Hypercarnivorous teeth and healed injuries to *Canis chihliensis* from early Pleistocene Nihewan beds, China, suggest social hunting 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, specialized toward increased cutting edges for meat consumption and robust p4-m1 complex for cracking bone. The deep history of canid pack hunting is, however, obscure 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. Another 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 is consistent with social hunting and family care (food-sharing) although alternative explanations exist. 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* may be traced back to the early Pleistocene, well before the appearance of modern wolves, but additional evidence is needed for confirmation.

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2 ***chihliensis* from early Pleistocene Nihewan beds,**
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4

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26

Abstract

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

37   trauma to heal. The long period required for healing the compound fracture is consistent with

38   social hunting and family care (food-sharing) although alternative explanations exist.

39   Comparison with abundant paleopathological records of the putatively pack-hunting late

40   Pleistocene dire wolf, *Canis dirus*, at the Rancho La Brea asphalt seeps in southern California,

41   U.S.A., suggests similarity in feeding behavior and sociality between Chinese and American

42   *Canis* across space and time. Pack hunting in *Canis* may be traced back to the early Pleistocene,

43   well before the appearance of modern wolves, but additional evidence is needed for

44   confirmation.

45

Introduction

47   Large, hypercarnivorous dogs (family Canidae)—such as gray wolves (*Canis lupus*), African

48   hunting dogs (*Lycaon pictus*), and Asian dholes (*Cuon alpinus*)—are known to be highly social

49   because of their need for collaborative hunting (Van Valkenburgh 1991). In all three species,

50   energetic requirements necessitate that they pursue prey species that are larger than themselves

51   (Carbone et al. 1999). But, unlike their felid (cat family) counterparts, canids lack retractile

52   claws and are usually unable to bring down their prey single-handedly (Wang et al. 2008),

53   making collaborative (pack) hunting a useful compensatory strategy. Despite the importance of

54   pack hunting as a key biological indicator for social interactions, trophic relationship, and diets,

55   however, fossil records rarely preserve direct information on behavior.

56   Discovery of an injured and healed skeleton and jaws of a large ancestral wolf, *Canis*

57   *chihliensis*, from the early Pleistocene hominin site of Nihewan Basin, northern China, is of

58   interest in inferring their social behavior. Evidence of healing raises the possibility that

59   individuals survived incapacitating injuries by sharing food with family members (Palmqvist et

60   al. 1999), a question to be explored in this paper.

61

Materials & Methods

63   The methods employed in this study include morphological observations, CT scanning, and X-

64   ray examination. CT slicing intervals followed that of Rothschild et al. (1994). The osteological

65   terms are from Mescher (2018). The stages of fracture healing follow Edge-Hughes & Nicholson

66   (2007). Age determination follows Sumner-Smith (1966) for epiphyseal fusion and Gipson et al.

67   (2000) for tooth wear. Body-mass estimates were calculated using regressions on canid femur

68   shaft diameter by Anyonge & Roman (2006) and m1 length by Van Valkenburgh (1990).

69   Permission for excavation was granted by the State Administration of Cultural Heritage with a

70   permit number of 2018-090.

71

72   **Institution and Locality Abbreviations. HPICR**, Hebei Province Institute of Cultural Relics;

73   **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology; **MNHN**,

74   Muséum national d'Histoire naturelle; **NM**, Nihewan Museum; **NNNRM**, Nihewan National
75   Nature Reserve Management; **SSMZ**, Shanshenmiaozui; **TNHM**, Tianjin Natural History
76   Museum; **V,** Prefix in the catalog numbers for vertebrate fossils in IVPP.
77   **Morphological Abbreviations: DAP:** anteroposterior diameter; **DT:** transverse diameter; **MC:**
78   medullar cavity; **NF:** nutrient foramen.
79
80   **Locality and Fauna**. The present large sample of early Pleistocene wolf, *Canis chihliensis*,
81   comprises more than 200 specimens including excellently preserved pathological conditions. A
82   left dentary (IVPP V17755.11), a right dentary (IVPP V17755.12), and a right tibia (IVPP
83   V18139.20) of *Canis chihliensis* are all from the Shanshenmiaozui (SSMZ) Site in Nihewan
84   Basin. *C. chihliensis* from SSMZ is dominated by older individuals as inferred from wear on
85   teeth (Chen 2018; Chen & Tong 2015). The SSMZ locality (40°13' 08"N, 114° 39' 54"E) lies at
86   the southern bank of the Sangganhe River, and at the edge of the Haojiatai fluviolacustrine
87   platform in Yangyuan County, Hebei Province (Fig. S1). The fossiliferous layer was dated to ca.
88   1.2 Ma by magnetostratigraphy and associated fauna (Liu et al. 2016; Tong et al. 2011).
89   Canids are the most abundant carnivorans in the Early Pleistocene Nihewan Fauna (Qiu
90   2000; Teilhard de Chardin & Piveteau 1930), as also confirmed by our recent excavations at
91   SSMZ (Fig. S2). The dominant taxon of the canid guild in the SSMZ Fauna is *Canis chihliensis*
92   (Tong et al. 2011; Tong et al. 2012). The mammalian fauna associated with *C. chihliensis* at the
93   SSMZ site are as follows: *Lepus* sp., *Ochotona* sp., Pantherinae gen. et sp. indet., *Pachycrocuta*
94   sp., *Mammuthus trogontherii*, *Coelodonta nihowanensis*, *Elasmotherium peii*, *Proboscidipparion*
95   sp., *Equus sanmeniensis*, *Sus* sp., *Eucladoceros boulei*, *Spirocerus wongi*, *Bison palaeosinensis*,
96   and *Gazella sinensis*. Our fieldwork between 2015-2018 recovered additional taxa, e.g. *Alactaga*
97   sp. (represented by metacarpal), *Acinonyx* sp. (radius), *Panthera* sp. (partial mandible and manus
98   bones), *Lynx* sp. (partial mandible with m1, mandible), *Paracamelus* sp. (partial metatarsal),
99   *Pseudodama* sp. (partial antler and metacarpal), and *Gazella subgutturosa* (metatarsal) (Tong &
100   Chen 2015; Tong et al. 2017; Tong et al. 2018; Tong et al. 2011; Tong et al. 2012; Tong & Wang
101   2014; Tong & Zhang 2019).
102
103   **Rancho La Brea *Canis dirus*.** The best records of paleopathology in extinct canids are from the
104   world's largest collection of late Pleistocene dire wolves, *Canis dirus*, from the Rancho La Brea
105   asphalt seeps in Los Angeles, California, U.S.A. The Rancho La Brea paleopathology collection
106   comprises about 3,200 specimens of dire wolves assembled from over 200,000 specimens
107   representing a minimum of 3,500 individuals (dire wolves represent greater than 50% of all
108   mammal specimens from the Rancho La Brea) (Shaw & Ware 2018). As the largest *Canis* that
109   ever lived and presumably preferring larger prey, dire wolves are widely considered a social
110   predator (Anyonge & Roman 2006; Carbone et al. 2009; Hemmer 1978; Merriam 1912; Stock
111   1930; Van Valkenburgh & Hertel 1998; Van Valkenburgh & Sacco 2002). The Rancho La Brea
112   dire wolf collection preserves a range of pathological conditions throughout the skeleton
113   (Hartstone-Rose et al. 2015; Lawler et al. 2017; Moodie 1918; Shaw & Howard 2015; Stock

114 1930; Ware 2005), with particularly debilitating examples offering evidence that strong social
115 bonds existed to allow weakened or disabled individuals to survive for extended periods of time
116 (Shaw & Howard 2015; Shaw & Ware 2018).
117   Focusing on *Canis dirus* from a single deposit (Pit 61/67) at Rancho La Brea, Brown et al.
118 (2017) quantified patterns of traumatic pathology—injuries that likely resulted from hunting,
119 including healed fractures and evidence of severe or chronic muscle strain as well as
120 osteoarthritis—and predicted skull injuries to be common because of the probability of being
121 kicked while chasing prey. Contrary to expectation, the cranium showed a low incidence of
122 traumatic injury (1.6%) and the dentary even less so (0.18%) (Brown et al. 2017). This study,
123 however, excluded dental injuries likely incurred from feeding—such as abscesses and alveolar
124 resorption stemming from infection—which were also sustained by and preserved in *C. dirus*
125 from Rancho La Brea. In the current study, we quantify these dental injuries, as well as traumatic
126 damage to the dire wolf tibia, for comparison with dental and tibial injuries in *C. chihliensis*.
127

Taxonomic and Phylogenetic Remarks

129 As far as we are aware, there are few reports of debilitating injuries to large hypercarnivorous
130 canines in the fossil record, including early Pleistocene *Canis falconeri* from Venta Micena of
131 Spain (Palmqvist et al. 1999), *Cuon* from late Pleistocene of Italy (Iurino & Sardella 2014), and
132 the latest Pleistocene occurrences of *Canis dirus* in the Rancho La Brea asphalt seeps (Shaw &
133 Howard 2015). This is despite a generally excellent fossil record for large canids in the late
134 Cenozoic because of canids' preference for mid-latitude open habitats, where terrestrial fossil
135 records are best preserved and most extensively explored (Tedford et al. 2009; Wang 1994;
136 Wang et al. 2008; Wang et al. 1999).
137   The holotype of *Canis chihliensis* was originally described based on a maxillary fragment
138 with P3-M2 from Feng-Wo at Huang-Lu village (Locality 64) in Huailai County, Hebei (Chihli)
139 Province by Zdansky (1924). Teilhard de Chardin & Piveteau (1930) referred additional
140 specimens to this species from Nihewan Basin. Rook (1994) synonymized *C. chihliensis* with *C.*
141 *antonii* Zdansky, 1924, but Tedford et al. (2009) returned to *C. chihliensis* by restricting the
142 concept to large Nihewan *Canis*. The systematics of *C. chihliensis* from SSMZ has been treated
143 by Tong et al. (2012)
144   Rook (1994) and Sotnikova (2001) referred the Pliocene-Early Pleistocene species *Canis*
145 *falconeri* from Europe, *C. antonii* from Asia and *C. africanus* from Africa to the supraspecific
146 group *Canis* (*Xenocyon*) ex gr. *falconeri*. All of them readily fall into the category of
147 hypercarnivores based on dentition and *C. falconeri* has also been hypothesized to be a
148 hypercarnivore similar to modern gray wolves (Palmqvist et al. 1999). *Canis chihliensis* shares
149 some similarities with *Sinicuon dubius* (Tong et al. 2012). Furthermore, *C. chihliensis* is among
150 the largest *Canis* species of Eurasia in the early Pleistocene.
151

152 ## Results

153

154 **Dental Fracture and Inflammations as Related to Bone-crushing and Hypercarnivory**. The
155 left dentary (IVPP V17755.11) and right dentary (IVPP V17755.12) belong to the same
156 individual. The left dentary (Fig. 1.A-D) has c, p1-3 and m2-3 intact, while the crown of p4,
157 trigonid of m1, and mesial root of m1 are fractured and lost, apparently due to injuries suffered
158 during life. Both root fragments of p4 are retained. On m1 only the talonid is preserved. Note on
159 Fig 1.A that the alveolar bone in the region of the missing mesial root of m1 shows no residual
160 socket, which indicates antemortem bone remodeling. This is consistent with the radiographic
161 evidence of periapical bone resorption associated with the apices of the retained roots of p4 and
162 the distal root of m1 (described below). There is also partial loss of the enamel on c and m1 and
163 fracturing of the crowns of p2, p3, and root of m1. The pulp cavities of p4 and m1 are exposed.
164 The dentin of all teeth is stained brown. All remaining cusps are moderately worn.
165   There are multiple fractures of the buccal and lingual cortical surfaces of the dentary,
166 primarily in the regions of p2-p3, m1-m2, and the posterior surface of the mandibular ramus
167 including the condylar process. All fractures appear to be postmortem as suggested by the
168 absence of any repair.
169   There is loss of the cortical bone on the alveolar ridge in the regions of p3, p4, and m1. This
170 was most likely caused by periodontitis *in vivo* although there may have also been some
171 postmortem fracturing of the alveolar bone around m1.
172   The right dentary (Fig. 1.E-H) preserves i2-3, c, p1-4, and m1-2 *in situ*; the crown of m3 is
173 missing, but one root tip remains deep in the alveolus. The crown of m1 is brownish due to loss
174 of most of the enamel cap, and with the pulp cavity exposed; m2 was broken during excavation;
175 and other teeth are moderately worn. There are multiple fractures of the buccal and lingual
176 cortical bone, predominantly in the regions of p1 and m2, that are postmortem defects.
177   The right dentary also suffered serious injury. The bone surrounding the m1 root is
178 perforate on the buccal cortex (purple arrow, fpp, on Fig. 1.H) by an apparent fistula and there is
179 extensive loss of alveolar bone over the buccal aspect of the mesial root of m1 (red arrow, pp, on
180 Fig. 1.H). The buccal cortical surface is porous adjacent to p4 and m1 (white arrows, vab, on Fig.
181 1.F). This is most likely the result of increased number and size of vascular canals associated
182 with inflammation in this region.
183

184 **Radiographic Observation.** The radiographic images of the right and left dentaries reveal
185 periapical bone loss (rarefying osteitis) (blue arrows, pi, on Figs. 1.D and 1.H) associated with
186 exposed pulp cavities, a periodontal pocket between the right p4 and m1 (red arrow, pp, on Fig.
187 1.H), and an apparent fistula from the periodontal pocket to the surface (purple arrows, fpp, on
188 Figs. 1.F and 1.H).
189

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

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

214 The above scenario suggests prolonged and possibly repeated injuries and infections, first to
215 the left p4-m1 (possibly broken in a single bite), and then to the right jaw perhaps after the left
216 side had partially healed. Such a scenario is consistent with a hypercarnivorous dentition in *C.*
217 *chihliensis* frequently used for bone consumption, as also seen in late Pleistocene European *Cuon*
218 (Iurino & Sardella 2014). Bone-crushing behavior in canids has been linked to collaborative
219 hunting and competitive consumption of carcasses within the same family group of predators
220 (Wang et al. 2008; Wang et al. 2018). Such a behavior is especially prevalent among large,
221 hypercarnivorous canids, and Van Valkenburgh et al. (2019) recently linked high tooth fractures
222 in extant gray wolves to limited prey availability.
223

224 **Comparison to Rancho La Brea *Canis dirus*.** In Pit 61/67 alone, 35 dentaries of adult age (14
225 left, 21 right)—out of 64 pathological adult dentaries (25 left, 39 right; 55%) and 617 dentaries
226 total (both pathological and non-pathological; 5.7%)—exhibit dental injuries similar to those in
227 the Nihewan *C. chihliensis* dentaries examined in this current study (Fig. S3). Across Rancho La
228 Brea deposits, abscesses and alveolar resorption likely due to infection were preserved in 43%
229 (Pit 16) to 77% (Pit 3) of pathological dentaries (Fig. 2.A). Most of the remaining pathological

230 dentaries also preserved dental anomalies, predominantly supernumerary teeth (particularly in
231 the first and second premolars) or a missing lower first premolar (p1) and/or third molar (m3).
232 Because both the p1 and m3 (Balisi et al. 2018; Buchalczyk et al. 1981; Wang 1994) vary in their
233 presence among canids, we excluded anomalies in these teeth from our comparison with
234 Nihewan *C. chihliensis*. Across 200 *C. dirus* jaws (both left and right) bearing abscesses and
235 alveolar infections, the lower first molar or carnassial showed the highest frequency of injury (87
236 total specimens with m1-associated injuries), likely inflicted by bone-crushing during the
237 consumption of prey, followed by the second premolar (79 total specimens with p2-associated
238 injuries), likely the result of biting and killing while chasing prey or in fighting with conspecifics
239 or competitors of other species (Fig. 2.B). The fourth premolar was the third most frequently
240 injured tooth (57 specimens); often, it was injured in conjunction with the lower first molar (34
241 specimens), as in the case of *C. chihliensis*. As *C. dirus* is a predator widely recognized to have
242 had a forceful bite capable of processing bone (Anyonge & Baker 2006; Brannick et al. 2015;
243 Van Valkenburgh & Hertel 1993), the high frequency of injury in its p4-m1 complex—similar to
244 that found in the specimens of *C. chihliensis* examined here—supports the inference that *C.*
245 *chihliensis* also processed bone using p4 and m1.

246

247 **Tibia Fracture**. A normal left tibia (IVPP V18139.21) and pathologic right tibia (IVPP
248 V18139.20) of *Canis* are present in the collection from Shanshenmiaozui (SSMZ). The
249 pathologic tibia has healed fractures at the lower one-third of the shaft. Compared with the
250 normal tibia on the left side (Fig. 3), the pathologic tibia is stouter; it is much broader distally,
251 especially at the fracture site, and is shorter, the maximum length for the normal tibia being
252 181.6 mm, in contrast to the pathologic one at 166.5 mm (Table 1). In addition, the nutrient
253 foramen is much more enlarged in the pathologic tibia. The partially healed bone has a rough and
254 porous surface (callus).
255   The porous bone surface indicates that the periosteal vessels also took part in the repair of
256 the fracture, which penetrated into the hard callus. Because the woven/primary bone is not
257 replaced with secondary lamellar bone, this individual did not survive to the stage of lamellar
258 bone formation, i.e. the fracture healing stage 6 by Edge-Hughes & Nicholson (2007).
259

260 **Foreshortening of tibia.** The pathologic tibia has fused overlapping components with
261 remodeling starting 4 cm from the proximal surface and extending throughout the length.
262 Accentuation (irregularities) of the entheseal region at the lateral margin of the tibial plateau
263 suggests increased stress at the proximal tibial-fibular joint. The tibia widens abnormally starting
264 6 cm distal to proximal surface, with concurrent alteration of surface color and texture,
265 continuing on to the fused distal component of the tibial fracture, where surface filigree reaction
266 (characteristic of infection) is more prominent. There are increased vascular markings at the
267 junction of proximal and middle third (related to current length) of the tibia. A shallow groove
268 identifies the original demarcation of the fracture components now fused. The fibula was also
269 fractured, and residual components are noted at the distal 6 cm. A linear defect is noted at the

270   mid-portion of the tibia, slightly medial to the sagittal line. It appears to be perforated in a
271   manner more suggestive of vasculature than of draining sinuses. It may be the residue of the
272   fracture. If so, it would mean that the injury not only caused fracture, separation and overlap of
273   components, but also caused a "splintering" or at least slight separation of the distal portion of
274   the proximal component. Increased vascularity is noted 2 cm from the distal end of the tibia.
275

276   **X-ray Examination.** Increased density of the medial tibial plateau is noted. If not related to an
277   artifact (e.g., glued component), this is suggestive of a healed, minimally displaced fracture.
278   There clearly is a displaced distal fracture, fused incompletely with overlap. The curvature of the
279   distal portion of the proximal component suggests torsion of the components related to each
280   other. Several layers of periosteal reaction are noted, with partial disruption of subjacent cortex.
281   The distal fibula is fused to the tibia, with focal loss of margin definition. Irregular cavities are
282   noted in the distal portion of the proximal component of the fracture and adjacent to the distal
283   junction of the tibia and fibula. Both contain radio-dense material. This suggests that this was a
284   compound fracture, with skin breach and exposure to environmental contamination. The fracture
285   was incompletely stabilized during the healing process, with continued movement of the
286   components.
287

288   **CT Scan.** The CT images show clearly that it was a comminuted fracture, and all three pieces of
289   the fractures are displaced, which resulted in the division of the medullary cavity into three
290   chambers whose broken ends were enclosed by callus or woven bones (Figs. 4.A-D).
291   CT longitudinal sections slice 1 (Figs. 4.A-B) – There is a focal area of trabecular loss just
292   distal to the proximal epiphyseal plate. It is irregularly ellipsoid in shape and contains slightly
293   thickened bone "fragments" of apparently increased density. Increased density is noted in the
294   subsequent proximal fracture component. Periosteal reaction is noted with multiple focal areas of
295   trabecular loss, bounded by sclerotic margins, characteristic of abscesses. There is massive loss
296   of cortical bone in the region of fragment fusion. Fibular fusion with a distal radio-dense
297   inclusion is noted. Presence of foreign bodies is consistent with the diagnosis of a compound
298   fracture.
299   CT longitudinal sections slice 2 (Figs. 4.C-D) – There is an area of increased density at the
300   median tibial plateau noted on the x-ray. The CT shows this area to be separated by a fracture
301   line from subjacent bone. The trabecular pattern is denser. The lateral portion of the proximal
302   epiphyseal plate is partially preserved, in contrast to the medial portion, which cannot be
303   distinguished from the epiphysis. This appears to be a non-displaced fracture through the
304   epiphyseal plate, only affecting a portion of that plate.
305   There is a linear focal disruption (partially occluded at the surface) of the medial aspect at
306   the midpoint of the current length and a U-shaped defect (also seen in CT slice 1) with thickened
307   margins at the distal fifth. The latter could represent a draining abscess, although the former
308   suggests the possibility of a penetrating injury. Radio-dense inclusions are noted, perhaps
309   representing environmental exposure at time of injury. The surface imperfection seen on the

310   reconstructed tibial image (Fig. 4.E) may be a CT averaging artifact. A series of 8 cross sections
311   (Figs. 4.F-M) allows comparisons of healthy cancellous (F), healthy cortical (G-H), and injured
312   and healed bones (I-M).

313

314   **Interpretation, Comparison, and Implications for Limb Injury.** That the injury, plus the
315   subsequent infections, suffered by IVPP V18139 must have been devastating seems not in doubt.
316   The displacement of the right hindlimb and the pain associated with a compound fracture with
317   skin breach and exposure to environmental contamination all but rule out hunting activities. For
318   modern domestic dogs of more than 1 year of age, fracture healing can take 7 weeks to 1 year
319   (Edge-Hughes & Nicholson 2007). Therefore, it is safe to assume that healing of the open
320   fractures in IVPP V18139 without medical intervention (broken bones not re-aligned nor cast to
321   immobilize wounds) would take a considerable amount of time, much longer than its metabolic
322   reserve can sustain. Such a long-term survival by an injured wolf requiring a high degree of meat
323   consumption thus suggests collaborative hunting and potentially family care.

324   In addition to abnormalities in the jaws and dentition, the Rancho La Brea dire wolf
325   collection has numerous healed fractures in the limb bones (Moodie 1918; Shaw & Howard
326   2015; Stock 1930; Ware 2005). Again focusing on Pit 61/67, which has a minimum number of
327   371 dire wolf individuals, Brown et al. (2017) showed that frequencies of traumatic injury—
328   including healed fractures—were higher than expected for most limb bones, especially the tibia.
329   Surveying dire wolf tibiae across all Rancho La Brea deposits, we found 11 specimens (5 left, 6
330   right) of 251 total pathologic tibiae (4.38%) to have suffered an oblique fracture with
331   foreshortening similar to that in IVPP V18139 (Fig. S4). In studies of modern Saskatchewan
332   gray wolves and sympatric coyotes, such bone fractures—which likely resulted from conflicts
333   with large prey—were found to be more common in wolves than in coyotes, a difference thought
334   to result from wolves' tendency to prey on larger animals like moose (Wobeser 1992). Similarly,
335   Rancho La Brea preserves no fractured and healed tibiae belonging to the coyote—which is also
336   found abundantly in the Pleistocene to Holocene-age asphalt seeps—though this lack may be
337   confounded by a coyote sample size an order of magnitude smaller than that of the dire wolf.

Discussions

339   Life is not easy for large predators. In modern canids, hypercarnivory is almost always
340   associated with social hunting, such as in the gray wolves (*Canis lupus*), African hunting dogs
341   (*Lycaon pictus*), and Asiatic dholes (*Cuon alpinus*). Of these, the latter two most
342   hypercarnivorous species almost invariably hunt cooperatively, whereas gray wolves regularly,
343   but not exclusively, hunt together for large prey (Macdonald 1983). Group hunting by these
344   highly social canids offers apparent advantages that are otherwise unavailable to individual
345   hunters, such as the ability to bring down prey much larger than the predators themselves, plus
346   coordinated attacks that seal off escape routes as well as relaying strategies that lessen the burden
347   of individual hunters. These strategies are especially critical to canids because, unlike felids,

348   canids never evolved fully retractile claws that are effective weapons for grappling and subduing
349   prey (Wang 1993). Therefore, for canids, group hunting is not optional, as it is for large cats
350   (only the lions are social hunters, as are occasionally the cheetahs), once canids have crossed the
351   critical body mass threshold of about 21 kg above which energetic costs necessitate feeding on
352   large prey (Carbone et al. 1999). For canids, it is possible that this body size threshold may even
353   be substantially lowered as in the case of the Asiatic dholes (10-13 kg) that have the most
354   extremely hypercarnivorous dentitions among living canids (Cohen 1978). The Nihewan *Canis*
355   *chihliensis* is larger than the dholes (13.7–16.8 kg based on femur shaft diameter; ~21.2 kg based
356   on the mean of m1 length).
357   Social hunting is characteristic of large canids, hyaenids, and some felids, and depending on
358   how such behavior is described, may even be quite common in carnivorans (Bailey et al. 2013).
359   Such behavior has important implications not only in the social organizations of large
360   carnivorans but also in their trophic relationships and diet. Among large, hypercarnivorous living
361   canids, the gray wolf (*Canis lupus*) is the best studied in its pack hunting behavior. The basic
362   social unit is the mated pair; prey size is a factor in pack sizes, which range from a few up to 20
363   individuals, with the largest packs preying on bison and moose and smaller packs preying on
364   deer (Mech & Boitani 2003). Social hunting, however, may not always be the most efficient in
365   terms of food intake per wolf because the packs must share their proceeds (Thurber & Peterson
366   1993). The formation of packs, therefore, offers the opportunity to kill prey too large to tackle by
367   one individual alone, as well as the opportunity both to better defend kills against carcass theft
368   and to steal carcasses from larger predators (Carbone et al. 1997; Eaton 1979; Van Valkenburgh
369   2001; Vucetich et al. 2004).
370   It has been long known that large *Canis* from the Nihewan Basin includes individuals with
371   highly trenchant lower molars (Teilhard de Chardin & Piveteau 1930). Hypercarnivorous
372   characteristics (dominance of cutting edge of m1 trigonid and enlargement of hypoconid at the
373   expense of entoconid, along with reductions of posterior molars) in *C. chihliensis* are variable
374   (Tong et al. 2012) but strongly converge on the morphology of living African hunting dogs and
375   Asiatic dholes (Fig. 5). Such a dental morphology is commonly associated with emphasis in
376   slicing meat using the sharp carnassial blades. Trenchant molars thus correlate well with
377   hypercarnivory (Crusafont-Pairó & Truyols-Santonja 1956), i.e., tendency to consume meat
378   exclusively, which also drives the evolution of larger body size as a macroevolutionary ratchet
379   (Van Valkenburgh et al. 2004).
380   Wolves have a dangerous life as long-distance pursuit predators. The traumas and infections
381   inflicted on *Canis chihliensis* likely are related to hunting behavior, feeding strategies, and
382   predator-prey interactions, as have also been suggested for other extinct carnivores (Shaw &
383   Ware 2018). Healing from such devastating injuries is also a testimony to its survival for long
384   periods of time during which the ability to hunt must have been seriously limited or nonexistent,
385   suggesting that assisted living was a possibility. Debilitating bone diseases in the Pleistocene
386   apex predator *Smilodon*, which were even more hypercarnivorous than canids, have also been
387   used to argue for social or gregarious behaviors (Akersten 1985; Heald 1989; Shaw 1992a; Shaw

388   1992b; Van Valkenburgh 2009; Van Valkenburgh & Sacco 2002) although the pathology-
389   sociality link has been challenged (McCall et al. 2003). Schleidt & Shalter (2004) also noted that
390   social predators should have more healed injuries than solitary predators. Often infirm animals
391   are allowed to feed on group kills, as observed in spotted hyaenas and African wild dogs.
392   Whereas sociality in sabertooth cats has been questioned given its rarity among extant large
393   felids, all of which are capable of killing on their own, pack hunting in dog-like carnivorans
394   (wolves, hunting dogs, dholes, hyenas) is the dominant mode of predation and may partly be
395   driven by the necessity of overcoming larger prey (Mech & Boitani 2003). Dental morphology
396   and pathology in our Nihewan *Canis chihliensis* strongly suggest processing of hard food (bone
397   cracking), which is commonly associated with hypercarnivory and pack hunting in large canids.
398   While herbivores, too, suffer from crippling injuries, comparisons to herbivores are irrelevant in
399   this case because injured herbivores can continue eating plant matter, foraging on food items that
400   do not move, while recovering from injuries. However, critical carnivore injuries, such as to the
401   running hindlimbs, blunt active predators' ability to hunt and chase animal prey. Although the
402   massive, healed tibial fracture may not be a definitive indication of social care, a predator's
403   recovery from such a devastating injury is suggestive of food provisioning that only social
404   groups can offer. This has been similarly proposed from an early Pleistocene Spanish record of
405   *C. falconeri* (Palmqvist et al. 1999), although temporary shift to a more omnivorous diet is also
406   possible. With this new record from Nihewan, we extend the history of *Canis* sociality to the
407   early Pleistocene, and likely to the Pliocene as well if the even larger *Canis antonii* from Fugu
408   area in Shanxi Province is taken into consideration (Tedford et al. 2009:appendix I).
409   Arguably the most definitive (though still correlative) pathological evidence to support
410   sociality in *Canis chihliensis* would be a significant prevalence of similar injuries not only in the
411   extinct *Canis dirus* but in the three extant hypercarnivorous canines whose pack-hunting
412   behavior can be observed directly, in contrast to a low prevalence of similar injuries in non-pack-
413   hunting carnivoran species. However, one common challenge in predator paleopathology is the
414   lack of sufficient samples of large-predator post-crania relative to crania in museum collections
415   of living mammals. Survival with just the leg or just the dental damage does have isolated
416   representation, but not the combination. This limitation—and the corresponding lack of
417   published systematic pathological surveys across large sample sizes within and among extant
418   species—prevents statistically robust inferences of injury prevalence in extant wild animals.
419   When isolated cases are available, lack of field documentation on behaviors related to
420   pathological specimens also hampers interpretations. Such deficiencies make it difficult to
421   ground-truth inferences of extinct behaviors based on extant relatives, even where large samples
422   of extinct predators are available (Brown et al. 2017). While such a systematic comparative
423   survey exceeds the scope of the current paper, future studies that calculate injury prevalence
424   across large museum and zoo collections of extant species of known behavior (e.g., Rothschild et
425   al. 1998) would bolster inferences of extinct behavior based on skeletal injuries.
426   As knowledge of the fossil history of hypercarnivorous canids in the Plio-Pleistocene of
427   Eurasia increases, more complexity than has been previously assumed is now emerging, both in

428   its chronology and its morphologic diversity. Recent molecular studies placed *Cuon* and *Lycaon*,
429   two of the most hypercarnivorous living canids, near the base of the *Canis* clade (Chavez et al.
430   2019; Koepfli et al. 2015; Lindblad-Toh et al. 2005), in contrast to morphological analysis
431   suggesting that hypercarnivorous forms are at the terminal end of the canine phylogeny (Tedford
432   et al. 1995; Tedford et al. 2009). If the molecular relationship is correct, then records of *Cuon*
433   and *Lycaon* are expected to be at least as old, if not older, than that of many species of *Canis*.
434   This new record pushes back the first occurrence of pack hunting likely accompanied by social
435   care by about 1.7 million years to when early *Homo erectus* was first recorded in Asia (Ao et al.
436   2013; Zhu et al. 2004). This record is important because it coincides with the initial
437   diversification of the large canids (such as *Canis* and *Lycaon*), also known as the Wolf Event in
438   Eurasia (Azzaroli 1983; Sardella & Palombo 2007), and *Lycaon*'s arrival in Africa (Hartstone-
439   Rose et al. 2010).
440   Although records of early wolves have been pushed back slightly (Martínez-Navarro et al.
441   2009; Rook & Martínez-Navarro 2010; Sardella & Palombo 2007), the wolf event is essentially
442   confined to the Early Pleistocene, i.e., Late Pliocene before recent redefinition (Gibbard et al.
443   2010). A recent new Tibetan record in the Middle Pliocene, *Sinicuon* cf. *S. dubius*, seems to
444   suggest that hypercarnivorous canines may have predated the genus *Canis* (Wang et al. 2014).
445   Whatever the detailed relationships of these records, it seems clear that hyper-predators, such as
446   large wolves and hunting dogs, were associated with the increasingly open habitats in Eurasia
447   during the onset of the Pleistocene. In this background of large-canine radiation at the beginning
448   of the Ice Age, our new record of a pathological wolf from the Early Pleistocene of Nihewan
449   hints at pack hunting as a major step toward social collaboration while procuring food and, as
450   such, signals a major step in the evolution of large canids.

Conclusions

452   We document dental injuries and infections and a healed tibia fracture in *Canis chihliensis* from
453   the early Pleistocene (~1.2 Ma) Nihewan Basin of northern China. This early species of wolf-like
454   *Canis* begins to have large body size and hypercarnivorous dentition. The dental injuries and
455   infections likely occurred while processing hard food, such as bones, whereas the tibia fractures
456   severely limited locomotion during recuperation. Dental injuries and healing of compound
457   fracture suggests social hunting and family care (food-sharing) although alternative explanations
458   exist. We made comparisons with abundant paleopathological records of the putatively pack-
459   hunting late Pleistocene dire wolf, *Canis dirus*, at the Rancho La Brea in southern California, and
460   demonstrate similarity in feeding behavior and sociality between Chinese and American *Canis*
461   across space and time.

Acknowledgments

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697 ## Captions of Figures

698 **Figure 1 Two dentaries of the same individual of *Canis chihliensis*.** (A-D) left dentary (IVPP
699 V17755.11); (E-H) right dentary (IVPP V17755.12). (A, E) occlusal views; (B, F) buccal views;
700 (C, G) lingual views; (D, H) X-ray images. White arrows (labeled vab) indicate areas of
701 increased vascularity of alveolar bone; red arrows (labeled pp) mark periodontal pocket, purple
702 arrows (labeled fpp) indicate probable fistula from periodontal pocket, and blue arrows (labeled
703 pi) mark periapical infections associated with exposed pulp chambers.

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

710 **Figure 3 Tibias of the same individual of *Canis chihliensis* from SSMZ, Nihewan.** (A-D)
711 normal tibia of left side (IVPP V 18139.21). (E-H) pathologic tibia of right side (IVPP V
712 18139.20). (A, E) anterior views; (B, F) posterior views; (C, G) medial views; (D, H) lateral
713 views. NF: nutrient foramen.

714 **Figure 4 CT scan images of the pathologic right tibia of *Canis chihliensis* (V18139-20) from
715 SSMZ, Nihewan.** (A-B) anteroposterior longitudinal sections; (C-D) mediolateral longitudinal
716 sections; (E) 3-D reconstruction of the pathologic tibia; (F-M) cross sections; (F-J) the upper part
717 of the tibia; (K) the upper and middle parts of the fracture; (L) the middle and lower parts of the
718 fracture; (M) lower part of the fracture, infection with subtle cortical loss. MC1-MC3, represent
719 the medullar cavities of the three fractions of the fractured tibia; NP, nutrient foramen.

720 **Figure 5 Lower molars from SSMZ as compared to living hypercarnivorous taxa.** Occlusal
721 views of lower molars, m1-3, of *Canis chihliensis* (A-C) from SSMZ in Nihewan, as compared

722 with those of *C. lupus* (D), *Cuon alpinus* (E) and *Lycaon pictus* (F). (A) right m1-3 (IVPP
723 V17755.6); (B) right m1-3 (IVPP V17755.4); (C) left (inverted) m1-2 (IVPP V17755.5); (D)
724 right m1-3 (IOZ no number, extant, China); (E) right m1-2 (IOZ 26747, extant, China); (F) right
725 m1-3 (T.M. No. 5560 and BPI/C 223, extant, South Africa). Modified from Tong et al. (2012).
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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.

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2   Table 1 Dimensional comparisons between the normal and pathologic tibiae of *C. chihliensis* (in:

3   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

5

6

Figure 1

Two dentaries of the same individual of *Canis chihliensis*

(A-D) left dentary (IVPP V17755.11); (E-H) right dentary (IVPP V17755.12). (A, E) occlusal views; (B, F) buccal views; (C, G) lingual views; (D, H) X-ray images. White arrows (labeled vab) indicate areas of increased vascularity of alveolar bone; red arrows (labeled pp) mark periodontal pocket, purple arrows (labeled fpp) indicate probable fistula from periodontal pocket, and blue arrows (labeled pi) mark periapical infections associated with exposed pulp chambers.
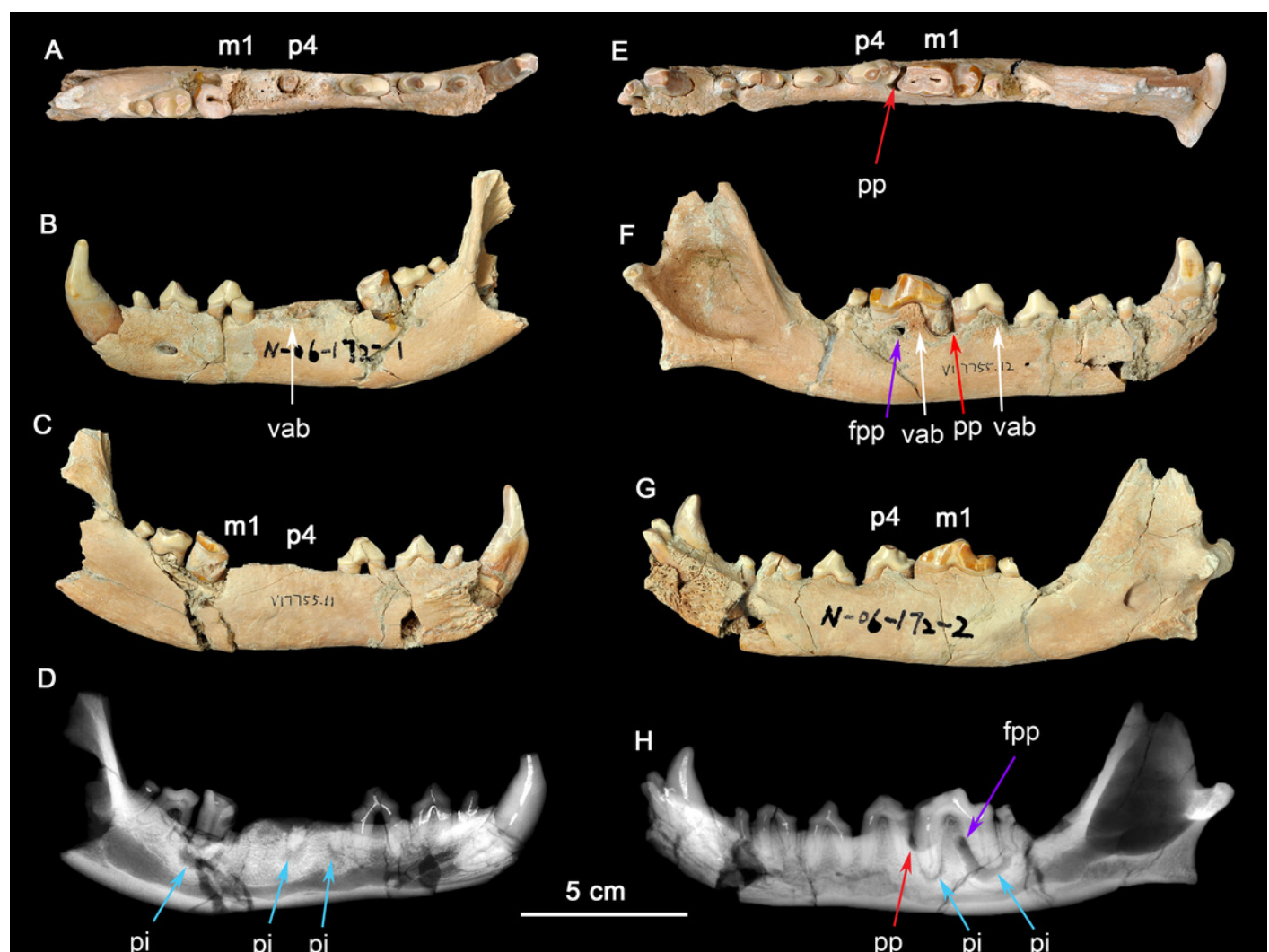
Figure 2

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.
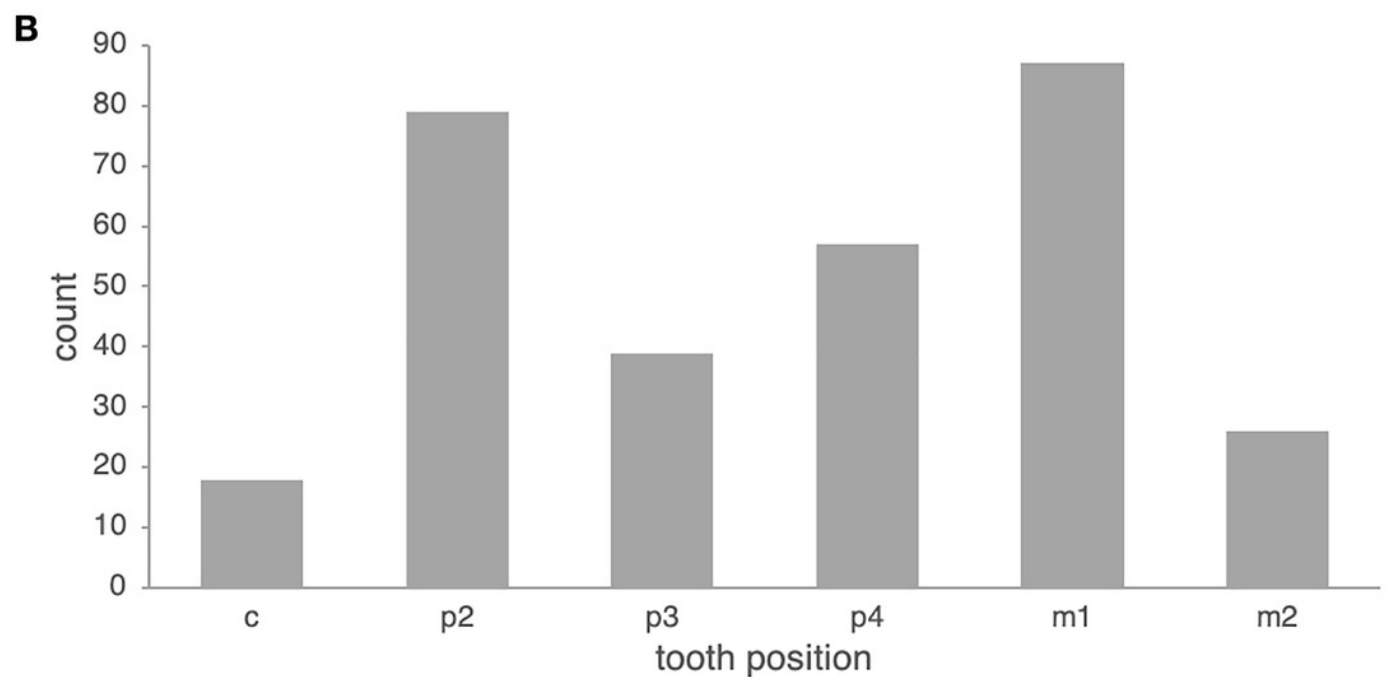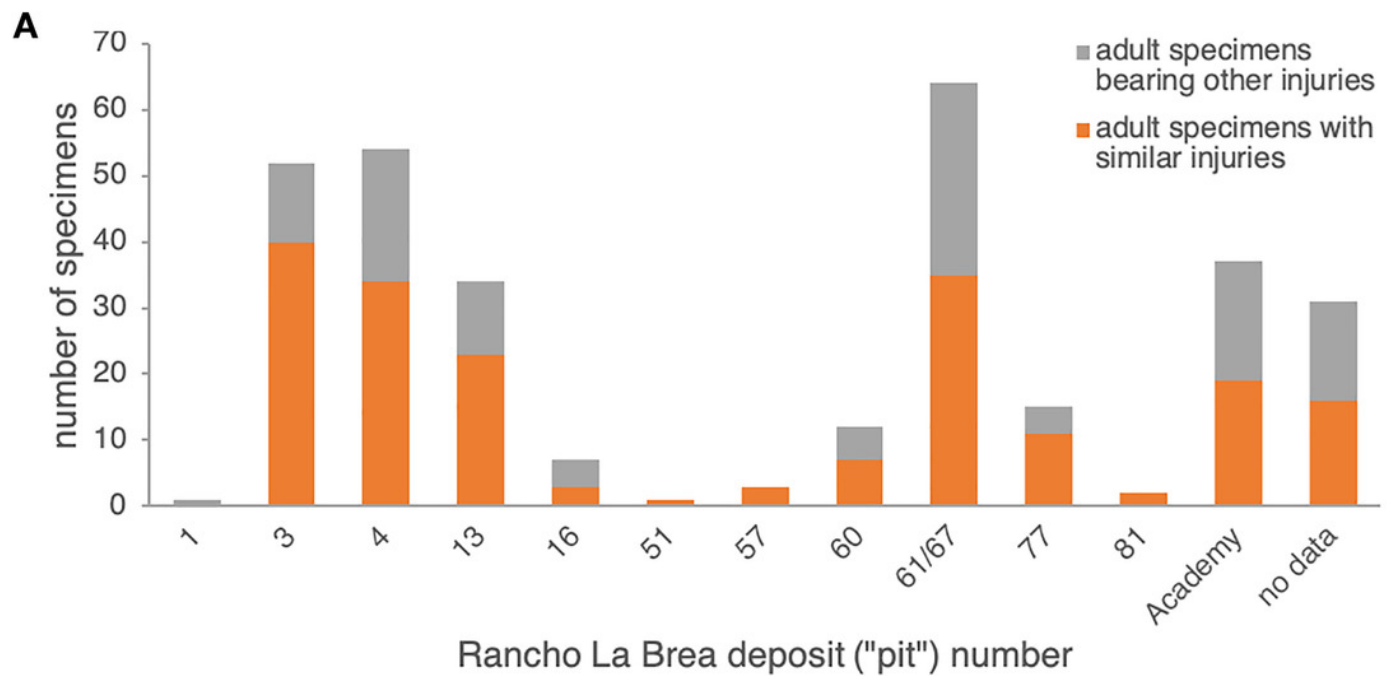
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Figure 3

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

(A-D) normal tibia of left side (IVPP V 18139.21). (E-H) pathologic tibia of right side (IVPP V 18139.20). (A, E) anterior views; (B, F) posterior views; (C, G) medial views; (D, H) lateral views. NF: nutrient foramen.

Figure 4

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

(A-B) anteroposterior longitudinal sections; (C-D) mediolateral longitudinal sections; (E) 3-D reconstruction of the pathologic tibia; (F-M) cross sections; (F-J) the upper part of the tibia; (K) the upper and middle parts of the fracture; (L) the middle and lower parts of the fracture; (M) 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.
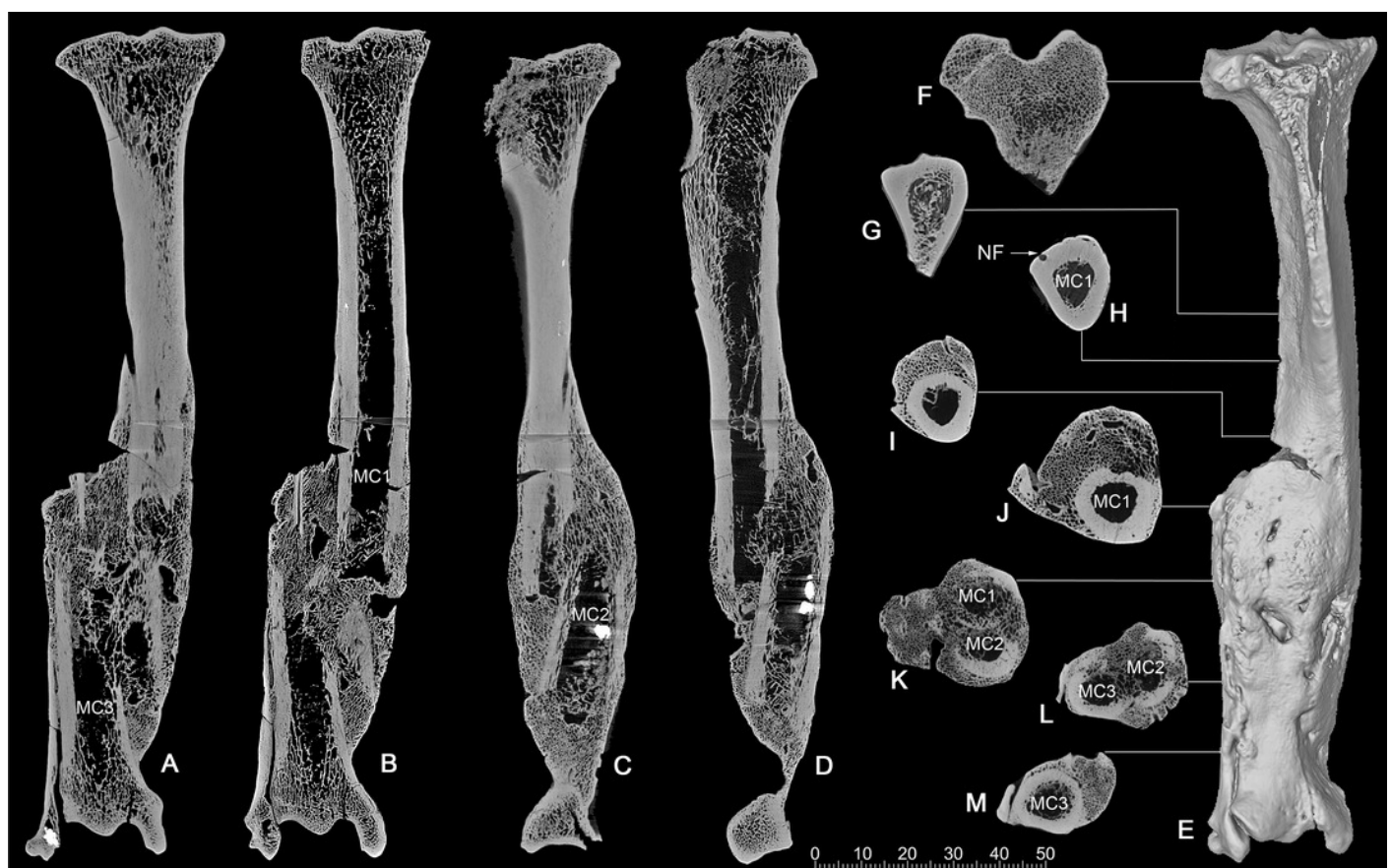
Figure 5

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).