THE APPENDICULAR SKELETON

OF

AELURODON *(PROHYAENA)* *TAXOIDES* (CANIDAE):

AN

ANALYSIS OF FUNCTIONAL MORPHOLOGY

AS RELATED TO PALEOECOLOGIC ROLE

by

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ABSTRACT

An unusually complete skeleton of Aelurodon (Prohyaena) taxoides from the Valentine Formation of Knox County, Nebraska, provides an opportunity to evaluate former speculations, based principally on tooth and jaw morphology, that Aelurodon held an ecologic role similar to that of the wolves, hyenas, or hunting dogs. Comparison of the appendicular skeleton of the wolf and the spotted hyena with that of this fossil specimen shows that the former species are distinctly more cursorially specialized than the latter. Robust limb bones of A. taxoides indicate that it was a heavy-set animal. Evidence from associated fossils (both plants and vertebrates) in Great Plains deposits, indicates that A. taxoides lived in a savanna environment. It is proposed that this species inhabited savanna forests where it could ambush prey. This habitat and behavior may have been similar to that of the modern South American bush dog. It is suggested that change of Barstovian and Clarendonian age savannas to grasslands in the Great Plains and Great Basin regions, caused the decline of Aelurodon by Hemphillian time.

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INTRODUCTION

Throughout the western United States, species of the carnivore genus Aelurodon have been found to be common components of Barstovian and Clarendonian fossil mammalian faunas. At least one species of Aelurodon persisted into Hemphillian times (Radinsky, 1973). It would seem that the osteology of such a common and wide ranging genus would be well known. In reality, however, nearly all the reports of Aelurodon material have been based on mandibles, skulls, and isolated teeth, so that knowledge of the post-cranial skeleton is quite limited. It is the purpose of this study to describe for the first time the post-cranial skeleton of Aelurodon (Prohyaena) taxoides, and, through analysis of body proportions and skeletal morphology, determine the paleoecologic role which the species held.

PREVIOUS WORK

Geographic Distribution

The following list of states from which Aelurodon remains have been reported illustrates the cosmopolitan nature of the genus in western North America; California (Merriam, 1919; Bode, 1935; Macdonald, 1948a), Montana (Thorpe, 1922), Nebraska (Leidy, 1858; Hatcher, 1894; Cook, 1914; Cope and Matthew, 1915; Barbour and Cook, 1917; Thorpe, 1922; Stirton and McGrew, 1935; Voorhies, 1969; Webb, 1969; Messenger and Messenger, 1977), Nevada (Vanderhoof and Gregory, 1940; Henshaw, 1942), New Mexico (Cope, 1877), Oklahoma (Kitts, 1957 and 1964), Oregon (Vanderhoof and Gregory, 1940; Shotwell and Russell; 1963), South Dakota (Matthew and Gidley, 1904; Gregory, 1942; Macdonald, 1960; Green, 1971), and Texas (Wilson, 1960; Dalquest and Hughes, 1966). Aelurodon is also known from as far east as Maryland (Whitmore, 1971), and as far South as Florida (White, 1947). Storer (1975) recently extended the known range of Aelurodon to Saskatchewan, Canada.

Postcranial Skeleton

It is worthwhile to present a summary of the skeletal material which has been referred to the various species of Aelurodon, due to the paucity of post-cranial material which is recognizably attributable to the genus. Cope (1883, p. 242) figured a calcaneum, astragalus, and three metatarsals of *A. saevus*, and stated that metacarpal II has a roughened area indicating that metacarpal I was present in the foot as is characteristic of *Canis* and unlike modern hyenas (p. 244). Hatcher (1894, p. 239) stated that an atlas was found with the holotype of *A. taxoides* (a mandible), but did not figure the vertebra. Cope and Matthew (1915, pls. CXVII-CXIX) figured a nearly complete skeleton of *A. saevus*, but provided no descriptive text. Merriam (1919, pp. 540-541, figs. 149-150) figured two incomplete metapodials which "possibly represent *Aelurodon ? aphobus*", and referred three other metapodials to *Aelurodon*? sp. (p. 540, figs. 151-153). Vanderhoof and Gregory (1940, p. 162) gave a brief description of the skeleton of *A. haydeni* in which they discussed the vertebral column, humerus, femur, and pelvis, but figured none of those elements. Gregory (1942, pp. 347-348) described two humeri which he referred to *Aelurodon* sp., and did not describe but also referred to *Aelurodon* sp. an ulna, the proximal end of a radius, the distal end of a radius, a cuneiform, a metacarpal III, and two astragali. Macdonald (1948b, p. 48, fig. 2c) figured the distal end of an

Aelurodon humerus which he incorrectly referred to *Pseudaelurus pedionomus* (Webb, 1969, p. 70). Macdonald provided measurements (p. 47), but no description of the bone.

The above account shows that while much of the skeleton of *A. saevus* has been figured, very little has been described. Only a few elements of the post-cranial skeleton of *A. haydeni* have been described. Most notably, no post-cranial material representative of the *A. taxoides* group has been previously described or figured (other than the atlas associated with the type specimen of *A. taxoides*).

Ecologic Role and Relationships

The lack of post-cranial material of *Aelurodon* has necessitated that speculations on the habits of the members of the genus be based primarily on analyses of tooth size and wear, and skull size. Most workers have equated the ecologic niche of *Aelurodon* with either that of the wolves (*Canis lupus*) or the hyenas (usually without specifying whether *Crocuta crocuta*, *Hyaena hyaena* or *Hyaena brunnea* was intended.)

In describing the type specimens of *A. saevus* (Leidy) and *A. haydeni* (Leidy), Leidy (1858, p. 21) referred to the specimens as the mandibles of wolves. He also stated (p. 22) that the type specimen of *A. ferox* Leidy was a sectorial the size of that of a wolf, but noted that it possessed an anterior cusp which is not found in modern canids but is found in modern felids (and in hyenas). Matthew (1924, p. 120) stated that the feet of *Aelurodon* are similar to that of the wolf; later, he commented that *A. haydeni*, though larger than the timber wolf "was probably of similar habits with some approach to the hyenoid dogs in the manner of life" (1930, p. 131).

Cope (1883, p. 244) speculated that the robust premolars of *Aelurodon* were used for crushing bones "as they are in *Hyena*."

He went on to state that "...this genus (*Aelurodon*) is the ancestor of the hyaenidae", and that *A. saevus* and *A. wheelerianus* were scavengers which ate "the remains of the antelopes and small camels of the Loup Fork epoch". Macdonald (1948a, p. 65) described *Aelurodon* as a long-faced dog, and stated that *Aelurodon* either scavanged carcasses or killed weak and dying individuals (p. 78). Other workers have referred to the teeth of *Aelurodon* as being hyena-like (Radinsky, 1973, p. 179), indicative of hyenoid specialization (Vanderhoof and Gregory, 1940, p. 163), or having morphology and wear indicative of bone crushing ability (Voorhies, 1969, p. 20). Schlosser (1890, p. 411) carried the relationship with hyenas a step further by claiming that the holotype of *A. wheelerianus* was the jaw of a true hyaenid, and used the specimen as the basis for establishing his new genus *Prohyaena*. Matthew (1912, p. 185) proposed that a future goal of paleontologic research should be to determine whether *Aelurodon* has any ancestral relationship with the Hyaenidae, stating that morphologic evidence from the family indicates remote canid affinities, while paleontologic evidence indicates a derivation from the Viverridae. Vanderhoof and Gregory (1940, p. 163) did not postulate a modern ecological analogue for *Aelurodon*, but stated that *A. haydeni* was an active predator whose shortness of limbs indicates that it was not as well suited for pursuit of prey as the wolf. Gregory (1942, p. 334) maintained this line of thought, saying that *Aelurodon* may have been a plains animal that also "haunted waterholes and ambushed its prey." Shotwell and Russell (1963) noted the presence of *Aelurodon* in their "savanna community", but made no speculations on ecological roles. Most recently, Galiano and Frailey (1977, p. 14) made the suggestion, based on tooth and jaw morphology, that the *A. taxoides* group held the niche of the wolves or hunting dogs, while *A. haydeni* held the eco-niche of the spotted hyenas (*Crocuta*). Radinsky (1973) studied endocranial casts of *Aelurodon* in order to determine how closely it resembled modern dogs in brain structure.

METHODS AND MATERIALS

My analyses and conclusions concerning functional skeletal morphology are based on the excellent studies of modern canid skeletons by Hildebrand (1952 and 1954) and more general studies of the mammalian skeleton (Hildebrand, 1974; Howell, 1965; Smith and Savage, 1956). Detailed comparisons are made between the skeleton of the wolf (*Canis lupus*), the spotted hyena (*Crocuta crocuta*), and a well preserved specimen of *Aelurodon* (*Prohyaena*) *taxoides* from Knox County, Nebraska. Another nearly complete skeleton of *Aelurodon* ? sp. from near Gordon, Nebraska provides a means to assess individual variation within the genus. Supplemental comparisons were made utilizing skeletons of the coyote (*Canis latrans*), the black bear (*Ursus americanus*), and the tiger (*Felis* (*Panthera*) *tigris*).

A list of specimens utilized in the study follows:

Aelurodon (*Prohyaena*) *taxoides*	Skull and skeleton-UNSM* 46815	
Aelurodon ? sp.	Skeleton	UNSM 4476
Canis lupus lycaon	Skull and skeleton-(UNSM)ZM12641-S	
Canis lupus lycaon	Skull and skeleton-(UNSM)ZM12642-S	
Canis lupus nobilus	Skull and skeleton-(UNSM)ZM590-S	
Canis latrans	Skull and skeleton-(UNSM)ZM14459	
Crocuta crocuta	Skull	USNM**282797
Crocuta crocuta	Skeleton	USNM 172685
Felis (*Panthera*) *tigris*	Skeleton	(UNSM)ZM14603
Ursus americanus	Skull and skeleton-(UNSM)ZM283	

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*University of Nebraska State Museum
**United States National Museum

Equi-length line drawings (figs. 2-6) were made via slide projection to compensate for differences between the species due to relative size differential.

The anatomical terminology follows Miller, et. al. (1964) unless otherwise indicated. Data on wolf behavior and habits is primarily based on observations by Murie (1944), Young and Goldman (1944), and Mech (1966). The recent work of Kruuk (1972 and 1975), provided excellent information on the habits of the spotted hyena.

ACKNOWLEDGEMENTS

Much credit and thanks must be given to Dr. Michael Voorhies for suggesting this project, and for his ready accessibility and desire to give guidance and take part in discussions throughout the study. Mike must also be credited as the discoverer, collector, and preparator of the *A.* (*Prohyaena*) *taxoides* skeleton. R. G. Corner and K. A. Richey of the University of Nebraska State Museum provided specimens of *Aelurodon* for comparison. Dr. R. Emry and R. Purdy of the Department of Paleobiology, Smithsonian Institution, provided access to Leidy's type specimens of *A. ferox*, *A. saevus*, and *A. haydeni*. Dr. F. C. Whitmore, Jr., of the U. S. Geological Survey, made his specimen of *Aelurodon* from Maryland available. Drs. C. O. Handley and J. G. Mead of the Division of Mammals, Smithsonian Institution, made an extended loan of the *Crocuta* specimens. Funds were provided through a scholarship from the Lincoln (Nebraska) Gem and Mineral Club (through the efforts of R. K. Pabian, Nebraska Geological Survey), and by the Department of Geology, University of Nebraska-Lincoln. Dr. H. Gunderson and R. Hunt reviewed the manuscript.

SYSTEMATIC PALEONTOLOGY

Mammalia
 Carnivora
  Canidae
   Borophaginae
    Aelurodon (Prohyaena) taxoides
     Aelurodon Leidy, 1858
     (Prohyaena) Schlosser, 1890
      A. taxoides Hatcher, 1894

Referred specimen: UNSM 46815, relatively complete skeleton consisting of nearly complete skull partially damaged in naso-frontal region, but possessing all teeth except crowns of left P^1 and right P^4, and lacking the M^1 and M^2 from the right side; well preserved mandible with all teeth except crowns of right I_2 and M_1, left P_1 and lacking the M_3 from both sides; left humerus, right humerus missing proximal end, right and left ulnae, left radius, distal half right radius, left pisiform, left Mc. II and IV, right Mc. III and IV, all tarsals and metatarsals of right hind foot, left astragalus, left calcaneum, left navicular, left Mt. II-III, 4 proximal phlanges, 4 distal phlanges, right innominate lacking proximal half of ilium, right femur, distal half left femur, 1 cervical bertebrae, 2 thoracic vertebrae, 4 lumber verbrae, cranial end of manubrium, 1 sternal element, and miscellaneous rib fragments.

Horizon and locality: Burge (?) Member, upper Valentine Formation. UNSM Locality Kx-119, Knox Co., Nebraska. (pl. 5A)

Generic Characters of Aelurodon

The genus Aelurodon was first erected by Leidy in 1858 when he described Aelurodon ferox. Leidy based the genus on the upper carnassial tooth of a canid collected in the Niobrara River valley, probably near Valentine, Nebraska (Vanderhoof and Gregory, 1940, p. 143). The genotypic specimen (USNM 523), is characterized by the presence of a parastyle anterior to the paracone. Such a parastyle is absent on the upper carnassial of modern canids, but is found in modern felids and also in the fossil canid genera Tomarctus and Osteoborus which were, in part, contemporaries of Aelurodon (Vanderhoof and Gregory, 1940, p. 143).

Vanderhoof and Gregory (1940) published a comprehensive review of Aelurodon, in which they proposed a combination of characters to distinguish that genus from other related members of the Canidae. A slightly modified list of the generic characters of Aelurodon recognized by Vanderhoof and Gregory (1938 and 1940) follows:

1. Well developed parastyle on P^4.
2. Small metaconid on M_1 (maybe absent), heel bicuspid.
3. M_2 with distinct trigonid and basin-shaped heel.
4. Premolar serier never abruptly reduced.
5. Anterior premolars have a strong principal cusp slightly anterior to the center of the tooth, with a smaller cusp between the principal cusp and a posterior basal cusp. (Presence of an anterior basal cusp is variable).
6. Dental formual as in Canis $\frac{3142}{3143}$
7. Skull as large or larger than modern wolf (Canis lupus).
8. Sagittal crest stronger than modern dogs, braincase relatively smaller.
9. Snout more elongate than Osteoborus and Borophagus.

The Knox County specimen agrees with all of these characters except for the presence of M_3. The minute remnants of alveoli for this tooth in both rami indicate that although the M_3 is absent from the specimen, the absence is probably due to a combination of advanced age and general reduction in the size of the tooth rather than a genetic loss (M. R. Voorhies, oral communication, 1977). Scott (1890) noted great variation in this tooth in specimens of A. haydeni. He stated that M_3 may be double-rooted, single-rooted, or not occur at all.

Due to wear on the M_2 of the Knox County specimen it is not ascertainable whether this tooth possessed a basin-shaped heel. However, the character may be variable since some specimens of A. taxoides possess heels on M_2 which appear trenchant rather than basined (Vanderhoof and Gregory, 1940, p. 149).

The most obvious characters differentiating UNSM 46815 from other borophagine genera are as follows; Tomarctus is smaller, Borophagus lacks a parastyle on P^4, and Osteoborus has reduced anterior premolars.

The knox County specimen is referred to Aelurodon due to the presence of only minor variations from typical Aelurodon characters and to the obvious lack of similarity to other borophagine genera.

Characters of Aelurodon Species

Many new species of Aelurodon were described in the latter half of the nineteenth and early twentieth centuries as more specimens were collected around the country. The large number of these species was due in part to an inability to compare new material with the genotype (most of the new species were based on lower jaws), and partly due to an ignorance of the range of individual variation within valid species of Aelurodon. Vanderhoof and Gregory (1940) clarified the confused status of the species of the genus, and McGrew (1944) simplified problems further by dividing the genus into two species groups; the A. saevus and A. taxoides groups. McGrew designated the type specimens of A. saevus (Leidy), A. haydeni (Leidy), A. inflatus Vanderhoof and Gregory and A. mortifer (Cook) to be representative of the A. saevus group (1944, p. 79). A. taxoides and some specimens which had been referred to A. wheelerianus were designated as representing the A. taxoides group. A. ferox Leidy, A. meandrinus Hatcher, A. brachygnathus Douglass, and A. wheelerianus (Cope) were considered to not possess sufficient characters for specific determination (McGrew, 1944, p. 79). Mawby (1964) added A. marshi to the A. taxoides group, and suggested that A. wheelerianus also probably belongs to that group, while A. ferox probably belongs to the A. saevus group.

Five characters distinguish the A. taxoides from the A. saevus group. These are (McGrew, 1944, p. 79):

1. Horizontal ramus not tapering anteriorly, symphysis deep.
2. Premolars little reduced.
3. Heel of M_1 short.
4. Entoconid of M_1 much reduced.
5. Paraconid, protoconid, and metaconid of M_2 reduced.

To determine whether the Knox County specimen should be referred to the A. saevus or A. taxoides group a graphical comparison of tooth size was made between the dentition of UNSM 46815 and the published measurements of Aelurodon holotype and referred specimens (figs. 1a-g). The graphs indicate that both groups widely overlap in their size ranges of P_4 and M_1 (figs. 1e, f), however the A. saevus group tends to have distinctly smaller sized anterior lower premolars than does the A. taxoides group. This portrays McGrew's (1944, p. 79)

Figure 1a-g. Graphs showing size of the lower dentition of UNSM 46815 relative to the published measurements of other species of *Aelurodon*. A = *A. aphobus*, A_1 from Merriam (1919), A_{2-3} from MacDonald (1948a); H = A. haydeni (holotype) from Matthew and Cook (1909), H_1 from Webb (1969); I = *A. inflatus* (holotype) from Gregory (1942), I_{1-2} from MacDonald (1960); M_1 = mean of 6 specimens of *A. mortifer* from Kitts (1957); Ma = *A. marshi* (holotype) from Thorpe (1922); P_1 = *A. platyrhinus* from Voorhies (1969); S = *A. saevus* (holotype) from Matthew and Cook (1909), S_1 from Matthew and Gidley (1904), S_2 from Green (1971); T = *A. taxoides* (holotype) from Thorpe (1922), T_1 from Gregory (1942), $T_{2,3,6}$ from MacDonald (1960), $T_{7,8}$ from Webb (1969); TM = *A. taxoides magnus* (holotype) from Thorpe (1922); W = *A. wheelerianus* (holotype) from Matthew and Cook (1909), $W_{1,2,4}$ from Merriam (1919), W_3 from Matthew and Gidley (1904); WA = *A. wheelerianus aesthenostylus* (holotype) from Henshaw (1942). Specimens referred to species of the *A. taxoides* group are designated by an "X"; others are designated by a dot. The range of the *A. saevus* group exclusive of *A. haydeni* (from McGrew, 1944) is shown in yellow. The range of *A. mortifer* (from Kitts, 1957) is shown in blue. UNSM 46815 is designated by a ⊗ . Scale in mm.

Figure 1a. Size range in canine teeth (lower) in *Aelurodon*.

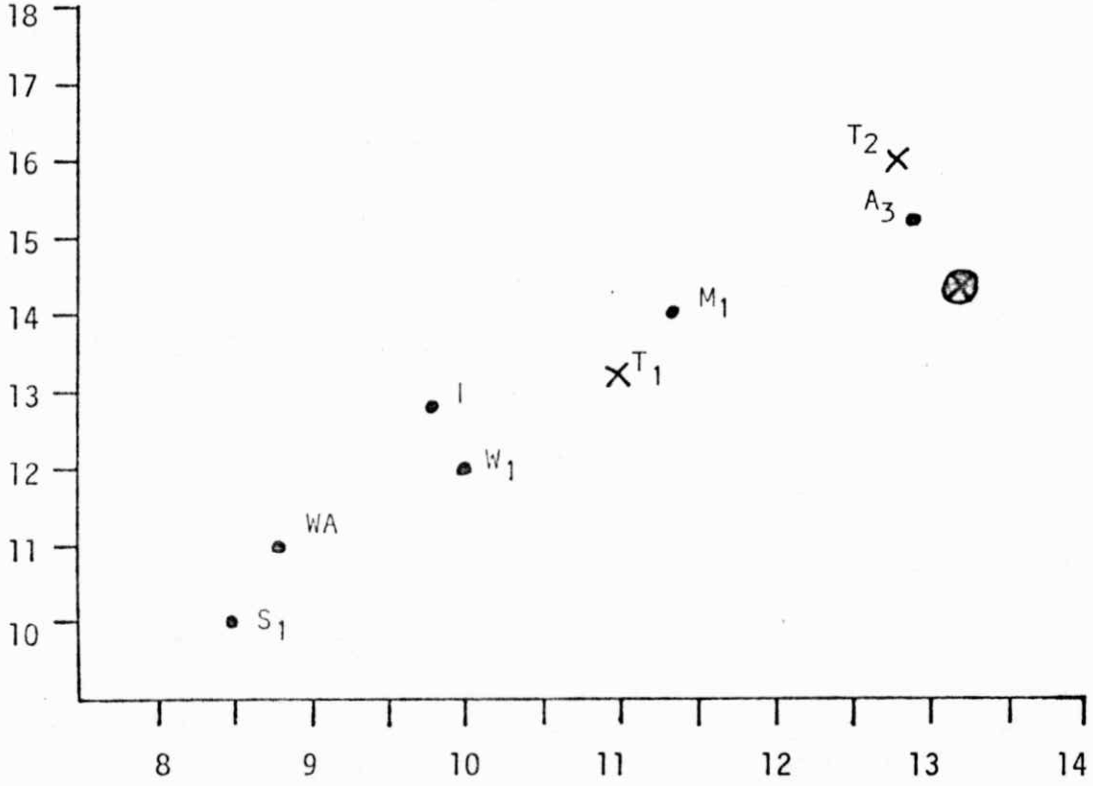
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Figure 1b. Size range in the P_1 of *Aelurodon*.

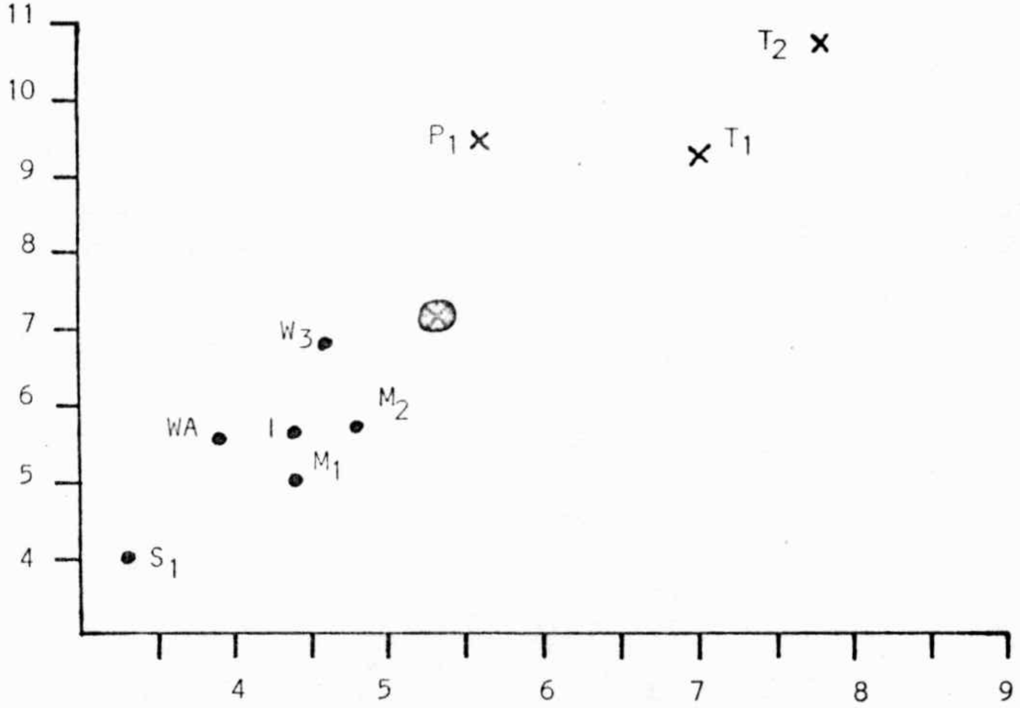

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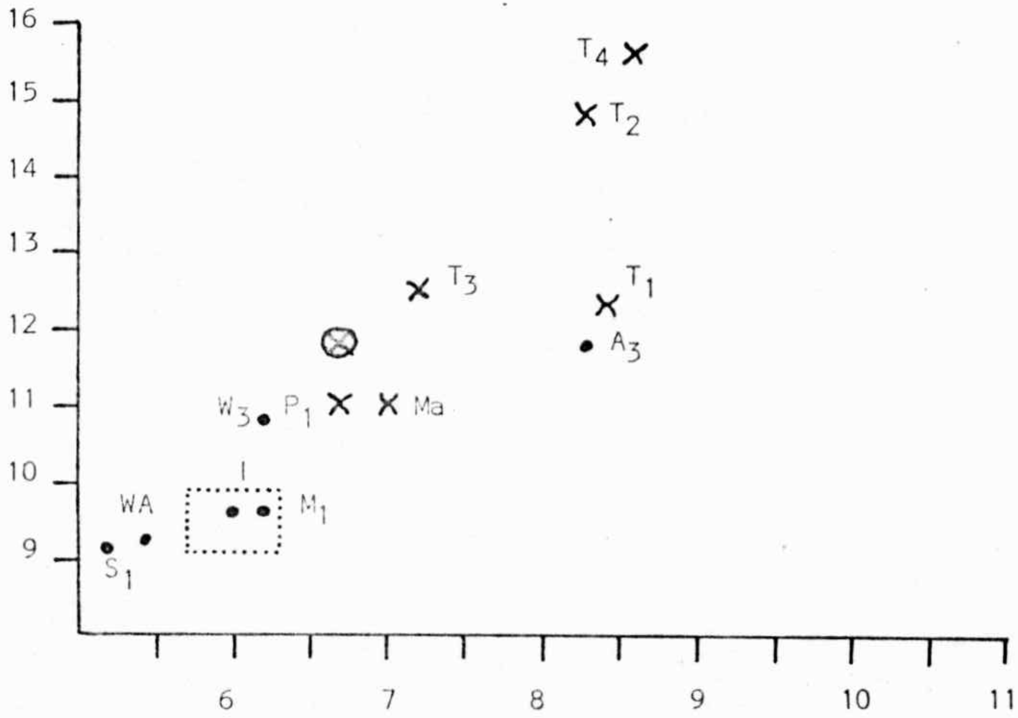
Figure 1c. Size range in the P_2 of *Aelurodon*.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M1
S1

Figure 1d. Size range in the P_3 of *Aelurodon*.

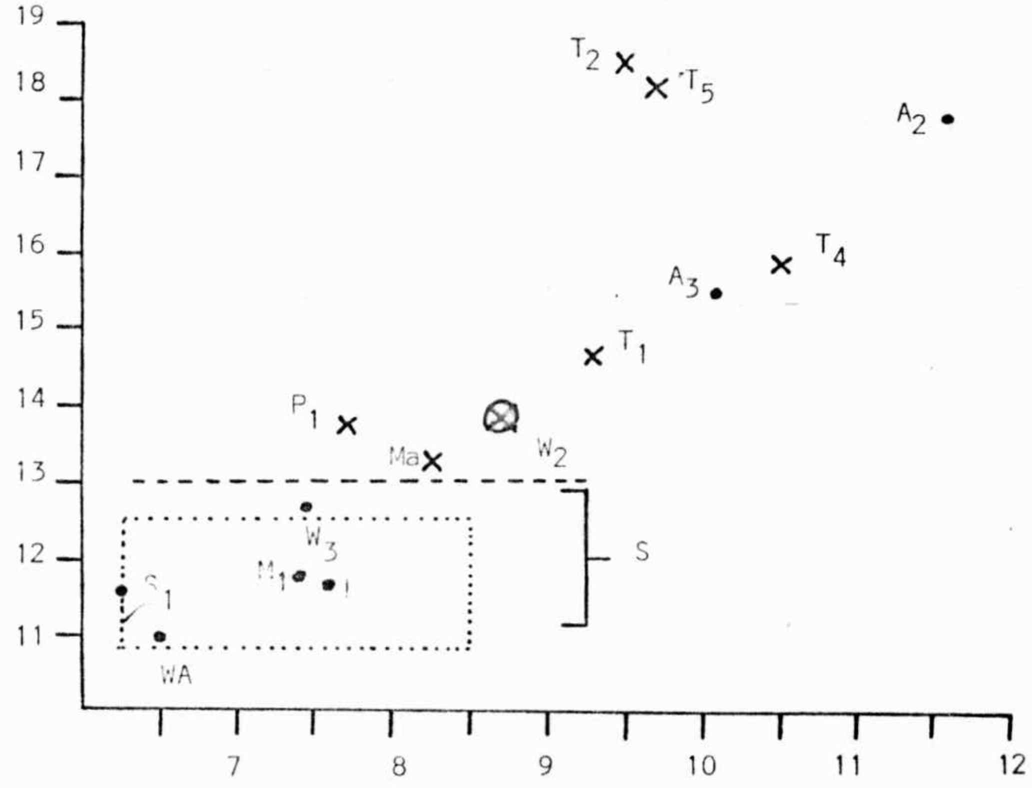
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Figure 1e. Size range in the P_4 of Aelurodon.

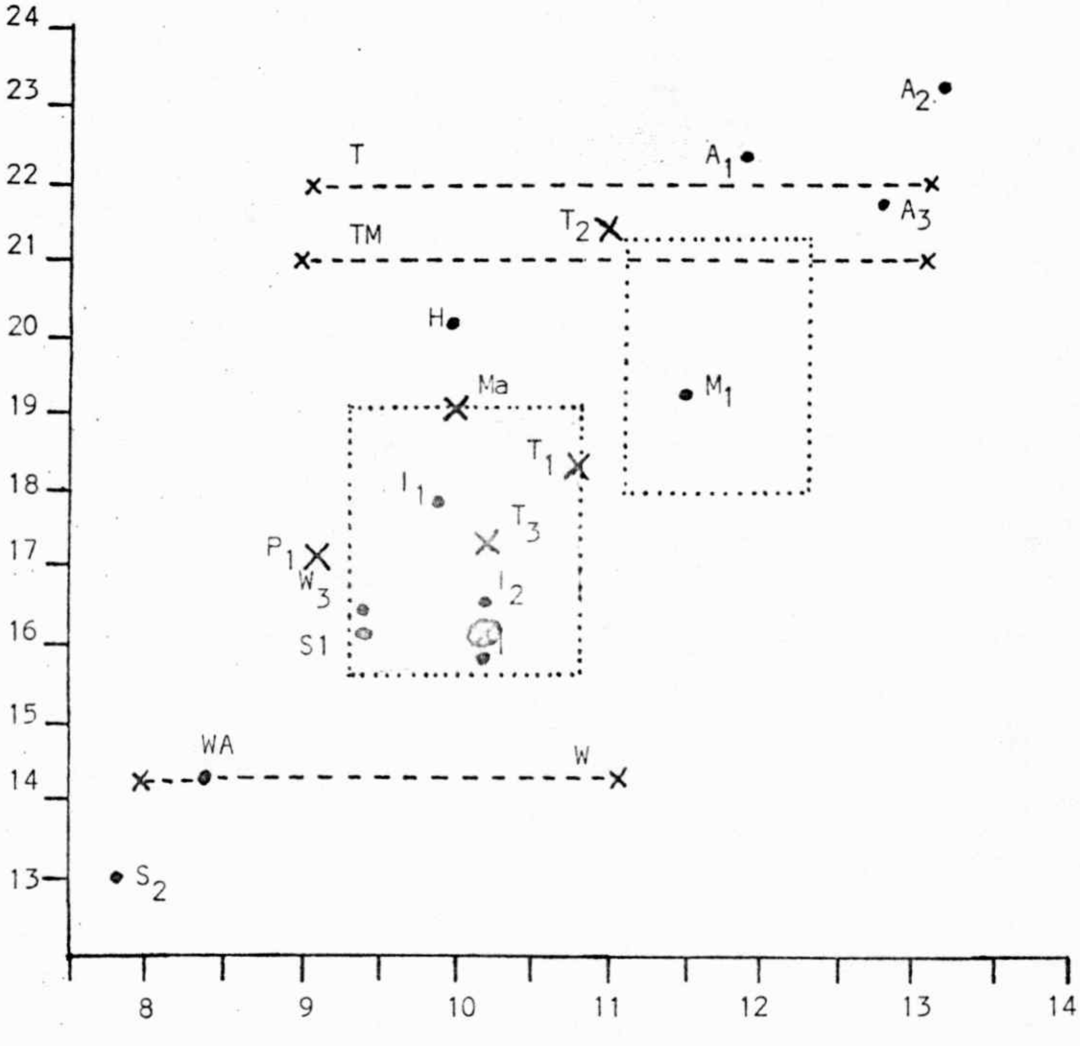
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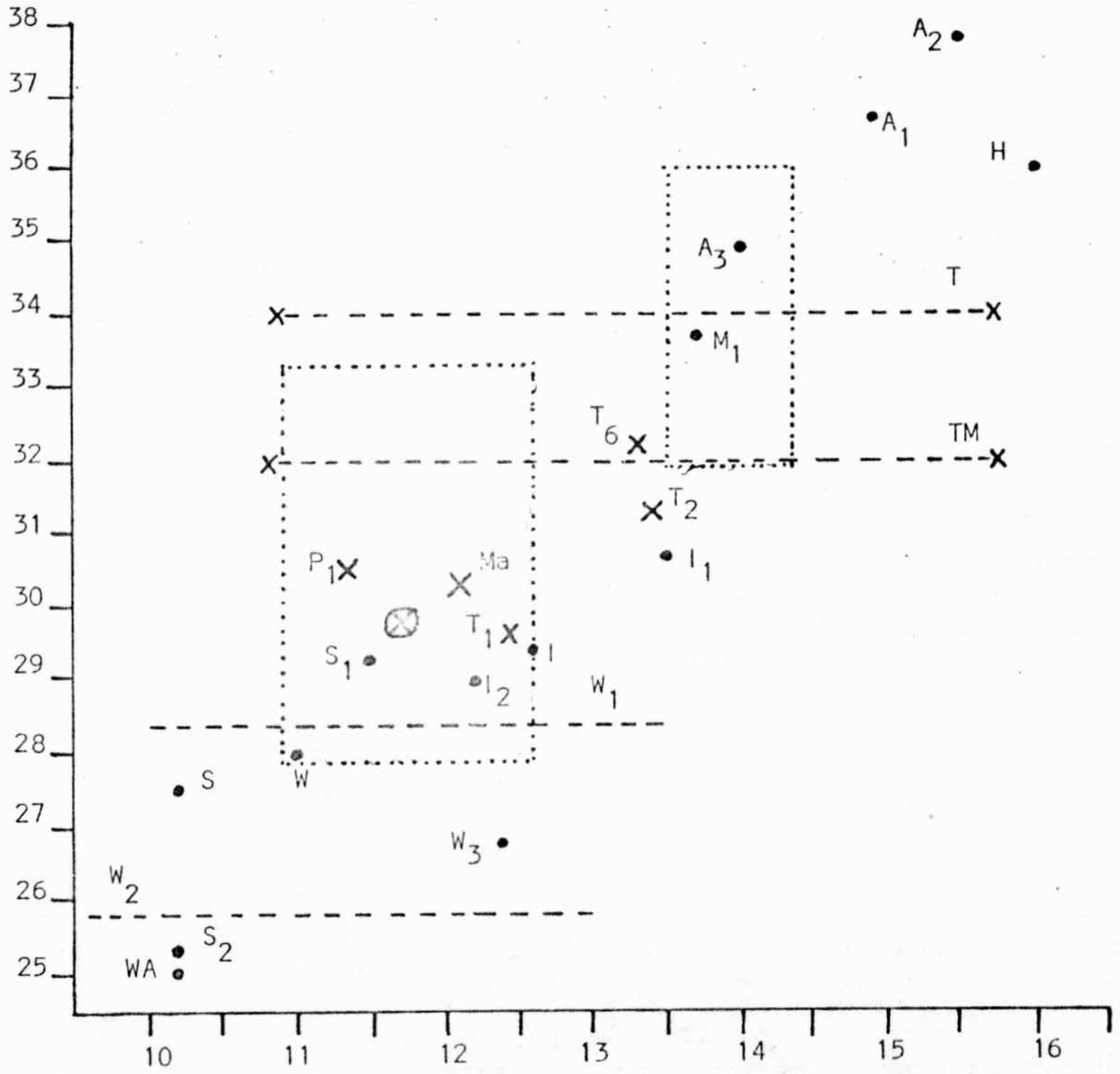
Figure 1f. Size range in the M_1 of <u>Aelurodon</u>.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A2
A1
H
A3
T
M1
T6
TM
T2
I1
P1
Ma
T1
S1
I
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W1
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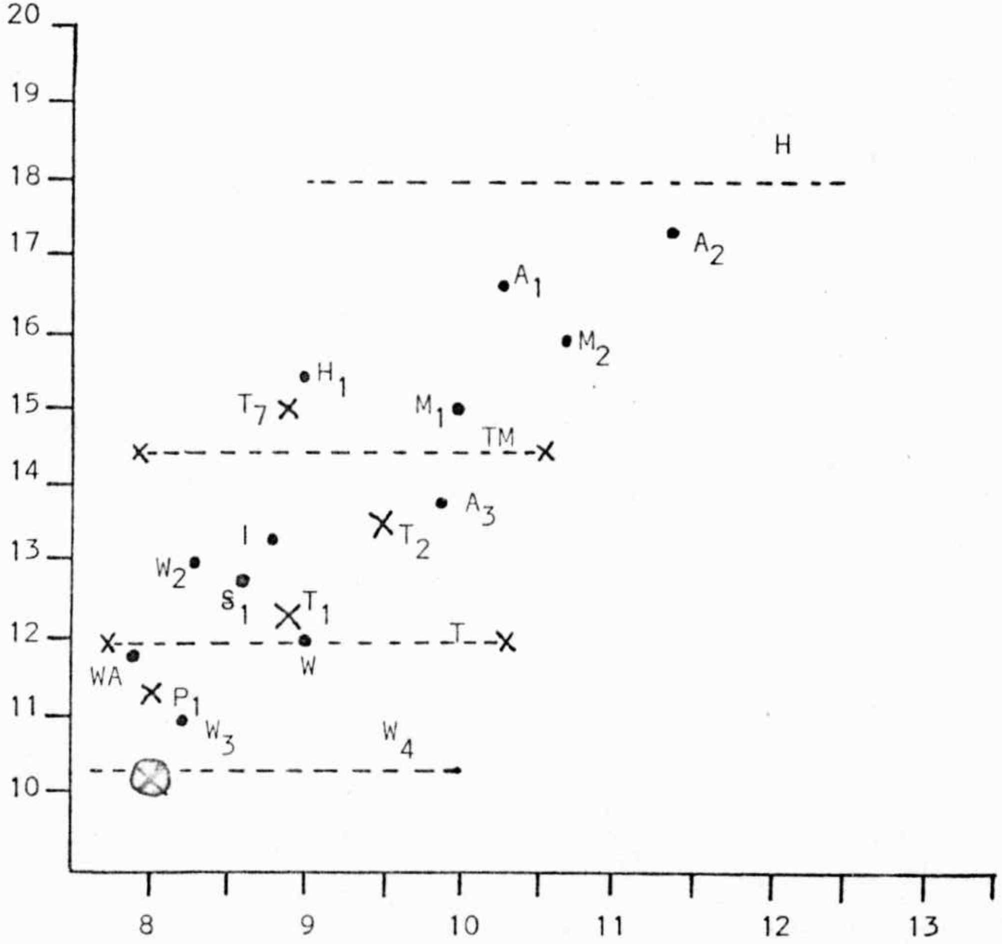
W
W3
W2
S2
WA

Figure 1g. Size range in the M_2 of *Aelurodon*.



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A_2
A_1
M_2
H_1
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M_1
TM
A_3
I
T_2
W_2
S_1
T_1
T
WA
W
P_1
W_3
W_4
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observation that the premolars of the *A. taxoides* group are not reduced in comparison to those of the *A. saevus* group. Although the Knox County specimen falls on the small end of the range of premolar sizes for the *A. taxoides* group, it appears to lie outside the range of the small premolars characteristic of the *A. saevus* group. Based on tooth size alone, UNSM 46815 appears to belong to the *A. taxoides* group.

The following qualitative characters were evaluated to check the results of the above statistical comparisons: relative cusp size and position, and mandibular morphology. The cusps on M_1 and M_2 were compared using descriptions presented by Vanderhoof and Gregory (1940) for *A. saevus* (p. 146), *A. haydeni* (p. 147), and *A. taxoides* (p. 149). The first lower molar of *A. saevus* and *A. haydeni* is characterized as possessing subequal hypoconid and entoconid cusps which enclose a basin. That of *A. taxoides* is described as having a larger and slightly more posteriorly placed hypoconid than entoconid, with a shorter heel on the tooth than is found in the two former species. The M_1 of UNSM 46815 agrees with *A. taxoides* in these characters. The M_2 of *A. taxoides* displays a larger and more anteriorly placed protoconid than metaconid, with a less distinct basin than occurs in *A. saevus* or *A. haydeni*. UNSM 46815 agrees with *A. taxoides* in these characters.

Abrupt anterior tapering of the mandible is characteristic of the *A. saevus* group, while the mandible of the *A. taxoides* group maintains an approximately equal depth throughout its antero-posterior length and possesses a deep angular symphysis (McGrew, 1944, p. 79). The latter contrasts with the characteristically rounded appearance of the symphysis in the *A. saevus* mandible (Vanderhoof and Gregory, 1940, p. 161). The mandible of the Knox County specimen is heavy throughout the entire antero-posterior length and possesses a robust symphysis in having an angular chin rather than a rounded one. This indicates that the general structure of the mandible of UNSM 46815 is of the A. taxoides type.

In separate comparisons of three different groups of characters; tooth size, relative size and position of the cusps of the lower molars, and general mandibular morphology; the Knox County specimen compares most closely with A. taxoides. It seems clear that the affinities of this specimen lie with the A. taxoides group.

The small size of M_2 and lack of M_3 (for whatever reasons) in UNSM 46815 agrees with Mawby's (1964) conclusion that the A. taxoides group is more Canis-like, than the A. saevus group which has affinities with Osteoborus. My use of (Prohyaena)for A. taxoides follows the usage of R. H. Tedford and Beryl Taylor (AMNH) who are currently revising the Borophaginae (personal communication to M. R. Voorhies, 1978). Emphasis on reduction in tooth size in Osteoborus occurred primarily in the anterior premolars (Stirton and Vanderhoof, 1933, p. 175), rather than in the posterior molars. The reverse is true of UNSM 46815.

The large canine of the Knox County specimen (fig. 1a, pl 5) probably in part reflects the lack of reduction in the anterior dentition of members of the A. taxoides group, but the disproportionate size of this tooth in UNSM 46815 in comparison to those of other Aelurodon specimens of equivalent size, may indicate that canine size was a sexually dimorphic character in the Knox County population. Unfortunately, although most of the appendicular skeletal material was found with UNSM 46815, there is no trace of a baculum with the specimen. Without a larger population sample it cannot be determined whether the unusually large canine of this specimen reflects individual variation, sexual dimorphism, or both.

SKELETAL DESCRIPTION

Tables 1-9 provide detailed comparisons of the appendicular skeleton of UNSM 46815 with that of the wolf and spotted hyena. Features of A. (Prohyaena) taxoides are grouped into three catagories: 1) C. lupus-like, 2) C. crocuta-like, and 3)different from both. Features which are common to all three species are not listed. Emphasis is placed on features which are useful in determining the lifestyle of A. taxoides.

FRONT LIMB

Humerus (Table 1; Pl. 7; Fig. 2)

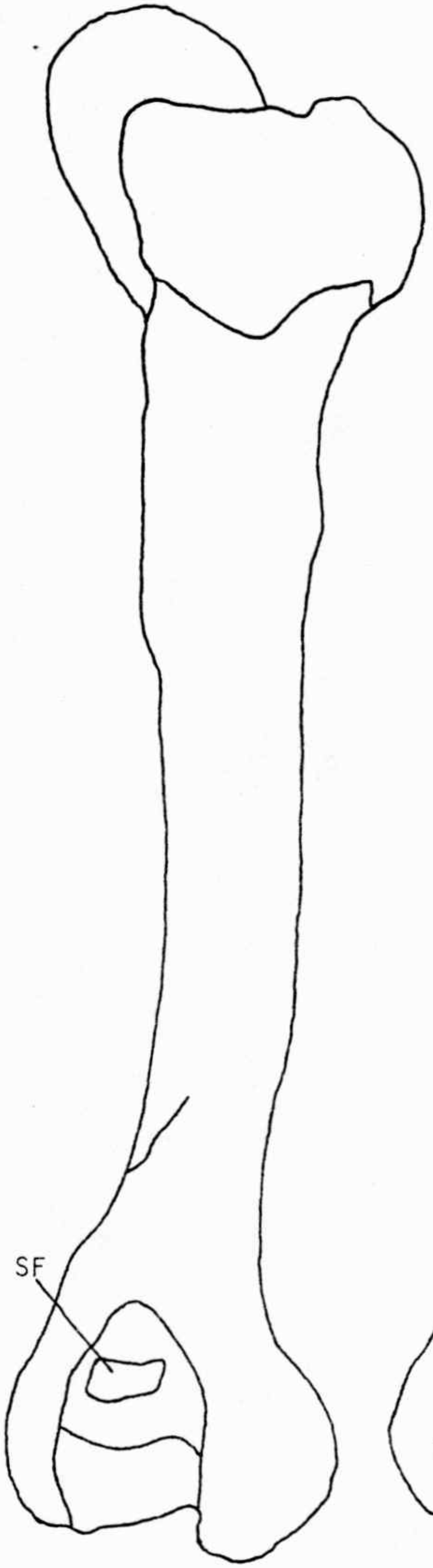
The heavy shaft of the A. taxoides humerus is similar to that of C. crocuta and greatly differs from the thin-shafted C. lupus humerus. It is interesting to note that Hildebrand (1954, p. 434) stated that two characters which distinguish the Canidae are the lack of an entepicondylar foramen and the presence of a supratrochlear foramen, while both humeri of UNSM 46815 possess an ent epicondylar foramen and lack the supratrochlear foramen. Presence or absence of a supratrochlear foramen appears to be a variable characteristic in A. taxoides, since a humerus referred to Aelurodon sp. from Verdigre Quarry in Knox County, Nebraska (Voorhies, 1969) has a distinct supratrochlear foramen. Miller, et. al. (1964, p. 69) state that the supratrochlear foramen is sometimes lacking from humeri of small individuals of Canis familiaris. The presence, of the entepicondylar foramen in A. taxoides is considered to be a primitive feature by Vanderhoof and Gregory (1940, p. 161).

Table 1. Comparison of features of the humerus.

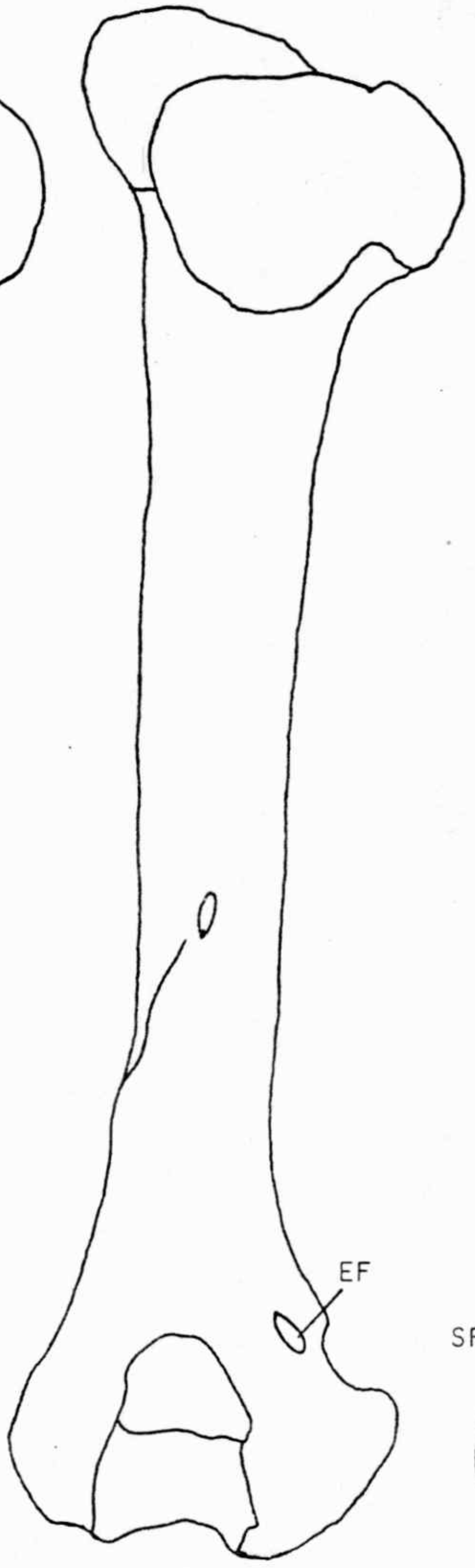
	FEATURE	C. crocuta	A. (P.) taxoides	C. lupus	FUNCTIONAL IMPLICATION IN AELURODON
Canis-like Features	Position of lateral epicondyloid crest	More medially directed, no nutrient foremen on caudal surface	Proximally directed, ending at nutrient foramen	Proximally directed, ending at nutrient foramen	Not known
	Shaft thickness	Heavy	Heavy	Slender	Greater support for heavy body
Crocuta-like Features	Width of olecranon fossa	Wide	Wide	Narrow	Accomodates wide proximal surface of trochlear notch of ulna
	Size of head relative to shaft	Large	Large	Small	Not known
	Size of greater tubercle	Large, high	Large, high	Moderate size and height	Not known
	Humeroradial index	112	94	105	Less cursorial than the other two species
Features Distinct From Canis or Crocuta	Size of proximal portion of lateral epicondyloid crest	Weak	Prominent	Weak	Large m. brachioradialis indicates ability to rotate forearm dorsolaterally
	Entepicondylar foramen	Absent	Distinct foramen present	Absent	Not known
	Supratrochlear foramen	Present	Absent*	Present	

*Present in some Aelurodon specimens in UNSM collections

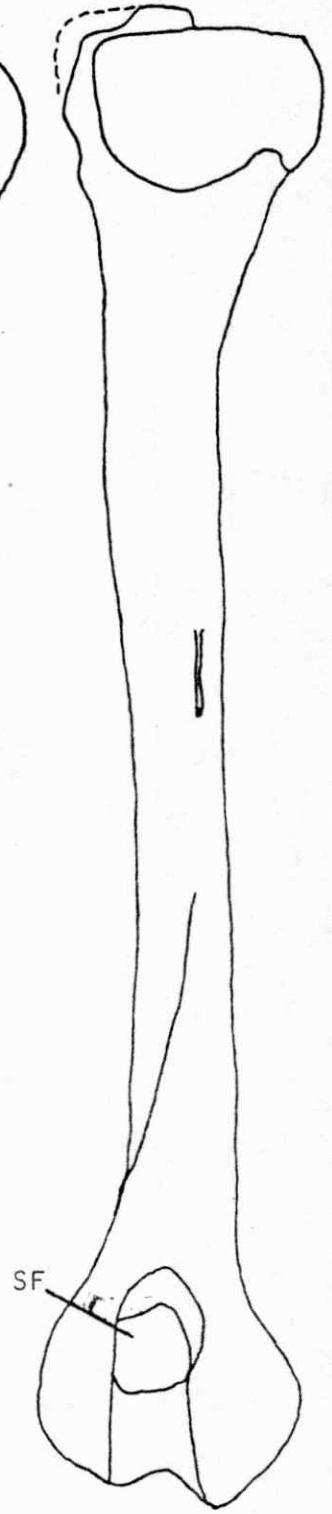
Figure 2. Proportions of humeri after equi-length adjustment made. EF- entepicondylar foramen, SF- supratrochlear foramen.



C. *crocuta*



A. (*P*) *taxoides*



C. *lupus*

Radius (Table 2; Pl. 8; Fig. 3)

The radius of *A. taxoides* is different from that of both *C. lupus* and *C. crocuta*, not only morphologically, but also in its length relative to the humeral length. In *A. taxoides*, the radius is shorter than the humerus, while in the other two species it is longer. Less obvious differences are present in the size of muscle attachments, implying that there were related differences in muscle size and use. The radial tuberosity which is the point of insertion for the distal tendon of the m. biceps brachii is distinctly larger in *A. taxoides* than in *C. lupus* or *C. crocuta*. A distinct ridge is present on the shaft of the *A. taxoides* radius at the point of insertion for the m. supinator. The same area on the shafts of *C. lupus* and *C. crocuta* is smooth, implying that the m. supinator in these species is smaller than that of *A. taxoides*. The m. pronator teres also appears to have been larger than that of *C. lupus* and *C. crocuta* for the same reasons. The insertion of the interosseous ligament occupies only 1/6 of the shaft length in *A. taxoides*, but extends for 1/3 the length of the *C. lupus* shaft and 2/3 of the shaft of *C. crocuta*. The manner of articulation between the distal ends of the radius and ulna is quite different in *A. taxoides* from that of *C. lupus* and *C. crocuta*. The ulnar notch facet is oriented proximo-laterally at a 45° angle in the former, while in the latter two species it is vertical.

Ulna (Table 3; Pls. 9, 10A; Fig. 4)

The ulna of *A. taxoides* resembles that of *C. crocuta* in general structure, but there are distinct differences in detailed structure. Similarities with *C. crocuta* include a robust shaft and distal end. The proximal surface of the olecranon process of *A. taxoides* resembles that of *C. lupus* (and *C. latrans*) in possessing a deep antero-

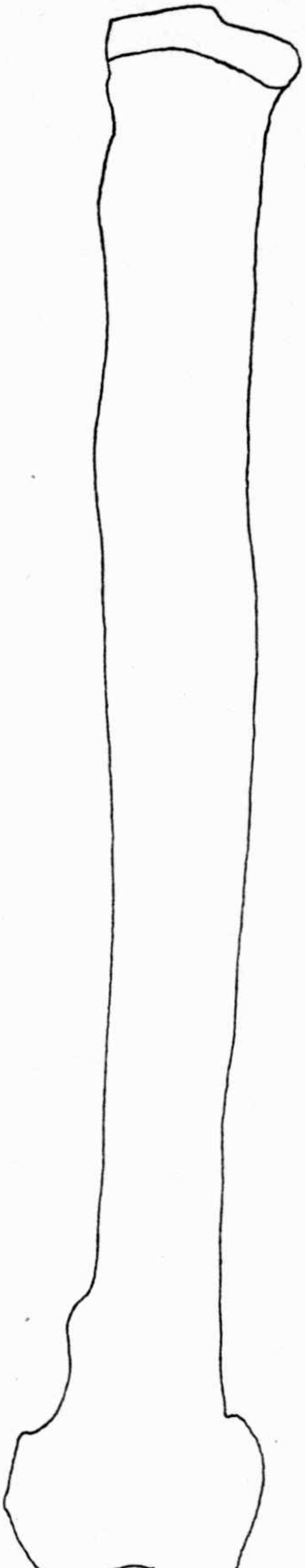
Table 2. Comparison of features of the radius.

	FEATURE	*C. crocuta*	*A.* (*P.*) *taxoides*	*C. lupus*	FUNCTIONAL IMPLICATION IN *AELURODON*
Canis-like Features	Largest tendinal attachment on distal end	Tendon of m. extensor digitorum communis	Tendon of m. extensor carpi radialis	Tendon of m. extensor carpi radialis	Priority on extension of the carpal joint and flexion of the elbow joint, rather than extension of the digits
	Size of process at proximal end of radial head	Very small	Prominent	Prominent	Not known
Crocuta-like Features	Arc of radial articular circumference	260°	270°	125°	Freer movement of the radius of *Aelurodon*
Features Distinct From *Canis* or *Crocuta*	Relation to length of humerus	Longer	Shorter	Longer	Less cursorial than other two species
	Ratio of transverse to anteroposterior diameter	2:1	1.5:1	2.5:1	Less blade-like shaft due to lack of cursorial specialization
	Size of radial tuberosity	Small	Large	Small	Large distal tendon of m. biceps brachii may indicate ability of forearm supination
	Size of prominence lateral to radial tuberosity	Small	Large	Small	Large cranial crus of ulnar collateral ligament provides point of insertion for large proximal tendon of m. supinator may indicate forearm rotational ability
	Area of insertion of m. supinator on proximal portion of shaft	Smooth	Low ridge present	Smooth	Well developed m. supinator indicates ability to rotate palm medially

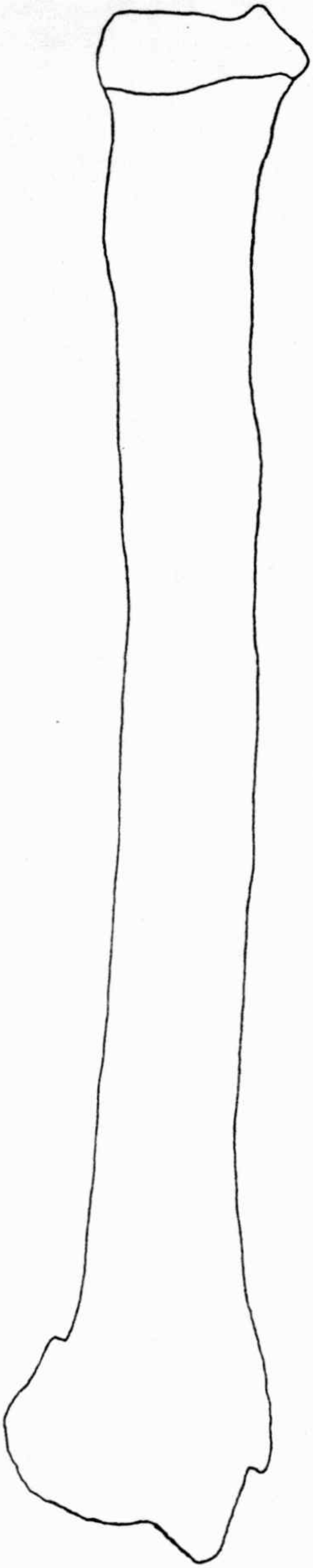
Table 2. (Continued)

	FEATURE	*C. crocuta*	*A. (P.) taxoides*	*C. lupus*	FUNCTIONAL IMPLICATION IN *AELURODON*
Features Distinct From *Canis* or *Crocuta*	Area of insertion of m. pronator teres	Roughened but lacks ridge	Low ridge present	Roughened but lacks ridge	Well developed m. pronator teres indicates ability to rotate dorsal forearm medially
	Length of insertion of inter osseous ligament	2/3 shaft	1/6 shaft	1/3 shaft	Radius and ulna not as tightly bound as in other two species
	Orientation of ulnar notch facet	Vertical	45° angle facing proximo-laterally	Vertical	Allows sliding articulation with ulna and provides support for weight transmitted through ulna
	Length of styloid process	Long, stout	Moderate, thin	Short, thin	Less cursorially specialized than *C. lupus*
	Shape of ulnar notch facet	Concave	Flat	Concave	Not known

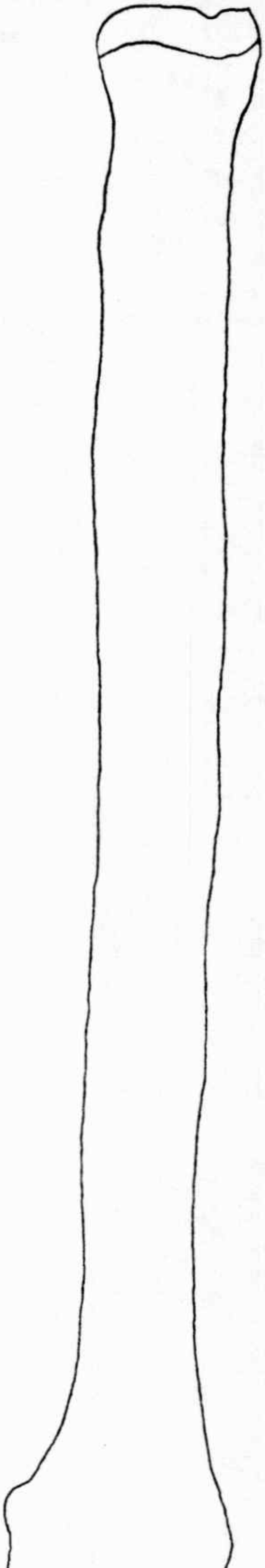
Figure 3. Proportions of radii after equi-length adjustment made.



C. crocuta



A. (*P.*) *taxoides*

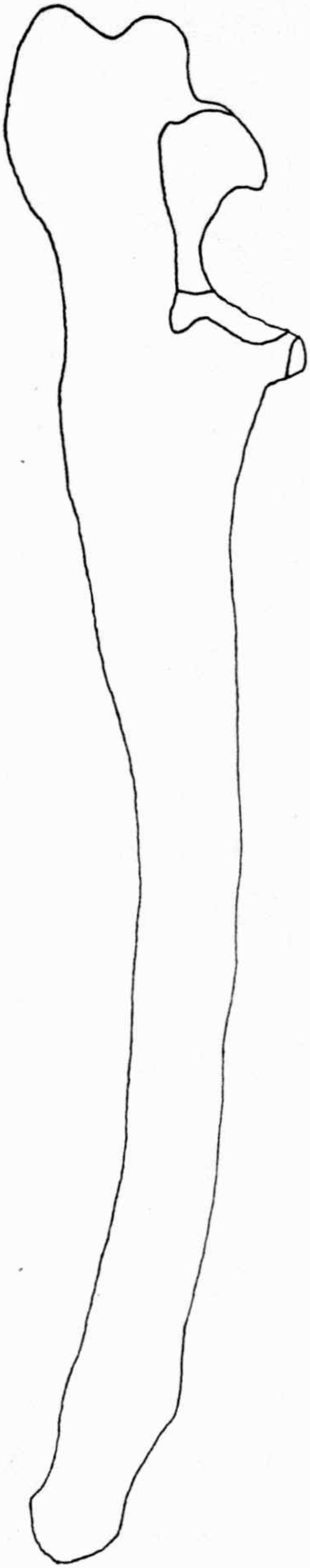


C. lupus

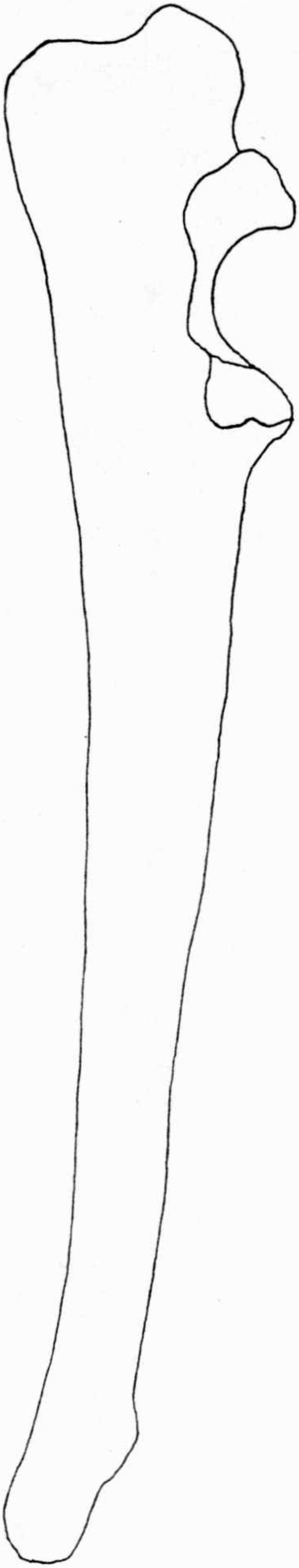
Table 3. Comparison of features of the ulna.

	FEATURE	*C. crocuta*	*A.* (*P.*) *taxoides*	*C. lupus*	FUNCTIONAL IMPLICATION IN *AELURODON*
Canis-like Features	Deep grove on proximal surface of olecranon process	Absent	Present	Present	Not known
	Height to width ratio of articular surface of radial notch	1/4	1/2	1/2	Not known
Crocuta-like Features	Shaft thickness	Stout	Stout	Slender	Greater support for heavy body
	Proportions of distal end	Robust	Robust	Slender	Thicker wrist correlated with heavy limbs
	Robustness of olecranon process	Very robust	Very robust	Moderately robust	Not known
	Orientation of olecranon process	Proximally directed	Proximally directed	Proximo-caudally directed	Not known
	Lateral articular surface of trochlear notch	Slightly notched	Slightly notched	Stongly notched	Not known
Features Distinct From *Canis* or *Crocuta*	Shaft curvature	Bowed	Straight	Bowed	Less cursorial than other two species
	Length interosseous crest/ length of ulna (minus olecranon process) X 100	84	17	38	Short interosseous ligament allows rotation of forearm
	Orientation of articular circumference facet	Vertical	45° angle facing cranio-distally	Vertical	Sliding articulation with radius allows rotation of forearm
	Facet on styloid process	Present	Absent	Present	Ulna does not articulate with cuneiform
	Groove distal to medial lip of trochlear notch	Absent	Deep	Shallow	Not known

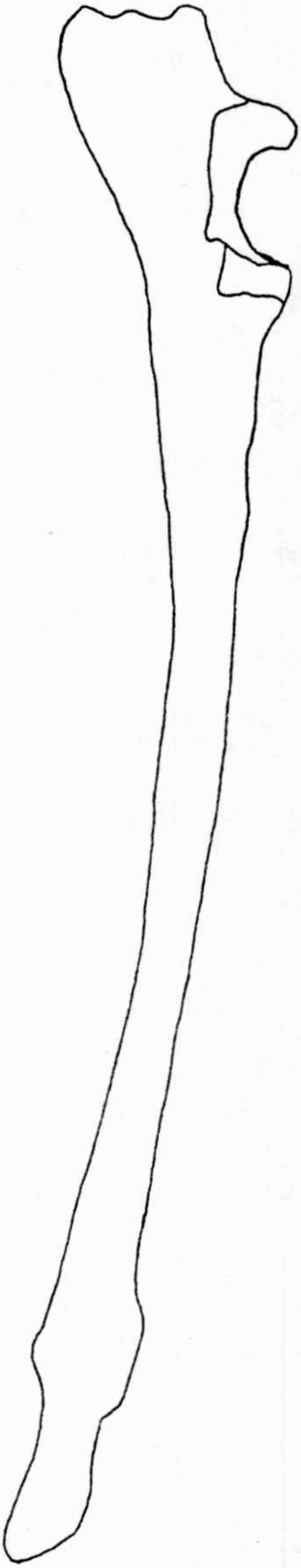
Figure 4. Proportions of ulnae after equi-length adjustment made (length of shaft from distal edge of semi-lunar notch to distal end of ulna equalized).



C. *crocuta*



A. (*P*.) *taxoides*



C. *lupus*

posteriorly directed groove (pl. 10A). A latero-medially directed and much shallower groove occupies the same area on the olecranon process of C. crocuta. The ulna of A. taxoides also has several features distinct from both C. lupus and C. crocuta. The shaft is nearly straight in the former species, but bowed in the latter two species. The interosseous crest is quite short in A. taxoides, of moderate length in C. lupus, and very long in C. crocuta. As mentioned above, the manner of distal radio-ulnar articulation is distinctly different in A. taxoides from that of the other two species. The articular circumference facet is oriented at a 45° angle and faces cranio-distally, while those of both C. lupus and C. crocuta are vertical and face cranially.

Forefoot (Pl. 17A-H)

The forefeet of UNSM 46815 are only partially preserved, therefore comparisons are confined to general morphology. The pisiform of A. taxoides is similar to that of C. crocuta in having a wide, deep facet on the dorsal surface for articulation with the styloid process of the ulna. This facet on the pisiform of C. lupus is narrow and shallow. The metacarpals of A. taxoides resemble those of C. crocuta in being straight and robust. The metacarpals of C. lupus are more slender and the distal ends of the second and fifth flare laterally. The third and fourth metacarpals of A. taxoides are distinctly shorter relative to total limb length (15%), than those of C. lupus (17%), or C. crocuta (18%).

Hind Limb

Innominate (Table 4; Pl. 10 B, C)

The innominate of A. taxoides is nearly equal in size to that of C. lupus, although the former is more robust. A. taxoides is also

[redacted]

Table 4. Comparison of features of the innominate.

	FEATURE	*C. crocuta*	*A.* (*P.*) *taxoides*	*C. lupus*	FUNCTIONAL IMPLICATION IN *AELURODON*
Canis-like Features	Fossa between ventral part of acetabular fossa and lunate surface	Present	Absent	Absent	Not known
	Shape of ischial tuberosity	Sub-circular	Oblong	Oblong	Not known
Crocuta-like Features	Orientation of acetabular fossa	45° from vertical	45° from vertical	Slightly anteriorly oriented	Not known
Features Distinct From *Canis* or *Crocuta*	Thickness of base of ilium anterior to acetabulum	Moderately thick	Thick	Thin	Body more massive than that of *C. lupus* and m. iliacus larger than in *C. crocuta* or *C. lupus*
	Position of ventral border of auricular surface	Above acetabulum	Nearly on horizontal plane with acetabulum	Above acetabulum	Less cursorially specialized than the other two species
	Width of ischial surface posterior to obturator foramen	Narrow	Wide	Very wide	M. obturator externus larger than that of *C.* but not as large as that of *C. lupus*
	Relief of iliopectinal emminence	Low	High	Low	Not known
	Shape of obturator foramen	Sub-circular	Intermediate	Oblong	Not known

similar to C. lupus in having a wide (but not as wide as the latter) ischial surface posterior to the obturator foramen, indicating a large area of origin for the m. obturator externus. This area is narrow in the C. crocuta pelvis. A. taxoides differs from both C. lupus and C. crocuta in having the ventral surface of the sacrum positioned on a horizontal plane with the acetabulum, as indicated by the ventral border of the auricular surface. The sacra of C. lupus and C. crocuta are positioned dorsal to the level of the acetabulum.

Femur (Table 5; Pl. 11; Fig. 7)

The femur of A. taxoides is similar to that of C. crocuta in having a robust shaft and a wide but only moderately deep patellar groove. The C. lupus femur has a slender shaft and a deep and narrow patellar groove. A. taxoides differs from both C. lupus and C. crocuta in displaying only a slight bow in the shaft, as compared to the distinct curvature present in the shafts of the latter two species; and having a larger lesser trochanter for insertion of the m. iliopsoas

Patella (Pl. 13 C)

The patellae of A. taxoides, C. lupus, and C. crocuta are not significantly different.

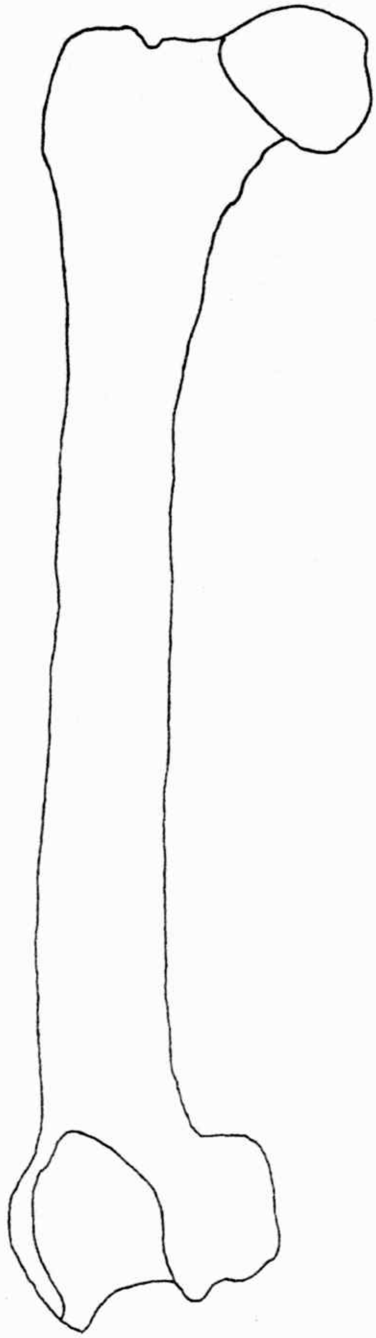
Tibia (Table 6; Pl. 12; Fig. 8)

As is true of the other long bones, the general structure of the A. taxoides tibia resembles that of C. crocuta more closely than that of C. lupus. Tibiae of the former two species have robust, straight shafts, large proximal ends, and are distinctly shorter than the femora with which they articulate. The tibia of C. lupus has a slender, curved shaft, a small proximal end, and is longer than the femur.

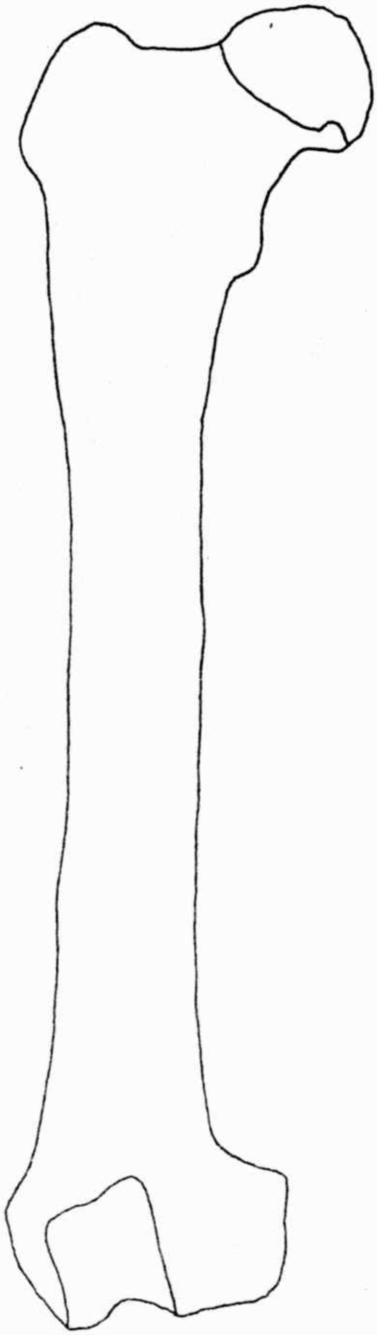
Table 5. Comparison of features of the femur.

	FEATURE	*C. crocuta*	*A. (P.) taxoides*	*C. lupus*	FUNCTIONAL IMPLICATION IN *AELURODON*
Crocuta-like Features	Femorotibial index	79	84	104	Less cursorial than *C. lupus*
	Thickness of shaft	Robust	Robust	Slender	Support for heavier body than that of *C. lupus*
	Depth of patellar groove	Moderately deep, wide	Moderately deep, wide	Deep, narrow	Less cursorial than *C. lupus*
	Position of facet for medial fabella	Not continuous with condyle, antero-medially positioned facing proximo-medially	Not continuous with condyle, antero-medially positioned facing proximo-medially	Adjacent and continuous with medial condyle, faces proximally	Not known
Features Distinct From *Canis* and *Crocuta*	Curvature of shaft	Bowed	Slightly bowed (distal end)	Bowed	Less cursorial than other two species
	Size of lesser trochanter	Moderate	Large	Small	M. iliopsoas stronger than in other two species
	Morphology of lateral supracondylar tuberosity	Flat roughened square	Pimple-like protuberence	Flat roughened rectangle	Not known
	Size of lateral supracondylar tuberosity	1.5 x 1.5 cm	.5 cm diameter, .5 cm height	2 x 1 cm	Not known

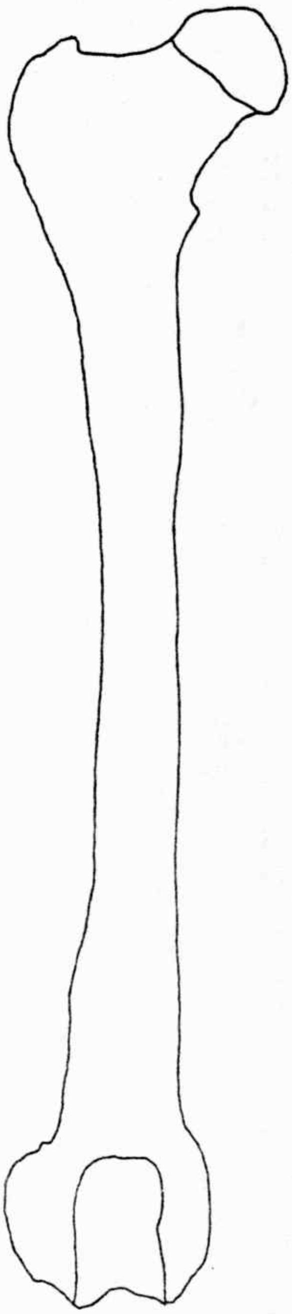
Figure 5. Proportions of femora after equi-length adjustment made.



C. *crocuta*



A. (*P*.) *taxoides*

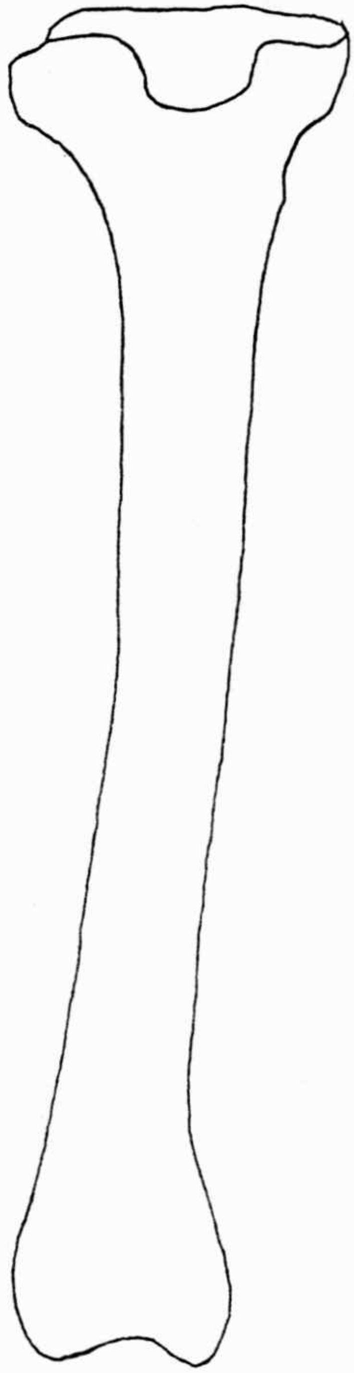


C. *lupus*

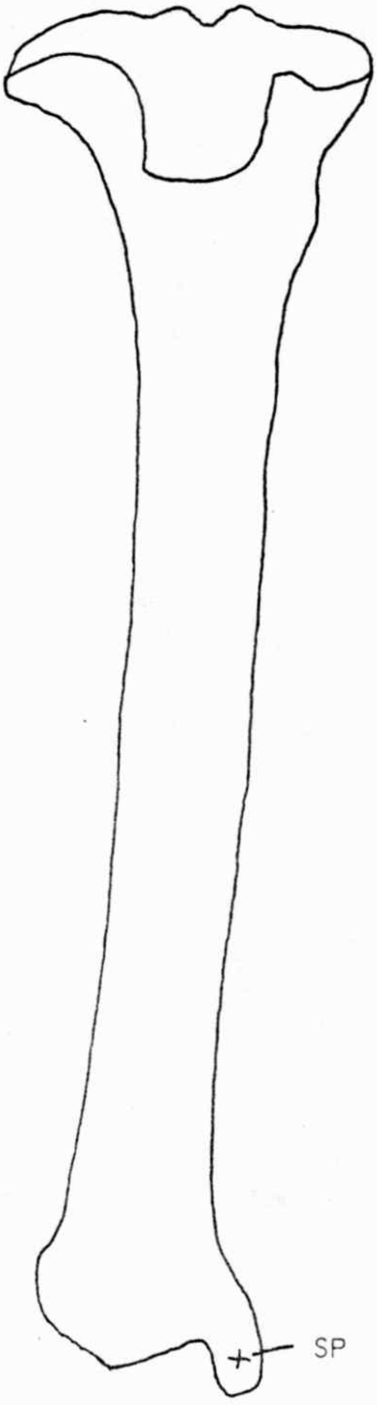
Table 6. Comparison of features of the tibia.

	FEATURE	*C. crocuta*	*A.* (*P.*) *taxoides*	*C. lupus*	FUNCTIONAL IMPLICATION IN *AELURODON*
Canis-like Features	Shape of tibial tuberosity	Squared-off	Rounded	Rounded	Not known
	Length of medial malleolus	Short	Long	Long	Not known
	Depth of cochlea tibiae	Shallow	Moderately deep	Deep	Not known
	Size of facets for distal articulation with the fibula	Lateral-small Distal-large	Lateral-large Distal-small	Lateral-large Distal-small	Not known
Crocuta-like Features	Relative length of tibia to length of femur	Shorter	Shorter	Longer	Less cursorial than *C. lupus*
	Shaft thickness	Robust	Robust	Slender	Support for heavier body than that of *C. lupus*
	Size of proximal end	Large	Large	Small	More massive upper hind limb than that of *C. lupus*
	Size of facet for proximal articulation with fibula	Large	Large	Small	Fibula less reduced than that of *C. lupus* due to less cursorial habits
	Tibial crest	Long	Long	Moderately long	Muscles more distally positioned than those of *C. lupus* indicating less cursorial specialization
Features Distinct From *Canis* and *Crocuta*	Tibioradial index	117	98	91	Lower limb elements in more generalized proportions than cursorially specialized limbs of *C. crocuta* (anteriorly elongated) or *C. lupus* (posteriorly elongated)
	Sulcus muscularis	Absent	Deep, narrow	Shallow, wide	Not known

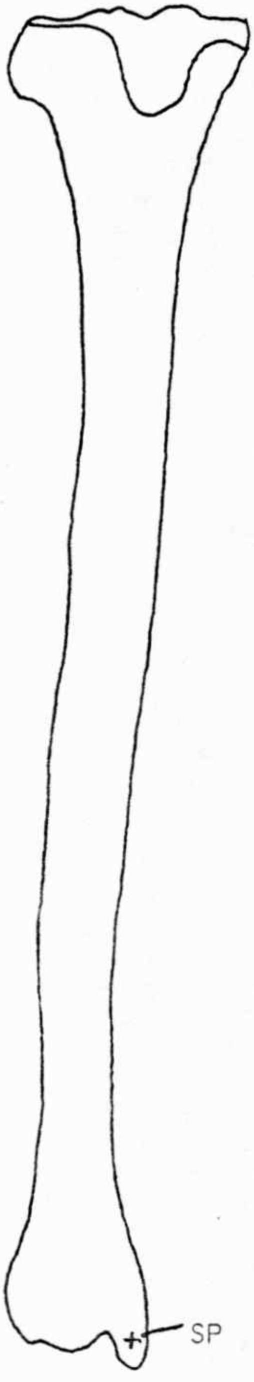
Figure 6. Proportions of tibiae after equi-length adjustment made.
SP- styloid process.



C. crocuta



A. (*P.*) *taxoides*



C. lupus

Fibula (Table 7; Pl. 13 A, B)

The fibula is in a reduced state in all three species, but the shafts of the *A. taxoides* and *C. crocuta* fibulae are distinctly less reduced than is the thin, flat shaft of *C. lupus*. The wide area of proximal articulation with the tibia in the *A. taxoides* fibula, shows that of the three, this species has undergone the least amount of fibular reduction.

Hindfoot (Table 19; Pl. 14-16)

Complete right hind feet (minus phalanges) are present in both UNSM 46815 and UNSM 4476, allowing an unusual opportunity to compare these structures. The tarsals of *A. taxoides* are very similar to those of *C. lupus*, although the calcaneal tuber is more elongate in the calcaneum of the latter. The tarsals of *C. crocuta* are generally more robust than those of *A. taxoides* or *C. lupus*. The lack of an interlocking articulation between the medial surface of the cuboid with the lateral surfaces of the navicular and cuneiform is a trait shared by *A. taxoides* and *C. crocuta*; but not *C. lupus* which possesses an interlocking fit.

A. taxoides and *C. crocuta* both possess short, straight, and robust metatarsals. The metatarsals of *C. lupus* are long and thin, and metatarsals II and V flare outward at their distal ends. The proximal breadth of the metatarsal bones (ankle) in *A. taxoides* and *C. crocuta* is nearly equal to the distal breadth, while the ankle of *C. lupus* is constricted relative to the width of the distal ends of the metatarsals. The length of metatarsal I in *A. taxoides* is 1/2 that of metatarsal II, while in *C. lupus* and *C. crocuta*, it is 1/7 and 1/9, respectively.

Table 7. Comparison of features of the fibula.

	FEATURE	*C. crocuta*	*A. (P.) taxoides*	*C. lupus*	FUNCTIONAL IMPLICATION IN *AELURODON*
Canis-like Features	Shape of proximal articular facet	Sub-circular	Oblong	Oblong	Not known
	Size of lateral malleolus	Large	Moderate	Moderate	Not known
	Orientation and size of distal articular facets	Proximal facet large medially directed facet small	Proximal facet small, medially directed facet large	Proximal facet small, medially directed facet large	Not known
Crocuta-like Features	Amount of reduction of bone size	Moderate	Moderate	Highly reduced	Less cursorially specialized in hind limb than *C. lupus*
	Shaft cross-section measurements	6.8 x 5.3mm	6.8 x 5.4mm	4.0 x 2.1mm	"
Features Distinct From *Canis* and *Crocuta*	Width proximal end	Narrow	Wide	Narrow	Less cursorially specialized than *C. crocuta* and *C. lupus*
	Shape of shaft in cross-section	Rounded	Oval-shaped	Flattened	Less reduced than in *C. crocuta* and *C. lupus*

Table 8. Comparison of features of the tarsals.

	FEATURE	*C. crocuta*	*A.* (*P.*) *taxoides*	*C. lupus*	FUNCTIONAL IMPLICATION IN *AELURODON*
Canis-like Features	Morphology of proximal trochlea of astragalus	Wide with shallow groove	Narrow with deep groove	Narrow with deep groove	Not known
	Morphology of proximal end of calcaneal tuber	Oval, not grooved	Sub-circular, grooved	Sub-circular, grooved	"
	Facies articularis cuboidea of calcaneum	Flat	Shallowly concave	Shallowly concave	"
	Morphology of sulcus tendinus fibularis longi of cuboid	Shallow, not seen in cranial view	Very deep, seen in cranial view	Deep, seen in cranial view	"
	Shape of cuboid	Slightly elongate	Elongate	Elongate	"
	Position of planter process of navicular	Medial	Lateral	Lateral	"
	Position of groove adjacent to planter process of navicular	Lateral, directed toward cuboid	Medial, directed toward internal cuneiform	Medial, directed toward internal cuneiform	"
	Planter process of internal cuneiform	Absent	Present	Present	"
	Position of planter process of external cuneiform	Medial	Proximal	Proximal	"

Table 8. Continued.

	FEATURE	*C. crocuta*	*A. (P.) taxoides*	*C. lupus*	FUNCTIONAL IMPLICATION IN *AELURODON*
Crocuta-like Features	Morphology of facet on middle articular surface of astragalus	Wide, right angled	Wide, right angled	Narrow, nearly flat	Not known
	Orientation of long axis of head of astragalus	Horizontal	Horizontal	45° above horizontal	"
	Orientation of calcaneal facies articularis talaris media	Facets face cranially and proximally	Facets face cranially and proximally	Cranially facing facet only	"
	Robustness of internal cuneiform	Moderately thick	Moderately thick	Thin	"
	Size of planter process of external cuneiform	Large	Large	Small	"
Features Distinct From *Canis* and *Crocuta*	Shaft size of calcaneal tuber	Robust	Moderately thick	Slender	"
	Size of calcaneal facies articularis talaris distalis	Small	Large	Small	"
	Calcaneal facet for articulation with navicular	Present	Absent	Present	"
	Facet on navicular for articulation with calcaneum	Present	Absent	Present	"

[redacted]

Table 9. Comparison of features of the metatarsals.

	FEATURES	*C. crocuta*	*A.* (*P.*) *taxoides*	*C. lupus*	FUNCTIONAL IMPLICATION IN *AELURODON*
Crocuta-like Features	Shape of metatarsals	Short, wide and straight	Short, wide and straight	Long and narrow, mt. II and IV curve outward distally	Short, wide foot for support of heavier body, and foot less cursorially specialized than that of *C. lupus*
	Width across distal ends of metatarsals/width across proximal ends of metatarsals X 100	111	114	127	Thicker wrist indicative of less cursorial specialization than *C. lupus*
Features Distinct From *Canis* and *Crocuta*	Length of metatarsal II/length of metatarsal I	7.0	2.0	9.0	Lack of extreme reduction in metatarsal I indicative of less cursorial specialization than that of *C. crocuta* or *C. lupus*

No phalanges were found in articulated position and thus could not be differentiated as coming from fore or hind feet. The phalanges of *A. taxoides* are intermediate between the robust form of the *C. crocuta* phalanges and the more elongate *C. lupus* phalanges. No terminal phalanges are present in UNSM 46815, although those of UNSM 4476 (pl. 16 C) indicate that both animals may have had claws similar to those of *C. crocuta*.

Note On Pathology

An interesting phenomenon common to both the Knox County *Aelurodon* (UNSM 46815) and the Gorden *Aelurodon* (UNSM 4476) is the presence of pathologic bone growths in the feet. Such growths are present on the ventral and dorsal sides of metatarsals of UNSM 46815, and some phalanges of this specimen also possess growths indicative of injury, arthritis, or both. The ventral surface of the left navicular of this animal also appears quite arthritic (pl. 17 G, H). Left metacarpals III and IV (pl. 17 E, F) of UNSM 4476 have excessive growth on the dorsal surface which nearly doubles the normal shaft thickness. Splintered and rehealed bone on the medial surface of metacarpal III shows that the animal suffered severe fracturing of this bone at an extended time prior to death. A phalanx of this animal also displays evidence of fracture and subsequent healing. One is tempted to speculate that the animal received a blow to this region of the forefoot from some potential hoofed prey, although less violent explanations are possible.

DISCUSSION

Body Build and Cursorial Ability

The robust limb and foot bones indicate that *A. taxoides* was a heavy animal, probably resembling *C. crocuta* in this respect (though not in limb proportions). Although its limbs are a little longer than those of a coyote, they far exceed those of the wolf in massiveness. Hildebrand (1954, p. 413) observed that the more cursorial canids (*Canis lupus*, *Lycaon pictus*, etc.) have lighter limb bones than species less well adapted for running (such as *Speothos venaticus*). Thus the heavy, short limbs indicate that *A. taxoides* was not well adapted for a cursorial lifestyle.

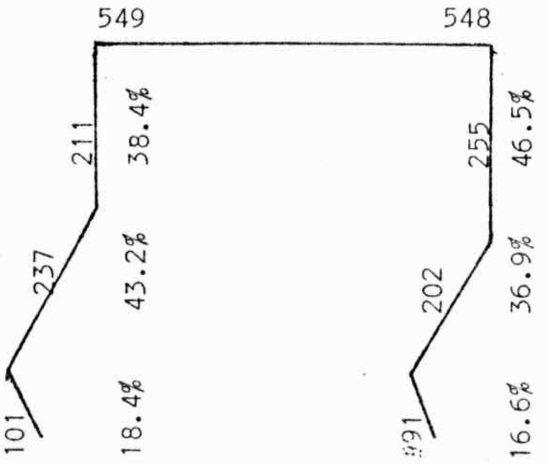
Several features of the forelimb indicate that *A. taxoides* may have had good rotational ability in the forearm. The prominent proximal portion of the lateral epicondyloid crest of the humerus implies that *A. taxoides* possessed a well developed m. brachioradialis for lateral rotation of the forearm. Muscle scars on the radius show that other muscles involved in forearm rotation were well developed in *A. taxoides*. These include a well developed m. supinator (for rotation of the dorsal palm medially) and m. pronator teres (for rotation of the dorsal forearm medially). The shortness of the interosseous ligament, which binds the radius to the ulna, would allow much more movement between these bones in *A. taxoides* than is possible in the wolf and hyena which have long interosseous ligaments. The large arc of the radial articular circumference, in association with the small arc of the articular facet on the coronoid process of the ulna of *A. taxoides* indicates a high degree of rotational freedom at the proximal end of the radius of this species (the arc of the radial articular circumference in *C. crocuta* is also large,but since the surface of articulation with the ulna is equally large, suppression rather than freedom of rotation is indicated). Hildebrand (1974, p. 503) and Howell (1965, p. 250) noted that loss of forearm rotational ability is a cursorial specialization. Presence of this ability in *A. taxoides* reinforces the proposition that the species was not cursorial.

Relative lengths of the humerus and radius of *A. taxoides* further evidence the lack of cursorial specialization in this species (fig. 7). The humeroradial index (radius/humerus x 100) of *A. taxoides* (94), is distinctly smaller than those of *C. lupus* (105) and *C. crocuta* (112). Howell (1965, p. 201) found that in generalized species of mammals the humeroradial index is approximately 100, and went on to state that high speed adaptations in mammals include reduction in the length of the proximal limb segment, and increase in the length of epipodials and metapodials. Hildebrand (1952, p. 243) found this relationship holds in modern Canidae, and observed that there is a correlation in the group between speed and humeroradial index.

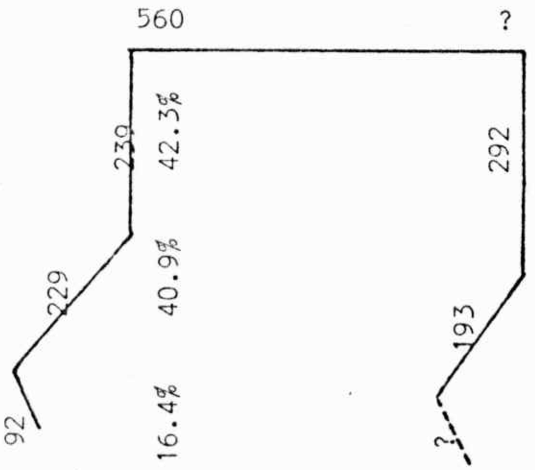
The hind leg of *A. taxoides* shows no more cursorial specialization than the fore leg, although there are more similarities between the hind limbs of *A. taxoides* and *C. crocuta*, than exist between the forelimbs of these species. This similarity may reflect a lack of cursorial specialization in the hind limb of *C. crocuta*, which would be consistent with Howell's (1965, p. 51) observation that the forelimbs are the primary locomotive limbs in the hyena, and the hind limbs serve principally to maintain balance. The femorotibial indices (tibia/femur x 100) of *A. taxoides* (84) and *C. crocuta* (79) are quite close, compared with that of *C. lupus* (104) whose tibia is longer than the femur. The short tibia is indicative of poor cursorial ability, for the same mechanical reasons discussed above

Figure 7. Proportions of limb elements relative to total limb length (humerus + radius + longest metacarpal; femur + tibia + longest metatarsal). Fore limbs on left, hind limbs on right, limb length at top of limb. Data for *A. taxoides* from UNSM 46815, *A. saevus* from Cope and Matthew (1915), *C. lupus* from UNSM-ZM 12642-S, *C. crocuta* from USNM 172685, *C. c. spelaea* from Kurten (1956), *O. cyonoides* from Dalquest (1969).

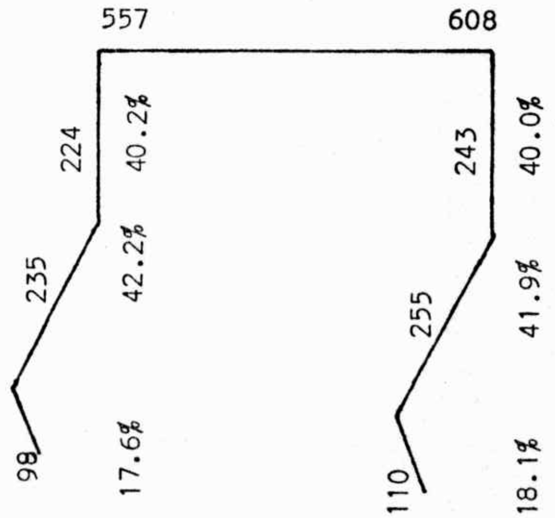
Crocuta crocuta



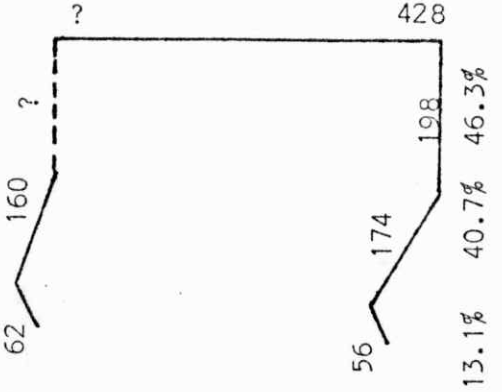
Crocuta crocuta spelaea



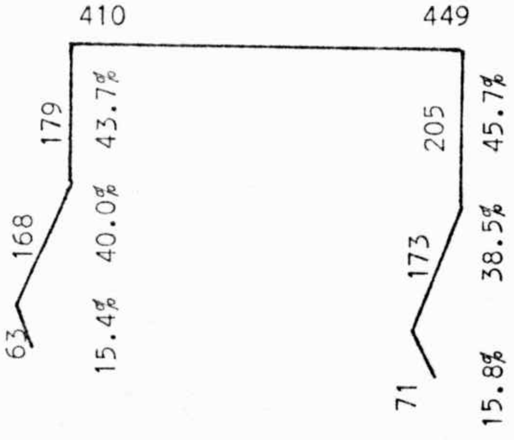
Canis lupus



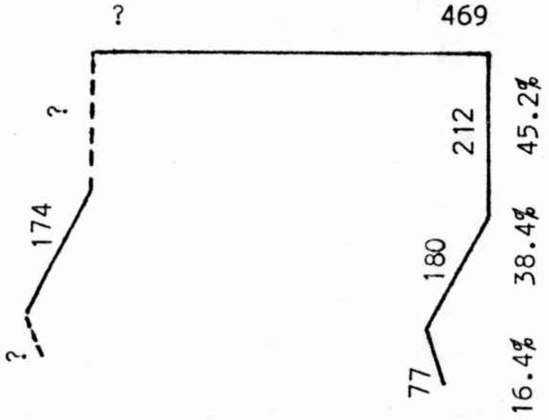
Osteoborus cyonoides



Aelurodon (Prohyaena) taxoides



Aelurodon saevus



in reference to the relative lengths of the radius and humerus.

The shallowness of the patellar groove of the femur of A. taxoides is further evidence of non-cursorial specialization, since both Hildebrand (1954, p. 441) and Howell (1965, p. 172) correlated depth in this structure with speed. This is also true of the relatively large, unreduced fibula and metatarsal I in A. taxoides, compared to those of C. lupus and C. crocuta. Howell (1965, p. 256) correlated reduction in the fibula, and reduction in the number of digits (p. 253) with increased speed.

Paleoecologic Role

Determining the paleoecologic role of an extinct species must always be in part a speculative venture. There are, however, several souces of information which can provide insight into the problem. Morphology provides the most direct evidence. Teeth and jaws are indicative of diet and longevity. The postcranial skeleton provides information on locomotive ability and body weight. Radinsky (1973) has shown that endocranial casts may be useful in determining certain aspects of the behavior of fossil species. Tracks, trails and burrows provide direct evidence of a species' activities. Association with other fossils may provide clues to life associations, although this relationship breaks down with increasing distance of transport prior to burial. Finally, the lithology of associated sediments and associated plant remains provide information on habitat; plants being especially good indicators of climatic conditions.

Aelurodon was a large and common carnivore which must have played an important part in the Barstovian and Claredonian land mammal age ecosystems in western North America. The presence of Aelurodon in nearly all the large North American faunas of these ages (e.g. Big

Spring Canyon, Niobrara River, Verdigre, Burge, Minnecheduza, Mission, Tonopah, Barstow, Ricardo, etc.) is well documented. One cannot avoid speculating on the relationship between Aelurodon, a high-level carnivore, and the herbivores which dominate these faunas. As mentioned above (see Previous Work), many workers have speculated on the behavior of Aelurodon based on tooth and jaw morphology. Analysis of the appendicular skeleton of A. (Prohyaena) taxoides provides another parameter with which to determine the paleoecologic role of the species, and thus evaluate the validity of former speculations. In the following pages this new information will be evaluated in light of four closely related parameters (habitat, social structure, diet, and hunting behavior).

HABITAT - MacGinitie's (1962) comprehensive analysis of the Kilgore flora from the Valentine Formation of north-central Nebraska, provides insight into the type of habitat in which Aelurodon lived in late Barstovian Nebraska. He concluded (op. cit., p. 67-68) climatic conditions were warm temperate to subtropical, and nearly frostless; while the flora was savanna-like, having mesic forests bordering streams with grassy forests in the interfluvial regions. Vertebrate evidence of climatic conditions provided by Hibbard (1960, p. 6-10) and Voorhies (1969, p. 61) agrees with MacGinitie's conclusions.

Gregory (1971, p. 70) compared the ratio of browsers to grazers in the Barstovian and Clarendonian faunas mentioned above and also concluded that what is presently the Great Plains grassland, was savanna at that time. The presence of Aelurodon in Shotwell and Russell's (1963) "savanna community" and absence from the "pond-bank and grassland communities" may further support the claim that

Aelurodon inhabited a savanna environment; however, their *Aelurodon* material was quite scrappy so absence from the other communities may not be significant. Also, Shotwell's methods have been criticized by Voorhies (1969, p. 53-56).

MacGinitie (1962, p. 76) and Voorhies (1969, p. 60) agreed that topographic relief between interfluvial highs and stream valley lows may not have been greater than 25 feet (8 m).

Conclusion: *Aelurodon* inhabited savanna of low relief.

SOCIAL STRUCTURE - Comparisons of endocranial casts of *Aelurodon* with those of modern canids by Radinsky (1973) provide additional insight into the habits of *Aelurodon*. He found (op. cit., p. 195) that all modern canids having a pack social structure (species of *Canis*, Cape hunting dog (*Lycaon pictus*), and the Asiatic dhole (*Cuon alpinus*) possess a large prorean gyrus. Modern foxes which lack the expanded prorean gyrus, also lack a pack social structure. The expanded prorean gyrus is also lacking in endocranial casts of *Aelurodon* (op. cit., p. 194). This may imply that members of the genus were not pack animals and may have been solitary. The lack of concentrations of *Aelurodon* remains in the faunas mentioned above is consistent with this hypothesis. Webb (1969, p. 25) showed that *Aelurodon* was represented by only 1.6% and 1.0% of the specimens collected in the Burge and Minnechaduza quarries, respectively. Voorhies (1969, p. 21, pl. 4) found a similar scarcity of *Aelurodon* (6 specimens) remains at Verdigre Quarry compared to the much more common *Merycodus* (2690 specimens) and *Protohippus* (321 specimens). Other *Aelurodon*-producing faunas alrady mentioned, have an equal paucity of material from the genus.

DIET - It has long been recognized on the basis of tooth morphology that Aelurodon was a carnivorous animal. Large canines, carnassial shear, and the morphology of the incisors and premolars indicate specialization for a meat-eating diet. Cope (1883, p. 244) suggested that heavy wear and robustness of teeth of Aelurodon indicate that it also possessed bone crushing ability. Since that time, Vanderhoof and Gregory (1940, p. 163), Voorhies (1969, p. 20), and Radinsky (1973, p. 179) have accepted Cope's opinion, although recently Galiano and Frailey (1977, p. 14) have suggested that A. haydeni was a bone crusher but that A. taxoides filled a more wolf-like niche. A survey of specimens of A. taxoides in the UNSM collections shows only slight wear on the carnassials of some (apparently younger) individuals, while those of other (apparently older) individuals are worn more excessively than the carnassials of wolves available for comparison. This indicates that although A. taxoides possessed bone crushing abilities, meat-eating was at least of equal importance, especially in younger individuals.

HUNTING BEHAVIOR - Young and Goldman (1944, p. 75) stated that the hunting behavior of wolves is based on exhaustion of their prey, and that their greater endurance over most big game animals is one of their main assets. Murie (1944), observed wolves traveling long distances to get to "choice herds" of caribou, and stated that trips of 10 miles (oneway) were not unusual. It is evident from the robustness and proportions of the limbs of A. taxoides that this species could not have hunted in the manner of the wolves.

The recent suggestion of Galiano and Frailey (1977, p. 14) that A. taxoides held the niche of the Cape hunting dog seems questionable for the same reasons. The van Lawick-Goodalls (1971) described the long-distance running capabilities of hunting dogs, stating that chases after prey averaged 3.2-4.8 km, with some as long as 8 km, and observed speeds up to 48 km per hour for 4.8 km. It seems doubtful that an animal having the build of *A. taxoides* could endure such chases averaging two minutes per mile for three miles.

When Cope (1883) equated *Aelurodon* to the hyenas, the latter were thought to be slow moving scavengers. Only recently did Kruuk (1972, 1975) show that the spotted hyena is actually a fast running and highly competitive predator in the Serengheti ecosystem, reporting chases at speeds of "perhaps 30-40 m.p.h." (1975, p. 25.) *A. taxoides* could not have possessed the cursorial ability of the spotted hyenas. It is of note that although the anterior limbs of the spotted hyena are unlike those of *A. taxoides* which are not cursorially specialized, the proportions of both the front and back limbs of the Pleistocene "cave" hyena (*Crocuta crocuta spelaea*) are quite similar to those of *A. taxoides* (fig. 7). On the basis of limb proportions alone and without knowledge of the detailed morphology of the limb elements of *C. c. spelaea*, it is tempting to suggest that *A. taxoides* has behavioral affinities with this fossil hyena. This raises the question of when did *C. crocuta* become cursorially specialized? The robust body of the spotted hyena, and the solitary rather than group hunting behavior of smaller ungulates such as gazelle (Kruuk, 1975, p. 25), may indicate that the present behavioral repertoire evolved from a relatively recent ancestral condition of solitary rather than gregarious social structure.

The proposals of Vanderhoof and Gregory (1940, p. 163) that *A. haydeni* was an active but slower predator than the wolf; and Gregory (1942, p. 334) that *Aelurodon* may have ambushed its prey; are consistent with observations made here on the appendicular skeleton of A. taxoides. It should also be added that the robust body of A. taxoides may have been an adaptation for solitary hunting. Hildebrand (1954, p. 450) suggested that the robustness of the dhole may compensate for small size when bringing down large game. Rotational freedom of the forearm of A. taxoides would also have been advantageous in wrestling down prey and such encounters with hoofed prey may explain a high incidence of foot injuries.

There appears to be no living canid the size of Aelurodon which fills the same eco-role; however, there are a surprising number of anatomical similarities between A. taxoides and the small South American bush dog (Speothos venaticus). The limb proportions of the bush dog are more similar to those of A. taxoides than are those of any other living canid. The percentage of humeral length and radial length to total limb length in A. taxoides (fig. 7) is 43.7% and 40.0% respectively, while Hildebrand (1952, p.226) shows values for the bush dog as 43.4% and 39.5%. The percentage of femoral and tibial lengths to total limb length is 45.7% and 38.5% in A. taxoides, and 41.2% and 41.1% in the bush dog. The hind limb proportions are not as close between the two species, but it is significant that Speothos is the only living canid having the tibia shorter than the femur. Hildebrand (1954, p. 413) mentions other characteristics of the bush dog which are similar to those of A. taxoides, including heavy, thick limb bones, a robust body, proportionately large head, broad muzzle and the ability to rotate the radius over the ulna. He also (op. cit., p. 408) states that the bush dog inhabits the banks of streams and rivers in heavy forest. While Langguth (1975, p. 199-200), reports that Speothos preys on pacas, capybara, deer, and rheas, as well as smaller animals. It seems logical to propose that A. taxoides also inhabited stream valley forests or wooded parts of the Barstovian and Clarendonian savannas, where it could ambush its prey, since it was obviously too slow to run down fast game. Gregory's (1971, p. 70) observation that the savanna had become grassland by Hemphillian time fits this model, because disappearance of the savanna habitat coincides with the disappearance of Aelurodon as a common faunal member.

The repeated association of Aelurodon with on primary suite of fossil herbivores throughout the Great Plains and Great Basin, indicates that these species cohabited the savanna environment, and that the herivorous species were potential prey of Aelurodon. Cope's (1883, p. 244) suggestion that species of Aelurodon ate antelopes (Antelocapridae) and small camels seems realistic; however, it is here suggested that they were actively preyed upon as well as scavenged. Less cursorial herbivores such as peccaries and oreodonts would probably have been relatively easy prey for A. taxoides. Healthy deer would probably have been too fast to chase down, but new born, unhealthy, or old individuals would have made potential meals. Kruuk (1975, p. 33) noted that modern zebra (Equus sp.) must be hunted by packs of spotted hyenas rather than solitary individuals due to defensive behavior of the stallion, however, the large size of A. taxoides relative to the size of its equid contemporaries could have served to overcome this defensive strategy (if it had developed by Barstovian time) in ambush situations. Rabbits and rodents probably made up part of the A. taxoides diet, but species of the smaller genus Tomamctus would have competed with Aelurodon for these smaller herbivores, as indicated by stomach contents of the Tomarctus skeleton reported by Green (1948, p. 86).

SUMMARY - Analysis of the appendicular skeleton of Aelurodon (Prohyaena) taxoides indicates that this species was not cursorially specialized. It is proposed that A. taxoides inhabited savanna forest and ambushed its prey, rather than scavenging most of its food. This lifestyle may be somewhat analogous to that of the South American bush dog. Transition of the savanna into a grassland habitat by Hemphillian times may have caused the decline of species of Aelurodon.

CONCLUSIONS

Comparison of the appendicular skeleton of Aelurodon (Prohyaena) taxoides with those of the wolf and spotted hyena shows that A. taxoides was a non-cursorially specialized animal, as evidenced by limb proportions, and rotational ability in the forearm; as well as more detailed bone structures such as a shallow patellar groove, and the relatively unreduced fibula and first metatarsal. Robustness of limb bones in A. taxoides is correlated with heavy body build.

Lack of cursorial ability indicates that previous workers who equated A. taxoides to wolves, hunting dogs, or spotted hyenas were in error, since these extant species depend on cursorial ability in bringing down prey. Faunal and floral remains associated with those of Aelurodon in Barstovian and Clarendonian age fossil deposits, and information provided by this analysis of the appendicular skeleton of A. taxoides, indicate that the species was an active predator which inhabited savanna stream valley forests and relied on an ambush form of hunting, rather than chasing down prey on open ground. This lifestyle may be analogous to that of the South American bush dog. Scavenging may have provided a source of food for A. taxoides when live prey could not be obtained, since heavy wear on the carnassials of older individuals indicates use of these teeth for bone crushing.

REFERENCES CITED

Barbour, E. H., and H. J. Cook, 1917, Skull of *Aelurodon platyrhinus* sp. nov.: Nebr. Geol. Survey, v. 7, pt. 19, p. 173-180.

Bode, F. D., 1935, The fauna of the *Merychippus* zone, north Coalinga District, California: Pub. Carn. Inst. Wash., 453; p. 65-96.

Colbert, E. H., 1939, Carnivora of the Tung Gur Formation of Mongolia: Bull. Amer. Mus. Nat. Hist., v. 66, art. 2, p. 47-81.

Cook, H. J., 1914, A new canid from the lower Pliocene of Nebraska: Nebr. Geol. Survey, v. 7, pt. 7, p. 49-50.

Cope, E. D., 1877, Report upon the extinct Vertebrata obtained in New Mexico by parties of the expedition of 1874: ch. 13. Fossils of The Loup Fork Epoch, Geog. Surveys West of the 100th Merid., 1st Lt. G. M. Wheeler, Corps of Eng., U.S. Army in Charge, v. 4, Paleontology, Washington, D.C., pp.1-370.

_____,1883, on the extinct dogs of North America: Am. Nat., v. 17, p. 235-249.

Cope, E. D., and W. D. Matthew, 1915, Hitherto unpublished plates of Tertiary Mammalia and Permian vertebrata: U.S. Geol. Survey and Amer. Mus. Nat. Hist., Monograph ser. 2, pl. 1-CLIV.

Dalquest, W. W., 1969, Pliocene carnivores of the Coffee Ranch, Bull. Tex. Mem. Mus., v. 15, p. 1-44.

Dalquest, W. W., and J. T. Hughes, 1966, A new mammalian local fauna from the Lower Pliocene of Texas: Trans. Kansas Acad. Sci., v. 69, p. 79-87.

Galiano, H., and D. Frailey, 1977, *Chasmaporthetes kani*, new species from China, with remarks on phylogenetic relationships of genera within the Hyaenidae (Mammalia, Carnivora): Amer. Mus. Nat. Hist. Nov., no. 2632, p. 1-16.

Green, M., 1948, A new species of dog from the Lower Pliocene of California: Univ. Cal. Pub., Bull. Dept. Geol. Sci., v. 28, no. 4, p. 81-90.

_____, 1971, Additions to the Mission vertebrate fauna, Lower Pliocene of South Dakota: Jour. Paleo., v. 45, no. 3, p. 486-490.

Gregory, J. T., 1942, Pliocene vertebrates from Big Spring Canyon, South Dakota: Univ. Cal. Pub., Bull. Dept. Geol. Sci., v. 26, no. 4, p. 307-446.

_____, 1971, Speculations on the significance of fossil vertebrates for the antiquity of the Great Plains of North America: Abh. Hess Landesamt Bodenforsch, v. 60, p. 64-72.

Hatcher, J. B., 1894, On a small collection of vertebrate fossils from the Loup Fork beds of northwestern Nebraska; with note on the geology of the region: Amer. Nat., v. 28, p. 236-248.

Henshaw, P. C., 1942, A Tertiary mammalian fauna from the San Antonio Mountains near Tonopah, Nevada: Pub. Carn. Inst. Wash., 530, p.77-168.

Hibbard, C. W., 1960, An interpretation of Pliocene and Pleistocene climates in North America: Mich. Acad. Sci., Arts and Letters, 62nd Ann. Rept., p. 5-30.

Hildebrand, M., 1952, An analysis of body proportions in the Canidae: Amer. Jour. Anat., v. 90, no. 1, p. 217-256.

_____, 1954, Comparative morphology in the body skeleton in recent Canidae: Univ. Cal. Pub. Zool., v. 52, no. 5, p. 399-470.

_____, 1974, Analysis of vertebrate structure: John Wiley and Sons, New York, 710p.

Howell, A. B., 1965, Speed in animals: Hafner Pub. Co., New York, p. 270.

Kitts, D. B., 1957, A Pliocene vertebrate fauna from Ellis County, Oklahoma: Circ. Okla. Geol. Survey, v. 45, p. 1-24.

_____, 1964, *Aelurodon*, an addition to the Durham local fauna, Roger Mills County, Oklahoma: Okla. Geol. Notes, v. 24, p. 76-78.

Kruuk, H., 1972, The spotted hyena: Univ. Chicago Press, Chicago.

_____, 1975, Hyaena: Oxford Univ. Press, London, 80 p.

Kurtén, B., 1956, The status and affinities of *Hyaena sinensis* Owen *Hyaena ultima* Matsumoto: Amer. Mus. Nov., no. 1764, p. 1-48.

Langguth, A., 1975, in:The wild canids: their systematics, behavioral ecology and evolution, M. W. Fox, ed., Van Nostrand Reinhold Co., New York, 508 p.

van Lawick-Goodall, H. and J., 1971, The innocent killers: Houghton-Mifflin, Boston. 222 p.

Leidy, J., 1858, Notice of remains of extinct vertebrata from the valley of the Niobrara River collected during the exploring expedition of 1857 in Nebraska, under the command of Lt. G. K. Warren, U.S. Top. Eng., by Dr. F. V. Hayden: Acad. Nat. Sci. Phila. Proc., v. 10, p. 20-29.

Macdonald, J. R., 1948a, The Pliocene carnivores of the Black Hawk Ranch fauna: Univ. Cal. Pub., Bull. Dept. Geol. Sci., v. 28, p. 53-80.

_____, 1948b, A new species of *Pseudaelurus* from the Lower Pliocene of Nebraska: Univ. Cal. Pub., Bull. Dept. Geol. Sci., v. 28, no. 2, p. 45-52.

_____, 1960, An Early Pliocene fauna from Mission, South Dakota: Jour. Paleo., v. 34, p. 961-982.

MacGinitie, H. D., 1962, The Kilgore flora: a late Miocene flora from northern Nebraska: Univ. Cal. Publ. Geol. Sci., v. 35, p. 67-158.

Matthew, W. D., 1912, Carnivora and Rodentia, in: Ten years progress in vertebrate paleontology: Bull. Geol. Soc. Amer., v. 23, p. 181-185.

_____, 1924, Third contribution to the Snake Creek fauna: Bull. Amer. Mus. Nat. Hist., v. 50, art. 2, p. 59-210.

_____, 1930, The phylogeny of the dogs: Jour. Mammalogy, v. 11, p. 117-138.

Matthew, W. D., and J. W. Gidley, 1904, New or little known mammals from the Miocene of South Dakota; American Museum expedition of 1903: Bull. Amer. Mus. Nat. Hist., v. 20, art. 22, p. 241-268.

Matthew, W. D., and H. J. Cook, 1909, A Pliocene fauna from western Nebraska: Bull. Amer. Mus. Nat. Hist., v. 25, p. 311-414.

Mawby, J. E., 1964, Species groups of the canid genus *Aelurodon*: Spec. Paper Geol. Soc. Amer., v. 82, p. 263. (abs.)

McGrew, P. O., 1944, The *Aelurodon saevus* group: Pub. Field Mus. Geol. Ser., v. 8, p. 79-84.

Mech, L. D., 1966, The wolves of Isle Royale: U.S. Nat. Park Serv. Fauna Ser., no. 7, Washington, D. C., 210 p.

Merriam, J. C., 1919, Tertiary mammalian faunas of the Mojave Desert: Univ. Cal. Pub., Bull. Dept. Geol. Sci., v. 11, no. 5, p. 437-585.

Messenger, K and C., 1977, Carnivores of the Jamber local fauna (Pliocene, Valentinian) Boyd County, Nebraska: Trans. Nebraska Acad. Sci., v. 4, p. 95-101.

Miller, M. E., et. al., 1964, Anatomy of the dog: W. B. Saunders, Philadelphia, 941 p.

Murie, A., 1944, The wolves of Mount McKinley: U.S. Dept. Inter. Fauna Ser., no. 5, Washington, D. C., 238 p.

Radinsky, L., 1973, Evolution of the Canid brain: Brain, Behav., Evol., v. 7, p. 169-202.

Schlosser, M., 1890, Die Affen, Lemuren, Chiropteren, Insectivoren, Marsupialier, Creodonten und Carnivoren des europaischen Tertiars; und deren beziehungen zu ihren lebenden und fossilen Aussereuropaischen verwandten: Beitrage zur Palaontologie Oesterreich-Ungarns, v. 8, p. 387-492.

Scott, W. B., 1890, Preliminary account of the fossil mammals from the White River and Loup Fork formations, contained in the Museum of Comparative Zoology; Pt. 2: Bull. Mus Comp. Zool., v. 20, p. 65-100.

Shotwell, J. A., and D. E. Russell, 1963, Mammalian fauna of the Upper Juntura Formation, the Black Butte local fauna; in: The Juntura Basin: studies in earth history and paleoecology, J. Shotwell, ed.: Amer. Philosoph. Soc. Trans., v. 53, pt. 1, 77 p.

Smith, M J., and R. J. G. Savage, 1956, Some locomotory adaptations in mammals: Jour. Linnean Soc. London-Zool., v. 42, p. 603-622.

Stirton, R. A., and V. L. Vanderhoof, 1933, *Osteoborus*, a new genus of dogs, and its relation to *Borophagus* Cope: Univ. Cal. Pub., Bull. Dept. Geol. Sci., v. 23, p. 175-182.

Storer, J. E., 1975, Tertiary mammals of Saskatchewan; Pt. III: The Miocene fauna: Life Sci. Contrib., Roy. Ontario Mus., no. 103, p. 1-134.

Thorpe, M. R., 1922, Some Tertiary Carnivora in the Marsh collection: Amer. Jour. Sci., Ser. 5, v. 3, p. 423-455.

Vanderhoof, V. L., and J. T. Gregory, 1938, Status of the later Tertiary dog *Aelurodon*: Proc. Geol. Soc. Amer.- 1937, p. 270. (abs.)

_____, 1940, A review of the genus *Aelurodon*: Univ. Cal. Pub., Bull. Dept. Geol. Sci., v. 25, p. 143-164.

Voorhies, M. R., 1969, Taphonomy and population dynamics of an early Pliocene vertebrate fauna, Knox County, Nebraska: Univ. Wyoming Contrib. Geol., Spec. Paper, no. 1, p. 1-69.

Webb, S. D., 1969, The Burge and Minnechaduza Clarendonian faunas of north-central Nebraska: Univ. Cal. Pub. Geol. Sci., v. 78, p. 1-191.

White, T. E., 1947, Additions to the Miocene fauna of north Florida: Bull. Mus. Comp. Zool. Harvard, v. 99, p. 497-515.

Whitmore, F. C., Jr., 1971, Vertebrate biofacies and paleoenvironments; in: Gernant, R., T. Gibson and F. C. Whitmore, Environmental history of the Maryland Miocene: Maryland Geol. Survey, Guidebook no. 3, p. 1-58.

Wilson, J. A., 1960, Miocene carnivores of the Texas coastal plain: Jour. Paleo., v. 34, no. 5, p. 983-1000.

Young, S. P., and E. A. Goldman, 1944, The wolves of North America; Pt. 1: Amer. Wildlife Inst., Washington, D.C., 385 p.

Plate 1. Ventral views of skulls: (left) Crocuta crocuta, USNM 282797 ; (center) Aelurodon taxoides, UNSM 46815; (right) Canis lupus, UNSM-ZM 12641-S.

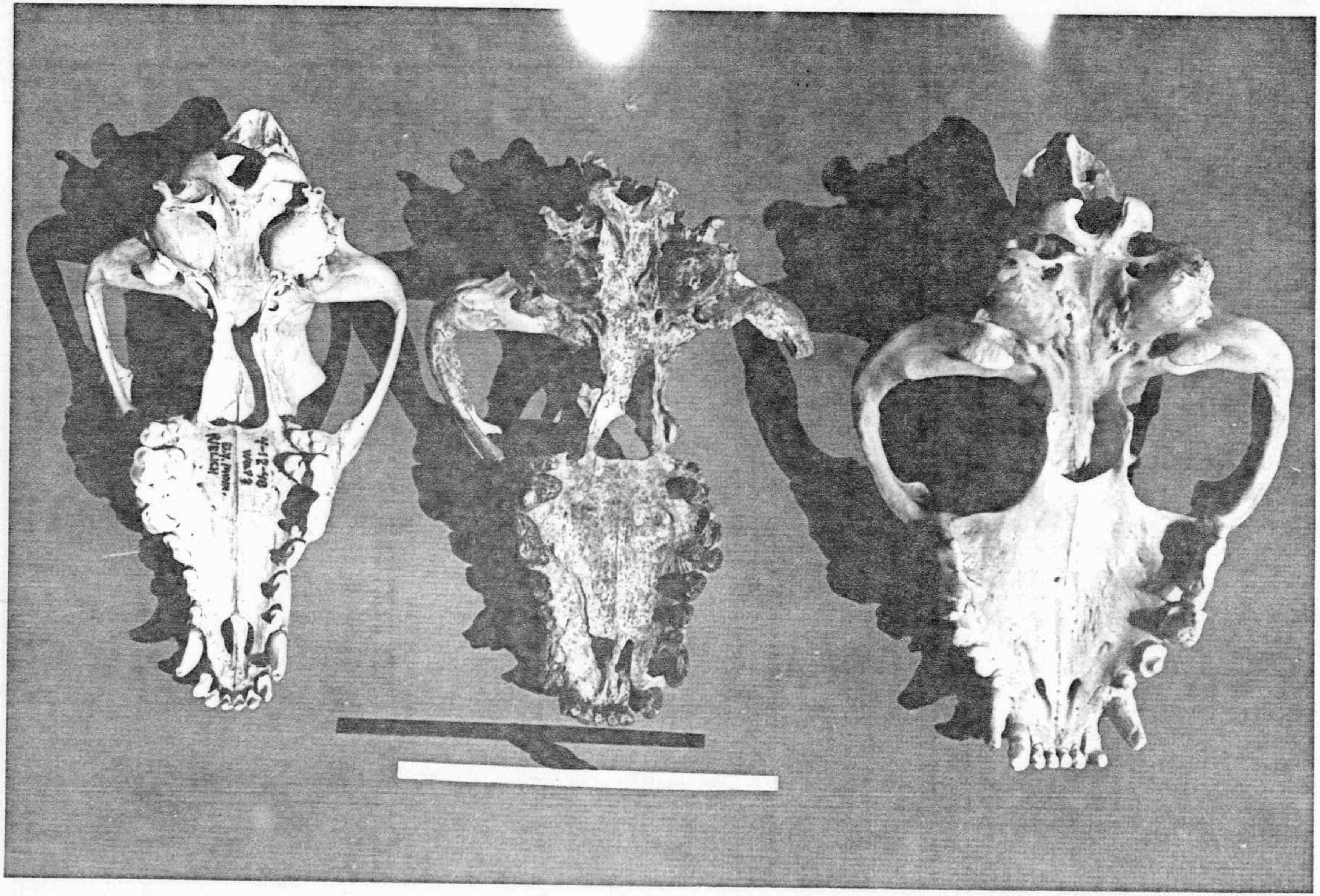

4-12-40
Wolf ♀

Plate 2. Skull of *Aelurodon taxoides*, UNSM 46815; ventral view.

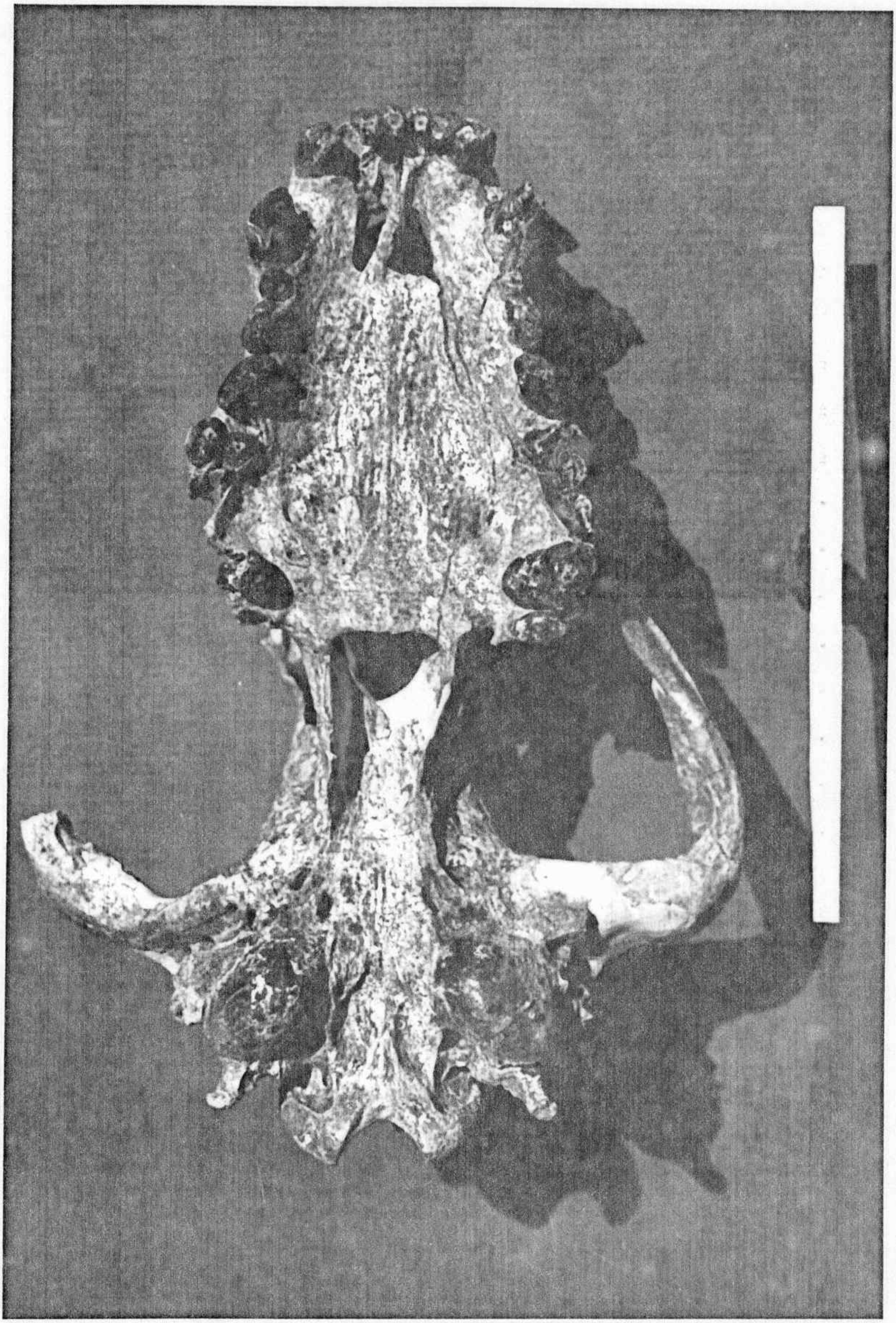


Plate 3. Skull of <u>Aelurodon</u> <u>taxoides</u>, UNSM 46815; dorsal view.

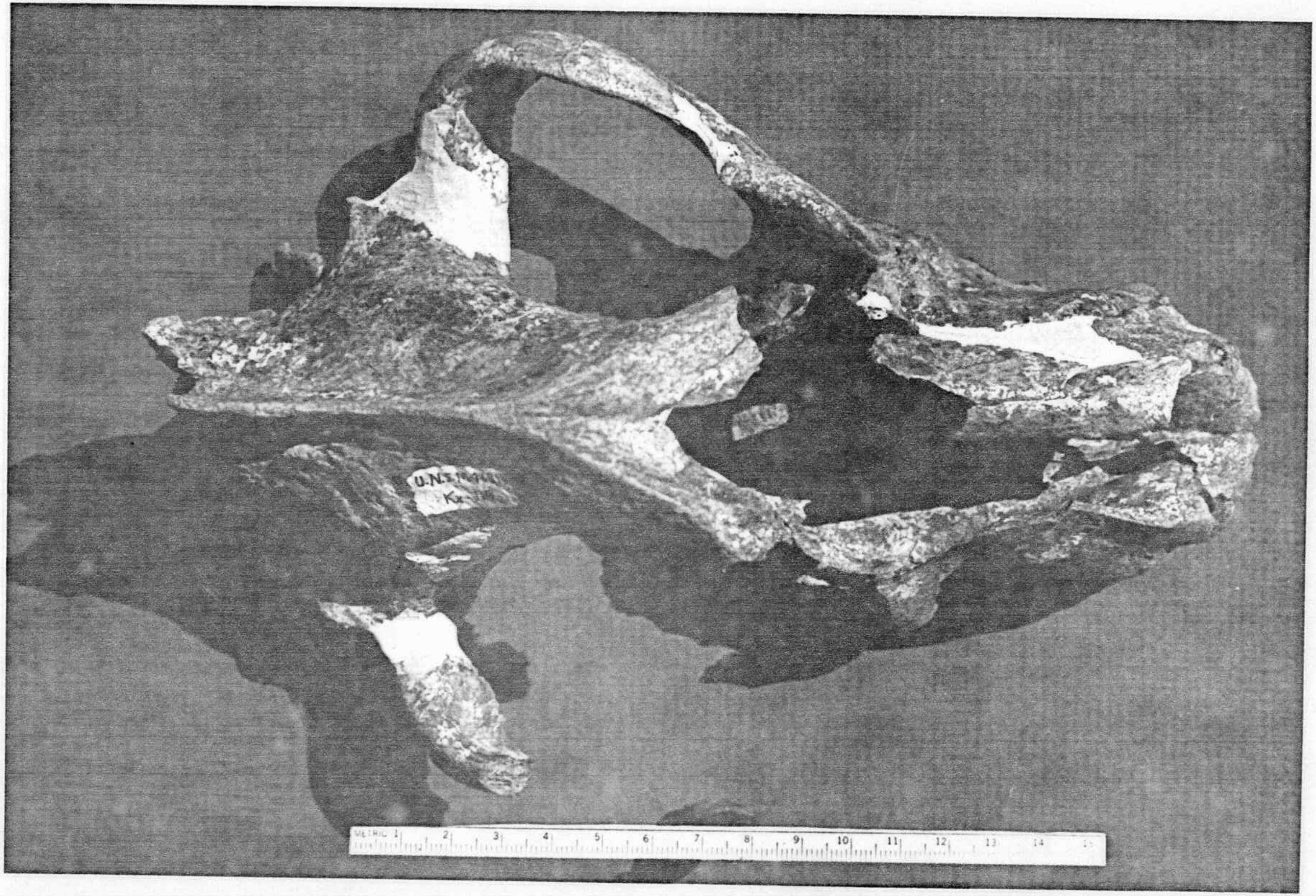

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Plate 4. Skull of _Aelurodon_ _taxoides_, UNSM 46815; left lateral view.

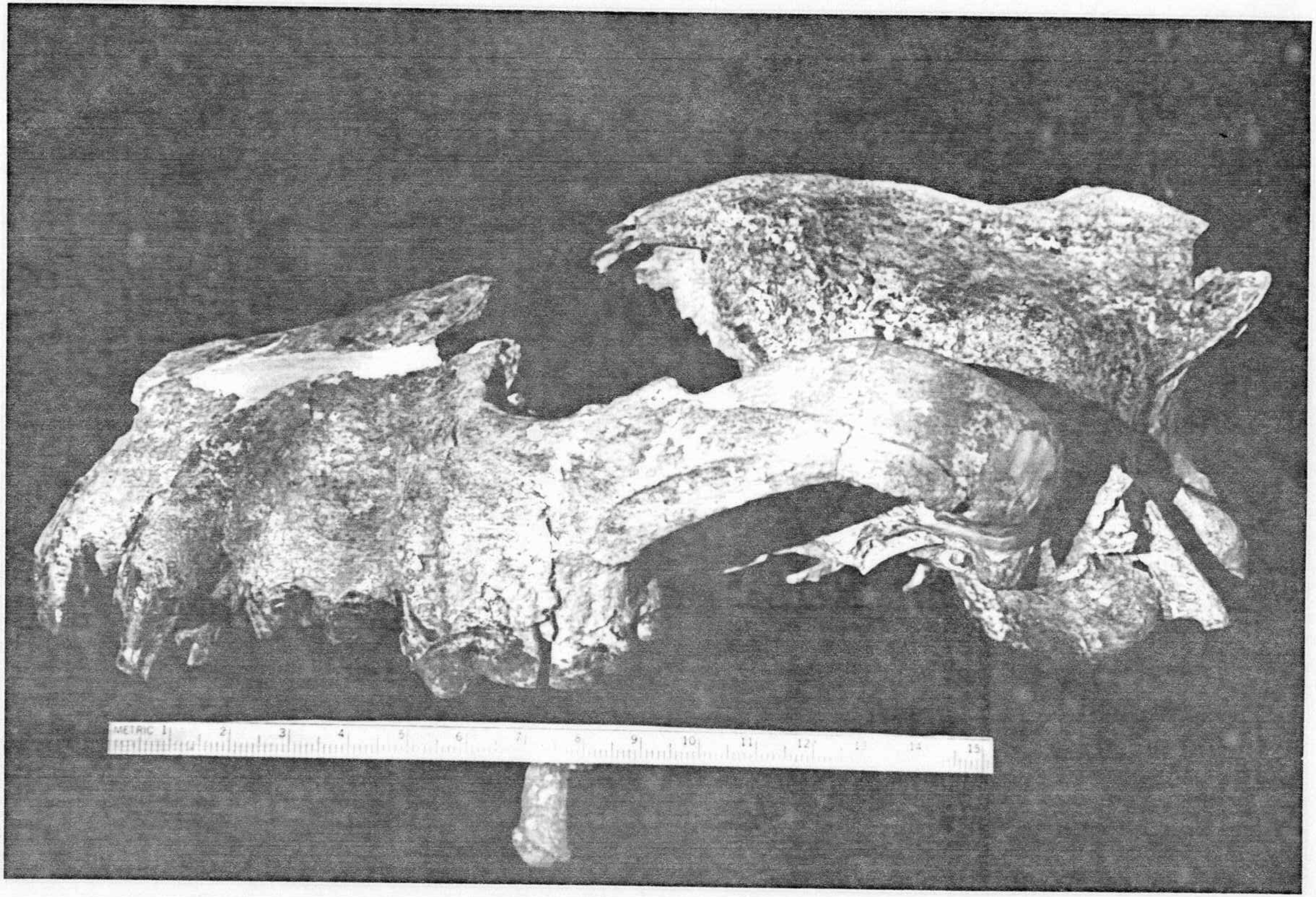
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Plate 5. Mandible of Aelurodon taxoides, UNSM 46815; left lateral view.

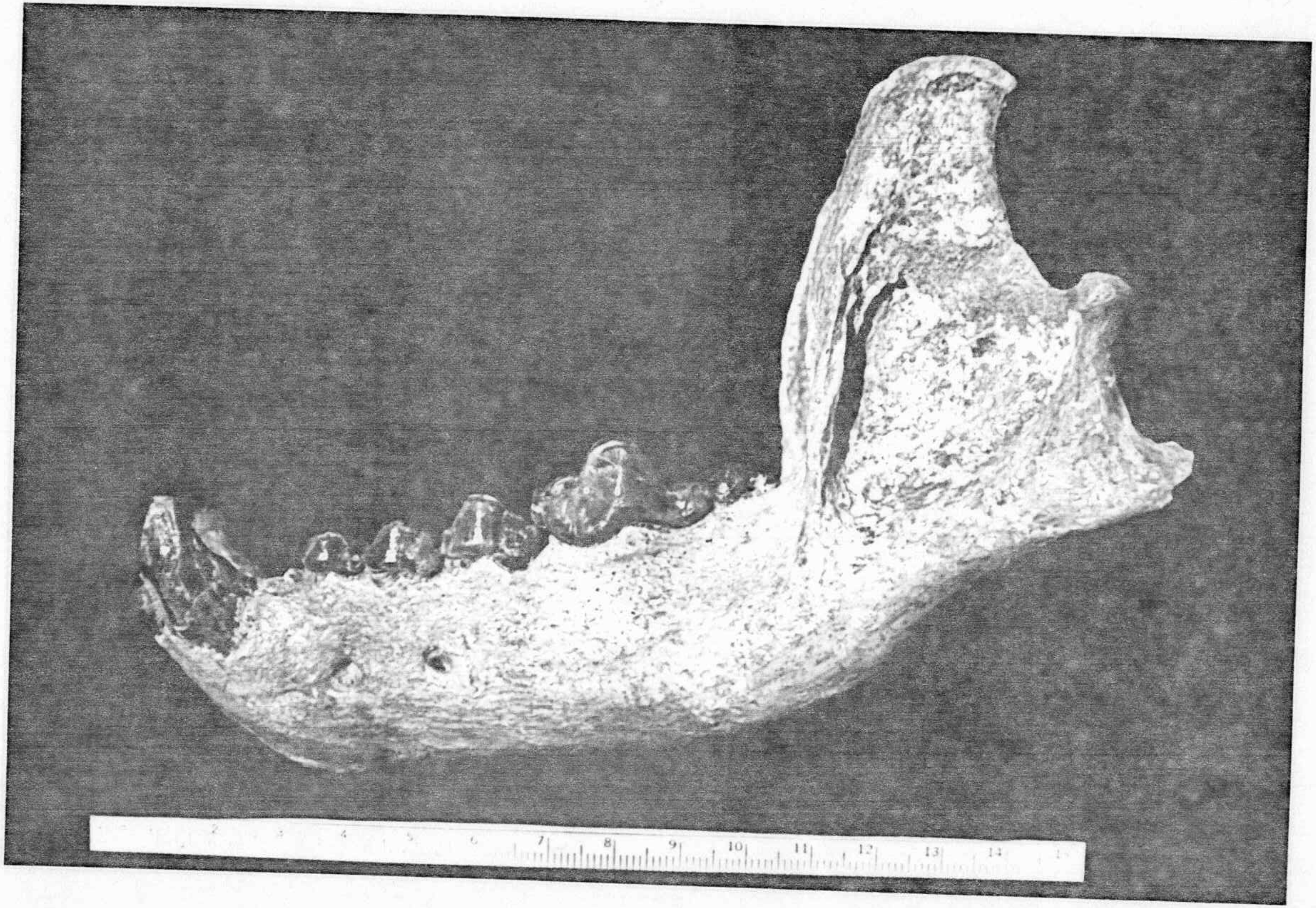
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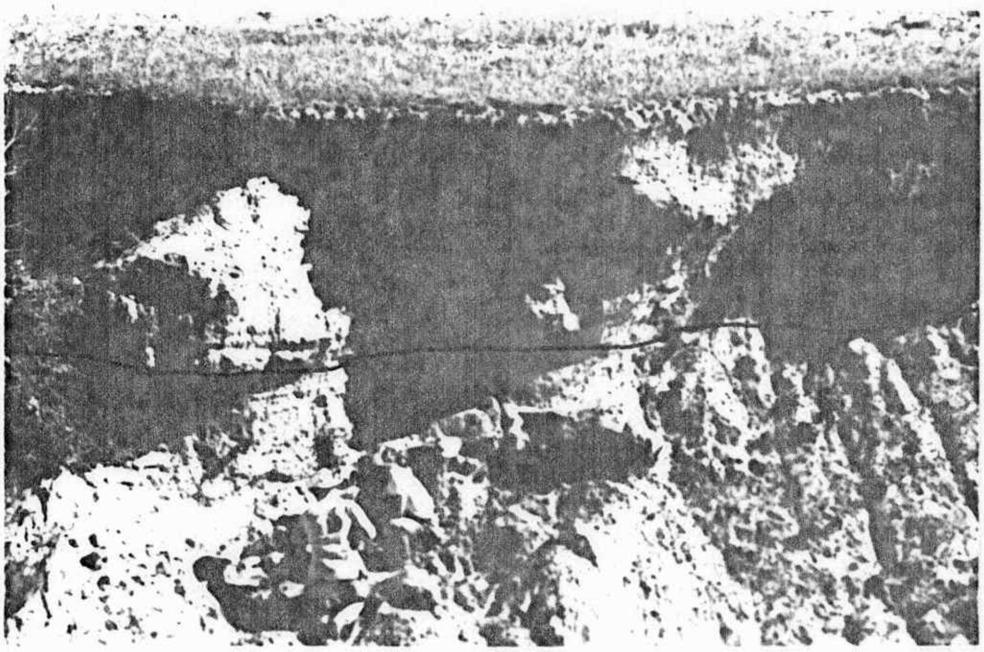
Plate 6. (A)- UNSM Locality Kx-119. M. Voorhies and W. Korth examining excavation site of UNSM 46815. Black line marks the contact between the Ash Hollow Fm. (Cap Rock Member) above, and the Valentine Fm. below.

(B)- Dorsal views of mandibles: (left) *Crocuta crocuta*, USNM 282797 ; (center) *Aelurodon taxoides*, UNSM 46815; (right) *Canis lupus*, UNSM-ZM 12641-S.

(C)- Close-up view of posterior teeth of *Aelurodon taxoides*, UNSM 46815, left mandible.



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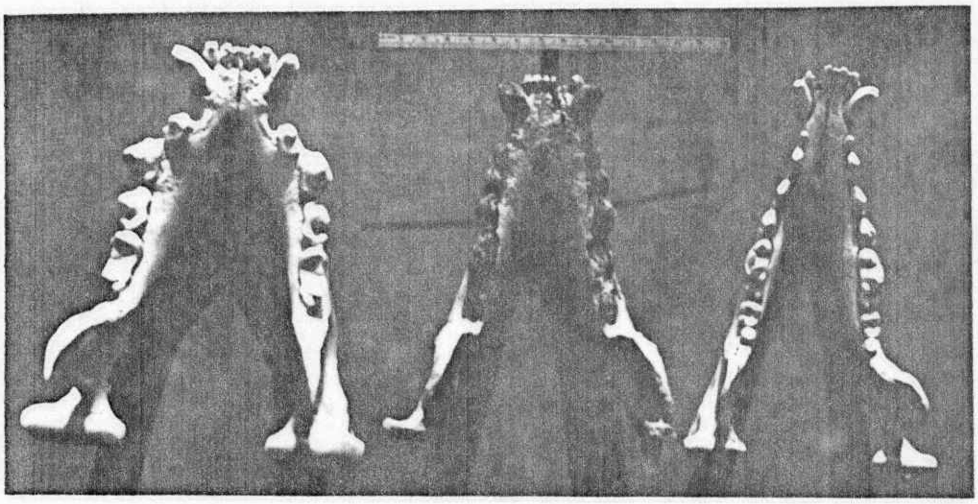

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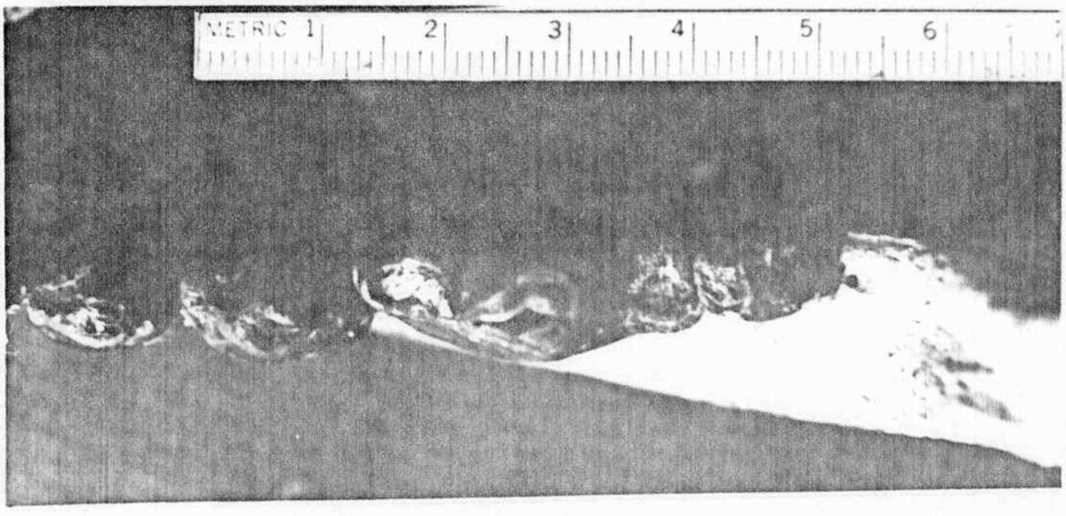

C

Plate 7. Postero-lateral view of humeri: (left) *Crocuta crocuta*, USNM 172685, left humerus; (center) *Aelurodon taxoides*, UNSM 46815, left humerus; (right) *Canis lupus*, UNSM-ZM 12642-S, right humerus.

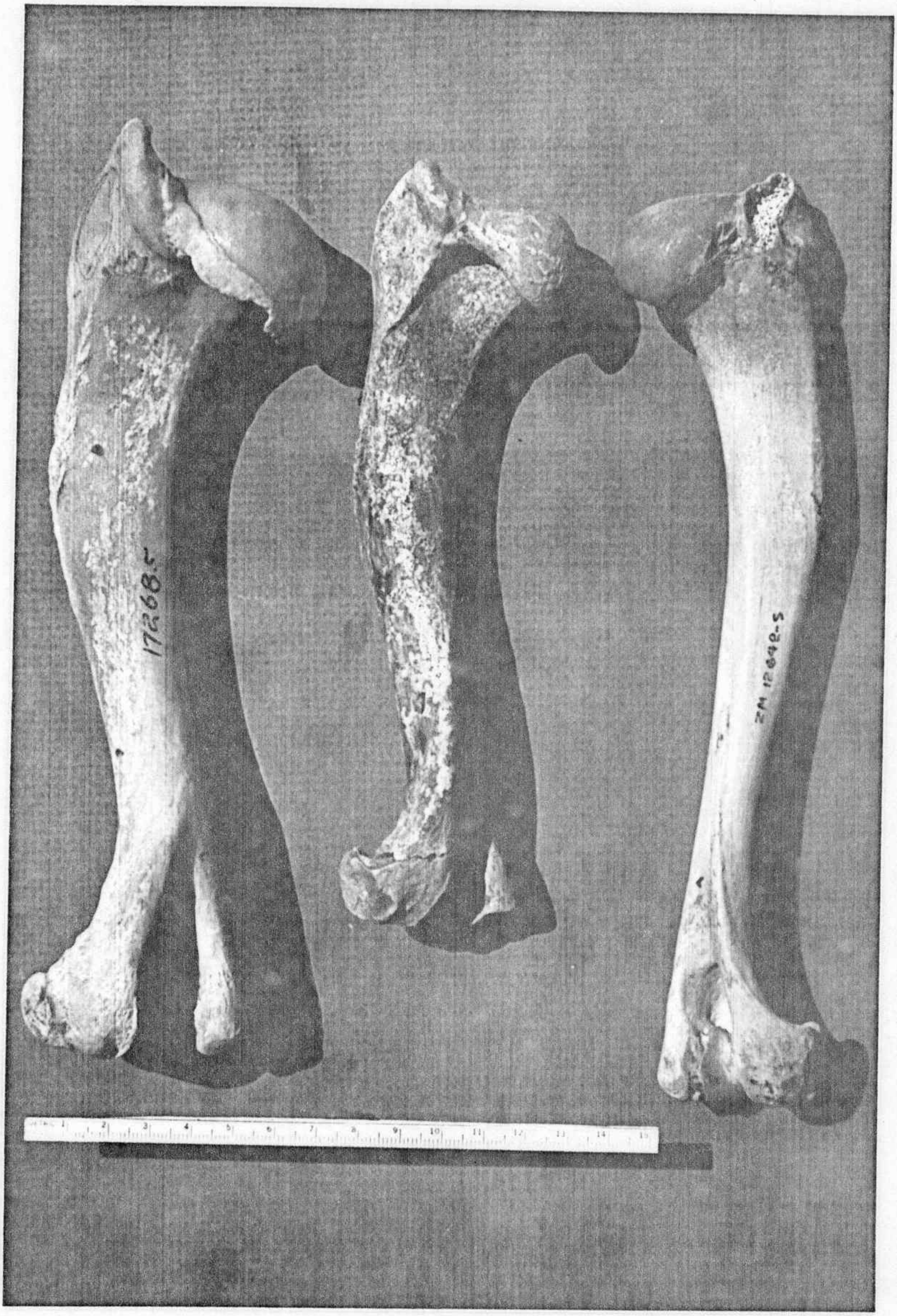
17268.5
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Plate 8. Posterior view of left radii: (left) <u>Crocuta crocuta</u>, USNM 172685; (center) <u>Aelurodon taxoides</u>, UNSM 46815; (right) <u>Canis lupus</u>, UNSM-ZM 12642-S.

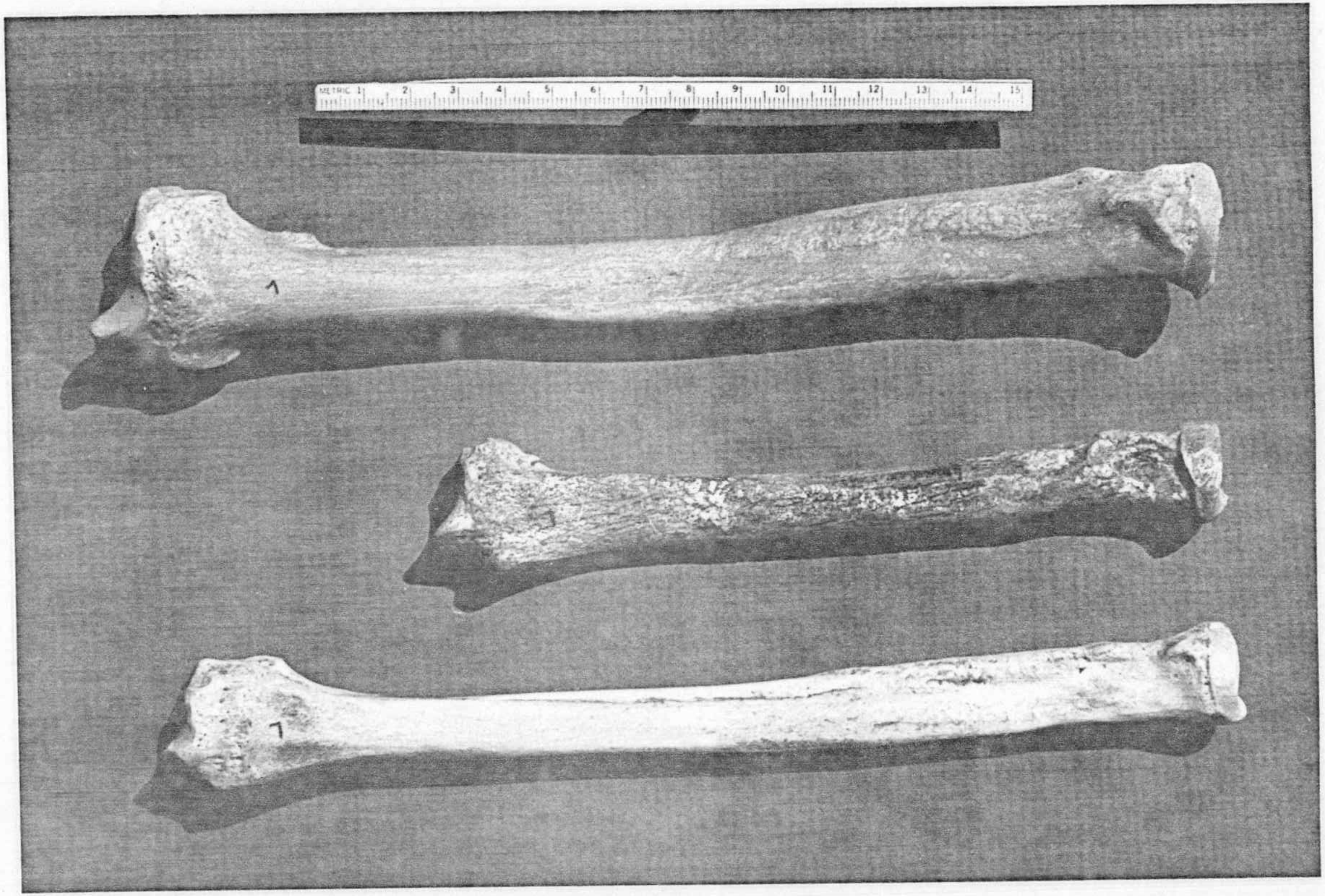
METRIC 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15

Plate 9. Antero-lateral view of right ulnae: (left) *Crocuta crocuta*, USNM 172685; (center) *Aelurodon taxoides*, UNSM 46815; (right) *Canis lupus*, UNSM-ZM 12642-S. The brackets show the length of attachment for the interosseous ligament.

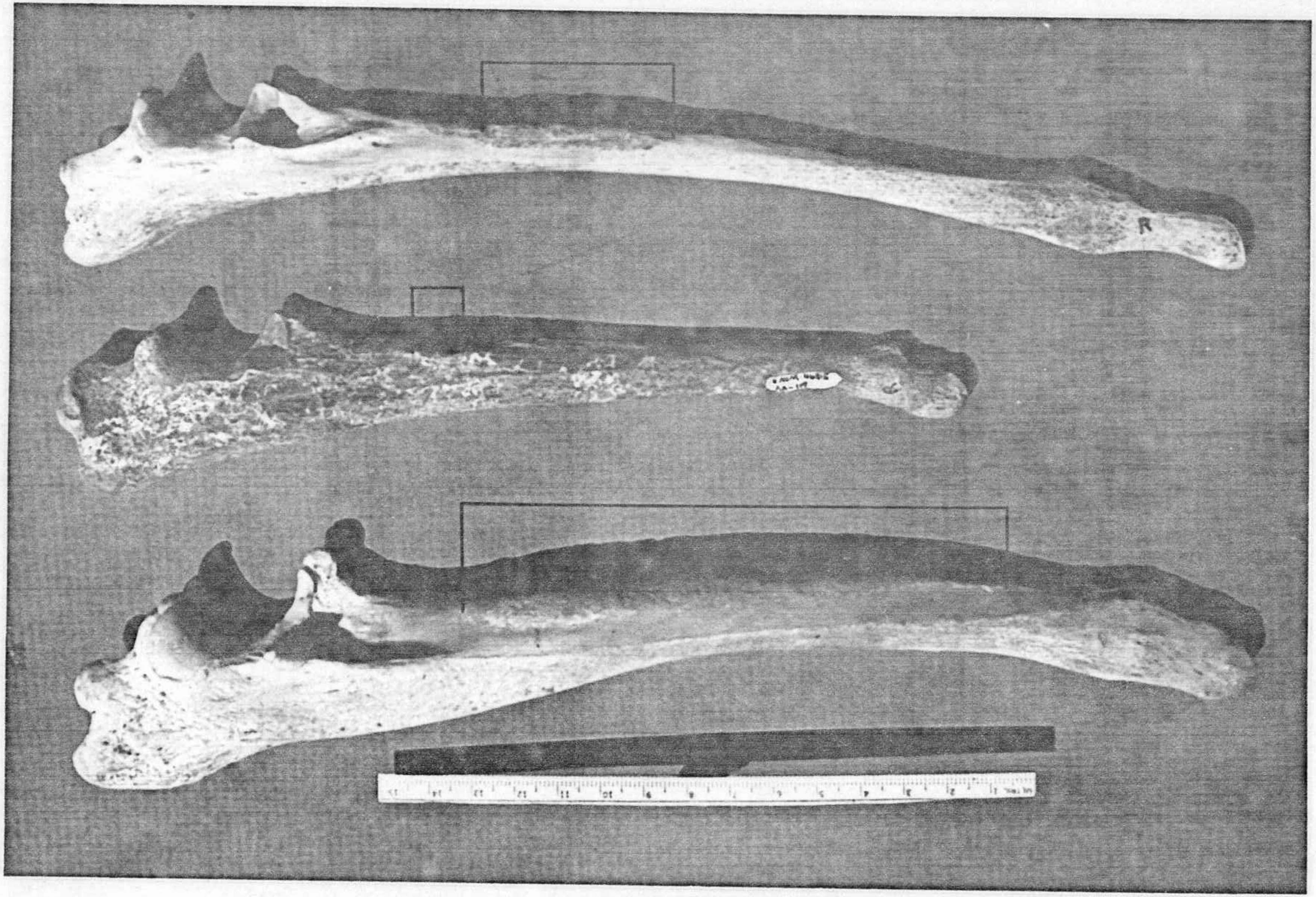

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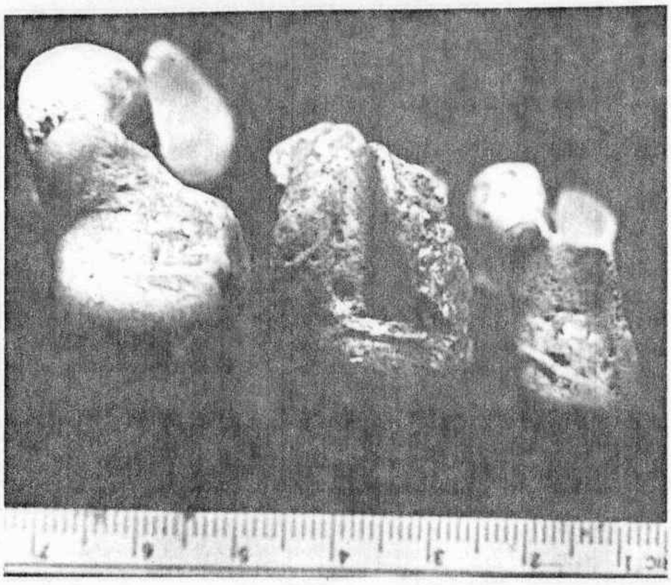
Plate 10. (A)- Dorsal view of olecranon process of left ulnae: (left) *Crocuta crocuta*, USNM 172685; (center) *Aelurodon taxoides*, UNSM 46815; (right) *Canis lupus*, UNSM-ZM 12642-S.

(B)- Lateral view of right pelves: (above) *Canis lupus*, UNSM-ZM 12642-S; (below) *Aelurodon taxoides*, UNSM 46815.

(C)- Right lateral view of pelvis, *Crocuta crocuta*, USNM 172685.



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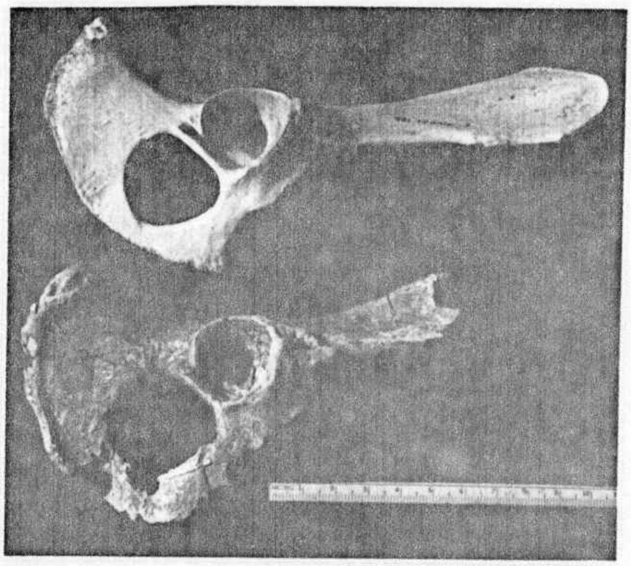

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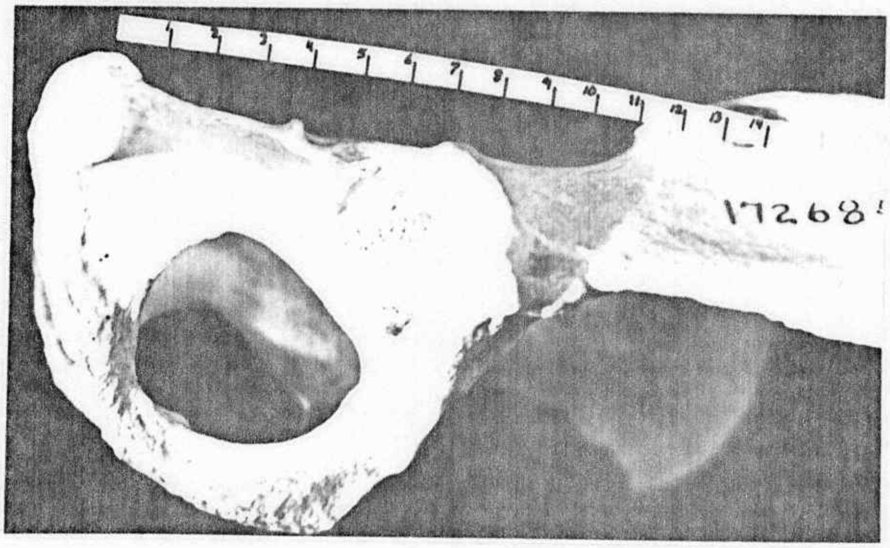

C

Plate 11. Anterior view of right femora: (left) *Crocuta crocuta*, USNM 46815; (center) *Aelurodon taxoides*, UNSM 46815; (right) *Canis lupus*, UNSM-ZM 12642-S.

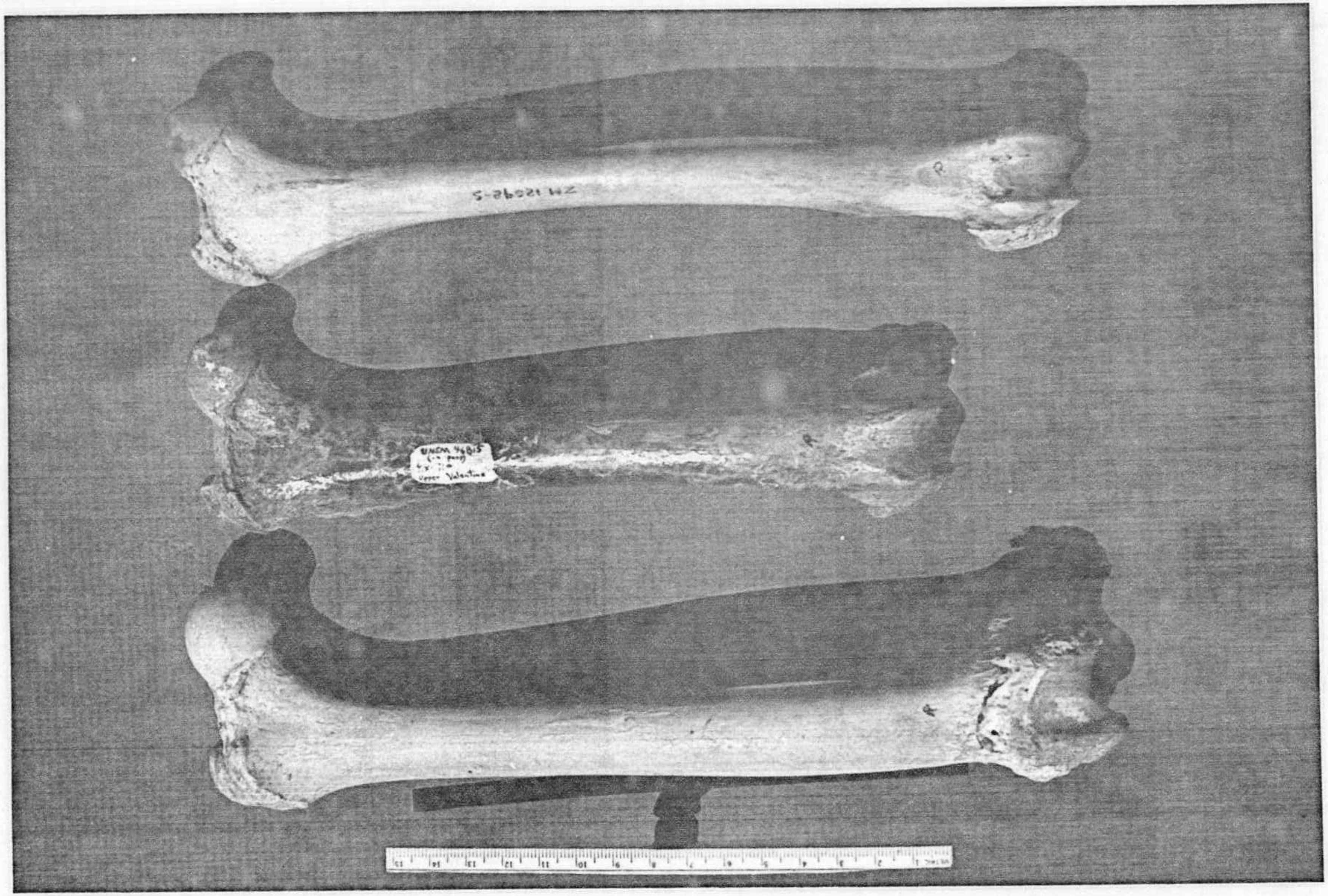
UNSM 46815
Upper Valentine
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Plate 12. Anterior view of tibiae: (left) *Crocuta crocuta*, USNM 172685; (center) *Aelurodon taxoides*, UNSM 46815; (right) *Canis lupus*, UNSM-ZM 12642-S.

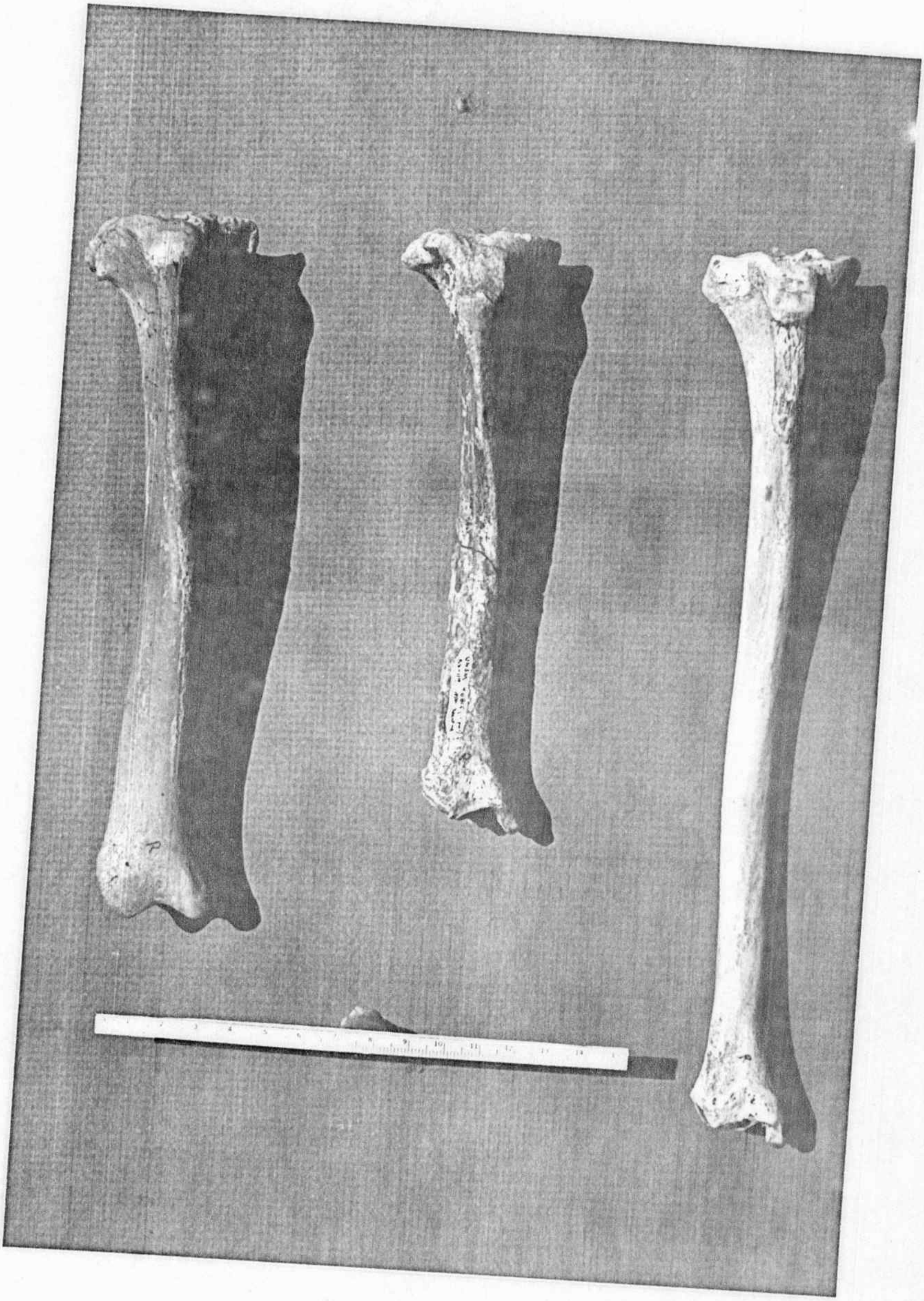
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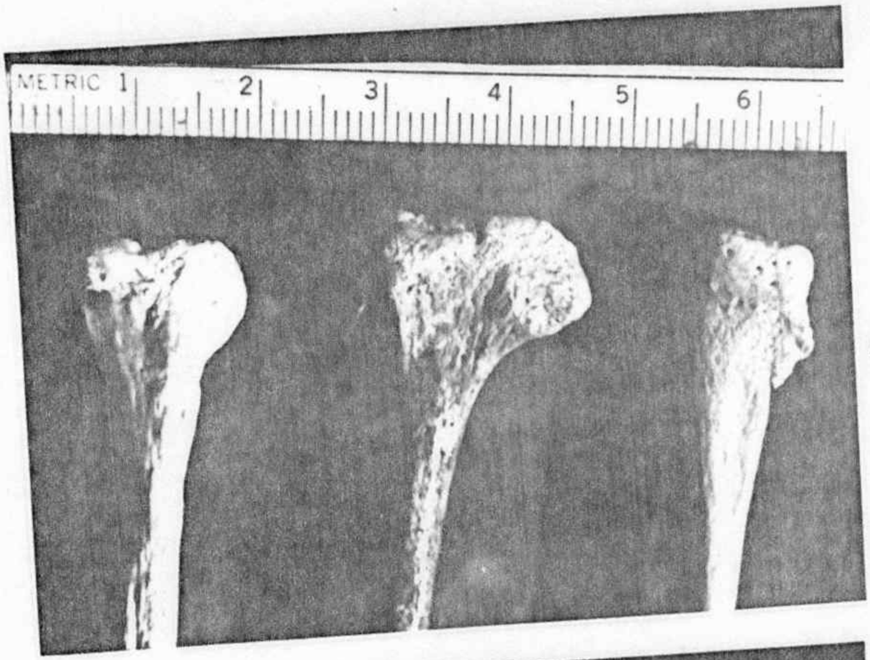
Plate 13. (A)- Lateral view of proximal end of fibulae: (left) *Crocuta crocuta*, USNM 172685; (center) *Aelurodon taxoides*, UNSM 46815; (right) *Canis lupus*, UNSM-ZM 12642-S.

(B)- Medial view of distal end of fibulae: (left) *Crocuta crocuta*, USNM 46815; (center) *Aelurodon taxoides*, UNSM 46815; (right) *Canis lupus*, UNSM-ZM 12642-S.

(C)- Anterior view of patellae: (left) *Crocuta crocuta*, USNM 172685; (right) *Aelurodon taxoides*, UNSM 46815.



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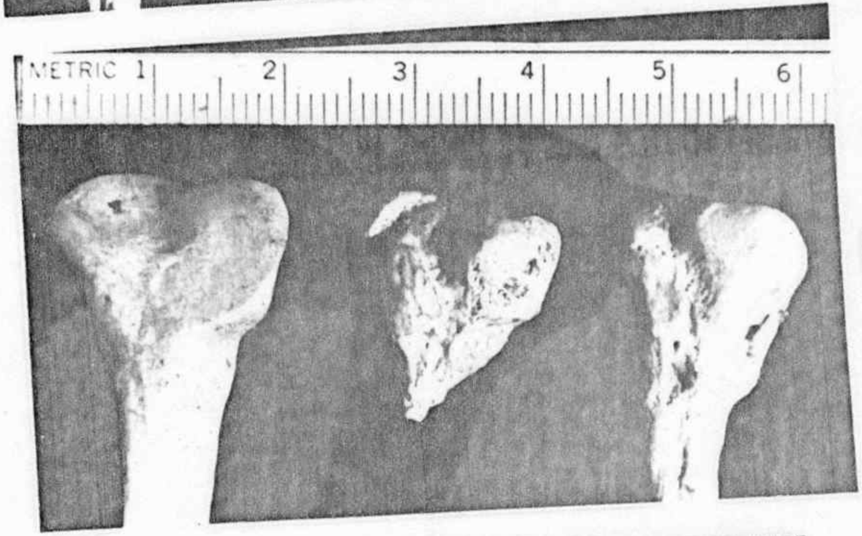

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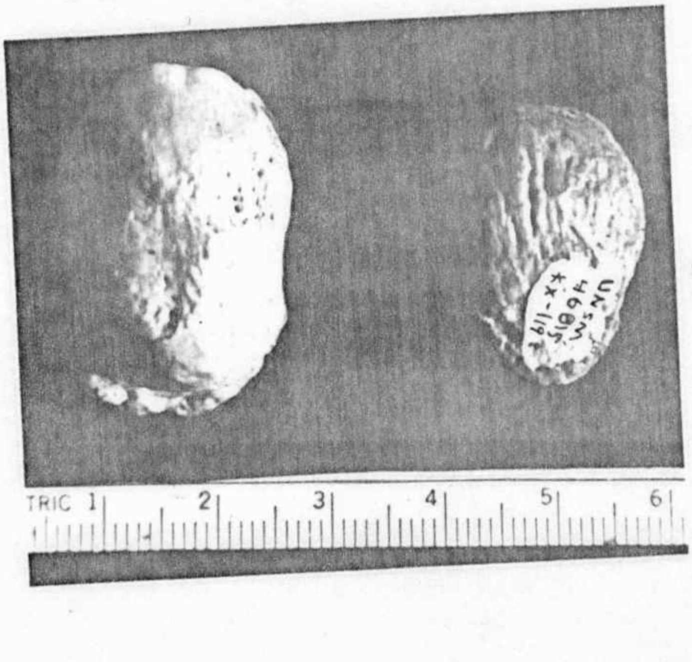
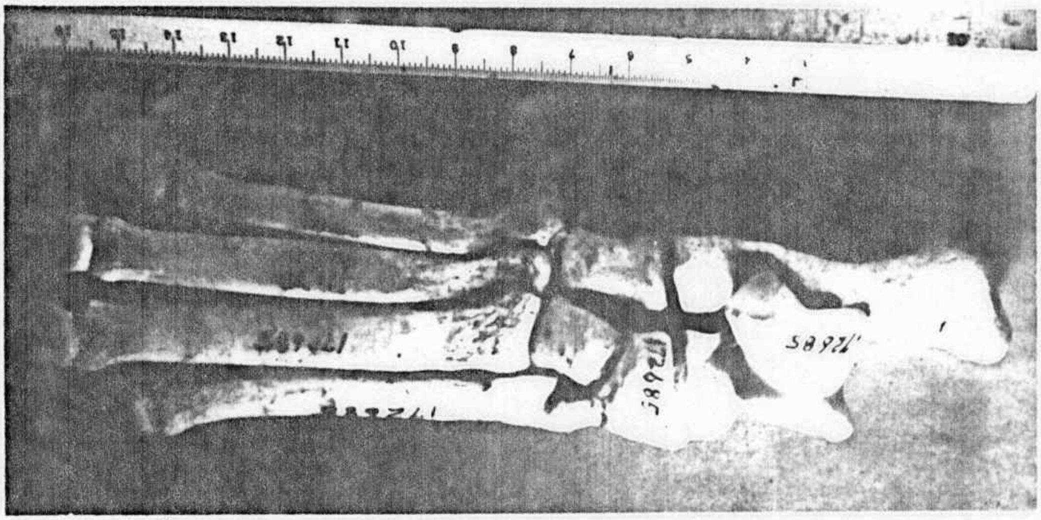


C

Plate 14. Anterior views of right hind feet. (A) *Crocuta crocuta*, USNM 172685; (B) *Aelurodon taxoides*, UNSM 46815; (C) *Canis lupus*, UNSM-ZM 12642-S.



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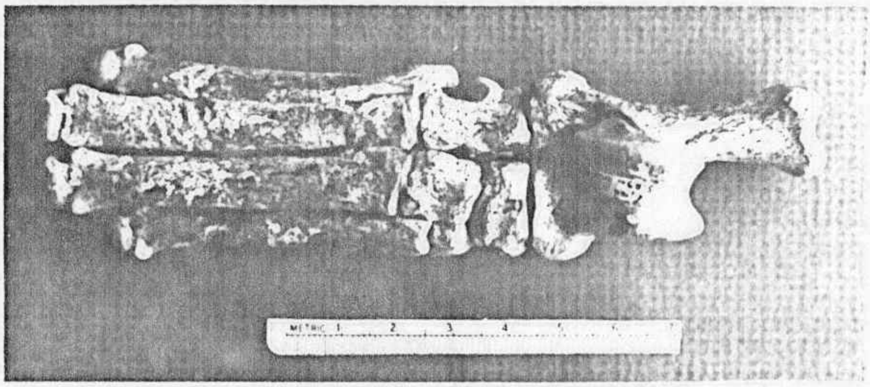

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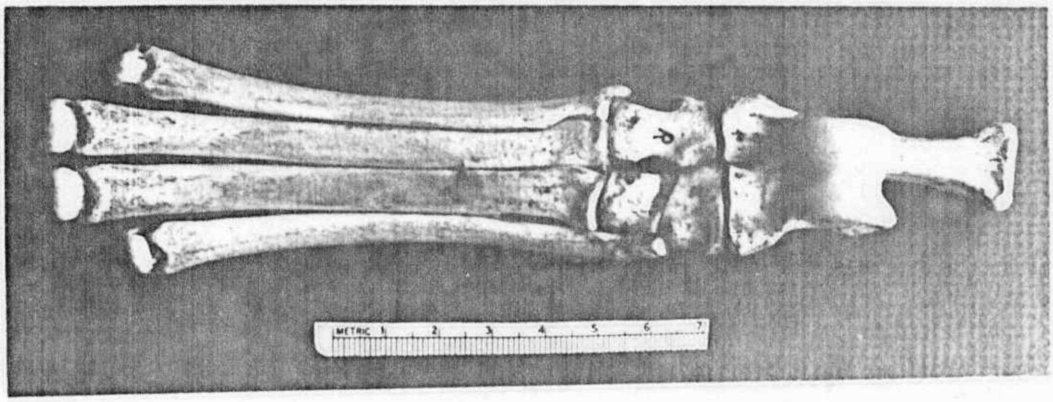
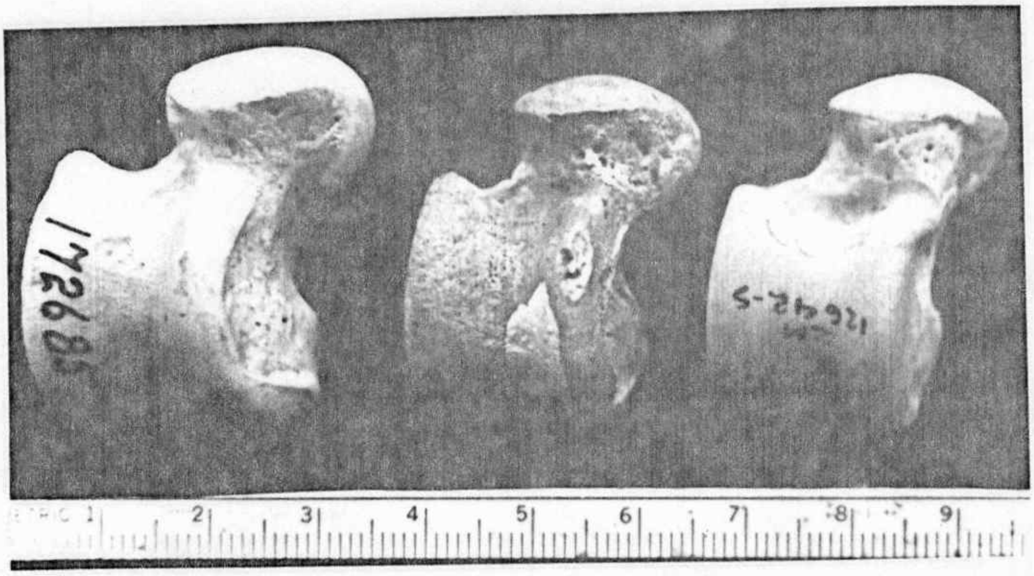


C

Plate 15. (A) Dorsal view of left astragalus: (left) Crocuta crocuta, USNM 172685; (center) Aelurodon taxoides, UNSM 46815; (right) Canis lupus, UNSM-ZM 12642-S.

(B) Ventral view of left astragalus: same specimens and order as (A).

(C) Dorsal view of left calcaneum: same order and specimens as (A).



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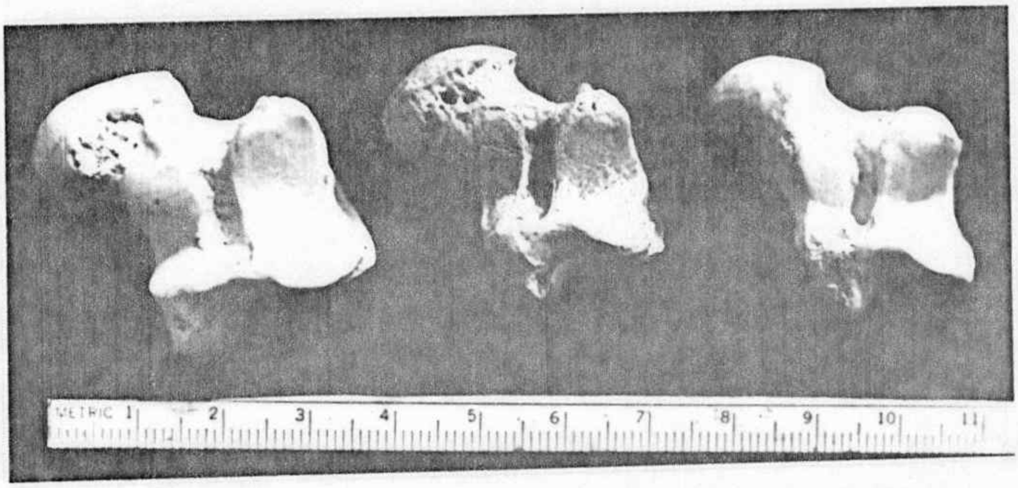

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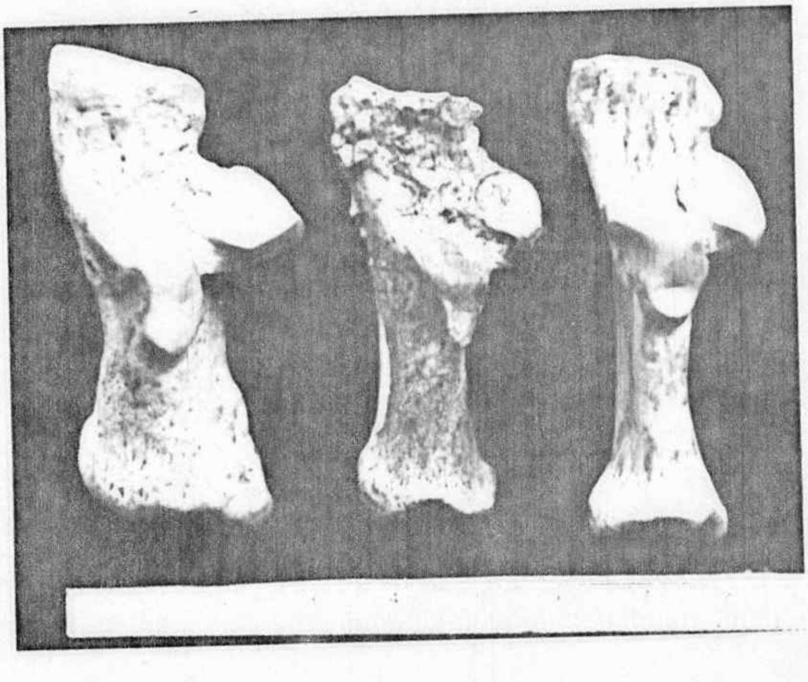
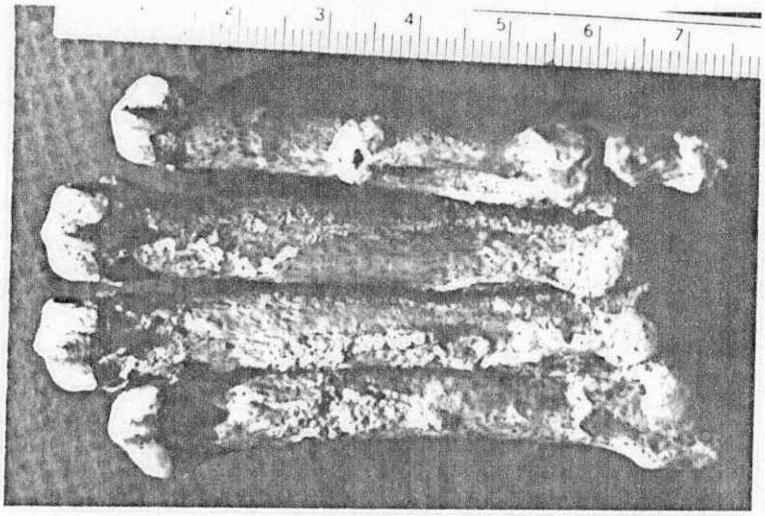


C

Plate 16. (A)- Ventral view of right metatarsals of *Aelurodon taxoides*, UNSM 46815. Note relatively unreduced Mt. I.

(B)- Dorsal view of phalanges: (below) *Crocuta crocuta*, USNM 172685; (center) *Aelurodon taxoides*, UNSM 46815; (above) *Canis lupus*, UNSM-ZM 12642-S.

(C)- Lateral view of terminal phalanges: (left) *Crocuta crocuta*, USNM 172685; (right) *Aelurodon* sp., UNSM 4476.



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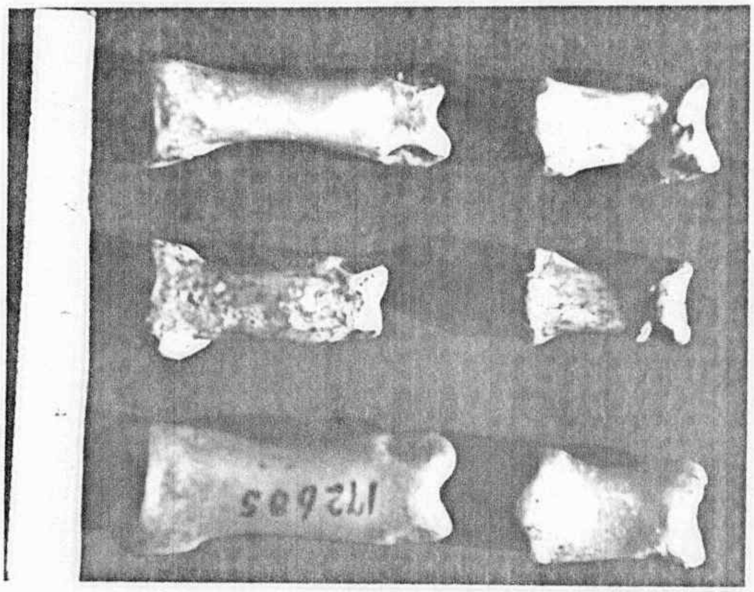

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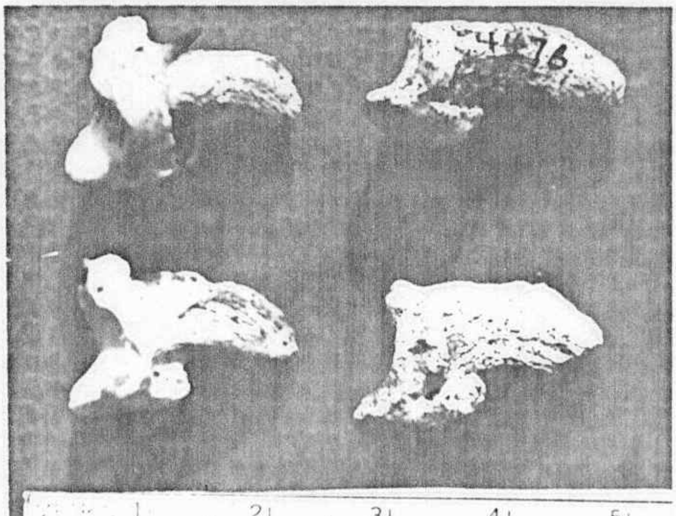


C

Plate 17. (A)- Dorsal view of right pisiform: (left) *Aelurodon taxoides*, UNSM 46815; (right) *Canis lupus*, UNSM-ZM 12642-S.

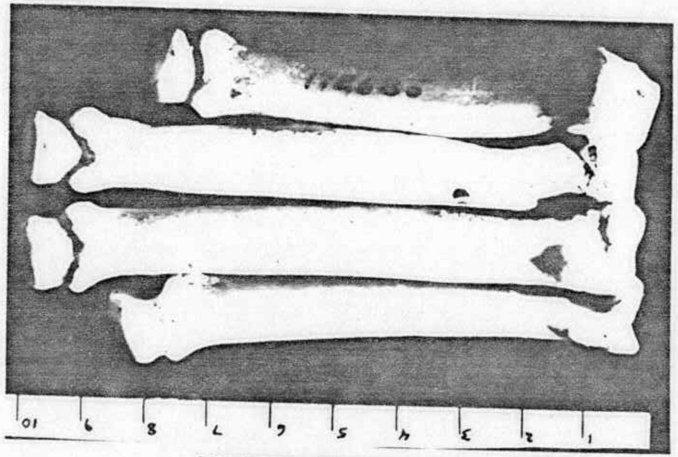
(B)- Dorsal view of metacarpals, *Crocuta crocuta*, USNM 172685.

(C)- Dorsal view of metacarpals III and V, *Aelurodon taxoides*, UNSM 46815.

(D)- Dorsal view of metacarpals, *Canis lupus*, UNSM-ZM 12642-S.

(E,F)- Fractured and rehealed metacarpals, *Aelurodon* sp., UNSM 4476. (E) Dorsal view. (F) Side view.

(G,H)-(Left) Arthritic navicular, *Aelurodon taxoides*, UNSM 46815. (Right) Fractured and rehealed phalanx, *Aelurodon* sp., UNSM 4476. (G) Dorsal view. (H) Ventral view.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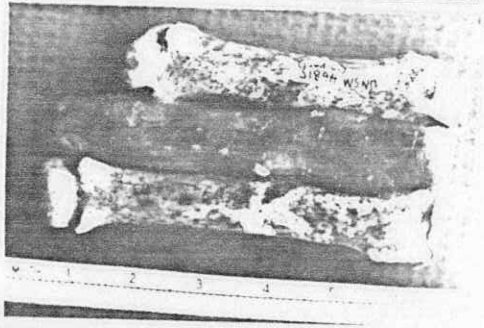
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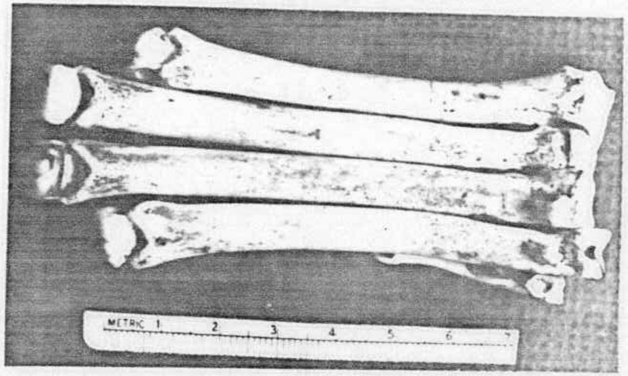
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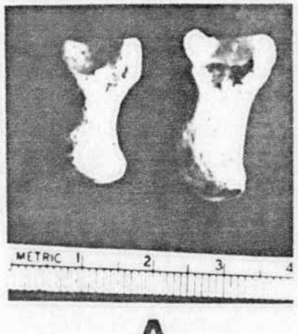
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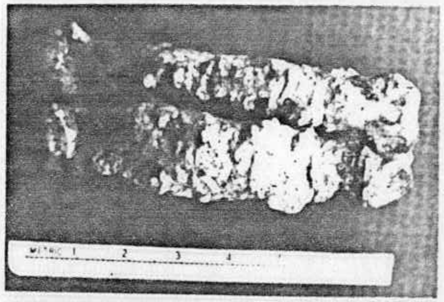
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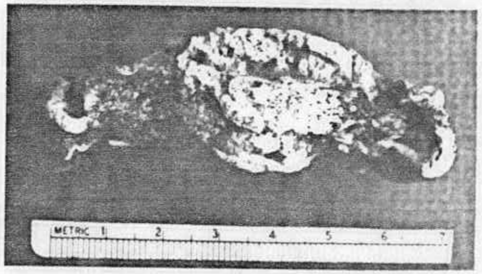
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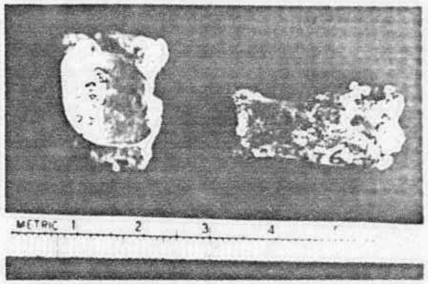
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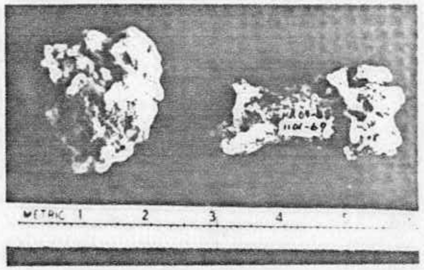
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