SEPARATUM

ACTA ZOOLOGICA FENNICA

A HISTORY OF COYOTE-LIKE DOGS (CANIDAE, MAMMALIA)

BJÖRN KURTÉN

HELSINKI — HELSINGFORS
1974

ACTA ZOOLOGICA FENNICA 140
EDIDIT
SOCIETAS PRO FAUNA ET FLORA FENNICA

A HISTORY OF COYOTE-LIKE DOGS (CANIDAE, MAMMALIA)

BJÖRN KURTÉN

Dedication

This paper is dedicated, with gratitude and admiration, to the memory of Claude W. Hibbard, leading student of North American Pleistocene mammals.

HELSINKI — HELSINGFORS
Oct. 1974

FI ISSN 0001—7299

Abstract

KURTÉN, BJÖRN (Department of Zoology and Department of Geology and Paleontology, University of Helsingfors): A History of Coyote-Like Dogs (Canidae, Mammalia). — Acta Zool. Fennica 140:1—38. 1974.

Fossil North American coyotes are listed and described under the names *Canis lepophagus* Johnston (Blancan), *C. priscolatrans* Cope (late Blancan and Irvingtonian) and *C. latrans* Say (Rancholabrean and Recent). Gradual evolutionary changes in size and in the proportions of the limbs, skulls and teeth are noted. The European *C. arnensis* Del Campana is regarded as a coyote probably conspecific with *C. priscolatrans*. A link between the European and North American populations is furnished by a number of Asiatic fossils. A relationship between *C. arnensis* and jackals is regarded as improbable.

Author's address: Dept. of Zoology, University of Helsingfors, N. Järnvägsgatan 13, SF-00100 Helsingfors 10, Finland.

Contents

I. INTRODUCTION

This is a comparative study of fossil and recent coyote-like canids in North America and Eurasia. The living coyote, *Canis latrans* Say, is evidently derived from a Blancan species in North America known as *C. lepophagus* Johnston, and originally described from Cita Canyon, Texas, but later identified in many other Blancan faunal associations. The gap between the ancestral and descendant form is bridged by Irvingtonian and latest Blancan fossils for which the name *C. priscolatrans* Leidy is availab-le. Wether in fact two fossil species can be upheld is somewhat uncertain and, if not, Leidy's name has priority.

In the Villafranchian of the Old World, several species of canids have been discovered; they have been related to wolves and jackals. In Europe there lived at this time three species of the genus *Canis: C. falconeri* Major, a large form; *C. etruscus* Major, a medium-sized form usually regarded as ancestral to the living Holarctic wolf *C. lupus* Linné; and *C. arnensis* Del Campana, a still smaller species that has usually been regarded as a jackal (e.g. KURTÉN 1968:109, TORRE 1967:136). More detailed comparisons, however, show that it should be regarded as a coyote. There is also Asiatic material belonging to this group. Thus it seems that for some time in the Pleistocene there was a Holarctic coyote population, which then became extinct in the Old World.

Acknowledgements. The material has been studied in the last decade during visits to various institutions in Europe and North America, as detailed in the survey of material examined. The study has been supported by the University of Helsinki, the Academy of Finland, the Societas Scientiarum Fennica, Harvard University, and the National Science Foundation of the United States of America. While the main part of the material was measured by myself, a few data have been taken from the literature, and measurements of two samples were taken according to my instructions by two other persons. Dr. E. Anderson measured part of the Recent sample of *C. latrans* in the National Museum of Natural History, Washington, and Mr. Martin E. McPike measured all of the canid material from Moonshiner Cave and Middle Butte Cave in the Idaho State University Museum, Pocatello. Many persons have helped by permitting me to study material in their care, among them Drs. A. Azzaroli, C. C. Black, W. A. Clemens, W. W. Dalquest, M. Dawson, T. Downs, G. Edmund, J. E. Guilday, O. Hawksley, C. A. Hibbard, J. Hürzeler, F. A. Jenkins, A. Johnels, K. A. Joysey, B. Lawrence, E. S. Lindsay, E. L. Lundelius, P. O. McGrew, P. Mein, J. Paradiso, B. Patterson, C. E. Ray, C. A. Repenning, H. Richards, K. Richey, D. E. Savage, C. B. Schultz, G. E. Schultz, E. Shapiro, B. Slaughter, A. J. Sutcliffe, R. H. Tedford, W. Turnbull, E. A. Vangengeim, S. D. Webb J. A. White and J. A. Wilson. Figure 1 is by Margaret Lambert. To all these persons and institutions I wish to express my sincere thanks.

Abbreviations

The following abbreviations have been used in the present paper:

ANSP, Academy of Natural Sciences, Philadelphia
BW, blade width
C, canine tooth (with super- or subscript)
CA, sample of *Canis arnensis*
CBL, condylobasal length of skull
CC, Çita Canyon sample
CL, sample of *Canis lupaster*
CM, Carnegie Museum, Pittsburgh
CMS, Central Missouri State College, Warrensburg
EP, sample from Idaho caves
F:AM, Frick Laboratory, American Museum of Natural History, New York
FM, Field Museum of Natural History, Chicago
FSL, Faculty of Science, Lyon
IGF, Institute of Geology, Florence
IGM, Institute of Geology, Academy of Sciences, Moscow
IR, Irvingtonian sample
ISUM, Idaho State University Museum
KUM, Kansas University Museum, Lawrence
L, left (in specimen list); length
LACM, Museum of Natural History, Los Angeles
LM, length of mandible
M, molar (with super- or subscript); mean
MC, metacarpal
MT, metatarsal
MU, Midwestern University, Wichita Falls, Texas
N, number of specimens
NHMB, Museum of Natural History, Basel
P, premolar (with super- or subscript)
R, right (in specimen list)
RE, Recent sample of *Canis latrans*
RL, Rancholabrean sample
s, standard deviation
SF, Santa Fe sample
SMU, Southern Methodist University, Dallas
TMM, Texas Memorial Museum, University of Texas, Austin
UA, University of Arizona, Tucson
UC, University of California, Museum of Paleontology, Berkeley
UCM, University of Colorado Museum, Boulder
UF, University of Florida, Florida State Museum, Gainesville
UMMP, University of Michigan, Museum of Paleontology, Ann Arbor
UNSM, University of Nebraska State Museum, Lincoln
USNM, National Museum of Natural History, Washington, D. C.
UW, University of Wyoming, Laramie
V, coefficient of variation
W, width
WT, West Texas State University, Canyon

II. MATERIAL

The following is an annotated list of localities and specimens of coyotes and coyote-like dogs. References are given to locality or faunal descriptions. The probable age for each sample is stated.

Coyotes are quite variable in size. Notes on the size of specimens found are given for most localities; more exact data are given in the tables of measurements. The standard of comparison has been the Cita Canyon coyote, representing an average-sized Blancan form.

Blancan

Hagerman, Twin Falls Conty, Idaho (BJORK 1970). UMMP V 54995 R, V 52280, V 56401 L maxillae, V 53910 RL, V 53452 L, V 50249, V 56282 R mandibles, V 55007 MC 3, all Glenns Ferry Formation, V 45222 L mandible (P_2 abnormality in FINE 1964), Hagerman Formation; LACM 122/1343, 118/1246[3] L, —1 R mandibles, 122/1343 L humerus, L MC 2, R MC 4, R MT 4, all Snake River. Additional material (not seen) in Bjork 1970: 13—14. Age: Early Blancan. A small to medium-sized form, no heterogeneity indicated.

Rexroad, Meade Country, Kansas (HIBBARD 1938, 1941b). UMMP 28442 M^1, 37132 P^4, M^1, V 56775 M^2, 45586 L Calcaneum. Age: Early Blancan. A comparatively small form.

Beck Ranch, Scurry County, Texas (DALQUEST 1972). MU 8651 R mandible, 8662 M^2. Age: Early Blancan. Small to medium.

Anita, Coconino County, Arizona (HAY 1921). Not seen, determined as *C. latrans* by Hay. Age: Blancan.

Grand View, Owyhee County, Idaho (SHOTWELL 1970). USNM 1186 M_1 (See also BJORK 1970). Age: Late Blancan. Size medium.

Sand Draw, Brown County, Nebraska (SKINNER & HIBBARD 1972). FM P 15511 RL P^4, UMMP V 57321 R maxilla, RL mandibles. Age: Late Blancan. Size medium.

Lisco, Morrill County, Nebraska (BARBOUR & SCHULTZ 1937). UNSM 26114, 907—38 L mandibles. Age: Blancan. Very small size of both specimens striking.

Broadwater, Morrill County, Nebraska (BARBOUR & SCHULTZ 1937). UNSM 26111, 26112 skulls, 26113 L maxilla, — P^4, M^1, M_1, M_2, R mandible, 26116 mandible. Age: Late Blancan. This fauna is usually regarded as identical with that from Lisco (HIBBARD 1970:414); the Broadwater coyote, however, is of average size, and markedly larger than that from Lisco.

Deer Park, Meade County, Kansas (HIBBARD 1938). UMMP 31945 LR M^1. Age: Late Blancan. Size fairly large.

Cita Canyon, Randall County, Texas (JOHNSTON & SAVAGE 1955). WT 881 skull, type *C. lepophagus* Johnston 1938, 722, 760, 2523 skulls, 1936 palate, 558, 560 2 L, 560 3 R maxillae, 722, 2287 2 RL, 558, 559, 560, 1027, 2631 13 L, 558, 559, 560, 1027, 2423, 2494, 1617 17 R mandibles, 560 isolated teeth. Age: Late Blancan. A homogeneous sample, representing the average-sized Blancan coyote.

Red Light Bolson, Hudspeth County, Texas (AKERSTEN 1970). TMM 40664—3, mandible without teeth, —10 L MC 5, —11 L radius. Age: Late Blancan.

Red Corral, Proctor Ranch, Oldham County, Texas (G. E. SCHULTZ, pers. com.). WT 4241 L, 4242 RL mandibles. Age: Late Blancan. The two specimens differ markedly in size but since both are within the variation range of *C. lepophagus,* and the large specimen is much smaller than wolf-like forms such as *C. texanus,* both are here regarded as coyote.

Curtis Ranch, Cochise County, Arizona (GAZIN 1942). USNM 12862 skull and mandible, type *C. edwardi* Gazin 1942; UA 1632 L, 1313, 1563, 3231 R mandibles. Age: Late Blancan (E. H. Lindsay, pers. com.). The type specimen is a very large individual on a par with the biggest coyotes from Rancho La Brea. The University of Arizona mandibles are somewhat smaller and so the apparent deviation from *C. lepophagus* is somewhat reduced; still, the Curtis Ranch coyote average very large.

Santa Fe 1, Gilchrist County, Florida (WEBB, MS.). UUF 10424 R, 10423, 10837 3 L mandibles, 7378 2 R humeri, — 4 L, radii, L tibia. Age: Late (?) Blancan. Size medium or slightly above.

Miñaca Mesa, Chihuahua, Mexico (REPENNING 1962). LACM 105/149, 1680, L mandibles. Age: Blancan. SAVAGE (1955) referred proboscidean material from this site to the early Blancan. The coyote locality has yielded *Nannippus phlegon, Equus,* and *Hipparion* (?); preservation of coyote bones is similar to that of *N. phlegon;* a late Blancan age is possible (T. DOWNS and L. BARNES, pers. com.). A large form, similar to that from Curtis Ranch.

Irvingtonian

Irvington, Alameda County, California (SAVAGE 1951). UC 38805 mandible, type *C. irvingtonensis* Savage 1951. Age: Irvingtonian. Like most Irvingtonian coyote, a large, powerful form.

Rome Beds, Malheur County, Oregon (WALKER & REPENNING 1966). USNM 23898 skull, Loc. 12 (fig. 1). Age: Probably Irvingtonian. Size very large.

Vallecito Creek, Anza-Borrego Desert, California (DOWNS & WHITE 1968). LACM 1638/6236 L, 6050 R, 1854/8235 LR, 1193/3258 LR mandibles, 1317/3805 R MT 2—5. According to the graph in DOWNS & WHITE 1968:44, material of »*Canis,* small» comes mainly from the lower part of the Vallecito Creek sequence and the modal age may perhaps be set as early Irvingtonian. The size is generally intermediate between the Cita and Irvington dogs.

Inglis, Citrus County, Florida (S. D. WEBB & J. KLEIN, pers. com.). UF — 2 R maxillae, teeth, radius, calcaneum, MC 3. Age: Irvingtonian. The size is, again, strikingly large.

Borchers, Meade County, Kansas (HIBBARD 1941a). KUM — M^1, UMMP V 33800 mandible fragments. Age: Irvingtonian, probably Aftonian (C. W. HIBBARD, pers. com.). Size much like Vallecito.

Rock Creek, Briscoe County, Texas (TROXELL 1915). UC V-2576 R MC 2; WT 2303 M^2. Age: Irvingtonian, probably Kansan (HIBBARD 1970:421). Size small.

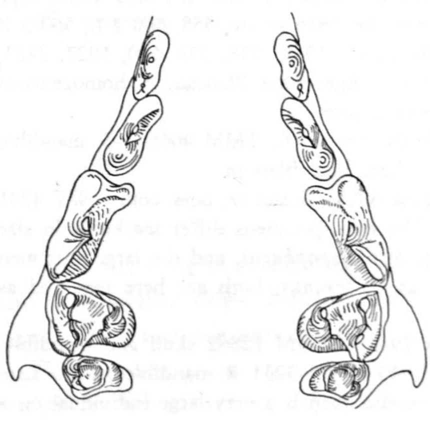

FIG. 1. USNM 23898, *Canis priscolatrans,* Rome Beds, Malber County, Oregon. Upper dentition, occlusal aspect. 2/3 natural size.

Gilliland, Baylor and Knox Counties, Texas (HIBBARD & DALQUEST 1966). UMMP 46464 MC. Age: Irvingtonian, probably Kansan.

Port Kennedy Cave, Montgomery County, Pennsylvania (COPE 1899). ANSP 57 R P^4, M^1, M^2 cotypes *C. priscolatrans* Cope 1899. Age: Irvingtonian. This is a large coyote, closely comparable to *C. edwardi*, *C. irvingtonensis,* and, for instance, the Rome and Inglis dogs. In addition, a wolf-sized form is known from this cave; it was compared by Cope with *C. dirus*.

Arkalon Gravel Pit, Seward County, Kansas (HIBBARD 1953). UMMP 29068 partial skeleton with RL radii and femora, tibia, calcanea, R MT 3, L MT 5. Age: Early Yarmouthian. A large, heavy form rather similar to the Inglis dog.

Mullen, Cherry County, Nebraska (SCHULTZ & MARTIN 1970:347, Loc. Cr—10). UNSM 26115 R mandible, 39218 L MC 4—5. Age: Late Irvingtonian (perhaps latest Yarmouthian or earliest Illinoian). Smaller than most other Irvingtonian coyotes.

Medicine Hat, Alberta (STALKER & CHURCHER 1970). Deposits of Kansan age by the South Saskatchewan River near Medicine Hat have yielded remains that were identified preliminarily as *Canis* cf. *latrans*.

Rancholabrean and Postglacial

American Falls, Power County, Idaho (GAZIN 1935). ISUM 17592 R, L mandibles. Age: Illinoian. Size large.

Fossil Lake, Lake County, Oregon (ELFTMAN 1931). UC 2972 R mandible, 78645 L MT 3, 78646 L MT 4, — LR radius fragments. Age: Illinoian. Size relatively small.

Hay Springs, Sheridan County, Nebraska (MATTHEW 1918). Not seen. Age: Illinoian.

Berends, Meade County, Kansas (STARRETT 1956). UMMP 29010 MT, 33319 mandible frag. Age: Illinoian.

Adams, Meade Country, Kansas. HIBBARD & TAYLOR 1960). UMMP 29021 L mandible. Age: Illinoian. Size relatively large.

Cumberland Cave, Allegany County, Maryland (GIDLEY & GAZIN 1938). USNM 7660 skull fragment. Age: Illinoian. Size relatively large.

Slaton Quarry, Lubbock County, Texas (DALQUEST 1967). MU 5043 R mandible, 6522 L maxilla, 6445 calcaneum 4630 L MT 5, 4627 R MC 3. Age: Illinoian (DALQUEST 1967) or early Sangamonian (HIBBARD 1970:405). The extremely small size of some of these remains was commented upon by Dalquest. Only the maxilla seems to be of »normal» size.

Cragin Quarry, Meade County, Kansas (HIBBARD 1970). KUM 5968 M^1. Age: Sangamonian. Size medium.

San Josecito Cave, Nuevo León, Mexico (Stock 1942). LACM 192/2246, 10574, 10576, 10577, 10578, 10579, 10580, 10586 R mandibles. Age: Wisconsin. Lack of time restricted the study to a series of right mandibles. The size is, on an average, larger than that of Recent coyote.

Valsequillo near Puebla, Mexico (KURTÉN 1967). University of Mexico, L mandible. Age: Rancholabrean. The fauna is heterochronic with an admixture of earlier forms; the coyote is thought by GUENTHER (1967) to belong to the late Pleistocene assemblage. The size is large.

Rancho La Brea tar pits, Los Angeles County, California (MERRIAM 1912). Time did not permit a thorough study of the great sample from this locality, which represents a minimum number of 239 individuals (MARCUS 1960). The following token sample was measured. UC 12249 type *C. andersoni* Merriam 1910, 24455, 24491, 24509 skulls, 19791 maxilla; FM P 14724 skull, 12529 palate, 12505 R, 12479, 14724 L mandibles, 12402, 14724 humeri, 12506, 3738 5 radii, 12506, 3737 4 femora, 12506 3 tibiae. From this locality also comes the type (UC 10842, MERRIAM 1912:256) of *C. orcutti* Merriam 1910. Age: Wisconsin. Rancho La Brea coyote average larger than Recent.

McKittrick tar pits, Kern County, California (SCHULTZ 1938). UC 518 L mandible, R maxilla. Age: Wisconsin. This may well represent a population similar to that of La Brea.

Tranquillity, Fresno County, California (HEWES 1943, 1946, BERGER et alii 1971). UC 78321 R mandible, 78322 R maxilla. Age: Late Wisconsin. Smaller than typical La Brea coyote.

Samwel Cave, Shasta County, California (GRAHAM 1959). UC 8856 M^1, 10072 L mandible. Age: Wisconsin. These specimens are very large. Graham describes a skull fragment CAS 36497 of more moderate size.

Hawver Cave, Eldorado County, California (STOCK 1918). Not seen. Age: Wisconsin. According to Stock's description, the specimen, a damaged skull, is similar to Recent California valley coyote *C. latrans ochropus.*

Costeau Pit, Orange County, California (MILLER 1971). Not seen. Age: Wisconsin. The sample (14 specimens) is stated to be indistinguishable from Recent and late Pleistocene *C. latrans.*

La Mirada, Los Angeles and Orange Counties, California (MILLER 1971). Not seen. Age: Wisconsin.

Papago Springs Cave, Santa Cruz County, Arizona (SKINNER 1942). F:AM 42800 skull, type *C. caneloensis* Skinner 1942 (not seen, data from Skinner). Age: Wisconsin. Large.

Ventana Cave, Santa Cruz County, Arizona (HAURY 1950). Not seen. Age: Wisconsin.

Double Adobe, Cochise County, Arizona (HAURY et alii 1959). UA 3334 L mandible. Age: Late Wisconsin. Small.

Tule Springs, Clark County, Nevada (MAWBY 1967). UC 64271 R mandible, 64362 P^4, 64354 femur. Age: Late Wisconsin. Size medium.

Burnet Cave, Eddy County, New Mexico (SCHULTZ & HOWARD 1935). ANSP 13454 P^4, 13455, 13583 L, 13561, 13997 R mandibles, 13994 L MC 3. Age: Wisconsin. Size near that of modern coyote.

Blackwater Draw, Curry County, New Mexico (STOCK & BODE 1936, LUNDELIUS 1972a). TMM 937-896 M_1, 897 C^s, SMU 2 L mandible, R maxilla, R MC 2, L MC 5. Age: Wisconsin. Large.

Isleta Cave, Bernalillo County, New Mexico (HARRIS & FINDLEY 1964). Not seen. Age: Late Wisconsin or Recent.

Dry Cave, Eddy County, New Mexico (HARRIS, 1970). Not seen. Age: Wisconsin.

Hill-Shuler fauna, Dallas and Denton Counties, Texas (SLAUGHTER 1961, 1966:481). TMM 30907-14 L mandible; SMU 60315 L mandible, type *C. latrans harriscrooki* Slaughter 1961. Age Wisconsin interstadial. Size large.

Clamp Cave, San Saba County, Texas (LUNDELIUS 1967). TMM 1295-1, -3 R, -7 LR mandibles. Age: Wisconsin. Size medium.

Cave without a Name, Kendall County, Texas (LUNDELIUS 1967). TMM 40450-1603, -1609 L, -1608 R mandibles, -345 R tibia. Age: Wisconsin. Size medium.

Levi Shelter, Travis County, Texas (Lundelius 1967). TMM 40449-68 R mandible. Age: Wisconsin. Size medium.

Ingleside Gravel Pit, San Patricio Countrry, Texas (Lundelius, 1972b). TMM 30967-1105 R maxilla. Age: Wisconsin. Size medium.

Laubach Cave, Travis County, Texas (Slaughter 1966). SMU 61269 skull (not seen; data from Slaughter). Age: Wisconsin. Size medium.

Carson Holloway Ranch, San Saba County, Texas (Lundelius, pers. com.). TMM 31036-7 P^4. Age: Wisconsin. The locality (»creek banks at and below Carson Holloway's windmill») has yelded *Mammuthus* and *Bison*. The coyote tooth is of moderate size.

Lubbock Reservoir Site, Lubbock County, Texas (Luadelius 1967). TMM 892- R mandible. Age: Wisconsin. Large.

Ben Franklin, Delta County, Texas (Slaughter & Hoover 1963). Not seen. Age: Wisconsin. »Slightly smaller than the average *C. 1. texanus*» (Slaughter & Hoover 1963: 141).

Clear Creek, Denton County, Texas (Slauhgter & Ritchie 1963). Not seen. Age: Wisconsin, probably same as the Hill-Shuler fauna. The specimen is referred to the same subspecies.

Schulze Cave, Edwards County, Texas (Dalquest et alii 1969). MU 7297 palate, 7298 R mandible, 7304 L MC 3—5, L humerus, L femur, L tibia, 7305 R femur, R tibia. Age: Wisconsin. Size relatively small.

Friesenhahn Cave, Bexar County, Texas (Hay 1920b, Evans 1961). Not seen. Age: Wisconsin.

Quitaque Creek, Motley County, Texas (Dalquest 1964). MU 1604 R tibia. Age: Wisconsin. Small.

Klein Cave, Kerr County, Texas (Roth 1972). Not seen. Age: Late Wisconsin.

Howard Ranch local fauna, Hardeman County, Texas (Dalquest 1965). Not seen Age: Wisconsin.

Afton, Ottawa Countrry, Oklahoma (Hay 1920a). Not seen. Age: Wisconsin.

Chimney Rock Animal Trap, Larimer County, Colorado (M. Hager, pers. com.). UW — R maxilla. Age: Post-Wisconsin. Size medium.

Little Box Elder Cave, Converse Countrry, Wyoming (Anderson 1968). UCM 22286 R mandible, — humerus, radius, R MT 2, 2 L, 1 R MT 3, LR MT 4, L MC 2, L MC 4. Age: Wisconsin. Size medium.

Bell Cave, Albany County, Wyoming (D. Walker, pers. com.). Not seen Age: Wisconsin.

Twin Falls, Twin Falls County, Idaho (Hay 1927:21). UC 34070 M_2. Age: Wisconsin.

Jaguar Cave, Lemhi County, Idaho (Kurtén & Anderson 1972). ISUM, see Kurtén & Anderson 1972, tables 5—7. Age: Late Wisconsin to early Recent.

Moonshiner Cave, Bingham County, Idaho. ISUM, 14 skulls, 9 R, 16 L maxillae, 28 L, 30 R mandibles, isolated teeth, 24 L, 23 R humeri, 23 L, 19 R radii, 19 L, 24 R ulnae, 21 L, 17 R femora, 20 L, 21 R tibiae, 12 L, 12 R astragali, 12 L, 7 R calcanea. Age: Wisconsin to Recent. The cave, a punctured lava blister, is still an active trap for animals. Size medium.

Middle Butte Cave, Bingham County, Idaho. ISUM, 11 skulls, 3 L, 5 R mandibles, 4 L, 5 R humeri, 2 L radii, 3 L, 1 R ulnae, 6 L, 3 R femora, 4 L, 5 R tibiae. Age: Post-Wisconsin. The cave is of the same type as Moonshiner Cave. Size medium.

Angus, Nuckolls County, Nebraska (L. D. Martin, unpublished thesis). Not seen. Age: Rancholabrean.

Dubuque, Dubuque County, Iowa (Hay 1923:334). Not seen. Age: Wisconsin.

Younger's Cave, St. Clair County, Missouri. KUM 5952 P^4, RL and R mandibles. Age: Post-Wisconsin.

Bat Cave, Pulaski County, Missouri (HAWKSLEY et alii 1963). CMS 35, 320 2 R M_1. Age: Wisconsin. Relatively large.

Brynjulfson Cave, Boone County, Missouri (PARMALEE & OESCH 1972). Not seen. Age: Wisconsin.

Herculaneum, Jefferson County, Missouri (OLSON 1940). Not seen. Age: Wisconsin.

Galena, Jo Daviess County, Illinois (HAY 1923:337). Not seen. Age: Wisconsin.

Boone County, Indiana (HAY 1923:334). Not seen. Age: Wisconsin.

South of Vicksburgh, Warren County, Mississippi. FM PM 527 femur. Age: Wisconsin? Large.

Frankstown Cave, Blair County, Pennsylvania (PETERSON 1926). CM 11027 RL mandible. Age: Wisconsin. Large.

Ichetucknee River, Suwannee County, Florida (KURTÉN 1965b). UF 1151 L mandible. Age: Wisconsin. Size medium to large.

Crystal River, Citrus County, Florida. UF 17073 maxilla R maxilla. Age: Wisconsin. Large.

Vero, Indian River County, Florida (HAY 1917). Not seen. Type locality of *C. riviveronis* Hay 1917. Age: Wisconsin.

Melbourne, Brevard Countrry, Florida (RAY 1958). Not seen. Age: Wisconsin.

Seminole Field, Pinellas County, Florida (SIMPSON 1929). Not seen. Age: Wisconsin.

Phillippi Creek, Sarasota County, Florida (SIMPSON 1929). Not seen. Age: Wisconsin.

Medicine Hat, Alberta (STALKER & CHURCHER 1970). Not seen. In addition to the Kansan-age record already mentioned, Sangamonian and mid-Wisconsin deposits have yielded material referred to *Canis* cf. *latrans*.

Villafranchian

Valdarno superiore, Tuscany, Italy (MOVIUS 1949). IGF, three skulls with mandibles, 4 partial skulls with mandibles, 3 mandibles, limb bone fragments (for detailed list see TORRE 1967). The material includes the type of *C. arnensis* Del Campana 1913. NHMB Va 368 C^s, M_1; BM M 415 frag. upper teeth; MHNP skull. Most specimens evidently from the Il Tasso locality. Age: Late Villafranchian. Size close to Cita Canyon form or slightly larger.

Senèze, Haute-Loire, France (SCHAUB 1944). FSL 3736 R maxilla; NHMB Se 1780 palate. Age: Late Villafranchian. Similar to Valdarno form.

Kuruksai, Tadzhikistan, USSR (E. A. VANGENHEIM, pers. com.). IGM 3120-356 L mandible. Age: Middle or late Villafranchian.

Beregovaia, Transbaikalia, USSR (E. A. VANGENGEIM, pers. com.). IGM Loc. 482, L mandible. Age: Early or middle Villafranchian.

Shamar, Mongolia (E. A. VANGENGEIM, pers. com.). IGM Loc. 970, L mandible. Age: Early or middle Villafranchian. The material from the three last-mentioned localities represents a relatively small form, comparable to Lisco or small Cita coyotes. They average somewhat smaller than the European specimens.

III. GROUPING INTO SAMPLES

The material comprises some fairly homogeneous samples of statistically respectable size, as well as various smaller samples and single specimens. For larger samples the degree of homogeneity was studied by averaging the Pearsonian coefficients of variation for 11 variates (dimensions of lower cheek teeth, lengths of premolar series and molar series). In apparently homogeneous samples such values were found to be about 6. Values between 7 and 8 were considered to indicate moderate heterogeneity. Values over 8 were regarded as evidence of strong heterogeneity and such samples were broken up into subsamples representing single localities.

The following samples were considered homogeneous or only moderately heterogeneous. They are denoted by abbreviations as indicated in each case.

CC: Cita Canyon sample, *C. lepophagus.* The low variability of the topotype sample (average V = 5.89) may suggest that it represents a limited part of the Blancan, not long enough for significant evolutionary change. Judging from skull and jaw size, these animals were about as big as modern coyotes, although the teeth tend to slightly smaller dimensions. This sample has been used as a standard of comparison in the construction of the ratio diagram (fig. 2) and in the computation of size indices.

IR: Irvingtonian coyotes, *C. priscolatrans.* This group may represent a time span of more than 1 million years; apart from the Irvingtonian material *sensu stricto,* it includes the latest Blancan Curtis Ranch sample, which has the same characters. The average V = 7.83, which indicates some slight heterogeneity in comparison with CC. These animals are clearly larger than the Cita coyote, and some Irvingtonian populations apparently represent the very culmination of size in this group, even though large coyotes persist in the late Pleistocene. Still these animals are smaller than any members of the true wolf group known from North America. The sample includes the types of *C. priscolatrans, C. edwardi* and *C. irvingtotensis;* the first-mentioned has priority.

RL: Late Rancholabrean coyotes, *C. latrans,* from the southern and western states and Mexico, mainly or exclusively of Wisconsin date. The average V = 7.4, or close to that in IR, and may suggest slight heterogeneity. These animals, though still quite large, average somewhat smaller than those of sample IR.

EP: End-Pleistocene and Holocene coyotes, *C. latrans,* from three caves in Idaho, — Jaguar Cave, Moonshiner Cave and Middle Butte Cave. This sample should be both temporally and geographically homogeneous and in fact has a low average V = 5.8. Due mainly to the remarkable number of specimens from Moonshiner, this is the largest sample at hand. Compared with EP, size has receded still further, and in fact some teeth even average smaller than their homologues in CC. The carnassials, however, are significantly larger than in CC.

RE: Recent coyotes, *C. latrans.* The main part of this sample is homogeneous geographically (Oklahoma); however, on these specimens only 8 variates were measured. Other specimens, on which the total set of variates was taken, are moderately scattered geographically. The average V = 5.63 and no heterogeneity is indicated.

CA: Villafranchian coyotes, *C. arnensis,* from Europe. This sample appears quite homogeneous (V = 5.68). Both localities date from the late Villafranchian and the geographic distance between them is short. In most characters, these dogs average slightly larger than the CC ones and agree closely with *C. latrans* (EP, RE). Although smaller than IR on average, this group has acquired some similar characters as will be shown in more detail below.

CL: Recent wolf jackal, *C. lupaster,* from North Africa. I have included this form as a representative of the true jackals; for details on the sample (and on fossil *C. lupaster* from the Levant, included in the bivariate studies below) see KURTÉN (1965a).

In addition to these main groups there are numerous smaller samples. If, for instance, all of the Blancan coyotes except CC are combined into one sample, it turns out to be very heterogeneous (V > 9). Some localities have small forms, others medium-sized or large ones. On the whole, early Blancan coyotes are small (Rexroad, Beck Ranch) and middle to late Blancan medium-sized (Grand View, Hagerman, Sand Draw, Broadwater) but there are exceptions. One is the great Curtis Ranch form, here included in sample IR; another the equally large Miñaca coyote, which is here treated separately since its date is somewhat uncertain. (The fauna from Miñaca Mesa has not yet been studied in detail.) On the other hand, the Lisco coyote, usually regarded as late Blancan, is an exceptionally small form.

Statistical data on teeth, skulls and jaws in the main samples are given in tables 1—2. Some individual data for small samples are in tables 3—4. In addition to the Blancan material discussed above, they also include early Rancholabrean specimens in which there is considerable variation.

For limb bone measurements (tables 5—6) the main samples are EP and RE. In addition, a number of specimens from scattered sites are recorded separately.

IV. COMPARISON OF SAMPLES

Ratio Diagram

The ratio diagram of SIMPSON (1941) may be used to compare various samples with a given standard which is set at 100 per cent. Figure 2 is such a diagram in which the means for lower teeth in sample CC form the standard. Corresponding means for other samples are expressed as percentages of the CC value (logarithmic percentage scale) or (which amounts to the same) as positive or negative log difference (upper scale). The samples compared with CC are IR, RE, CA and CL.

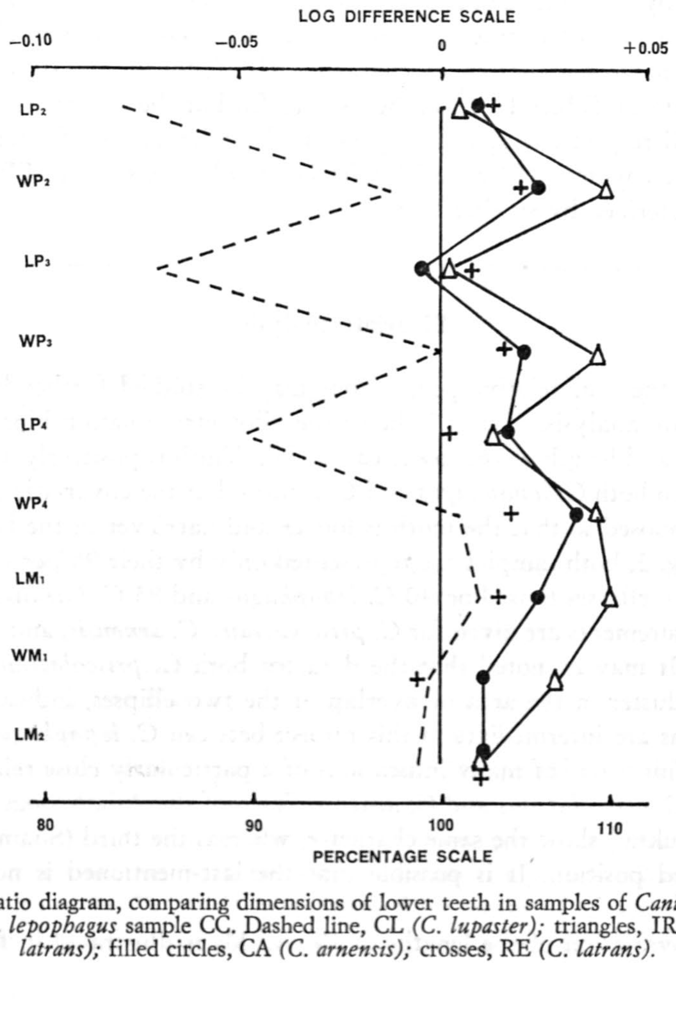

FIG. 2. Ratio diagram, comparing dimensions of lower teeth in samples of *Canis;* standard (100 %) *C. lepophagus* sample CC. Dashed line, CL *(C. lupaster);* triangles, IR *(C. priscolatrans);* filled circles, CA *(C. arnensis);* crosses, RE *(C. latrans).*

We may initially note that the pattern formed by CL, *C.lupaster*, deviates very markedly from the others. The premolars are relatively short and broad, compared with those in coyotes. The molars, on the other hand, are of coyote size. Thus the relative proportions of the jackal dentition are quite different from those of the coyote.

Sample IR, *C. priscolatrans,* also deviates from CC but in a different way and to a lesser degree. The Irvingtonian coyotes are larger than CC; the premolars are somewhat broader; the lower carnassial is clearly elongated. Very similar characters, although slightly less deviant from CC, are seen in sample CA, the European *C. arnensis*. It is evident that the resemblance between *C. arnensis* and *C. priscolatrans* is very close.

Sample RE, Recent coyote, shows a regression of size from the stage represented by IR, so that in overall size it is very close to CC. It does, however, retain such IR characters as more robust premolars and an elongated, relatively narrow carnassial — characters also found in *C. arnensis.*

The data in Tables 1—2 can be used to fill but the picture to some extent. In all respects, sample IR represents the culmination of size; the late Pleistocene coyotes (RL) are still quite large, whereas samples EP and RE are characterized by smaller body size.

Bivariate analysis

The changes in relative proportions may be studied further by means of bivariate analysis. Figure 3 shows the allometric relationships between the width and length of the lower carnassial. Width is positively allometric to length in both *C. lepophagus* and *C. latrans,* but the covariation axis has been transposed so that the tooth is longer and narrower in the latter species. In fig. 3, both samples are represented only by their 95 per cent equiprobability ellipses (based on 40 *C. lepophagus* and 93 *C. latrans).* Individual measurements are given for *C. priscolatrans, C. arnensis,* and the Asiatic dogs. It may be noted that the data for both *C. priscolatrans* and *C. arnensis* cluster in the area of overlap of the two ellipses, indicating that both forms are intermediate in this respect between *C. lepophagus* and *C. latrans.* This is one of many indications of a particularly close relationship between *C. priscolatrans* and *C. arnensis.* Two of the Asiatic dogs (Beregovaia, Kuruksai) show the same character, whereas the third (Shamar) takes an isolated position. It is possible that the last-mentioned is not a true coyote.

The covariation of the lengths of P_4 and M_1 is illustrated in fig. 4 (on

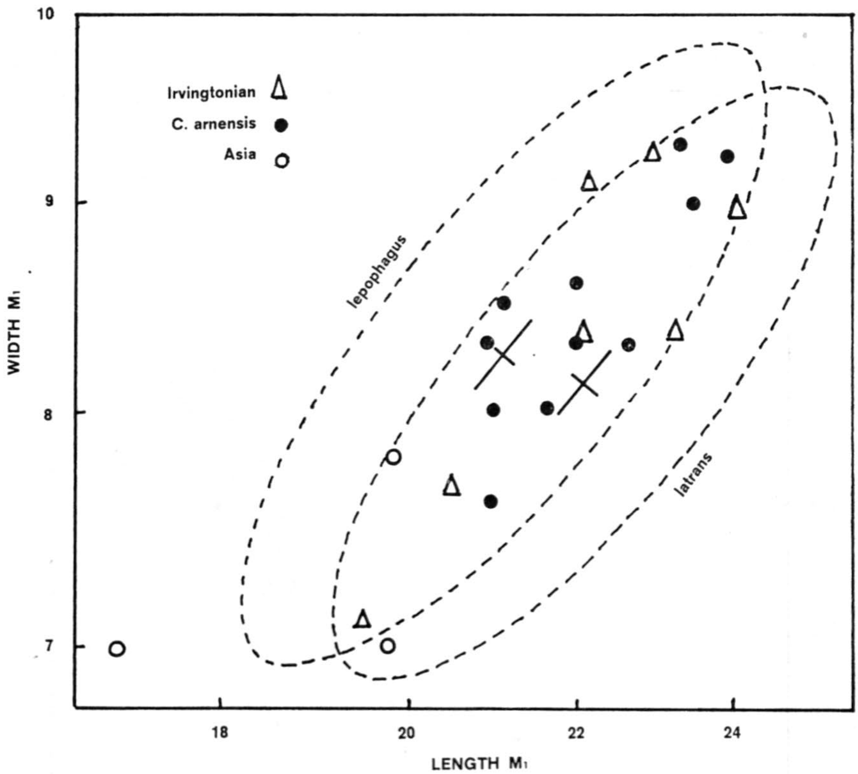

FIG. 3. Width and length of M1, double logarithmic plotting. *C. lepophagus* and *C. latrans* represented by 95 per cent equiprobability ellipses, other samples by individual observations as labelled.

an arithmetic scale). There is, again, a transposition from *C. lepophagus* to *C. latrans*, involving a shortening of P4 and elongation of M1. In this case, it can be shown that *C. arnensis* agrees most closely with *C. lepophagus*, and is significantly different from *C. latrans*. The same may be true for *C. priscolatrans* but the data are too few to be conclusive. The Asiatic dogs agree with the Blancan in having relatively long P4 and short M1.

The diagram also shows the mean and major axis for *C. lupaster* in which P4 is even shorter than in *C. latrans*. The jackal type is thus quite different from *C. arnensis* and other early coyotes.

The difference in relative width of the lower premolars was commented upon in connection with the ratio diagram comparison. Width/length relationships of P2, P3 and P4 were studied by means of bivariate analysis, and it was found that in each case the *C. latrans* tooth differed significantly from the *C. lepophagus* homologue, in being relatively broader. For *C. arnensis* and *C. priscolatrans* the *latrans* relationship was found in P4, and this is apparently true for P2 and P3 also, although the material was somewhat too small for definite conclusions.

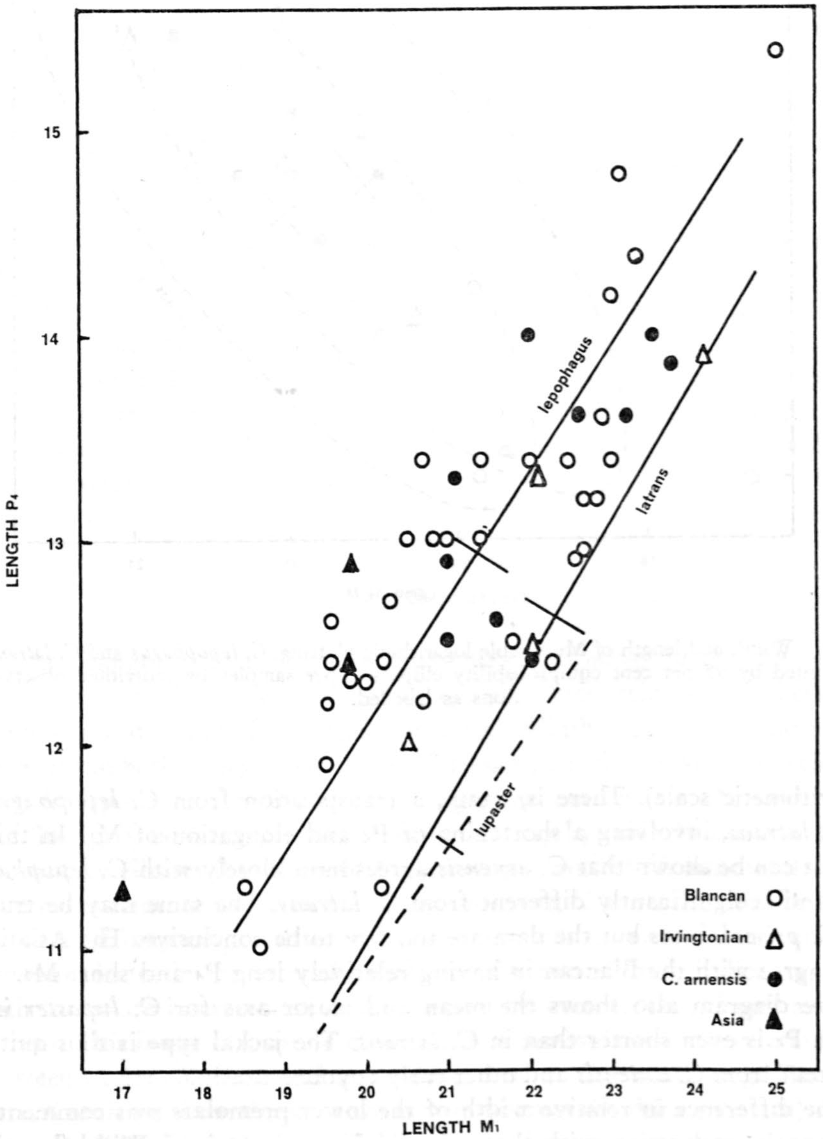

FIG. 4. Length relationships of P4 and M1 with major axes and means for *C. lepophagus, C. latrans* and *C. lupaster*. Individual measurements for the two latter omitted; other samples as labelled.

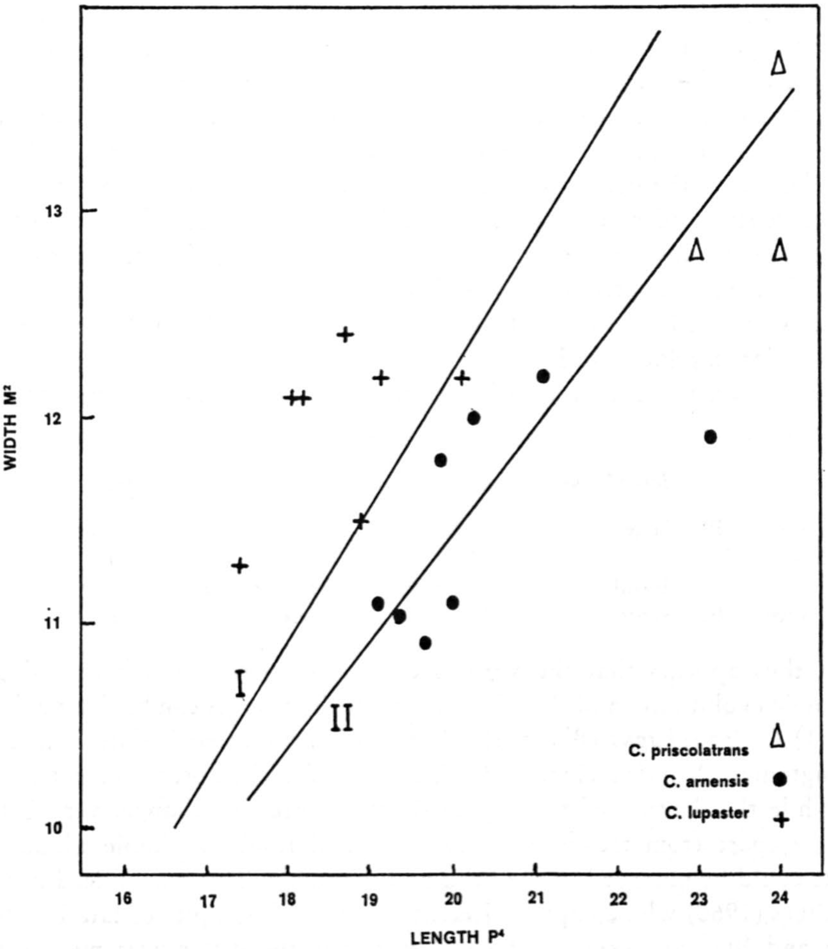

FIG. 5. Relationship between width of M² and length of P⁴. Axis I (N=48) is based on *C. lepophagus* combined with *C. latrans* samples RL and RE, axis II (N=38) on *C. priscolatrans* (IR), *C. arnensis* (CA) and *C. latrans* sample EP. Individual observations indicated for some samples, as labelled; note divergent position of *C. lupaster*.

It was more difficult to study the changes of proportions in the upper dentition. The available material of anterior upper premolars is small, and little change except for overall size can be observed in the carnassial and molars. However, the second upper molar — a strongly reduced tooth in *Canis* — is more reduced in some coyote populations than in others. This can be studied, for instance by relating the width of the second molar to the length of the carnassial (fig. 5).

In the Blancan *C. lepophagus* the molar is relatively large and this relationship is also found in the RL and RE samples of late Pleistocene and Recent coyote. In samples IR, EP and CA, on the other hand, the molar is relatively smaller. The reduction of M^2 might be a character that appeared in *C. priscolatrans* and which is now retained in the northwestern part of the range of the species, whereas the larger-M^2 relationship survives from the Blancan to the present day in other parts of the Recent population. A thorough study of modern coyote would be necessary to substantiate this suggestion. In any case, it is of great interest to note that the European form, *C. arnensis*, agrees closely with *C. priscolatrans*, in this character as in many others. In the jackal *C. lupaster*, on the other hand, M^2 is comparatively large, relative to P^4.

The differences observed in bivariate relationships may be summarized as follows.

	lepophagus	*priscolatrans*	*arnensis*	*latrans*
M^2 relative to P^4	large	small	small	large or small
P_2, P_3, P_4	narrow	broad	broad	broad
M_1	broad	intermediate	intermediate	narrow
M_1 relative to P_4	short	short	short	long

It thus appears that the various changes occurred at different times (»mosaic evolution») and that three fairly distinct stages can be distinguished: (1) *C. lepophagus* (Blancan), (2) *priscolatrans-arnensis* (late Blancan-Irvingtonian, Villafranchian), (3) *C. latrans* (Rancholabrean-Recent).

While the dention of the coyote shows progressive change, very little change apart from trends in overall size and resulting simple-allometry shifts could be observed in the head and mandible. This was indeed noted by GILES (1960) who compared Recent coyote with samples of late Pleistocene and Blancan forms, and concluded that the differences were very slight. Bivariate comparison of a number of skull measurements confirm this opinion. The only notable difference revealed by my data (see table 2) is a tendency for Blancan and Irvingtonian skulls to have a somewhat more tapering snout; the width across the rostrum, in relation to that across the carnassials, is somewhat greater in *C latrans* than in *C. lepophagus* and *C. priscolatrans.* The European form is indeterminate in this respect.

Limb bones

It was only possible to study a limited number of limb bones. Six Recent skeletons were measured. A larger number of long bones was available from Moonshiner Cave; the mean lengths of these (sample EP) were practically identical with those for the Recent (RE). A small sample of long bones from Rancho La Brea gave significantly higher values, averaging 9—10 per cent longer than in EP and RE; the relative length proportions, however, remained the same in all instances.

The relative lengths of bones referred to *C. lepophagus* and *C. priscolatrans*, on the other hand, turned out to be markedly different. In *C. latrans* the radius is as long as the humerus, or longer; the average radius length is 103.6 per cent of that of the humerus. For 2 humeri and 6 radii of *C. lepophagus* from Santa Fe 1 the corresponding value is only 93.4 per cent. The humeri average longer and the radii shorter than those of RE and EP, and the differences are highly significant. Thus, although the total arm length was about the same in the Blancan coyote as in the Recent, the forearm was shorter.

A humerus and some metacarpals from the Snake River Blancan also indicate a relative shortening of the distal parts of the arm. The length of this humerus is 157 mm. which is close to the RE and EP means. The three metacarpals, although almost certainly not from a single individual, have length relationships that are normal for one manus and thus give collective evidence on the size of the hand. The length of MC 3 is well below the RE mean. Its length is 40.8 per cent of the Snake River humerus, while the Recent mean figure is 42.3.

It may also be observed that a single radius from the Blancan of Red Light Bolson is strikingly short, well below the observed range in samples RE and EP. A distal shortening is also indicated by the shortness of the associated MC 5 from the same locality (TMM 40664). Its length is only 51, while the lengths of MC 5 in six Recent coyote skeletons range from 56 to 60. Its length is 33.8 per cent of that of the radius from the same locality, while the corresponding average for the modern sample is 35.1 per cent. There is thus a suggestion that the hand in *C. lepophagus* was relatively even shorter than the forearm; there would then be a proximodistal gradient in the differentiation between *C. lepophagus* and *C. latrans*.

Length relationships in the hind limb probably have changed in much the same way. Unfortunately, there is no femur from Santa Fe. A tibia from here, however, appears rather short when compared with the humerus; its length is 107.0 per cent of that of the humerus, while the Recent average is 114.8.

The partial skeleton from Arkalon, which probably belonged to a very large, powerful *C. priscolatrans* of the early Irvingtonian, gives interesting information on the limb relationships in the coyotes of this time. Radius, femur, tibia and two metatarsals are preserved. The tibia and metatarsals are only slightly longer than the values for sample RE, the femur much longer. The tibia in the Arkalon canid has a length of 100 per cent of that of the femur, while the length of MT 3 is 42.3 per cent of the femoral length. Corresponding means for sample RE are 106.5 and 44.6 per cent. The radius of the Arkalon dog is also relatively short, when compared with the femur. Its length is 90.0 per cent of that of the femur, while the modern figure is 95.9.

An animal of about the same size as the Arkalon coyote is represented by a radius and MC 3 from Inglis. It is presumably of somewhat later date, although still well within the Irvingtonian. The length of the metacarpal is 40.8 per cent of that of the radius, which does not differ significantly from the modern mean (41.8). Whether the Inglis canid retained the relationship of the Santa Fe form, or had acquired the modern relation-

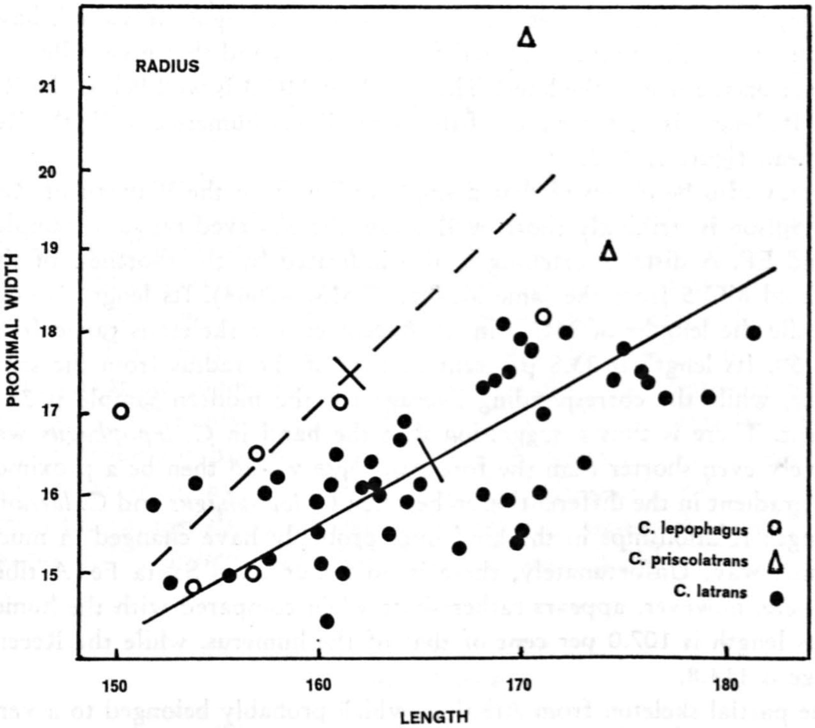

Fig. 6. Proximal width and length of radius in *Canis* as labelled, with means and major axes for *C. lepophagus-priscolatrans* (dashed line) and *C. latrans.*

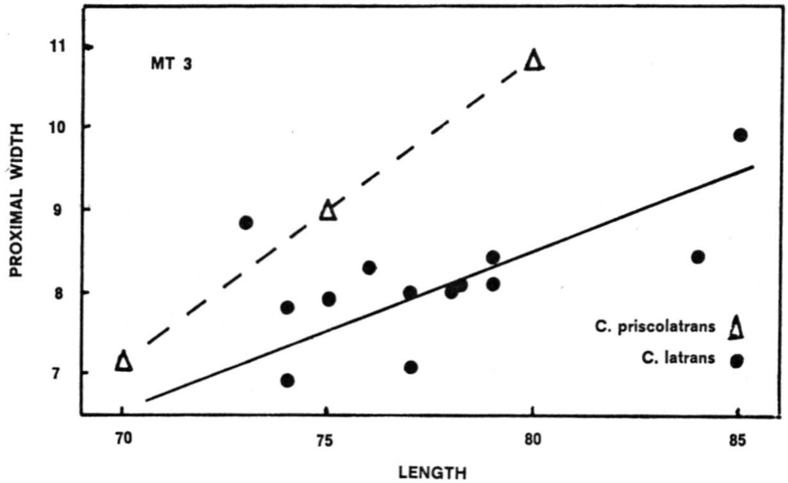

FIG. 7. Proximal width and length of third metatarsal in *Canis* as labelled, with major axes for *C. priscolatrans* (dashed line) and *C. latrans.*

ship, cannot thus be decided on the present evidence. Possibly such a change occurred in the course of the Irvingtonian. The metacarpals from Mullen, of latest Irvingtonian or earliest Ranchobrean date, are very close in dimensions to the modern. On the other hand, an MC 3 from Slaton, of Illinoian or Sangamon date, is strikingly short, well below the observed range in sample RE. It is thus possible that the primitive type of limb may have persisted in some populations even in earlier Rancholabrean times. In the later Rancholabrean, however, the distal parts of the coyote limb are clearly lengthened, and of modern type.

The differences in limb segment lengths are necessarily associated with differences in the relative proportions of individual bones. Thus the distal limb bones, while shorter in *C. lepophagus* than in *C. latrans,* have about the same width, indicating that the body weight was much the same. In relation to their own length, they will thus be plumper. This relationship continues into the larger *C. priscolatrans* but is here exaggerated by positive allometry (JOLICOEUR, 1963; KURTÉN, 1965b:230), and the robustness of the bones is often striking. For instance, the proximal width of the radius, as related to radius length, shows a continuation in the Arkalon and Inglis canids of the trend for *C. lepophagus,* with the result that these values fall well outside the range in later coyotes (fig. 6). Again, the metatarsals of Fossil Lake, Vallecito and Arkalon coyotes *(C. priscolatrans)* are relatively plumper than Rancholabrean and Recent *C. latrans* (fig. 7). This, too, is good indication that the type of limb seen in *C. lepophagus* was retained in the Irvingtonian *C. priscolatrans* and that the striking robustness of some of the specimens, e.g. the Arkalon and Inglis canids, simply results from the adaptation of such a limb to the large body size of the Irvingtonian form.

Such changes in the limb skeleton as the elongation of the distal segments in *C. latrans* are related to the mode of locomotion. When the distal segments are lengthened and the proximal are shortened, the leverage of the muscles is also shortened and running speed increased at the cost of power. Thus it would appear that the transition from *C. priscolatrans* to *C. latrans* coincided with a definite ecological change, and very likely one that had something to do with the predator-prey relationship.

V. EVOLUTION IN SIZE

The Size Index

For detailed studies of the evolution in size, the size index introduced in an earlier paper (Kurtén, 1959) has proved useful. With fragmentary fossil material, comparison of homologus structures is often difficult because the material may be too small to give meaningful results. A larger body of data becomes available if several different variates are compared with a given standard and their size expressed as a percentage of the standard. In the present case I have used the Cita Canyon means (CC) as a standard with the value 100. The measurements used in obtaining the size index were the lengths of the lower premolars, the upper and lower carnassials, and the width of M^1. These values, expressed as percentages of the Cita Canyon means, were averaged for each locality or group of localities (table 7). The standard deviations were calculated on the basis of N_1 (number of measurements used), but standard errors from N_2 (minimum number of individuals represented by sample). The index does reflect changes in overall size, which is its main purpose, but it is also to some extent affected by changes in relative size (e.g. the change in the relation of P_4 and M_1 discussed above) and for fragmentary material this may lead to bias. In most cases, however, several different tooth measurements go into the index and they tend to average out.

Absolute chronology

An absolute chronology would be necessary for any accurate study of evolutionary rates. In the case of the Plio-Pleistocene, important advances have been made in recent years (e.g. RICHMOND 1970; IZETT et alii 1970; BIRKELAND et alii 1971; COOKE 1972).

The beginning of the Blancan, with the early Blancan faunas of Rexroad and Fox Canyon, may be placed at about 4.5 m.y. BP. The Blancan/Irvingtonian transition is still quite uncertain but can hardly be later than 1.5 m.y. BP. Mid-Blancan samples like that of Glenns Ferry may thus be set at about 3 m.y. while the later Sand Draw and Broadwater may lie in the range 2—2.5 and the Curtis Ranch locality is dated at about 2 m.y. BP.

The glacial-interglacial chronology in Richmond's and Cooke's scheme identifies the Nebraskan with the Washakie Point Glaciation at about 1.3 m.y. This would give us very tentative dates for the lower Vallecito and other early Irvingtonian faunas such as the Arkalon (pre-Borchers according to HIBBARD 1970, and so pre-Aftonian). Borchers (Aftonian) would be about 1 m.y. in this scheme and the modal age of the Kansan some 0.8 m.y. The Inglis fauna has been considered as possibly Kansan in age but may well be older (presence of *Chasmaporthetes* and ?*Megantereon).*

The Yarmouth Interglacial, about 0.65 m.y. in this chronology, is rather a blank as far as coyote history is concerned, unless the Mullen canid is late Yarmouthian in age. The Illinoian with the modal date 0.5 m.y. would be represented by such faunas as Fossil Lake, Adams and possibly Slaton, unless the latter is Sangamonian. The Sangamon, with Cragin Quarry, is dated at about 0.25 m.y. This, of course, is not the same interglacial as that immediately preceding the Wisconsin and which is surely correlatable with the European Eemian at about 80—100,000 BP (FLINT 1971). Obviously, also, much remains to be done before the mammalian faunas can be definitely correlated with the radiometrically dated sequence.

Wisconsinan material, finally, is plentiful; the Rancho La Brea coyote has been selected as a representative.

The European chronology was compared with the American by RICHMOND (1970) and COOKE (1972) suggesting a correlation between Donau and Nebraskan Glaciations. The Villafranchian specimens from Valdarno and Senèze may be late pre-Donau or Tiglian with dates of 1.5 m.y. or more and thus be close to the Blancan/Irvingtonian transition.

Changes in size

Plotting the mean size index of dated samples against absolute age (fig. 8) indicates that sustained trends of evolution in size can be established in coyote history. There is a gradual size increase in the Blancan, from the small early forms of the Rexroad through larger mid-Blancan and

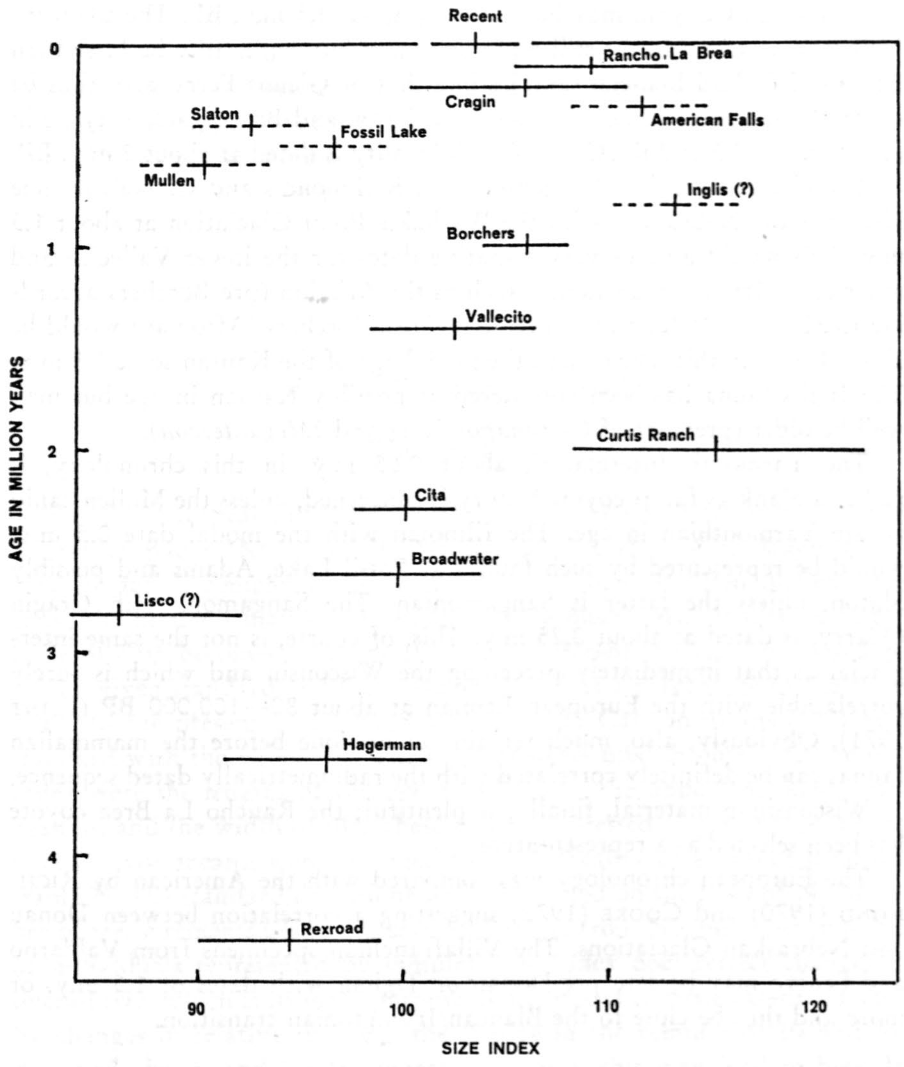

Fig. 8. Tentative plot of size index (see Table 7) against time for North American coyote. Crossbar indicates position of mean, horizontal bar M ± 2s; very uncertain values indicated by dashed lines. Time scale provisional.

later Blancan forms and up to the great *C. priscolatrans* type near the end of the Blancan. The small Lisco dog may be late Blancan, but its position is uncertain. If it is to be accommodated into the same evolving lineage, there must have been a considerable oscillation in size, not just a steady phyletic growth, during the Blancan.

The culmination in size comes in the late Blancan and early Irvingtonian with average size index in the range 108—113. Later on there seems to be a slight decrease in size, but fairly large coyotes continue in evidence to the middle (American Falls) and late Rancholabrean (Rancho La Brea). However, the presence of distinctly smaller forms throughout the sequence (Borchers, Vallecito, Fossil Lake, Slaton) suggests that locally and/or temporally distinct forms evolved from time to time, perhaps in an oscillation of size related to the climatic shifts. The more intense climatic changes of the Irvingtonian and particularly the Rancholabrean may have brought forth a greater temporal and local differentiation in size than the more equable regimen of the Blancan.

The values at hand suggest that the average rate of size change in the Blancan may have been of the order of two or three per cent per million years, with episodes at a higher rate. Still higher rates may have obtained in the Irvingtonian. Good data for study of the rate of change in the late Rancholabrean and Recent are not yet at hand. The absolute amount of reduction from, say, the Rancho La Brea coyote to the present-day form was more than 5 per cent. Comparable or greater values were found in North America for *Panthera onca* and *Lynx rufus* (KURTÉN 1965b), in Europe for *Ursus arctos, Martes martes, Felis silvestris* and *Gulo gulo* (KURTÉN 1959), and in the Levant for *Canis lupus, Felis silvestris, Crocuta crocuta, Martes foina, Vulpes vulpes, Ursus arctos* (KURTÉN 1965a) and *Bos primigenius* (JARMAN 1969). All of these recent changes occurred at much higher time-rates than those suggested here for the Blancan and Irvingtonian coyotes.

Does this mean that such rapid changes did not occur in earlier times? Not necessarily; dating techniques at present are not adequate for establishing such rapid trends, necessarily during a very short time interval, back in the Blancan. If the Lisco and Broadwater assemblages are approximately coeval, it might be argued that the differences between their coyotes resulted from a phase of rapid size change. But we do not yet have a detailed comparison between the two assemblages and it is not certain that they are contemporaneous. The dwarf coyote from Slaton may provide somewhat better evidence of a rapid size change, but it may also be a stunted individual.

VI. TAXONOMIC IMPLICATIONS

From the foregoing survey of coyote evolution it can be seen that the transformation from Blancan to modern coyotes occurred gradually. The changes in size differ in rate and direction but there is always overlap between ancestral and descendant populations as represented in the fossil record. While some (e.g. dental) characters changed from Blancan to Irvingtonian coyotes, others persisted through Irvingtonian times and changed at a later date, and, of course, many characters of the Blancan coyotes appear to persist unchanged in the modern population.

How should these changes be interpreted taxonomically? Should more than one species be recognized in the sequence from Rexroad early Blancan to the present day? If so, how many, and where should the species boundaries be drawn?

GILES (1960) concluded that the Blancan coyote did not differ more than subspecifically from living *C. latrans*. His study concerned mainly cranial and mandibular dimensions, which have indeed changed but little. Dental and limb characters, however, show very considerable differences and I think this definitely supports specific distinction.

What about the Irvington coyotes? They agree with Blancan coyotes in relative limb proportions and in some dental characters; with modern coyotes in some dental characters, but not in limb proportions; and they differ from both Blancan and Recent coyotes in some characters, notably average size. From this it would appear that they form a distinct taxon, for which the name *C. priscolatrans* is available.

If we recognize three species stages in the sequence, they would then be *C. lepophagus* (Blancan), *C. priscolatrans* (latest Blancan — Irvingtonian) and *C. latrans* (Rancholabrean — Recent).

If it is decided to recognize only two species stages, some difficulties are encountered. Which is the »most important» change in the sequence? Personally I am inclined to regard the change in limb proportions as the major shift and in this case *C. lepophagus* would become a synonym or subspecies of *C. priscolatrans*. It is hoped that future studies will throw additional light on this problem.

The large Rancholabrean coyote, although exceeding the living form in average size, should not be regarded as more than subspecifically distinct, and the earliest name available for this group would appear to be *C. latrans orcutti*.

Finally, we have to consider the problems raised by the identification of *C. arnensis* as a coyote. TORRE (1967) made a bivariate study of the lengths of M_1 and M_2 and showed that jackals and wolves could be separated on this character, and that *C. arnensis* agreed with jackals. This is true, but coyotes and jackals are not separable on this character (except for quite large samples) and *C. arnensis* also agrees with coyote. As we have seen, there are numerous other characters that do separate jackals and coyotes and for all of them *C. arnensis* agrees with coyotes. More precisely, *C. arnensis* shows special and very detailed agreement with the Irvingtonian coyote *C. priscolatrans.* Unfortunately, Asiatic material connecting the two populations is still very scarce. Future studies may verify the suggestion that *C. arnensis* and *C. pristolatrans* formed parts of a single, Holarctic coyote population, in which case *C. arnensis* should be regarded as a synonym or subspecies of *C. priscolatrans.* The probability that this is indeed so is much strengthened by the discovery of Holarctic jaguar at the same time (see KURTÉN 1973); similar conclusions have been formed as regards the hyaenid *Chasmaporthetes* (KURTÉN, in the press) and restudy of other groups of mammals may well lead to similar conclusions as regards early Pleistocene species. The existence of Holarctic mammalian species in Rancholabrean and Recent times is, of course, well documented; for earlier forms, however, a provincial taxonomy still tends to persist.

An incompletely known Asiatic form which may turn out to be a link in the coyote population chain is *Canis chihliensis* Zdansky (1924). However, such scanty data as are available indicate that this form may be somewhat larger, and perhaps more closely allied to the early wolf *C. etruscus.* A more likely candidate is the form described as *Canis* sp. by ZDANSKY (1925) from Loc. 1, Chikusan, Chihli (not the same as Loc. 1 of Choukoutien, which is Loc. 53 of the Sino-Swedish Expedition) and from Diske, Mongolia. Lengths of M_1 are given as 20.4 and 22.0 respectively, which corresponds to coyote (and also, as ZDANSKY noted, to jackal).

SUMMARY

The history of the coyote line may be traced from small early Blancan forms to gradually larger, and eventually very large forms in the late Blancan and early Irvingtonian, followed by considerable size fluctuation in later Irvingtonian and Rancholabrean populations; there is a final size decrease of about 5 per cent leading to the present-day form. The evolving line can be divided into three successive species stages. *Canis lepophagus* of the Blancan differs from the Recent and Rancholabrean *C. latrans* in its

shorter distal limb segments, more tapering snout, relatively larger M^2 (this character is however retained in some Recent populations), narrower P_2—P_4, and shorter M_1 (relative to its own width, and also to the length of P_4). The late Blancan and Irvingtonian *C. priscolatrans,* typically a very large form, retains some of the *C. lepophagus* characters (snout and limb bone proportions, length of M_1 relative to P_4), is intermediate in some (width/length relationship in M_1), and resembles *C. latrans* in the others. Alternatively, only two species stages are recognized, in which case *C. lepophagus* would be a subspecies of *C. priscolatrans.* The evolution thus documented is apparently adaptive in nature, for the characters concerned are of great functional importance; the change in the limb bones, for instance, probably reflects an increase in running speed.

The European canid *C. arnensis* shows detailed resemblance to the *C. priscolatrans* stage (s. str.) in the sequence, and is regarded as the European representative of a Holarctic coyote population. A small number of Asiatic canids of the same age may represent other segments of the population. Although *C. arnensis* is usually referred to as a jackal, it is in fact quite different from jackals.

TABLE 1. Measurements of dentition in samples of *Canis.*

	Sample	N	M	s
Length P^2	CC	4	10.28±0.40	—
	IR	2	13.6	—
	RL	4	11.80±0.18	—
	EP	5	10.92±0.31	0.70
	RE	6	11.05±0.26	0.63
	CA	8	10.50±0.21	0.60
	CL	7	9.94±0.27	0.71
Width P^2	CC	4	4.25±0.19	—
	IR	1	5.3	—
	RL	5	4.38±0.20	0.44
	EP	5	3.74±0.13	0.30
	RE	6	4.22±0.20	0.48
	CA	8	4.11±0.09	0.24
	CL	7	3.97±0.11	0.28
Length P^3	CC	4	11.90±0.40	—
	IR	2	15.55	—
	RL	10	12.39±0.32	1.01
	EP	13	12.15±0.25	0.90
	RE	6	13.06±0.40	0.97
	CA	10	12.05±0.18	0.58
	CL	7	11.41±0.28	0.75
Width P^3	CC	4	4.82±0.36	—
	IR	2	5.9	—
	RL	10	4.63±0.14	0.46
	EP	10	4.19±0.13	0.40
	RE	6	4.67±0.15	0.45
	CA	9	4.51±0.09	0.27
	CL	7	4.54±0.08	0.20
Length P^4	CC	8	19.06±0.55	1.57
	IR	5	23.44±0.35	0.78
	RL	18	20.70±0.32	1.36
	EP	60	20.22±0.13	1.02
	RE	26	20.04±0.21	1.08
	CA	8	20.31±0.44	1.25
	CL	7	18.57±0.32	0.84
Width P^4	CC	8	9.03±0.28	0.80
	IR	4	11.52±0.13	—
	RL	17	10.32±0.18	0.72
	EP	57	9.67±0.10	0.76
	RE	6	9.85±0.17	0.41
	CA	10	10.14±0.18	0.57
	CL	7	9.77±0.23	0.60

	Sample	N	M	s
Blade width P^4	CC	9	7.02±0.21	0.64
	IR	3	8.60±0.47	—
	RL	17	7.91±0.14	0.57
	EP	58	7.16±0.06	0.49
	RE	6	7.32±0.20	0.50
	CA	10	7.32±0.14	0.43
	CL	4	7.00±0.17	—
Width M^1	CC	10	17.20±0.37	1.16
	IR	6	20.02±0.31	0.76
	RL	12	18.29±0.35	1.21
	EP	68	17.38±0.09	0.74
	RE	26	17.62±0.18	0.91
	CA	9	17.89±0.30	0.89
	CL	7	17.50±0.22	0.58
Length M^1	CC	10	12.54±0.35	1.11
	IR	6	14.70±0.14	0.33
	RL	12	13.32±0.23	0.80
	EP	68	12.94±0.07	0.60
	RE	6	13.25±0.38	0.92
	CA	9	13.28±0.33	0.99
	CL	7	12.94±0.17	0.46
Width M^2	CC	7	11.89±0.37	0.98
	IR	5	12.56±0.38	0.84
	RL	10	12.29±0.28	0.90
	EP	37	11.76±0.12	0.75
	RE	26	12.19±0.17	0.85
	CA	9	11.60±0.19	0.56
	CL	7	11.93±0.17	0.45
Length P_2	CC	15	10.31±0.18	0.69
	IR	4	11.42±0.42	—
	RL	14	10.49±0.22	0.81
	EP	21	10.41±0.15	0.69
	RE	6	10.60±0.28	0.69
	CA	8	10.50±0.20	0.57
	CL	6	8.45±0.22	0.54
Width P_2	CC	13	4.29±0.09	0.32
	IR	2	4.9	—
	RL	14	4.44±0.10	0.36
	EP	22	4.24±0.04	0.20
	RE	6	4.48±0.13	0.31
	CA	8	4.52±0.10	0.27
	CL	6	3.93±0.17	0.41
Length P_3	CC	19	11.58±0.13	0.58
	IR	5	12.06±0.50	1.11
	RL	13	11.75±0.20	0.71
	EP	40	11.29±0.10	0.62

	Sample	N	M	s
	RE	6	11.78±0.27	0.65
	CA	9	11.43±0.21	0.64
	CL	7	9.75±0.25	0.66
Width P_3	CC	17	4.49±0.08	0.32
	IR	5	4.98±0.31	0.69
	RL	13	4.77±0.14	0.50
	EP	41	4.35±0.05	0.30
	RE	6	4.63±0.14	0.34
	CA	9	4.69±0.11	0.33
	CL	7	4.34±0.15	0.40
Length P_4	CC	22	12.84±0.13	0.59
	IR	6	13.67±0.39	0.97
	RL	21	12.72±0.18	0.82
	EP	44	12.44±0.12	0.77
	RE	6	12.88±0.34	0.84
	CA	10	13.29±0.20	0.65
	CL	7	11.64±0.24	0.63
Width P_4	CC	21	5.50±0.07	0.33
	IR	5	6.22±0.33	0.74
	RL	20	5.72±0.12	0.53
	EP	39	5.40±0.06	0.38
	RE	6	5.70±0.17	0.41
	CA	10	5.91±0.10	0.33
	CL	7	5.41±0.13	0.34
Length M_1	CC	28	20.91±0.22	1.18
	IR	9	23.03±0.37	1.11
	RL	26	22.90±0.27	1.36
	EP	61	21.86±0.15	1.15
	RE	21	21.59±0.21	1.09
	CA	11	22.05±0.33	1.08
	CL	7	20.86±0.37	0.99
Width M_1	CC	30	8.28±0.10	0.56
	IR	8	9.14±0.17	0.47
	RL	28	8.35±0.09	0.49
	EP	63	8.07±0.08	0.66
	RE	7	8.15±0.13	0.34
	CA	11	8.47±0.16	0.53
	CL	7	8.12±0.15	0.39
Length M_2	CC	25	9.92±0.13	0.66
	IR	7	10.21±0.22	0.58
	RL	20	9.94±0.21	0.95
	EP	10	9.72±0.14	0.43
	RE	26	10.13±0.12	0.61
	CA	10	10.15±0.17	0.54
	CL	7	9.70±0.14	0.36

TABLE 2. Measurements of skull and mandible in samples of *Canis*.

	Sample	N	M	s
Condylo-	CC	4	177.2±2.6	—
basal	IR	2	198.5	—
Length	RL	3	191.0±1.0	—
	EP	4	180.8±5.7	—
	RE	26	187.0±1.5	7.6
	CA	3	184.0±8.6	—
	CL	7	163.0±4.1	10.7
Rostral	CC	4	30.6±0.7	—
Width	IR	2	35.5	—
at C^s	RL	8	33.5±0.9	2.6
	EP	8	30.8±0.5	1.5
	RE	6	31.4±0.8	2.0
	CA	2	31.2	—
	CL	7	28.5±0.6	1.7
Mandible	CC	11	139.8±2.3	7.5
Length	IR	1	157	—
	RL	12	140.3±3.0	10.4
	EP	38	138.9±0.9	5.7
	RE	26	144.4±1.0	5.2
	CA	6	139.8±2.8	6.9
	CL	7	127.6±2.7	7.0
Length	CC	21	36.6±0.3	1.4
P_2—P_4	IR	7	39.3±0.9	2.3
	RL	22	38.5±0.6	2.6
	EP	15	38.5±0.5	1.9
	RE	6	37.7±0.5	1.2
	CA	8	37.6±0.6	1.7
	CL	7	31.1±0.9	2.5
Length	CC	20	35.9±0.5	2.1
M_1—M_3	IR	2	38.5	—
	RL	20	37.0±0.6	2.7
	EP	10	36.5±0.5	1.7
	RE	6	36.0±0.5	1.3
	CA	10	36.9±0.7	2.2
	CL	7	34.3±0.5	1.4

TABLE 3. Measurements of upper teeth and skull in individual fossil coyote specimens.

	..	LP^2	WP^2	LP^3	WP^3	LP^4	WP^4	BWP^4	WM^1	LM^1	WM^2	CBL^1
Rexroad	UMMP V37132	—	—	—	—	19.1	10.0	7.5	16.5	—	—	—
	V56775	—	—	—	—	—	—	—	—	—	10.4	—
	V28442	—	—	—	—	—	—	—	14.9	10.6	—	—
Beck Ranch	MU 8662	—	—	—	—	—	—	—	—	—	10.5	—
Hagerman	UMMP V52280	—	—	—	—	17.0	9.0	6.7	14.8	11.3	10.4	—
	V54995	—	—	—	—	19.7	10.0	7.5	—	—	—	—
	V56401	—	—	—	—	16.1	8.0	6.0	15.0	11.5	10.0	—
Broadwater	UNSM 26111	10.5	3.8	12.7	4.3	19.0	9.1	7.0	17.8	13.5	11.8	185
	26112	—	—	—	—	19.7	10.7	8.0	18.2	14.8	12.8	193
	26113	—	—	—	—	20.0	10.0	8.0	18.2	14.6	11.6	—
Sand Draw	UMMP V57321	—	—	12.5	—	20.2	9.8	7.3	—	12.8	—	—
	FM P 15511	—	—	—	—	17.8	9.1	6.8	—	—	—	—
Deer Park	UMMP V31945	—	—	—	—	—	—	—	—	14.3	—	—
Rock Creek	WT 2303	—	—	—	—	—	—	—	—	—	10.3	—
Cragin Quarry	KUM 5968	—	—	—	—	—	—	—	18.5	—	—	—
Slaton Quarry	MU 6522	—	—	—	—	20.1	9.7	—	17.0	13.1	—	—

TABLE 4. Measurements of lower teeth and mandible in individual fossil coyote specimens.

Locality	Specimen	LP_2	WP_2	LP_3	WP_3	LP_4	WP_4	LM_1	WM_1	LM_2	LM	P_{2-4}	M_{1-3}
Beck Ranch	MU 8651	—	—	—	—	—	—	—	—	11.0	—	—	—
Hagerman	UMMP V53910	10.1	3.8	11.7	4.0	12.2	5.0	19.5	7.6	10.0	—	37	—
	V45222	9.7	3.6	12.5	4.2	13.4	5.3	—	—	—	—	—	—
	V50249	—	—	—	—	—	—	—	—	10.0	—	—	—
	V53452	—	—	—	—	—	—	—	—	9.0	—	—	—
	V56282	—	—	—	—	—	—	—	—	10.0	—	—	—
	LACM 122/1343	9.7	4.0	10.8	4.6	—	—	21.1	8.4	—	—	39	36
	118/1246	—	—	12.7	4.8	13.6	5.8	22.9	8.3	—	—	43	—
	—	—	—	—	—	—	—	—	—	—	—	38	—
	—	—	—	—	—	—	—	—	—	—	—	40	—
Grand View	USNM 1186	—	—	—	—	—	—	20.3	8.1	—	—	—	—
Lisco	UNSM 26114	8.7	3.5	—	—	11.0	4.5	18.7	7.2	8.2	123	32.5	32
	907-38	—	—	10.5	3.5	11.3	4.5	18.5	—	7.7	104	—	30
Broadwater	UNSM 26116	10.6	4.5	—	—	—	—	20.9	8.7	10.1	—	37	36
	—	—	—	—	—	—	—	20.4	7.8	9.8	—	—	35
	—	—	—	—	—	—	—	18.7	—	9.5	—	—	—
Red Corral	WT 4241	—	—	—	—	14.4	—	23.3	8.4	11.0	—	—	38
	4242	9.1	3.5	10.5	3.9	11.9	5.0	19.5	7.1	8.4	120	33.5	32.0
Santa Fe 1	UF 10423	—	—	—	—	12.9	5.5	22.6	8.8	—	—	36	39
	10424	10.6	—	12.4	—	12.9	—	22.6	9.0	10.9	142	40	38
	10837	—	—	13.4	6.0	—	—	—	—	—	—	41	—
	—	—	—	—	—	11.3	5.6	20.2	8.3	—	116	33	31
Sand Draw	UMMP V57321	10.2	4.4	11.5	4.7	13.2	5.4	22.8	8.2	9.7	143	—	37
Miñaca Mesa	LACM 105/149	—	—	13.3	5.2	14.8	6.4	23.1	9.8	12.3	—	—	40
	105/1680	12.1	5.0	—	—	—	—	—	—	—	—	—	—
Borchers	UMMP V33800	10.8	4.7	—	—	—	6.0	22.1	9.1	10.4	—	—	—
Mullen	UNSM 26115	9.0	4.0	10.5	4.7	12.0	5.9	20.5	7.7	8.9	—	35	34
American Falls	ISUM —	—	—	—	—	—	—	24.2	9.6	11.4	—	40	40
	17592	—	—	—	—	—	—	24.5	—	9.7	—	41	—
Fossil Lake	UC 2972	—	—	—	—	—	—	—	7.6	8.8	—	34	33
Slaton Quarry	MU 5043	8.3	—	9.7	—	—	—	—	—	—	—	—	—
Valsequillo	Mexico	—	—	—	—	—	—	23.1	8.6	10.0	—	—	—
Kuruksai	IGM3120-356	9.7	4.5	10.2	4.3	12.9	5.4	19.8	7.8	10.0	—	34.5	—
Beregovaia	IGM 482-	9.5	3.8	10.6	3.9	12.4	5.4	19.8	7.0	8.6	—	34.7	31.5
Shamar	IGM 970-	8.6	3.8	9.8	4.2	11.3	5.4	17.0	7.0	8.0	—	35.5	28.5

TABLE 5. Measurements of limb bones in samples of *Canis*.

	Sample[1]	N	M	s
Humerus Length	RL	2	174	—
	EP	32	158.6 ±1.1	6.0
	RE	6	159.0 ±2.3	5.6
— Shaft width	RL	2	12.7	—
	EP	31	10.49±0,10	0.53
	RE	6	10.68±0.12	0.29
Radius Length	SF	6	160.7 ±2.8	6.8
	RL	5	178.8 ±3.1	6.8
	EP	35	164.7 ±1.1	6.6
	RE	6	164.8 ±2.3	5.6
— Proximal width	SF	5	16.3 ±0.6	1.4
	RL	5	17.48±0.15	0.33
	EP	43	16.20±0.16	1.02
	RE	6	16.22±0.18	0.43
Femur Length	RL	4	189.5 ±3.7	7.4
	EP	24	173.7 ±0.9	4.4
	RE	6	171.5 ±2.5	6.2
— Distal width	RL	4	31.4 ±0.9	1.9
	EP	33	27.73±0.25	1.42
	RE	6	28.3 ±0.5	1.2
Tibia Length	RL	3	199.0	—
	EP	33	183.3 ±1.4	7.8
	RE	6	182.6 ±2.9	7.0
— Proximal width	RL	3	35.5 ±1.9	
	EP	35	30.26±0.35	2.05
	RE	6	31.2 ±0.4	1.03
Calcaneum Length	EP	21	41.4 ±0.5	2.5
	RE	5	41.5 ±0.5	1.1
Astragalus Length	EP	26	23.94±0.30	1.53
	RE	5	23.9 ±0.4	0.9
MC II Length	RE	6	60.7 ±0.8	2.0
— Shaft width	RE	6	5.95±0.19	0.46
MC III Length	RE	6	68.8 ±1.0	2.6
— Shaft width	RE	6	5.80±0.16	0.39
MC IV Length	RE	6	67.8 ±0.9	2.3
—Shaft width	RE	6	5.50±0.10	0.24
MC V Length	RE	6	57.8 ±0.7	1.8
— Shaft width	RE	6	6.27±0.11	0.27
MT II Length	RE	6	68.8 ±0.7	1.7
— Shaft width	RE	6	5.92±0.25	0.61
MT III Length	RE	6	76.5 ±1.0	2.4
— Shaft width	RE	6	6.23±0.18	0.45
MT IV Length	RE	6	77.5 ±0.9	2.2
— Shaft width	RE	6	6.05±0.22	0.54
MT V Length	RE	6	70.3 ±0.8	1.8
— Shaft width	RE	6	5.90±0.13	0.31

[1] RL only Rancho La Brea; SF Santa Fe 1; other samples as in Tables 1—2.

TABLE 6. Measurements of fossil coyote limb bones.

				Length	Width		
					Prox.	Shaft	Dist.
Humerus	Santa Fe 1		UF 7378	171	31.4	10.8	30.5
			UF —	173	32.7	12.0	32.2
	Hagerman		LACM 122/1343	157	—	11.0	28.2
	Little Box Elder Cave		UCM 52—72	169	31	12.5	—
	Schulze Cave		MUVP 7304	155	28	10.0	29.6
Radius	Arkalon Gravel Pit		UMMP V29068	170	21.7	—	28.0
	Inglis		UF —	174	19.0	—	25.0
	Little Box Elder Cave		UCM 95—92	171	17.0	—	25.0
	Red Light Bolson		TMM 40664—11	151	17.0	—	24.0
Femur	Arkalon Gravel Pit		UMMP V29068	189	42.0	15.9	36.0
	Tule Springs		UC 64354	181	38.0	12.8	29.0
	Schulze Cave		MUVP 7303	168	33.7	10.8	27.9
			MUVP —	173	36.0	12.1	29.0
Tibia	Santa Fe 1		UF —	184	30.7	11.8	22.0
	Arkalon Gravel Pit		UMMP V29068	189	40.0	15.2	27
	Quitaque Creek		MUVP 1604	164	31.0	10.4	20.8
	Schulze Cave		MUVP 7304	171	30.8	11.0	20.5
			MUVP 7305	173	31.5	10.7	20.8
	Cave without a Name		TMM 40450—345	177	—	10.0	18.9
Calcaneum	Rexroad		UMMP V45586	38.3	—	—	—
	Arkalon Gravel Pit		UMMP V29068	49	—	—	—
	Inglis		UF —	44	—	—	—
	Slaton Quarry		MUVP 6445	36.0	—	—	—
Metacarpus	Red Light Bolson	MC V	TMM 40664—10	51	9.2	6.0	7.5
	Hagerman	MC III	UMMP V55007	64	7.4	5.5	8.4
		MC II	LACM 122/1343	56	6.2	6.5	8.6
		MC IV	LACM 122/1343	63	—	5.7	8.1
	Inglis	MC III	UF —	71	8.8	7.0	9.3
	Rock Creek	MC II	UC V-2576	64	7.2	7.0	9.5
	Mullen	MC IV	UNSM 39218	68	—	6.0	8.8
		MC V	UNSM 39218	62	—	7.7	10.6
	Slaton Quarry	MC III	MUVP 4627	57	6.4	4.9	6.0
	Little Box Elder Cave	MC II	UCM —	62	—	7.5	9.3
		MC IV	UCM 52—73	75	—	7.5	12.1
	Blackwater Draw	MC II	SMU —	59	5.5	6.0	7.7
		MC V	SMU —	57	9.7	5.5	7.9
	Burnet Cave	MC III	ANSP 13994	66	6.4	5.6	—
	Schulze Cave	MC III	MUVP 7304	69	7.5	5.4	7.8
		MC IV	MUVP 7304	68	5.9	5.2	7.5
		MC V	MUVP 7304	59	9.7	6.5	9.1
Metatarsus	Hagerman	MT IV	LACM 122/1343	77	—	6.7	8.5
	Arkalon Gravel Pit	MT III	UMMP V29068	80	10.8	8.0	—
		MT V	UMMP V29068	76	—	—	9.5

			Length	Prox.	Shaft Width	Dist.
Vallecito	MT II	LACM 1317/3805	68	—	6.5	9.5
	MT III	LACM 1317/3805	75	9.0	7.2	9.3
	MT IV	LACM 1317/3805	77	—	6.9	8.6
	MT V	LACM 1317/3805	69	—	6.5	8.6
Fossil Lake	MT III	UC 78645	70	7.2	5.8	8.0
	MT IV	UC 78646	71	—	5.5	7.7
Slaton Quarry	MT V	MUVP 4630	60	—	4.2	6.4
Little Box Elder Cave	MT II	UCM —	66	—	5.0	6.7
	MT III	UCM 52—14	87	8.1	6.5	9.0
	MT III	UCM 52—60	73	8.8	7.0	9.0
	MT III	UCM —	76	8.3	6.8	8.0
	MT IV	UCM 52—38	86	—	8.1	10.5
	MT IV	UCM —	76	—	6.5	7.8

N.B. For data on Jaguar Cave material, see Kurtén & Anderson (1972).

TABLE 7. Size index for samples of coyote (Cita Canyon = 100)

Sample	N_1	N_2	M	s	Age
Recent	96	26	103.5±1.1	5.7	Recent
Rancho La Brea	15	10	109.1±1.9	6.0	Wisconsinan
Cragin Quarry etc.	10	3	105.9±2.8	4.9	Sangamon
American Falls	4	2	111.5±6.4	9.0	Sangamon? Illinoian?
Slaton Quarry	4	2	92.2±7.3	—	Sangamon? Illinoian?
Fossil Lake etc.	7	4	96.3±6.0	11.9	Illinoian
Mullen	5	1	90.2±4.2	—	Yarmouth? Illinoian?
Inglis	6	3	113.2±5.2	9.1	Kansan?
Vallecito	12	6	102.4±2.0	5.0	Irvingtonian
Valdarno + Senèze	53	13	102.6±1.5	5.6	Villafranchian
Borchers	4	2	106.0±1.0	—	Aftonian
Miñaca Mesa	5	2	116.8±3.3	4.7	?Late Blancan
Curtis Ranch	12	4	115.2±3.7	7.5	Late Blancan
Cita Canyon	102	21	100.0±1.2	5.6	Late Blancan
Sand Draw	6	2	99.7±3.1	4.4	Late Blancan
Broadwater	16	7	99.5±2.0	5.2	Late Blancan
Lisco	8	2	86.0±3.0	4.2	?Late Blancan
Hagerman	21	10	96.1±2.5	8.1	Middle Blancan
Rexroad	5	3	94.4±2.2	6.6	Early Blancan

N_1, number of measurements used
N_2, number of individuals in sample

References

AKERSTEN, W. A. 1970: Interpretation of sediments and vertebrate fossils in fill of Red Light Bolson, southeastern Hudspeth County, Texas. — Soc. Econ. Paleontol. Mineral. Publ. 70—12:82—87.
ANDERSON, E. 1968: Fauna of the Little Box Elder Cave, Converse County, Wyoming. The Carnivora. — Univ. Colorado Stud. Earth Sci. 6:1—59.
BARBOUR. E. & SCHULTZ, C. B. 1937: An early Pleistocene fauna from Nebraska. — Amer. Mus. Novitates 942:1—10.
BERGER, R., PROTSCH, R., REYNOLDS, R., ROZAIRE, C. & SACKETT, J. R. 1971: New radiocarbon dates based on bone collagen of California Palaeoindians. — Contr. Univ. California Archaeol. Res. Facil. 12:43—49.
BIRKELAND, P. W., CRANDELL, D. R. & RICHMOND, G. M. 1971: Status of correlation of Quaternary stratigraphic units in the Western conterminous United States. — Quaternary Res. 1:208—227.
BJORK, P. R. 1970: The Carnivora of the Hagerman local fauna (late Pliocene) of southwestern Idaho. — Trans. Amer. Philosoph. Soc. 60(7):1—54.
COOKE, H. B. S. 1972: Pleistocene chronology: Long or short? — Maritime Sediments 8: 1—12.
COPE, E. D. 1899: Vertebrate remains from Port Kennedy bone deposit. — Jour. Acad. Nat. Sci. Philadelphia (2)11:193—267.
DALQUEST, W. W. 1964: A new Pleistocene local fauna, Motley County, Texas. — Trans. Kansas Acad. Sci. 67:499—505.
—»— 1965: New Pleistocene formation and local fauna from Hardeman County. Texas. — Jour. Paleontol. 39:63—79.
—»— 1967: Mammals of the Pleistocene Slaton local fauna of Texas. — Southwestern Naturalist 12:1—30.
—»— 1972: On the upper Pliocene skunk, *Spilogale rexroadi* Hibbard. — Trans. Kansas Acad. Sci. 74:234—236.
DALQUEST, W. W., ROTH, E. & JUDD, F. 1969: The mammal fauna of Schulze Cave, Edwards County, Texas. — Bull. Florida State Mus. 13:205—276.
DEL CAMPANA, D. 1913: I cani pliocenici di Toscana. — Palaeontograph. Italica 19: 189—254.
DOWNS, T. & WHITE, J. A. 1968: A vertebrate faunal succession in superposed sediments from late Pliocene to middle Pleistocene in California. Proc. XXIII Int. Geol. Congr. 10:41—47.
ELFTMAN, H. O. 1931: Pleistocene mammals of Fossil Lake, Oregon. — Amer. Mus. Novitates 481:1—21.
EVANS, G. L. 1961: The Friesenhahn Cave. — Bull. Texas Memorial Mus. 2:5—22.
FINE, M. D. 1964: An abnormal P_2 in *Canis* cf. *C. latrans* from the Hagerman fauna of Idaho. — Jour. Mammal. 45:483—485.
FLINT, R. F. 1971: Glacial and Quaternary geology. — New York.
GAZIN, C. L. 1935: Annoted list of Pleistocene Mammalia from American Falls, Idaho. — Jour. Washington Acad. Sci. 25:297—307.
—»— 1942: The late Cenozoic vertebrate faunas from the San Pedro Valley, Ariz. — Proc. U. S. National Mus. 92:475—518.
GIDLEY, J. W. & GAZIN, C. L. 1938: The Pleistocene vertebrate fauna from Cumberland Cave, Maryland. — Bull. U. S. National Mus. 171:1—99.
GILES, E. 1960: Multivariate analysis of Pleistocene and Recent coyotes *(Canis latrans)* from California. — Univ. California Publ. Geol. Sci. 36:369—390.
GRAHAM, R. 1959. Additions to the Pleistocene fauna of Samwel Cave, California. I. *Canis lupus* and *Canis latrans*. — Cave Stud. 10:54—67.
HARRIS, A. H. 1970: The Dry Cave mammalian fauna and late pluvial conditions in southeastern New Mexico. — Texas Jour. Sci. 22:3—27.
HARRIS, A. H. & FINDLEY, J. S. 1964: Pleistocene-Recent fauna of the Isleta Caves, Bernalillo County, New Mexico. — Amer. Jour. Sci. 262:114—120.
HAURY, E. W. 1950: The stratigraphy and archaeology of Ventana Cave, Arizona. — Albuquerque.
HAURY, E. W., SAYLES, E. B. & WASLEY, W. W. 1957: The Lehner mammoth site, southeastern Arizona. — Amer. Antiquity 25:2—30.

HAWKSLEY, O., REYNOLDS, J. & McGOWAN, J. 1963: The dire wolf in Missouri. — Missouri Speleol. 5:63—72.
HAY, O. P. 1917: Vertebrata mostly from stratum No. 3, at Vero, Florida, together with descriptions of new species. — Rep. Florida Geol. Surv. 9:43—68.
—»— 1920a: Report of work on Pleistocene paleontology. — Publ. Carnegie Inst. Washington Year Book 18:361—362.
—»— 1920b: Descriptions of some Pleistocene vertebrates found in the United States. — Proc. U. S. National Mus. 58: 83—146.
—»— 1921: Descriptions of species of Pleistocene Vertebrata, types of specimens of most of which are preserved in the United States National Museum. — Proc. U. S. National Mus. 59:599—642.
—»— 1923: The Pleistocene of North America and its vertebrated animals from the States east of the Mississippi River and from the Canadian Provinces east of longitude 95°. — Publ. Carnegie Inst. Washington 322:1—499.
—»— 1927: The Pleistocene of the western region of North America and its vertebrated animals. — Publ. Carnegie Inst. Washington 322 B:1—346.
HEWES, G. W. 1943: Camel, horse and bison associated with human burials and artifacts near Fresno, California. — Science 97:328—329.
—»— 1946: Early man in California and the Tranquillity site. — Amer. Antiquity 11: 209—215.
HIBBARD, C. W. 1938: An upper Pliocene fauna from Meade County, Kansas. — Trans. Kansas Acad. Sci. 40:239—265.
—»— 1941a: The Borchers fauna, a new Pleistocene interglacial fauna from Meade County, Kansas. — Bull. Kansas Geol. Surv. 41:261—269.
—»— 1941b: Mammals of the Rexroad fauna from the upper Pliocene of southwestern Kansas. — Trans. Kansas Acad. Sci. 44:265—313.
—»— 1953: Equus (Asinus) calobatus Troxell and associated vertebrates from the Pleistocene of Kansas. — Trans. Kansas Acad. Sci. 56:111—126.
—»— 1970: Pleistocene mammalian local faunas from the Great Plains and Central Lowland provinces of the United States. — Univ. Kansas Dept. Geol. Spec. Publ. 3: 395—433.
HIBBARD, C. W. & DALQUEST, W. W. 1966: Fossils from the Seymour Formation of Knox and Baylor Counties, Texas, and their bearing on the late Kansan climate of that region. — Contr. Mus. Paleontol. Univ. Michigan 21:1—66.
HIBBARD, C. W. & TAYLOR, D. W. 1960: Two late Pleistocene faunas from southwestern Kansas. — Contr. Mus. Paleontol. Univ. Michigan 16:1—223.
IZETT, G. A., WILCOX, R. E., POWERS, H. A. & DESBOROUGH, G. A. 1970: The Bishop Ash Bed, a Pleistocene marker bed in the Western United States. — Quaternary Res. 1:121—132.
JARMAN, M. R. 1969: The prehistory of upper Pleistocene and Recent cattle. Part I: East Mediterranean, with reference to north-west Europe. — Proc. Prehist. Soc. 35: 236—266.
JOHNSTON, C. S. 1938: Preliminary report on the vertebrate type locality of Cita Canyon and the description of an ancestral coyote. — Amer. Jour. Sci. (5)35:383—390.
JOHNSTON, C. S. & SAVAGE, D. E. 1955: A study of various late Cenozoic vertebrate faunas of the Panhandle of Texas. Part I. Introduction, description of localities, preliminary faunal lists. — Univ. California Publ. Geol. Sci. 31:27—50.
JOLICOEUR, P. 1963: The degree of generality of robustness in Martes americana. — Growth 27(652):1—27.
KURTÉN, B. 1959: Rates of evolution in fossil mammals. — Cold Spring Harbor Symp. Quantit. Biol. 24:205—215.
—»— 1965a: The Carnivora of the Palestine caves. — Acta Zool. Fennica 107:1—74.
—»— 1965b: The Pleistocene Felidae of Florida. — Bull. Florida State Mus. 9:215—273.
—»— 1967: Präriewolf und Säbelzahntiger aus dem Pleistozän des Valsequillo, Mexico. — Quartär 18:173—178.
—»— 1968. Pleistocene mammals of Europe. — London & Chicago.
—»— 1973: Pleistocene jaguars in North America. — Comment. Biol. Soc. Sci. Fennica 62:1—23.
KURTÉN, B. & ANDERSON, E. 1972: The sediments and fauna of Jaguar Cave: II — The fauna. — Tebiwa 15:21—45.

LUNDELIUS, E. L. Jr. 1967: Late-Pleistocene and Holocene faunal history of central Texas. — In: MARTIN, P. S. & WRIGHT, H. E. (ed.), Pleistocene extinctions: 287—319. New Haven.
—»— 1972a: Vertebrate remains from the Gray Sand. — Fort Burgwin Rec. Center Publ. 8 (Blackwater Loc. 1): 148—163.
—»— 1972b: Fossil vertebrates from the late Pleistocene Ingleside fauna, San Patricio County, Texas. — Rep. Invest. Bureau Econ. Geol. Univ. Texas 77:1—74.
MARCUS, L. F. 1960: A census of the abundant large Pleistocene mammals from Rancho La Brea. — Contr. Sci. Los Angeles County Mus. 38:1—11.
MATTHEW, W. D. 1918: Contributions to the Snake Creek fauna; with notes upon the Pleistocene of western Nebraska; American Museum Expedition of 1916. — Bull. Amer. Mus. Nat. Hist. 38: 183—229.
MAWBY, J. E. 1967: Fossil vertebrates of the Tule Springs site, Nevada. — Nevada State Mus. Anthropol. Papers 13:105—128.
MERRIAM, J. C. 1910: New mammalia from Rancho La Brea. — Univ. California Publ. Dept. Geol. 5:391—395.
—»— 1912: The fauna of Rancho La Brea. Part II. Canidae. — Mem. Univ. California 1: 215—272.
MILLER, W. E. 1971: Pleistocene vertebrates of the Los Angeles basin and vicinity (exclusive of Rancho La Brea). — Bull. Los Angeles County Mus. Nat. Hist., Sci. 10: 1—124.
MOVIUS, H. 1949: Villafranchian stratigraphy in southern and southwestern Europe. — Jour. Geol. 57:380—412.
OLSON, E. C. 1940: A late Pleistocene fauna from Herculaneum, Missouri. — Jour. Geol. 48:32—56.
PARMALEE, P. & OESCH, R. D. 1972: Pleistocene and Recent faunas from the Brynjulfson Caves, Missouri. — Illinois State Mus. Rep. Invest. 25:1—52.
PETERSON, O. A. 1926: The fossils of the Frankstown Cave, Blair County, Pennsylvania. — Ann. Carnegie Mus. 16:249—315.
RAY, C. E. 1958: Additions to the Pleistocene mammalian fauna from Melbourne, Florida. Bull. Mus. Comp. Zool. 119:421—451.
REPENNING, C. A. 1962: The giant ground squirrel Paenemarmota. — Jour. Paleontol. 36: 540—556.
RICHMOND, G. M. 1970: Comparison of the Quaternary stratigraphy of the Alps and Rocky Mountains. — Quatern. Res. 1:3—28.
ROTH, E. L. 1972: Late Pleistocene mammals from Klein Cave, Kerr County, Texas. — Texas Jour. Sci. 24:75—84.
SAVAGE, D. E. 1951: Late Cenozoic vertebrates of the San Francisco Bay region. — Univ. California Publ. Geol. Sci. 28:215—314.
—»— 1955: A survey of various late Cenozoic vertebrate faunas of the Panhandle of Texas. Part II. Proboscidea. — Univ. California Publ. Geol. Sci. 31:51—74.
SCHAUB, S. 1944: Die oberpliocaene Säugetierfauna von Senèze (Haute-Loire) und ihre verbreitungsgeschichtliche Stellung. — Eclogae Geol. Helvetiae 36: 270—289.
SCHULTZ, C. B. & HOWARD, E. B. 1938: The fauna of Burnet Cave, Guadalupe Mountains, New Mexico. — Proc. Acad. Nat. Sci. Philadelphia 87:273—298.
SCHULTZ, C. B. & MARTIN, L. D. 1970: Quaternary mammalian sequence in the Central Great Plains. — Univ. Kansas Dept. Geol. Spec. Publ. 3:341—353.
SCHULTZ, J. R. 1938: A late Quaternary mammal fauna from the tar seeps of McKittrick, California. — Publ. Carnegie Inst. Washington 487:111—215.
SHOTWELL, J. A. 1970: Pliocene mammals of southeast Oregon and adjacent Idaho. — Bull. Mus. Nat. Hist. Univ. Oregon 17:1—103.
SIMPSON, G. G. 1929: Pleistocene mammalian fauna of the Seminole Field, Pinellas County, Florida. — Bull. Amer. Mus. Nat. Hist. 56:561—599.
—»— 1941: Large Pleistocene felines of North America. Amer. Mus. Novitates 1136:1—27.
SKINNER, M. F. 1942: The fauna of Papago Springs Cave, Arizona. — Bull. Amer. Mus. Nat. Hist. 80:143—220.
SKINNER, M. F. & HIBBARD, C. W. 1972: Early Pleistocene pre-glacial and glacial rocks and faunas of north-central Nebraska. — Bull. Amer. Mus. Nat. Hist. 148:1—148. 1—148.

SLAUGHTER, B. H. 1961: A new coyote in the late Pleistocene of Texas. — Jour. Mammal. 42:503—509.

—»— 1966: Platygonus compressus and associated fauna from the Laubach Cave of Texas. — Amer. Midland Naturalist 75:475—494.

SLAUGHTER, B. H. & HOOVER, B. R. 1963: Sulphur River Formation and the Pleistocene mammals of the Ben Franklin local fauna. — Jour. Graduate Res. Center 31:132—148.

SLAUGHTER, B. H. & RITCHIE, R. 1963: Pleistocene mammals of the Clear Creek local fauna, Denton County, Texas. — Jour. Graduate Res. Center 31:117—131.

STALKER, A. MACS. & CHURCHER, C. S. 1970: Deposits near Medicine Hat, Alberta, Canada. — Diagram, Geol. Surv. Canada.

STARRETT, A. 1956: Pleistocene mammals of the Berends fauna of Oklahoma. — Jour. Paleontol. 30:1187—1192.

STOCK, C. 1918: The Pleistocene fauna of Hawver Cave. — Bull. Dept. Geol. Univ. California 10:461—515.

—»— 1942: Rancho La Brea. A record of Pleistocene life in California. — Sci. Ser. Los Angeles County Mus. 4:1—73. (Also later editions.)

STOCK, C. & BODE, F. D. 1936. The occurrence of flints and extinct animals in pluvial deposits near Clovis, New Mexico. Part III. Geology and vertebrate paleontology of the late Quaternary near Clovis, New Mexico. — Proc. Acad. Nat. Sci. Philadelphia 88:219—241.

TORRE, D. 1967: I cani villafranchiani della Toscana. — Palaeontograph. Italica 63:113—138.

TROXELL, E. L. 1915: The vertebrate fossils of Rock Creek, Texas. — Amer. Jour. Sci. 39:613—638.

WALKER, G. W. & REPENNING, C. A. 1966. Reconnaissance geological map of the west half of the Jordan Valley Quadrangle, Malheur County, Oregon. — U. S. Geol. Surv. Misc. Geol. Invest. Map. I—457.

ZDANSKY, O. 1924: Jungtertiäre Carnivoren Chinas. — Palaeontol. Sinica, ser. C, 2(1):1—155.

—»— 1925: Quartäre Carnivoren aus Nord-China. — Palaeontol. Sinica, ser. C, 2(2):1—29.

PRINTACO