

DIRE WOLF, *CANIS DIRUS* (MAMMALIA; CARNIVORA; CANIDAE), FROM THE  
LATE PLEISTOCENE (RANCHOLABREAN) OF EAST-CENTRAL  
SONORA, MEXICO

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**ABSTRACT**—We describe the first occurrence of the extinct dire wolf, *Canis dirus*, from the late Pleistocene deposits of east-central Sonora, Mexico. Remains include a partially complete left mandible and a left distal fragment of humerus collected from the deposits at Térapa. Local environments are interpreted to have been a tropical marsh with thorn-scrub to deciduous forest including some component of a nearby grassland. Although the mandible is nearer to the size of other large species of *Canis* known to occur in Mexico, the deep and robust mandible, presence of an accessory cuspid on the p2, an enlarged and robust p4, and accessory cuspids on the posterior margin of the trigonid ally the *Canis* from Térapa with *C. dirus*. Length of p4 suggests a possible closer affiliation to *C. d. guildayi* than to *C. d. dirus*.

**RESUMEN**—Describimos el primer registro del ya extinto lobo (*Canis dirus*) de depósitos del Pleistoceno tardío del centro-este de Sonora, México. Los restos incluyen una mandíbula izquierda parcialmente completa y un fragmento izquierdo distal de húmero colectados de depósitos en Térapa. Se piensa que el clima local fue pantano tropical con matorral espinoso a bosque deciduo, incluyendo algún componente de un pastizal cercano. A pesar de que el tamaño de la mandíbula es más similar al de otras especies grandes de *Canis* que ocurren en México, la profundidad y robustez de la mandíbula, la presencia de una cúspide accesoria en el p2, un p4 alargado y robusto, y cúspides accesorias en el margen posterior del trigónido colocan el *Canis* de Térapa en *C. dirus*. La longitud de p4 lo asocia más con *C. d. guildayi* que con *C. d. dirus*.

Mexico has a rich and diverse record of canids in the late Pleistocene (Mammalia, Carnivora, Canidae). At present, six species and two genera of medium-to-large-sized canids are recorded from the late Pleistocene; Rancholabrean North American Land Mammal Age of Mexico, which include the dhole, *Cuon alpinus* (Kurtén and Anderson, 1980), coyote, *Canis latrans* (Kurtén, 1974; Nowak, 1979), gray wolf, *C. lupus* (Nowak, 1979), red wolf, *C. rufus* (Nowak, 1979), extinct dog, *C. cedazoensis* (Mooser and Dalquest, 1975), and dire wolf, *C. dirus* (Nowak, 1979; Dundas, 1999); the latter is of interest here.

Dundas (1999) has provided the most recent review of known localities of *C. dirus*, which has an extensive fossil range. *Canis dirus* is known to occur as far north as southern Alberta (Canada) and south into South America to southern

Bolivia (Dundas, 1999). Ten localities in Mexico are known to contain *C. dirus*: Cedazo, Aguascalientes (Mooser and Dalquest, 1975); Comondu, Baja California (Berta, 1979); El Cedral, San Luis Potosí (J. L. Lorenzo and L. Mirambell, in litt.); El Tajo Quarry (Furlong, 1925; Berta, 1979; Kurtén, 1984), Tequiquiac (Freudenberg, 1910), and Valsequillo, all in Distrito Federal, Mexico (Maldonado-Koerdell, 1955; Thenius, 1970; Berta, 1988); Lago de Chapala, Jalisco (Downs, 1958; Nowak, 1979); Lotlun Cave, Yucatán (Alvaerz and Polaco, 1982); Potrecito, Sinaloa (Kurtén, 1984); and San Josecito Cave, Nuevo León (Nowak, 1979; Kurtén, 1984). The majority of these localities occur in the central and southeast-central portions of Mexico with few localities occurring in the north or west. Of the central localities, San Josecito Cave and

Cedazo have the greatest number of individuals of *C. dirus* collected from a single locality; other localities in Mexico are known by only a few specimens.

San Josecito Cave has a rich record of Pleistocene carnivores (Stock, 1950; Hall, 1960; Kurtén and Anderson, 1980). Fossils of  $\geq 30$  individuals of *C. dirus* were collected along with *C. latrans*, *C. lupus*, and *Cuon alpinus* (Nowak, 1979; Kurtén, 1984). Occurrence of *Cuon alpinus* in the Pleistocene of central Mexico is something of an enigma as the only other known occurrence of this species in North America is the Old Crow River locality near Fairbanks, Alaska (Cohen, 1978). This distribution is unexplained at present (Kurtén and Anderson, 1980; Anderson, 1984). The Cedazo locality also has an extensive record of carnivores; four lower jaws and a tibia of *C. dirus* were collected, along with *C. latrans* and *C. cedazoensis* (Mooser and Dalquest, 1975).

The northwestern states of Mexico at present have an enigmatic Pleistocene record. Only localities at Comondu, Baja California (Berta, 1979), and Potrecito, Sinaloa (Kurtén, 1984), contain *C. dirus*. The small number of northern and western localities of *C. dirus* may not indicate the rarity of *C. dirus* from this region of Mexico, or more likely, reflects the lack of intensive prospecting. New collecting in Sonora in the late 20th century and the early 21st century have yielded new RanchoLabrean localities (Lindsay, 1984; Van Devender et al., 1985; Mead et al., 2006). Here we present the first specimens of *C. dirus* from the state.

**LOCALITY**—Vertebrate history of the late Pleistocene of Sonora is beginning to be understood in greater detail with analysis of fossils recovered from deposits at Térapa, located along the Río Moctezuma in interior east-central Sonora (29°41'N; 109°39'W, 605 m elevation). The fossil-rich deposits of Térapa contain >70 zoological taxa, many with tropical affinities such as *Crocodylus* (crocodile) and *Hydrochaeris* (capybara), along with many birds and *Bison* (bison; Mead et al., 2006). Carranza-Castañeda and Roldán-Quintana (2007) briefly mentioned their recovery of surface finds of *Bison* and *Equus* (horse) from Térapa. Teeth and postcranial remains of *Bison* recovered by Mead et al. (2006) from throughout the 11 m of stratified sediments prescribe an assignment for the deposit and encased fauna to the RanchoLabrean

North American Land Mammal Age of the late Pleistocene (Bell et al., 2004). Avian remains (D. W. Steadman and J. I. Mead, in litt.) and glyptodont and pampathere xenarthrans have been described (Mead et al., 2007). Geological context and stratigraphy of deposits at Térapa were described in Mead et al. (2006). A lava flow within the Moctezuma volcanic field (Paz-Moreno et al., 2003) created at least one catchment basin ca. 1 by 2 km adjacent to the Río Moctezuma. The Río Moctezuma joins the Río Yaqui and enters the Gulf of California (28°N, 111°W), positioning Térapa 350 km inland.

All fossil specimens from Térapa are archived temporarily into the Laboratory of Quaternary Paleontology, Northern Arizona University (NAU QSP), Flagstaff. Within this system, all specimens are curated into a numbering classification specifically for Térapa (TERA) and eventually will be returned to Sonora.

**SYSTEMATIC PALEONTOLOGY**—Materials described below were collected during the 2003 and 2005 field seasons. Dental nomenclature follows Van Valen (1966) and Wang et al. (1999). Postcranial nomenclature follows Reighard and Jennings (1925) and Munthe (1989). Two skulls and skeletons of *Canis lupus* (NAUQSP 5936 and 7344) were available for comparison with fossil material. All other comparisons are based on literature and text figures.

Order Carnivora Bowdich, 1821  
 Family Canidae Gray, 1821  
 Subfamily Caninae Gill, 1872  
 Genus *Canis* Linnaeus, 1758  
*Canis dirus* Leidy, 1858

**Referred Specimens**—TERA-154 left mandible with c1-m2 from Long Wolf site and TERA-155 left distal humerus fragment from Santiago site. Specimens are from the Bp2 marsh sediments as described in Mead et al. (2006).

**Description**—The left lower jaw (TERA-154; Table 1) is missing the anterior portion of the ascending ramus, coronoid process, and condyloid process (Figs. 1a and 1b). The ramus is deep and robust. The anterior mental foramen is enlarged and situated below and between p1 and p2. The posterior mental foramen is small and is positioned below and between the p3 and p4. The canine is slightly mediolaterally compressed with a medial ridge that is situated from the tip of the tooth down to just above the base of the

TABLE 1—Measurements of mandibular ramus of *Canis dirus* from Térapa, Sonora (in mm): \* = estimated.

Character	Measurement
Ramus	
Depth between p2 and p3	29.6
Width between p2 and p3	13.5
Depth between m1 and m2	35.1
Width between m1 and m2	15.2
c1	
Anteroposterior diameter	14.3
Transverse diameter	10.2
p1	
Anteroposterior diameter	7.3
Transverse diameter	5.5
p2	
Anteroposterior diameter	14.5
Transverse diameter	6.9
p3	
*Anteroposterior diameter	15.6
Transverse diameter	6.8
p4	
Anteroposterior diameter	19.5
Transverse diameter	9.4
m1	
Anteroposterior diameter of entire tooth	32.6
Transverse diameter of entire tooth	12.9
Anteroposterior diameter of trigonid	22.8
Transverse diameter of trigonid	12.9
Anteroposterior diameter of talonid	10.2
Transverse diameter of talonid	12.2
m2	
Anteroposterior diameter	12.5
Transverse diameter	9.4
m3 (alveolus)	
*Anteroposterior diameter	5.7
*Transverse diameter	9.4
Lengths of toothrow	
Length of p1-m2	100.9
Length of m1-m2	44.9

enamel, which is typical of the genus *Canis*. The canine possesses wear on the tip of the tooth and along one-half of the upper posterior margins. The p1 is small and single rooted with the principal cusp slightly more anterior of the tooth. Slight wear on the dorsal surface occurs on the p1. The p2 is as large as the p3 with a tall principal cusp with presence of a small posterior accessory cusp. There is a slight ridge for the

posterior cingular cusp. Wear occurs on the dorsal tip of the p2. Only the anterior one-half of the crown and anterior root of p3 are preserved. The principal cusp has wear on the dorsal tip. The p4 is larger than the p3. The primary cusp is about the same height as the paraconid on m1. The posterior accessory cusp is large with a large posterior cingular cusp. Wear occurs on both the principal cusp and posterior accessory cusp. The m1 is large and robust. The trigonid is long and massive with a short heel. The paraconid is only slightly smaller than the protoconid and not as tall, with heavy dorsal wear. The protoconid is tall and massive, with heavy wear on the anterior, dorsal and posterior margins of the crown. The metaconid is reduced, with wear on the dorsal tip. A slight secondary cuspid occurs just below the metaconid. The hypoconid is larger than the entoconid, both having heavy wear on the dorsal surface. A slight cingulum is present on the lateral posterior margins of the heel. The m2 has an enlarged protoconid and a small hypoconid. There are small cusps for the entoconulid and the entoconid. A single alveolus for the m3 is present.

A left distal fragment of humerus (TERA-155; Table 2) is the only known postcranial material of *Canis* from Térapa (Fig. 1c). The fragment preserved is the lower portion of the mid-shaft and the capitulum, trochlea, lateral and medial epicondyles of the distal end. The shaft is straight and flairs slightly near the medial and lateral epicondyles. The ulnar fossa foramen is moderately wide.

*Comparison*—The mandible of *Canis*, TERA-154, is about the size of that from a large *C. lupus*, and is near the size of the extinct Irvingtonian *Canis armbrusteri*. In comparison of TERA-154 with *C. lupus*, proportions suggest a more robust animal lived in Térapa. TERA-154 is deeper and heavier than those mandibles seen in *C. lupus*. The p2 of *C. lupus* lacks the posterior accessory cuspid as is on *C. dirus* and TERA-154. The p4 of *C. lupus* is as massive as that on TERA-154 from Térapa.

Mandibles in *C. armbrusteri* are neither as deep nor as massive compared to TERA-154. The p2 and p3 in *C. armbrusteri* are simpler, with the p2 not having accessory cuspid and the p3 varying from having no additional cusps, to having a small simple posterior accessory cusp (Gidley, 1913; Gidley and Gazin, 1938). The p4 in *C. armbrusteri* is not as large proportionally as compared to TERA-154. Gidley (1913) described

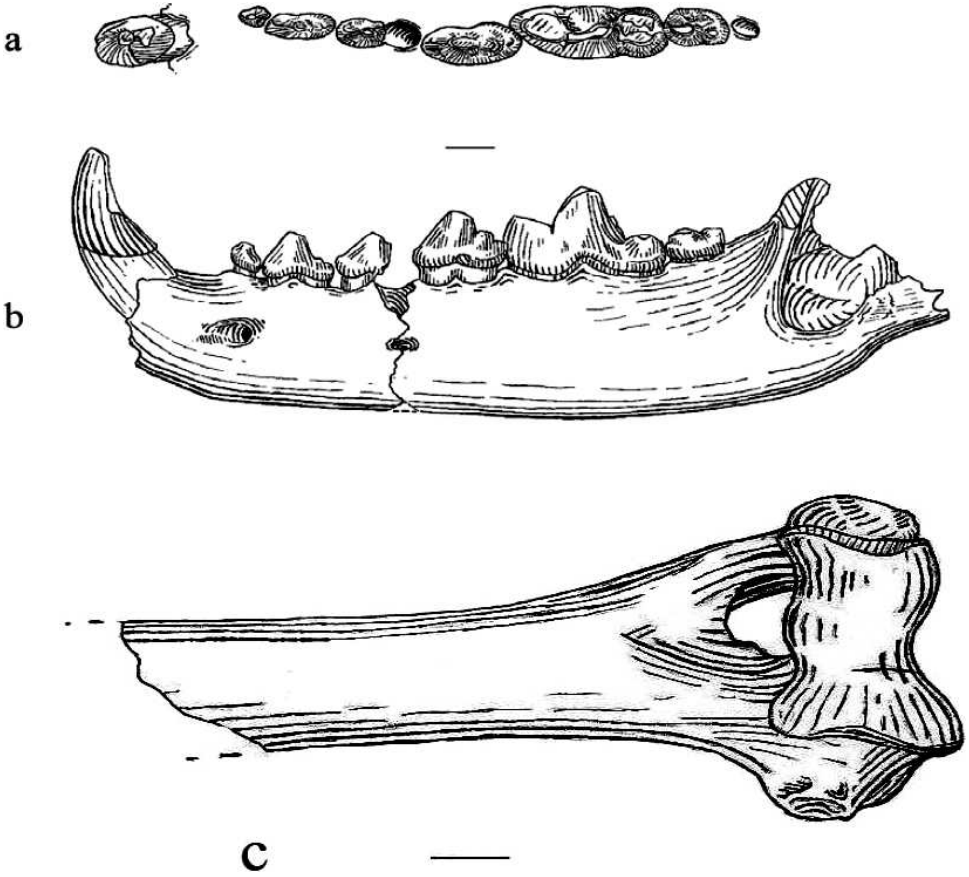


FIG. 1—a) Occlusal view of dentition and b) lateral view of ramus and dentition of left mandible of *Canis dirus* (TERA-154) from Térapa, Sonora, and c) anterior view of fragment of left distal humerus of *C. dirus* from Térapa, Sonora (TERA-155). Scale bar equals 1 cm.

*C. arnbrusteri* as having a dentition more coyote-like than wolf-like, although the skull and postcranial materials from Cumberland Cave (Maryland) suggest a slender wolf similar in proportion to the extant *C. rufus* (Gidley and Gazin, 1938).

*Canis rufus* has a long-slender ramus with a long-slender canine (Paradiso and Nowak,

1972), while TERA-154 is deeper and shorter yet has a heavier canine. Premolars of *C. rufus* are reduced in height but are longer proportionally than TERA-154. There is a small posterior accessory cuspid on the p2, although the p4 is not enlarged (see Paradiso and Nowak, 1972:figure 1) in *C. rufus* like that in TERA-154.

*Canis dirus*, *C. gezi*, and *C. nehringi* have been recovered from tropical deposits of South America and would be appropriate for comparison to the *Canis* from Térapa due to the tropical nature of the Sonoran fauna. *Canis gezi* is a species of wolf from the Ensenadan South American Land Mammal Age, which is about equivalent to the late Irvingtonian and early Rancholabrean (Berta, 1988). The ramus of *C. gezi* is massive and deep, such as on TERA-154, with a short and broad canine; the p1 that is single rooted with a single primary cusp (Berta, 1988).

TABLE 2—Measurements of a humerus of *Canis dirus* from Térapa, Sonora (in mm).

Character	Measurement
Transverse width of distal end	44.6
Transverse width of epicondyles	34.6
Depth of epicondyles	18.2
Anteroposterior depth of epicondyles	19.5
Width of ulnar fossa foramen	12.2
Depth of ulnar fossa foramen	13.5

*Canis gezi* has a p2 that does not have a small accessory cuspid, a single cusped p3, and a p4 that is not proportionally enlarged or robust. *Canis nehringi* is a large species of wolf from the Lujanian South American Land Mammal Age that is about equivalent to the late Rancholabrean (Berta, 1988). The ramus of *C. nehringi* is not as deep as that on TERA-154, *C. gezi*, or *C. dirus*. In *C. nehringi*, the p2 does not have a posterior accessory cuspid, the p3 has a small posterior accessory cuspid, and the p4 is not enlarged. *Canis nehringi* has an enlarged m1 as on TERA-154, but lacks accessory cuspids on the posterior margin of the trigonid as on the specimen from Térapa.

The *Canis* from Térapa compares best with *C. dirus*, a Pleistocene species that has an extensive distribution in North, Central, and South America (Dundas, 1999). *Canis dirus* has a deep and robust mandible, a short and robust canine, a p1 that is single rooted and with a single principal cuspid, a p2 that is double rooted with a small posterior accessory cuspid, a p3 with a large posterior accessory cuspid, a large and robust p4 that is larger than the p3, and a massive and heavy m1 with small accessory cuspids on the posterior margin of the trigonid (Merriam, 1912; Berta, 1988). Variation occurs in the p2 in the presence of the posterior accessory cuspid. Merriam (1912) noted that most mandibles of *C. dirus* from Rancho La Brea (California) did not have the posterior accessory cuspid. Berta (1988), however, in her emended diagnosis of *C. dirus*, listed the accessory cuspids on p2 as one of the characteristic traits of the species, based on material from South America and elsewhere. Posterior accessory cuspids on p2 are not present in most North and South American *Canis* with the exception of *C. rufus* and *C. dirus*. We consider this a possible apomorphic character for distinguishing *C. dirus*. The enlarged p4 is perhaps the most characteristic trait seen in *C. dirus*. Although noted as having a massive m1 (Merriam, 1912; Nowak, 1979; Berta, 1988), *C. gezi* and *C. nehringi* also possess an enlarged m1 (Berta, 1988). The enlarged p4 is unique to *C. dirus*, another possible apomorphy.

In regards to the humerus TERA-155, literature describing the postcranial skeleton of *C. dirus* is inadequate. Most descriptions of postcranial material of *C. dirus* focuses on limb proportions in comparison to those of *C. lupus* (Stock et al., 1946; Nigra and Lance, 1947; Stock and Lance, 1948) and limb proportions relative

to running speed (Kurtén, 1984; Dundas, 1999). Merriam's (1912) evaluation of the humerus of *C. dirus* from Rancho La Brea was to state that it was similar to the living gray wolf, only larger. The TERA-155 fragment is similar to, yet larger than, the humerus of *C. lupus*.

Kurtén (1984) suggested that two forms of dire wolf occurred in North America, based on length of limb and tooth proportions. One form from west of the Rocky Mountains and from Mexico, which he referred to as *C. d. guildayi*, had shorter limb and longer tooth proportions. The other form, *C. d. dirus*, is known from east of the Rocky Mountains and had longer limb and shorter tooth proportions (Kurtén, 1984; Wang, 1990). Dental proportions (Table 3) and geographic position of *C. dirus* from Térapa would suggest association with the *C. d. guildayi* form.

DISCUSSION AND CONCLUSIONS—The Térapa deposit, with its diverse fauna, adds significantly to the knowledge about the Rancholabrean of Sonora. Presence of *C. dirus* at Térapa is the first for the state. Its presence expands the number of known predators in the fauna and helps to understand the predator scheme within these deposits. The only other large predator reported thus far from this location is cf. *Crocodylus acutus* (Mead et al., 2006). The large body mass of *C. dirus* can be correlated with the living gray wolf of northern North America, which prefers larger prey (such as bison) over smaller prey (Anyonge and Roman, 2006). New studies using stable isotopes on bone collagen of dire wolves from Rancho La Brea show a higher degree of prey preference toward species of ruminants over non-ruminants (Coltrain et al., 2004). Fox-Dobbs et al. (2007) recently suggested that *Equus* from Rancho La Brea was a major component in the diet of *C. dirus*, while bison and large camelids might have been secondary. *Canis dirus* would have filled the pursuit-predator niche in the tropical environment of Térapa, hunting large mammals such as *Bison*, *Equus*, large antilocaprids, and camelids that frequented the local environments, which are interpreted to have been a marsh with thorn-scrub to deciduous forest including some component of a grassland.

The presence of both *C. dirus* and glyptodont-pampathere xenarthrans (Mead et al., 2007) is shared with the locality at Cedazo, Aguascalientes (Mooser and Dalquest, 1975). The thick armor

TABLE 3—Comparison of subspecies of *Canis dirus* with *C. dirus* from Térapa, Sonora (modified from Kurtén, 1984; in mm).

Character	Sample	n	Range	Mean
Length of p2	Rancho La Brea ( <i>C. d. guildayi</i> )	20	14.4–17.9	15.72 ± 0.20
	San Josecito Cave ( <i>C. d. guildayi</i> )	30	13.2–16.4	15.22 ± 0.30
	<i>C. d. dirus</i> (Sangamon-early Wisconsin)	4	15.2–16.1	15.70 ± 0.23
	<i>C. d. dirus</i> (late Wisconsin)	9	12.2–15.8	14.78 ± 0.40
	<i>C. dirus</i> from Térapa	1	14.5	14.5
Width of p2	Rancho La Brea ( <i>C. d. guildayi</i> )	20	6.3–8.2	7.43 ± 0.09
	San Josecito Cave ( <i>C. d. guildayi</i> )	30	6.5–8.1	7.21 ± 0.07
	<i>C. d. dirus</i> (Sangamon-early Wisconsin)	4	6.5–7.6	7.15 ± 0.25
	<i>C. d. dirus</i> (late Wisconsin)	10	5.2–7.5	6.70 ± 0.21
	<i>C. dirus</i> from Térapa	1	6.9	6.9
Length of p4	Rancho La Brea ( <i>C. d. guildayi</i> )	26	17.6–21.8	19.95 ± 0.19
	San Josecito Cave ( <i>C. d. guildayi</i> )	32	15.0–17.3	16.04 ± 0.11
	<i>C. d. dirus</i> (Sangamon-early Wisconsin)	6	15.8–17.5	16.70 ± 0.31
	<i>C. d. dirus</i> (late Wisconsin)	13	13.5–17.4	16.06 ± 0.30
	<i>C. dirus</i> from Térapa	1	19.5	19.5
Width of p4	Rancho La Brea ( <i>C. d. guildayi</i> )	25	9.4–11.1	10.28 ± 0.10
	San Josecito Cave ( <i>C. d. guildayi</i> )	33	9.3–11.9	10.20 ± 0.10
	<i>C. d. dirus</i> (Sangamon-early Wisconsin)	8	9.0–10.8	10.15 ± 0.23
	<i>C. d. dirus</i> (late Wisconsin)	16	8.4–10.8	9.61 ± 0.18
	<i>C. dirus</i> from Térapa	1	9.4	9.4
Length of trigonid of m1	Rancho La Brea ( <i>C. d. guildayi</i> )	27	22.3–27.0	24.36 ± 0.20
	San Josecito Cave ( <i>C. d. guildayi</i> )	33	22.0–27.9	24.64 ± 0.14
	<i>C. d. dirus</i> (Sangamon-early Wisconsin)	6	23.5–26.3	24.53 ± 0.44
	<i>C. d. dirus</i> (late Wisconsin)	15	21.0–26.4	24.01 ± 0.44
	<i>C. dirus</i> from Térapa	1	22.8	22.8
Length of m1	Rancho La Brea ( <i>C. d. guildayi</i> )	33	32.9–40.2	13.31 ± 0.27
	San Josecito Cave ( <i>C. d. guildayi</i> )	44	31.5–39.3	35.50 ± 0.23
	<i>C. d. dirus</i> (Sangamon-early Wisconsin)	10	32.5–39.1	36.09 ± 0.61
	<i>C. d. dirus</i> (late Wisconsin)	14	32.1–37.4	35.16 ± 0.52
	<i>C. dirus</i> from Térapa	1	32.6	32.6
Width of m1	Rancho La Brea ( <i>C. d. guildayi</i> )	29	12.3–14.9	13.31 ± 0.13
	San Josecito Cave ( <i>C. d. guildayi</i> )	40	12.4–15.0	13.62 ± 0.10
	<i>C. d. dirus</i> (Sangamon-early Wisconsin)	11	12.8–15.5	14.10 ± 0.36
	<i>C. d. dirus</i> (late Wisconsin)	22	11.8–16.3	13.40 ± 0.24
	<i>C. dirus</i> from Térapa	1	12.9	12.9

and large size of adult glyptodonts and pampatheres probably would have been a deterrent even for a pack of dire wolves. The only known preserved predator attack on a large armored xenarthran is that of two elliptical punctures in the roof of the skull of a young glyptodont from the Blancan 111 Ranch locality in Arizona made by the canines of a large machairodont felid (sabertoothed cat; Gillette and Ray, 1981).

Bone-cracking abilities have been proposed for *C. dirus* based on the enlarged p4, heavy wear on its dentition, its massive jaws, and craniodental ratios (Merriam, 1912; Biknevicius and Van Valkenburgh, 1996). However, Hill (1991) argued that *C. dirus* lacked specializations that the

extant bone crusher *Crocota crocuta* (spotted hyaena; Hyaenidae) has for resisting forces needed to crush dense bone. Recently, Anyonge and Baker (2006) suggested the craniofacial morphology of the dire wolf was similar to the gray wolf differing only in a more powerful bite used in the former to hold and subdue prey longer. With the nature of the dense bony armor that glyptodonts and pampatheres share, it would be unlikely that the dire wolf would have pursued adult, armored, cingulate xenarthrans as prey. This would have been due to difficulty of holding such a large and bulky mammal that did not have the exposed areas of attack (neck and limbs) that living wolves target in ruminants.

In conclusion, the *Canis* from Térapa is near the size of other large modern and fossil species of *Canis* from North and South America. However, presence of characters such as a deep massive ramus, short and robust canine, p2 with an accessory posterior cuspid, an enlarged p4, a massive m1 with small accessory cuspids on the trigonid, and a large and robust humerus allies specimens from Térapa with the extinct *C. dirus*. Presence of *C. dirus* from the Rancholabrean deposits at Térapa is the first for the state of Sonora. The dire wolf from Térapa likely would have filled the niche of a large pursuit predator for the local fauna, preying on medium-to-large ungulates.

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