6 Discussion

6.1 Subfossils

The Iceman site is unique not just in Quaternary bryology but in all Quaternary and archaeological studies. Though there are archaeological sites at great altitude elsewhere, there is nothing quite like it. Immediately around the Iceman site there are about 21 different bryophytes present today (24 in the whole 1 km² square of the site) and in the extended vicinity (along the trail to the Similaunhütte) there are 36 species in all to be found. This stands in great contrast to a total of more than 75 species recovered from the site as subfossils. Some of the species can be found growing at the site now, but there are also low to moderate altitude mosses, which could never have grown there. The latter are highly interesting and tell about the Iceman's origin and last journey (Dickson 2003, 2011b; Dickson et al. 2003a, b; 2005; Oeggl et al. 2007). Dickson (2003) gave a preliminary discussion of how some of these numerous species came to be preserved and the topic has been greatly augmented by Dickson et al. (2019). The 6 cm long mass of *Neckera complanata* that the Iceman had carried can plausibly be explained as wrapping for provisions (Dickson 2000, 2011b). In all the gut samples, apart from the stomach, there are tiny fragments of *Neckera* and there are five more species but each of these five was extracted from only one gut sample. These samples represent at least three meals, and so the *Neckera* was ingested three times or more. Therefore, the use of *Neckera* as a wrapping material by the Iceman seems all the more likely (Dickson et al. 2019). Furthermore, *Neckera* also is crucially involved in the deduction of the Iceman's provenance (Dickson et al.1996, 2019). The botanical evidence, i.e. the remains of both flowering plants and bryophytes, clearly points to the south. Today, though only in moderate amount, *Neckera* grows close to Vernagt, only at 5 km distance, whereas on the northern valleys this moss occurs only at many times that distance at northernmost Ötztal or Inntal. Similarly, other mosses found with the Iceman, such as *Anomodon viticulosus*, grow in southern to mid Schnalstal but not in Ventertal. Three other mosses such as *Antitrichia curtipendula*, *Amblystegium serpens* and *Plagiomnium affine* occur at Zwieselstein, at the northernmost end of Ventertal.

A tentatively identified very small piece of *Sphagnum* cf. *teres* adhered to the Iceman's equipment may attest his last journey. That the Iceman passed through the Vernagt – Kurzras area (1,750 – 2,200 m.s.l.) before his very last climb into the nival zone is also supported by the presence of that species in eight adjacent squares in the Vernagt – Kurzras area. The discovery of a very small piece of the low altitude species *Sphagnum* cf. *affine* in the Iceman's colon supports the pollen evidence that he was low down (1,200 m a.s.l. or less) before entering Schnalstal (Oeggl et al. 2007, Dickson 2011b).

Many of the bryophyte remains that had become preserved in the hollow of the Iceman site provide palaeoenvironmental information about that very high-altitude terrain (see Dickson 2011b). *Polytrichastrum sexangulare* has been recovered from 69 % of the samples. Clearly, it had been growing within the hydrological catchment. The significance of that particular moss is that it only inhabits areas of snow beds. Therefore it is certain that, no matter how warm or cold it was during the period of sedimentation, which lasted thousands of years, the area had held snow beds with snow persisting long into summer.

Growing only on rocks wetted by snow and glacier melt water, the moss *Grimmia mollis* has been recovered from 26 % of the samples, but at present, this moss is not known from the hydrological catchment of the site though from typical habitats nearby, both in Austria and Italy. The abundant occurrence of this moss shows that cold water had flowed into the hollow of the site for much or all of the period of sediment deposition.

A very important matter is the recovery of subfossil fragments of further bryophyte species from low altitudes from the sediment in the hollow at the site that could never have grown around the hollow at any time during the last 5000 and more years such as *Amblystegium serpens*, *Anomodon viticulosus, Antitrichia curtipendula*, *Hymenostylium recurvirostre*, *Leucodon sciuroides*, *Neckera crispa*, etc. This whole topic is discussed at length by Dickson et al. (2019). A good example is the large species *Antitrichia curtipendula*. It is common and locally abundant in Schnalstal, mostly on shaded rocks in woodland to an altitude of about 1,950 m a.s.l. Fragments of this moss were found in four samples, two certainly connected with the Iceman perhaps also a third; one was from a sediment sample. The species could never have grown around the hollow and its habitats make dispersal uphill by wind very unlikely though perhaps not impossible. Did these fragments come from the hoofs or hair of herbivores, or on the feet and clothes of people? This scatter of bryophyte fragments of species that never grew in the nival zone is certainly overwhelmingly connected with the Iceman. However, other people may well have crossed the Alps before and after the Iceman, as is indicated by the recovery of artefacts from both before and after the Iceman's time (Dickson 2011b).

As a very relevant discovery, *Heterocladium dimorphum* was identified in caprine dung recovered from the sediments in the hollow (Oeggl et al. 2005; 2009, Dickson et al. 2019). To present there are only very few records of this species growing in the nival zones of the Alps (Vaccari 1913, 1914; Düll 1991; Grims 1999; Moosflora der Schweiz 2011 – www.swissbryophytes.ch). It does grow above the timberline but in all of Austria the altitudinal limit is 2,800 m a.s.l. but it has not been recorded in the investigated area above 2,600 m a.s.l. So, an animal such as alpine ibex that produced the dropping may have carried the moss internally up some 400 – 600 m.

6.2 Present bryoflora

For the studied area of "only" 200 km², the total amount of ca. 500 species of bryophytes seems large, as it represents about 2.5 % of all bryophytes known so far. Furthermore, we can surmise that even more species may well occur in the entire study area of this central part of the Alps considering other studies dealing with the area or parts of it (e.g. Düll 2006, Grims 1999).

With regard to the geographic location and the difference in the lowest elevations, we found a higher species diversity and more thermophilic species in the Italian part of the study area such as *Leptodon smithii* and *Ptychomitrium polyphyllum* which only occured in the low lying squares of the Vinschgau.

According to the main bedrock types, species which prefer acidic ground, are common. Since at some summits and other parts of the study area calciferous rock may occur, a few calcareous species were widespread, like *Tortella tortuosa* or *Tortella fragilis*. These species obviously could thrive if only traces of lime were present. In contrast, other species were confined to few localities where the presence of lime was more pronounced, e.g. *Ctenidium molluscum*, *Hymenostylium recurvirostrum* and *Eucladium verticillatum*. The former was found on bare calciferous rock and the latter two grew only on lime tufa.

The geographic, climatic and edaphic conditions define the vegetation pattern and the plant communities have also consequences for the distribution of the bryophytes. Steppe communities and their typical bryophytes, like *Crossidium squamatum*, are confined to the South Tyrolean area of the study. Boggy areas, which are much more widespread in the North Tyrolean part, harbour different *Sphagnum* spp. and a greater abundance of so called "brown mosses", e.g. *Warnstorfia* spp., *Calliergon* spp. and *Paludella squarrosa*.

6.3 Red list status and rare/new species

Regarding the red list status of the recorded bryophytes, it can be recognised that the classification varies in the single countries. However, considering all categories of the red lists, 80 % of all recorded bryophytes are listed in any of the considered countries (AT, IT, CH, DE, FR). In AT 40 % of the recorded bryophytes in the study area are listed in the red list, in IT 24 %.

Seligeria brevifolia is recorded for the first time for Italy.

Aulacomnium androgynum, *Barbula sinuosa*, *Pohlia andalusica*, and *Tortula obtusifolia* were newly documented for South Tyrol / Alto Adige.

6.4 Altitudinal ranges

In this study, it was possible to define the altitudinal ranges of the bryophytes more accurately and the knowledge was even extended substantially. Some of our results (such as those for *Schistidium flaccidum*, *Pogonatum urnigerum*) are overall in line with recent studies of Bertram (2009) and Amann et al. (2013). For many other species, the altitudinal data could be corrected in comparison to the literature and for several bryophytes we confirmed that they do not grow at the altitude of the Iceman site. For this topic, important recent sources, apart from Pitschmann & Reisigl (1954) and Reisigl and Pitschmann (1958), were the publications of Düll (1991), who focused on North Tyrol and Eastern Tyrol, but gave some information on South Tyrol, and Grims (1999) and Köckinger (2017), both covering the whole area of Austria and providing substantial information on the knowledge of the region, including information from former publications such as those of Dalla Torre & Sarnthein (1904).

In recent studies, altitudinal and range changes of biota have been discussed widely in connection to global climate change. It is axiomatic that the changes in plant communities since the 1950s are caused by global warming (Gottfried et al. 1994; Pauli et al. 2007). In general, many taxonomic groups (not only plants) are expanding poleward as well as to higher elevations (Hickling et al. 2006). Such studies depend on accurate data. Especially with regard to the present changes in climate and landscape, actual surveys of the local distribution patterns of species become more and more valuable for modelling future distribution, for biodiversity research and conservation purposes (Krisai et al. 2002; Grytnes et al. 2006; Costa da et al. 2015; Potemkin et al. 2018). Under these circumstances, our survey provides detailed data on bryophyte distribution within the study area.

Several publications have discussed how climate change might influence the distribution of bryophytes. There are strong indications that some bryophytes from the lowlands have already altered their distributional range further north and further inland in Europe due to climate change (Frahm & Klaus 1997, 2001; Frahm 2003, 2009; Bergamini et al. 2009b; He et al. 2016). Many bryophyte species are highly specialised and are dependent on peculiar microhabitats. The occurrence of these stenotopic bryophytes is not strongly bound to elevation, thus, it is rather difficult to assess vertical migration tendencies. Nevertheless, there are already signs that some bryophytes are shifting their ranges and some specialised bryophytes adapted to low temperatures may even lose their habitats (Bergamini et al. 2009b). Bryophytes in general and certain species in particular may be used as indicators for climatic changes (Gignac 2001; Hohenwallner et al. 2002; Sérgio et al. 2011).

Considering our results, range expansions of the bryophytes are difficult to evaluate. At a first sight, it might seem that some bryophytes have moved to higher elevations compared to previous investigations. However, we have to admit that the altitudinal records of several species may be merely a consequence of intensified work in the study area. As the recording was performed in detail (in squares of 1 km^2), our species range data offer the possibility to check the development of the local bryoflora in the future. We also recommend a detailed statistical analysis of historical and present data on the elevational distribution ranges.

6.5 Conclusions

All in all, it can be concluded that the Tyrol is one of the best, most intensely bryologically investigated regions of the world.

Even at present new information on the bryophyte flora of the Tyrol can be obtained. Detailed information on the distribution of bryophytes within the investigated area and several new altitudinal records were obtained. Whether the occurrences of bryophytes in altitudes not measured before are due to climate change or not cannot be solved now, but our data will be a base for further work.

Finally, we may ask if the Iceman was the earliest known bryologist? If he had deliberately selected *Neckera complanata* to carry it on his last journey, which is not a wildly implausible thought, then this may be true. Therefore, we may conclude that bryology in the Tyrol looks back to a 5,300 years long history. The last 24 years of Iceman research combined with the actual bryological fieldwork has produced an abundance of details of the Tyrolean bryoflora, present and past.