Healed injuries to *Canis chihliensis* from early Pleistocene Nihewan beds, China, suggest family care for ancestral wolves (#48717)

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Healed injuries to *Canis chihliensis* from early Pleistocene Nihewan beds, China, suggest family care for ancestral wolves

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Collaborative hunting by complex social groups is a hallmark of large dogs (Mammalia: Carnivora: Canidae), whose teeth also tend to be hypercarnivorous, showing a specialization toward increased cutting edges for meat consumption and robust p4-m1 complex for cracking bone. The deep history of canid pack hunting is obscure, however, because behavioral evidence is rarely preserved in fossils. Dated to the early Pleistocene (~1.2 Ma), *Canis chihliensis* from the Nihewan Basin of northern China is one of the earliest canines to feature a large body size and hypercarnivorous dentition. We present the first known record of dental infection in *C. chihliensis*, likely inflicted by processing hard food, such as bone. An individual also suffered a displaced fracture of its tibia and, despite such an incapacitating injury, survived the trauma to heal. The long period required for healing the compound fracture implicates social hunting and family care (food-sharing). Comparison with abundant paleopathological records of the putatively pack-hunting late Pleistocene dire wolf, *Canis dirus*, at the Rancho La Brea asphalt seeps in southern California, U.S.A., suggests similarity in feeding behavior and sociality between Chinese and American *Canis* across space and time. Pack hunting in *Canis* can thus be traced back to the early Pleistocene, well before the appearance of modern wolves.

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Abstract

Collaborative hunting by complex social groups is a hallmark of large dogs (Mammalia: Carnivora: Canidae), whose teeth also tend to be hypercarnivorous, showing a specialization toward increased cutting edges for meat consumption and robust p4-m1 complex for cracking bone. The deep history of canid pack hunting is obscure, however, because behavioral evidence is rarely preserved in fossils. Dated to the early Pleistocene (~1.2 Ma), *Canis chihliensis* from the Nihewan Basin of northern China is one of the earliest canines to feature a large body size and hypercarnivorous dentition. We present the first known record of dental infection in *C. chihliensis*, likely inflicted by processing hard food, such as bone. An individual also suffered a displaced fracture of its tibia and, despite such an incapacitating injury, survived the trauma to

heal. The long period required for healing the compound fracture implicates social hunting and family care (food-sharing). Comparison with abundant paleopathological records of the putatively pack-hunting late Pleistocene dire wolf, *Canis dirus*, at the Rancho La Brea asphalt seeps in southern California, U.S.A., suggests similarity in feeding behavior and sociality between Chinese and American *Canis* across space and time. Pack hunting in *Canis* can thus be traced back to the early Pleistocene, well before the appearance of modern wolves.

Introduction

Large, hypercarnivorous dogs (family Canidae)—such as gray wolves (*Canis lupus*), African hunting dogs (*Lycaon pictus*), and Asian dholes (*Cuon alpinus*)—are known to be highly social because of their need for collaborative hunting (Van Valkenburgh 1991). In all three species, energetic requirements necessitate that they pursue prey species that are larger than themselves (Carbone et al. 1999). But, unlike their felid (cat family) counterparts, canids lack retractile claws and are usually unable to bring down their prey single-handedly (Wang et al. 2008), making collaborative (pack) hunting a useful compensatory strategy. Despite the importance of pack hunting as a key biological indicator for social interactions, trophic relationship, and diets, however, fossil records rarely preserve direct information on behavior.

Discovery of an injured and healed skeleton and jaws of a large ancestral wolf, *Canis chihliensis*, from the early Pleistocene hominine site of Nihewan Basin, northern China, is of considerable interest in inferring their social behavior. Evidence of healing raises the possibility that individuals survived incapacitating injuries by sharing food with family members (Palmqvist et al. 1999), a question to be explored in this paper.

Materials & Methods

The methods employed in this study include morphological observations, CT scanning, and X-ray examination. CT slicing intervals followed that of Rothschild et al. (1994). The osteological terms are from Mescher (2018). The stages of fracture healing follow Edge-Hughes & Nicholson (2007). Age determination follows Sumner-Smith (1966) for epiphyseal fusion and Gipson et al. (2000) for tooth wear. Body-mass estimates were calculated using regressions on canid femur shaft diameter by Anyonge & Roman (2006) and m1 length by Van Valkenburgh (1990). Permission for excavation was granted by the State Administration of Cultural Heritage with a permit number of 2018-090.

Institution and Locality Abbreviations. HPICR, Hebei Province Institute of Cultural Relics; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology; **MNHN**, Muséum national d'Histoire naturelle; **NM**, Nihewan Museum; **NNNRM**, Nihewan National

Nature Reserve Management; **SSMZ**, Shanshenmiaozui; **TNHM**, Tianjin Natural History Museum; **V,** Prefix in the catalog numbers for vertebrate fossils in IVPP.
Morphological Abbreviations: DAP: anteroposterior diameter; **DT:** transverse diameter; **MC:** medullar cavity; **NF:** nutrient foramen.

Locality and Fauna. A large sample of early Pleistocene wolf, *Canis chihliensis*, comprising more than 200 specimens including excellently preserved pathological conditions, affords an opportunity to examine the social consequences of family care for the disabled. A left dentary (IVPP V17755.11), a right dentary (IVPP V17755.12), and a right tibia (IVPP V18139.20) of *Canis chihliensis* are all from the Shanshenmiaozui (SSMZ) Site in Nihewan Basin. *C. chihliensis* from SSMZ is dominated by older individuals as inferred from wear on teeth (Chen 2018; Chen & Tong 2015). The SSMZ locality (40˚13' 08"N, 114˚ 39' 54"E) lies at the southern bank of the Sangganhe River, and at the edge of the Haojiatai fluviolacustrine platform in Yangyuan County, Hebei Province (Fig. S1). The fossiliferous layer was dated to ca. 1.2 Ma by magnetostratigraphy and associated fauna (Liu et al. 2016; Tong et al. 2011).

Canids are the most abundant carnivorans in the Early Pleistocene Nihewan Fauna (Qiu 2000; Teilhard de Chardin & Piveteau 1930), as also confirmed by our recent excavations at SSMZ (Fig. S2). The dominate taxon of the canid guild in the SSMZ Fauna is *Canis chihliensis* (Tong et al. 2011; Tong et al. 2012). The mammalian fauna associated with *C. chihliensis* at the SSMZ site are as follows: *Lepus* sp., *Ochotona* sp., Pantherinae gen. et sp. indet., *Pachycrocuta* sp., *Mammuthus trogontherii*, *Coelodonta nihowanensis*, *Elasmotherium peii*, *Proboscidipparion* sp., *Equus sanmeniensis*, *Sus* sp., *Eucladoceros boulei*, *Spirocerus wongi*, *Bison palaeosinensis*, and *Gazella sinensis*. Our fieldwork between 2015-2018 recovered additional taxa, e.g. *Alactaga* sp. (represented by metacarpal), *Acinonyx* sp. (radius), *Panthera* sp. (partial mandible and manus bones), *Lynx* sp. (partial mandible with m1, mandible), *Paracamelus* sp. (partial metatarsal), *Pseudodama* sp. (partial antler and metacarpal), and *Gazella subgutturosa* (metatarsal) (Tong & Chen 2015; Tong et al. 2017; Tong et al. 2018; Tong et al. 2011; Tong et al. 2012; Tong & Wang 2014; Tong & Zhang 2019).

Rancho La Brea *Canis dirus*. The best records of paleopathology in extinct canids are from the world's largest collection of late Pleistocene dire wolf, *Canis dirus*, from the Rancho La Brea asphalt seeps in Los Angeles, California, U.S.A. The Rancho La Brea paleopathology collection comprises about 3,200 specimens of dire wolves assembled from over 200,000 specimens representing a minimum of 3,500 individuals (dire wolves represent greater than 50% of all mammal specimens from the Rancho La Brea) (Shaw & Ware 2018). As the largest *Canis* that ever lived and presumably preferring larger prey, dire wolves are widely considered a social predator (Anyonge & Roman 2006; Carbone et al. 2009; Hemmer 1978; Merriam 1912; Stock 1930; Van Valkenburgh & Hertel 1998; Van Valkenburgh & Sacco 2002). The Rancho La Brea dire wolf collection preserves a range of pathological conditions throughout the skeleton (Hartstone-Rose et al. 2015; Lawler et al. 2017; Moodie 1918; Shaw & Howard 2015; Stock

1930; Ware 2005), with particularly debilitating examples offering evidence that strong social bonds existed to allow weakened or disabled individuals to survive for extended periods of time (Shaw & Howard 2015; Shaw & Ware 2018).

Focusing on *Canis dirus* from a single deposit (Pit 61/67) at Rancho La Brea, Brown et al. (2017) quantified patterns of traumatic pathology—injuries that likely resulted from hunting, including healed fractures and evidence of severe or chronic muscle strain as well as osteoarthritis—and predicted skull injuries to be common because of the probability of being kicked while chasing prey. Contrary to expectation, the cranium showed a low incidence of traumatic injury (1.6%) and the dentary even less so (0.18%) (Brown et al. 2017). This study, however, excluded dental injuries likely incurred from feeding—such as abscesses and alveolar resorption stemming from infection—which were also sustained by and preserved in *C. dirus* from Rancho La Brea. In the current study, we quantify these dental injuries, as well as traumatic damage to the dire wolf tibia, for comparison with dental and tibial injuries in *C. chihliensis*.

Results

Taxonomic and Phylogenetic Remarks. As far as we are aware, there are few reports of debilitating injuries to large hypercarnivorous canines in the fossil record, including early Pleistocene *Canis falconeri* from Venta Micena of Spain (Palmqvist et al. 1999), *Cuon* from late Pleistocene of Italy (Iurino & Sardella 2014), and the latest Pleistocene occurrences of *Canis dirus* in the Rancho La Brea asphalt seeps (Shaw & Howard 2015). This is despite a generally excellent fossil record for large canids in the late Cenozoic because of canids' preference for mid-latitude open habitats, where terrestrial fossil records are best preserved and most extensively explored (Tedford et al. 2009; Wang 1994; Wang et al. 2008; Wang et al. 1999).

The holotype of *Canis chihliensis* was originally described based on a maxillary fragment with P3-M2 from Feng-Wo at Huang-Lu village (Locality 64) in Huailai County, Hebei (Chihli) Province by Zdansky (1924). Teilhard de Chardin & Piveteau (1930) referred additional specimens to this species from Nihewan Basin. Rook (1994) synonymized *C. chihliensis* with *C. antonii* Zdansky, 1924, but Tedford et al. (2009) returned to *C. chihliensis* by restricting the concept to large Nihewan *Canis*. The systematics of *C. chihliensis* from SSMZ has been treated by Tong et al. (2012)

Rook (1994) and Sotnikova (2001) referred the Pliocene-Early Pleistocene species *Canis falconeri* from Europe, *C. antonii* from Asia and *C. africanus* from Africa to the supraspecific group *Canis* (*Xenocyon*) ex gr. *falconeri*. All of them readily fall into the category of hypercarnivores based on dentition and *C. falconeri* has also been hypothesized to be a hypercarnivore similar to modern gray wolves (Palmqvist et al. 1999). *Canis chihliensis* shares some similarities with *Sinicuon dubius* (Tong et al. 2012). Furthermore, *C. chihliensis* is among the largest *Canis* species of Eurasia in the early Pleistocene.

Dental Fracture and Inflammations as Related to Bone-crushing and Hypercarnivory. The left dentary (IVPP V17755.11) and right dentary (IVPP V17755.12) belong to the same individual. The left dentary (Fig. 1.A1-4) has c, p1-3 and m2-3 intact, while the crown of p4 and trigonid of m1 and mesial root of m1 are fractured and lost, apparently due to injuries suffered during life. Both root fragments of p4 are retained. On m1 only the talonid is preserved. Note on Fig 1.A1 that the alveolar bone in the region of the missing mesial root of m1 shows no residual socket, which indicates antemortem bone remodeling. This is consistent with the radiographic evidence of periapical bone resorption associated with the apices of the retained roots of p4 and the distal root of m1 (described below). There is also partial loss of the enamel on c and m1 and fracturing of the crowns of p2, p3, and root of m1. The pulp cavities of p4 and m1 are exposed. The dentin of all teeth is stained brown. All remaining cusps are moderately worn.

There are multiple fractures of the buccal and lingual cortical surfaces of the mandible primarily in the regions of p2-p3, m1-m2, and the posterior surface of the mandibular ramus including the condylar process. All fractures appear to be postmortem as suggested by the absence of any repair.

There is loss of the cortical bone on the alveolar ridge in the regions of p3, p4, and m1. This was most likely caused by periodontitis in vivo although there may have also been some postmortem fracturing of the alveolar bone around m1.

The right dentary (Fig. 1.B1-4) preserves i2-3, c, p1-4, and m1-2 in situ; the crown of m3 is missing, but one root tip remains deep in the alveolus. The crown of m1 is brownish due to loss of most of the enamel cap, and with the pulp cavity exposed; m2 was broken during excavation; and other teeth are moderately worn. There are multiple fractures of the buccal and lingual cortical bone, predominantly in the regions of p1 and m2, that are postmortem defects.

The right dentary also suffered serious injury. The bone surrounding the m1 root is perforate on the buccal cortex (purple arrow on Fig. 1.B4) by an apparent fistula and there is extensive loss of alveolar bone over the buccal aspect of the mesial root of m1 (red arrow on Fig. 1.B4). The buccal cortical surface is porous adjacent to p4 and m1 (white arrows on Fig. 1.B2). This is most likely the result of increased number and size of vascular canals associated with inflammation in this region.

Radiographic Observation. The radiographic images of the right and left hemi-mandibles reveal periapical bone loss (rarefying osteitis) (blue arrows on Figs. 1.A4 and 1.B4) associated with exposed pulp cavities, a periodontal pocket between the right p4 and m1 (red arrow on Fig. 1.B4), and an apparent fistula from the periodontal pocket to the surface (purple arrows on Figs. 1.B2 and 1.B4).

Interpretation and Implications for Dental Injury. IVPP V17755 suffered from repeated dental injuries in similar locations on both left and right sides. Although both lever models and *in vivo* experimentation (Ellis et al. 2008) show that biting forces are greatest on the posterior-most molars, patterns of tooth wear suggest that the lower p4-m1 are used more frequently than more posterior molars (Tseng & Wang 2010; Wang et al. 2008; Werdelin 1989), although in the case of the most hypercarnivorous canid, *Lycaon*, bone consumption may be at a more posterior location (Van Valkenburgh 1996). Dental modifications for bone consumption in fossil borophagine canids are most apparent in the p4-m1 region, indicating that this was the location of most bone-cracking behavior (Wang et al. 1999). We interpret the loss of the left p4-m1 in IVPP V17755 as owing to bone-cracking—the p4 and m1 are the largest lower cheek teeth in *Canis* and their loss must have been inflicted by a strong biting force. Preservation of the roots of both the p4 and the m1 trigonid (Fig. 1.A4) suggests tooth fracture from a strong bite and/or encountering hard objects. The alveolar bone in the region of the missing m1 mesial root eventually healed, but the periapical infections associated with both retained root fragments of p4 and the distal root of m1 still show active lesions.

The need for bone-crushing in IVPP V17755 would have continued during and after the healing of the wounds on the left side. Accordingly, the right p4-m1 suffered excessive wear, likely to compensate for the loss of the same function on the left side. Again, we infer that the heavy wear is due to chewing on bones. The wear on the crown of m1 led to exposure of the pulp chamber through two pulp horns in the mesial cusp and directly to the periapical lesions (abscess) (blue arrows in Figs. 1.A4 and 1.B4). This lesion grew sufficiently that it created a fistula to the buccal surface of the dentary to allow drainage of pus. It is also likely that excessive use on the right side led to bone splinters (shards, fragments) being imbedded into the gum tissue between p4 and m1, causing a periodontal pocket.

The above scenario suggests prolonged and possibly repeated injuries and infections, first to the left p4-m1 (possibly broken in a single bite), and then to the right jaw perhaps after the left side had partially healed. Such a scenario is consistent with a hypercarnivorous dentition in *C. chihliensis* frequently used for bone consumption, as also seen in late Pleistocene European *Cuon* (Iurino & Sardella 2014). Bone-crushing behavior in canids has been linked to collaborative hunting and competitive consumption of carcasses within the same family group of predators (Wang et al. 2008; Wang et al. 2018). Such a behavior is especially prevalent among large, hypercarnivorous canids, and Van Valkenburgh et al. (2019) recently linked high tooth fractures in extant gray wolves to limited prey availability.

Comparison to Rancho La Brea *Canis dirus*. In Pit 61/67 alone, 35 dentaries of adult age (14 left, 21 right)—out of 64 pathological adult dentaries (25 left, 39 right; 55%) and 617 dentaries total (both pathological and non-pathological; 5.7%)—exhibit dental injuries similar to those in the Nihewan *C. chihliensis* dentaries examined in this current study (Fig. S3). Across Rancho La Brea deposits, abscesses and alveolar resorption likely due to infection were preserved in 43% (Pit 16) to 77% (Pit 3) of pathological dentaries (Fig. 2.A). Most of the remaining pathological dentaries also preserved dental anomalies, predominantly supernumerary teeth (particularly in the first and second premolars) or a missing lower first premolar (p1) and/or third molar (m3). Because both the p1 and m3 (Balisi et al. 2018; Buchalczyk et al. 1981; Wang 1994) vary in their presence among canids, we excluded anomalies in these teeth from our comparison with Nihewan *C. chihliensis*. Across 200 *C. dirus* jaws (both left and right) bearing abscesses and alveolar infections, the lower first molar or carnassial showed the highest frequency of injury (87 total specimens with m1-associated injuries), likely inflicted by bone-crushing during the consumption of prey, followed by the second premolar (79 total specimens with p2-associated injuries), likely the result of biting and killing while chasing prey or in fighting with conspecifics or competitors of other species (Fig. 2.B). The fourth premolar was the third most frequently injured tooth (57 specimens); often, it was injured in conjunction with the lower first molar (34 specimens), as in the case of *C. chihliensis*. As *C. dirus* is a predator widely recognized to have had a forceful bite capable of processing bone (Anyonge & Baker 2006; Brannick et al. 2015; Van Valkenburgh & Hertel 1993), the high frequency of injury in its p4-m1 complex—similar to that found in the specimens of *C. chihliensis* examined here—supports the inference that *C. chihliensis* also processed bone using p4 and m1.

Tibia Fracture. A normal left tibia (IVPP V18139.21) and pathologic right tibia (IVPP V18139.20) of *Canis* are present in the collection from Shanshenmiaozui (SSMZ). The pathologic tibia has healed fractures at the lower one-third of the shaft. Compared with the normal tibia on the left side (Fig. 3), the pathologic tibia is stouter; it is much broader distally, especially at the fracture site, and is shorter, the maximum length for the normal tibia being 181.6 mm, in contrast to the pathologic one at 166.5 mm (Table 1). In addition, the nutrient foramen is much more enlarged in the pathologic tibia. The partially healed bone has a rough and porous surface (callus).

The porous bone surface indicates that the periosteal vessels also took part in the repair of the fracture, which penetrated into the hard callus. Because the woven/primary bone is not replaced with secondary lamellar bone, this individual did not survive to the stage of lamellar bone formation, i.e. the fracture healing stage 6 by Edge-Hughes & Nicholson (2007).

Foreshortening of tibia. The pathologic tibia has fused overlapping components with remodeling starting 4 cm from the proximal surface and extending throughout the length. Accentuation (irregularities) of the enthesial region at the lateral margin of the tibial plateau suggests increased stress at the proximal tibial-fibular joint. The tibia widens abnormally starting 6 cm distal to proximal surface, with concurrent alteration of surface color and texture, continuing on to the fused distal component of the tibial fracture, where surface filigree reaction (characteristic of infection) is more prominent. There are increased vascular markings at the junction of proximal and middle third (related to current length) of the tibia. A shallow groove identifies the original demarcation of the fracture components now fused. The fibula was also fractured, and residual components are noted at the distal 6 cm. A linear defect is noted at the mid-portion of the tibia, slightly medial to the sagittal line. It appears to be perforated in a manner more suggestive of vasculature than of draining sinuses. It may be the residua of the fracture. If so, it would mean that the injury not only caused fracture, separation and overlap of components, but also caused a “splintering” or at least slight separation of the distal portion of the proximal component. Increased vascularity is noted 2 cm from the distal end of the tibia.

X-ray Examination. Increased density of the medial tibial plateau is noted. If not related to an artifact (e.g., glued component), this is suggestive of a healed, minimally displaced fracture. There clearly is a displaced distal fracture, fused incompletely with overlap. The curvature of the distal portion of the proximal component suggests torsion of the components related to each other. Several layers of periosteal reaction are noted, with partial disruption of subjacent cortex. The distal fibula is fused to the tibia, with focal loss of margin definition. Irregular cavities are noted in the distal portion of the proximal component of the fracture and adjacent to the distal junction of the tibia and fibula. Both contain radio-dense material. This suggests that this was a compound fracture, with skin breach and exposure to environmental contamination. The fracture was incompletely stabilized during the healing process, with continued movement of the components.

CT Scan. The CT images show clearly that it was a comminuted fracture, and all three pieces of the fractures are displaced, which resulted in the division of the medullary cavity into three chambers whose broken ends were enclosed by callus or woven bones (Fig. 4.B1-2, C1-2).

CT longitudinal sections slice 1 (Fig. 4.B1-2) – There is a focal area of trabecular loss just distal to the proximal epiphyseal plate. It is irregularly ellipsoid in shape and contains slightly thickened bone “fragments” of apparently increased density. Increased density is noted in the subsequent proximal fracture component. Periosteal reaction is noted with multiple focal areas of trabecular loss, bounded by sclerotic margins, characteristic of abscesses. There is massive loss of cortical bone in the region of fragment fusion. Fibular fusion with a distal radio-dense inclusion is noted. Presence of foreign bodies is consistent with the diagnosis of a compound fracture.

CT longitudinal sections slice 2 (Fig. 4.C1-2) – There is an area of increased density at the median tibial plateau noted on the x-ray. The CT shows this area to be separated by a fracture line from subjacent bone. The trabecular pattern is denser. The lateral portion of the proximal epiphyseal plate is partially preserved, in contrast to the medial portion, which cannot be distinguished from the epiphysis. This appears to be a non-displaced fracture through the epiphyseal plate, only affecting a portion of that plate.

There is a linear focal disruption (partially occluded at the surface) of the medial aspect at the midpoint of the current length and a U-shaped defect (also seen in CT slice 1) with thickened margins at the distal fifth. The latter could represent a draining abscess, although the former suggests the possibility of a penetrating injury. Radio-dense inclusions are noted, perhaps representing environmental exposure at time of injury. The surface imperfection seen on the reconstructed tibial image (Fig. 4.A) may be a CT averaging artifact. A series of 8 cross sections (Figs. 4D.1-8) allows comparisons of healthy cancellous (D1), healthy cortical (D2-3), and injured and healed bones (D4-8).

Interpretation, Comparison, and Implications for Limb Injury. That the injury, plus the subsequent infections, suffered by IVPP V18139 must have been devastating seems not in doubt.

The displacement of the right hindlimb and the pain associated with a compound fracture with skin breach and exposure to environmental contamination all but rule out hunting activities. For modern domestic dogs of more than 1 year of age, fracture healing can take 7 weeks to 1 year (Edge-Hughes & Nicholson 2007). It is safe to assume that healing of the open fractures in IVPP V18139 without medical intervention (broken bones not re-aligned nor cast to immobilize wounds) would take a considerable amount of time, much longer than its metabolic reserve can sustain. Such a long-term survival by an injured wolf requiring a high degree of meat consumption thus suggests family care and collaborative hunting.

In addition to abnormalities in the jaws and dentition, the Rancho La Brea dire wolf collection has numerous healed fractures in the limb bones (Moodie 1918; Shaw & Howard 2015; Stock 1930; Ware 2005). Again focusing on Pit 61/67, which has a minimum number of 371 dire wolf individuals, Brown et al. (2017) showed that frequencies of traumatic injury—including healed fractures—were higher than expected for most limb bones, especially the tibia. Surveying dire wolf tibiae across all Rancho La Brea deposits, we found 11 specimens (5 left, 6 right) of 251 total pathologic tibiae (4.38%) to have suffered an oblique fracture with foreshortening similar to that in IVPP V18139 (Fig. S4). In studies of modern Saskatchewan gray wolves and sympatric coyotes, such bone fractures—which likely resulted from conflicts with large prey—were found to be more common in wolves than in coyotes, a difference thought to result from wolves' tendency to prey on larger animals like moose (Wobeser 1992). Similarly, Rancho La Brea preserves no fractured and healed tibiae belonging to the coyote—which is also found abundantly in the Pleistocene to Holocene-age asphalt seeps—though this lack may be confounded by a coyote sample size an order of magnitude smaller than that of the dire wolf.

Discussion

Life is not easy for large predators. In modern canids, hypercarnivory is almost always associated with social hunting, such as in the gray wolves (*Canis lupus*), African hunting dogs (*Lycaon pictus*), and Asiatic dholes (*Cuon alpinus*). Of these, the latter two most hypercarnivorous species almost invariably hunt cooperatively, whereas gray wolves regularly, but not exclusively, hunt together for large prey (Macdonald 1983). Group hunting by these highly social canids offers apparent advantages that are otherwise unavailable to individual hunters, such as the ability to bring down prey much larger than the predators themselves, plus coordinated attacks that seal off escape routes as well as relaying strategies that lessen the burden of individual hunters. These strategies are especially critical to canids because, unlike felids, canids never evolved fully retractile claws that are effective weapons for grappling and subduing prey (Wang 1993). Therefore, for canids, group hunting is not optional, as it is for large cats (only the lions are social hunters), once canids have crossed the critical body mass threshold of about 21 kg above which energetic costs necessitate feeding on large prey (Carbone et al. 1999). For canids, it is possible that this body size threshold may even be substantially lowered as in the case of the Asiatic dholes (10-13 kg) that have the most extremely hypercarnivorous dentitions among living canids (Cohen 1978). The Nihewan *Canis chihliensis* is larger than the dholes (13.7–16.8 kg based on femur shaft diameter; ~21.2 kg based on the mean of m1 length).

Social hunting is characteristic of large canids, hyaenids, and some felids. Such behavior has important implications not only in the social organizations of large carnivorans but also in their trophic relationships and diet. Among large, hypercarnivorous living canids, the gray wolf (*Canis lupus*) is the best studied in its pack hunting behavior. The basic social unit is the mated pair; prey size is a factor in pack sizes, which range from a few up to 20 individuals, with the largest packs preying on bison and moose and smaller packs preying on deer (Mech & Boitani 2003). Social hunting, however, may not always be the most efficient in terms of food intake per wolf because the packs must share their proceeds (Thurber & Peterson 1993). The formation of packs, therefore, offers the opportunity to kill prey too large to tackle by one individual alone, as well as the opportunity both to better defend kills against carcass theft and to steal carcasses from larger predators (Carbone et al. 1997; Eaton 1979; Van Valkenburgh 2001).

It has been long known that large *Canis* from the Nihewan Basin includes individuals with highly trenchant lower molars (Teilhard de Chardin & Piveteau 1930). Hypercarnivorous characteristics (dominance of cutting edge of m1 trigonid and enlargement of hypoconid at the expense of entoconid, along with reductions of posterior molars) in *C. chihliensis* are variable (Tong et al. 2012) but strongly converge on the morphology of living African hunting dogs and Asiatic dholes (Fig. 5). Such a dental morphology is commonly associated with emphasis in slicing meat using the sharp carnassial blades. Trenchant molars thus correlate well with hypercarnivory (Crusafont-Pairó & Truyols-Santonja 1956), i.e., tendency to consume meat exclusively, which also drives the evolution of larger body size as a macroevolutionary ratchet (Van Valkenburgh et al. 2004).

Wolves have a dangerous life as long-distance pursuit predators. The traumas and infections inflicted on *Canis chihliensis* likely are related to hunting behavior, feeding strategies, and predator-prey interactions, as has also been suggested for other extinct carnivores (Shaw & Ware 2018). Healing of such devastating injuries is also a testimony to its survival for long periods of time during which the ability to hunt must have been seriously limited or nonexistent, suggesting that some kind of assisted living was necessary. Debilitating bone diseases in the Pleistocene apex predator *Smilodon*, which is even more hypercarnivorous than canids, have also been used to argue for social or gregarious behaviors (Akersten 1985; Heald 1989; Shaw 1992a; Shaw 1992b; Van Valkenburgh 2009; Van Valkenburgh & Sacco 2002) although the pathology-sociality link has been challenged (McCall et al. 2003). Schleidt & Shalter (2004) also noted that social predators should have more healed injuries than solitary predators. Often infirm animals are allowed to feed on group kills, as observed in spotted hyaenas and African wild dogs.

Whereas sociality in sabertooth cats has been questioned given its rarity among extant large felids, all of which are capable of killing on their own, pack hunting in dog-like carnivorans (wolves, hunting dogs, dholes, hyenas) is the dominant mode of predation and is primarily driven by the necessity of overcoming larger prey. Dental morphology and pathology in our Nihewan *Canis chihliensis* strongly suggest processing of hard food (bone cracking), which is commonly associated with hypercarnivory and pack hunting in large canids. Although the massive, healed tibial fracture may not be a definitive indication of social care, such a devastating injury is highly suggestive of the necessity of food provisioning that only social groups can offer, as has been similarly proposed from an early Pleistocene Spanish record of *C. falconeri* (Palmqvist et al. 1999). With this new record from Nihewan, we extend the history of *Canis* sociality to the early Pleistocene, and—by phylogenetic extension, given the probable divergence date between the lineages leading to *Canis chihliensis* and the social dire wolf *Canis dirus*—likely to the Pliocene as well.

Arguably the most definitive (though still correlative) pathological evidence to support sociality in *Canis chihliensis* would be a significant prevalence of similar injuries not only in the extinct *Canis dirus* but in the three extant hypercarnivorous canines whose pack-hunting behavior can be observed directly, in contrast to a low prevalence of similar injuries in non-pack-hunting carnivoran species. However, one common challenge in predator paleopathology is the lack of sufficient samples of large-predator post-crania relative to crania in museum collections of living mammals. This limitation—and the corresponding lack of published systematic pathological surveys across large sample sizes within and among extant species—prevents statistically robust inferences of injury prevalence in extant wild animals. When isolated cases are available, lack of field documentation on behaviors related to pathological specimens also hampers interpretations. Such deficiencies make it difficult to ground-truth inferences of extinct behaviors based on extant relatives, even where large samples of extinct predators are available (Brown et al. 2017). While such a systematic comparative survey exceeds the scope of the current paper, future studies that calculate injury prevalence across large museum and zoo collections of extant species of known behavior (e.g., Rothschild et al. 1998) would bolster inferences of extinct behavior based on skeletal injuries.

As knowledge of the fossil history of hypercarnivorous canids in the Plio-Pleistocene of Eurasia increases, more complexity than has been previously assumed is now emerging, both in its chronology and its morphologic diversity. Recent molecular studies placed *Cuon* and *Lycaon*, two of the most hypercarnivorous living canids, near the base of the *Canis* clade (Lindblad-Toh et al. 2005), in contrast to morphological analysis suggesting that hypercarnivorous forms are at the terminal end of the canine phylogeny (Tedford et al. 1995; Tedford et al. 2009). If the molecular relationship is correct, then records of *Cuon* and *Lycaon* are expected to be at least as old, if not older, than that of many species of *Canis*. This new record pushes back the first occurrence of social care, and pack hunting by extension, by about 1.7 million years to when early *Homo erectus* was first recorded in Asia (Ao et al. 2013; Zhu et al. 2004). This record is important because it coincides with the initial diversification of the large canids (such as *Canis* and *Lycaon*), also known as the Wolf Event (Azzaroli 1983; Sardella & Palombo 2007), and is associated with pack hunting behavior by large carnivorans in increasingly open habitats.

Although records of early wolves have been pushed back slightly (Martínez-Navarro et al. 2009; Rook & Martínez-Navarro 2010; Sardella & Palombo 2007), the wolf event is essentially confined to the Early Pleistocene, i.e., Late Pliocene before recent redefinition (Gibbard et al.

2010). A recent new Tibetan record in the Middle Pliocene, *Sinicuon* cf. *S. dubius*, seems to suggest that hypercarnivorous canines may have predated the genus *Canis* (Wang et al. 2014). Whatever the detailed relationships of these records, it seems clear that hyper-predators, such as large wolves and hunting dogs, were associated with the increasingly open habitats in Eurasia during the onset of the Pleistocene. In this background of large-canine radiation at the beginning of the Ice Age, our new record of a pathological wolf from the Early Pleistocene of Nihewan hints at pack hunting as a major step toward social collaboration while procuring food and, as such, signals a major step in the evolution of large canids.

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Captions of Figures

Figure 1 Two dentaries of the same individual of *Canis chihliensis*. A, left dentary (IVPP V17755.11); B, right dentary (IVPP V17755.12). A1, B1, occlusal views; A2, B2, buccal views; A3, B3, lingual views; A4, B4, X-ray images. White arrows mark resorption of alveolar bone; red arrows mark periodontal pocket, purple arrows indicate probable fistula from periodontal pocket, blue arrows mark periapical infections associated with exposed pulp chambers, and white arrows indicate porous cortical bone.

Figure 2 Frequencies of dental injury in the mandible of Rancho La Brea dire wolves, *C. dirus*. A, numbers of specimens of adult age bearing injuries similar to those in *C. chihliensis* (orange) compared with other dental injuries (gray). Most dental injuries in *C. dirus* involve abscesses and alveolar resorption stemming from infection. B, categorization of dental injuries by tooth position. The m1 shows the highest frequency of infection or injury, followed by p2 and p4.

Figure 3 Tibias of the same individual of *Canis chihliensis* from SSMZ, Nihewan. A, normal tibia of left side (IVPP V 18139.21); B, pathologic tibia of right side (IVPP V 18139.20); A1, B1, anterior views; A2, B2, posterior views; A3, B3, medial views; A4, B4, lateral views. NF: nutrient foramen.

Figure 4 CT scan images of the pathologic right tibia of *Canis chihliensis* (V18139-20) from SSMZ, Nihewan. A, 3-D reconstruction of the pathologic tibia; B1-B2, anteroposterior longitudinal sections; C1-C2, mediolateral longitudinal sections; D1-D8, cross sections; D1-D5, the upper part of the tibia; D6, the upper and middle parts of the fracture; D7, the middle and lower parts of the fracture; D8, lower part of the fracture, infection with subtle cortical loss. MC1-MC3, represent the medullar cavities of the three fractions of the fractured tibia; NP, nutrient foramen.

Figure 5 Lower molars from SSMZ as compared to living hypercarnivorous taxa. Occlusal views of lower molars, m1-3, of *Canis chihliensis* (A-C) from SSMZ in Nihewan, as compared with those of *C. lupus* (D), *Cuon alpinus* (E) and *Lycaon pictus* (F). A, right m1-3 (IVPP V17755.6); B, right m1-3 (IVPP V17755.4); C, left (inverted) m1-2 (IVPP V17755.5); D, right m1-3 (IOZ no number, extant, China); E, right m1-2 (IOZ 26747, extant, China); F, right m1-3 (T.M. No. 5560 and BPI/C 223, extant, South Africa). Modified from Tong et al. (2012)

Table 1(on next page)

Dimensional comparisons between the normal and pathologic tibiae of *C. chihliensis* (in: mm).

Abbreviations: DAP: anteroposterior diameter; DT: transverse diameter.

Table 1 Dimensional comparisons between the normal and pathologic tibiae of *C. chihliensis* (in: mm). Abbreviations: DAP: anteroposterior diameter; DT: transverse diameter.

Dimensions	Normal (left) tibia (IVPP V 18139.21)	Pathologic (right) tibia (IVPP V 18139.20)
Maximum length	181.6	166.5
Proximal DAP	37.5	>32.2
Proximal DT	36.5	35.8
Distal DAP	17.6	>17.3
Distal DT	24.1	25.7
Shaft DAP at nutrient foramen	15.4	17.2
Shaft DT at nutrient foramen	13.2	14.8
Shaft DAP at the fracture	-	25.5
Shaft DT at the fracture	-	29.2

Figure 1

Two dentaries of the same individual of *Canis chihliensis*.

A, left dentary (IVPP V17755.11); B, right dentary (IVPP V17755.12). A1, B1, occlusal views; A2, B2, buccal views; A3, B3, lingual views; A4, B4, X-ray images. White arrows mark resorption of alveolar bone; red arrows mark periodontal pocket, purple arrows indicate probable fistula from periodontal pocket, blue arrows mark periapical infections associated with exposed pulp chambers, and white arrows indicate porous cortical bone.

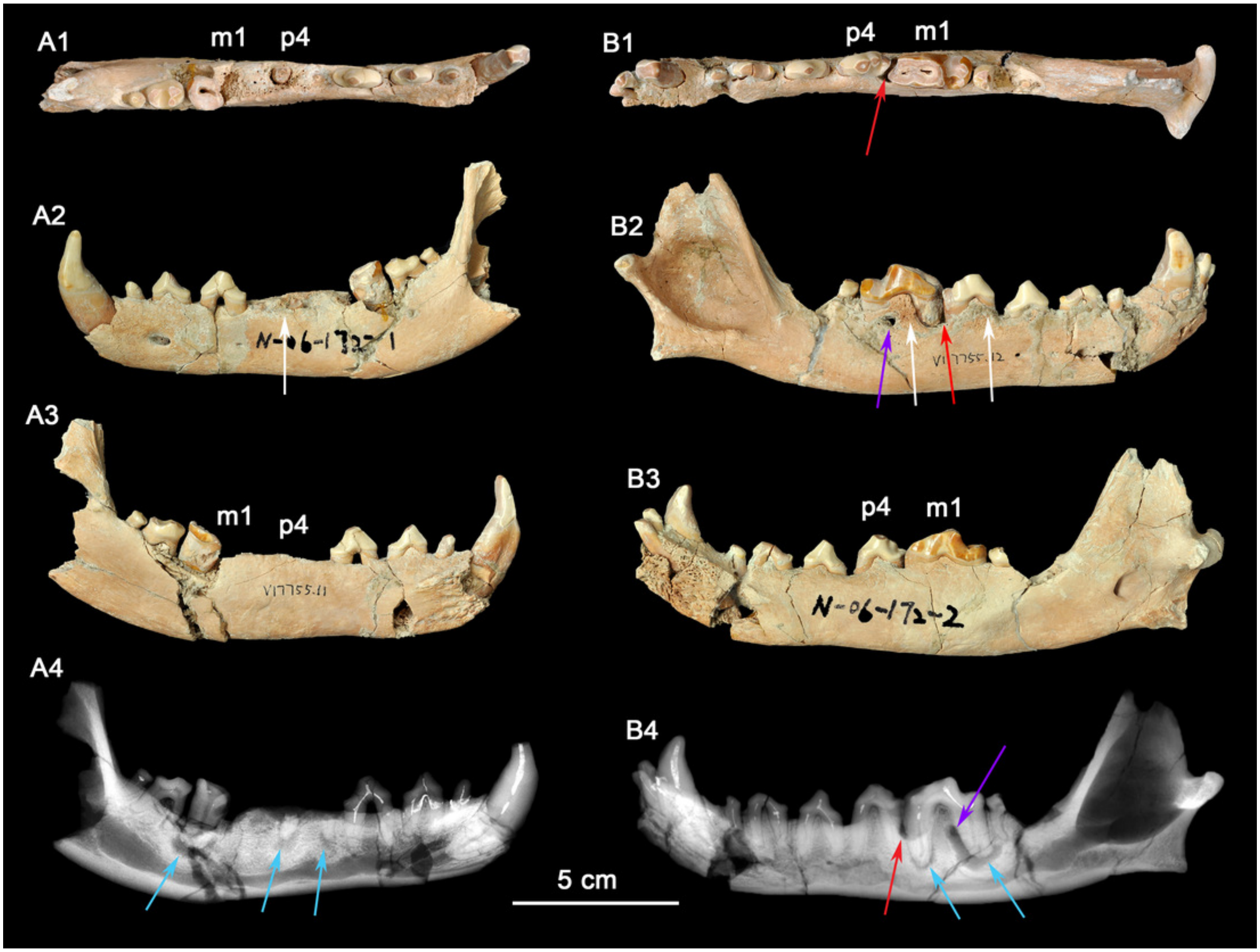

Figure 2

Frequencies of dental injury in the mandible of Rancho La Brea dire wolves, *C. dirus*.

A, numbers of specimens of adult age bearing injuries similar to those in *C. chihliensis* (orange) compared with other dental injuries (gray). Most dental injuries in *C. dirus* involve abscesses and alveolar resorption stemming from infection. B, categorization of dental injuries by tooth position. The m1 shows the highest frequency of infection or injury, followed by p2 and p4.

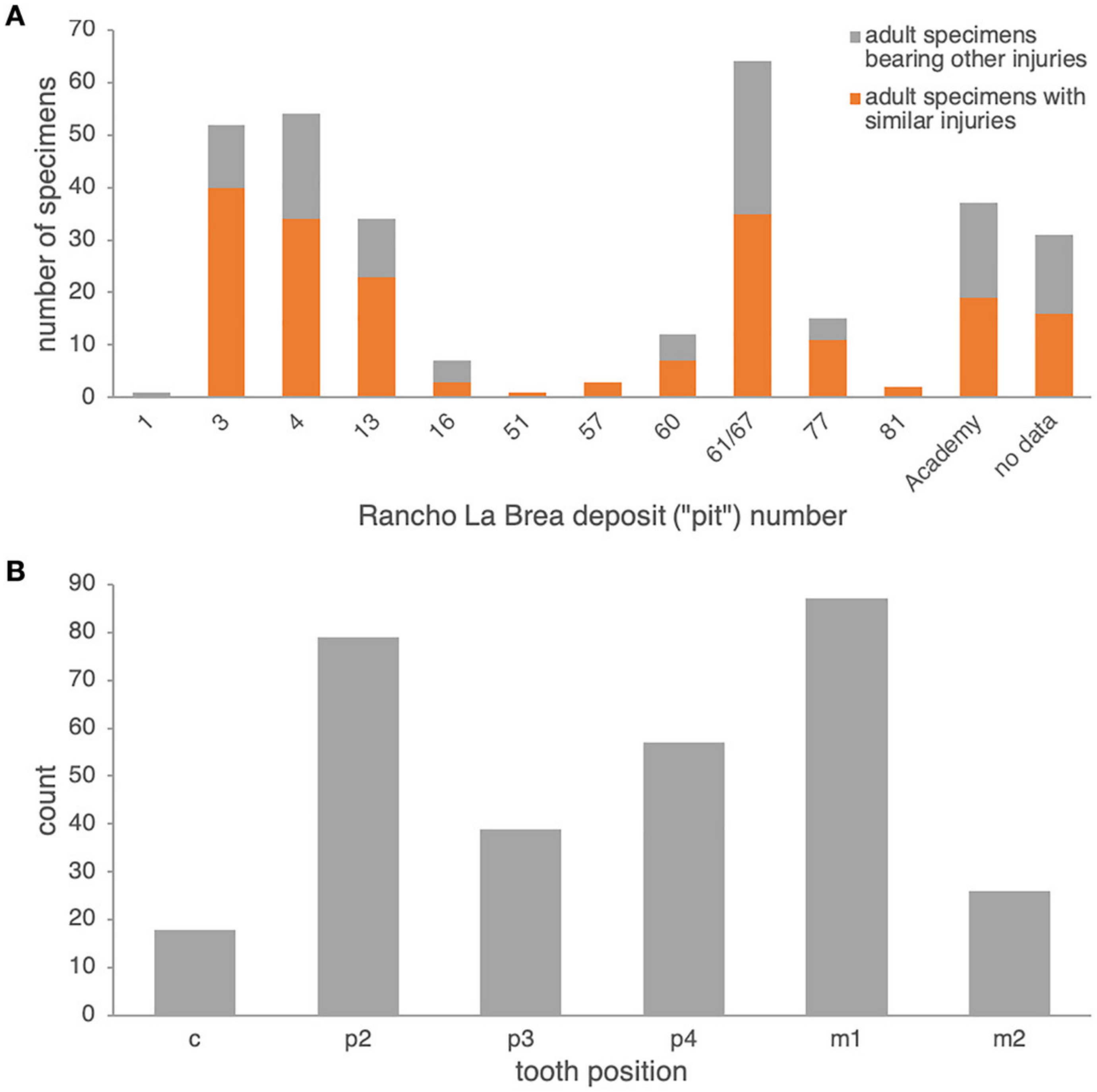
A
■ adult specimens bearing other injuries
■ adult specimens with similar injuries
number of specimens
0
10
20
30
40
50
60
70
1
3
4
13
16
51
57
60
61/67
77
81
Academy
no data
Rancho La Brea deposit ("pit") number
B
count
0
10
20
30
40
50
60
70
80
90
c
p2
p3
p4
m1
m2
tooth position

Figure 3

Tibias of the same individual of *Canis chihliensis* from SSMZ, Nihewan.

A, normal tibia of left side (IVPP V 18139.21); B, pathologic tibia of right side (IVPP V 18139.20); A1, B1, anterior views; A2, B2, posterior views; A3, B3, medial views; A4, B4, lateral views. NF: nutrient foramen.

Figure 4

CT scan images of the pathologic right tibia of *Canis chihliensis* (V18139-20) from SSMZ, Nihewan.

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