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Mammalian Biology
Zeitschrift für Säugetierkunde

ISSN 1616-5047

Mamm Biol
DOI 10.1007/s42991-020-00079-x



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ORIGINAL ARTICLE



Assessing molar wear in narrow-headed voles as a proxy for diet and habitat in a changing Arctic

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Received: 2 June 2020 / Accepted: 13 October 2020
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Abstract

This paper investigates the potential of mesoscale tooth wear (mesowear, chipping, facets, and other wear attributes) in rodents as a proxy for Arctic habitat. It presents a pilot study of narrow-headed voles, *Microtus gregalis*, at three sites along a latitudinal gradient of ecological subzones in the Yamal Peninsula of the Russian Arctic. These sites include Kharp in the forest–tundra ecotone, Erkuta in the low Arctic, and Sabetta at the border between the low and the high Arctic. A total of 117 specimens were included and eight variables were used to characterize mesoscale tooth wear. Results show significant differences between the sites, suggesting that these variables can distinguish populations from different subzones. Kharp has the flattest tooth wear, whereas Sabetta has the most M1 occlusal relief and dentin exposure. These results are consistent with and interpreted in the light of published experimental work on captive voles. In addition, the Kharp sample has the tallest M1 crowns, whereas Sabetta has the most vertically implanted M1s. The general directional trends toward separation of values by latitude of samples suggests that mesoscale wear in hypselodont rodents (those with open-rooted, ever-growing molar teeth) reflects variation in food abrasivity and, by extension, may be valuable for tracking habitat and ecological changes in the Arctic.

Keywords Rodents · Teeth · Climate change · Habitat assessment

Introduction

Global warming and increasingly extreme weather have led to fundamental and irreversible habitat changes and disruptions of ecosystems that threaten many mammalian species today. This is particularly so for the Arctic, which is warming at more than twice the average rate as the rest of the planet (Przybylak and Wyszyński 2020). Global warming and increasingly extreme weather beg for new proxies

to assess impacts of climate-driven habitat changes on endemic Arctic mammalian communities. Proxies designed to measure fine-scale ecological change in the past, document it today, and monitor it in the future will be especially valuable.

The first step in developing a proxy to track impacts of climate change on mammalian ecology in the Arctic is to demonstrate the efficacy to parse individuals living in different environmental settings. This paper investigates the potential of mesoscale dental wear (mesowear, chipping, faceting, and other millimeter-scale wear attributes) to separate rodents by habitat. More specifically, it presents a pilot study on narrow-headed voles, *Microtus gregalis*, at three sites along a latitudinal gradient of bioclimatic subzones on the Yamal Peninsula of the Russian Arctic to determine whether mesoscale dental wear patterning reflects aspects of the environment.

Handling editor: Eva Bärmann.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s42991-020-00079-x>) contains supplementary material, which is available to authorized users.

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Why mesoscale wear?

Many mesoscale tooth wear studies have focused on dental mesowear. This technique was developed originally two

decades ago as a rapid, simple tool for characterizing gross tooth wear in fossil herbivores to reconstruct diets and habitats of the past (Fortelius and Solounias 2000). Mesowear studies have been widely adopted by the paleontological community since with more than 200 publications to date on more than 700 species (Ackermans 2020; Green and Croft 2018). We believe that this approach holds equal potential for addressing ecological questions about elusive neontological species that are difficult to observe directly, such as rodents in the tundra, but for which dental remains are readily available.

The basic theory, as proposed originally by Fortelius and Solounias (2000), is grounded in observations that cheek teeth wear by attrition resulting from tooth-to-tooth contact and by abrasion resulting from tooth-to-food contact. Attrition and abrasion each evince distinctive and distinguishable wear signatures. So, for example, ruminant grazers consuming tough grasses with endogenous (i.e., silica phytoliths) and/or exogenous (i.e., quartz grit) abrasives have well-worn cheek teeth with low, blunt cusps, whereas browsers consuming less abrasive dicots have honed facets with higher, sharper cusps (Fortelius and Solounias 2000). Methods for characterizing mesowear have been refined and the variety of taxa studied using them have expanded over the past two decades (e.g., Danowitz et al. 2016; Mihlbachler and Solounias 2006; Solounias et al. 2014).

Much of the focus of mesowear studies has been on paleoenvironmental reconstruction. Such work is predicated on associations between diet and habitat and assumptions that individuals are limited to whatever foods are available at a given time and place. It has been demonstrated, for example, that extant grazers, browsers, and mixed feeders inhabit more open, closed, and mosaic or seasonal environments, respectively (Gagnon and Chew 2000).

Mesowear and other studies of tooth wear have several advantages over more traditional ecomorphological analyses, which associate tooth form with diet and habitat. First, these are “foodprints” (Ungar 2017), or traces of actual behavior, free from the assumptions that an individual in the past ate what its own ancestors evolved to eat and what closely related forms eat today (e.g., see Sponheimer et al. 1999). This also means that conspecifics with a given tooth shape, rather than just different species with different tooth shapes, can be compared because pattern differences develop during life. In addition, tooth wear reflects both foods eaten (an indirect proxy for habitat) and exogenous grit/dust load resulting from other aspects of habitat, such as vegetative cover (Wolfe and Nickling 1993) and annual rainfall (Eronen et al. 2010).

Another advantage of mesowear specifically is that this proxy has typically been considered a reflection of time-averaged diet and habitat exposure at scales beyond single seasons (Rivals et al. 2013), though recent *in vivo*

experiments suggest that changes in pattern can occur quickly or can last a lifetime depending on the species and situation (Ackermans et al. 2018, 2020; Kropacheva et al. 2017; Martin et al. 2020; Solounias et al. 2014).

Why rodents?

Most mesoscale tooth wear studies to date have focused on larger-bodied mammals, especially ungulates (Ackermans 2020; Green and Croft 2018). But rodents are the most speciose, widely distributed (except for us) of the terrestrial mammals and are ubiquitous in many fossil assemblages. Moreover, rodents are important keystone members and engineers of ecosystems (e.g., Legagneux et al. 2012). They control prey and predator species abundances, aerate and increase groundwater recharge through soil turbation, aid in decomposition and nutrient cycling, control plant productivity and species richness and composition, promote ecological succession, and provide habitats for other species, among other things (e.g., Ballová et al. 2019; Prugh and Brashares 2012; Tschumi et al. 2018; Zhang et al. 2003). Hence, no mammalian order is more important for regulating and understanding biospheric activity than Rodentia.

There is no place this is more evident than the Arctic. Rodent densities are especially sensitive to changing climate (e.g., Ehrich et al. 2017; Fufachev et al. 2019; Gilg et al. 2009; Ims et al. 2011; Morris and Dupuch 2012). This makes them excellent model mammals for monitoring changes in the tundra biome (Christensen et al. 2013), and researchers associated with the Circumpolar Biodiversity Monitoring Program have focused on rodents over the past two decades at 49 sites across the Arctic (38 of which are currently active), from Alaska to Canada, Greenland, Fennoscandia, and Russia (Ehrich et al. 2020). Further, because of this monitoring, Arctic rodent teeth are readily available for study.

It has already been demonstrated that patterns of rodent tooth wear at micron scales reflect diet and habitat. Studies of rodent molars, for example, have shown distinctive patterns of scratching and pitting dependent on broad food preferences (e.g., Nelson et al. 2005; Rodrigues et al. 2009; Townsend and Croft 2008), and microwear on these teeth may even be able to resolve subtler differences among species with versatile diets (Burgman et al. 2016; Robinet et al. 2020). Indeed, a recent microwear analysis of Arctic field vole molars showed marked seasonal differences in texture pattern consistent with changes in diet between autumn and spring (Calandra et al. 2016). Rodent incisor microwear is also well suited to separating groups by habitat type, and preliminary analysis has shown that incisor microwear texture patterns parse species in wetter, closed settings from those in more open habitats (Caporale and Ungar 2016).

If rodents are such important keystone species in ecosystems and their dental microwear reflects diet and habitat, why have their teeth been understudied at the mesoscale? This might be due in part to the perception that these mammals are not well suited to mesowear analysis, as originally envisioned, because their masticatory movements are propalinal (rear-to-front) rather than transverse (Kaiser and Fortelius 2003). But recent studies have suggested that, in fact, mesowear in rodents can provide valuable insights into diet and habitat (Kropacheva et al. 2017; Ulbricht et al. 2015).

Ulbricht et al. (2015) studied murines, which have propalinal chewing, but also brachydont or mesodont teeth that are rooted and have finite growth like many other mammals. These authors focused on the distal edges of maxillary and mandibular first molars (M1 and m1, respectively) of mice and rats from habitats ranging from forest to savanna. Their results showed a trend for flatter cusps with lower relief along the gradient from low to high abrasion environments. The study, although preliminary, suggested strongly that mesowear does reflect diet and habitat in rodents that engage in propalinal chewing. The question of whether pattern differences would hold for within-species comparisons (i.e., no genetically mediated differences in tooth form) was left open. The question of whether pattern differences would hold for hypselodont rodents, those with open tooth roots and ever-growing molars that continue to erupt throughout life to compensate for wear, was also not addressed. There are many such species, including the arvicolines (voles, lemmings, and muskrats), which often dominate Arctic rodent communities.

Kropacheva et al. (2017) were the first to consider dental mesowear and other mesoscale tooth wear attributes in the arvicoline voles, *Microtus*. These have, in addition to propalinal mastication and hypselodont molars, a complex zigzag occlusal outline formed by triangular prisms with sharp salient angles separated by equally sharp reentrant angles (see Fig. 1). This work followed observations that some voles form lateral wear facets on their molar teeth (Kropacheva et al. 2012), the incidence of which seems to vary between populations within species depending on the site from which they are wild trapped (Smirnov and Kropacheva 2015). Kropacheva et al. (2017) combined analyses of wild-trapped voles and in vivo laboratory experiments on individuals fed either tough and abrasive foods, or less abrasive but more pliant items. Both continuous and discrete metrics showed significant differences in mesowear and other mesoscale wear attributes between experimental groups, with wild-trapped individuals more closely resembling those fed tough, abrasive foods (see discussion). This demonstrates that mesoscale dental wear on the distinctive hypselodont, prismatic molars of voles holds potential as a diet and/or habitat proxy.

Why Yamal?

Yamal is well suited to studying impact of habitat on Arctic rodents. The peninsula extends over 700 km north to south, with no insurmountable geographical barriers, such as impassable mountains or unfordable rivers. Moreover, it presents a continuous biogeographic gradient between bioclimatic subzones C and E, from the border between low and high Arctic to forest–tundra ecotone (see Walker et al. 2005). Yamal is among the best studied areas for tundra ecology in the Russian Arctic, with long-term uninterrupted research since Soviet times (e.g., Dunaeva 1948) and expanding studies of terrestrial ecosystems today (Ehrich et al. 2017; Fufachev et al. 2019; Sokolov et al. 2012, 2016; Sokolova et al. 2014). Furthermore, unprecedented support from the Government of Yamal-Nenets Autonomous District has funded state-of-the art scientific infrastructure and research initiatives at Yamal. Rodent specialists at the Institute of Plant and Animal Ecology (IPAЕ) Arctic Research Station in Labytnangi prepare, preserve, and archive skulls of collected individuals after snap-trapping for use in morphometric and phenetic studies. Thus, Yamal boasts a research infrastructure, collections, and collaborative environment well suited to documenting high-latitude variation in mesoscale tooth wear patterning among endemic rodents.

Much of the recent ecological work in Yamal has focused on contextualizing the impacts of global warming and increasingly extreme weather on endemic and invasive floras and faunas. To this end, there are three research sites strategically placed along a latitudinal gradient on the peninsula from which rodents are sampled: (1) Kharp in the forest–tundra ecotone (66.7° N, 66.4° E), (2) Erkuta in the low Arctic (68.2° N, 69.1° E), and (3) Sabetta at the border between the low and the high Arctic (71.2° N, 71.5° E).

Overall vegetation properties at the sites vary with bioclimatic subzone, as has been described for the Arctic as a whole (Walker et al. 2005). Kharp is situated just south of the most southern subzone (E) and is the only site interspersed with trees (mostly Siberian larches, *Larix sibirica*). Willow thickets (*Salix* spp.) at Kharp trapping areas extend more than 2 m in height. Bioclimatic subzone E is characterized by 80–100% vascular plant cover, with a total phytomass reaching 100 t ha^{-1} . In contrast, Sabetta, on the border between subzones C and D, has the most open setting. Based on the Circumpolar Arctic Vegetation Map (Team 2003), Sabetta has approximately 50% cover of vascular plants with interrupted closed or patchy vegetation. Total phytomass at Sabetta is estimated to be 30 t ha^{-1} . Willow thickets in Sabetta trapping areas are up to “knee height” (approximately 0.40 m maximum). Vegetation height, variety, and density are intermediate at Erkuta, which is in the middle of subzone E. Erkuta has willow thickets averaging 1–2 m in height. We expect that environmental grit loads would

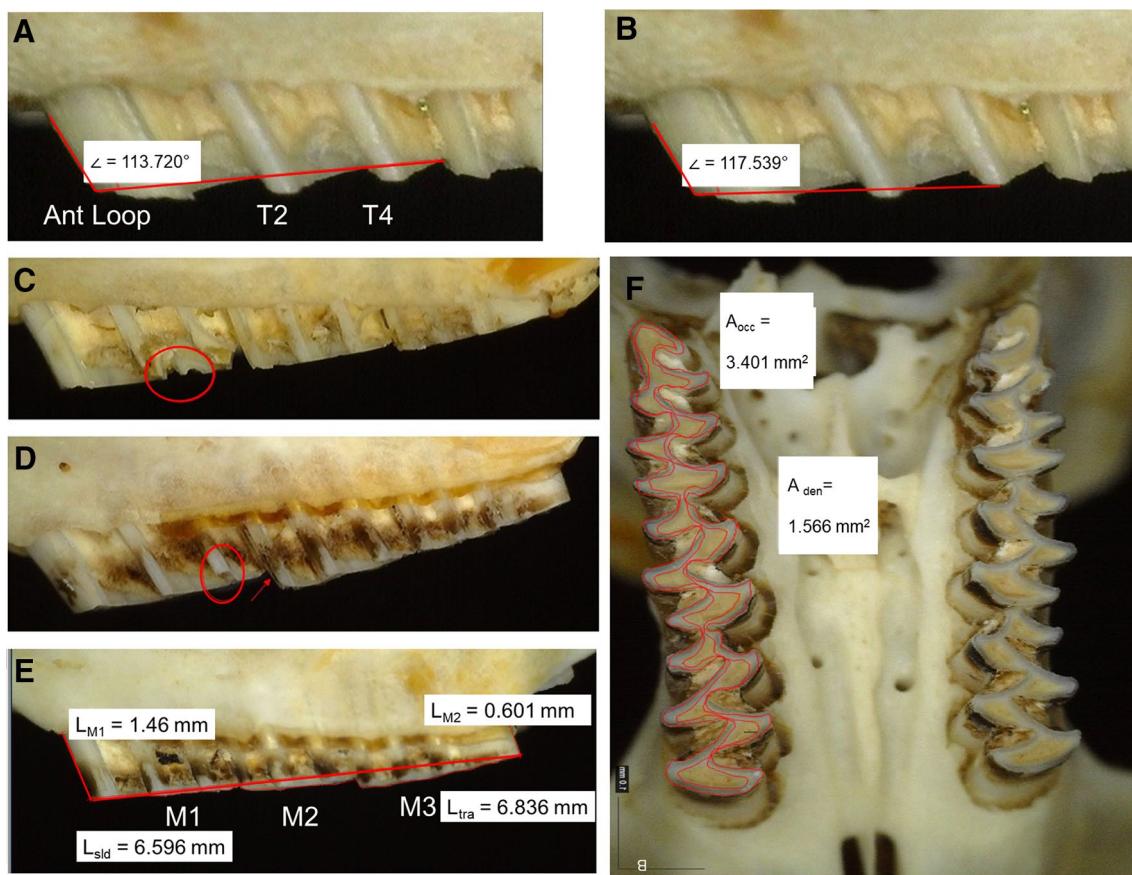


Fig. 1 Measurements taken: **a** angle formed in buccal view between the anterior surface of the M1 crown and a line formed between the anterior and posterior edges of the occlusal table (M1 occlusal angle = \angle_{Occ}), **b** angle formed between the anterior surface of M1 and the line formed between the anterior edge and the highest point on T4 (= \angle_{T4}), **c** chipping, **d** lateral wear facet, **e** straight-line distance and tracing measured between the anterior edge of the anterior

loop of M1 to the posterior edge of the posterior loop of M3 as well as M1 anterior and M3 posterior crown height (L_{sld} straight-line distance, L_{tra} length of occlusal surface tracing), **f** planimetric area of dentin and total area of the occlusal table in occlusal view (A_{occ} area of occlusal surface, A_{den} area of exposed dentin). See text for details concerning measurements and resultant data variables

be highest at Sabetta, followed by Erkuta and, finally, lowest at Kharp. This should, in principle, affect tooth wear of narrow-headed voles living at these sites.

It can also be noted that endogenous silica concentration (by weight) in tundra plants averages more than four times that in lower latitude boreal forests (Carey and Fulweiler 2012). This is due in large part to the presence of phytolith-rich grasses and sedges in the tundra. Likewise, soil amorphous silica concentration tends to be twofold to threefold higher in graminoid tundra than wetlands (Alfredsson et al. 2016).

The variation in habitat ground cover and plant type (boreal forest fringe to high-Arctic tundra) make Yamal well suited to assessing variation in tooth wear patterning among high-latitude rodents. It is expected that narrow-headed voles at higher latitudes have more abrasive diets in terms of both endogenous silicates from tundra graminoids and exogenous quartz grit/dust common to more open settings.

In this study, we test the hypothesis that the pattern of mesoscale molar wear of narrow-headed voles on Yamal tracks variation in habitat along the peninsula. This is a first and necessary step toward determining whether mesoscale tooth wear holds potential as a proxy for environmental change and impacts on rodent communities of the Arctic over time.

Materials and methods

Narrow-headed voles in Yamal are attributed to the subspecies *Microtus (Stenocranius) gregalis* major Ognev, 1918 (per Borodin 2009). These rodents typically live in colonies consisting of individual burrows connected by paths and underground tunnels (Pal'chekh et al. 2003). They are endemic to and widespread across the region, from northern ridge of taiga zone in the south to 72nd parallel in the north (Dunaeva 1948). Published data on the diets of

narrow-headed voles within the Yamal-Nenets Autonomous District are limited to two Soviet-era studies (Dunaeva 1948; Kopein 1958). Dunaeva (1948) collected data around Erkuta and 50–100 km to the south. Dunaeva's work was limited to a survey of gnaw marks on plants found within *M. gregalis* ranges. Kopein (1958), on the other hand, worked on the western side of Baydaratskaya Bay at the same latitudes, closer to the seashore. Kopein's work included identification of plants with gnaw marks, remains of stored food within narrow-headed vole burrows, and items consumed during ad libitum feeding experiments with captive individuals. A list of plant foods reported in these studies is presented in the Appendix I electronic supplementary file.

Both Dunaeva's (1948) and Kopein's (1958) reports were largely anecdotal, with no quantitative data presented. Further, it is difficult to be certain that the bite marks and food remains were all left by narrow-headed voles given the presence of other rodent species in the research areas. Nevertheless, Dunaeva (1948) and Kopein (1958) both suggest consumption of sedges, grasses, and herbs. It is possible that diets differed somewhat between localities given more reported grass consumption by Dunayeva, but more herb consumption by Kopein. Further, both claim that narrow-headed voles vary seasonally in their diets, including more green parts of sedges, grasses, and herbs as well as leaves of shrubs in the summer but more roots of *Salix* in the spring. These observations imply that narrow-headed voles on Yamal have flexible diets, driven, at least in part, by food availability at a given time and in a given place. Nevertheless, a comprehensive and systematic study of diets of these rodents at Sabetta, Erkuta, and Kharp today is needed to confirm the details.

Specimen collection

Specimens were trapped and processed by NAS, IAF, and AAS and dental wear data were generated from digital photomicrographs of original dentitions by PSU and JP. These specimens were first collected during snap-trap sessions at Kharp (2011–2019), Erkuta (1999–2019), and Sabetta (2014–2019). As was mentioned above, all three study sites are spatially separated, and situated in different bioclimatic subzones along a latitudinal gradient. Erkuta is ca. 250 km to the north of Kharp, and Sabetta is ca. 350 km north of Erkuta. At each site, three traps were baited with raisins and rolled oats at each corner of a 15 × 15 m permanent quadrat following small-quadrat field protocol (Myllymäki et al. 1971), i.e., 12 traps per quadrat for two nights, with 8 (Kharp), 12 (Sabetta) and 18 (Erkuta) replications of quadrats at each habitat to sample microhabitat variability. The trapping protocol used is described in detail in Sokolova et al. (2014) and in Fufachev et al. (2019). At Kharp,

sampling usually occurs in June and September, at Erkuta in June and August, and at Sabetta in July.

Specimen preparation and metadata

All trapped specimens were dissected in the field, and sex, age category and other metadata were documented. Heads were removed and kept in a 20–40% ethanol solution. Skulls were then processed back in the laboratory at the IPAE Arctic Research Station in Labynangi by boiling and drying. Because of sample size limitations and the preliminary nature of this study, only site and age are considered here, but microhabitat metadata and sex, along with the raw tooth wear data, are included for reader consideration in the Appendix II electronic supplementary file.

Only adult and subadult individuals were considered in this study. Age categories follow Bashenina (1962). Subadult (sad) I was defined by weight between 4.3 and 8.5 g, and by uniform gray coat color (age ~ 9–14 days). Subadult II was defined by weight between 8.0 and 37.0 g, with gray coat and light endings of the outer hair (age ~ 15–50 days). Adults (ad) typically weigh 15.0–60.0 g, and have red tone fur color.

Sample analyzed

A total of 117 specimens ($n=54$ from Sabetta, $n=51$ from Erkuta, and $n=12$ from Kharp) were included in this study. These were sampled from processed crania curated in Labynangi. Only complete molar rows with unbroken teeth unobscured in buccal and occlusal view by detritus or remnant organic material were included in this study. The focus was the maxillary molar row, following the original protocol of Fortelius and Solounias (2000). Sample sizes average those from other rodent mesoscale tooth wear analyses (Ulbricht et al. 2015; Kropacheva et al. 2017) and should be sufficient to suggest the potential of this approach to reflect diet/habitat variation in Yamal voles, noting that Fortelius and Solounias (2000) suggested a minimum sample of $n=10$ for such studies.

Data acquisition

Molar rows were examined using an AM4113ZT polarizing digital microscope (Dinolite Corp). JPEG images were generated of both buccal and occlusal views (see Fig. 1) with a resolution of 1280 × 1024 pixels. The magnification was fixed at 43.4× for all specimens to confine the field of view to the molar row, but maximize resolution of imaging for individual teeth. All measurements were taken directly from digital photomicrographs using DinoCapture 2.0 measurement software (Dinolite Corp).

Data collected represent a modified subset of those developed by Kropacheva et al. (2017), focused on the maxillary molar row, and especially the first maxillary molar (M1). *Microtus gregalis* has classic arvicoline prismatic molars and continuous eruption to compensate for rapid wear induced by propalinal grinding or milling of tough, abrasive vegetation (Markova et al. 2013). The M1 occlusal surface has an anterior loop with staggered triangles formed on the lingual (T1, T3) and buccal sides (T2, T4), from front to back, with re-entrant angles separated by salient angles formed as the apices of the triangles (Fig. 1, see van der Meulen, 1973 for terminology). Traits were selected to characterize occlusal surface chipping, relief, dentin exposure, and wear facet shape—all elements expected to vary with food fracture properties and abrasive load given propalinal masticatory movements. Six continuous and two discrete variables were considered (see Fig. 1):

1. Height of M1 crown at anterior edge (*M1 height*). This was measured along the anterior margin of the M1 crown and the posterior margin of the M3 crown.
2. Quotient of M1 to M3 crown height (*M1/M3 height*). This was measured along the anterior margin of the M1 crown and the posterior margin of the M3 crown.
3. Vertical displacement of occlusal outline in buccal view (*M1-M3 displacement*). This was measured as the quotient of the tracing length and straight-line distance measured between the anterior edge of the anterior loop of M1 and the posterior edge of the posterior loop of M3.
4. Dentin exposure on the occlusal table (*dentin area*). This was measured as the quotient of planimetric area of dentin and total area of the M1-M3 occlusal tables on one side in occlusal view. This attribute is similar to that considered for other rodents (Rensberger 1973; Schmidt-Kittler 2002) and larger mammals (e.g., Gailer and Kaiser 2014).
5. M1 occlusal relief at triangle T4 (*M1 relief*). This was measured as the difference in angle formed in buccal view between the anterior surface of the crown and a line formed between the anterior and posterior edges of the occlusal table on the one hand, and between the anterior surface and the line formed between the anterior edge and the highest point on T4 on the other.
6. Angle formed between M1 anterior edge and occlusal table plane (*M1 occlusal angle*). This is also a measure of vertical implantation of the crown relative to the anterior face of the tooth, with higher values indicating more oblique implantation.
7. Presence/absence of enamel chip(s) on the M1 occlusal surface in buccal view (*chips*).
8. Presence/absence of lateral wear facet(s) in buccal view (*facets*) following Kropacheva et al. (2012).

These attributes together are used to characterize mesoscale wear of narrow-headed vole molars. Two of the eight variables, M1 relief and M1 occlusal angle, can be considered mesowear as originally defined by Fortelius and Solounias (2000). The others are millimeter-scale measurements and discrete attributes expected to vary with diet and abrasive load. This aggregate of variables was selected to characterize mesoscale tooth wear in a species that lacks cuspidate dental morphology (see Fraser and Theodor 2010).

Statistical analyses

Continuous and discrete traits were analyzed separately. Statistical analyses were conducted using Systat 13 (SYSTAT Software, Inc.). First, the continuous variable data were rank transformed to mitigate violation of assumptions inherent to parametric statistical analyses (Conover and Iman 1981). A multivariate analysis of variance (MANOVA) model was applied to the continuous variables to determine whether there is significant variation in mesoscale wear when samples are parsed by location of capture. Individual ANOVAs were used for each variable, along with pairwise comparisons tests, to identify the sources of significant variation identified using the MANOVA. Both Tukey's HSD and Fisher's LSD tests were used to balance the risks of Type I and Type II error (Cook and Farewell 1996). Where Fisher's but not Tukey's test *p* values were < 0.05, results were considered suggestive but of marginal significance. A second set of tests was used to compare the Subadult I specimens only (the one age category with adequate samples at all three sites), to assure that results did not conflate age-related variation in tooth wear (see Rivals et al. 2007).

The two discrete variables (incidence of chipping and lateral wear facets on M1) were considered separately to compare samples from the three sites using Pearson's chi-square tests, with pairwise tests applied to determine the sources of significant variation as needed. Note that the degree of chipping and extent of facet development were not recorded, so these data were limited to presence/absence reporting. Also note that all age classes were combined because separate consideration would have meant more than one-fifth of fitted cells were sparse (frequency < 5).

Results

Descriptive statistics are presented in Table 1 and analytical statistics are presented in Tables 2 and 3 (continuous variables) and Table 4 (discrete variables). Results are illustrated in Figs. 2, 3, 4. In sum, there is a general trend for Kharp to have flatter wear than Erkuta and Sabetta. There is also a trend for M1 relief and dentin area to show flatter/more wear for the Erkuta sample than Sabetta (though not for

Table 1 Descriptive statistics for dental mesowear of *Microtus gregalis* from the Yamal Peninsula ($n=117$). All individuals in all age classes parsed by site (see supplemental information for raw data)

	M1 height	M1/M3 height	M1–M3 displacement	Dentin area	M1 relief	M1 occlusal angle
Erkuta ($n=51$)						
Median	1.102	2.518	1.076	0.474	2.737	114.025
Mean	1.074	2.586	1.088	0.473	2.939	114.237
SD	0.225	0.805	0.052	0.059	0.798	3.262
Kharp ($n=12$)						
Median	1.183	2.449	1.036	0.479	1.534	116.119
Mean	1.165	2.698	1.041	0.478	1.617	116.374
SD	0.173	1.121	0.019	0.043	0.596	2.000
Sabettia ($n=54$)						
Median	1.062	2.444	1.06	0.454	3.247	112.045
Mean	1.084	2.669	1.069	0.449	3.237	112.046
SD	0.204	1.305	0.038	0.045	0.998	3.645
						Facets
						Chips
Erkuta ($n=51$)						
Absent			41			20
Present			10			31
Kharp ($n=12$)						
Absent			11			7
Present			1			5
Sabettia ($n=54$)						
Absent			44			34
Present			10			20

M1–M3 displacement for the combined age sample). The M1 occlusal angle is more obtuse in Kharp than Erkuta and in Erkuta than Sabetta.

MANOVA results indicate significant variation by site for the combined-age sample (Table 2) and for the subadult I age class considered separately (Table 3). For the combined-age sample, single-classification ANOVAs indicate sites vary by M1 relief, dentin area, M1–M3 displacement, and M1 occlusal angle. Differences are illustrated in Figs. 2 and 3. There is a general trend for the Kharp sample to show flatter wear than either Erkuta or Sabetta specimens (note that the y-axis values for M1 relief and M1–M3 displacement are reversed so that higher positioned medians reflect flatter wear). M1 relief is significantly lower for Kharp than for Erkuta or Sabetta. M1–M3 displacement also shows significantly flatter occlusal surfaces for Kharp than for Erkuta or Sabetta, though Sabetta also has marginally lower M1–M3 displacement than Erkuta. On the other hand, Sabetta has marginally lower average dentin area than either Kharp or Erkuta. Finally, the M1 occlusal angle is significantly less obtuse in Sabetta than Erkuta and Erkuta than Kharp.

Results specific to subadult I individuals (again, tested because of concerns over conflating results across age and because this was the only age category with sufficient

samples for separate analysis) also show significant variation in the MANOVA model (Table 3, Fig. 3). In this case, there is a clear trend for increasing relief (=decreasing molar flatness) from Kharp to Erkuta to Sabetta, with Karp significantly different from Erkuta and Sabetta by Tukey's and Fisher's tests, and Erkuta marginally different from Sabetta by Fisher's test. Kharp also has significantly lower M1–M3 displacement (again, flatter wear) than either Erkuta or Sabetta. In addition, Kharp has significantly higher M1 heights than Erkuta and marginally higher M1 heights than Sabetta. Finally, Kharp has significantly higher M1 occlusal angles than Sabetta, and Erkuta has marginally higher M1 occlusal angles than Sabetta.

Results for the discrete attributes show no significant difference between locations in the presence/absence of lateral wear facets on the M1s (Table 4, Fig. 4). On the other hand, Pearson's chi-square test results do indicate variation between sites in chipping incidence. Specifically, Erkuta has a higher chipping incidence than does Sabetta. We caution against over-interpreting results for Kharp chipping incidence, because the sample sizes in individual cells are small for a log-linear model ($n=5$ chipped, $n=7$ unchipped).

Table 2 Analytical statistics for dental mesowear of *Microtus gregalis* from the Yamal Peninsula ($n=117$)

	Value	F	df	p
(A)				
Wilk's Lambda	0.539	6.567	12, 218	0.000
M1 relief	14,518.81	15.851	2, 114	0.000
Dentin area	4130.17	3.761	2, 114	0.026
M1/M3 height	35.699	0.031	2, 114	0.970
M1–M3 displacement	8630.62	8.467	2, 114	0.000
M1 height	1271.42	1.107	2, 114	0.334
Occlusal angle	13,106.416	13.932	2, 114	0.000
(B)				
M1 relief	Kharp	44.127**		
	Sabetta	– 10.252	– 54.38**	
Dentin area	Kharp	– 8.059		
	Sabetta	14.663*	22.722*	
M1–M3 displacement	Kharp	– 41.172**		
	Sabetta	– 13.07*	28.102**	
Occlusal angle	Kharp	– 24.922**		
	Sabetta	21.597**	46.519**	

(A) MANOVA (Wilk's Lambda) followed by individual ANOVA test results for each variable, (B) pairwise comparisons for variables that show significance at $p < 0.05$

** $p < 0.05$ for both Tukey's HSD and Fisher's LSD tests

* $p < 0.05$ for Fisher's LSD test only

Table 3 Analytical statistics for dental mesowear of subadult I age individuals of *Microtus gregalis* from the Yamal Peninsula ($n=48$)

	Value	F	df	p
(A)				
Wilk's Lambda	0.392	3.986	12, 80	0.000
M1 relief	1694.43	13.094	2, 45	0.000
Dentin area	101.802	0.509	2, 45	0.605
M1/M3 height	112.302	0.562	2, 45	0.574
M1–M3 displacement	811.219	4.81	2, 45	0.013
M1 height	716.18	4.143	2, 45	0.022
Occlusal angle	1020.80	6.406	2, 45	0.004
(B)				
M1 relief	Kharp	17.458**		
	Sabetta	– 7.729*	– 25.188**	
M1–M3 displacement	Kharp	– 15.625**		
	Sabetta	– 0.062	22.722**	
M1 height	Kharp	– 15.313**		
	Sabetta	– 2.281	13.031*	
Occlusal angle	Kharp	– 8.958		
	Sabetta	9.854*	18.813**	

Analytical statistics for the sample. (A) MANOVA (Wilk's Lambda) results followed by individual ANOVA test results for each variable, (B) pairwise comparisons for variables that show significance at $p < 0.05$

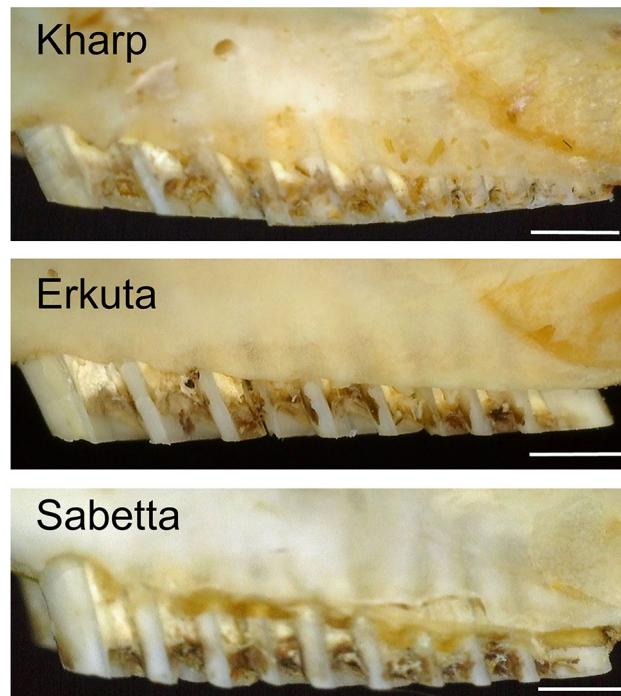
** $p < 0.05$ for both Tukey's HSD and Fisher's LSD tests

* $p < 0.05$ for Fisher's LSD test only

Table 4 Pearson's chi-square tests for incidence of lateral wear facets and chipping of *Microtus gregalis* from the Yamal Peninsula ($n=117$): (A) comparison of lateral wear facet incidence on M1s across sites, (B) comparison of chip incidence on M1s, both across sites (chips all) and pairwise between sites (to determine sources of significant variation)

	χ^2	df	p
(A)			
Facets all	0.861	2	0.650
(B)			
Chips all	6.133	2	0.047
Kharp × Sabetta	0.089	1	0.765
Kharp × Erkuta	1.45	1	0.229
Sabetta × Erkuta	5.921	1	0.015

All age classes are combined

**Fig. 2** Buccal views of M1–M3 of specimens from Kharp (#1884, top), Erkuta (#2960, middle) and Sabetta (#2580, bottom). Note the difference in triangle/prism relief. Scale bars = 1.0 mm

Discussion

This study shows differences in mesoscale tooth wear patterning between *Microtus gregalis* specimens collected at different latitudes in the Yamal Peninsula. For most variables, the samples from Kharp (forest–tundra ecotone at 66.7° N, 66.4° E) and Sabetta (border between low and high Arctic at 71.2° N, 71.5° E) are at opposite ends of the spectrum, and those from Erkuta (low Arctic, 68.2° N,

69.1° E) are in between. While sample sizes are limited and there are exceptions to the trends, these results suggest that mesoscale arvicoline tooth wear does hold potential as an environmental proxy for Arctic ecosystems.

While most of the specimens considered here were trapped in willow thicket microhabitats (see supplemental online information for specifics), the larger environments at the three sites vary along a gradient expected to differ in both food availability and environmental grit/dust load. Given more open habitat to the north, and more phytoliths associated with tundra than boreal forest plants, concomitant differences in food abrasivity (both extrinsic and intrinsic abrasives) are expected. The overall pattern of variation in mesoscale tooth wear between sites can be interpreted in this light, especially when compared with results from previous studies of rodent tooth wear.

Comparisons of results with those from previous studies of rodent tooth wear

Ulbricht et al. (2015) compared mesowear of museum samples of rodents and hares. Their rodent sample included yellow-necked mice (*Apodemus flavicollis*), African pygmy mice (*Mus minutoides*), and African grass rats (*Arcicanthis niloticus*). These murines have rounded, cuspidate molars with closed roots, so their mesowear is perhaps more comparable to that of better-studied larger mammalian herbivores than that of voles with ever-growing, prismatic cheek teeth. Furthermore, Ulbricht and colleagues compared different species rather than a single species in different habitats; so they did not control for the effect of phylogeny on occlusal morphology or susceptibility to cusp rounding and relief changes. Nevertheless, the species are known to live in different habitats, with *Ap. flavicollis* inhabiting forest, *Ar. niloticus* in grasslands with more abrasive vegetation, and *M. minutoides* in intermediate deciduous forest–woodland savannas. Thus, they serve as an excellent initial baseline of mesowear in propalinal rodents. Results for these murines conform to the expected gradient from low to high abrasion diets, with *A. niloticus* and *M. minutoides* molars having significantly flatter cusps than *A. flavicollis*. Furthermore, *M. minutoides* tends to possess sharper cusps and higher occlusal relief than *A. niloticus*. In sum, more open habitats and more abrasive foods equal flatter cusps and less occlusal relief for these rodents, as has been found for mesowear of larger herbivores (see Green and Croft 2018; Ackermans 2020 for review).

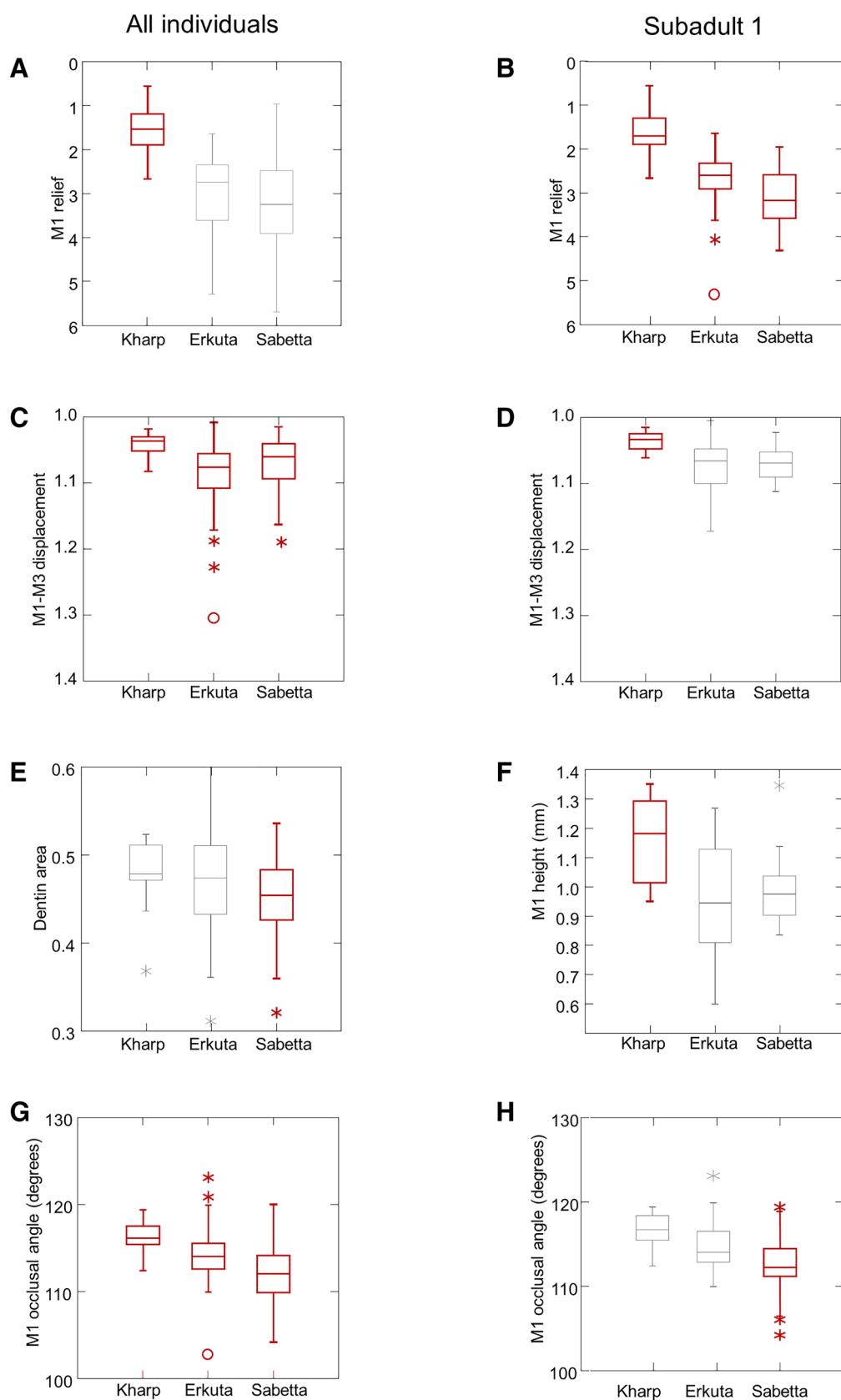
Kropacheva et al. (2017) were the first to consider mesowear and other mesoscale wear attributes in *Microtus* voles. Their study combined *in vivo* experiments on *M. gregalis* and *M. oeconomus* in a laboratory setting with data for field trapped specimens of *M. gregalis* and *M. arvalis*. The captive voles were fed either “soft foods” (cleaned dandelion

leaves, cleaned carrots, and cored apples) or “hard diets” (monocot leaves and hay, carrots with adherent soil). While these experiments conflate food fracture properties with abrasives, and endogenous abrasives (phytoliths) with exogenous ones (grit, dust), and there are other food properties, such as water content, likely to affect tooth wear (e.g., Winkler et al. 2019), Kropacheva and colleagues do present the first published study of mesowear and other mesoscale dental wear attributes in hypselodont rodents that we are aware of. This is also the only such study to examine *Microtus gregalis*, the species considered here.

Results from Kropacheva et al. (2017) were at first glance unexpected and largely inconsistent with those for mammals with fixed-growth teeth, including murines. Voles fed “hard” (more abrasive) foods had higher M1 crowns and more occlusal relief than those on “soft” diets. As far as mesoscale tooth wear is concerned then, hypselodont rodents seem play by a different set of rules. Other results indicate that soft diets lead to more enamel chipping, lateral wear facets, and vertically implanted (lower occlusal angle) M1s. Kropacheva and colleagues speculated that food dimensions and material properties affecting the biomechanics of mastication—the distribution of masticatory loads and inclination of jaw movements (e.g., vertical compared with horizontal chewing strokes)—might account for the patterns seen.

Occlusal relief and vertical displacement differences among Yamal vole molars are also unexpected in light of molar mesowear in non-hypselodont rodents and other herbivorous mammals. The sample from Kharp (with tall shrubs and trees) has the flattest occlusal wear with the lowest M1 relief and vertical displacement of the upper molar row, whereas the sample from Sabetta (mostly mossy tundra and low shrubs) has the highest occlusal relief, at least for the subadult specimens—though vertical displacement for the overall sample from Erkuta was marginally higher than that for Sabetta. Assuming environmental grit load decreases with plant cover/phytomass and increases with latitude, and that phytolith load is higher in tundra than boreal forest fringe foods, the pattern for occlusal relief is opposite of expectation. On the other hand, it is in accord with the laboratory feeding experiments on voles by Kropacheva et al. (2017). Those fed more abrasive foods had more occlusal relief.

While Kropacheva et al. (2017) suggested that food dimensions, material properties, and resulting occlusal dynamics might explain occlusal relief patterns in different vole samples, we propose an alternative explanation, based on the interplay between tooth growth and wear associated with hypselodont. In hypselodont species, epithelial cells proliferate and differentiate into ameloblasts continuously, allowing for enamel extension and tooth growth throughout life to compensate for wear (Müller et al. 2014; Rensberger 1986; Zuri et al. 1999). In fact, the prismatic, hypselodont



◀Fig. 3 Box-and-whisker plots for continuous variables showing significant variation between sites for all individuals (left, **a**, **c**, **e**, and **g**) and subadult I age category (right, **b**, **d**, **f**, and **h**). The hinges mark the first and third quartiles, the horizontal lines between them are medians, each whisker represents a value 1.5 times the interquartile range, asterisks are outliers, and circles are far outliers. Note that M1 relief (**a**, **b**) and M1–M3 displacement (**c**, **d**) are plotted with lower values at the top of the y-axis, so more flatly worn specimens appear higher on the y-axis. Groups that are not significantly different from one another within each graph appear in gray, whereas those significantly different from others appear with thicker lines (red in the online version)

molars of arvicoline (including voles) are thought to have evolved specifically for grinding tough, abrasive vegetation (Markova et al. 2013).

An important feature of hypselodonty is the fact that dental extension (growth) rate varies with rate of wear to maintain occlusal relationships between opposing teeth. Marked variation of rodent incisor extension rate with diet is well established (Hua et al. 2015), and the presence of a regulatory mechanism matching growth with tissue loss has been confirmed by clipping anterior teeth of glirids (Schour and Medak 1951). Further, Müller et al. (2014) demonstrated with *in vivo* study that cheek teeth of hypselodont rabbits fed more abrasive diets have more rapid tooth wear and compensatory growth (see also Martin et al. 2019, 2020). Growth rate is flexible and responds to wear. Perhaps then, the greater relief seen in higher latitude Yamal voles reflects a more abrasive diet and higher rate of enamel extension. If so, less abrasive diets may lead to slower tooth eruption and less occlusal relief given the balance between surface wear on a given tooth and extension rate. Whether this hypothesis holds and how broadly it can be applied needs further study, though, given that Ulbricht et al. (2015) failed to show similar differences when comparing museum samples of two hypselodont hare species, one from a more open habitat and the other from a more closed setting.

In other attributes, the Yamal vole results do not correspond to those predicted given Kropacheva et al.'s (2017) study. For example, Kropacheva and colleagues found a higher M1 height in their "hard" (=abrasive) diet sample, whereas in our study, M1 height is highest in the Kharp sample (though Erkuta and Sabetta samples do not differ in this attribute). It makes sense that M1s are taller in a less abrasive environment, though not necessarily so if wear is matched by compensatory molar extension. Note also that only the subadult I (age 9–14 days) sample show significant differences between Kharp and the other sites. Further, as Müller et al. (2014) noted, crown growth rate can vary week by week, and Kropacheva and colleagues experiments lasted 1–3 months.

The other attribute for which our results differ from those of Kropacheva et al. (2017) is the occlusal angle. Kropacheva and colleagues reported a higher angle for

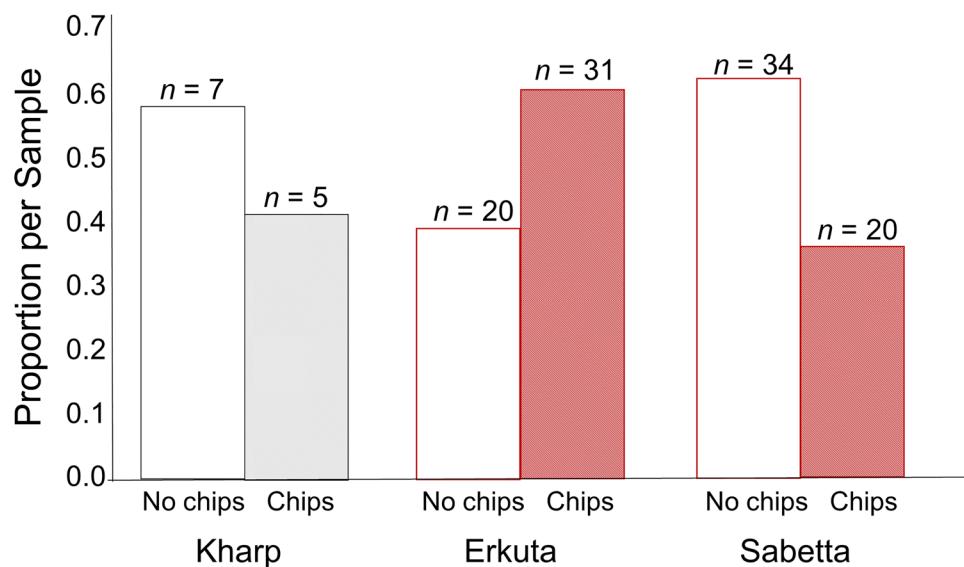
their "hard" (=abrasive) diet sample, whereas in our study, the occlusal angle is highest in Kharp followed by Erkuta and lowest in Sabetta. Because higher occlusal angle corresponds with more obliquely implanted molars, the Yamal voles at higher latitudes presumably have more vertically implanted molars. Kropacheva and colleagues speculated that their results relate to more posterior loading and a stronger wear gradient with their "harder" foods. While variation in the distribution of masticatory loads related to food fracture properties may well play a role in alveolar bone growth and orientation of molar implantation, more work is needed on vole diets and masticatory biomechanics to evaluate this hypothesis. It is also plausible that tooth extension rate, related to food abrasivity, may play in occlusal surface inclination though, again, more work is needed to assess this possibility.

Finally, as far as the discrete variables go, none of the specimens from Yamal show the extreme lateral wear facet development of the specimen illustrated in Fig. 3 of Kropacheva et al. (2017). Facet development for the Yamal voles is at most, slight, and there are no significant differences noted among the samples. On the other hand, the Erkuta sample does have significantly higher incidences of M1 chipping than Sabetta, which is consistent with Kropacheva and colleagues' finding that voles fed "soft" (less abrasive) foods had more chipping than those fed "hard/abrasive" diets. While more Kharp specimens have unchipped teeth than chipped ones, the lack of a significant difference from Erkuta or Sabetta may relate more to small sample size than a biologically meaningful signal. We hope that future collection will help clarify variation in chipping between sites.

The higher apparent chipping incidence for soft food-than hard/abrasive food-fed voles (and those at Erkuta compared with Sabetta) is surprising. While Towle et al. (2017) suggested that dental chipping rate is associated with dietary abrasiveness in primates, this does not seem to be the case for narrow-headed voles. Constantino et al. (2012) argued, alternatively, that dental chipping rate in primates increases with the consumption of large, hard objects, such as seeds and nuts. The relationships between visible dental chipping on vole molars and the abrasive, fracture, and dimensional properties of food are likely complex, especially given effect of varying rate of surface turnover on chip erasure. More detailed study of antemortem chipping, including chip size, number, location, and turnover, would likely yield important insights into their etiology.

Finally, results presented here can be cast in light of ongoing discussions concerning the etiology of tooth wear. While there is consensus that exogenous quartz grit wears teeth, some argue that endogenous silica phytoliths within plant foods contribute substantially to enamel loss, whereas others claim they do not (e.g., Lucas et al. 2014;

Fig. 4 Percent of individuals with at least one chip on the M1 by site for all individuals. Note that groups significantly different from one another appear with thicker lines (red in the online version). Each sample location has two bars. The first bar (white) and second bar (shaded) indicate the proportion of the sample for a given location without any chips and with at least one chip, respectively



Rabenold and Pearson 2014; Sanson et al. 2007). Indeed, whether tooth wear in grassland mammals relates more to exogenous grit in open, erosive settings or to phytoliths within the grasses themselves has been debated for decades (e.g., Janis 1988; MacFadden 1997). A survey of herbivorous ungulates from different environments and with varying proportions of phytolith-rich grass in their diets suggests that endogenous abrasives may be important to mesowear pattern (Kaiser et al. 2013), but there are certainly cases where a high dust load impacts tooth wear signal (Schulz et al. 2013).

Unfortunately, given that tundra is both open and dominated by phytolith-rich plants, it is equally difficult to parse effects of exogenous from endogenous abrasives for the current study. This is especially so given that phytolith concentration varies by individual plant species and part (Piperno 2006). We expect that future analyses of vole diets and environmental grit in Yamal will help us better understand the causes of tooth wear differences between the sites. While narrow-headed voles across the Yamalo-Nenets Autonomous Okrug seem to prefer (presumably phytolith-rich) grasses, along with sedges and herbs supplemented by shrubs and other parts to varying degrees (Dunaeva 1948; Kopein 1958), the diets of individuals studied should be considered in future analyses, given individual food preferences and local plant species availability. Whether grit or phytoliths explain these differences though, variation between the forest–tundra ecotone at Kharp and the boundary between low and high Arctic at Sabetta suggests that mesoscale tooth wear of narrow-headed voles holds potential as proxy for high-latitude habitat.

Conclusions

The results of this pilot study demonstrate that mesowear patterns of *Microtus gregalis* samples from the Yamal peninsula vary between sites in different environments at different latitudes. While our results are preliminary, they do show some general trends separating samples from the forest–tundra ecotone site of Kharp and the boundary between low and high Arctic at Sabetta. In many cases, values for the low tundra sample at Erkuta are intermediate. This work suggests the potential of dental wear of arvicoline as a proxy for habitat and ecological context—a first step toward the goal of developing a new method for assessing the impact of climate change on Arctic mammalian communities.

Our study also suggests that, compared with most other mammals analyzed for mesoscale tooth wear, narrow-headed voles dance to the beat of a different drummer. The general rule relating low, blunt cusps to attrition (abrasive diets) evidently does not hold for the ever-growing, prismatic molars of *Microtus gregalis*. More work is needed to understand the etiology and progress of tooth wear patterning in these rodents, including studies of diet and food fracture properties, documentation of both environmental grit and endogenous silicates, biomechanics of chewing, and regulatory mechanisms matching tooth growth and attrition. We expect that such research would lead to insights that improve and hone interpretations of mesoscale tooth wear in hypselodont arvicoline, with the ultimate goal being a new tool for documenting habitat variation across both space and time in the Arctic.

Acknowledgements We are grateful to the reviewers for their helpful comments and suggestions on an earlier draft of this paper. We thank Violetta Filippova and Svetlana Sokovnina for discussions and Olivier Gilg for making the connection that established this collaboration.

Author contributions PSU, AAS, and NAS conceived the project, analyzed the data and wrote the paper. NAS, IF, and AAS collected the specimens analyzed in this paper. PSU and JP generated the data used in this paper.

Funding NAS, IF and AAS were supported through grant of Russian Foundation for Basic Research No: 18-05-60261, by the Russian Center of Development of the Arctic, “Yamal-LNG” company and Government of the Yamal Nenets Autonomous District. PSU developed the collaboration through support from US National Science Foundation Award No: 1927793.

Data availability All raw data presented in this study are presented in Appendix II. The original specimens are curated and kept at the Arctic Research Station in Labytnangi, Russia.

Compliance with ethical standards

Conflict of interest The authors have no conflicts of interest or competing interests.

Ethics approval No ethics approvals were required to conduct this research.

References

- Ackermans NL (2020) The history of mesowear: a review. PeerJ 8:e8519
- Ackermans NL, Martin LF, Codron D, Hummel J, Kircher PR, Richter H, Kaiser TM, Clauss M, Hatt JM (2020) Mesowear represents a lifetime signal in sheep (*Ovis aries*) within a long-term feeding experiment. Palaeogeogr Palaeoclimatol 553:109793
- Ackermans NL, Winkler DE, Schulz-Kornas E, Kaiser TM, Muller DWH, Kircher PR, Hummel J, Clauss M, Hatt JM (2018) Controlled feeding experiments with diets of different abrasiveness reveal slow development of mesowear signal in goats (*Capra aegagrus hircus*). J Exp Biol. <https://doi.org/10.1242/jeb.186411>
- Alfredsson H, Clymans W, Hugelius G, Kuhry P, Conley DJ (2016) Estimated storage of amorphous silica in soils of the circum-Arctic tundra region. Glob Biogeochem Cycle 30:479–500
- Ballová Z, Pekárik L, Piš V, Šibík J (2019) How much do ecosystem engineers contribute to landscape evolution? A case study on Tatra marmots. CATENA 180:104121
- Bashenina N (1962) Ecology of common vole with some features of its geographical variability (In Russian). Moscow University Press, Moscow
- Borodin AV (2009) Guide on teeth of voles of ural and western Siberia (late Pleistocene—Today) (In Russian). Ural Branch of the Russian Academy of Sciences, Ekaterinburg
- Burgman JHE, Leichliter J, Avenant NL, Ungar PS (2016) Dental microwear of sympatric rodent species sampled across habitats in southern Africa: Implications for environmental influence. Int Zool 11:111–127
- Calandra I, Labonne G, Schulz-Kornas E, Kaiser TM, Montuire S (2016) Tooth wear as a means to quantify intra-specific variations in diet and chewing movements. Sci Rep 6:34037
- Caporale SS, Ungar PS (2016) Rodent incisor microwear as a proxy for ecological reconstruction. Palaeogeogr Palaeoclimatol 446:225–233
- Carey JC, Fulweiler RW (2012) The terrestrial silica pump. PLoS ONE 7:e52932
- Christensen TR, Payne J, Doyle G, Ibarguchi G, Taylor NM, Schmidt M, Gill M, Svoboda M (2013) The arctic terrestrially biodiverse monitoring plan. CAFF International Secretariat, Akureyri
- Conover WJ, Iman RL (1981) Rank transformations as a bridge between parametric and nonparametric statistics. Am Stat 35:124–129
- Constantino PJ, Markham K, Lucas PW (2012) Tooth chipping as a tool to reconstruct diets of great apes (*Pongo*, *Gorilla*, *Pan*). Int J Primatol 33:661–672
- Cook RJ, Farewell VT (1996) Multiplicity considerations in the design and analysis of clinical trials. J R Stat Soc A 159:93–110
- Danowitz M, Hou SK, Mihlbachler M, Hastings V, Solounias N (2016) A combined-mesowear analysis of late Miocene giraffids from North Chinese and Greek localities of the Pikermian Biome. Palaeogeogr Palaeoclimatol 449:194–204
- Dunaeva TN (1948) Comparative ecology of the tundra voles of Yamal Peninsula. (In Russian). Proc Inst Geogr USSR Acad Sci 41:78–143
- Ehrich D, Cerezo M, Rodnikova AY, Sokolova NA, Fuglei E, Shtro VG, Sokolov AA (2017) Vole abundance and reindeer carcasses determine breeding activity of Arctic foxes in low Arctic Yamal, Russia. BMC Ecol 17:32
- Ehrich D, Schmidt NM, Gauthier G, Alisauskas R, Angerbjörn A, Clark K, Ecke F, Eide NE, Framstad E, Frandsen J, Franke A, Gilg O, Goiroux M-A, Henttonen H, Bierger H, Ims RA, Kataev GD, Kharitonov SP, Krebs CJ, Killengreen ST, Lanctot RB, Lecomte N, Menyushina IR, Morris DW, Morrison G, Oksanen L, Oksanen T, Olofsson J, Pokrovsky IG, Popov IY, Reid D, Roth JD, Samelius G, Sittler B, Sleptsov SM, Smith P, Sokolov AA, Sokolova NA, Soloviev MY, Solovyeva D (2020) Documenting lemming population change in the Arctic: can we detect trends? Ambio 49:786–800
- Eronen JT, Puolamaki K, Liu L, Lintulaakso K, Damuth J, Janis C, Fortelius M (2010) Precipitation and large herbivorous mammals I: estimates from present-day communities. Evol Ecol Res 12:217–233
- Fortelius M, Solounias N (2000) Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. Am Mus 3301:1–36
- Fraser D, Theodor JM (2010) The use of gross dental wear in dietary studies of extinct lagomorphs. J Paleontol 84:720–729
- Fufachev IA, Ehrich D, Sokolova NA, Sokolov VA, Sokolov AA (2019) Flexibility in a changing arctic food web: can rough-legged buzzards cope with changing small rodent communities? Glob Change Biol 25:3669–3679
- Gagnon M, Chew AE (2000) Dietary preferences in extant African Bovidae. J Mammal 8:490–511
- Gailer JP, Kaiser TM (2014) Common solutions to resolve different dietary challenges in the ruminant dentition: the functionality of bovid postcanine teeth as a masticatory unit. J Morphol 275:328–341
- Gilg O, Sittler B, Hanski I (2009) Climate change and cyclic predator-prey population dynamics in the high Arctic. Glob Change Biol 15:2634–2652
- Green JL, Croft DA (2018) Using dental mesowear and microwear for dietary inference: a review of current techniques and applications: reconstructing Cenozoic terrestrial environments and ecological communities. In: Croft DA, Su D, Simpson SW (eds) Methods in paleoecology: reconstructing cenozoic terrestrial environments and ecological communities. Springer International Publishing, Cham, pp 53–73

- Hua LC, Ungar PS, Zhou ZR, Ning ZW, Zheng J, Qian LM, Rose JC, Yang D (2015) Dental development and microstructure of bamboo rat incisors. *Biosurf Biotribol* 1:263–269
- Ims RA, Yoccoz NG, Killengreen ST (2011) Determinants of lemming outbreaks. *Proc Natl Acad Sci U S A* 108:1970–1974
- Janis CM (1988) An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preference. In: Russell DE, Santoro J-P, Sigogneau-Russell D (eds) *Teeth revisited: proceedings of the VIIth international symposium on dental morphology*, Paris, 1986. Muséum national d'Histoire naturelle, Paris, pp 367–387
- Kaiser TM, Fortelius M (2003) Differential mesowear in occluding upper and lower molars: opening mesowear analysis for lower molars and premolars in hypsodont horses. *J Morphol* 258:67–83
- Kaiser TM, Muller DWH, Fortelius M, Schulz E, Codron D, Clauss M (2013) Hypsodonty and tooth facet development in relation to diet and habitat in herbivorous ungulates: implications for understanding tooth wear. *Mammal Rev* 43:34–46
- Kopein KI (1958) Materials on the biology of the siberian lemming and the narrow-headed vole (in Russian). *Bul MOIP Ural Dept* 1:109–133
- Kropacheva JE, Smirnov NG, Markova EA (2012) Individual age and odontologic characteristics of root vole. *Dokl Biol Sci* 446:302–305
- Kropacheva YE, Sibiryakov PA, Smirnov NG, Zykov SV (2017) Variants of tooth mesowear in *Microtus* voles as indicators of food hardness and abrasiveness. *Russ J Ecol* 48:73–80
- Legagneux P, Gauthier G, Berteaux D, Bety J, Cadieux MC, Bilodeau F, Bolduc E, McKinnon L, Tarroux A, Therrien JF, Morissette L, Krebs CJ (2012) Disentangling trophic relationships in a High Arctic tundra ecosystem through food web modeling. *Ecology* 93:1707–1716
- Lucas PW, van Casteren A, Al-Fadhalah K, Almusallam AS, Henry AG, Michael S, Watzke J, Reed DA, Diekwißch TGH, Strait DS, Atkins AG (2014) The role of dust, grit and phytoliths in tooth wear. *Ann Zool Fenn* 51:143–152
- MacFadden BJ (1997) Origin and evolution of the grazing guild in New World terrestrial mammals. *Trends Ecol Evol* 12:182–187
- Markova EA, Smirnov NG, Kourova TP, Kropacheva YE (2013) Ontogenetic variation in occlusal shape of evergrowing molars in voles: an intravital study in *Microtus gregalis* (Arvicolinae, Rodentia). *Mamm Biol* 78:251–257
- Martin LF, Krause L, Ulbricht A, Winkler DE, Codron D, Kaiser TM, Muller J, Hummel J, Clauss M, Hatt JM, Schulz-Kornas E (2020) Dental wear at macro- and microscopic scale in rabbits fed diets of different abrasiveness: a pilot investigation. *Palaeogeogr Palaeocl* 556:109886
- Martin LF, Winkler D, Tutken T, Codron D, De Cuyper A, Hatt JM, Clauss M (2019) The way wear goes: phytolith-based wear on the dentine-enamel system in guinea pigs (*Cavia porcellus*). *Proc R Soc B Biol Sci* 286:20191921
- Mihlbachler MC, Solounias N (2006) Coevolution of tooth crown height and diet in oreodonts (Merycoidodontidae, Artiodactyla) examined with phylogenetically independent contrasts. *J Mam Evol* 13:11–36
- Morris DW, Dupuch A (2012) Habitat change and the scale of habitat selection: shifting gradients used by coexisting arctic rodents. *Oikos* 121:975–984
- Müller J, Clauss M, Codron D, Schulz E, Hummel J, Fortelius M, Kircher P, Hatt JM (2014) Growth and wear of incisor and cheek teeth in domestic rabbits (*Oryctolagus cuniculus*) fed diets of different abrasiveness. *J Exp Zool A Ecol Genet Physiol* 321:283–298
- Myllymäki A, Paasikallio A, Pankakoski E, Kanervo V (1971) Removal experiments on small quadrats as a mean of rapid assessment of the abundance of small mammals. *Ann Zool Fenn* 8:177–185
- Nelson S, Badgley C, Zakem E (2005) Microwear in modern squirrels in relations to diet. *Palaeontol Electron* 8:1–15
- Pal'chev NA, Mal'kova MG, Kuz'min IV, Yakimenko VV (2003) The structure of narrow-skulled vole (*Microtus gregalis* Pall.) colonies in western Siberia. *Russ J Ecol* 34:327–331
- Piperno DR (2006) Phytoliths: a comprehensive guide for archaeologists and paleoecologists. Alta Mira Press, Oxford
- Prugh LR, Brashares JS (2012) Partitioning the effects of an ecosystem engineer: kangaroo rats control community structure via multiple pathways. *J Anim Ecol* 81:667–678
- Przybylak R, Wyszyński P (2020) Air temperature changes in the Arctic in the period 1951–2015 in the light of observational and reanalysis data. *Theor Appl Climatol* 139:75–94
- Rabenold D, Pearson OM (2014) Scratching the surface: A critique of Lucas et al. (2013)'s conclusion that phytoliths do not abrade enamel. *J Hum Evol* 74:130–133
- Rensberger JM (1973) Occlusion model for mastication and dental wear in herbivorous mammals. *J Paleontol* 47:515–528
- Rensberger JM (1986) Early chewing mechanisms in mammalian herbivores. *Paleobiology* 12:474–494
- Rivals F, Mihlbachler MC, Solounias N (2007) Effect of ontogenetic age distribution in fossil and modern samples on the interpretation of ungulate paleodiets using the mesowear method. *J Vert Paleontol* 27:763–767
- Rivals F, Rindel D, Belardi JB (2013) Dietary ecology of extant guanaco (*Lama guanicoe*) from Southern Patagonia: seasonal leaf browsing and its archaeological implications. *J Archaeol Sci* 40:2971–2980
- Robinet C, Merceron G, Candela AM, Marivaux L (2020) Dental microwear texture analysis and diet in caviomorphs (Rodentia) from the Serra do Mar Atlantic forest (Brazil). *J Mamm* 101:386–402
- Rodrigues HG, Merceron G, Viriot L (2009) Dental microwear patterns of extant and extinct Muridae (Rodentia, Mammalia): Ecological implications. *Naturwissenschaften* 96:537–542
- Sanson GD, Kerr SA, Gross KA (2007) So silica phytoliths really wear mammalian teeth? *J Archaeol Sci* 34:526–531
- Schmidt-Kittler N (2002) Feeding specializations in rodents. *Senckenb Lethaea* 82:141–152
- Schour I, Medak H (1951) Experimental increase in rate of eruption and growth of rat incisor by eliminating attrition. *J Dent Res* 30:521
- Schulz E, Fraas S, Kaiser TM, Cunningham PL, Ismail K, Wronski T (2013) Food preferences and tooth wear in the sand gazelle (*Gazella marica*). *Mamm Biol* 78:55–62
- Smirnov NG, Kropacheva JE (2015) Patterns of lateral wear facets on molar teeth of voles (Arvicolinae). *Dokl Biol Sci* 460:20–22
- Sokolov AA, Sokolova NA, Ims RA, Brucker L, Ehrich D (2016) Emergent rainy winter warm spells may promote boreal expansion into the Arctic. *Arctic* 69:121–129
- Sokolov V, Ehrich D, Yoccoz NG, Sokolov A, Lecomte N (2012) Bird communities of the arctic shrub tundra of Yamal: habitat specialists and generalists. *PLoS ONE* 7:e50335
- Sokolova NA, Sokolov AA, Ims RA, Skogstad G, Lecomte N, Sokolov VA, Yoccoz NG, Ehrich D (2014) Small rodents in the shrub tundra of Yamal (Russia): density dependence in habitat use? *Mamm Biol* 79:306–312
- Solounias N, Tariq M, Hou SK, Danowitz M, Harrison M (2014) A new method of tooth mesowear and a test of it on domestic goats. *Ann Zool Fenn* 51:111–118
- Sponheimer M, Reed KE, Lee-Thorp JA (1999) Combining isotopic and ecomorphological data to refine bovid paleodietary reconstruction: a case study from the Makapansgat Limeworkshominin locality. *J Hum Evol* 36:705–718

- Team C (2003) Circumpolar Arctic Vegetation Map, scale 1:7 500,000. Conservation of Arctic Flora and Fauna (CAFF) Map No. 1. U.S. Fish and Wildlife Service, Anchorage, AK
- Towle I, Irish JD, De Groote I (2017) Behavioral inferences from the high levels of dental chipping in *Homo naledi*. Am J Phys Anthropol 164:184–192
- Townsend KEB, Croft DA (2008) Enamel microwear in caviomorph rodents. J Mammal 89:730–743
- Tschumi M, Ekoos J, Hjort C, Smith HG, Birkhofer K (2018) Rodents, not birds, dominate predation-related ecosystem services and dis-services in vertebrate communities of agricultural landscapes. Oecologia 188:863–873
- Ulbricht A, Maul LC, Schulz E (2015) Can mesowear analysis be applied to small mammals? A pilot-study on leporines and murines. Mamm Biol 80:14–20
- Ungar PS (2017) Evolution's bite: a story of teeth, diet, and human origins. Princeton University Press, Princeton
- van der Meulen AJ (1973) Middle Pleistocene smaller mammals from the Monte Peglia (Orvieto, Italy) with special reference to the phylogeny of *Microtus* (Arvicidae, Rodentia). Quaternaria 17:1–144
- Walker DA, Raynolds MK, Daniels FJA, Einarsson E, Arve E, Gould WA, Kaitenin AE, Kholod SS, Markon CJ, Melnikov ES, Moskalenko NG, Talbot SS, Yurtsev BA (2005) The circumarctic vegetation map. J Veg Sci 16:267–282
- Winkler DE, Schulz-Kornas E, Kaiser TM, De Cuyper A, Clauss M, Tutken T (2019) Forage silica and water content control dental surface texture in guinea pigs and provide implications for dietary reconstruction. Proc Natl Acad Sci U S A 116:1325–1330
- Wolfe SA, Nickling WG (1993) The protective role of sparse vegetation in wind erosion. Prog Phys Geogr 17:50–68
- Zhang YM, Zhang ZB, Liu JK (2003) Burrowing rodents as ecosystem engineers: the ecology and management of plateau zokors *Myospalax fontanieri* in alpine meadow ecosystems on the Tibetan Plateau. Mammal Rev 33:284–294
- Zuri I, Kaffe I, Dayan D, Terkel J (1999) Incisor adaptation to fossorial life in the blind mole-rat, *Spalax ehrenbergi*. J Mammal 80:734–741

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