL	1-150	141	76	53	64	51	80	17.4				11.0	5	3	10
300	UKL	1-151	154	79	55	69	55	85	16.0	9.4	4.0	9.7	10.2	5	3	10
301	UKL		153	81	56	70	55	84	16.9	9.6	4.0	8.0	10.9	5	3	10
Ward (15MCL11)																
302	UKL	1-70	157	80	55	72	56	84	16.6	9.7	4.9	8.4	10.7	4	3	10
303	UKL	1-72	146	80	56	64	53	83	16.4	9.1		9.8	9.9	4	3	10
304	UKL	1-98	148	80	55		51	83	16.6	9.7	3.9	8.3	9.4	5	3	10
305	UKL	1-99	163	82	57	73	57	87	16.4	9.5	4.6	8.8	10.6	5	3	10
Chiggerville (15OH1)																
306	UKL	1-61	151	78	51	71	51	85	17.2	10.7	4.4	9.8	11.0	5	3	10
Read (15BT10)																
307	UKL	1-144	160	80	59		64	88	18.2	9.7	4.8	10.3	12.1	5	3	10
308	UKL	71-1	156	81	56	71	58	85	18.3	8.7	4.0	9.8	10.8	5	3	10
Perry (1LU25)																
309	UKL	2-43	144	74	51	64	53	79	15.4	8.0	3.9	7.9	10.0	5	3	10
310	UKL	2-45	145	76	53	65	57	81	16.4	10.0		9.5	11.1	5	3	10
311	UKL	2-52	146	76	52	65	57	79	15.3	9.1	3.8	8.7	9.2	5	3	10
312	UKL	2-53	141	73	54	61	52	80	15.8	8.3	4.0	8.6	10.3	5	3	10
313	UKL	2-55	129	70	49	59	49	73	15.1	8.2	3.6	7.9	9.5	5	3	10
314	UKL	2-73	142	73	53	64	50	80	17.5	9.0	3.9	9.3	10.8	5	3	10
315	UKL	2-82	154	79	59	69	60	82	17.4	12.2	4.6	8.5	9.8	5	3	10

Table 51 (continued).

Group/ Case	Specimen	Measurements (mm) CL	PL	PW	OI	MCW	IM2	P4	CAN	P1	P2	P3	Observations A	S	SG
Canis familiaris North America (continued)															
Whitesburg Bridge (1MA10)															
316 UKL	40-25	155	82	57	72	55	86	17.6	9.5	4.3	9.1	11.5	5	3	10
Flint River (1MA48)															
317 UKL	40-7	156	82	57	72	56	85	15.7	8.9	4.1	8.3	9.9	5	3	10
318 UKL	40-9	167	86	57	78	59	91	17.0	11.3	4.9	9.8	10.8	5	3	10
Little Bear Creek (1CT78)															
319 UKL	2-93	148	78	58	71	52	84	16.6	9.7	4.0	9.8	9.9	5	3	10
320 UKL	2-97	156	83	58	71	60	86	17.1	10.8	4.4	9.6	11.1	5	3	10
Mulberry Creek (1CT27)															
321 UKL	2-3	152	79	50	69	53	82	16.1	9.3	4.1	8.3	9.6	5	3	10
322 UKL	2-5	151	78	54	68	55	86	17.7	10.0	4.5	9.3	10.9	5	3	10
323 UKL	2-9	157	82	56	70	56	86	18.1	9.4		10.1	11.5	5	3	10
Bailey (40GL26)															
324 MCL	86-157	141	72	52	61	54	78	15.2	8.2	4.0	8.1	9.0	5	3	10
Cherry (40MCL84)															
325 MCL	84-22	151	80	53	69	51	82	15.5	9.5	4.2	8.2	9.8	5	3	10
326 MCL	84-49	133	69	50	59	46	73	14.1	7.9	4.2	8.4	9.3	4	3	10
Eva (40MCL6)															
327 MCL	6-16	149	80	57	67	53	82	17.2	9.7	4.5	9.4	10.9	5	3	10
328 MCL	6-49	153	82	58	72	54	83	17.1	10.7	4.3		10.3	5	3	10
Koster															
329 ISM	F2357	158			77		86	18.9	10.9	5.1	10.7	11.8	5	3	11
330 ISM	F2256	165	85	61	78	60	91	18.5	10.6	5.3	10.3	12.9	5	3	11
Modoc															
331 ISM	B-2	162	86	59	75	56	90	17.9	10.5	3.9	9.9	11.8	5	3	11
Canis familiaris Europe															
Ringkloster															
332 IPA	1592AVEN	156	80	56	71	57	84	17.3	9.0	4.8	9.8	10.6	5	3	33
333 IPA	1592AYPG	158	80	57	71	58	84	15.5	9.7	3.7	9.2	10.1	5	3	33
Ertebølle															
334 ZMC		168	86	57		56	90	18.1	10.5	3.8	9.6	11.0	5	3	33

Table 51 (continued).

Group/ Case	Specimen	Measurements (mm) CL	PL	PW	OI	MCW	IM2	P4	CAN	P1	P2	P3	Observations A	S	SG
Canis familiaris Europe (continued)															
Vedbæk Boldbaner															
335	ZMC 1944-45	161	84	61	74	59	88	18.7	10.1	4.9	10.7	11.3	5	3	33
Saltpetersmosen															
336	ZMC H.7-1	178	93	63	82	62	96	18.1	12.0	5.2	9.9	11.4	5	3	33
337	ZMC H.7-2	163	83	60	75	59	87	17.3	10.8	5.3	10.1	11.5	5	3	33
Bundsø															
338	ZMC BII	136	72	52	61	54	76	15.1	8.7	3.7	8.8	10.3	5	3	33
339	ZMC F.A 62	137	71	50	62	51	74	14.2	8.6	4.2	7.4	9.2	5	3	33
340	ZMC DS 3	154	76	53	69	56	79	14.3	8.5	4.1	7.4	8.5	5	3	33
341	ZMC KV A.1	160	84	57	73	60	87	16.9	10.2	4.4	8.8	10.3	5	3	33
342	ZMC KV B	158	83	57	71	56	84	17.5	9.6	4.6	9.5	10.9	5	3	33
343	ZMC BS 2	159	80	59	68	58	86	18.1	10.0	4.4	9.4	10.8	5	3	33
344	ZMC DS 5	149	77	51	66	53	80	16.9	9.5	4.1	9.2	10.4	5	3	33
Spodsbjerg															
345	ZMC 9688:941	149	78	54	70	57	82	17.1	9.7	4.0	8.4	9.8	5	3	33
Lidsø															
346	ZMC	141	77	53	68	56	80	15.6	10.2	3.4	6.5	9.1	5	3	33
347	ZMC	157	80	53	72	57	86	16.3	9.2	3.9	8.7	10.5	5	3	33
348	ZMC	148	78	54	67	58	78	16.4	10.0	4.9	9.2	10.4	5	3	33
Senckenberg															
349	ZMC	178	93	63	81	59	99	19.0	13.5	5.4	11.6	12.8	5	3	34

*Institutional acronym, followed by institutional catalog number

**A=age category, S=sex, SG=subspecies or geographic region

Table 52. Key to coding information on canid specimens used in analysis.

Variable/ Value	Description
Institutional Acronym	
JFB	James Ford Bell Museum of Natural History, Minneapolis, Minnesota
SNM	Smithsonian Institution, National Museum of Natural History, Washington, D.C.
UIM	University of Illinois Natural History Museum, Urbana, Illinois
KUM	Kansas University Natural History Museum, Lawrence, Kansas
ISM	Illinois State Museum, Springfield, Illinois
UKL	University of Kentucky Museum of Anthropology, Lexington, Kentucky
MCL	Frank H. McClung Museum, University of Tennessee, Knoxville, Tennessee
IPA	Institute for Prehistory, University of Århus, Moesgård, Denmark
ZMC	Zoological Museum, University of Copenhagen, Denmark
Subspecies or Geographic Region	
1	unknown
2	*Canis lupus lycaon*
3	*Canis lupus baylei*
10	Midsouth: Kentucky, Alabama, or Tennessee
11	Illinois River Valley, Illinois
15	*Canis lupus nubilus*
16	*Canis lupus irremotus*
20	*Canis lupus youngi*
21	*Canis rufus rufus*
22	*Canis rufus gregoryi*
23	*Canis aureus indicus*
24	*Canis aureus lanka*
25	*Canis aureus lupaster*
26	*Canis aureus morracanus*
27	*Canis aureus anthus*
28	*Canis aureus algirensis*

Table 52 (continued).

Variable/ Value	Description
Subspecies or Geographic Region (continued)	
33	Denmark
34	Germany
36	*Canis latrans thamnos*
Sex	
1	Male
2	Female
3	Unknown

APPENDIX B

BIVARIATE PLOTS OF CRANIAL AND DENTAL MEASUREMENTS AGAINST CL FOR ADULT CANID SPECIES

Figures 28-37 present bivariate plots of each cranial and dental measurement against CL for adult canids used in analysis. All measurements are log transformed. Because of the quantity of data many observations--over 100 in some cases--are masked. With two exceptions, each plot illustrates two static regression lines. The longer line is the regression for all groups combined. The shorter line is the regression for wild canids only, with domestic dogs excluded. The two exceptions are the plots for OI and P4. In these cases the two regression lines were virtually identical. Consequently, only the regression for all groups is illustrated.

Different species are represented by different numbers, as follows:

1--*Canis lupus lycaon/baylei*
2--*Canis familiaris* NA/EU
3--*Canis latrans*
4--*Canis rufus*
5--*Canis aureus*

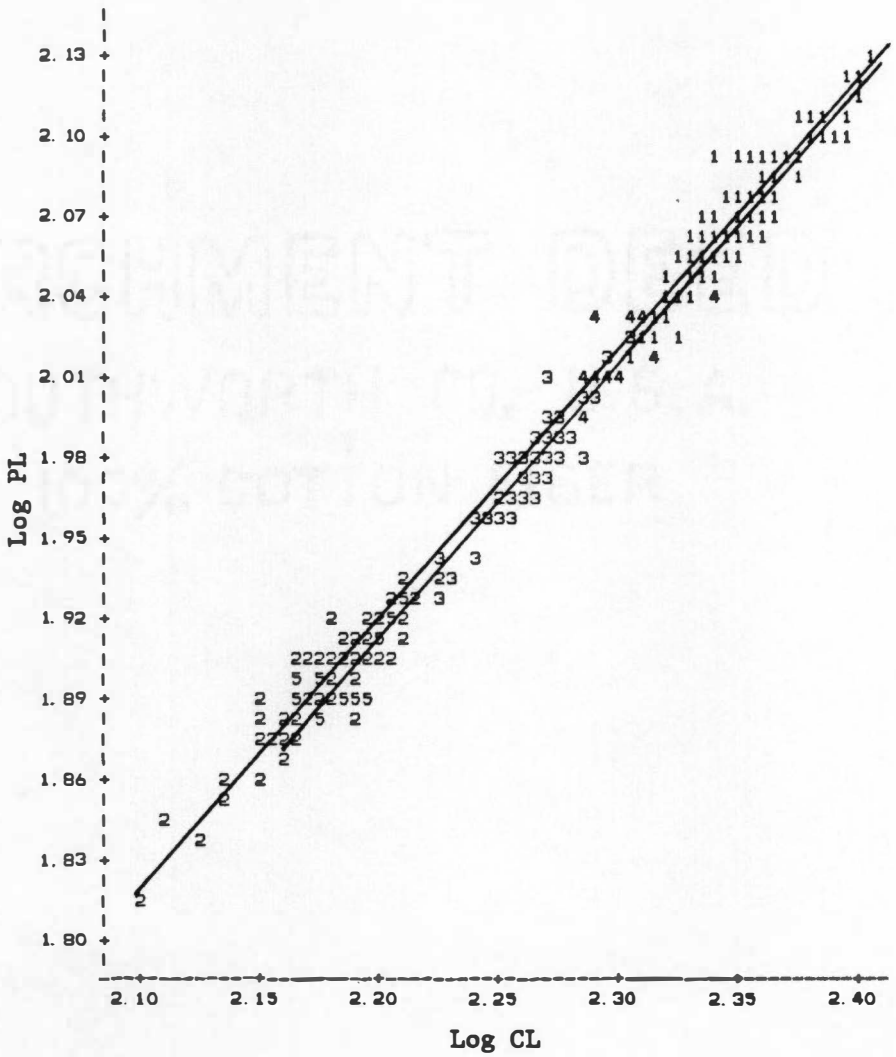


Figure 28. Bivariate plot of PL x CL for adult specimens of five canid species, with interspecific regression lines shown for all groups (longer line) and wild canids only (shorter line).

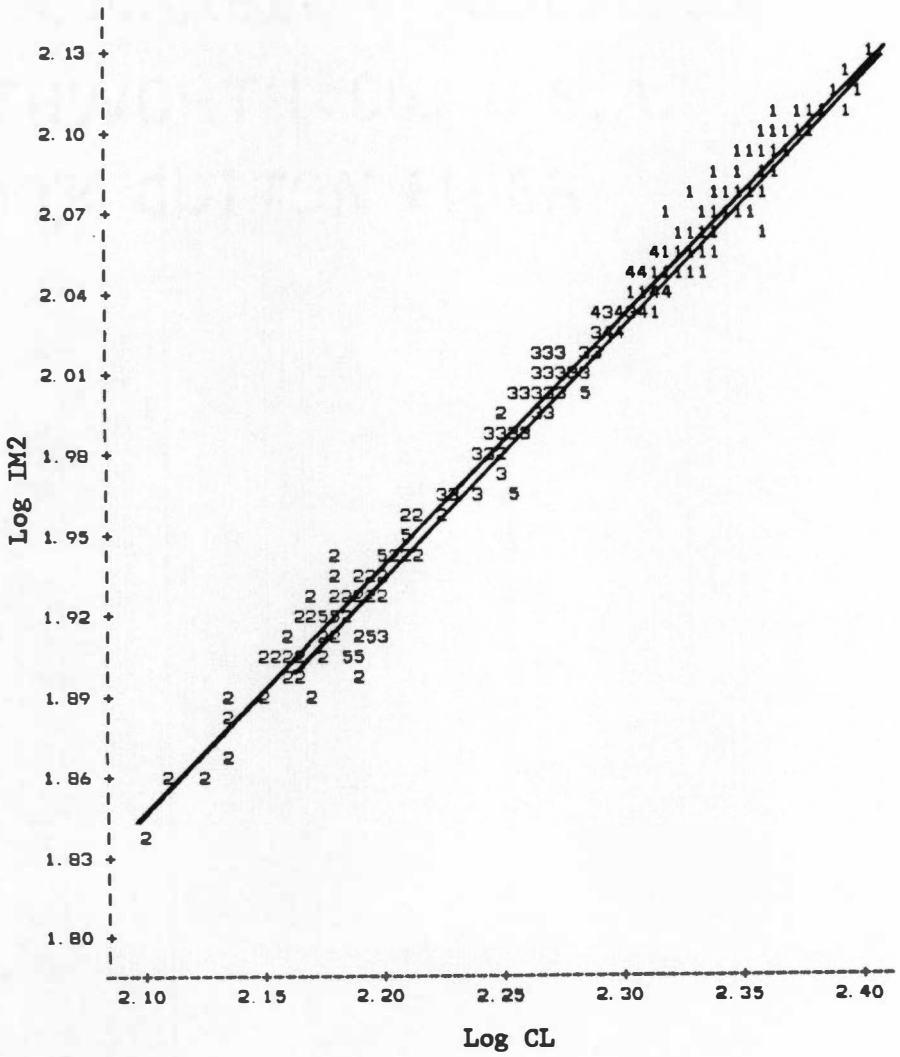


Figure 29. Bivariate plot of IM2 x CL for adult specimens of five canid species, with interspecific regression lines shown for all groups (longer line) and wild canids only (shorter line).

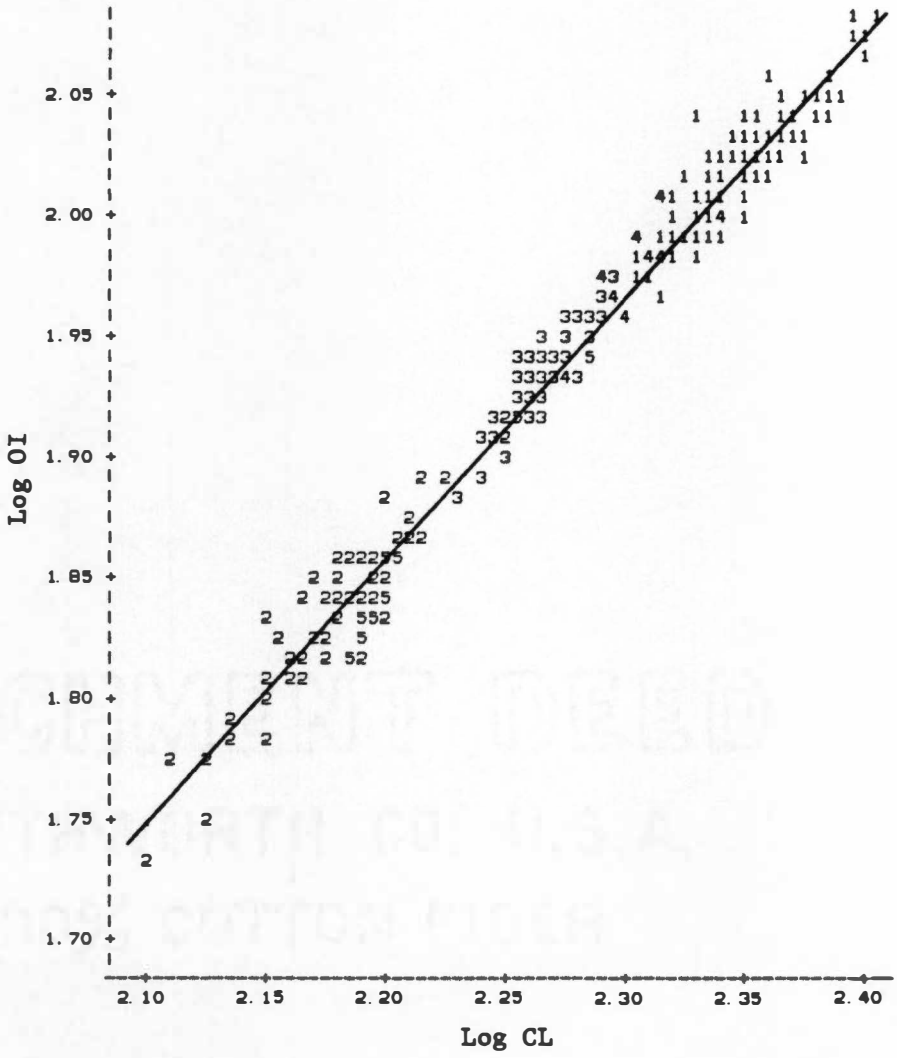


Figure 30. Bivariate plot of OI x CL for adult specimens of five canid species, with interspecific regression line shown for all groups.

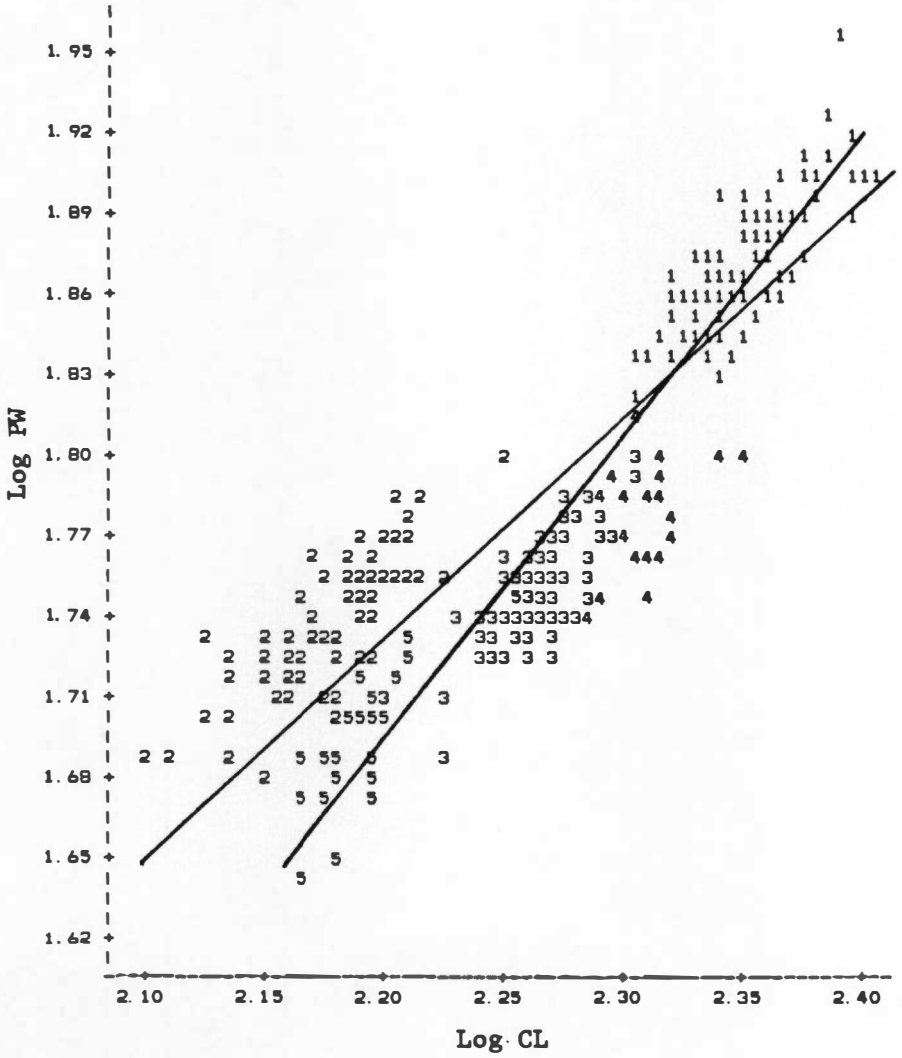


Figure 31. Bivariate plot of PW x CL for adult specimens of five canid species, with interspecific regression lines shown for all groups (longer line) and wild canids only (shorter line).

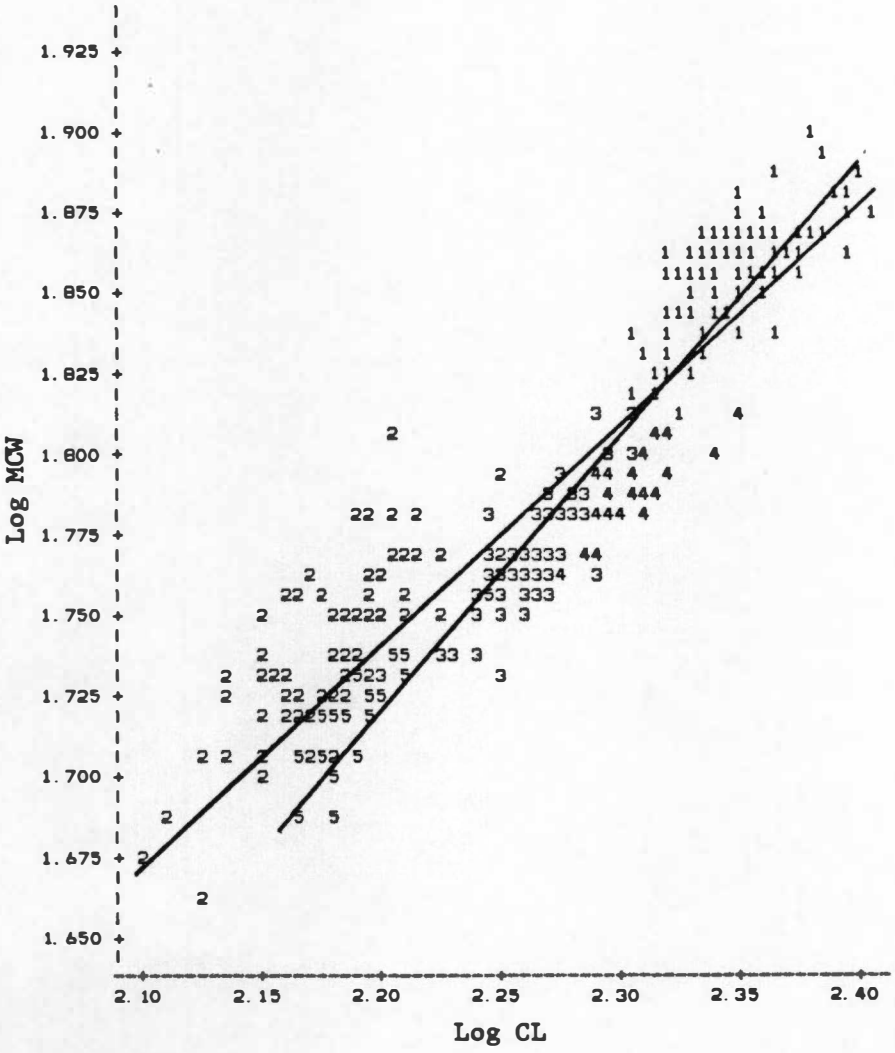


Figure 32. Bivariate plot of MCW x CL for adult specimens of five canid species, with interspecific regression lines shown for all groups (longer line) and wild canids only (shorter line).

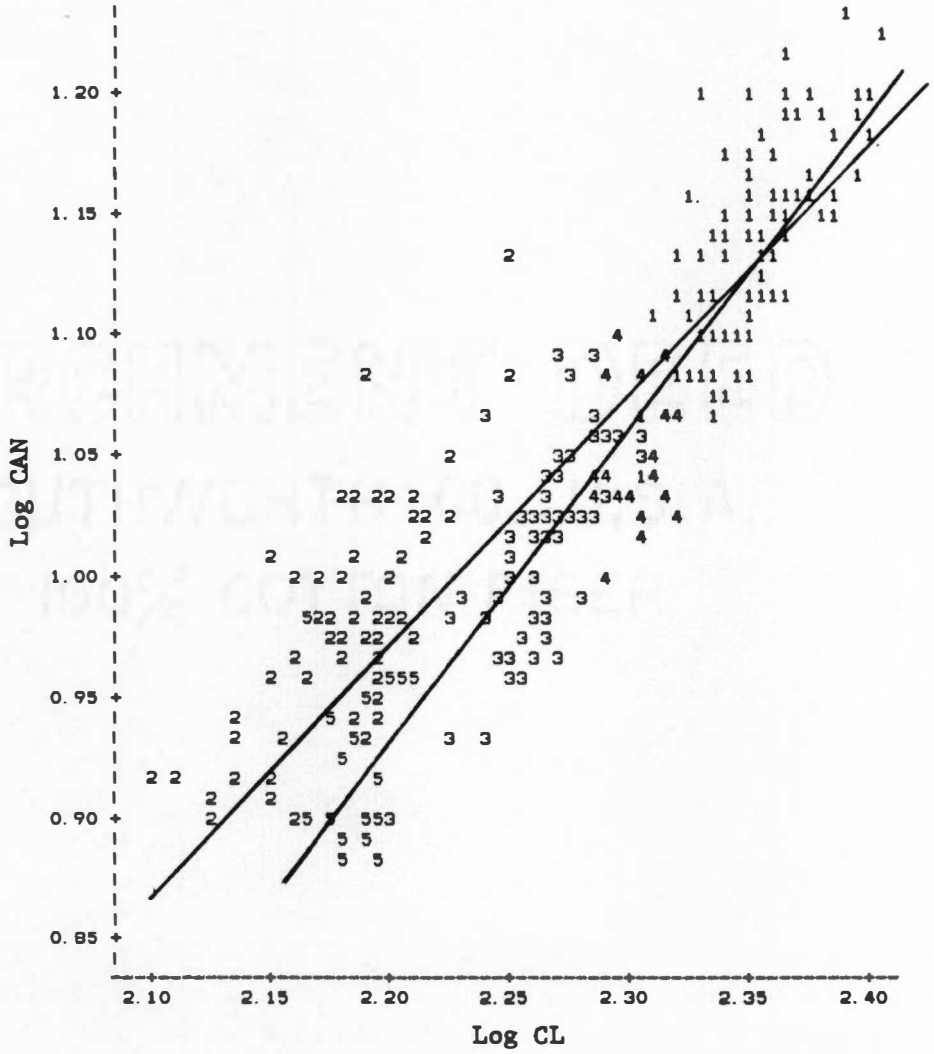


Figure 33. Bivariate plot of CAN x CL for adult specimens of five canid species, with interspecific regression lines shown for all groups (longer line) and wild canids only (shorter line).

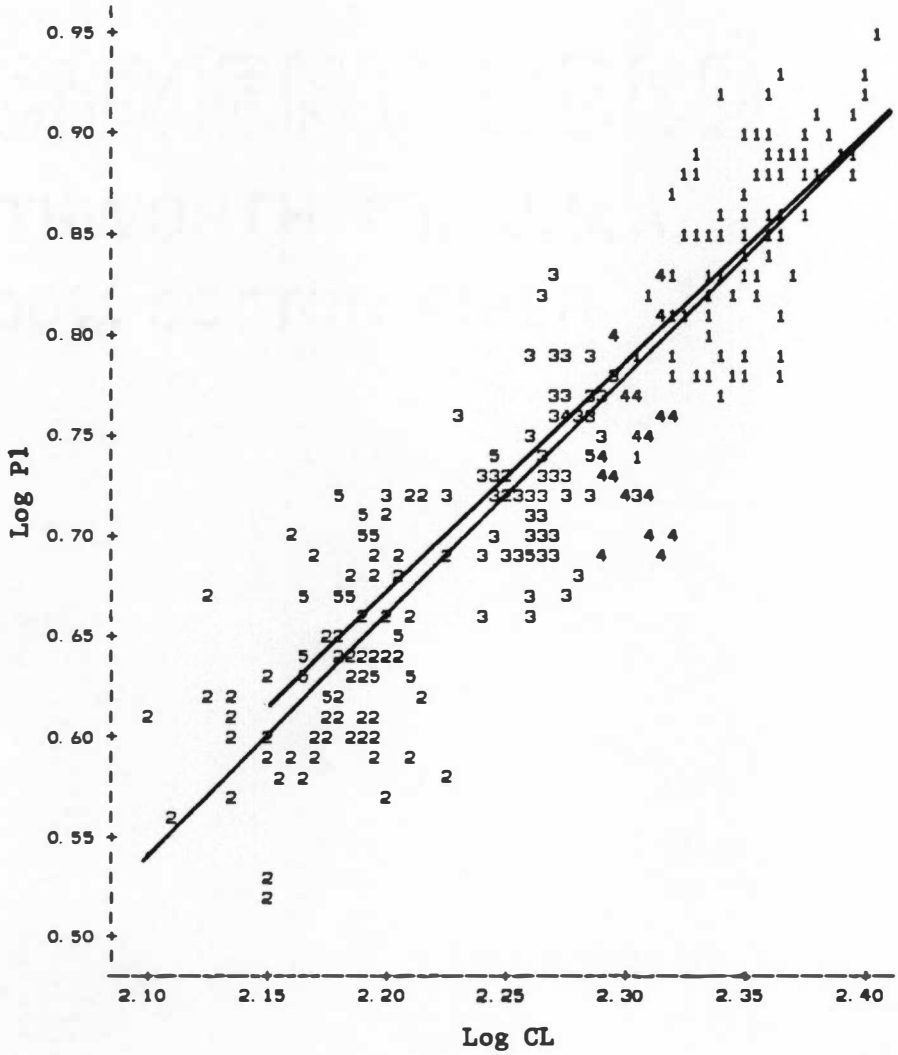


Figure 34. Bivariate plot of P1 x CL for adult specimens of five canid species, with interspecific regression lines shown for all groups (longer line) and wild canids only (shorter line).

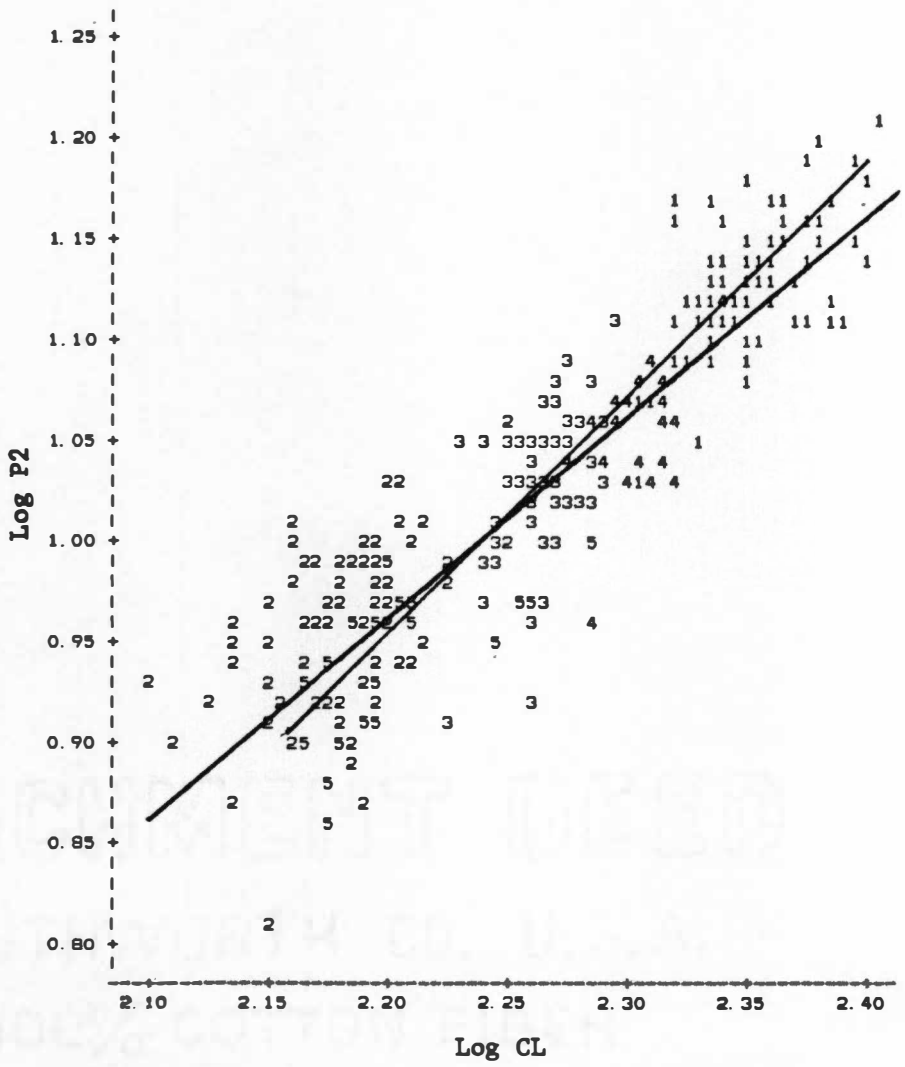


Figure 35. Bivariate plot of P2 x CL for adult specimens of five canid species, with interspecific regression lines shown for all groups (longer line) and wild canids only (shorter line).

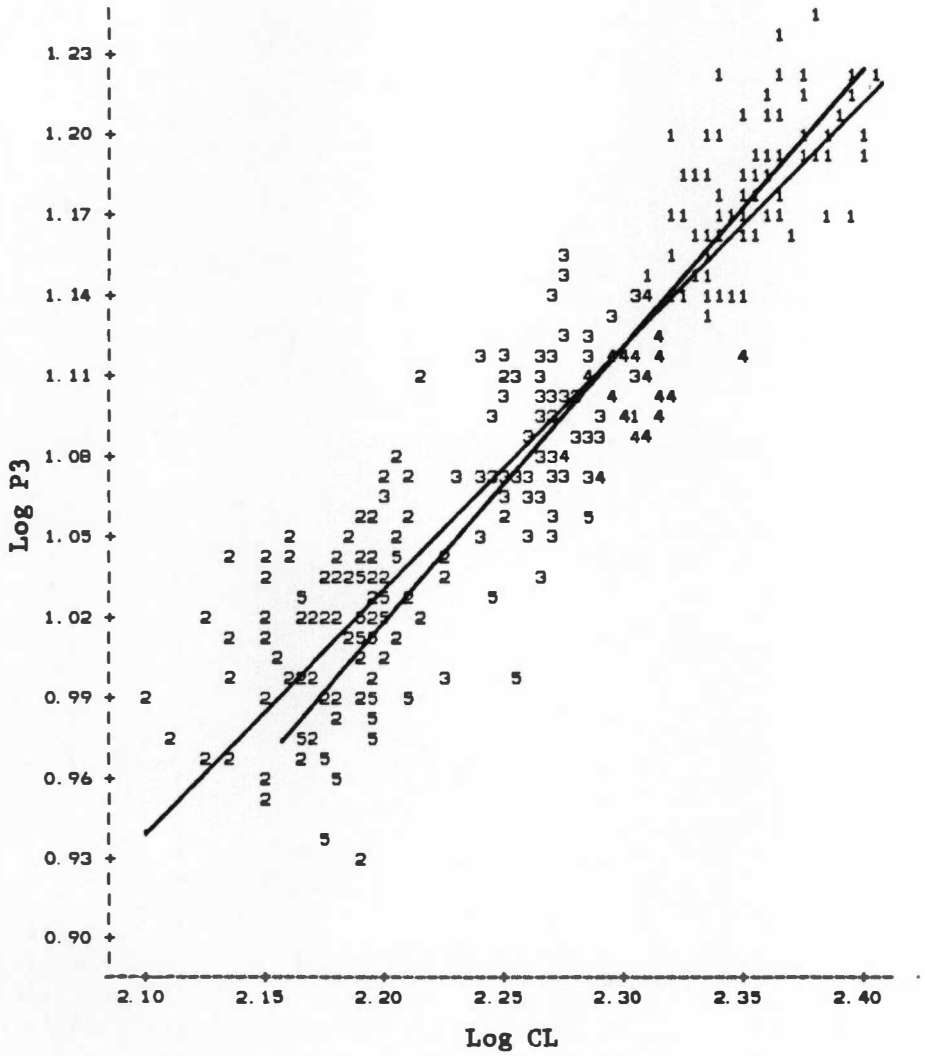


Figure 36. Bivariate plot of P3 x CL for adult specimens of five canid species, with interspecific regression lines shown for all groups (longer line) and wild canids only (shorter line).

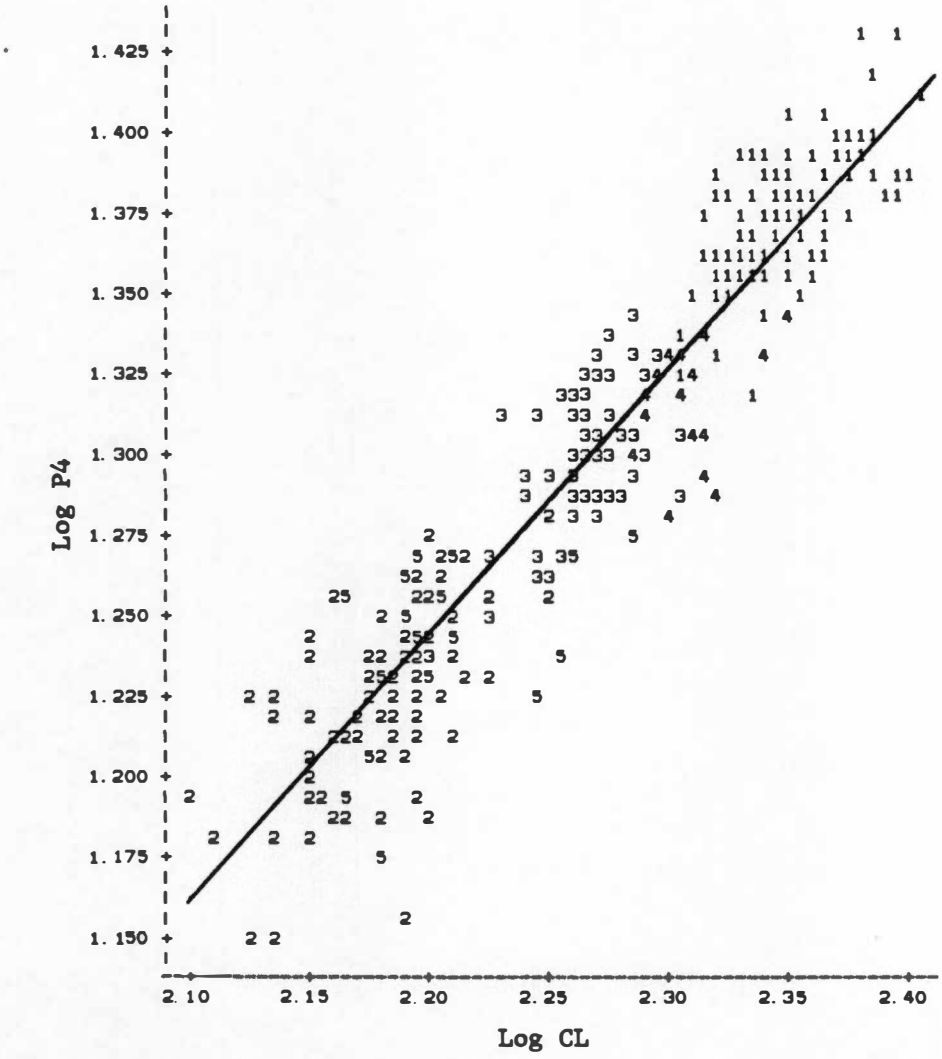


Figure 37. Bivariate plot of P4 x CL for adult specimens of five canid species, with interspecific regression line shown for all groups.

APPENDIX C

BIVARIATE PLOTS OF CRANIAL MEASUREMENTS AGAINST CL FOR JUVENILE WOLF SPECIES

Tables 38-46 present bivariate plots of cranial measurements against CL for juvenile C. lupus and juvenile C. rufus samples. All measurements are log transformed. In each case the regression line fit to the data is illustrated. Data points are represented by a number that identifies the age category (see Table 2, page 81) of the individual represented. Only age categories 1, 2 and 3 are represented. In all cases several observations are masked.

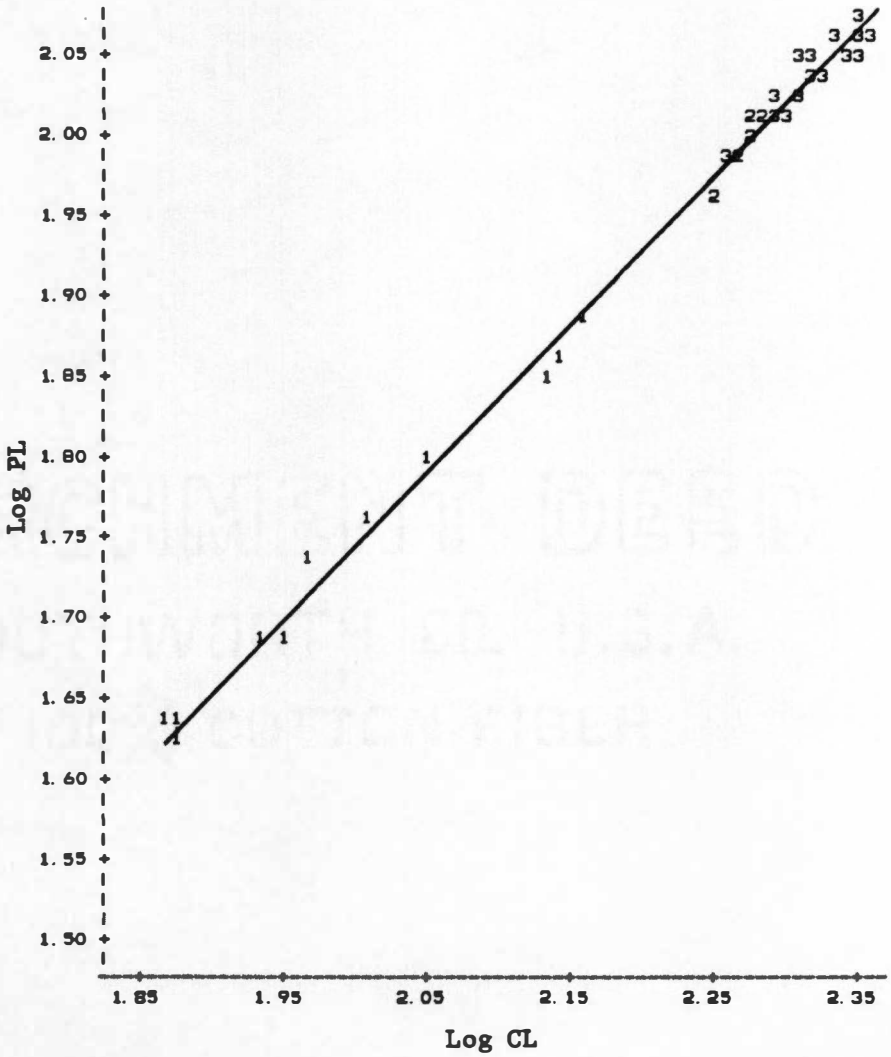


Figure 38. Bivariate plot of PL x CL for juvenile C. lupus (age categories 1, 2, and 3) with regression line shown.

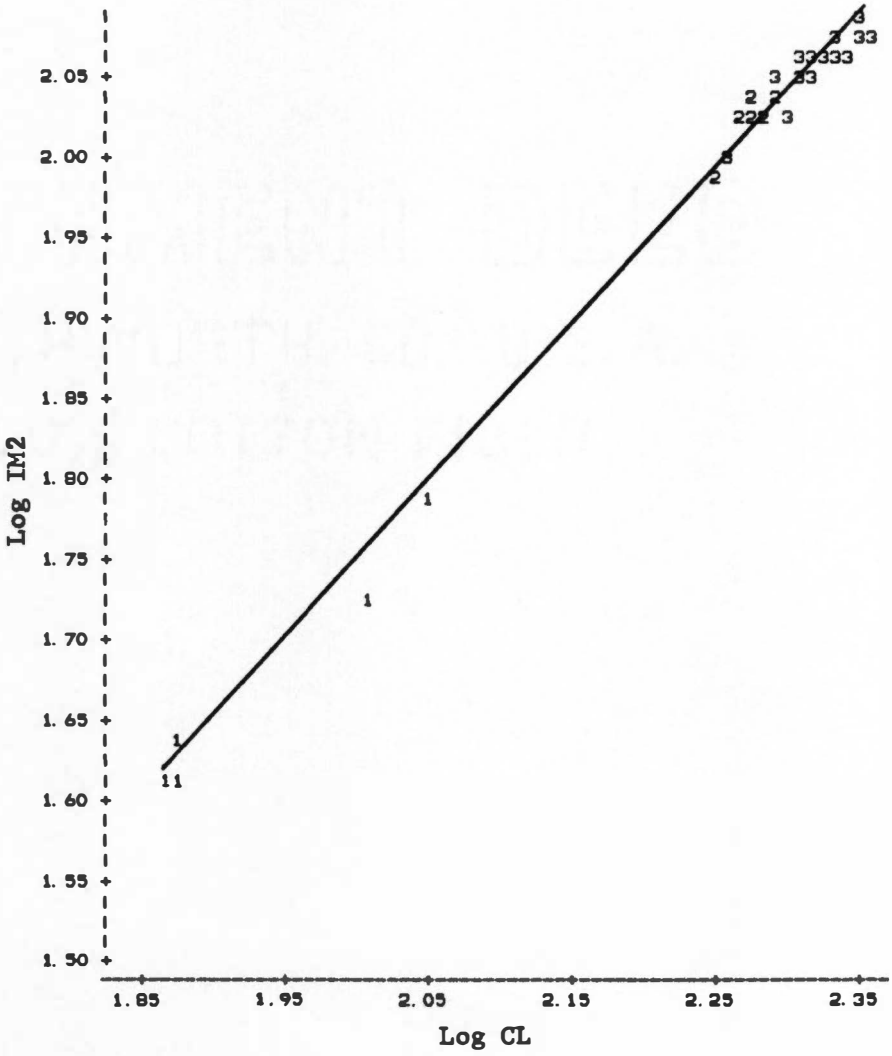


Figure 39. Bivariate plot of IM2 x Cl for juvenile C. lupus (age categories 1, 2, and 3) with regression line shown.

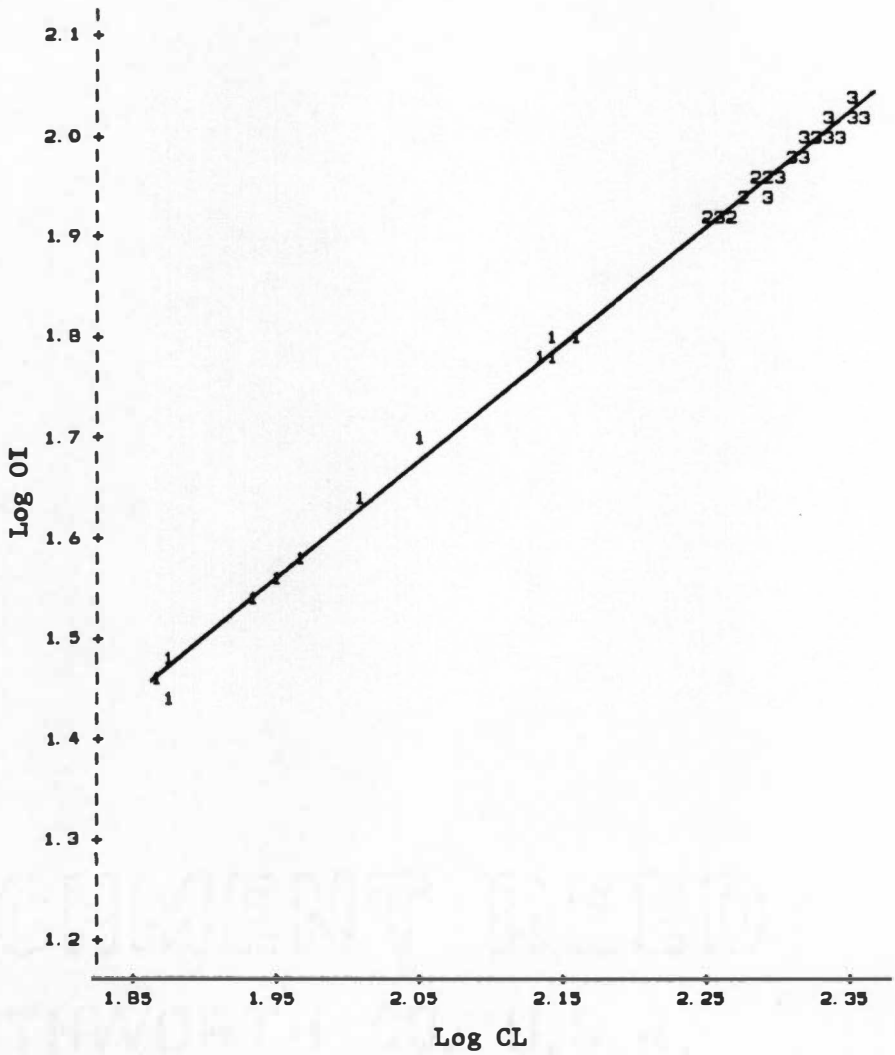


Figure 40. Bivariate plot of OI X CL for juvenile C. lupus (age categories 1, 2, and 3) with regression line shown.

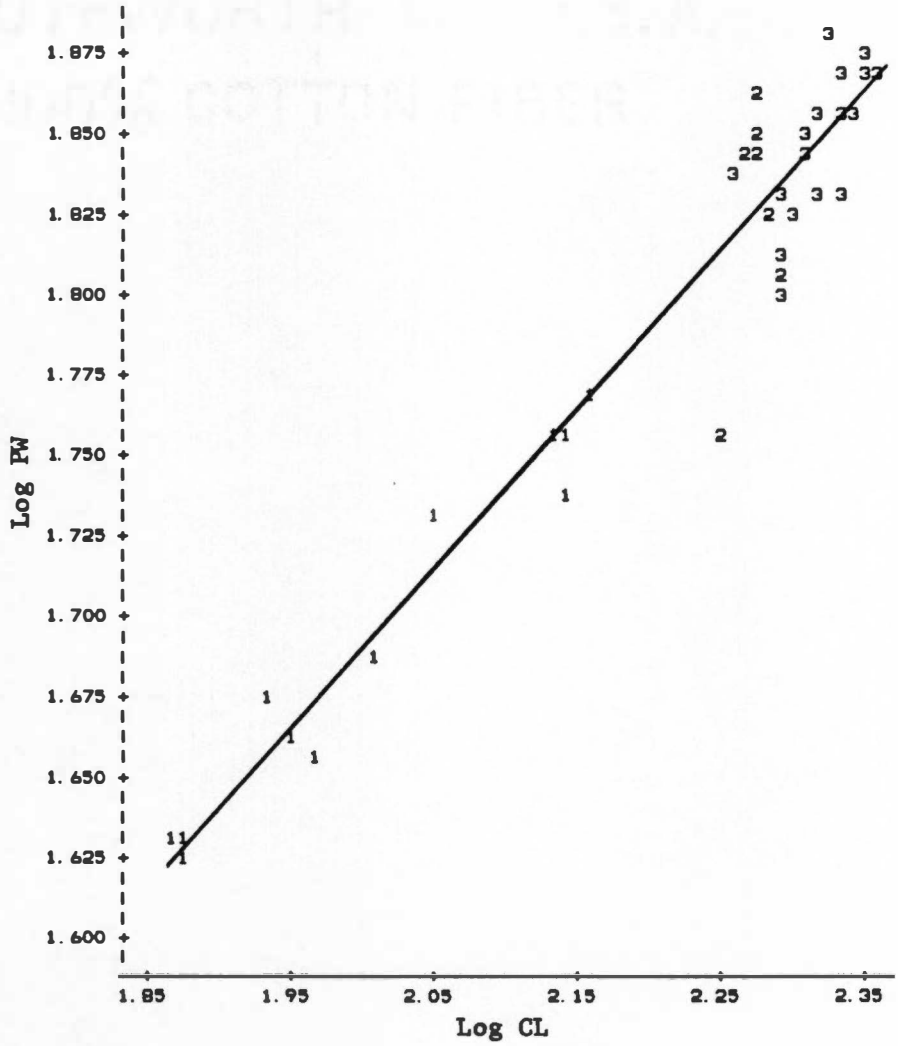


Figure 41. Bivariate plot of PW x CL for juvenile C. lupus (age categories 1, 2, and 3) with regression line shown.

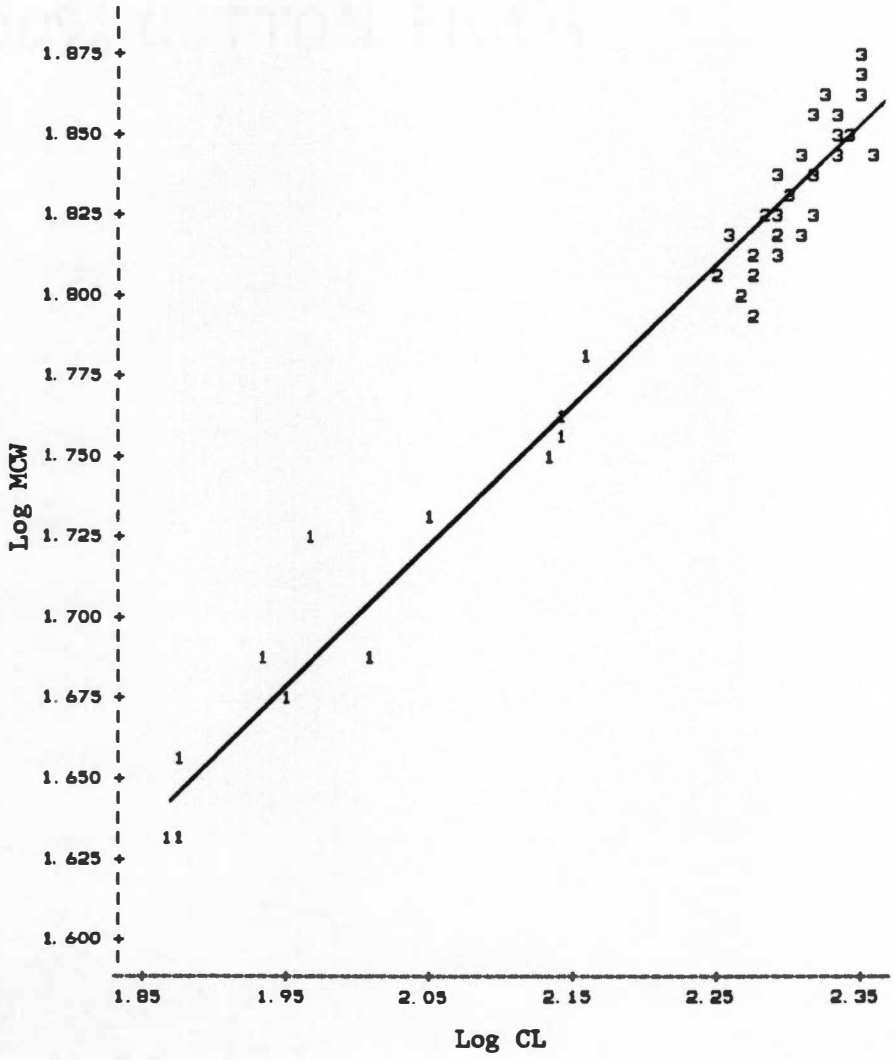


Figure 42. Bivariate plot of MCW x CL for juvenile C. lupus (age categories 1, 2, and 3) with regression line shown.

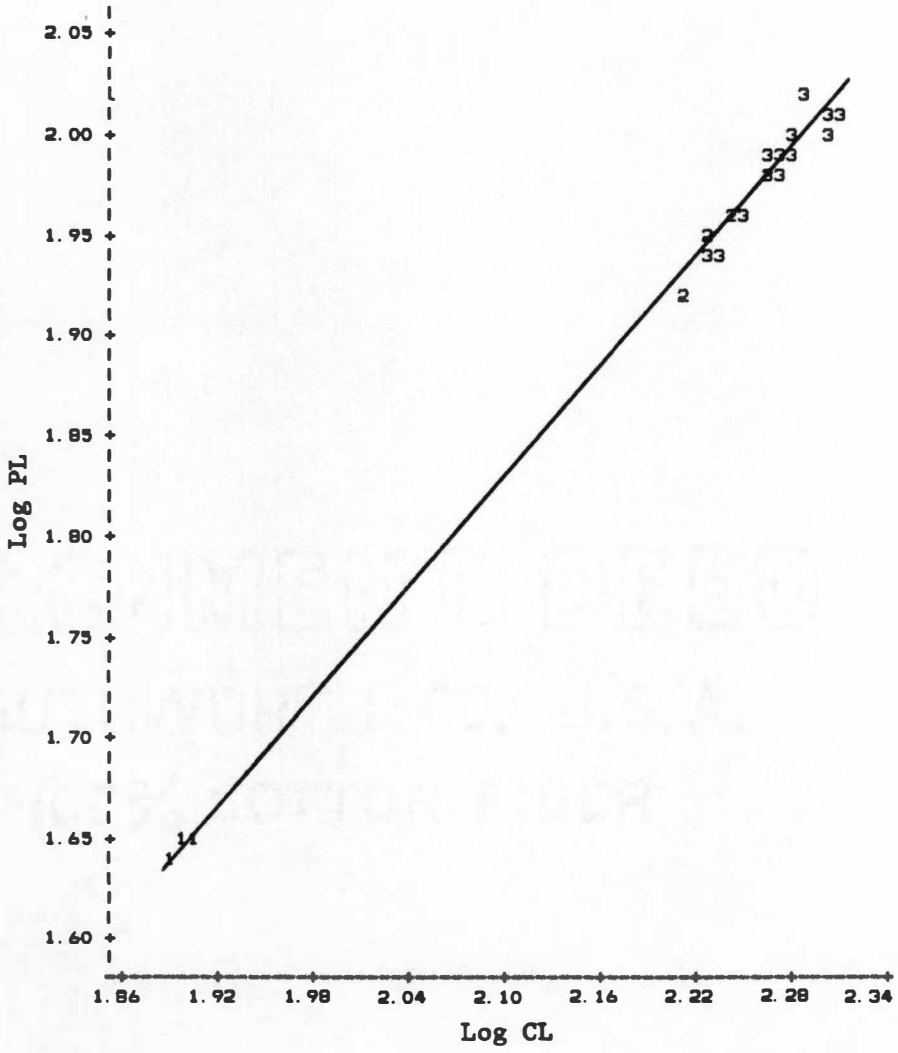


Figure 43. Bivariate plot of PL x CL for juvenile C. rufus (age categories 1, 2, and 3) with regression line shown.

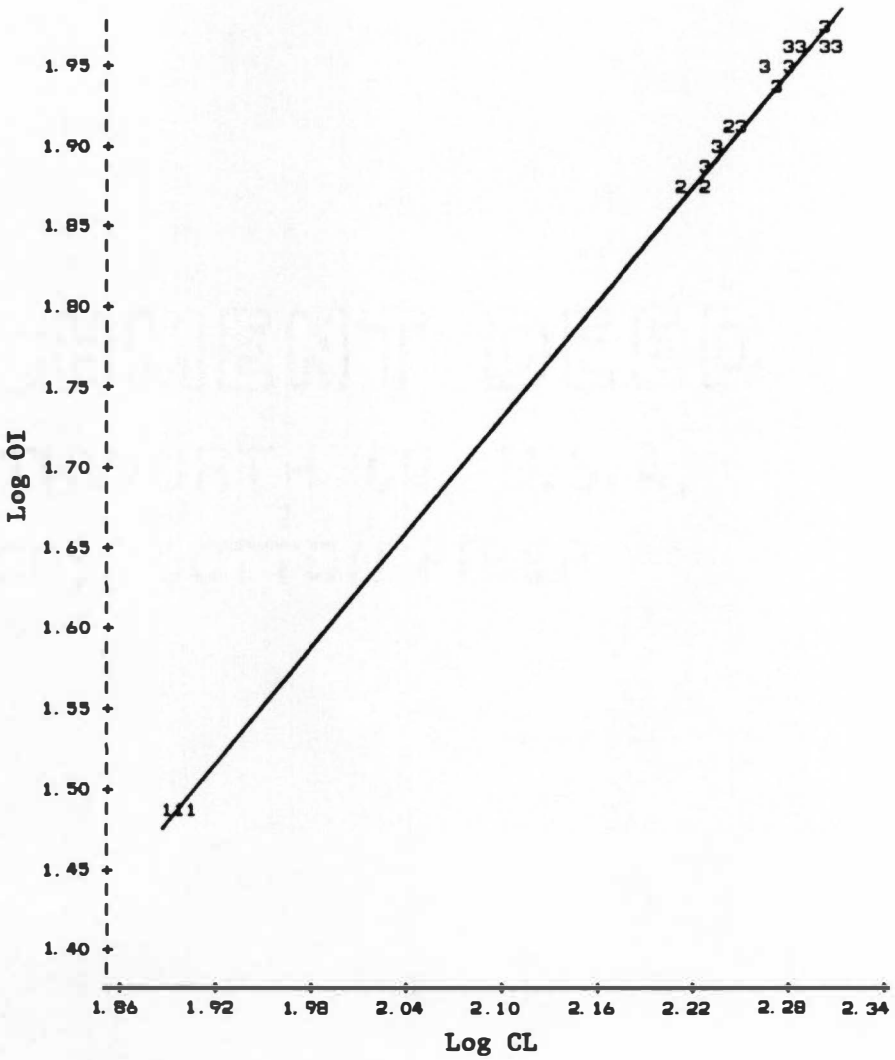


Figure 44. Bivariate plot of OI x CL for juvenile C. rufus (age categories 1, 2, and 3) with regression line shown.

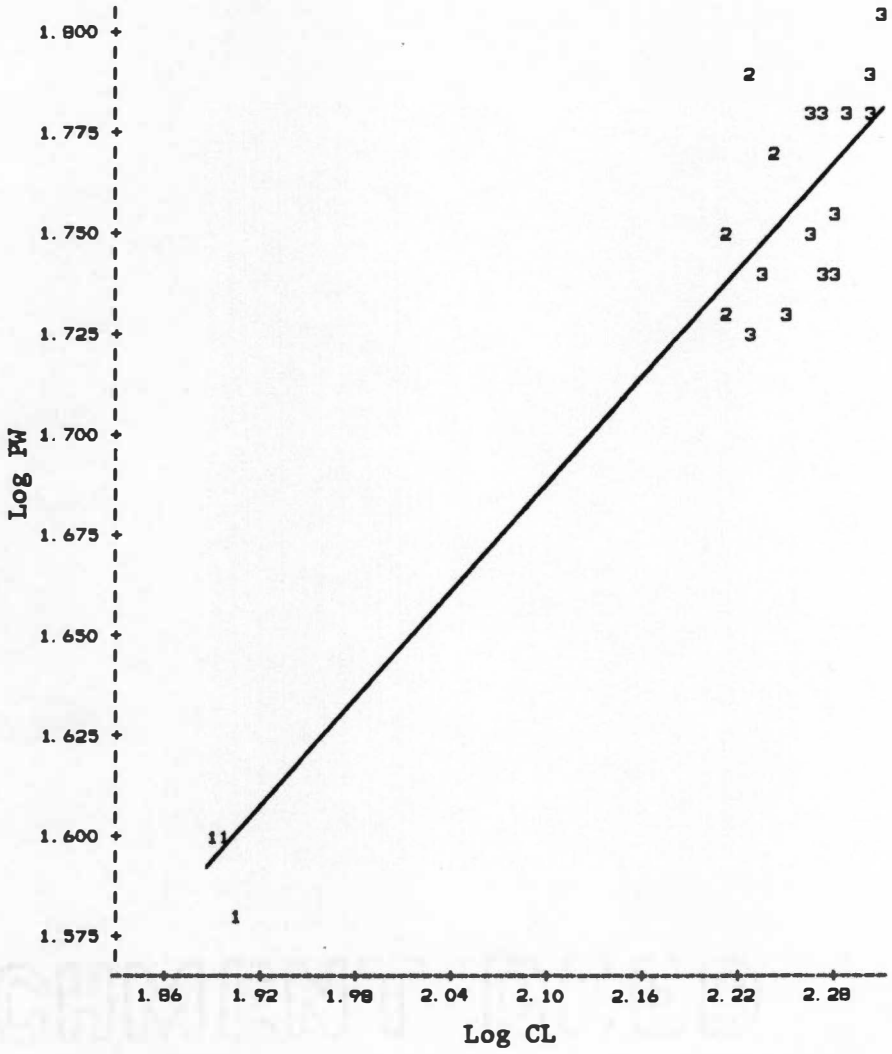


Figure 45. Bivariate plot of PW x CL for juvenile C. rufus (age categories 1, 2, and 3) with regression line shown.

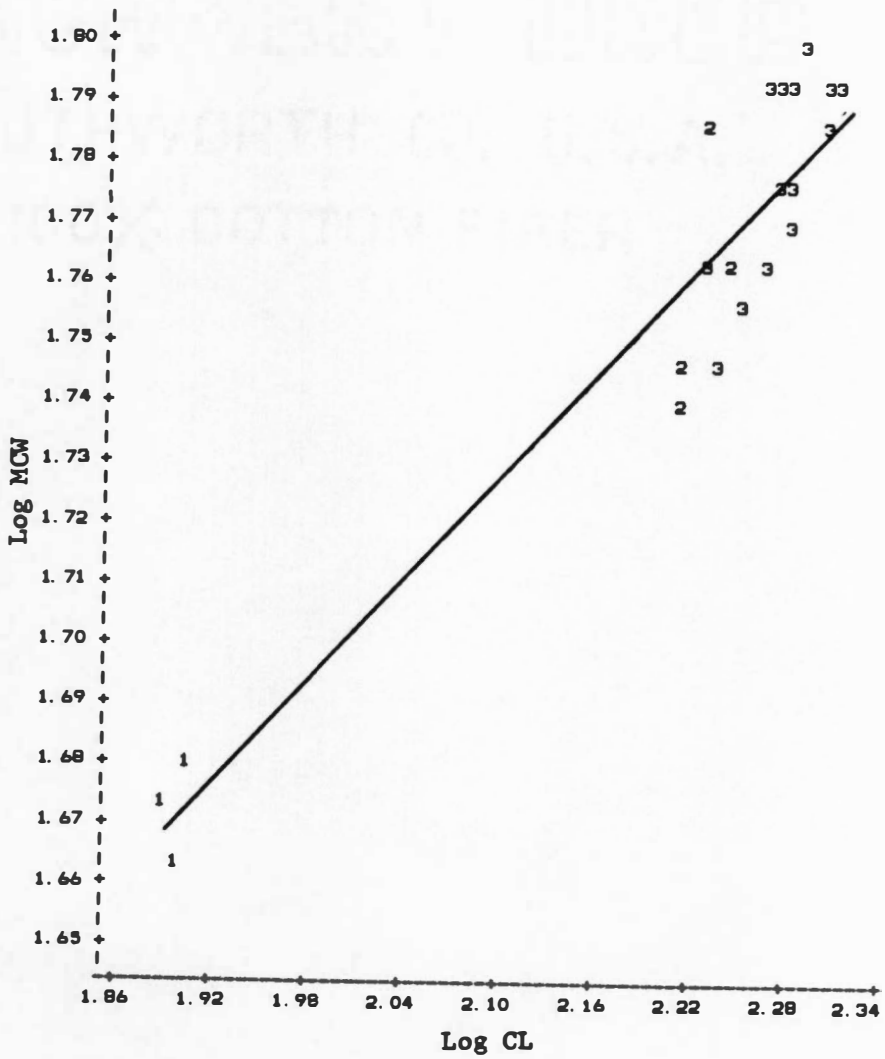


Figure 46. Bivariate plot of MCW x CL for juvenile C. rufus (age categories 1, 2, and 3) with regression line shown.

VITA

Darcy F. Morey was born on September 29, 1956 in Manhattan, New York. He received his primary and secondary education in the public schools of Liberty, Missouri, graduating from Liberty High School in 1974. He attended the University of Nebraska, Lincoln, receiving a B.A. cum laude in Anthropology from that Institution in 1978. During those years he participated in a variety of archaeological field research projects in the Central and Northern Plains.

He began graduate studies at the University of Tennessee, Knoxville in 1979, graduating with the M.A. in Anthropology in 1982. Upon completing the M.A. he began full time employment with the University of Tennessee, Department of Anthropology's Columbia Archaeological Project in middle Tennessee. He began doctoral studies in the University of Tennessee in 1984. Since that time he has participated in archaeological field research projects in France and Denmark. Upon completion of the Ph.D. he will pursue a career in archaeology.