Family care for early wolves as evidenced by healed injuries to *Canis chihliensis* from early Pleistocene Nihewan beds, China

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Abstract: Collaborative hunting by complex social groups is a hallmark of large canids (dog family), whose teeth also tend to be hypercarnivorous, ~~specialization~~ specialized toward increased cutting edges for meat consumption. The deep history of canid pack hunting is obscure because behavioral evidence is rarely preserved in fossils. We present the first known evidence of family care in *Canis chihliensis* and by extension, group hunting. Dated to early Pleistocene (~1.2 Ma), *C. chihliensis* from the Nihewan Basin is one of the earliest canines to feature a large body size and hypercarnivorous dentition. It suffered injuries and infections inflicted by processing hard food, likely related to bone-cracking. 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 indicates social hunting and family care (food sharing). Comparison with abundant paleopathological records of the late Pleistocene dire wolf, *Canis dirus*, at the Rancho La Brea in California, 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.

Key words: *Canis chihliensis*, dental fracture, limb fracture, early Pleistocene, Nihewan of northern China, bone cracking, pack hunting

Introduction

Large, hypercarnivorous canids (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[1]. At their body sizes (10-80 kg), energetic requirements necessitate that they pursue prey species that are larger than themselves[2]. But,

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unlike their felid (cat family) counterparts, canids lack a retractile claws and are usually unable to bring down their prey single-handedly[3], 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, 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 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 clan members, a question to be explored in this paper.

Results

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.

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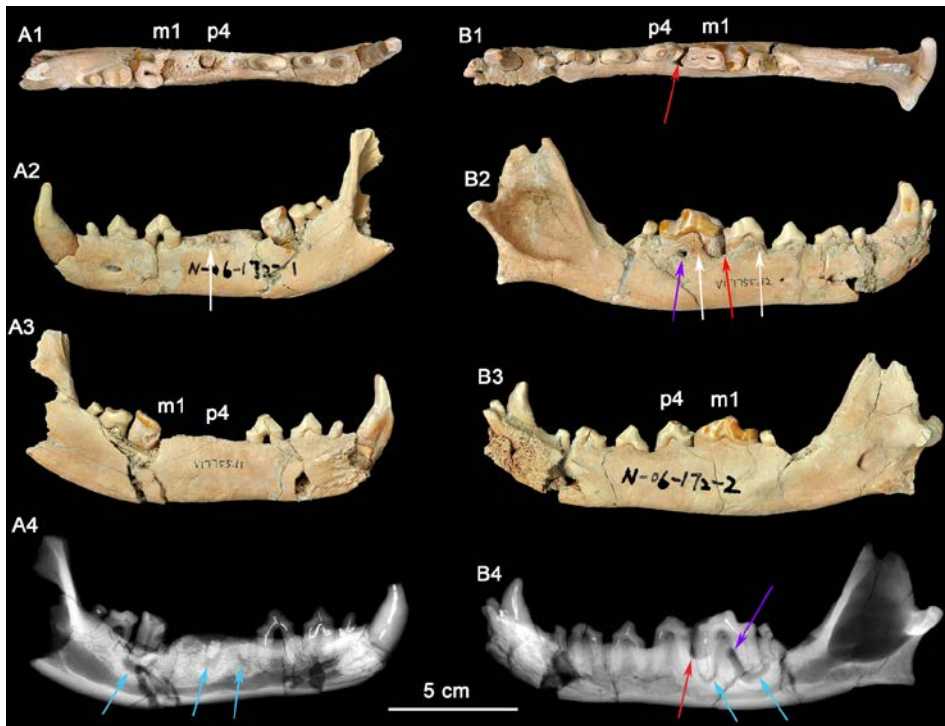**Formatted:** Font: Italic

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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.

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, Comparison, 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[4] show that biting forces are greatest on the posterior-most molars, cranial morphological evidence indicates that canids actually use the upper P4 and lower p4-m1 to process hard food[3,5,6], where the bulk of food can be accommodated most readily at the corner of the lip. Abundant fossil evidence from bone-crushing borophagine canids shows that this is where selection pressure is most intense, where localized bone-cracking at p4-m1 drives relative enlargement of the p4 through successive lineages, i.e., achieving the most morphological change at this location[7]. We interpret the loss of the left p4-m1 in IVPP V17755 as owing to bone cracking behavior—the p4 and m1 are two of the strongest lower cheek teeth in *Canis* and their loss must have been inflicted by a strong biting force. Preservation of the roots of both its p4 and m1 trigonid (Fig. 1.A4) suggests tooth fracture while biting 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*[8]. Bone-crushing behaviors in canids have been linked to collaborative hunting and competitive consumption of carcasses within the same clan of predators[3,9]. Such a behavior is especially prevalent among large, hypercarnivorous canids, and Van Valkenburgh et al.[10] also linked high tooth fractures in extant gray wolves to limited prey availability.

The best records of paleopathology in extinct canids are from the world's largest collection of late Pleistocene dire wolves, *Canis dirus*, from the Rancho La Brea asphalt seeps in Los Angeles, California. A paleopathology collection of about 3,200 specimens of dire wolves was 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 Tar Pits)[11]. As the largest

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Canis that ever lived and presumably preferring larger prey, dire wolves are widely considered a social predator[12-18]. The Rancho La Brea dire wolf collection preserves a range of pathological conditions throughout the skeleton[14,19-23], with particularly debilitating examples offering evidence that strong social bonds existed to allow weakened or disabled individuals to survive for extended periods of time.

Focusing on *Canis dirus* from a single deposit (Pit 61/67) at Rancho La Brea, Brown et al.[24] 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 head-first. Contrary to expectation, the cranium showed a low incidence of traumatic injury (1.6%) and the dentary even less so (0.18%)[24]. 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, and which we quantify here.

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. S1). 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 canids, in general, have tended to be particularly labile in p1 and m3[25-27], 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 (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 and likely processed bone[28-30], 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.
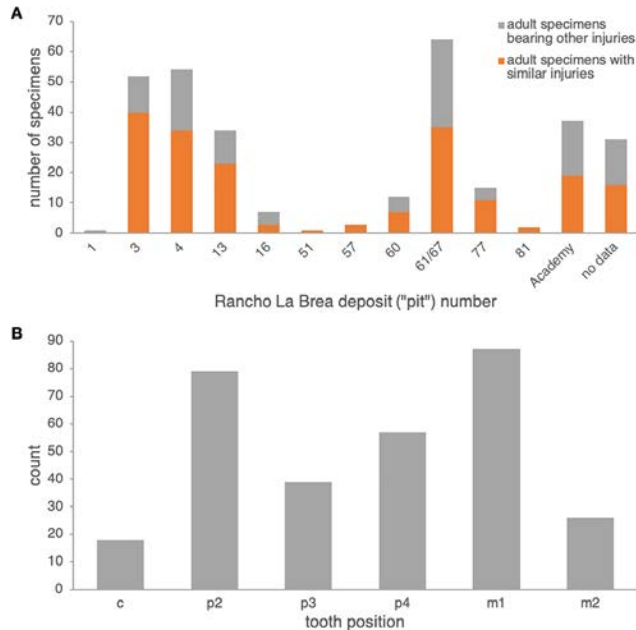
Figure 2. Frequencies of dental injury in the mandible of Rancho La Brea dire wolves, *C. dirus*. A, numbers of specimens of adult age bearing injuries similar to those in *C. chihliensis* (orange) compared with other dental injuries (gray). Most dental injuries in *C. dirus* involve abscesses and alveolar 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.

Tibia Fracture. A normal left tibia (IVPP V18139.21) and pathological right tibia (IVPP V18139.20) are among our *Canis* 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 prominently stouter, especially at the fracture site; on the other hand, it 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 than the normal one. 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 and Nicholson[31] or the remodeling stage by others.

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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.

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~~entheseal 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 residue~~ua~~ 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.

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

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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

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).

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.

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 radiodense 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. Radiodense 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) allow 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[31]. 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 points to 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 limb bones[14,19-21]. Again focusing on Pit 61/67, which has a minimum number of 371 dire wolf individuals, Brown et al.[24] 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. S2). 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[32]. 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[33]. 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[34]. 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[2]. 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[35]. The Nihewan *Canis chihliensis* reached this threshold (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 relationship 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 mating 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 smaller deer[36]. Social hunting, however, may not always be the most efficient in terms of food intake per wolf because the packs must share their proceeds[37]. The formation of packs, therefore, offers the opportunity to kill prey too large to tackle by one individual alone; but the opportunity to defend kills against carcass theft, and the ability to steal carcasses from larger predators, are also factors in forming packs[38-40].

It has been long known that large *Canis* from the Nihewan Basin features individuals with highly trenchant lower molars[41]. Hypercarnivorous characteristics (dominance of cutting edge of m1 trigonid and enlargement of the hypoconid at the expense of entoconid, along with reductions of posterior molars) in *C. chihliensis* are variable[42], 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[43], i.e., tendency to consume meat exclusively, which also drives larger body size as a macroevolutionary ratchet[44].
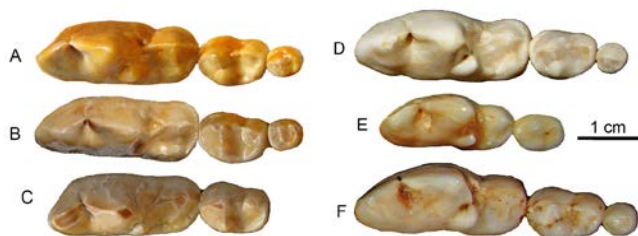

Figure 5. Occlusal views of lower molars, m1-3, of *Canis chihliensis* (A-C) from SSMZ in

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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.[42]

Wolves make a dangerous living as long-distance pursuit predators. The traumas and infections inflicted on *Canis chihliensis* are related to hunting behavior, feeding strategies, and predator-prey interactions, as ha~~s~~ve also been suggested for other extinct carnivores [11]. Healing from~~of~~ such devastating injuries is also a testimony of its adaptive ability to survive for long periods of time during which provisioning of food must have been seriously limited if not completely ceased, suggesting that ~~some kind of~~ assisted living was necessary. Debilitating bone diseases in Pleistocene apex predator *Smilodon*, which were~~is~~ even more hypercarnivorous than canids, have also been used to argue for social or gregarious behaviors[15,45-49] although the pathology-sociality link has been challenged[50]. Schleidt and Shalter[51] 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.

While the case for a social sabertooth cat is rare among mostly solitary hunters in felids and may have been driven by intraspecific competition[12], 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. Whereas its massive, healed tibial injury may not be an exclusive indication of social care, such a devastating injury is highly indicative of assisted living that only social groups can offer. 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 (see Taxonomic and Phylogenetic Remarks below).

Methods

The methods employed in this study include morphological observations, CT scanning and X-ray examination; CT slicing intervals are as those of Rothschild et al.[52] The osteological terms are from Mescher[53]. The stages of fracture healing follow Edge-Hughes and Nicholson[31]. The age determination is according to Sumner-Smith[54] by epiphyseal fusion and Gipson et al.[55] by tooth wear. Body-mass estimates are calculated using regressions on canid femur shaft diameter by Anyonge and Roman[16] and m1 length by Van Valkenburgh[56].

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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[57,58]. 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. S3). The fossiliferous layer was dated to ca. 1.2 Ma by magnetostratigraphy and associated fauna[59,60].

Canids are the most abundant carnivorans in the Early Pleistocene Nihewan Fauna[41,61], as also confirmed by our recent excavations at SSMZ (Fig. S4). The dominantte taxon of the canid guild in the SSMZ Fauna is *Canis chihliensis*[42,59]. 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), *Paracamelus* sp. (partial metatarsal), *Pseudodama* sp. (partial antler and metacarpal), *Gazella subgutturosa* (metatarsal) and *Lynx* sp. (mandible)[42,59,62-66].

Taxonomic and Phylogenetic Remarks. As far as we are aware, debilitating injuries to large, hypercarnivorous canines have not been reported before, besides the latest Pleistocene occurrences of *Canis dirus* in the Rancho La Brea tar pits[20] and late Pleistocene Italian *Cuon*[8]. 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[3,7,26,67].

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[68]. Teilhard de Chardin and Piveteau[41] referred additional specimens to this species from Nihewan Basin. Rook[69] synonymized *C. chihliensis* with *C. antonii* Zdansky, 1924,

but Tedford et al.[67] 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.[42]

Rook[69] and Sotnikova[70] 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 (Fig. 5) and *C. falconeri* has also been hypothesized to be a hypercarnivore similar to modern gray wolves[71]. *Canis chihliensis* shares some similarities with *Sinicuon dubius*[42]. Furthermore, *C. chihliensis* is among the largest *Canis* species of Eurasia in the early Pleistocene.

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[72], in contrast to morphological analysis suggesting that hypercarnivorous forms are at the terminal end of the canine phylogeny[67,73]. 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[74,75]. 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[76,77], and is associated with pack hunting behavior by large carnivorans in increasingly open habitats. Although records of early wolves have been pushed back slightly[76,78,79], the wolf event is essentially confined to the Early Pleistocene, i.e., Late Pliocene before recent redefinition[80]. A recent new Tibetan record in Middle Pliocene, *Sinicuon* cf. *S. dubius*, seems to suggest that hypercarnivorous canines may have predated the genus *Canis*[81]. 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 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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Author Contributions

H.-W. T. and X.W. designed the project and collected data. H.-W. T. led the field excavations that recovered the fossils described, with contributions from X.C. and B.Z. X.C. worked on the taphonomic context. X.W. and H.-W. T. co-wrote the manuscript, with contributions on tibial pathology by B.R., dental pathology by S.W., and La Brea wolf pathology by M.B.