

Large-bodied wolverines *Gulo gulo berelechii* from the Late Pleistocene of north-eastern Yakutia, Russia

Marina V. Sotnikova, Aisen I. Klimovsky, Vera V. Polyanskaya & Alexander V. Sizov*

ABSTRACT. New material of Pleistocene wolverines (*Gulo gulo*) from north-eastern Yakutia is described, comprising eight complete crania from the Indigirka River basin (Badyarikha, Ogorokha and Tirekhteeh) and New Siberia Island, together with associated fragments. AMS radiocarbon dates obtained at ETH Zürich (c. 24–45 cal ka BP) place these specimens in the Late Pleistocene (MIS 3–MIS 2). Their large size, strongly developed cranial crests and prominent muscle attachment areas indicate that all crania except DSMF GG/Og1 are probably male. Fused nasals, extensive suture obliteration and advanced dental wear indicate that the Indigirka sample comprises adult individuals. Craniometric analysis (cranial length, mastoid and interorbital breadths and additional measurements) shows that the Yakutian specimens consistently exceed the size range of extant Eurasian wolverines and are comparable to the Late Pleistocene form *Gulo gulo berelechii* from the Berelekh mammoth-fauna locality (Yakutia). We discuss the distinctive taxonomic status of the Yakutian wolverines and their role in the Late Pleistocene biodiversity of Western Beringia, as well as possible ecological drivers of their large body size, which may have been linked to climatic phases and trophic resource structure.

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Крупные росوماхи *Gulo gulo berelechii* из позднего плейстоцена северо-востока Якутии (Республика Саха), Россия

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РЕЗЮМЕ. Описан новый материал из северо-восточной Якутии (бассейн Индигирки: Бадяриха, Огороха, Тирэхтээх; о. Новая Сибирь), представленный восемью полными черепами плейстоценовых росوماх *Gulo gulo* и их фрагментами. Радиоуглеродные датировки (ETH Zürich; 24–45 тыс. лет назад) уверенно относят находки к позднему плейстоцену (MIS 2–3). Крупные размеры, развитые краниальные гребни и рельефно выраженные места прикрепления мышц позволяют предположить, что все черепа за исключением DSMF GG/Og1 принадлежат самцам. Сросшиеся носовые кости, высокая степень облитерации черепных швов и выраженная стираемость зубов свидетельствуют о зрелом возрасте индигирских особей. Краниометрический анализ таких показателей как длина черепа, а также общая, мастоидная и орбитальная ширина в совокупности с другими размерами показывают, что якутские экземпляры всегда крупнее современного вариативного ряда росوماх Евразии и по размерам сопоставимы с позднеплейстоценовой формой *Gulo gulo berelechii* из Берелёхского местонахождения мамонтовой фауны (Якутия). Обсуждаются особый таксономический статус якутских росوماх и их место в позднеплейстоценовом биоразнообразии Западной Берингии, а также возможные экологические причины их крупного телосложения, которые могли быть связаны с климатическими фазами и структурой трофических ресурсов.

КЛЮЧЕВЫЕ СЛОВА: поздний плейстоцен, Якутия, мамонтовая фауна, росوماхи, *Gulo gulo*, черепа, морфология, морфометрия.

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Introduction

Extant wolverines, *Gulo gulo* (Linnaeus, 1758), are the largest terrestrial mustelids and today occupy a circumboreal range. The early fossil record of the genus is sparse and fragmentary. The oldest occurrences are from the Pliocene of North America (Gray Fossil Site, Tennessee; latest Hemphillian, 4.9–4.5 Ma; *Gulo sudorus* Samuels, Bredehoeft & Wallace, 2018) and from Asia (Udunga, Transbaikalia; MN 16a, 3.4–3.2 Ma; *G. minor* Sotnikova, 1982) (Sotnikova, 1982, 2010; Samuels *et al.*, 2018). The North American record predates the Asian record by roughly one million years, although the finds are not comparable in completeness: the North American specimen is represented by a single isolated upper tooth, similar in size to that of extant *G. gulo*, whereas Udunga has yielded fragments of two mandibles, probably belonging to the same individual. Both occurrences are associated with thermophilous faunal assemblages, suggesting that early *Gulo* initially occupied milder environments and later followed a relatively short evolutionary trajectory towards boreal adaptation (Sotnikova, 2010; Wolsan & Sotnikova, 2013; Samuels *et al.*, 2018).

A subsequent well-documented occurrence is recorded in the late Early Pleistocene, represented by the small form *Gulo schlosseri* Kormos, 1914 in Eu-

rope and Asia (Kormos, 1914; Kretzoi, 1941; Kurtén, 1968; Bonifay, 1971; Sotnikova, 1978, 1982, 2010), seemingly restricted to ~1.0–0.8 Ma (van Kolfschoten, 2001). A closely similar North American form has been described as *Gulo gidleyi* Hall, 1936 (Gidley & Gazin, 1938; Kurtén & Anderson, 1980). Several authors have noted the few diagnostic characters and the contentious taxonomic status of these forms (Bryant, 1987). This further highlights the fragmentary character of the Early Pleistocene wolverine record.

In Eurasia, the distribution of extant wolverines is currently confined to the boreal zone. In contrast, during the Late Pleistocene, the range extended much farther south, reaching the Mediterranean region in Europe and as far as China in Asia. Fossil wolverines were frequent components of Late Pleistocene mammal communities and formed part of the Eurasian *Mammuthus–Coelodonta* faunal complex (Kahlke, 1999). During the Last Glacial, they were widespread across Europe, as indicated by numerous records from France, Poland, Ukraine, Hungary, Austria, Germany, Slovakia, and the Netherlands, as well as from the Balkans and Italy (Kurtén, 1968; Döppes, 2001; Sabol, 2006; Mol *et al.*, 2007; Diedrich, 2009; Vlačíky, 2009; Diedrich & Copeland, 2010; Marciszak & Kovalchuk, 2011; Marciszak *et al.*, 2017; Döppes, 2019). In eastern Europe and Asia, Last Glacial occurrences are known from the



Fig. 1. Localities with the Late Pleistocene record of wolverines (*Gulo* sp.) in north-eastern Yakutia.

1 — Berelekh mammoth graveyard (ZIN 34907; Vereshchagin, 1977); 2 — Tumus Yar, middle reaches of the Alazeya River (Lazarev & Tomskaya, 1987); 3 — DSMF GG/Bd1; 4 — DSMF GG/Bd2; 5 — DSMF GG/Og1; 6 — DSMF GG/Og2; 7 — DSMF GG/EA1; 8 — DSMF GG/EA2; 9 — DSMF GG/Sm1; 10 — DSMF GG/Ms1; 11 — GIN1197/NS-1.

Russian Plain, the Urals, Siberia, and China (Kuzmina, 1971; Vereshchagin, 1977; Sotnikova, 1978, 1982; Xu & Wei, 1987; Boeskorov & Baryshnikov, 2013).

Many authors treat both extant and Late Pleistocene wolverines as a single species, *Gulo gulo*. However, large-bodied Late Pleistocene forms have often been referred to as the subspecies *G. gulo spelaea* Goldfuss, 1818 (also cited as *Gulo spelaea*) in Europe (e.g., Kurtén & Rausch, 1959) and as *G. gulo berelechii* Novikov, 1993 in Asia (Boeskorov & Baryshnikov, 2013). Their pronounced size and broad distribution during the Late Pleistocene suggest that this interval of the Quaternary may have been particularly favourable for wolverines.

Despite the relative abundance of Late Pleistocene wolverine finds in Europe, most are fragmentary and occur as isolated remains, predominantly in cave contexts (e.g., Reynolds, 1912; Pacher & Döppes, 1997; Döppes, 2001; Diedrich & Döppes, 2004). Complete crania remain rare, both in Western Europe — where they are often associated with human activity (Döppes, 2001; Marciszak *et al.*, 2017) — and at Palaeolithic sites in European Russia (Sotnikova, 1982). By contrast, Eastern Siberia stands out for the richness and preservation of its material: notable finds are known from Bol'shoy Lyakhovsky Island, the Berelekh mammoth graveyard, the Tumus Yar exposure, and Mal'ta archaeological site (Gromov, 1948; Vereshchagin, 1977; Lazarev & Tomskaya, 1987; Boeskorov & Baryshnikov, 2013). The region of north-eastern Yakutia (Western Beringia) is recognised as a distinct biogeographical province that was

long isolated by the Mомsky, Chersky and Verkhoyansk ranges (Sher, 1971; Yurtsev, 1976). Its biota was strongly affected by Pleistocene glacial and interglacial climatic oscillations, including the Last Glacial Maximum.

Material and methods

Abbreviations. ELMA, European Land Mammal Ages; ALMA, Asian Land Mammal Ages; MN, Mammal Neogene biozones (Neogene Mammal units). Berelekh, the Berelekh mammoth graveyard in the middle Indigirka River basin, Sakha Republic (Yakutia), Russia.

Institutional abbreviations. GIN RAS, Geological Institute of the Russian Academy of Sciences (Moscow, Russia); DSMF AS RS(Y), Department for the Study of Mammoth Fauna, Academy of Sciences of the Republic of Sakha (Yakutia) (Yakutsk, Russia); ZIN RAS, Zoological Institute, Russian Academy of Sciences (St Petersburg, Russia); ZMMU (MSU), Zoological Museum, Lomonosov Moscow State University (Moscow, Russia); MSU, Lomonosov Moscow State University (Moscow, Russia).

Material. In this study, we examine a new assemblage of Late Pleistocene cranial material from the Indigirka River basin representing eight adult individuals (seven males and one female), together with a previously undescribed fossil skull of a large male from New Siberia Island (summarised in Table 1).

Extant wolverine cranial material from the Zoological Museum of Moscow State University (ZMMU);

Table 1. New Late Pleistocene cranial material of wolverines (*Gulo gulo*)

No. of specimen	Material	Locality
DSMF GG/Bd1	Skull associated with a mandible (Fig. 7)	The right bank of the Badyarikha River (Yakut: Бадьяариха), near the locality of Meten (Yakut: Мэтэн) — 67.6849°N, 146.7681°E (Fig. 1/3)
DSMF GG/Bd2	Skull (Fig. 9B)	The right bank of the Badyarikha River (Yakut: Бадьяариха), at the Sypnoy Yar locality (Russian: Сыпной Яр) — 68.2190°N, 146.6273°E (Fig. 1/4)
DSMF GG/Og1	Female skull (Fig. 9A)	The left bank of the Ogorokha River (Russian: Огороха), a right-bank tributary of the Badyarikha River (Yakut: Бадьяариха) — 68.2319°N, 146.8579°E (Fig. 1/5)
DSMF GG/Og2	Skull (Fig. 8C)	The left bank of the Ogorokha River (Russian: Огороха), a right-bank tributary of the Badyarikha River (Yakut: Бадьяариха) — 68.3064°N, 146.4737°E (Fig. 1/6)
DSMF GG/EA1	Skull (Fig. 8B)	The left bank of the Ekhe Arghakhtaakh River (Yakut: Эһэ Арҕахтаах), within the basin of the Tirekhteech River (Yakut: Тирэхтээх) — 68.5682°N, 147.1162°E (Fig. 1/7)
DSMF GG/EA2	Skull (Fig. 8A)	The left bank of the Ekhe Arghakhtaakh River (Yakut: Эһэ Арҕахтаах), within the basin of the Tirekhteech River (Yakut: Тирэхтээх) — 68.5785°N, 147.1649°E (Fig. 1/8)
DSMF GG/Sm1	Skull (Fig. 9E)	The left bank of the Syomyuyeleekh River (Yakut: Сөмүөйэллээх), within the Tirekhteech River basin (Yakut: Тирэхтээх) — 68.5825°N, 147.2199°E (Fig. 1/9)
DSMF GG/Ms1	Skull (Fig. 9C)	The left bank of the Muostakh River (Yakut: Мюостах), also within the Tirekhteech River basin (Yakut: Тирэхтээх) — 68.5947°N, 147.2023°E (Fig. 1/10)
GIN1197/NS-1	Skull (Fig. 8D)	Cape Utyos Derevyannykh Gor (Russian: Утес Деревянных Гор), southern shore of New Siberia Island (Fig. 1/11)

S-68188, S-188020, S-1612, S-1613, S-95909, S-95910, S-10852), comparable in size and age to the fossil specimens, was used for comparison. The Berelekh skull, the holotype of *Gulo gulo berelechii* (ZIN 34907), was included in the analysis. Published craniometric datasets for extant and Late Pleistocene Eurasian wolverines (Vereshchagin, 1977; Novikov, 1993; Döppes, 2001; Boeskorov & Baryshnikov, 2013) and for Alaskan wolverines (Anderson, 1977) were incorporated. Data from Döppes (2001) were also used to assess variation in the morphology of the upper carnassial (P4).

Localities and Age. The material examined was recovered from Late Pleistocene deposits in the Indigirka River basin, Republic of Sakha (Yakutia). Most specimens were obtained from artificial exposures created during mammoth-tusk excavations, where high-pressure water pumps were used to wash out bone-bearing lenses. These recovery conditions likely resulted in a pronounced sampling bias: the assemblage is dominated by relatively complete crania of adult males, whereas more fragile or smaller remains — those of juveniles and old adults, lighter female crania, postcranial elements, and mandibles — are scarce or absent. This necessarily limits the representativeness of the assemblage with respect to natural population structure. Nevertheless, the metric similarity of the studied crania to the type specimen of *Gulo gulo berelechii* from Berelekh (also within the Indigirka basin), recovered from a natural faunal assemblage, suggests that large size was probably characteristic of wolverines from the Indigirka region.

All fossil remains considered here derive from bone-bearing lenses within Yedoma (Ice Complex) deposits. Across the Indigirka basin and its tributaries, these deposits form a substantial succession of loess-like silt and sandy loam deposits that are extremely ice-rich and formed syngenetically with the growth of polygonal ice wedges. In sections at Sypnoy Yar, Meten, Ogorokha, Ekhe Arghakhtaakh, Muostakh and Syomyuyeleekh, the upper part consists of thawed loess-like silts overlying a perennially frozen, stratified unit of silty and sandy loams containing wedge-ice bodies, abundant ice lenses, and thin humus-rich and peaty interbeds. Exposures commonly reach 20–40 m in thickness, with local thicknesses of 50–70 m. Bone concentrations are typically confined to humic layers within the loess-like succession or to contacts between loess-like and more ice-rich packets; field evidence for secondary reworking by seasonal thaw, solifluction, and downslope creep is widespread.

In all of the listed localities, the wolverine remains are associated with typical representatives of the Late Pleistocene mammoth faunal complex: *Mammuthus primigenius* (Blumenbach, 1799), *Coelodonta antiquitatis* (Blumenbach, 1799), *Bison priscus* (Bojanus, 1825), *Ovibos moschatus* (Zimmermann, 1780), *Equus lenensis* Russanov, 1968, *Lepus timidus* Linnaeus, 1758, *Lepus tanaiticus* Gureev, 1964, *Ursus arctos* Linnaeus, 1758, *Panthera spelaea* (Goldfuss, 1810), *Canis*

lupus ssp., *Vulpes vulpes* (Linnaeus, 1758), *Vulpes lagopus* (Linnaeus, 1758), *Martes zibellina* (Linnaeus, 1758), *Mustela erminea* Linnaeus, 1758 (Boeskorov & Baryshnikov, 2013). The age of the studied specimens was determined based on associated fauna and supported by radiocarbon dating.

Chronologically, these deposits span the Late Pleistocene. The thawed upper loess-like beds generally formed during MIS 2 (Sartanian cryochron) and overlie units attributed to MIS 3 (Karginian Interstadial); below, horizons correlated with MIS 4 (Zyryanian Glaciation) and MIS 5 (Kazantsevo Interglacial) are frequent, with locally older, faunistically uncharacterised levels. Radiocarbon data obtained for several of the crania examined in this study fall within the MIS 3–MIS 2 interval and thus correspond to Late Pleistocene facies of the Ice Complex, documenting the presence of wolverines in north-eastern Yakutia throughout Late Pleistocene climatic oscillations. Conventional ^{14}C ages were calibrated using IntCal20 and plotted on the GICC05 (b2k) timescale alongside the Greenland $\delta^{18}\text{O}$ records (GRIP, GISP2, NGRIP) (Fig. 2); in Fig. 2, sample labels show conventional ages in ^{14}C yr BP (AD 1950 = 0), whereas the time axis is expressed in cal ka b2k (AD 2000 = 0). Stratigraphically, the finds occur in the upper part of the Yedoma succession, where significant accumulations of mammoth bones are concentrated.

Radiocarbon data were obtained by AMS and reported as conventional radiocarbon ages (^{14}C) in years BP with $\delta^{13}\text{C}$ normalisation (Stuiver & Polach, 1977). In the text and tables, these are formatted as xx xxx \pm yyy ^{14}C yr BP. Calibration was performed in OxCal v4.4 (Bronk Ramsey, 2009) using the IntCal20 Northern Hemisphere terrestrial curve (Reimer *et al.*, 2020). For each sample, we report the posterior median, along with the 68.3% and 95.4% highest posterior density ranges in cal yr BP (and, where appropriate, in cal ka BP); where the posterior is multimodal, all 2σ ranges are listed. For plotting against the Greenland $\delta^{18}\text{O}$ records on the GICC05 timescale, calibrated ages were converted to b2k by a constant offset (b2k = cal BP – 50 yr; Andersen *et al.*, 2006; Rasmussen *et al.*, 2014). No marine reservoir correction was applied (terrestrial material). Calibrated bounds were rounded to the nearest ten years.

Calibrated ranges (2σ): DSMF GG/Og2, 20 860 \pm 200 \rightarrow 25–24 cal ka BP; DSMF GG/Bd2, 25 900 \pm 600 \rightarrow 30.5–29.5 cal ka BP; DSMF GG/Ms1, 38 100 \pm 600 \rightarrow 42–41 cal ka BP; DSMF GG/Sm1, 41 200 \pm 800 \rightarrow 45–44 cal ka BP. The wolverine mummy ZIN32214 (Berelekh) dates to 12 420 \pm 55 ^{14}C yr BP (OxA-19216; AMS), calibrating to c. 14.6–14.1 cal ka BP (2σ ; bimodal due to IntCal20 wiggles). In conventional radiocarbon years, this age falls within the reported formation interval of the Berelekh mammoth graveyard (13 700–11 800 ^{14}C yr BP; Pitulko *et al.*, 2014).

Measurements. Cranial measurements for the Late Pleistocene wolverines are given in Table 2; tooth measurements, taken according to standard procedures,

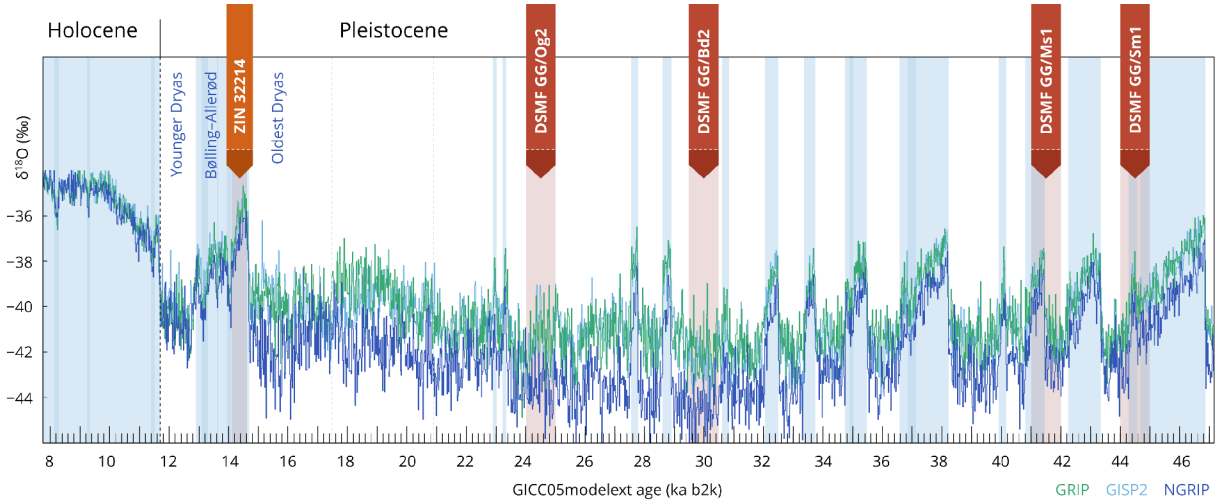


Fig. 2. Radiocarbon data for Late Pleistocene wolverine (*Gulo gulo*) crania from north-eastern Yakutia (this study). Conventional ¹⁴C ages (labels) were calibrated with IntCal20; the resulting 2σ ranges (shaded vertical reddish bands) are plotted on the GICC05 (b2k) timescale against the Greenland δ¹⁸O records (GRIP, GISP2, NGRIP). Arrowheads mark posterior medians. Calibrated ranges (2σ): ZIN 32214, 12 420 ± 55 ¹⁴C yr BP → 14.6–14.1 cal ka BP (potentially bimodal); DSMF GG/Og2, 20 860 ± 200 → 25–24 cal ka BP; DSMF GG/Bd2, 25 900 ± 600 → 30.5–29.5 cal ka BP; DSMF GG/Ms1, 38 100 ± 600 → 42–41 cal ka BP; DSMF GG/Sm1, 41 200 ± 800 → 45–44 cal ka BP.

Table 2. Cranial measurements for fossil male wolverines (*Gulo gulo*).

Measurements	GG/EA2	GG/EA1	GG/Bd1	GG/Og2	GG/Bd2	GG/Sm1	GG/Ms1	ZIN 34907	GIN1197/NS-1
GL	167.9	185.40	181.7	182.7	178.8	–	–	174.4	176.8
CL	154.2	172.2	165.1	165.5	165.7	161.6	–	161.6	162.4
BL	142.6	160.6	153.6	154.1	155.2	151.2	–	150.8	151
PL	83.9	92.5	91.1	90.4	88	87.7	87.7	84	87.7
FL	72.8	75.6	76.8	75	78.5	76.90	75.2	71.3	74.5
OL	108.6	120.6	115.3	118.3	108.3	–	–	116.9	114.5
WIO	46.9	50.5	49.7	44.6	45.8	48.5	41.9	46.8	46.5
WC	44.1	46.7	48.2	49.2	49.2 (alv.)	45.5 (alv.)	45.5 (alv.)	44.6	47.7
WF	57.8	55.5	57.3	51.4	52.1	57.8	49.3	53.1	54.6
WPC	39.1	35.5	34.9	–	38.3	37.2	35.2	–	–
WZ	113	120.7	127.7	122.1	113.9	–	–	117.6	114.6
WB	68.5	69.3	67	62.1	65.3	65.2	–	64.9	67
WPM	72.9	75.9	75.8	76.7	77	75.3	68.1	–	77.5
WM	95.4	98.8	101.0	100.2	96.6	97.6	–	99.6	96.2

are presented in Table 3. All measurements were taken with callipers to the nearest 0.1 mm and are reported in millimetres.

Cranial abbreviations: GL — Greatest length: Distance from anterior tip of premaxillae to the posterior point of inion; CL — Condylbasal length: Distance from anterior tip of premaxillae to posterior point of condyles; BL — Basal Length: Distance from the incisor row to the foramen magnum notch; PL — palatal length; FL — Facial length: Distance from anterior tip of premaxillae to the middle point between postorbital processes; OL — Occipital length: Distance from middle point between postorbital processes to poste-

rior end of sagittal crest, along the middle line of the skull; WIO — Interorbital width: Minimum breadth across dorsal margins of orbit; WC — Skull width at the level of canines: Maximum width above canines; WF — Frontal shield width: Maximum breadth between postorbital processes; WPC — Postorbital constriction width: Minimum width across frontals behind postorbital process; WZ — Zygomatic width: Greatest distance across zygoma; WB — Braincase width: Maximum breadth across braincase; WPM — Greatest palatal width between distal ends of P4; WM — Mastoid width: Maximum width across mastoid processes.

Table 3. Upper tooth measurements for fossil male wolverines (*Gulo gulo*).

Measurements	GG/EA2	GG/EA1	GG/Bd1	GG/Og2	GG/Bd2	GG/Sm1	GG/Ms1	ZIN 34907	GIN1197/NS-1
W I3–I3	23.3	25.1	25	25.7	26.1	24	24.1	23.5	25.1
L C1–M1	57.40	61.80	61.40	59.30	59.30	58.4	54.8	58.9	57.9
L P1–M1	45.20	50.90	46.80	45.50	–	–	–	47.30	46.50
L P1–P4	40.50	47.30	45	41.80	–	–	–	45.50	44.60
L / WP3	–	–	11.5 / 7.4	–	11.9 / 7.1	12.6 / 7.1	10.1 / 5.9	–	11.2 / 7.2
L / WP4	21.9 / 12.9	23.1 / 13.3	23.2 / 13.6	22.5 / 15.0	24.2 / 14.4	23.7 / 15.0	21.1 / 12.5	23.0 / 12.0	24.5 / 14.1
L / WM1	8.7 / 15.1	7.3 / 14.8	8.7 / 15.5	8.9 / 15.4	9.0 / 15.3	8.4 / 14.7	7.6 / 13.4	8.4 / 14.0	7.9 / 15.3

Dental abbreviations: I1-3/i1-3, upper and lower incisors; C1/c1, upper and lower canines; P1/p1, upper and lower 1st premolars; P2/p2, upper and lower 2nd premolars; P3/p3, upper and lower 3rd premolars; P4/p4, upper and lower 4th premolars; and M1/m1-m2, upper and lower 1st and 2nd molars; alv., alveolar measurement.

Graphical representation of cranial measurements.

For the comparative diagrams of cranial size and proportions, we used six standard linear measurements: condylobasal length (CL), basal length (BL), interorbital width (WIO), zygomatic width (WZ), mastoid width (WM) and braincase width (WB) (see Table 2 for definitions). Cranial measurements of extant wolverines were compiled from published datasets: Novikov (1993) for Scandinavia, the Ural region, Eastern Siberia, the Russian Far East and Yakutia; and Boeskorov & Baryshnikov (2013) for Yakutian populations from the Olekma and Kolyma River basins. For each region and variable, we used the observed minimum, maximum and mean values for adult skulls; these are shown as point-and-whisker plots, with the mean indicated by a solid circle and whiskers extending to the minimum and maximum values.

For the Late Pleistocene Yakutian wolverines, individual cranial measurements were used to construct box-and-whisker plots. In these plots, the central line marks the median, the box spans the interquartile range (25th–75th percentiles), and the whiskers extend to the minimum and maximum values; potential outliers were not plotted separately. This approach provides a consistent visual comparison between regional samples of extant wolverines (summarised by their ranges and means) and the fossil Yakutian sample (summarised by the distribution of individual measurements).

Results

A total of eight Late Pleistocene wolverine crania from the Indigirka River basin were examined: seven large male skulls (one with an associated mandible) and one female skull. In addition, one additional male skull from New Siberia Island, housed in the GIN RAS collection, was included in the analysis.

Sex assessment and individual age of the Yakutia wolverines

Sexual dimorphism in extant wolverines is strongly expressed in cranial size. According to Novikov (1993), of the 19 cranial measurements taken across the extant range of *Gulo gulo*, only two (nasal length and m1 width) overlap between males and females; the remaining 17 parameters show little or no overlap in linear dimensions. Consequently, male and female cranial series are usually analysed separately in both extant (Novikov, 1993) and fossil material (Döppes, 2001; Boeskorov & Baryshnikov, 2013). Using these data, together with the morphology and measurements of the material studied here, we infer that the sample comprises eight male skulls and one female skull, DSMF GG/Og1 (Fig. 9A; cf. Fig. 4), which in all respects falls within the size range of females.

Individual age variation in extant wolverines is relatively slight. Novikov (1993) showed that the skull of a young wolverine reaches its full length within the first year, while cranial breadth attains adult values by the age of two; subsequent ageing is expressed mainly in progressive suture obliteration, which is largely complete by about five years. On this basis, the Indigirka and New Siberia Island skulls DSMF GG/Bd1, DSMF GG/Og2, DSMF GG/EA1, DSMF GG/Sm1, DSMF GG/Ms1 and GIN1197/NS-1 can be assigned to the adult age class (Figs 7–9). They display moderate tooth wear, a well-developed sagittal crest, and extensive suture fusion, suggesting an age of 5–7 years or older. All of these features, apart from large cranial size, are also present in DSMF GG/Og1 (Fig. 9A), which we therefore interpret as an adult, moderately sized female. Within the cranial sample, the only exceptions are the skulls from Sypnoy Yar (DSMF GG/Bd2) and the Ekhe Arghakhtaakh River (DSMF GG/EA2), in which the nasal sutures remain clearly visible on the dorsal surface of the snout (Figs 8–9), suggesting young adult individuals.

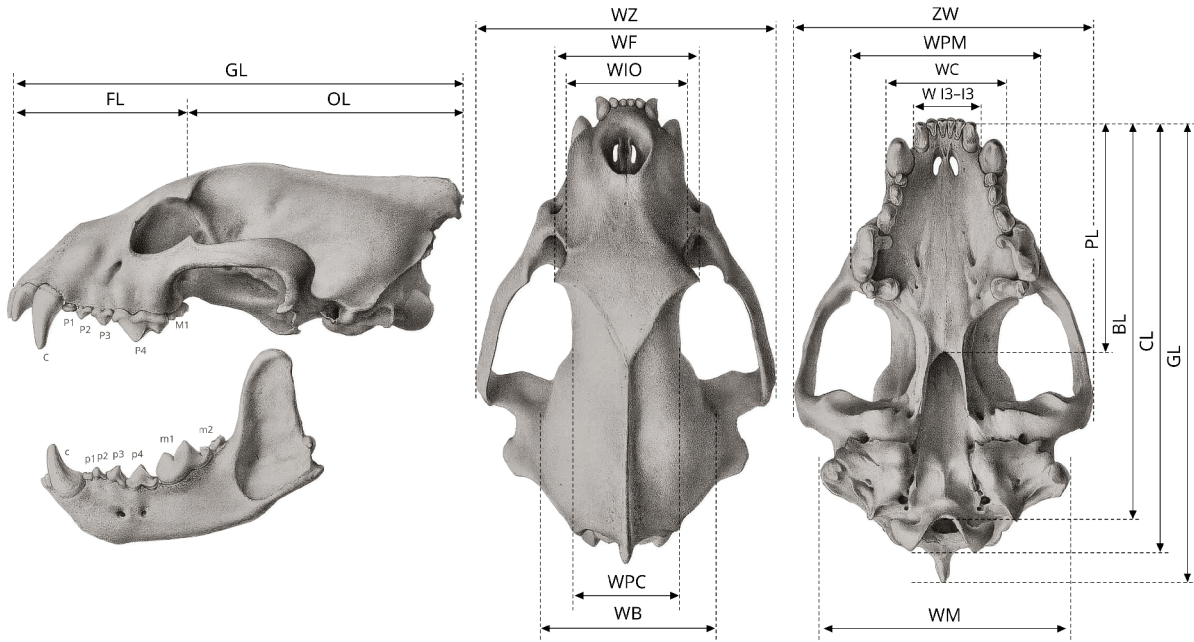


Fig. 3. Cranial measurements and abbreviations.

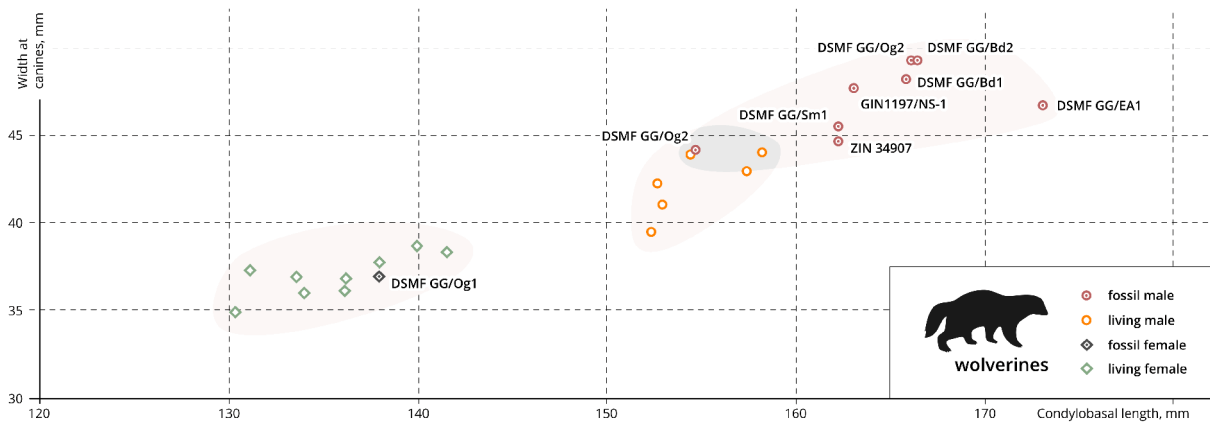


Fig. 4. Scatter plot of condylobasal length (CL) versus width at canines (WC) in fossil and extant wolverines. The diagram illustrates both the differences in overall skull size between fossil and modern males and females, and the higher WC/CL ratios in fossil males compared with recent males. Cranial measurements of extant individuals are based on material from the collection of the ZMMU.

Brief morphological and metric characterisation of the Yakutian wolverines. Cranial morphology and distinguishing features

The examined crania are very large (Tables 2–3; Figs 7–9). Their greatest cranial length exceeds the maximum values reported for extant male wolverines. Among the male skulls studied, the largest, DSMF GG/EA1, has a greatest length of 185.4 mm; by comparison, Novikov (1993) reported maxima of 172.5 mm for Scandinavian males, 168.8 mm for males from the Urals, 170.6 mm for specimens from Eastern Siberia, and 176.5 mm for males from the northern Russian Far East, including Yakutia.

As in extant forms, the Late Pleistocene wolverines have short, broad and robust muzzles with a clear lateral expansion at the level of the canines and upper carnassials. The nasal bones are preserved only in DSMF GG/Bd2 and DSMF GG/EA2, both of which likely represent individuals younger than c. 5 years. The nasal aperture is relatively small and oval in outline. The infraorbital foramina are comparatively small and slit-like. In some skulls, the preorbital fossa is well developed, especially in DSMF GG/Bd1 (Fig. 7F, arrows). The temporal crests are strongly expressed and converge to form a sagittal crest anterior to, or at the level of, the postorbital constriction.

In the lateral view, the muzzle slopes gently from the posterior frontal region towards the nasal opening. A high, elongated sagittal crest runs along the main cranial axis. Posteriorly, it becomes particularly prominent, projecting beyond the level of the occipital condyles and providing an extensive surface for attachment of the *m. temporalis*. Its height at the level of the occipital condyles reaches 25.5 mm in DSMF GG/Bd1.

Among the fossil specimens, DSMF GG/Bd1 best preserves the occipital region. It shows a well-developed paroccipital process directed distally from the auditory bulla and ending in a prominent free tip, together with a long, broad and robust mastoid process with a bulbous ventral margin. In the posterior view, this specimen displays a high, trapezoidal supraoccipital shield, whereas in some other skulls the shield tends to be more fan-shaped. Overall, DSMF GG/Bd1 is distinguished by the greatest expansion of the zygomatic arches ($WZ = 127.7$ mm) and a very broad mastoid region ($WM = 101.0$ mm).

Across the 14 cranial variables measured, the five best-preserved Indigirka skulls and the New Siberia Island specimen closely match the type specimen from Berelekh (ZIN 34907). Their dimensions fall between our largest fossil specimen, DSMF GG/EA1 (greatest length 185.4 mm; $CL = 172.2$ mm), and the smaller crania DSMF GG/Sm1 ($CL = 161.6$ mm) and GIN1197/NS-1 ($CL = 162.4$ mm). The maximum zygomatic breadth ($WZ = 127.7$ mm) is recorded in DSMF GG/Bd1, which also shows the largest mastoid width ($WM = 101.0$ mm). All other skulls have broadly comparable measurements and differ little from one another in both absolute and proportional values (Table 2).

Within the studied series, DSMF GG/EA2 stands out as an exception. In most parameters considered, it matches the other male skulls in the Indigirka sample. Still, its cranial length is markedly lower than even the mean values for this group. It should be noted that this specimen is younger than the others, as indicated by unfused sutures in the nasal region, and it also shows distinctive features related to dental anomalies, most likely reflecting the congenital absence of several teeth (Fig. 8A). These factors may have constrained the growth of cranial elements, and DSMF GG/EA2 was therefore excluded from some analyses, particularly those involving proportional indices.

The morphology of the upper dentition differs only slightly from that of extant wolverines. The broad, curved incisor row is moderately projected anteriorly. The incisors are set without diastemata, and the third incisors are enlarged and caniniform. In extant forms, small diastemata between the outer incisors and the canines are common. In contrast, in the material studied, the incisor row meets the canines in close contact in most cases. An upper canine is preserved in only a single specimen, DSMF GG/EA2 (Fig. 8A); it is massive, relatively low-crowned, only weakly curved, and bears distinctly wrinkled enamel. The tooth row shows a marked inflexion between P3 and P4, with the buccal wall of the upper carnassial P4 strongly protruding buccally beyond the line of the cheek teeth.

The premolars are large, robust and arranged almost without diastemata. The single-rooted P1 is invariably present and is situated at the posterior margin of the canine alveolus. In the fossil material, it is more fully integrated into the tooth row, whereas in extant wolverines, it is often slightly displaced lingually relative to the tooth row. The double-rooted second and third premolars are massive, each with a single principal cusp bounded by anterior and posterior crests. In extant *Gulo gulo*, the second premolar is aligned with the main axis of the tooth row, whereas in Yakutian Late Pleistocene specimens it is often slightly rotated lingually. Occlusal outlines of P3 are variable in both extant and fossil forms; distal expansion of the crown is rare, and in most cases, the anterior and posterior crown widths differ only slightly. However, in unworn fossil P3, the basal cingulum encircling the crown is more strongly developed than in extant material.

The massive, broad P4 (Figs 5–6A) exhibits a large, well-defined protocone, the anterior margin of which, as in extant *Gulo gulo*, lies slightly behind the anterior margin of the paracone. Two well-developed ridges run along the anterior face of P4: the medial ridge descends towards the protocone, whereas the anterior ridge terminates in the region of the anterior cingulum. In some cases, the lower part of this ridge is split into two short crests, as observed in specimen DSMF GG/Bd3 and in some extant P4 (Fig. 5).

In the occlusal view, the buccal margin of P4 is slightly curved at about mid-paracone level, and the broad metacone shows a subquadrate posterior outline. The metacone also bears two posterior vertical ridges and two roughly parallel ridges delimiting its occlusal surface. This configuration is most clearly visible on young, unworn teeth and is less pronounced on carnassials affected by wear (Fig. 5). This pattern appears to be characteristic of the genus *Gulo*.

The relatively broad M1 shows a slight constriction, more pronounced on the mesial side of the crown. The tooth is transversely elongated, with its length markedly shorter than its width. The metacone is much smaller than the paracone. The cingulum is well developed around the buccal styler shelf. Fossil specimens share a consistent feature that distinguishes them from extant wolverines: the cingulum extends onto the anterior side of the trigon. It encircles the paracone anteriorly, whereas in extant material this anterior cingulum is strongly reduced (Fig. 5, arrows).

Both mandibular rami associated with the skull DSMF GG/Bd1 (Fig. 7) have a deep corpus beneath the lower carnassial and a broad ascending ramus with a well-developed angular process. The large, deep masseteric fossa bears a conspicuous internal depression (hereafter referred to as the “pocket”; Fig. 7E, yellow arrow), corresponding to the impression of the deep portion of the masseter muscle. In contrast to extant material, the masseteric fossa of DSMF GG/Bd1 shows pronounced internal sculpturing and a more rounded anterior margin. Two moderately large mental foramina (c. 3 mm in anteroposterior length) are visible below



Fig. 5. P4 and M1 of *Gulo gulo* (fossil and extant wolverines). Not to scale. Arrows indicate the differing degree of development of the anterior cingulum around the paracone in fossil versus extant forms.

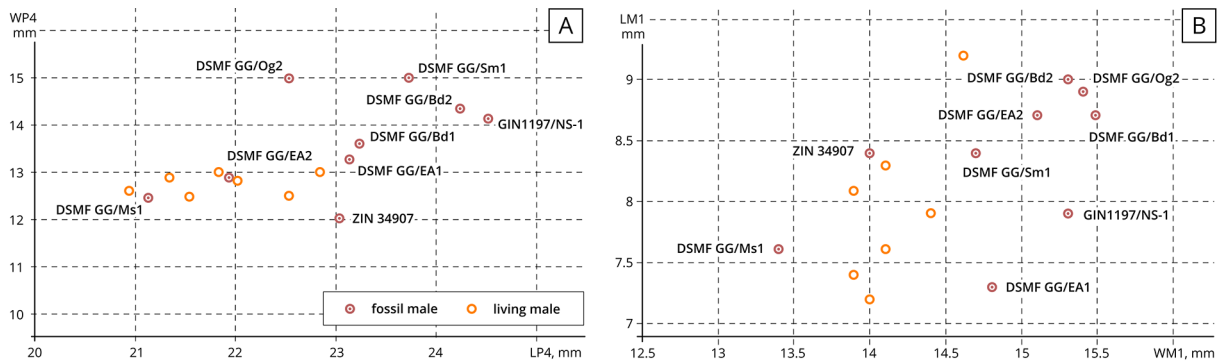


Fig. 6. Scatter plots of premolar and molar dimensions in fossil and extant male wolverines. A — bivariate plot of P4 length (LP4) versus width (WP4); B — bivariate plot of M1 length (LM1) versus width (WM1).

the anterior roots of p3 and p4. The incisors are represented by the right and left alveoli of i3 and by scarcely worn right and left i1–2; all incisors are slightly staggered and occupy a very small incisal space.

The tooth row is strongly curved laterally. All premolars show slight distal expansion; for example, in p4, the anterior width is 7.1 mm, and the posterior width is 8.1 mm. Crown length increases posteriorly, with p2, p3 and p4 measuring 7.0, 9.0 and 13.9 mm, respectively. The long axes of p4 and m1 are set at an angle to one another. The single-rooted p1 lies against

the lingual wall of the canine alveolus, whereas p2 and p3 are slightly rotated buccally. The disproportionately elongate p4 preserves fragments of a cingulid which, in the unworn state, evidently encircled the entire base of the crown, as is typical of both extant and fossil wolverines. The lower carnassial m1 is preserved on both sides and exhibits the same pattern of damage. The surviving crown fragments indicate that these long, robust teeth were initially fractured and subsequently abraded, most likely due to bone-crushing behaviour. The second molar is represented only by its alveolus.

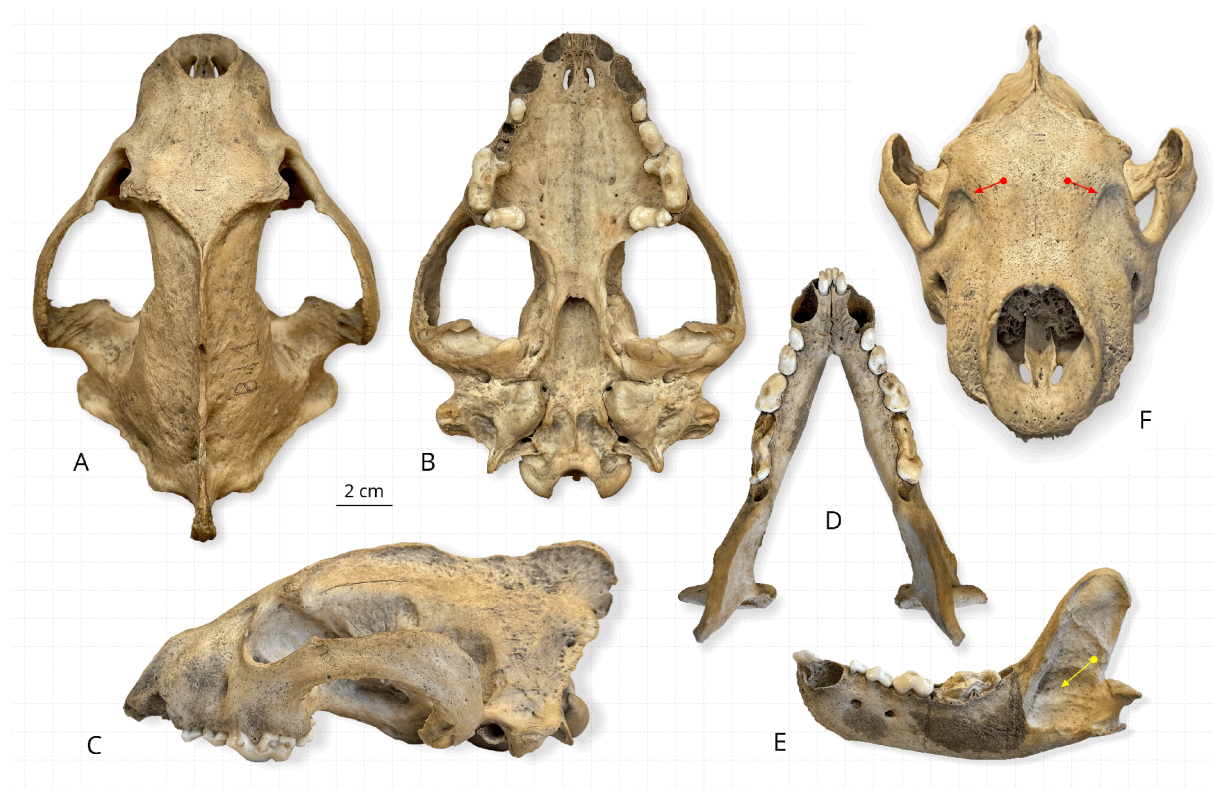


Fig. 7. Skull and mandible of *Gulo gulo* from the Meten locality (DSMF GG/Bd1). (A) dorsal view; (B) palatal view; (C) left lateral view; (D) occlusal view of mandible; (E) lateral view of left mandible (yellow arrow points to the “pocket” in the masseteric fossa); (F) anterior view of rostrum showing well-developed preorbital fossae (red arrows). Scale bar for A – E = 2 cm; F not to scale.

The principal measurements of the left mandibular ramus are as follows: length from i3 to the angular process, 111.0 mm; alveolar length c1–m2, 70.8 mm; alveolar length p4–m2, 42.1 mm; alveolar length m1, 23.4 mm; mandibular height between p4 and m1, 24.3 mm.

Discussion and comparison

Indigirka material in the context of the Late Pleistocene wolverine record

The new specimens described in this study constitute the most complete Late Pleistocene cranial assemblage of fossil wolverines (*Gulo gulo*) currently documented from Eurasia. Wolverine finds are numerous in Europe; however, they are typically represented by single, often fragmentary specimens, and complete skulls remain rare in Western and Central European deposits (Döppes, 2001; Diedrich, 2014). In Eastern Europe, wolverine remains are relatively abundant at the Avdevo Palaeolithic site (Kursk Region, Russia), where they are mainly represented by mandibles (a minimum of c. 40 individuals) and isolated teeth, while complete crania are lacking (Sotnikova, 1982). Against this background, the Indigirka series, including several

well-preserved male skulls and one skull with associated mandibles, provides an exceptional basis for assessing Late Pleistocene variation in *Gulo gulo* at both the individual and population levels.

General cranial and dental morphology in Late Pleistocene and recent *Gulo gulo*

The wolverine skull, in addition to its large size, exhibits a suite of features that distinguish it from other extant mustelids. These include a relatively short and broad muzzle, widely flared zygomatic arches, small slit-like infraorbital foramina, a powerful sagittal crest, robust mastoid processes, and a moderately inflated auditory bulla with an elongated meatal tube, combined with a strongly developed dentition. The dental formula of *Gulo* is the same as that of *Martes*. However, the carnassial teeth of wolverines are conspicuously larger, both absolutely and relatively, than those of other marten-like mustelids.

The upper carnassial P4 in *Gulo* is particularly distinctive. In occlusal view, its distal margin has a subquadrate outline, in contrast to the more triangular carnassials of other gulonines and martens. The cutting system of the paracone–metacone complex is also

specialised. A substantial portion of the metacone ridge is displaced lingually, then runs along the broad posterior margin of the tooth and turns onto the buccal side, where it occupies almost two-thirds of the metacone length. As a result, the metacone of P4 in *Gulo gulo* forms two parallel, well-separated cutting edges, rather than a single blade as in most other carnivorans. As emphasised by Sokolov (1968), this configuration makes the wolverine carnassials functionally closer to secateurs or metal shears than to “paper scissors”, and is likely related to bone-crushing and to processing tough connective tissues in large prey.

Our observations indicate that Late Pleistocene Yakutian wolverines closely match extant *Gulo gulo* in this suite of cranial and dental characters. The general cranial architecture (short, broad rostrum; strongly developed sagittal crest; robust mastoid region) and the basic pattern of the upper and lower carnassials fall within the extant morphological range, with differences largely expressed in size and in a few more detailed features of muscle attachment, cheek-tooth alignment, and dental cingulum development, which are discussed below.

European Late Pleistocene wolverines and the status of “*Gulo spelaea*”

Late Pleistocene wolverine remains from Europe are generally referred to the extant species *Gulo gulo*. They have been reported across a broad geographic range, from the Iberian Peninsula through central Europe to the Carpathians and the western flank of the Urals (e.g., Döppes, 2001, 2005; Diedrich & Döppes, 2004). Published radiocarbon ages for some of these occurrences fall largely within the ~12–40 ka interval (as reported in the original sources): for example, 18–44 ka in Austria, 35–46 ka in Slovenia, 12–36 ka in Croatia, and 11 950 ± 300 to 23 400 ± 700 ¹⁴C yr BP at Avdeev in European Russia (Döppes, 2001; Dolukhanov *et al.*, 2001).

When first described, the European Late Pleistocene wolverine was assigned to a separate species, *Gulo spelaea* Goldfuss, 1818 (later treated by some authors as *Gulo gulo spelaea*). The type specimen originates from the classical Zoolithenhöhle, long known as Gailenreuth Cave in Franconia (Germany), and is housed in the Museum für Naturkunde, Berlin (MB). Accord-

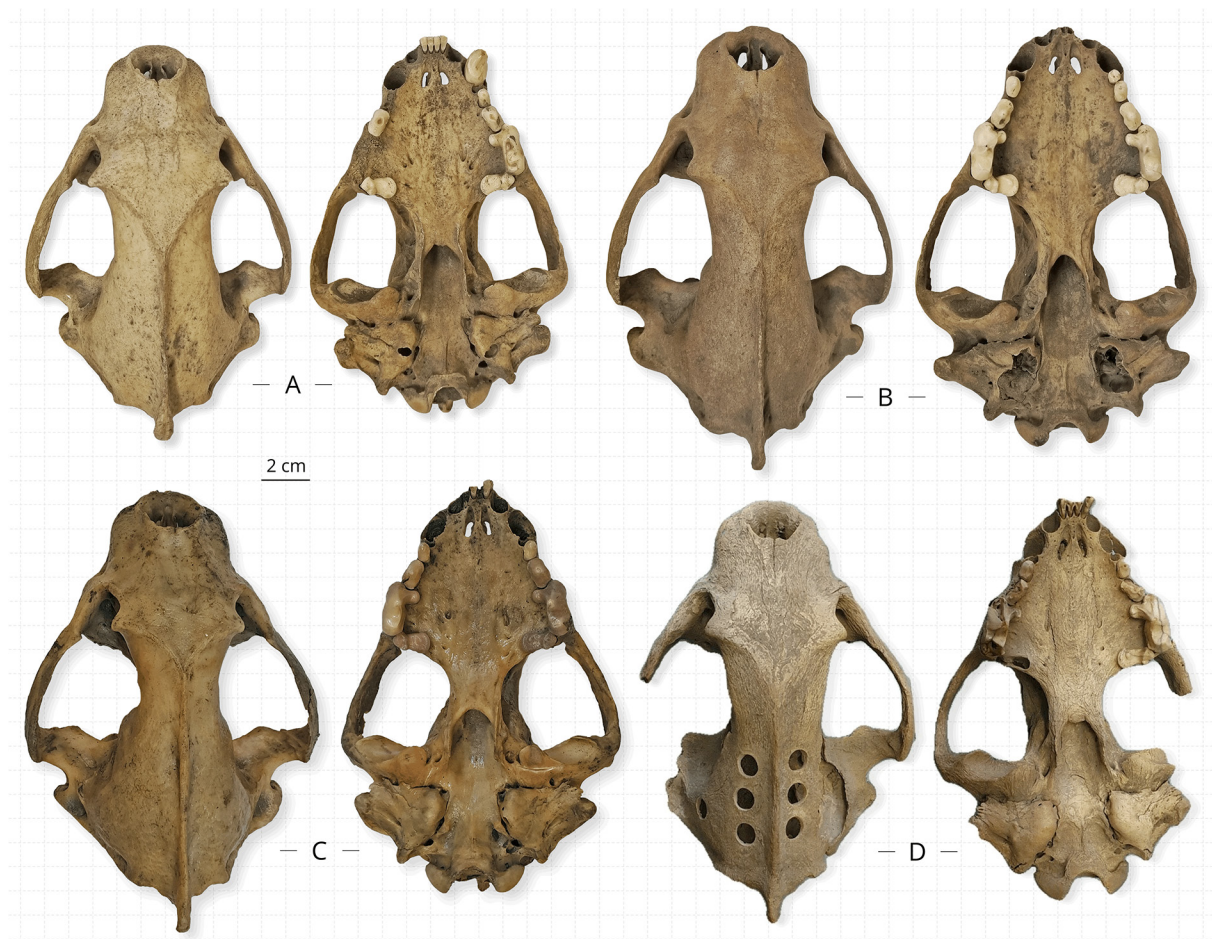


Fig. 8. Skulls of *Gulo gulo*. (A) Ekhe Arghakhtaakh River, DSMF GG/EA2; (B) Ekhe Arghakhtaakh River, DSMF GG/EA1; (C) Ogorokha River, DSMF GG/Og2; (D) New Siberia Island, GIN1197/NS-1. Scale bar = 2 cm.

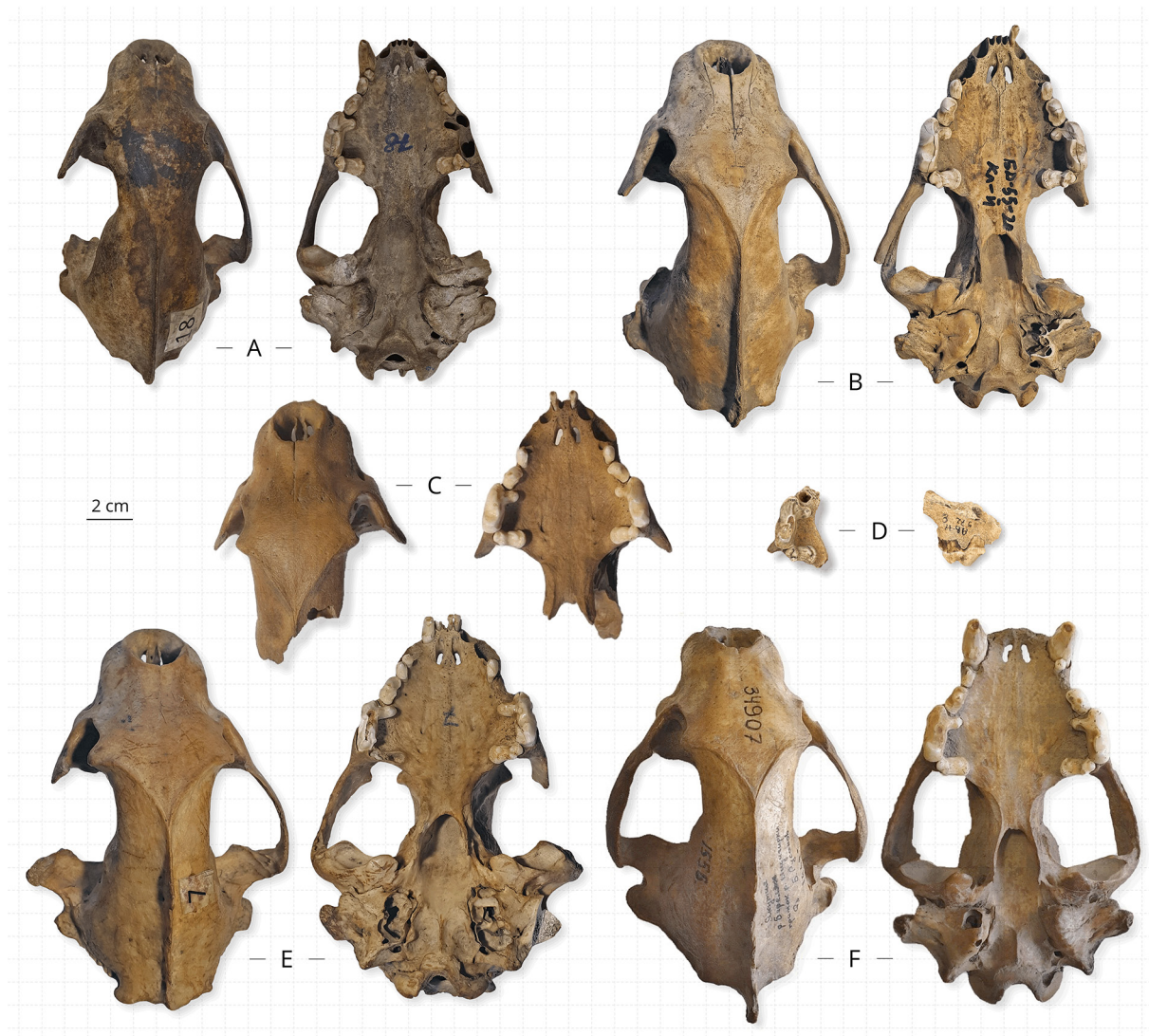


Fig. 9. Skulls and cranial fragments of *Gulo gulo*. (A) Ogorokha River, DSMF GG/Og1; (B) Synoy Yar locality, DSMF GG/Bd2; (C) Muostakh River, DSMF GG/Ms1; (D) DSMF GG/Bd3; (E) Syomyuyeleekh River, DSMF GG/Sm1; (F) Berelekh mammoth graveyard, ZIN 34907. Scale bar = 2 cm.

ing to Novikov's (1993) detailed account, the holotype is a well-preserved adult skull (MB-435) lacking the mandible and zygomatic arches, as well as the auditory bullae and several anterior teeth, but otherwise exhibiting the diagnostic cranial characters of *Gulo*. Diedrich (2014) illustrated this specimen together with a mandible, and Döppes (2001) provided metric data for European Late Pleistocene wolverines.

Subsequent work has suggested that the cranial proportions and dentition of the Zoolithenhöhle (=Zoolithen Cave) specimen fall within the broader range of variation of *Gulo gulo*. Accordingly, the taxonomic status and diagnostic value of the name *spelaea* remain debated, and many recent treatments refer the European Late Pleistocene material simply to *Gulo*

gulo, without recognising *spelaea* as a distinct taxon. Metric data compiled by Döppes (2001) indicate that European Late Pleistocene wolverines are, on average, smaller than both the type material of *G. g. berelekhii* from Berelekh in Yakutia and the new material from the Indigirka basin described here. In addition, the published photograph of the mandible associated with the type specimen of "*Gulo spelaea*", MB 435 (Diedrich, 2014, Fig. 6), shows no trace of the distinct "pocket" in the masseteric fossa documented in the Indigirka and Berelekh series. On this basis, European Late Pleistocene wolverines provide an important comparative background but cannot be regarded as direct morphological analogues of the Yakutian large-bodied form.

Comparison with extant *Gulo gulo*: cranial proportions and braincase size

Late Pleistocene male wolverines from north-eastern Yakutia are, on average, larger than extant males in the ZMMU collection, with this difference affecting both cranial and dental variables (Figs 4, 6). Geographical variation in skull size of extant male wolverines was analysed by Novikov (1993, pp. 122–125, Appendix). Unfortunately, only minimum, mean and maximum values are provided in his tables, and not all measurements follow a fully standardised protocol. As a result, only six cranial measurements are directly comparable with our dataset: BL (basal length), CL (condylobasal

length), WZ (breadth across the zygomatic arches), WIO (interorbital breadth), WM (mastoid breadth) and WB (maximum breadth of the neurocranium). Novikov’s extant samples represent four major Eurasian regions: Scandinavia ($n = 15$), the Ural region ($n = 43$), Eastern Siberia including Yakutia ($n = 17$), and the northern part of the Russian Far East ($n = 57$).

Comparative analysis of these regional samples with our Yakutian Late Pleistocene material shows that, across all linear dimensions available for comparison, fossil males exceed the ranges documented for extant Eurasian wolverines; the only exception is braincase breadth, which falls within the variation observed in extant males (Fig. 10). Analysis of relative values, based

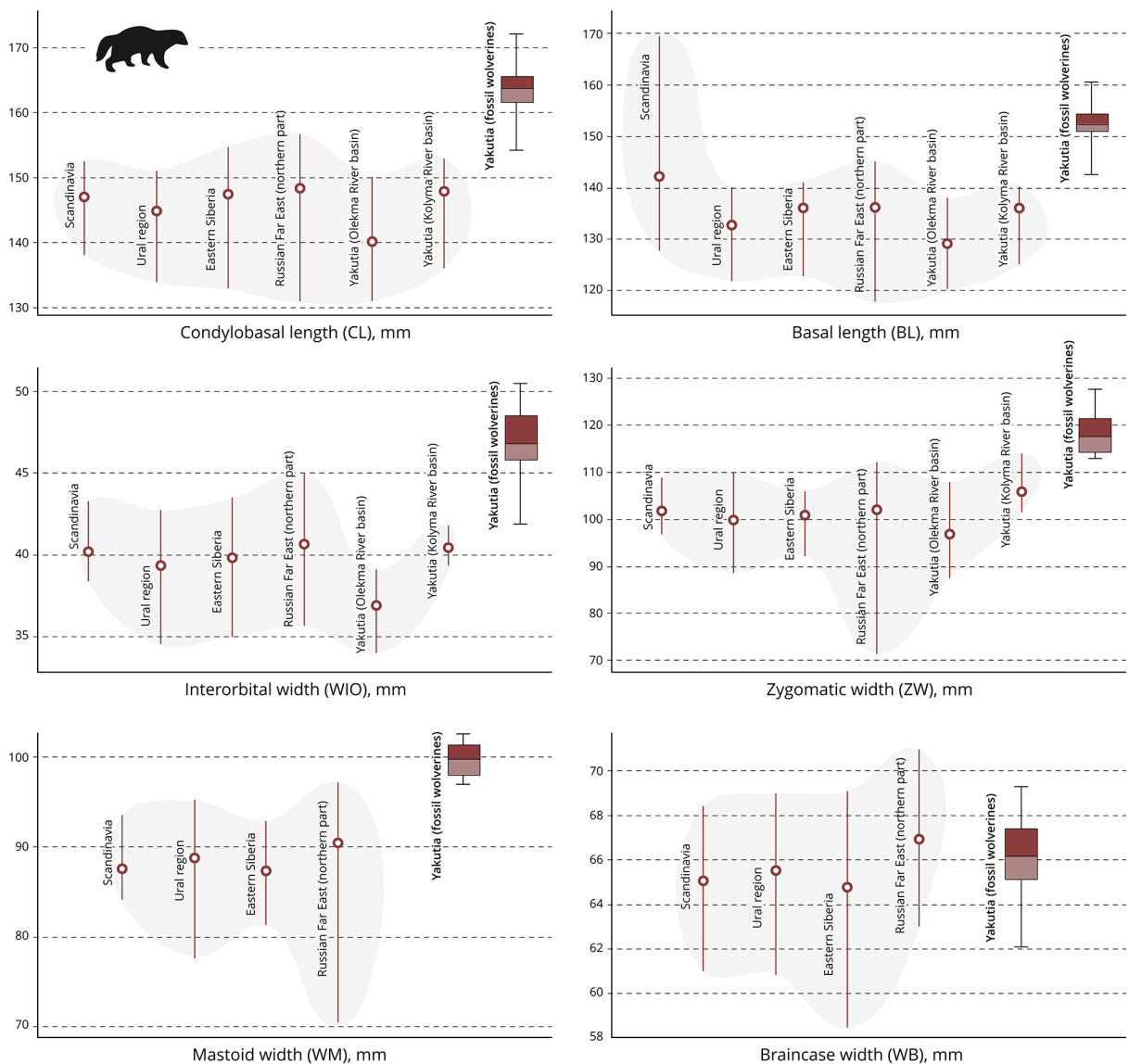


Fig. 10. Comparative cranial measurements in extant and Late Pleistocene wolverines. Regional samples of extant *Gulo gulo* from Scandinavia, the Ural region, Eastern Siberia, the Russian Far East, and Yakutia (Olekma and Kolyma River basins) are shown as point-and-whisker plots (solid circle = mean; whiskers = observed minimum and maximum). Late Pleistocene Yakutian wolverines (fossil sample) are shown as box-and-whisker plots (median, interquartile range, and minimum–maximum range).

on seven of the largest extant males from the ZMMU collection and seven fossil skulls, further indicates that the neurocranium of extant males is proportionally broader than in the Late Pleistocene sample: maximum neurocranial breadth averages 44.2% of basal skull length in the former, compared with 42.7% in the latter. This feature, identified here for the first time, may indicate a slightly more primitive cranial condition in the Late Pleistocene wolverines relative to extant forms. In terms of dental metrics, the upper cheek teeth P4 and M1 are also noticeably larger and more massive in the fossil males than in extant Eurasian *Gulo gulo* (tooth plots, Fig. 6).

Comparison with large extant male skulls in the ZMMU collection shows that the overall cranial morphology of the fossil and extant specimens is virtually identical, except for a few details noted in the descriptive section. These differences are most clearly expressed in the dentition rather than in the basic cranial architecture. The cranial distinctions are best interpreted as reflecting the development of more powerful musculature in the fossil form, rather than any fundamental evolutionary reorganisation, whereas the dental traits may record ongoing processes of dental specialisation and remodelling.

Among cranial features, two characters are noteworthy. First, a deep preorbital fossa is well developed in DSMF GG/Bd1, whereas it is only weakly expressed in extant analogues. Second, the presence of a distinct “pocket” within the masseteric fossa of the mandible appears to be stable in Late Pleistocene material: it is documented in c. 40 mandibles from Avdevo (Polyanskaya, 2025), as well as in the type mandible from Berelekh ZIN 34907 and in the Indigirka mandible associated with DSMF GG/Bd1 (Fig. 7E, arrow). This structure has not been observed in extant Eurasian wolverines.

Differences in dental morphology between fossil and extant wolverines include the absence of a diastema between the upper third incisor and the canine in the fossil sample, a less lingual position of the P1 alveolus and of the anterior margin of P3 relative to the main axis of the tooth row, and consistent retention of the anterior portion of the anterobuccal cingulum on the first upper molar M1 (Fig. 5, arrows). Collectively, these characters may indicate a higher degree of functional specialisation in Late Pleistocene forms.

The Berelekh subspecies *Gulo gulo berelekhii* and the Indigirka wolverines

The subspecies *Gulo gulo berelekhii* is based on material from the classic mammoth graveyard at Berelekh on the middle course of the Indigirka River, one of the key Late Pleistocene localities of north-eastern Yakutia. The first series of finds, recovered in 1966, comprised a well-preserved skull with an associated mandible and a separate mandible; in 1968, a wolverine mummy was discovered in the same area (Vereshchagin, 1977). Based on the cranial material, Novikov

(1993) erected the species *Gulo berelekhii* Novikov, designating ZIN 34907 as the holotype and emphasising its distinctive cranial proportions, notably a comparatively large mastoid breadth combined with a reduced braincase breadth (i.e. relative “lagging” of the neurocranium with respect to the basicranium).

Boeskorov and Baryshnikov (2013), using combined evidence from cranial dimensions, dental characters and limb proportions, argued that the Berelekh form is best treated as a subspecies, *Gulo gulo berelekhii*, characterised by very large body size (especially in adult males) and somewhat elongated limbs that differ in segmental proportions from those of recent wolverines. They also reported a radiocarbon age of $12\,420 \pm 55$ ^{14}C yr BP for the mummy. In terms of dental metrics, the Berelekh wolverine is conspicuously large: the length of the lower carnassial m1 in the Berelekh series is around 23–25 mm, compared with 19–22 mm in extant populations (Vereshchagin, 1977).

The two Berelekh crania described by Vereshchagin (1977) and re-analysed by Boeskorov and Baryshnikov (2013) have the greatest cranial lengths at 187.5 mm (mummified specimen ZIN 32214) and 174.7 mm (holotype ZIN 34907). These values bracket the Indigirka series: our largest skull (DSMF GG/EA1) measures 185.4 mm, whereas smaller Indigirka skulls (e.g., DSMF GG/Sm1, GIN 1197/NS-1) are close in size to the holotype ZIN 34907. Morphologically, the Indigirka skulls share with the Berelekh material the same combination of a very robust mastoid region, a powerful sagittal crest, greater zygomatic and mastoid breadths, and a relatively less inflated braincase compared with extant wolverines. The presence of a distinct internal “pocket” in the masseteric fossa, first recognised in Late Pleistocene mandibles from Avdevo (Polyanskaya, 2025), is clearly expressed in the mandible associated with the Berelekh holotype (ZIN 34907) and in the Indigirka mandible associated with DSMF GG/Bd1, whereas it appears to be absent in extant wolverines and in the European Late Pleistocene material. Given the close geographic proximity within the Indigirka basin, the very large cranial dimensions (overlapping those of the Berelekh skulls), and the shared cranial and mandibular specialisations, we consider it justified to assign the Indigirka male skulls described here to *Gulo gulo berelekhii*.

Conclusions

Genetic and phylogeographic data on extant wolverines (*Gulo gulo*) provide a key framework for interpreting the Late Pleistocene record from north-eastern Siberia. The circumarctic mitochondrial study by Zigouris *et al.* (2013) revealed a complex intraspecific structure associated with postglacial population reorganisation, comprising three well-defined clades (Beringian, American and Fennoscandian), each characterised by distinct haplotypes and geographic separation. The Beringian clade, which includes individuals from Alaska and Eastern Siberia, including the Arctic regions

of Yakutia, shows the highest genetic diversity and is interpreted as reflecting survival in a Beringian refugium during the Last Glacial Maximum (~26–19 ka). According to Zigouris *et al.* (2013), postglacial colonisation of most of Canada and the subarctic belt occurred predominantly from Eastern and Western Beringian source populations, whereas the Fennoscandian population remained largely isolated. This haplotype structure may indicate long-term geographic stability of some lineages, particularly in north-eastern Siberia, which is directly relevant to assessing the affinities of Late Pleistocene forms from Yakutia.

Our material shows that Yakutian Late Pleistocene wolverines represent a consistently large-bodied morphotype, particularly pronounced in males. Radiocarbon dates obtained from these specimens span several discrete intervals within MIS 3–2, encompassing both cold phases and relatively warm interstadial episodes up to the Bølling–Allerød. Throughout this period, male cranial and carnassial dimensions remain uniformly large, with no detectable trend toward size reduction in the terminal Pleistocene. These observations indicate that the enlargement of Yakutian wolverines was not a short-lived response to individual climatic oscillations, but rather a long-term ecophysiological adaptation to the mammoth-steppe environments of north-eastern Siberia. The most likely drivers of this large-bodied morphotype of *G. g. berelechii* were both thermoregulatory factors (persistently cold climatic conditions during MIS 3–2) and trophic factors (high herbivore biomass and diversity, providing a rich and predictable food base). In this context, our results support earlier suggestions that wolverines attained their maximum body size during the last glaciation and subsequently decreased to extant dimensions (Kurtén, 1968; Vereshchagin, 1977; Sotnikova, 1982; Novikov, 1993; Boeskorov & Baryshnikov, 2013), in broad agreement with Bergmann's rule, which predicts larger body size in mammals inhabiting colder climates.

Beyond size alone, the Late Pleistocene males from Yakutia share a distinctive cranial morphotype, defined by an elongate, massive skull with strongly developed temporal crests, pronounced occipital sculpturing and a high sagittal crest that, in most cases, rises above the level of the occipital condyles. Standard measurements of zygomatic and mastoid breadth exceed those known for extant populations, and the same holds for the dimensions and robustness of the carnassial teeth. At the same time, these fossils exhibit a relatively less inflated braincase compared with extant wolverines, in which the neurocranial region is more expanded. We interpret this conservative braincase morphology as a plesiomorphic feature distinguishing the fossil form from extant populations.

Taken together, the genetic and morphological evidence is consistent with the hypothesis that the large wolverines of the Late Pleistocene of Eastern Siberia, including Yakutia, represent a stable Beringian refugial population rather than west-to-east migrants. The large-bodied *G. g. berelechii* documented here and at

Berelekh can be regarded as the Late Pleistocene morphological expression of a Beringian lineage that likely persisted locally during Late Pleistocene climatic oscillations and may have contributed to postglacial recolonisation of the Holarctic range. Mitochondrial studies indicate that modern north-eastern wolverines possess distinctive phylogeographic signatures that may, in part, be inherited from their Pleistocene predecessors in this region, and our morphometric results underscore the uniqueness of the Yakutian wolverines in both size and cranial morphology, suggesting a partly independent evolutionary trajectory for this lineage within Beringia from the Late Pleistocene onward.

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