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Developing graminoid cuticle analysis for application to Beringian palaeoecology

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ABSTRACT

Much of Beringia was composed of graminoid (grass and sedge) dominated habitats during the Late-Pleistocene, yet the account of the actual gramioids that were present is relatively vague. The spatial and temporal variabilities of palaeoclimate, mega-fauna, archaeology, and vegetation interactions could be significantly enhanced with accounts of Beringian graminoids. Fossil graminoid foliage is well preserved in permafrost sediments from Beringia and is available for identification using the micro-morphologies of the leaf epidermis (cuticles), which are often consistent with taxonomic identity. We present a scanning electron microscope (SEM) guide to the leaf cuticles of 38 graminoid species shown to be, or suspected of being present in former Eastern Beringian habitats during marine isotope stages (MIS) 2 and 3 (~56,000–12,000 cal. yrs BP). We examine whether modern specimens have sufficient cuticle variability to identify fossil foliage. We surveyed SEM images from herbarium specimens for 50 quantitative and qualitative features on both sides (adaxial and abaxial) of leaves, and entered these into an interactive key program (Delta Editor). Individual species were unique based on the combined presence of 2–4 cuticle features. Replicate samples ($n = 5$) of 10 species were integrated into a cluster analysis and visually compared using a dendrogram. Overall, fossils that match modern specimens with a Gower's similarity coefficient of 0.80 or higher can be considered a reliable identification match. Several fossil graminoid specimens were compared and identified with our reference collection. Cuticle identification appears to be a viable method for future macrofossil analysis in Beringia.

1. Introduction

During intervals of the last global glaciation (125,000–12,000 calibrated radiocarbon years before present; cal. yrs BP), Alaska and the Yukon Territory made up the eastern part of an unglaciated land bridge (Beringia) that connected North America and Eurasia (Hopkins et al., 1982; Brigham-Grette, 2001). Some combination of aridity, temperature, disturbance, species competition and soil development contributed to shaping the mammoth steppe biome, a vegetation community without an apparent modern analogue (Hopkins et al., 1982; Guthrie, 1990; Zimov et al., 1995; Guthrie, 2001; Ager, 2003; Zazula et al., 2006a; Zazula et al., 2006b). This vegetation has been described as an intermingling of steppe plants (semi-xeric grass and herb species growing beyond tree line governed by aridity) and tundra plants (cryo-mesic, low shrub, and herb species growing beyond tree line governed by temperature) or steppe–tundra (Hopkins et al., 1982; Yurtsev, 2001; Zazula et al., 2006b). Questions concerning the composition of steppe–tundra have been related to a transition to a grass-rich tundra during future warming (Chapin and Starfield, 1997; Rupp et al., 2000; Post et al., 2009), mega-faunal extinction (Guthrie, 2003; Shapiro et al., 2004; Guthrie, 2006), human migration into the new world (Goebel et al., 2008), and the existence of a relatively productive and diverse ecosystem at high latitudes (Zimov et al., 1995; Guthrie, 2001; Walker et al., 2001).

The composition of past graminoid (grass and sedge)-dominated vegetation has generated considerable debate regarding the spatial variability of vegetation types in response to climate, edaphic and herbivore controls over time (Cwynar and Ritchie, 1980; Guthrie, 1990; Elias et al., 1997; Ager, 2003; Elias and Crocker, 2008). Although debate and speculation persist with regard to the Beringian vegetation, it is undisputed that graminoids regionally dominated Beringia and were the keystone for a grazing mega-fauna (Hopkins et al., 1982; Guthrie, 1990; Anderson and Brubaker, 1994; Anderson et al., 1994; Swanson, 2006; Zazula et al., 2006a; Zazula et al., 2006b).

A detailed taxonomic account of past graminoids in Beringia could provide improved ecological reconstructions and clarify palaeobotanical distributions relative to modern biogeography, but graminoid reconstruction of sites within Beringia have been limited due to the morphological similarity of all grass or sedge pollen (e.g. Cwynar and Ritchie, 1980; Anderson et al., 1994; Ager, 2003). Recent work by

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Oswald et al. (2003b) used fossil pollen indicator taxa preserved in tundra lake sediments to detail the landscape level changes of two adjacent vegetation communities during the Holocene. This approach of high spatial resolution is key to understanding vegetation landscapes that can be quite variable such as those at high latitudes, and a focus on the common taxa that are not defined by pollen analysis will enhance palaeoecological interpretations. Beringian graminoid species are variable in their habitat preferences (i.e. moisture, disturbance, and temperature; Cody, 2000; Hulten, 1968), resulting in undefined graminoid pollen providing a void in the taxonomic history of Beringia. Improved taxonomic resolution of graminoids can be achieved by identifying ancient plant remains that are a common constituent of Late-Pleistocene permafrost sediments in Beringia (Goetcheus and Birks, 2001; Zazula et al., 2006a; 2006b; 2007; Wooller et al., 2007). Some of this material consists of fossil seeds that can be identified (Goetcheus and Birks, 2001; Zazula et al., 2007). The abundant graminoid foliage present in fossil assemblages could add an alternative and potentially more comprehensive palaeobotanical resource, because seeds may not always be present as they may be shed or consumed before preservation.

Identification of fossil graminoid cuticles based on their taxa-specific micro-morphological features has enhanced paleoecological reconstructions of grass-dominated environments in the tropics (Palmer, 1976; Wooller et al., 2000; Ficken et al., 2002; Wooller et al., 2003). The technique has not, however, been applied to graminoid environments at high latitudes. Microscopic surveys of the size, abundance, location, and nature of features such as stomata, papillae, prickles and cell structure on either side of graminoid leaves can yield dozens of morphological features to be used for identification of fossil plant fragments (Palmer et al., 1981; Dugas and Retallack, 1993; Wooller et al., 2000; Wooller, 2002; Wooller and Agnew, 2002; Wooller et al., 2007). Ancient foliage from sites in Beringia often retains these features, which are available for potential identification (Wooller et al., 2007).

To initiate the application of fossil cuticle analysis in Beringia, we surveyed modern graminoid cuticles belonging to a variety of sub-Arctic graminoid species that are allegedly or evidently common in Late-Pleistocene steppe–tundra (Table 1). Some researchers have proposed that these species were common by drawing from relict steppe–tundra communities in modern Beringia. For instance, Swanson (2006) generated a list of 25 grass species that were likely common in Late-Pleistocene Beringian lowlands based on Amphi–Beringian (Asian and American sides of Beringia) distributed grass species that presently dominate well-drained, moderately basic soils. Other researchers have suggested that the past Beringian vegetation was composed of xeric grasses, associated with modern *Artemesia* and *Juniperus* communities found on south facing slopes in continental Eastern Beringia (Edwards and Armbruster, 1989; Wesser and Armbruster, 1991; Lloyd et al., 1994; Guthrie, 2001). Young (1982) and Yurtsev (1982) used indicator forb pollen (i.e. *Plantago* and *Chenopod*/*Amanranth* types) as well as disjunct plant communities to infer the former widespread occurrence of certain graminoids. All of

Table 1
Evidence and habitat of graminoid species in Eastern Beringia during MIS 2 and 3 with University of Alaska Museum accession numbers of specimens sampled in this study.

Species	Source[1]	Habitat[2]	Accession number[‡]
Alopecurus alpinus Sm.	d*	Wet, sandy soil	V155902
Arctagrostis latifolia (R. Br.) Griseb.	d*	Wet tundra meadows	86860
Arctophila fulva (Trin.) Rupr.	b c*	Polygon tundra	145087
Bromus inermis Leyss.	b c*	Meadows, dry slopes	V73988
Calamagrostis canadensis (Michx.)	d*	Meadows, wet places	93031
Calamagrostis purpurascens R. Br.	d*	Rocky calcareous soil	96831
Calamagrostis stricta (Timm) Koeler	d*	Wet places, variable	V135709
Carex albonigra Mackenzie	a c g* h i j*	Mountainsides	86204
Carex duriuscula C.A. Mey.	a c f* g h i j	Meadows, sandy soils	V124106
Carex filifolia Nutt.	a c f* g h i j	Dry ridges	V124869
Carex pediformis C.A. Mey.	a c f* g h i j	Steppe[3]	74272
Carex petasata Dewey	a c f* g h i j	Meadows, woods	78628
Carex rossii Boott	a c f* g h i j	Rocky slopes	82887
Carex rupestris All.	a c f* g h i j	Dry ridges	V145071
Carex siccata Dewey	a c f* g h i j	Dry open areas	60026
Deschampsia caespitosa (L.) Beauv.	d* g* h* i* j*	Moist places	17143
Dupontia fisheri R. Br.	e*	Sandy, wet meadows	V117398
Elymus alaskanus (Scribn. & Merr.)	c d* f g h i j	Sandy soil	51909
Elymus trachycaulus (Link) Gould	c d e* f g h* i j*	Sandy river bars	V156315
Festuca altaica Trin.	c* d* f g h i j	Variable	32371
Festuca brachyphylla J.A. Schultes	c d* f g h i j	Sandy places on tundra	V125043
Festuca kolymensis Drobow	c d f* g h i j	South facing slopes[3]	V90289
Festuca lenensis Drobow	c* d* f g h i j	Alpines slopes	V134587
Festuca rubra L.	c d* f g h i j	Moist and sandy soil	V155875
Hierochloe alpina (Sw. ex Willd.)	d* g h i j	Alpine meadows	V142605
Hierochloe hirta (Schrank) Borbás	d* g* h i* j*	Dry areas	V137323
Hordeum jubatum L.	d*	Sandy soils, riverbanks	44206
Kobresia myosuroides (Vill.) Fiori	b* e* h* i* j*	Dry, calcareous soils	80990
Koeleria asiatica Domin	d*	Dry tundra, sandy soil	V123100
Koeleria cristata auct. p.p. non Pers.	f*	Variable	77053
Poa arctica R. Br.	c* d* g h i j	Dry tundra	80878
Poa arctostepporum Jurtzev & Prob.	c d f* h i j	Steppe[3]	V158139
Poa botryoides (Trin. ex Griseb.) Kom.	c* d f* g h i j	Mouintains, dry soils[3]	V106269
Poa glauca Vahl	c d* g h i j	Dry sandy places	25692
Poa paucispicula Scribn. & Merr.	c d* h i j	Rock, snow beds	V137424
Poa pratensis L.	c d* g h i j	Waste places	V142809
Puccinellia hauptiana (Trin. ex Krecz.)	c* d*	Wet places	V128741
Trisetum spicatum (L.) Richter	b d* f g h i j	Tundra, variable	39541

[1] References showing evidence for genera and species listed: a = Elias et al., 1997, b = Goetcheus and Birks, 2001, c = Gubin et al., 2003, d = Swanson 2006, e = Young 1982, f = Yurtsev 2001, g = Zazula et al., 2005, h = Zazula et al. 2006a, i = Zazula et al. 2006b, j = Zazula et al. 2007. [2] All habitat descriptions from Hulten, 1968, unless otherwise stated. [3] Tomalchev et al., 1995. *indicates species was found. ‡University of Alaska Museum of the North.