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Mosses and the beginning of plant succession on the Walker Glacier, southeastern Alaska

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Three mosses, a basidiomycete fungus (perhaps *Mycena*) and seedlings (perhaps *Epilobium*) are reported as growing on dead ice of a glacier in southeastern Alaska. By far the most abundant species was *Racomitrium fasciculare* which appears to begin directly on the ice, and trapping mineral particles, grows up mostly into irregularly shaped patches but it can become more or less hemispheroidal on pedestals of ice. Many of the tufts of which there are thousands, develop to face southeast on tiny mounds of ice and protect the ice to the northwest. However, none appear to become 'glacier mice' (more or less spheroidal and lying loose on the ice surface). *Sanionia uncinata* invades the *Racomitrium*, as does *Pohlia filum*. The fungus and three seedlings also occurred only on the moss tufts. In its precise features and topographic situation, this beginning of plant succession on dead ice is of a classical Clementsian type and contrasts strongly with many of the other occurrences of mosses on glaciers in North America, Iceland and Svalbard.

That mosses can grow on glacier ice has been reported from widespread areas of the world. However, there appear to be no reports from Europe apart from a not very convincing one of "moss balls" from the Grosser Aletschgletscher in the Swiss Alps (Bertram 2000). By contrast, from Svalbard, the high arctic archipelago, there are occurrences on nine or more glaciers (Belkina and Mavlyudov 2011, Belkina et al. 2013). For over 60 years there have been reports of mosses growing on Icelandic glaciers (Eythórsson 1950, 1951). These 'jökla-mýs' (glacier mice) of undetermined species were found on the ice of the Hrútárjökull. Such glacier mice are more or less spheroidal mosses which lie unattached on the ice surface. In 1968 G. F. Mitchell of Trinity College Dublin, Ireland gave JHD such a glacier mouse from the Breiðamerkurjökull, Iceland; it is *Racomitrium fasciculare* (Hedw.) Brid.

Much more recently regarding Iceland, Porter et al. (2008) have produced a detailed study of glacier mice on Falljökull. The mosses were *Racomitrium fasciculare* and *R. ericoides* (Brid.) Brid. The authors consider that the glacier mice are produced by the slow downhill movement of the ice. They claim that initially the mosses had grown up on clasts (rock fragments ranging from coarse sand to granules to pebbles). As they grow up the mosses protect the underlying ice from melting and end up on top of little pedestals of ice as the general surface of the ice ablates or melts. Eventually the mice fall from their pedestals and become larger and spheroidal as they move downhill. Coulson and Midgley (2012) have studied the formation of glacier mice on Falljökull in greater detail by placing data loggers inside five mice of which they traced the movements over several days. They found the small invertebrates, Collembola, Nematoda and Tardigrada, inside the glacier mice; no doubt there are other biota awaiting study inside mosses on glaciers there and elsewhere.

There are at least two reports from the South America. According to Seki (1974) the mosses on the Ventisquero Soler Glacier of Chile grow at 400 m a.s.l. *Racomitrium crispulum* var. *rupestre* (Hook. f. & Wils.) Dix., *Holodontium pumilum* (Mitt.) Broth. and *Dicranoweisia brevistea* Card. were found growing on angular pebbles partially embedded in muddy ice and growth was more luxuriant on the underside. Perez (1991) found 'globular mosses' (*Grimmia longirostris* Hook.) at Paramo de Piedras Biancas, Venezuela.

There are several reports from North America, especially Alaska. Referring to the Mantanuska Glacier (Fig. 1), Benninghof (1955) found that "Small spheroidal, silt-packed moss cushions are abundant on the terminus of the glacier" and went to describe concentric moss layers in which sandy silt and a few small pebbles have been incorporated during growth. He listed *Ditrichum flexicaule* (Schwaegr.) Hampe, *Andreaea rupestris* Hedw., *Pohlia nutans* (Hedw.) Lindb., *Ceratodon purpureus* (Hedw.) Brid. and *Polytrichum juniperinum* Hedw. They "sometimes lay in shallow wells thawed by their insolation". That situation is the very opposite of the occurrences at Falljökull.

Shacklette (1966) discussed "moss spheroids" from Alaska, Iceland, northwest Greenland, Jan Mayen and Japan; many of these occurrences are not on glacier ice. However the bryological findings made by Norton Miller (as reported by Shacklette) on the glacier near Berners Bay, southeastern Alaska (Fig. 1) are noteworthy. There Norton Miller found "at quite a number of locations, flat polsters of species of *Grimmia* and *Racomitrium*.…directly on the ice.… at many places the polsters had become slightly sunken into the surface of the glacier, presumably as a result of the moss having absorbed heat which melted the ice… "

Heusser (1972) studied the Gilkey Glacier, 45 km north of Juneau (Fig. 1) and stated that "Hundreds of polsters rested on gently sloping ice surface over an area estimated to be 400–500 m^2". They were mainly spheroidal and "most of them were growing directly on bare ice partially covered by a thin film of dust". The only moss was *Drepanocladus berggrenii* (C.Jens.) Broth. [now synonymised with *Warnstorfia fluitans* (Hedw.) Loeske.]. These colonies of mosses invading the glacier surface appear to represent the earliest stages of a lithosere or, more precisely, a cryosere. Initial stages of growth, however, are probably not directly on the ice but rather in surface drainage or in shallow pools that are seasonal and ephemeral and in which the temperature is above freezing point. Later development is controlled by differential ablation of the glacier, subsequent fluvial transport, and wind. This action during growth tumbles the polsters about and moulds their spheroidal shape, as Benninghoff (1955) points out.

Figure 1. Map of Alaska and adjacent Canada showing glaciers mentioned in the text.

Moss balls have been found on the 'lower Kaskawulsh Glacier' in the southwest Yukon, Canada (Fig. 1). Wilfred Schofield of the University of British Columbia gave JHD a slide taken in the 1980s. There are no further details.

In both the bryoflora and the other colonists of the Walker Glacier and the precise features of the habitat and dynamics of the vegetation, this particular colonization of the ice may be unusual, perhaps unique, not just in Alaska but elsewhere.

Fieldwork on the Walker Glacier

The snout of the glacier is situated at about 138°10´W and 59°16´N, some 5 miles (8 km) southwest of the frontier with Canada, at an altitude of about 400 feet (122 m) a. s. l. (Fig. 1–5). River rafting guides refer to the glacier as the Walker Glacier (Lyman et al. 2000) but there is no name on the map consulted (US Geological Survey, Yakutat B-1, 1:163 360, 1959). The site is inside the Glacier Bay National Park and Wilderness, close to the northern extremity. The active ice flows northwest and then turns to the south and southwest. There is dead ice (ice no longer pushing forward) at the north of the glacier (Fig. 3, 4). Compared to the rugged active ice, the dead ice is much smoother, though scattered with angular boulders and smaller clasts here and there. Gently sloping in various directions, it is not far off the horizontal. There are some cracks, both narrow and wide, and many shallow little channels in which melt water drains away. It is this dead ice that supports the plant and fungus colonists.

Because of studies of the archaeobotany of the frozen human remains discovered in 1999 in northernmost British Columbia (Dickson et al. 2004, Dickson 2011) JHD had occasion to be in the Pacific Northwest for short periods in the summers of 2000 to 2003. While on a guided rafting trip down the Tatshenshini-Alsek Rivers through

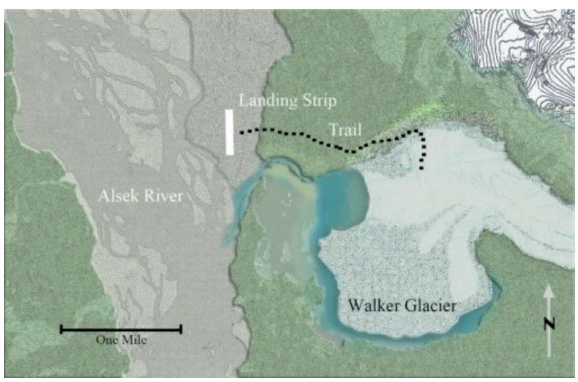

Figure 2. Map of the Walker Glacier and surroundings.

Figure 3. View from the moraine on the north side of the glacier looking down on the greyish dead ice with the white and blue active ice behind.

Figure 5. Numerous irregular patches of *Racomitrium* facing southeast partly on the general surface of the dead ice and partly on little mounds of ice

the Yukon, British Columbia and Alaska on 29 June 2001 JHD came across three species of mosses growing in abundance over a large part of the dead ice (Fig. 4, 5). The demands of schedule of the rafting trip were such that only a very short time (about one hour) was available to make observations. Two years later, however, on 23 August 2003 JHD had the chance to make a more thorough study for several hours. That time JHD was accompanied by Robert E. Johnston who took many landscape and moss photographs. All too conscious of the deficiencies produced by these very brief periods of study, JHD is now 77 years old and will never be there again. Perhaps, however, there is sufficient bryological and general ecological interest to place these findings on record.

Results and discussion

Racomitrium fasciculare (Hedw.) Brid. (Fig. 4–6). In the field JHD felt confident he had found a *Racomitrium* but

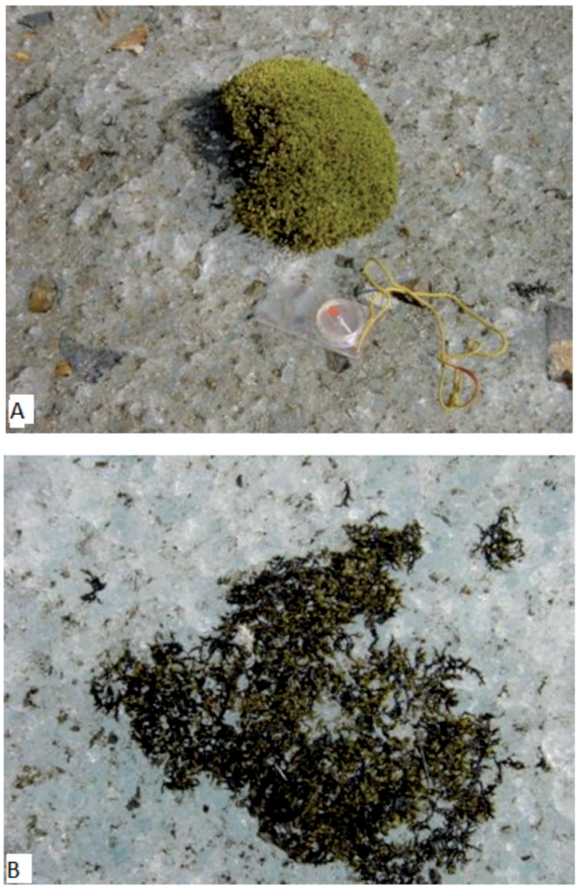

Figure 6. (A) Looking down on a hemispheroidal tuft of *Racomitrium* on a pedestal and facing the eastern half of the compass. (B) A large irregularly shaped patch of *Racomitrium* directly on the ice with many smaller patches scattered around. JHD.

Figure 4. A hemispheroid of *Racomitrium* on a pedestal, clearly raised above the general surface of the dead ice. Notice that the boulders also protect the ice on the northwest side.

was unsure of the species and at the time did not consider *R. fasciculare* because it was not immediately reminiscent of that moss in Britain and elsewhere in Europe. However, microscopic examination revealed the features of the species: elongate cells throughout the leaves which are long acuminate and muticous with crenulate margins at the apices. As the figures show, there were very many of patches, certainly thousands, some only a few cm or less across and others up to 18 cm and more of the longest axis. No sporophytes on any of the patches examined in 2001 and 2003.

Sanionia uncinata (Hedw.) Loeske (Fig. 7). Readily recognisable in the field, there were not many patches of this species. The stems were to about 3 cm long and the only sporophytes seen in 2001 had very immature capsules but in 2003 fully mature capsules were encountered. Hedenäs (1989) recognised three species within *Sanionia uncinata* sensu lato, with peristome characters important in making the distinctions: *S. uncinata* (Hedw.) Loeske, *S. nivalis* Hedenäs and *S. orthothecioides* (Lindb.) Loeske. These tufts are *Sanionia uncinata* sensu stricto. All the patches were within *Racomitrium* tufts. This species and *Bryum cryophilum* Mårtensson have been found colonizing tufts of *Hygrohypnella polare* (Lindb.) Loeske growing on glacier ice in Svalbard (Belkina and Mavlyuduv 2011, Belkina et al. 2013).

Pohlia filum (Schimp.) Mårt. (Fig. 8A–B). The slender stems of the voucher specimen were up to about 3 cm long; axillary gemmae were obvious and have the morphology distinctive for this species, as described by Shaw (1982, p. 262–263) who states "Common on glacial outwash in northwestern North America…". No sporophytes were seen in 2001 but in 2003 one patch had nearly mature capsules. This species was found as stems scattered within the both the *Racomitrium* and the *Sanionia* and on a few tufts it was growing as many densely packed stems. Shaw (1981, p. 36) states that *P. filum* is ecologically specialized and is almost entirely restricted to soils with very low levels of organic matter."

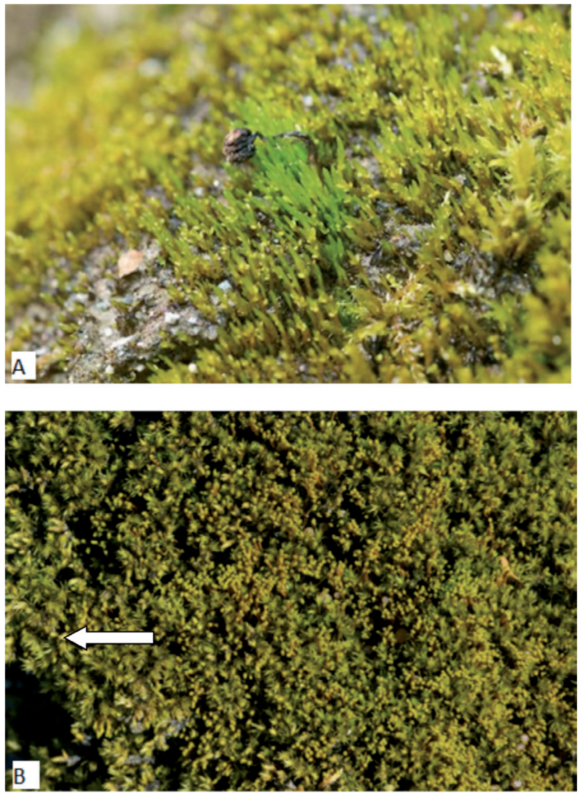

Figure 8. (A) Slender stems of *Pohlia* on a *Racomitrium* tuft with mineral particles at bottom left. (B) A mass of *Pohlia* on *Racomitrium* visible on the left. The yellow green spots are the bulbils on the *Pohlia*.

Mycena sp. (Fig. 9). There were little mushrooms, apparently identical, on three of the *Racomitrium* tufts. To judge from only the photograph they may be claimed tentatively to have been a species of *Mycena*.

Epilobium sp. (Fig. 10). One *Racomitrum* tuft had two identical dicotyledonous seedlings with no true leaves and another tuft had one seedling, resembling the first two,

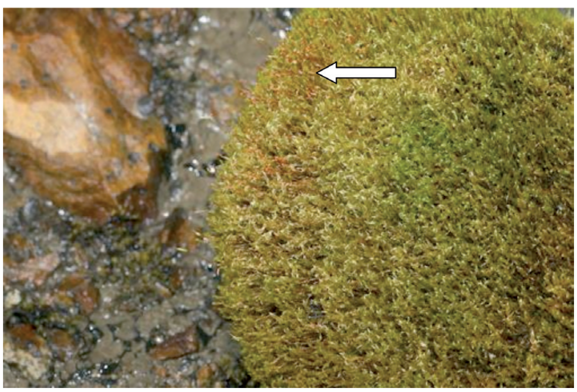

Figure 7. *Sanionia* with sporophytes top left obliterating the *Racomitrium* below.

Figure 9. A *Racomitrium* tuft colonized by a small brown mushroom with a striated cap, perhaps a species of *Mycena.*

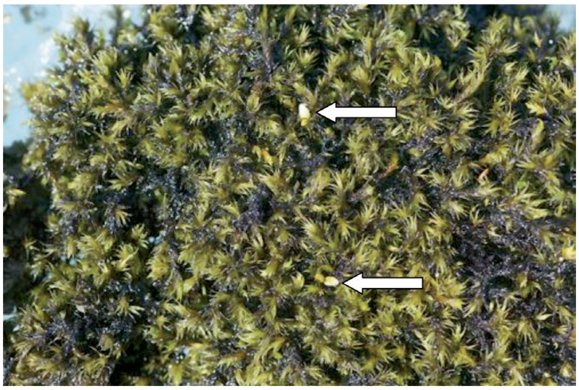

Figure 10. Two seedlings of perhaps *Epilobium* above and below the middle of a *Racomitrium* tuft.

but with the beginnings of tiny true leaves. They were taken to be seedlings of either *Epilobium latifolium* L. or *E. angustifolium* L. which both grow on nearby moraine and are locally abundant in the region. No other vascular plants were seen.

On the dead ice are sparse *Alnus* leaves and twigs, as well as other organic material such as a fragment of the lichen, *Cladina* sp. This debris has been blown or washed onto the surface of the glacier. There were many clasts from very fine particles to scattered boulders, large and small, especially in the northwest and north where there were some ice cones covered in mineral matter. Small thin patches of brown mud were numerous on the ice. JHD wondered if the mud or the clasts allowed the establishment of the *Racomitrium* tufts. However, Fig. 6B shows that the *Racomitrium* growth begins as prostrate fragments directly on the ice.

The colonies start to grow upwards and they trap fine mineral particles. Among the stems of all three moss species were sparse particles of coarse sand and angular quartz fragments up to 1 mm, sometimes more, across. In becoming approximately hemispheroidal, some of the patches reach a diameter of about 18 cm and a thickness of several cm. They end up facing southeast on their own little mounds of ice with tails of ice pointing northwest. Figure 5 also shows that the irregular patches, certainly the larger ones, also face southeast.

The observations by Benninghof on the mosses at Mantanuska, Miller on Berners Bay and Heusser on Gilkey revealed that the mosses were in shallow little hollows and both Benninghof and Miller claimed that the hollows formed because the sun's heat absorbed by the mosses melted the underlying ice. Figure 4 to 6 show that on the Walker Glacier the moss patches are not in hollows but on top of or on the side of tiny mounds of ice and in some cases on pedestals. So the situation compares with Iceland but is unique in North America. Put forward very tentatively, an explanation for this orientation may be the flow of katabatic winds down the glacier northwestwards and so the *Racomitrium* tufts protect the ice from melting.

Not a single *Racomitrium* tuft that could be called a 'moss ball', or a 'spheroid' or a 'glacier mouse' loose on the ice. Nor did JHD notice that any of the patches of the *Sanionia* had colonized the ice directly. The patch shown in Fig. 7 shows clearly that the *Sanionia* had covered the *Racomitrium*, which was spread beneath. The same lack of direct growth on the ice is also true for the *Pohlia*. As for *Sanionia*, there was one tuft on which the *Pohlia* seemed to be suppressing the *Racomitrium*.

What accounts for the very irregular shape of the great majority of the *Racomitrium* patches? Following Benninghoff, it seems feasible to suggest that the patches are disturbed by water or wind or both and fragments spread around. Dispersal of bulbils of the *Pohlia* may account for the establishment of that moss. Leafy stem fragments can spread the *Sanionia*. Nonetheless, establishment of spores from mosses on the glacier and even off the glacier cannot be totally excluded; all three mosses are common in the Pacific Northwest.

This paper is not the first publication to mention the moss colonization of the Walker Glacier. In their guide to rafting down the Tatshenshini River, Lyman et al. (2000) comment (p. 124): "Once on the glacier the first thing you notice are the moss colonies that are growing there. This indicates a history of relative stability for this section of ice". On p. 127 they say: "Once on the ice you'll see where moss spores have blown in and begun to grow on the silty mud on the relatively stable toe of the glacier". However, such confidence that spores are responsible for the moss colonizations on the mud may well not be true for any of the three species despite two of them producing sporophytes on the glacier.

These earliest stages of succession on the extensive area of dead ice of the Walker Glacier are strikingly Clementsian. The first stage, the *Racomitrium* tufts are totally indispensable to the continuing process. It is the only plant to grow directly on the ice. Regarded as stage 2, the growth of the other plants and the fungus is possible beacuse of stage 1. Mostly the *Racomitrium* patches become broken up by water or wind. None of the moss patches become spheroidal and are loose on the ice. Therefore they cannot be called glacier mice as are found in Svalbard, Iceland and elsewhere in North America. However, as the *Racomitrium* grows up, accumulating mineral particles, it sometimes develops into neat hemispheroids which allow the two other mosses to invade as well as the fungus and seedlings. Miniature ecosystems are the result. Raised above the ablating and melting surface of the ice, the hemispheroids may get some protection from the flow of shallow melt water.

Whatever the longevity of the moss patches, the final fate of at least some, perhaps many or all, is to be lost down the cracks in the ice or carried away by channels produced by melt water. Given by the photographer Al

Harvey, JHD has a photograph which proves that the colonization was abundant by at least 1988. It may well have started long before then. That further stages of the succession take place before the dead ice disappears remains to be seen.

Much more could be done by some vigorous young bryologist to test the ideas presented in this paper and a detailed comparison with the mosses growing on other North American glaciers could be very informative.

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