

## RESEARCH PAPER

# First Fossils of Hyenas (*Chasmaporthetes*, Hyaenidae, Carnivora) from North of the Arctic Circle

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The northern region of Beringia is ecologically and biogeographically significant as a corridor for biotic dispersals between the Old and New Worlds. Large mammalian predators from Beringia are exceedingly rare in the fossil record, even though carnivore diversity in the past was much higher than it is in this region at present. Here we report the first fossils of cursorial hyenas, *Chasmaporthetes*, in Beringia and north of the Arctic Circle. Two isolated teeth recovered in the Old Crow Basin, Yukon Territory, Canada, were identified amongst over 50,000 known fossil mammal specimens recovered from over a century of collecting in the Old Crow Basin. These rare records fill an important intermediary locale in the more than 10,000 km geographic distance between previously known New and Old World records of this lineage. The Pleistocene age of these fossils, together with its Arctic Circle occurrence, necessitate a rethinking of the role of large-bodied hunter-scavengers in Ice Age megafaunas in North America, and the implications of lacking an important energy flow modifier in present day North American food webs.

**Keywords:** Yukon; Pleistocene; Beringia; Carnivore; Predator

## Introduction

Pleistocene vertebrate faunas from Beringia – the unglaciated region between northeast Asia and northwest North America straddling the Bering Isthmus – are of particular importance for our understanding of intercontinental dispersals (Hopkins et al., 1982). These faunas record the movement, persistence, and extinction during the Pleistocene and establishment of present-day guilds and food webs. Members of the family Hyaenidae (part of Order Carnivora, which also includes wolves, cats, seals, weasels, and relatives) have an extensive fossil record across the Old World beginning in the early Miocene, with >60 extinct hyaenid taxa having been described. They are often the most abundant predators at fossil localities across Eurasia, and are considered to have played key ecological roles as mesopredators and scavengers (Turner et al., 2008). They were, however, absent from North America until dispersal (presumably via the Beringian land bridge) during the Blancan North American Land Mammal Age (NALMA, Figure S1), ~4.7 Ma (mega-annum) ago. The hitherto northernmost record of the hyaenid *Chasmaporthetes* in North America is from Meade County, Kansas at approximately 37°N latitude. In this report, we describe the first known fossil records of hyaenids in the Arctic

latitudes of Beringia, represented by two isolated teeth of *Chasmaporthetes* cf. *C. ossifragus*, a member of the cursorial hyaenid clade, adding to the exclusively southern United States and Mexico fossil records of hyenas in North America.

**Geographic Region and Geologic Context**—The Old Crow Basin, in the unglaciated region of northern Yukon Territory, Canada, has been the focus of paleontological, paleoenvironmental, and stratigraphic investigations for over a century (Harrington, 1989, Harrington, 2011, Irving and Beebe, 1984). Numerous exposures of unconsolidated, perennially frozen alluvial sediments are present along the Old Crow River and its tributaries, and reveal rich records of Quaternary biotic communities and environmental change. However, most fossils are recovered from numerous alluvial point bars, where admixture of anachronistic fossils from various Pleistocene and Holocene stratigraphic units makes geologic age constraint of the re-worked fossils difficult. One particular point bar near the downstream end of the basin known as Locality CRH 11A has been a focus for palaeontologists and is, by far, the richest and most diverse (Harrington, 2011). Stratigraphic investigations on river bluffs, including biochronology, tephrochronology, and magnetostratigraphy suggest that exposed sediments in the basin are no older than early Pleistocene, ~1.4 Ma; thus, these re-worked fossils can be considered to span the Irvingtonian to Rancholabrean NALMA (Figure S1) (Westgate et al., 2017, Kuzmina et al., 2014).

Over 50,000 vertebrate fossils, representing at least 80 species from over 200 bluffs and point bar localities along Old Crow River, have been amassed in the

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collections of the Canadian Museum of Nature and Yukon Government Palaeontology Program. These faunas are dominated by common Quaternary Holarctic herbivores such as *Mammuthus*, *Bison*, *Equus* and *Rangifer*, whereas remains of large carnivorans including the bear *Arctodus*, and the felids *Homotherium* and *Panthera* are relatively rare (Harington, 2011). However, it is the exceedingly rare specimens from the Old Crow Basin that have proved most important. For example, a single fossil of the flat-headed peccary *Platygonus compressus* extended the known range for this species northward by over 3000 km (Beebe, 1980). Rare specimens of the canid *Xenocyon lycaonoides* provide a glimpse of a brief dispersal of this typically Eurasian carnivoran into the North American Arctic (Tedford et al., 2009). Rare specimens of the large bodied camel cf. *Paracamelus* provide an intermediary fossil locale for this taxon, which ranged from the Canadian High Arctic to western Europe (Rybczynski et al., 2013). Although the chronological uncertainties with these re-worked faunas are difficult to resolve, these proverbial “needle-in-a-hay-stack” rare fossils from the Old Crow Basin have provided major advances in our knowledge of Quaternary biotic history and biogeography.

**Institutional Abbreviations**

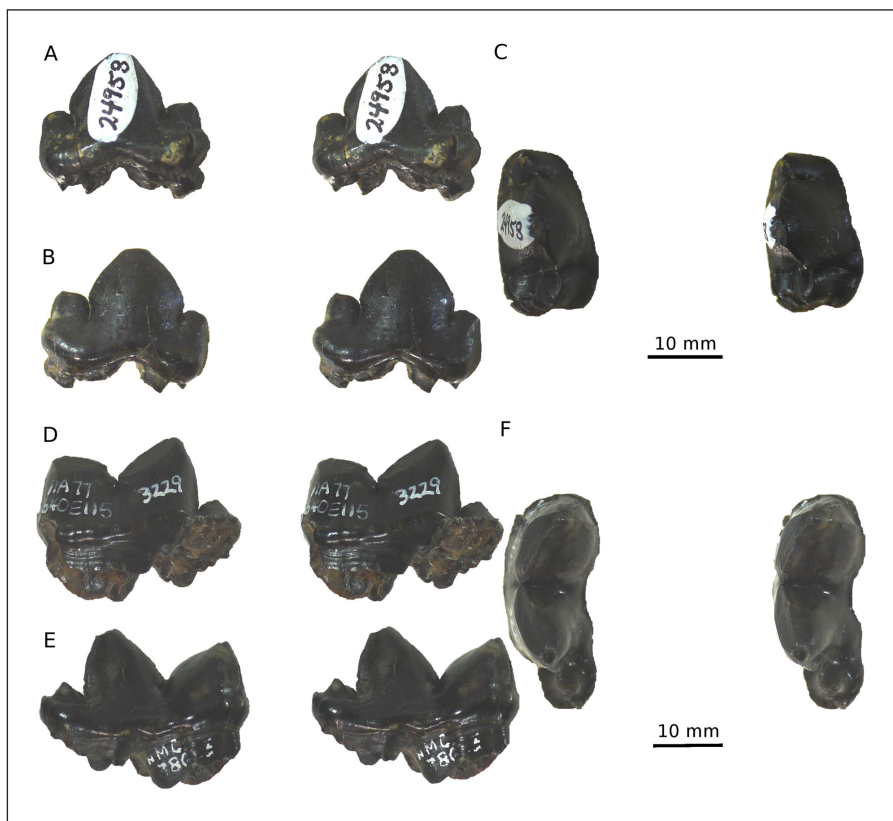
CMN, Canadian Museum of Nature, Ottawa, Canada; F:AM, Frick fossil mammals collection, Division of Paleontology, American Museum of Natural History, New York, USA; IGM, Geological Institute, Mongolian Academy

Sciences, Ulan Baatar, Mongolia; IPM, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; MAN, Museo Archeologico, Nuoro, Sardinia, Italy; MNHN, Muséum National d’Histoire Naturelle, Paris, France; NMT, National Museum of Tanzania; OGU, Odessa I.I. Mechnikov State University, Ukraine; PIU, Paleontology Collection, Museum of Evolution, Uppsala University, Sweden; PPM, Panhandle Plains Historical Museum, Canyon, Texas, USA; SAM, Iziko South African Museum, Cape Town, South Africa; Sk, Swartkrans Collection, Ditsong National Natural History Museum, Pretoria, South Africa; TM, Toros-Menalla locality, National Museum of Chad; UCB, Claude Bernard University, Lyon, France; UF, University of Florida Museum of Natural History, Gainesville, Florida, USA; USNM, United States National Museum (Smithsonian Institution)/National Museum of Natural History, Washington D.C., USA.

**Systematic Palaeontology**

Order CARNIVORA Bowdich, 1821  
 Family HYAENIDAE Gray, 1869  
*CHASMAPORTHETES* Hay, 1921  
*CHASMAPORTHETES* cf. *C. OSSIFRAGUS* Hay, 1921  
**(Figure 1A–1F; Table 1)**

*Adcrocuta* sp. Harington, 1989  
 “Hyaena”, Hyaenidae Harington, 2011



**Figure 1:** Hyena fossils from Old Crow, Yukon Territory, Canada. *Chasmaporthetes* cf. *C. ossifragus*, CMN 24958, right p3: **A.** lingual stereopair views, **B.** labial stereopair views, **C.** occlusal stereopair views. CMN 38053, left m1: **D.** labial stereopair views, **E.** lingual stereopair views, **F.** occlusal stereopair views.

**Table 1:** Measurements of *Chasmaporthetes* specimens from the Old Crown Basin, Yukon Territory. Abbreviations: mac, mesial accessory cusp; dac, distal accessory cusp; L, length; H, height; HSB, Hunter-Schreger Bands; b, bottom 1/3 of crown; m, middle 1/3 of crown; t, top 1/3 of crown; u, undulating HSB layers; a, acute undulating HSB layers.

Specimen No.	CMN 24958	CMN 38053
Element	Rp3	Lm1
Length (mm)	19.11	29.08
Width (anterior, mm)	9.94	13.12
Width (posterior, mm)	11.58	8.24 (partial)
L, mac (mm)	4.97	–
L, main cusp (mm)	10.38	–
Height, main cusp (mm)	13.34	–
L, dac (mm)	4.92	–
L, trigonid (mm)	–	22.25
L, talonid (mm)	–	6.41
H, paraconid (mm)	–	13.4
H, protoconid (mm)	–	15.55
HSB (b, m, t)	u, a, ?	u, a, a

**Referred specimens**—CMN (Canadian Museum of Nature, Ottawa, Canada) 24958, isolated right p3; collected by Richard Harington and team from the Canadian Museum of Nature in 1973. CMN 38053, isolated left m1, collected by William Irving and Brenda Beebe of the University of Toronto in 1977 (Irving and Beebe, 1984).

**Locality**—Old Crown Basin CRH (C. Richard Harington) Locality 11A, Yukon Territory, Canada. The locality is a point bar along the lower Old Crow River (67.819° N, 139.904° W). The area is very remote, only accessible by plane to the village of Old Crow, and from there either on the river or by helicopter.

**Age**—Approximately Irvingtonian to Rancholabrean NALMA, or from about 1.4 Ma to 0.012 Ma (Harington, 2011). We interpret the most likely age of the Old Crow *Chasmaporthetes* to be no younger than the end of Irvington I (approximately 0.85 Ma; see discussion), likely closer to 1.4 Ma.

### Description

CMN 24958, right p3: The main cusp is slightly worn, and has distinct, smooth ridges running down the mesial and distal faces. A well-developed mesial accessory cusp (MAC) is separated from the main cusp by a pronounced notch. No mesial cingulum is visible. A well-developed distal accessory cusp (DAC) is similar in size to the MAC, with a similarly notched boundary with the main cusp. Bulging cingula are developed on the buccal and labial sides of the DAC. The distal face of the DAC forms a depression on the distal edge of the tooth, separating the lingual and labial cingula. Vertical surface furrows are visible throughout the tooth, being most pronounced on the surface of the main cusp.

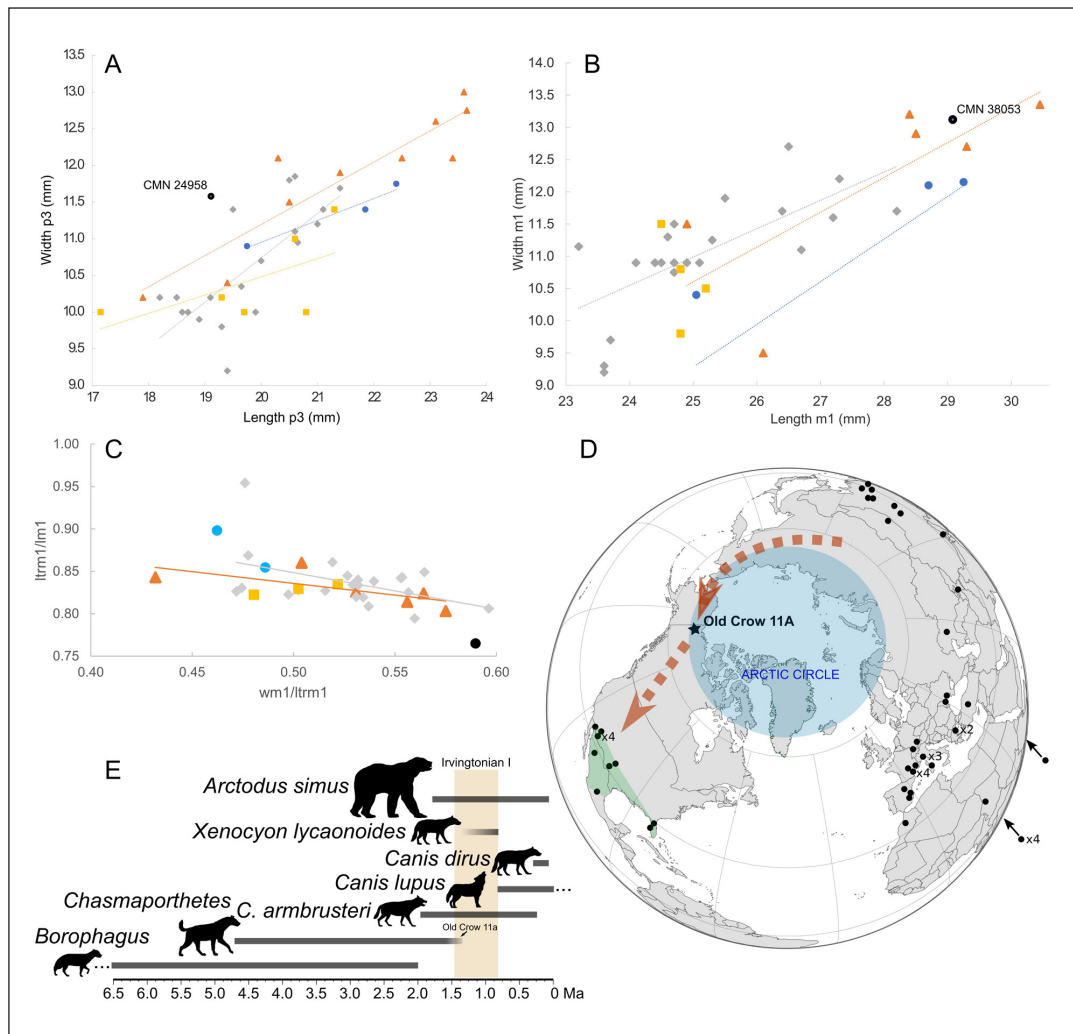
CMN 38053, left m1: A moderate shear facet is developed on the carnassial blade, exposing dentine within a rim of enamel. The protoconid is taller than the paraconid; both cusps are only slightly worn at the apices. There is no metaconid. A low cingulum is present around the base of the crown. The talonid has a single centrally situated cuspid, the hypoconid, with a raised ridge connecting its apex to the base of the protoconid forming a notch at their contact point. There are three small accessory cuspid formed on the lingual to distal rim of the talonid basin. The labial edge of the talonid is broken, so the possible presence of additional cuspid cannot be determined. For additional details see Electronic Supplemental Material (ESM).

CMN 24958 has an overall black sheen. Small regions of milky yellow to white preservation allows Hunter-Schreger bands to be observed under a dissection microscope at 30–40× magnification. The specimen is broken off at the base of the crown. Two roots are visible, with the distal being larger than the mesial one. Preservation of CMN 38053 is similar to CMN 24958. There are two broken roots at the base of the crown, with the mesial being the larger. Both CMN 38053 and CMN 24958 exhibit transitional, acute-undulating Hunter-Schreger Band enamel microstructure, indicating moderate capability to resist abrasive and/or hard foods (Tseng, 2011).

### Comparison with other *Chasmaporthetes*

The nearly symmetrical arrangement of p3 MAC and DAC around the main cusp, the linear alignment of the three cusps on p3 in occlusal view, and the centrally situated and trenchant hypoconid in the talonid basin are all characteristic of *Chasmaporthetes*, and are present on the referred specimens from Old Crow. Compared to specimens of *C. ossifragus* and other species of *Chasmaporthetes*, the p3 from Old Crow is relatively wide for its length (Figure 2A; Table S1). Lower first molar (m1) dimensions of the Old Crow specimen fall in line with the proportions observed in the global *Chasmaporthetes* sample (Figure 2B; Table S1). However, the m1 trigonid of the Old Crow specimen is relatively broad and short compared to the majority of the *Chasmaporthetes* measured (Figure 2C; Table S1). The MAC on CMN 24958 is relatively larger than the MAC on PPM (Panhandle-Plains Historical Museum) 2343 (*C. ossifragus*, Cita Canyon, Texas) and UF (Florida Museum of Natural History, University of Florida) 18088 (*C. ossifragus*, Inglis 1A, Florida), whereas the m1 trigonid and talonid proportions are similar among all three specimens, as well as to the isolated m1 from Inglis 1A (UF 18089).

Because there are only two teeth from the Old Crow Basin in this report, other characteristics such as degree of curvature of the dentition and p4 to m1 length ratios cannot be used to assign the specimens to an existing species, nor are there enough characters to warrant naming a new species. The main dental feature that has been described as characteristic of *C. ossifragus* (Berta, 1981) is consistent with our observations of the Old Crow specimen: a well-developed MAC is present in the Old Crow p3 (CMN 24957), similar to *C. ossifragus* specimens from Florida, and relatively larger in size compared to p3 MAC in other *Chasmaporthetes* species, especially Old World species



**Figure 2:** *Chasmaporthetes* measurements and distributions. **A.** p3 length versus width. **B.** m1 length versus width. **C.** relative m1 width and trigonid blade length in *Chasmaporthetes*. Wm1, m1 width; ltrm1, m1 trigonid length; lm1, m1 length. Symbols: triangle, Africa specimens; diamond, Asia specimens; square, Europe; blue circle, North America; black circle, Old Crow Basin specimens. **D.** Fossil localities containing *Chasmaporthetes*. New material described in this study from Old Crow Basin (Locality 11A) is marked with a star. Dashed arrows indicate likely dispersal route evidenced by new fossils. Locality information for other fossil occurrences taken from Tseng et al. (2013). Regions with more than one fossil locality are indicated with a quantity after the locality marker. Globe image by Connormah (CC BY-SA 3.0). **E.** Stratigraphic occurrence of *Chasmaporthetes* and other large carnivorans discussed in the text. Age ranges are taken from Wang et al., (1999), Tedford et al., (2009), Tseng et al., (2013) and Paleobiology Database via Fossilworks (<http://fossilworks.org>). Silhouettes are modified from Phylopic (*Arctodus* and *Canis lupus*: T. Heath [public domain]; *Canis dirus*: Zimices [CC BY-NC 3.0]; *Canis armbrusteri* image based on *C. lupus* by S. Traver [public domain]), modified from artwork by M. Antón, or generated for this study.

such as *C. lunensis*. Following previous reviews of dental (Kurtén and Werdelin, 1988), and lacking more specific evidence to unambiguously assign the Old Crow fossils to any one of existing species of *Chasmaporthetes* other than from geographic delineation, we reserve judgment on species designation and instead identify the new fossils as *Chasmaporthetes* cf. *C. ossifragus*.

**Discussion and Conclusion**

New records from the Old Crow Basin extend the geographic range of *Chasmaporthetes* in North America northward by more than 4,000 km (~2,500 miles) from the hitherto known localities ranging from the south-

ern United States to central Mexico. Furthermore, the Old Crow locality is roughly 6,500 km (~4,000 miles) from the nearest Old World *Chasmaporthetes* locality in Shamar, Mongolia (Tseng et al., 2013, Qiu, 1987), dramatically reducing the distance between the Old and New World occurrences of the genus (**Figure 2D**). The occurrences from Old Crow provide the first physical evidence of the long-suspected Beringian dispersal route of *Chasmaporthetes* from northern Asia into North America.

The Nearctic occurrence of *Chasmaporthetes* during the Pleistocene suggests that the genus may have ranged throughout much of North America from its initial arrival during the Pliocene, to the Early Pleistocene. Although

the majority of the fossil records of North American *Chasmaporthetes* are Blancan in age, the Mexican locality of El Golfo is Irvingtonian. Given the well-documented Middle and Late Pleistocene fossil records in North America, and the absence of any hyaenid specimens younger than Irvingtonian even at extremely well-sampled sites such as Rancho La Brea, or in Rancholabrean age faunas of central Yukon and Alaska (Guthrie, 1990, Harington, 2011), it is unlikely that the geologic age of the Old Crow *Chasmaporthetes* is much younger than around 1.4 Ma.

An analysis of stratigraphic ranges of similarly sized and/or coeval species that have been interpreted as hunter-scavengers suggests that potential competitors of *Chasmaporthetes* in North America include the canids *Borophagus*, *Canis armbrusteri*, and *Xenocyon lycaonoides*, and the short-faced ursid *Arctodus simus* (Figure 2E). Of these, *Borophagus* had the longest temporal overlap with *Chasmaporthetes*. Based on the timing of last occurrences of *Borophagus* and *Chasmaporthetes*, and the first occurrences of *Canis armbrusteri* and *Arctodus simus*, we hypothesize that competition between these two pairs of predators were in part responsible for the extinction of *Borophagus* and *Chasmaporthetes*.

**Blancan Competitors**—Although postcranial remains of *Chasmaporthetes* suggest that they were likely the most cursorial of the hyaenids (Berta, 1981, Tseng et al., 2013), skull biomechanical traits indicate that some species were capable bone-crackers (Tseng et al., 2011). This would have placed *Chasmaporthetes* into potential competition with the morphologically robust bone-cracking and bone-consuming borophagine canids from 4.7 to ~1.4 Ma (Tseng and Wang, 2011, Tseng and Wang, 2010, Wang et al., 2018, Werdelin, 1989) (Figure 2E). For most of the Blancan NALMA (4.7 to 1.4 Ma), *Chasmaporthetes* and the canid *Borophagus* were both found in the southern U.S. and into Mexico (Berta, 1981, Wang et al., 1999), with *Borophagus* going extinct in the late Blancan (Tseng and Geisler, 2016). This suggests that *Chasmaporthetes* eventually outlasted and/or outcompeted borophagine canids in North America. However, the two lineages coexisted in North America for almost three million years, so any potential competition may have been dampened by finer scale niche differentiation or lack of extensive geographic overlap. Out of ten Blancan-aged localities with *Chasmaporthetes* fossils, four of them (Benson, AZ, Cita Canyon, TX, Dry Mountain, AZ, and Santa Fe, FL) also contain *Borophagus* fossils (Berta, 1981, Wang et al., 1999).

**Irvingtonian Competitors**—The first large-bodied, wolf-like species to appear in North America was *Canis armbrusteri*, a possible predecessor to the extinct dire wolves (*C. dirus*) and/or extant gray wolves (*C. lupus*). *Chasmaporthetes* became extinct in North America within about 0.6 million years after the first occurrence datum of *C. armbrusteri* (Tedford et al., 2009). Shortly after the appearance of *C. armbrusteri* during the beginning of Irvingtonian I (~1.4 to ~0.85 Ma), the giant short-faced bear *Arctodus simus* appeared (Figure 2E). Whereas potential competition between *C. armbrusteri* and *Chasmaporthetes* is possible given comparable body sizes, *A. simus* would

have completely dominated any carcass or kill site because of their very large size. Furthermore, evidence from functional morphology studies suggests that *A. simus* may not have been a specialized scavenger as previously inferred (Figueirido et al., 2010). *Canis armbrusteri* is known from early Irvingtonian sites in Arizona, but is not found in *Chasmaporthetes* localities. *Arctodus* localities are known throughout North America (including in Old Crow and Alaska), but co-occurrence with *Chasmaporthetes* in the Old Crow cannot be confirmed because temporal constraints on the appearance of *Arctodus* in the Arctic are not resolved (Harington, 2011). The hunting dog-like *Xenocyon lycaonoides* made a brief appearance in the New World during the latter half of Irvingtonian I as an immigrant from Eurasia; its occurrence in Old Crow is suggestive of potential sympatry with *Chasmaporthetes*, but its record in Beringia is too poor for confident conclusions (Tedford et al., 2009). Two common elements of later Pleistocene and Holocene megafaunas, *Canis dirus* and *Canis lupus*, appeared too late (during Irvingtonian II) to have been in potential contact or competition with *Chasmaporthetes*.

Lastly, as recently suggested (Tseng et al., 2013), the relative rarity of complete *Chasmaporthetes* fossil materials even in some of the richest carnivoran fossil localities, is indicative of relatively low population densities. The presence of only two *Chasmaporthetes* specimens from the Old Crow Basin establishes this record as a critically important new datum in the Arctic for understanding the evolution of Hyaenidae and Pleistocene turnover patterns leading to present-day ecological communities. Together with the extinction of bone-cracking borophagine canids prior to the end-Pleistocene megafaunal extinctions, the Early Pleistocene extinction of *Chasmaporthetes* contributed to a permanent change in the profile of the North American predator guild. The effects of losing these specialized bone-cracking hunter-scavengers likely had an impact on energy flow in North American food webs (DeVault et al., 2003, Wilson and Wolkovich, 2011), perhaps in a way similar to trophic cascades in African ecosystems following extirpation of large predators there (Atkins et al., 2019). It remains to be quantified to what extent potential successors (*Arctodus* and *Canis*) played comparable ecological roles in North America after bone-crackers disappeared, or whether this loss of a key ecological player was detrimental to ecosystem stability leading up to the megafaunal extinctions.

#### Data Accessibility Statement

All data used in the study are included in the publication.

#### Additional File

The additional file for this article can be found as follows:

- **Electronic Supplemental Material.** DOI: <https://doi.org/10.5334/oq.64.s1>

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#### Competing Interests

The authors have no competing interests to declare.

#### Author Contributions

ZJT, GZ, LW designed the study and wrote the manuscript; ZJT made the figures and table; all authors approved the final version of the manuscript for publication.

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