

Quaternary records of the dire wolf, *Canis dirus*, in North and South America

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The dire wolf was an important large, late Pleistocene predator in North and South America, well adapted to preying on megaherbivores. Geographically widespread, *Canis dirus* is reported from 136 localities in North America from Alberta, Canada, southward and from three localities in South America (Muaco, Venezuela; Talara, Peru; and Tarija, Bolivia). The species lived in a variety of environments, from forested mountains to open grasslands and plains ranging in elevation from sea level to 2255 m (7400 feet). *Canis dirus* is assigned to the Rancholabrean land mammal age of North America and the Lujanian land mammal age of South America and was among the many large carnivores and megaherbivores that became extinct in North and South America near the end of the Pleistocene Epoch.

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Because of the large number of *Canis dirus* localities and individuals recovered from the fossil record, the dire wolf is the most commonly occurring large predator in the Pleistocene of North America. By contrast, the species is rare in South America. What is the reason for this discrepancy in the distribution of *Canis dirus* between the American continents? This and many other fundamental questions about the dire wolf remain to be answered. For example, in North America, why are there no records of *Canis dirus* farther north than southern Canada? What environmental factors most significantly influenced the biogeography of the dire wolf? Did the species originate in South America or North America, and when? Why did such an apparently successful species become extinct at the end of the Pleistocene? By summarizing our current knowledge of the dire wolf's paleobiogeography, this article helps to set the foundation for developing future studies that will provide answers to these questions.

History of study

The dire wolf was first recognized in 1854 by Joseph Leidy from a fossil fauna on the banks of the Ohio River near Evansville, Indiana (Leidy 1854). Few additional specimens were discovered in North America during the remainder of the 1800s (Merriam 1912). However, with the initiation of major fossil recovery efforts at the tar pits of Rancho La Brea, Los Angeles, California, in 1906, an abundance of dire wolf material soon became available, making possible the reconstruction of complete skeletons. Merriam (1912) provided a detailed description of the *Canis dirus* skeletal elements from

Rancho La Brea, comparing them with *Canis lupus* and dire wolf specimens from other localities. Although knowledge of the animal's biology had greatly increased by 1912, little was known about its stratigraphic or geographic ranges. Merriam (1912) speculated that the stratigraphic range was Pleistocene, based on associated taxa at a few sites from Indiana, Mississippi, Kansas, Texas, California, and Mexico.

Canis dirus received little attention during the subsequent three decades. Then several studies in the mid-1940s examined the postcranial dimensions of the Rancho La Brea dire wolf specimens (Stock *et al.* 1946; Nigra & Lance 1947; Stock & Lance 1948). In the late 1950s, *Canis dirus* remains were first discovered in South America (Churcher 1959; Lemon & Churcher 1961; Royo y Gomez 1960). Kisko (1967) studied the metapodials of the South American dire wolves from Talara, Peru, and compared them with North American Rancho La Brea specimens.

Since the mid-1970s several studies have involved *Canis dirus*, the most comprehensive being Nowak's (1979) monograph 'North American Quaternary *Canis*'. For each species, Nowak (1979) discussed taxonomy and geographic and stratigraphic distributions, provided descriptions and comparisons with other canids, and suggested a phylogenetic position within the genus *Canis*. In a study contradicting previous speculations regarding *Canis dirus* limb proportions and running speed, Kurtén (1984) considered geographic variation within the North American dire wolf populations and established two subspecies: *Canis dirus guildayi* for material from California and Mexico, and *Canis dirus dirus* for all specimens east of the North American Continental Divide. In evaluating the large South American Quaternary canids, Berta (1988) used cladis-

tic methodology to show the phylogenetic position of *Canis dirus* as the most derived member of the genus *Canis* in the New World. Her study also provides the most detailed synopsis of the South American dire wolf material to date. Hill (1991) determined that the dire wolf lacked the adaptations of a habitual bone-crushing carnivore such as the spotted hyena (*Crocuta crocuta*). Evaluation of the Rancho La Brea dire wolf population failed to show any significant microevolutionary change through time (Ruddell 1992), but problems with sample size, chronology, and taphonomic bias make it impossible to ascertain whether *Canis dirus* underwent dwarfing toward the end of the Pleistocene at Rancho La Brea. Dundas (1994) concluded that competition with other large carnivores did not cause the extinction of the dire wolf and that the loss of prey remains the prime hypothesis for the demise of *Canis dirus*.

Stratigraphic and geographic distribution

Canis dirus is documented from 139 sites in North and South America (Figs. 1 and 2). Data gleaned from both literature and personal communications were used to compile the list of known dire wolf localities presented in Table 1. The map numbers reported in Table 1 correspond to the locality numbers used in Fig. 1 and 2.

The age of most dire wolf localities is determined solely by biostratigraphy, although some sites have been radiocarbon dated. As a result, the precision and accuracy of locality age determinations vary greatly. Thirty-four sites are 'poorly' dated, being referred to a land mammal age or to the late Pleistocene; 16 sites are referred to the Sangamonian interglacial, while 87 localities are assigned to the Wisconsinan (or late Wisconsinan). Forty-three of the Wisconsinan and two of the Lujanian localities have radiocarbon dates associated with them.

The oldest North American occurrences of *Canis dirus* appear to be Rancholabrean in age. Nowak (1979) determined that specimens of *Canis dirus* reported from Blancan and Irvingtonian age sites were either misidentified, assignable to other taxa, or inadequate for specific identification. One of these accounts warrants further note. Savage (1951) reported a left dentary fragment, distal tibia, right metacarpal, and lumbar vertebra of a large canid from Irvington, California, which he called *Canis* cf. *C. dirus*. Although the specimens are from a very large wolf, no diagnostic features are present that permit their definite assignment to *Canis dirus*. Nowak (1979) referred the material to *Canis armbrusteri*, an Irvingtonian wolf species. However, the specimens are large for *Canis armbrusteri*, and given the lack of diagnostic characters, they remain problematic. Interestingly, a partial baculum recovered from the Irvington site is identical to *Canis dirus* bacula from Rancho La Brea. The baculum of the dire wolf is

very different from that of all living canids. Unfortunately, bacula of other extinct Pleistocene wolf species are not well known.

The oldest Rancholabrean locality containing *Canis dirus* has been a matter of debate. For many years, the Cedazo Local Fauna in Mexico was inferred to be one of the earliest occurrences of the species. Mooser & Dalquest (1975) reported the site to be Illinoian in age, but they also remarked that it could be as young as Sangamonian. Kurtén & Anderson (1980) noted the presence of *Panthera leo atrox* in the Cedazo fauna, a species that is unknown in pre-Sangamonian faunas in North America. This, coupled with the presence of *Bison latifrons*, suggests a Sangamonian age. Recent work at Salamander Cave in the Black Hills of South Dakota has produced the currently recognized oldest known record of the dire wolf. The site preserves a fauna approximately 252 000 years old, based on uranium-series dating. This is considered a minimum age for the fossils; they may be older (Mead *et al.* 1996).

Apart from Salamander Cave, the oldest known occurrences of *Canis dirus* in North America are the widely distributed Sangamonian localities. During that time the species is recorded from Medicine Hat, Alberta, Canada, in the north, to Slaton Quarry, Texas, in the south, and from the Atlantic to the Pacific coasts. Wisconsinan sites expand the known range to include much of Mexico. However, the more numerous Wisconsinan sites do not necessarily suggest a greater abundance and wider distribution of dire wolves during the last glacial period in North America, because Wisconsinan sites are much more common than Sangamonian ones. Sampling bias may account for the difference.

In contrast to North America, the dire wolf is rare in South America, being reported from only three localities, which are inferred to be Lujanian in age: Muaco, Venezuela; Talara, Peru; and Tarija, Bolivia (Fig. 2). Radiocarbon dates associated with the Muaco and Talara faunas indicate a latest Pleistocene age younger than 17 000 BP for these sites. However, the Tarija fauna is diachronous. Numerous fossil-bearing deposits in the Tarija basin range in age from Ensenadan to Lujanian. The dire wolf material was collected from Quebrada del Puente Alto, 6 km southeast of Tarija. The exact age of the specimens is uncertain, but they are inferred to be Lujanian (Berta 1988).

The terminal dates for *Canis dirus* in North and South America are uncertain. Given the large number of Wisconsinan dire wolf localities in North America, many of which are radiocarbon dated, it might be anticipated that the timing of the dire wolf's extinction is well understood. It is not, because there is a lack of radiocarbon dates needed to determine both the timing of extinction and local extirpations of dire wolf populations. Even though the fossil record preserves thousands of individual skeletal elements of *Canis dirus*, only three specimens have been directly radio-

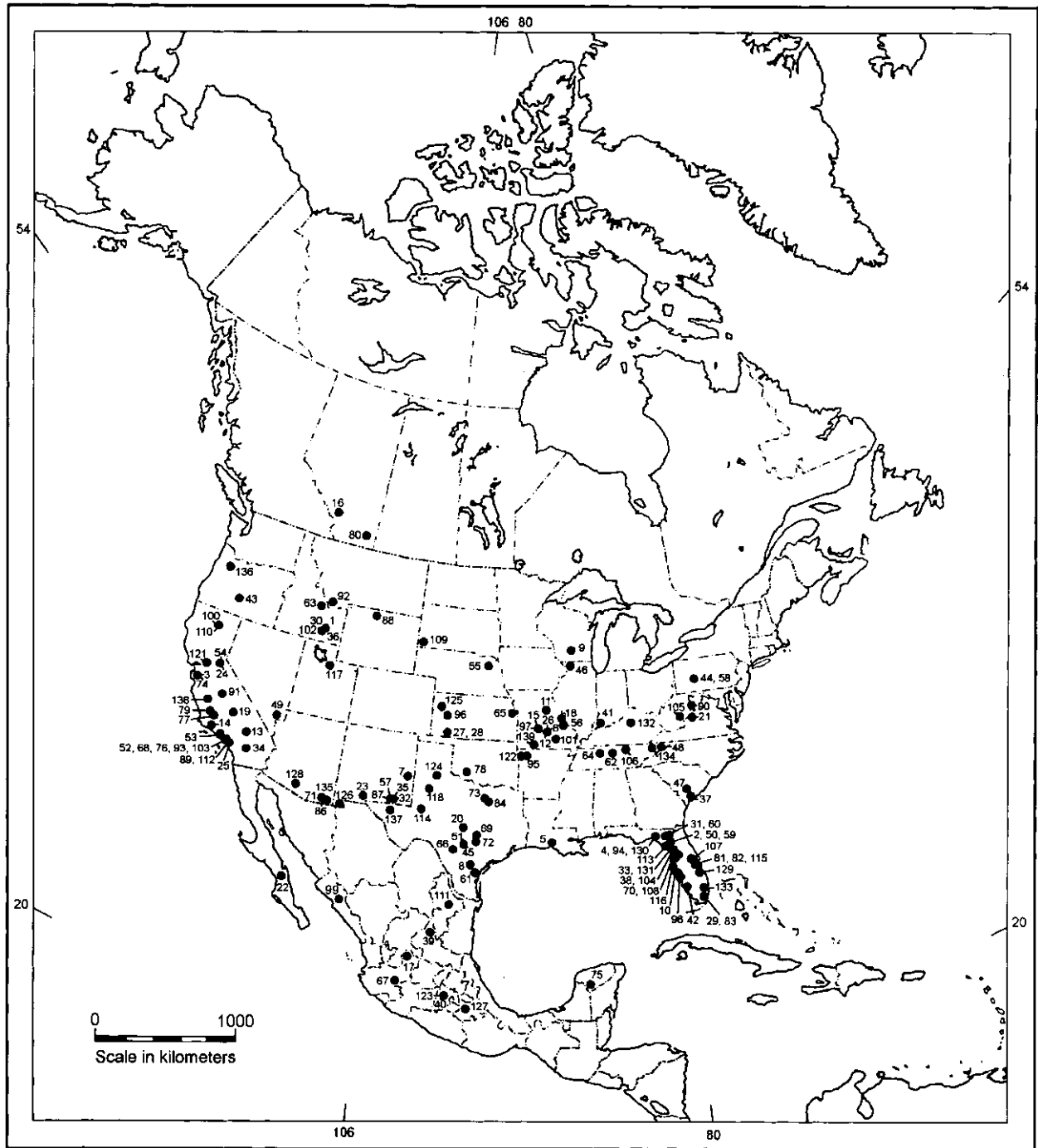


Fig. 1. Map of North America showing the distribution of dire wolf (*Canis dirus*) localities (numbered dots). The numbers correspond to the locality names in Table 1.

carbon dated. Two Rancho La Brea dire wolf specimens yielded dates of 9850 ± 550 BP and $10\,710 \pm 320$ BP, both based on bone carbonate (Marcus & Berger 1984), but the accuracy of the dates is suspect because bone carbonate is known to produce unreliable age determinations. Dire wolf ribs from Powder Mill Creek Cave,

Missouri, were dated at $13\,170 \pm 600$ BP (Krueger & Weeks 1965). This date is likewise considered unreliable because bone carbonate was analyzed. Although 45 dire wolf localities have radiocarbon dates associated with them, the strength of the association between the dates and the dire wolf remains is weak. Because the

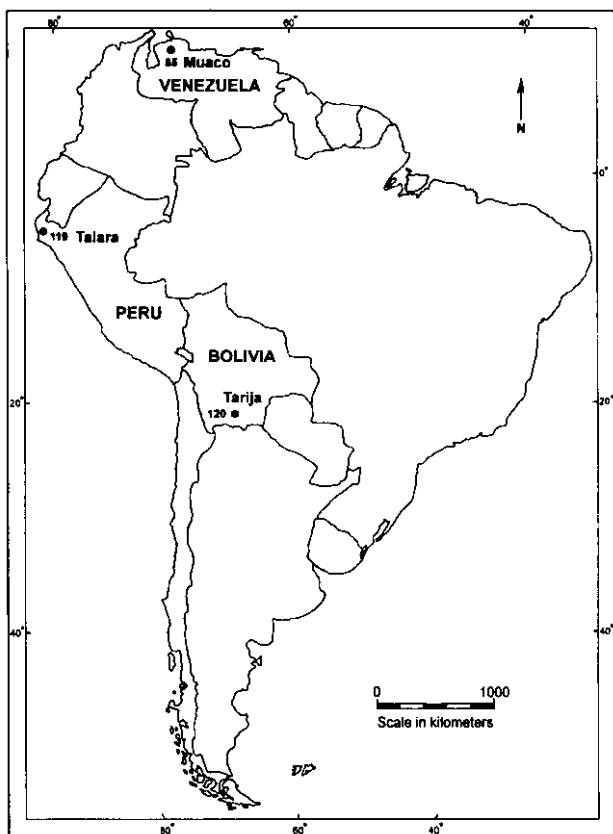


Fig. 2. Map of South America showing the distribution of dire wolf (*Canis dirus*) localities (numbered dots). The numbers correspond to the locality names in Table 1.

dire wolf occurs in many faunas dated at or near the Pleistocene/Holocene boundary, and because there are no confirmed Holocene records, the dire wolf is inferred to have become extinct near the end of the Pleistocene in both North and South America.

The dire wolf ranged widely in North and South America. Late Pleistocene sites are concentrated in the United States, particularly in California, Texas, Florida, and Missouri (Fig. 1). Most localities record a minimum of one to a few individuals, but mass occurrences of skeletal remains are known, particularly from Rancho La Brea, California, which records at least 2250 dire wolves (Marcus 1960; Dundas pers. obs.). A minimum of 25 individuals occur at Talara, Peru (Kisko 1967). Cutler Hammock, Florida, preserves at least 42 individuals and is interpreted to have been used by dire wolves as a denning or rendezvous site (Emslie & Morgan 1995). Another large collection is known from San Josecito Cave, Mexico, although a count of the minimum number of individuals is not available (Nowak 1979).

The dire wolf occupied a broad range of habitat types throughout its geographic distribution. In South America the species occurred in areas characterized by arid

savannah conditions. In North America most of the sites are on the plains and grasslands, although records also come from forested mountain areas. The sites range in elevation from sea level to 2255 m (7400 feet) (Dundas 1994). While the dire wolf is found at fairly high altitudes in temperate areas, such as Jaguar Cave, Idaho (2255 m) (Sadek-Kooros 1972), the species has not been found at high latitudes. *Canis dirus* may have ranged farther north than southern Canada during interglacial periods, but its remains would likely have been obliterated by subsequent glacial activity.

Center of origin

Most authors who have considered the question tend to favor a North American origin for the dire wolf (Martin 1974; Nowak 1979; Berta 1988) based on: (1) more potential progenitors are present in the middle Pleistocene of North America, (2) the distribution of *Canis dirus* is much better represented in North America, with 136 sites versus only three localities in South America, although South America is not nearly as well explored as North America, and (3) *Canis dirus* appears earlier in the fossil record in North America.

If *Canis dirus* originated in North America, the species likely dispersed into South America via the Andean corridor (Berta 1988), a proposed pathway for temperate mammals to migrate from Central to South America because of the favorable cool, dry, open habitats that characterized the region at times (Webb 1978, 1991). This interpretation is consistent with the distribution pattern of *Canis dirus* in South America. Additionally, the migration would likely have occurred during a glacial period, when the pathway consisted of open, arid regions and savannah, because during interglacial periods the pathway from Central America into South America was characterized by tropical rainforest habitat (Webb 1991). Overall, the present biogeographic data for *Canis dirus* in North and South America contribute little to answering the question of the species' area of origin.

Phylogenetic position

Although the geographic and stratigraphic data suggest a North American origin for the dire wolf, systematic data may indicate the opposite; a South American origin. Phylogenetic relationships within the *Canis* wolf group are unclear. Many wolf species appear in the Pleistocene of Eurasia, North America, and South America. *Canis falconeri*, *Canis armbrusteri*, *Canis lupus*, *Canis* cf. *C. dirus*, *Canis gezi*, and *Canis nehringi* have been suggested as close relatives of *Canis dirus* and therefore are important in determining the phylogenetic position of the dire wolf (Berta 1988). *Canis falconeri* is a large wolf from the middle-late Villa-

Table 1. Quaternary fossil localities of *Canis dirus* in North and South America.

Locality	Map No.	Age	Reference(s)
American Falls, ID	1	Sang.	Hopkins <i>et al.</i> 1969; Pinosof 1992
Arredondo 1B & 2A, FL	2	Sang.	Bader 1957; Webb 1974; Kurtén 1984; Webb & Wilkins 1984
Arroyo Las Positas, CA	3	Rancho.	Nowak 1979
Aucilla River 1A, FL	4	Wisc.	Webb 1974; Kurtén 1984
Avery Island (Petite Anse), LA	5	?Sang.	Gagliano 1967; Domning 1969; Nowak 1979
Bat Cave, MO	6	l. Wisc.	Hawksley 1965; Hawksley <i>et al.</i> 1973; Nowak 1979
Blackwater Draw Localities 1 & 6, NM	7	l. Wisc.	Lundelius 1972b
GBlanco Creek (Berclair Terrace), TX	8	Wisc.	Sellards 1940
Blue Mounds, WI	9	l. Pleist.	Allen 1876; Nowak 1979; Kurtén 1984
Bradenton, FL	10	Sang.	Webb 1974; Nowak 1979
Brynjulfson Caves, MO	11	l. Wisc.	Parmalee & Oesch 1972; Kurtén 1984
Bushwacker Cave, MO	12	?Wisc.	Hawksley 1986
Camp Cady, CA	13	Rancho.	Jefferson 1991a, 1991b
Carpinteria, CA	14	?Wisc.	Wilson 1933
Carroll Cave, MO	15	Wisc.	Hawksley <i>et al.</i> 1963; Hawksley 1965; Hawksley & Weaver 1981
Castleguard Icefield, Alberta, Canada	16	Rancho.	Cowan 1954
Cedazo, Aguascalientes, Mexico	17	?Illin/Sang.	Mooser & Dalquest 1975; Nowak 1979
Cherokee Cave, MO	18	l. Wisc.	Simpson 1949; Nowak 1979
China Lake, CA	19	l. Wisc.	Davis 1978; Fortsch 1978
Clamp Cave, TX	20	l. Wisc.	Lundelius 1967
Clark's Cave, VA	21	l. Wisc.	Guilday <i>et al.</i> 1977
Comondu, Baja California, Mexico	22	l. Pleist.	Berta 1979
Conkling Cave, NM	23	l. Wisc.	Nowak 1979
Cool Quarry, CA	24	Rancho.	Jefferson 1991a
Costeau Pit, CA	25	m. Wisc.	Miller 1971
Cox Cave, MO	26	l. Pleist.	Mehl 1962; Hawksley 1986
Cragin Quarry locality 1, KS	27	e. Sang.	Hibbard 1939, 1949; Hibbard & Taylor 1960
Cragin Quarry, XI Ranch, KS	28	e. Sang.	Hibbard 1939, 1949; Nowak 1979
Cutler Hammock, FL	29	l. Wisc.	Emslie & Morgan 1995
Dam, ID	30	l. Wisc.	Kurtén 1984; Pinosof 1992
Dampier's Landing, FL	31	l. Wisc.	Webb 1994 pers. comm.
Dark Canyon Cave, NM	32	l. Wisc.	Harris 1985a
Devil's Den, FL	33	l. Wisc.-?Holo.	Martin & Webb 1974; Seymour 1993
Domenigoni Valley, CA	34	Rancho.	Springer & Scott 1994 pers. comm.
Dry Cave, NM	35	l. Wisc.	Harris 1980; Harris 1989
Duck Point, ID	36	Wisc.	Hearst 1990; Pinosof 1992
Edisto Island, SC	37	l. Pleist.	Roth & Laerm 1980
Eichelberger Cave, FL	38	l. Wisc.	Nowak 1979
El Cedral, San Luis Potosi, Mexico	39	l. Pleist.-e. Holo.	Lorenzo & Mirambell 1981
El Tajo Quarry, Mexico, Mexico	40	l. Pleist.	Furlong 1925; Berta 1979; Kurtén 1984
Evansville, IN	41	Wisc.	Leidy 1854; Nowak 1979
Flamingo Waterway, FL	42	Wisc.	Kurtén 1984
Fossil Lake, OR	43	e.-m. Wisc.	Elftman 1931; Allison 1966; Kurtén 1984
Frankstown Cave, PA	44	l. Wisc.	Peterson 1926; Nowak 1979
Friesenhahn Cave, TX	45	l. Wisc.	Lundelius 1960; Kurtén 1984
Galena, IL	46	Wisc.	Hay 1923; Nowak 1979
Giant Portland Quarry, SC	47	l. Pleist.	Bohaska 1990 pers. comm.
Guy Wilson Cave, TN	48	l. Wisc.	Guilday <i>et al.</i> 1975; Corgan 1976
Gypsum Cave, NV	49	l. Wisc.	Harrington 1933
Haile 8A, FL	50	Sang.	Webb 1974
Hall's Cave, TX	51	l. Wisc.	Toomey 1993
Harbor Freeway (I-110), CA	52	Rancho.	Miller 1971
Harold Beds, CA	53	Rancho.	Nowak 1979
Hawver Cave, CA	54	Wisc.	Stock 1918
Heckendorf Gravel Pit, NB	55	l. Pleist.	Nowak 1979
Herculaneum, MO	56	Rancho.	Olson 1940
Hermit's Cave, NM	57	l. Wisc.	Schultz <i>et al.</i> 1970; Nowak 1979
Hollidaysburg Fissure, PA	58	l. Wisc.	Fonda & Czebieniak 1986
Hornsby Springs, FL	59	l. Wisc.	Bader 1957; Kurtén 1984
Ichetucknee River, FL	60	l. Wisc.	Nowak 1979; Kurtén 1984
Ingleside Gravel Pit, TX	61	?e. Wisc.	Lundelius 1972a
Jaguar Cave, TN	62	l. Wisc.	Robbins <i>et al.</i> 1981
Jaguar Cave, ID	63	l. Wisc.	Kurtén & Anderson 1972
Jewell Cave, TN	64	l. Pleist.	Nowak 1979
Kansas River, KS	65	l. Wisc.	Wang 1990
Kincaid Shelter, TX	66	Rancho.	Lundelius 1967

Table 1. Continued.

Locality	Map No.	Age	Reference(s)
Lago de Chapala, Jalisco, Mexico	67	1. Pleist.	Downs 1958; Nowak 1979
La Mirada, CA	68	1. Wisc.	Miller 1971
Laubach Cave, TX	69	1. Wisc.	Slaughter 1966b
Lecanto 2A, FL	70	Rancho.	Webb 1994 pers. comm.
Lehner, AZ	71	1. Wisc.	Haynes 1982
Levi Shelter, TX	72	1. Wisc.	Lundelius 1967
Lewisville, TX	73	1. Wisc.	Winkler 1982
Livermore Valley, CA	74	Rancho.	Leidy 1873; Nowak 1979
Loltun Cave, Yucatan, Mexico	75	1. Wisc.	Alvarez & Polaco 1982; Arroyo-Cabrales 1992 pers. comm.
Los Angeles Police Station, CA	76	Rancho.	Langenwalter 1975; Jefferson 1991a
Maricopa, CA	77	1. Wisc.	Shakespeare 1975; Nowak 1979
Marlow, OK	78	1. Pleist.	Nowak 1979
McKittrick, CA	79	1. Wisc.	Schultz 1938; Nowak 1979
Medicine Hat, Alberta, Canada	80	?Sang. or ?Wisc.	Harington 1978; Nowak 1979
Melbourne, FL	81	1. Wisc.	Gazin 1950; Ray 1958; Nowak 1979
Merritt Island, FL	82	Wisc.	Kurtén 1984
Monkey Jungle Hammock, FL	83	1. Wisc.	Webb 1994 pers. comm.
Moore Pit, TX	84	Sang. or Wisc.	Slaughter <i>et al.</i> 1962; Slaughter 1966a; Kurtén 1984
Muaco, Falcon state, Venezuela	85	1. Lujan.	Berta 1988
Murray Springs, AZ	86	1. Wisc.	Nowak 1979
Muskox Cave, NM	87	1. Wisc.	Logan 1981
Natural Trap Cave, WY	88	1. Wisc.	Walker 1987; Chomko & Gilbert 1987
Newport Bay Mesa, CA	89	Sang.	Miller 1971
New Trout Cave, WV	90	1. Wisc.	Grady 1982
Oil Springs, CA	91	Rancho.	Merriam 1903; Merriam 1912
Orr Cave, MT	92	Wisc.	Kurtén 1984; Dawson 1994 pers. comm.
Pacific Ave./Oliver St. San Pedro, CA	93	Sang.	Miller 1971; Langenwalter 1975
Page/Ladson, FL	94	1. Wisc.-Holo.	Dunbar <i>et al.</i> 1988; Webb 1994 pers. comm.
Peccary Cave, AR	95	1. Wisc.-Holo.	Davis 1969; Quinn 1972
Pendennis, KS	96	Rancho.	Hay 1924; Nowak 1979
Perkins Cave, MO	97	?Wisc.	Hawksley 1965; Nowak 1979
Phillipi Creek - Fruitville Ditch, FL	98	Wisc.	Simpson 1929; Nowak 1979
Potrecito, Sinaloa, Mexico	99	Rancho.	Kurtén 1984
Potter Creek Cave, CA	100	1. Wisc.-e. Holo.	Sinclair 1904; Jefferson 1991a
Powder Mill Creek Cave, MO	101	1. Wisc.	Galbreath 1964; Hawksley 1986
Rainbow Beach, ID	102	1. Wisc.	McDonald & Anderson 1975
Rancho La Brea, CA	103	1. Wisc.	Merriam 1912; Marcus 1960; Miller 1968; Nowak 1979
Reddick 1A, FL	104	Sang.	Gut & Ray 1963; Nowak 1979; Kurtén 1984
Rennick Cave, WV	105	Wisc.	Nowak 1979
Robinson Cave, TN	106	1. Wisc.	Guilday <i>et al.</i> 1969
Rock Springs, FL	107	Sang. - Wisc.	Webb 1974; Wilkins 1983
Sabertooth Cave, FL	108	Sang. or Wisc.	Simpson 1928; Kurtén 1984
Salamander Cave, SD	109	Rancho.	Mead 1994 pers. comm.
Samwel Cave, CA	110	1. Wisc.	Nowak 1979
San Josecito Cave, Nuevo Leon, Mexico	111	Wisc.	Nowak 1979; Kurtén 1984
San Pedro Lumber Company, CA	112	Sang.	Miller 1971
Sante Fe River IIA, FL	113	1. Pleist.	Webb 1974
Scharbauer, TX	114	Wisc.	Nowak 1979
Sebastian Canal, FL	115	Wisc.	Webb 1974
Seminole Field, FL	116	Wisc.	Simpson 1929; Nowak 1979
Silver Creek, UT	117	1. Wisc.	Miller 1976
Slaton Quarry, TX	118	Illin. or e. Sang.	Dalquest 1967
Talara, Peru	119	1. Lujan.	Churcher 1959; Kisko 1967; Berta 1988
Tarija, Bolivia	120	Lujan.	Berta 1988
Teichert Pit, CA	121	Sang.	Nowak 1979
Ten Mile Rock, AR	122	1. Wisc.	Medlock 1978
Tequiquiac, Mexico, Mexico	123	1. Pleist.	Freudenberg 1910; Maldonado-Koerdell 1955; Berta 1988
Tule Canyon, TX	124	Pleist.	Cope 1895; Merriam 1912
Twelve-Mile Creek, KS	125	Rancho.	Hay 1924; Nowak 1979
U-Bar Cave, NM	126	1. Wisc.	Harris 1985b, 1989
Valsequillo, Mexico, Mexico	127	1. Pleist.	Thenius 1970; Berta 1988
Ventana Cave, AZ	128	1. Wisc.	Colbert 1950
Vero (stratum 2), FL	129	1. Wisc.	Weigel 1962; Nowak 1979
Ward Island, FL	130	1. Wisc.	Graham 1993 pers. comm.
Wekiva River, FL	131	Rancho.	Nowak 1979

Table 1. Continued.

Locality	Map No.	Age	Reference(s)
Welsh Cave, KY	132	l. Wisc	Guilday <i>et al.</i> 1971
West Palm Beach, FL	133	l. Wisc.	Converse 1973; Webb 1994 pers. comm.
Whitesburg, TN	134	?Wisc.	Hay 1920; Corgan 1976
Whitewater Draw, AZ	135	l. Wisc.-e. Holo.	Nowak 1979; Harris 1985a
Willamette Valley, OR	136	Rancho.	Nowak 1979
Williams Cave, TX	137	l. Wisc.	Ayer 1936
Witt (or Dudley Ridge), CA	138	Wisc.	Jefferson 1991a; Gobalet & Fenenga 1993
Zoo Cave, MO	139	l. Wisc.-e. Holo.	Hood & Hawksley 1975; Nowak 1979

e. = early; m. = middle; l. = late; Pleist. = Pleistocene; Holo. = Holocene; Rancho. = Rancholabrean; Lujan. = Lujanian; Illin. = Illinoian glacial; Sang. = Sangamonian interglacial; Wisc. = Wisconsinan glacial; ? = questionable age.

franchian of Europe. Similarities with the North American species *Canis armbrusteri* have been noted (Kurtén & Anderson 1980). *Canis armbrusteri*, a large wolf about the size of *Canis lupus*, first appears in the Irvingtonian of North America and has been recovered from several localities across the United States, suggesting that the species had a continent-wide distribution. *Canis armbrusteri* became extinct near the end of the Irvingtonian, about the same time *Canis lupus* arrived in North America (Kurtén & Anderson 1980). *Canis lupus* originated in the early-middle Pleistocene in Europe and later migrated to North America in the late Irvingtonian via the Bering Land Bridge (Kurtén & Anderson 1980). *Canis gezi*, a poorly known small wolf from the Ensenadan of South America, appears to have given rise to *Canis nehringi*, a Lujanian species from Argentina, known only from the type specimen. Using the above taxa in a cladistic analysis, Berta (1988) suggested that *Canis dirus* has a more recent common ancestry with the South American wolves *Canis gezi* and *Canis nehringi* than with North American Pleistocene wolf species. In fact, Berta's (1988) analysis places *Canis dirus* and *Canis nehringi* as sister taxa and are the most derived members of the genus *Canis* in the New World. From this preliminary analysis, it is possible to suggest a South American origin for *Canis dirus*. However, additional phylogenetic studies are needed to clarify the relationships among the *Canis* wolf species.

Extinction

As previously noted, the timing of the extinction of *Canis dirus* is not precisely known, and very few radiocarbon dates are directly associated with dire wolf fossils. Over the past 30 years considerable research has focused on investigating the demise of megaherbivores at the end of the Pleistocene in North and South America (Martin & Wright 1967; Martin & Klein 1984; Stuart 1991), but the extinction of large predators has attracted little attention. It generally has been assumed that the large carnivore extinctions resulted from the

contemporaneous loss of megaherbivore prey species (Graham & Mead 1987; Barnosky 1989; Stuart 1991). Did *Canis dirus* become extinct as the result of the loss of its prey? Many factors of the environment contribute to the extinction of species. Extinction results from the elimination of a species' geographic range and the reduction of its population size to zero. Factors affecting biogeographic range and population size include competition, predator/prey interactions, variables of the physical environment, and chance events (Stanley 1987). In order to investigate possible extinction models, it is important to have a precise understanding of the biogeography of not only *Canis dirus* but also its potential competitors and prey, and how all of these organisms responded to environmental changes that occurred near or at the time of extinction. Currently, these data are unavailable.

Summary and conclusions

Our present understanding of the dire wolf's biogeography poses more questions about the animal than it answers. Several important questions arise from the following: (1) There is a large discrepancy in the number of dire wolf localities between the American continents. While common in the Rancholabrean of North America, the species is rare in the Lujanian of South America. (2) The dire wolf's center of origin remains uncertain. The geographic and stratigraphic data suggest a possible North American origin for the species, but this conflicts with the results of phylogenetic studies. (3) Though capable of adapting to a wide range of habitat types and altitudes, *Canis dirus* does not occur at high latitudes, unlike its close relative, *Canis lupus*. (4) An apparently very successful predator, particularly in North America for several hundred thousand years, the dire wolf became extinct on both American continents at the end of the Pleistocene. Clearly, *Canis dirus* requires additional studies to gain a better understanding of its biology and role in the late Pleistocene ecosystems of North and South America.

Future work should proceed in several directions.

More field studies are needed in South America to determine whether the discrepancy in numbers of localities between the two American continents is a real phenomenon or whether it is an artefact of our present knowledge (i.e. sampling bias). Furthermore, description and publication of Mexico's rich Pleistocene faunal collections should be encouraged. This work could help to resolve the question of the species' area of origin, along with comprehensive and detailed systematic studies needed to clarify the phylogenetic position of *Canis dirus*. To determine the timing of extinction of *Canis dirus*, many dire wolf specimens need to be directly dated. In addition, the timing of extinction needs to be determined for other large carnivores and megaherbivores that closely interacted with *Canis dirus*. The dates will permit more comprehensive tests of paleoecological extinction models relating to predator/prey interactions and interspecific competition. Future studies along these lines will help to shed new light on this important Pleistocene predator.

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