

The lichen *Allocetraria madreporiformis* in high-arctic steppes on Svalbard: a result of out-of-Tibet migration?

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Allocetraria madreporiformis is a small, finger-like, fruticose lichen with isolated occurrences in the inner fiord section of the long, straight fiord Wijdefjorden in Svalbard. Several new localities are added and mapped here, and we show that the species is confined to exclusive high-arctic steppe habitats on fine-textured, moderately alkaline soil, exposed to wind erosion and aeolian transport of silt and sand. It avoids the most saline steppes and adjacent tundra areas, as indicated by numerous pH samples of mineral soils from sites with and without occurrences of *A. madreporiformis*. In this open habitat, all otherwise common arctic-alpine fruticose lichen species were absent or extremely rare, and a cryptogamic cover was very depauperate. On Svalbard, this species is an exclusive character species of the steppe areas in Inner Wijdefjorden National Park. The genus *Allocetraria* is strongly centred in the Sino-Himalayan area. It is discussed here that it probably evolved as a response to the very extensive new habitats formed during a series of Qinghai-Tibetan Plateau uplift and orogeny events taking place 25–1.6 Ma. This and other aspects affecting current classification alternatives of cetrarioid lichens are also discussed. The habitat preferences of *A. madreporiformis* appear to have been largely defined by the conditions of its probable area of origin in steppe-like habitats of the northern part of the Qinghai-Tibetan Plateau.

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Introduction

Svalbard has a high biodiversity of lichens, most of them being widespread. Of the 748 species included in the lichen flora of Svalbard by Øvstedal et al. (2009), 93 % are also found in Fennoscandia and 34 % are bipolar. Still, there is a large element of high-arctic species, with *Aspicilia* excluding *Circinaria* as clearly the largest genus in this respect. However, this element also includes several conspicuous members of Parmeliaceae, with species such as *Arctocetraria nigricascens* (Nyl.) Kärnefelt & Thell, *Cetraria racemosa* (Lyngé) Øvstedal and *Masonhalea inermis* (Nyl.) Lumbsch, M. Nelsen & Thell. Lyngé (1933) and Printzen (2008) reviewed the phyto- and phylogeography of arctic lichens, and highlighted the following species: *Allocetraria madreporiformis* (Ach.) Kärnef. & Thell, *Dactylina arctica* (Richardson) Nyl. and *D. ramulosa* (Hook.) Tuck. The latter was stated to be absent from Fennoscandia by Printzen (2008), however, it is known from a small area on both sides of the Finnish-Norwegian border (Tindal 2004).

Of the high-arctic species occurring in Svalbard, *Allocetraria madreporiformis* is distinguished by a deviating distribution pattern. Lyngé (1933) cited two Svalbard collections,

both from Wijdefjorden, one by Wulff (UPS) with no further geographical information, and one from the entrance of the valley Kartdalen (O, TRH, leg. O.A. Høeg in 1928). Lyngø (1933) also stated that Høeg had observed the species at additional localities. Eilif Dahl also collected it in the area in 1936, but it was published much later (Øvstedal et al. 2009). A report of *A. madreporiformis* from NW Svalbard by Elvebakk & Spjelkavik (1981) has proven to represent a particularly well-branched specimen of *Dactylina arctica*.

In 2001 and 2002, we carried out botanical investigations in the Wijdefjorden area on behalf of the County Governor of Svalbard, and the report from these studies (Elvebakk & Nilsen 2002) served as a basis for the establishment of Inner Wijdefjorden National Park in 2005. A major criterion for this establishment was the occurrence of an exclusive high-arctic steppe landscape. Steppes cannot normally be developed at such low high-arctic temperatures. Elvebakk & Nilsen (2002) argued that the very long and straight fiord acts as a wind tunnel that removes much of the humidity in air and soil. At the same time, the inner parts of Wijdefjorden are in a very continental area, surrounded by several chains of high mountains on all sides, resulting in extremely low precipitation rates, although this has not been measured. Tributary valleys not exposed to these winds are dominated by normal middle-arctic tundra vegetation, whereas the central areas of the National Park instead have alkaline soils in the pH range 9.0–10.5 at depths down to 30 cm. Such soil is found up to altitudes of 300 m above sea level. These can only have been formed by exposure to long-lasting droughts. This steppe is characterized by *Potentilla pulchella* vegetation (Møller 2000, Elvebakk & Nilsen 2002, Nilsen & Elvebakk 2014) with occurrences of very rare vascular plants such as *Puccinellia svalbardensis* (Elvebakk & Nilsen 2011) and *Calamagrostis purpurascens* (Elvebakk & Nilsen 2016). A predominantly temperate steppe lichen, now named *Xanthomendoza trachyphylla* (Tuck.) Frödén, Arup & Søchting, has also been reported from the area (Elvebakk & Øvstedal 2009).

The aim of the present paper is to describe and discuss the distribution and ecology of the exclusive species *Allocetraria madreporiformis* in Svalbard, related to the rather recently defined High-Arctic steppe landscape in the Wijdefjorden area of Svalbard. It is red-listed as VU in Norway (Timdal et al. 2015), and a detailed ecological description is valuable for directing proper management measures for the conservation of this vulnerable species.

Divakar et al. (2017) very recently proposed a dramatic reclassification of cetrarioid lichens, where 13 previously accepted genera in the cetrarioid core were reduced to two, *Cetraria* and *Nephromopsis*, and *Allocetraria* was included in *Cetraria*. This classification alternative is also discussed in the present study.

Study area, material and methods

The archipelago of Svalbard is dominated by its largest island Spitsbergen. A general description of its tundra biodiversity was given by Elvebakk (1997). The warmest areas of the islands are the inner parts of Spitsbergen, which have been classified as middle arctic tundra zone (Elvebakk 1997). Mean July temperature at Svalbard Airport, Longyearbyen, is 5.9°C, the sum of mean monthly values above zero is 12.9°C, and annual precipitation is 190 mm (Førland et al. 1997). A strong temperature increase, especially in winter (Vikhamar-Schuler et al. 2016), has taken place subsequently, but the cited data are the most relevant ones to the field studies during 2001 and 2002. There are no meteorological stations at Wijdefjorden, but the general flora indicates that temperature probably is in the same range as in the valleys near Longyearbyen, which have somewhat higher temperature than at Svalbard Airport (Brosø & Elvebakk 2000), but precipitation must be much lower.

The western side of the fjord is composed of Devonian sandstones, mostly decomposing into alkaline soil, and the eastern side is dominated by Proterozoic basement rocks, like quartzites and gneisses (Winsnes 1988). The soil is strongly modified by marine, glaciofluvial and morainic deposits, and also by aeolian soil transport. Elvebakk & Nilsen (2002) show that strongly alkaline soils predominate both on the eastern and western sides, and formation of saline soils visible as white surface crusts is locally common up to altitudes of 300 m. In this report, the massive steppe landscape dominated by such soils is mapped as Sector I, a less pronounced steppe area as Sector II, whereas normal middle-arctic tundra along the fjords is mapped as Sector III. The latter is also present in lowland areas outside of the mapped sector areas, which are also shown in Fig. 1.

The whole interior part of the Wijdefjorden fiord system (the fiord is renamed Austfjorden south of its branching with Vestfjorden) was studied on both sides, south of the entrance of the valley Purpurdalen (79°20'N), on the western side, and Ringhorndalen (79°18'N), on the eastern side (Fig. 1). Fieldwork was done in the vicinities of four huts. Several additional sites were surveyed during short helicopter stopovers. The western side, including Vestfjorden, was surveyed in 2001 and the eastern side was surveyed in 2002. Altogether, 40 sites were investigated. In 33 plots, most of them as large as 1 km × 1 km, the frequency and dominance of all vascular plants as well as the lichens *Allocetraria madreporiformis* and *Dimelaena oreina* (Ach.) Norman, were recorded, using the following scale: 1 = rare (present at a single site); 2 = scattered; 3 = common (Elvebakk & Nilsen 2002). Brosø & Elvebakk (2000) provided a more precise definition of this field method, including values for dominant species.

Soil samples were taken at all visited sites. Altogether, 102 soil surface samples of mineral soil at dry sites, which are potential habitats of *A. madreporiformis*, were taken and related to the presence or absence of this species. Based on the homogeneity of the vegetation cover and soil structure, single samples were considered to be valid for an area of at least 100 m², often up to the range of 1 km². Most of these samples were collected from the upper 5 cm of the soil, but a top-soil saline crust was in some cases sampled separately. pH values of these samples were measured by using a standard laboratory pH meter, based on one volume part of soil, mixed and shaken with two volume parts of distilled water. Non-linear relationship between pH and the occurrence of *A. madreporiformis* was tested using XLfit ver. 5.3.1.3 (ID Business Solutions Ltd., Guildford, UK). The secondary chemistry of *A. madreporiformis* was studied by TLC, following Culberson (1972) and Orange et al. (2001), using the solvents A, B and C. Collected samples are deposited at TROM. The nomenclature of vascular plants and bryophytes in this article follows Elvebakk & Prestrud (1996).

Results

Allocetraria madreporiformis was found as rare to common in 12 of the studied sites, whereas it was not recorded at another 28 study sites (Fig. 1). It was defined as scattered at all the five sites on the western side. The older collections by Høeg and Dahl are from the northern part of this area (Fig. 1). At its two northernmost sites on the eastern side of the fiord, the species was recorded as rare, although the stopovers were of quite short duration. Further south on the eastern side, it was common on the north-western slope of Einsteinfjellet and north of Austbotnhytta, and scattered at the two localities between these two locations.

All localities are concentrated to parts of Austfjorden and the western side of Wijdefjorden with a moderate steppe character, marked as Sector II in Fig. 1. Within this sector, it occurs at 73% of the studied sites. The species was not found in the innermost part of Austfjorden or elsewhere within Sector III (Fig. 1). The species was also lacking from a total of 16 sites in Sector I, except

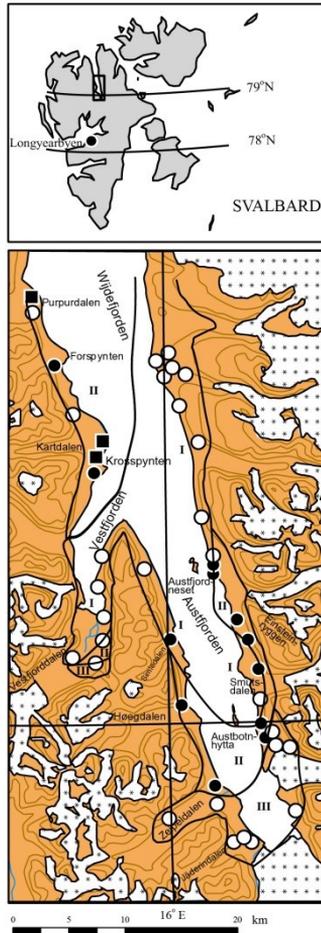


Figure 1. The Svalbard archipelago showing the study area in Wijdefjorden. Filled circles show localities where *Allocetraria madreporiformis* was found in 2001–2002, and open circles show investigated areas where the species was not found. Filled squares, with approximate positions, represent older collections, one Høeg collection from 1928 and two Dahl collections from 1936 reported by Lyng (1933) and Øvstedal et al. (2009). Landscape subdivisions affecting the distribution of *A. madreporiformis* are shown on the map as Sectors I–III; I = massive steppe landscape dominated by strongly alkaline soils; II = a less pronounced steppe area, III = normal middle-arctic tundra.

for two occurrences as rare near the boundary to Sector II at Austfjorden. All recorded occurrences are from dry ridges, either between gravelly or stony parent material or on silty soils. The species was absent from the most extremely exposed ridges and from areas with much white surface soil deposits, with measured pH values ranging from 9.0 to 10.3 (Elvebakk & Nilsen 2002).

The species showed strong preferences for the *Potentilla pulchella* steppe vegetation which consists of ca. 95 % open mineral soil, gravel and stones and is characterized by high-arctic species like *Potentilla pulchella*, *Puccinellia angustata*, *Poa hartzii* and *P. abbreviata*. Bryophytes

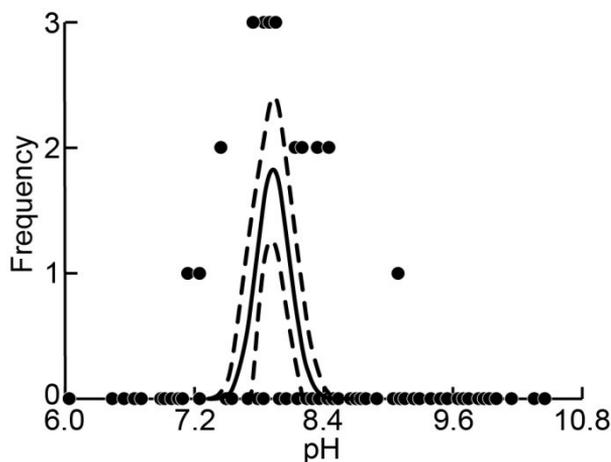


Figure 2. Best non-linear model for relationship between pH and occurrence (0 = absent, 1 = rare, 2 = scattered, 3 = common) of *Allocetraria madreporiformis*. The model showing best fit was a vapour pressure model ($y = \exp(A+(B/x) + (C \times \log(x)))$). The middle line shows the best fit, while the stippled lines show the upper and lower confidence limits at $p = 0.05$. $R = 0.571$.

are very scarce in this community, mostly consisting of depauperate mats of *Ditrichum flexicaule*, which were found to have a surface cover of 1–2 % (own unpublished data). The most commonly associated lichens were *Physconia muscigena* (Ach.) Poelt and crustose species within the genera *Ochrolechia*, *Mycobilimbia* and *Lecanora*. Fruticose and foliose terricolous lichens of other genera were very rare. *Cetraria aculeata* (Schreb.) Fr., *Cladonia symphycarpa* (Flörke) Fr. and *Thamnolia vermicularis* (Sw.) Schaer. were recorded as a few single thalli at a limited number of sites, while other species of *Cetraria* and *Cladonia*, as well as species of *Alectoria*, *Cetrariella* and *Flavocetraria* were not recorded in associations with *A. madreporiformis*.

Allocetraria madreporiformis also grows in a transitional zone between the *Potentilla pulchella* and the *Dryas octopetala* communities, and within the latter. The *Dryas* community is in this area restricted to lower elevations than elsewhere in Svalbard, probably because of the strong aridity in the area, and *A. madreporiformis* was only found in the driest version of this community.

At most sites, *A. madreporiformis* grows directly on fine-textured soil, and only occasionally within a sparse cover of bryophytes and lichens, although its contact with soil may, in some cases, be blocked by gravel and stones. Here, the surfaces are instable because of strong drought and wind transport of particles. Desiccation cracks are common, and hemispherical polygons are formed between the cracks in the driest parts of the *Dryas* communities, particularly on the western side of the main fjord, where there are almost no stabilizing bedrock outcrops. The soil is rarely stabilized by a crust of bryophytes, crustose lichens and free-living cyanobacteria like in alkaline soils in most flat and non-disturbed soils elsewhere in Svalbard (e.g. Pushkareva & Elster 2013). We observed sand storms, which even included white salt dust, at Vestfjorden and Ringhorndalen in both 2001 and 2002.

Fig. 2 shows the non-linear relationship between pH and the frequency of *A. madreporiformis*, where the value 0 represents sites where it was absent. This shows that *A. madreporiformis* is concentrated to soils with pH from 7.0 to 8.5. It is absent from the few sites with pH lower than 7.0 and from the numerous sites with pH higher than 8.5, except for one low-

frequency occurrence on soil with a measured pH value of 9.1. Thus, the species is concentrated to alkaline soils, but avoids saline habitats.

All the 10 collections studied by TLC contain usnic and protolichesterinic acids as major secondary compounds, with lichesterinic acid present in minor quantities. This is in agreement with previous chemical studies of this species (Randlane et al. 2001). Two collections, one from Canada cited below, and one from Svalbard, have three additional substances, i.e. gyrophoric acid, an unidentified UV + blue substance, one unknown substance, all occurring in minor or trace amounts, as shown as spot characters. The species is homogeneously usnic-acid yellow on Svalbard (Fig. 3), and with only weak traces of a brown melanin-like pigment, which appears to be more common in more sunny areas, e.g. in the Rocky Mountains, as illustrated in Brodo et al. (2001).

Samples studied: **Norway:** Svalbard, Wijdefjorden, Krosspynten, 73°19'N, 15°45'E, *A. Elvebakk* 01:108, *E. Elverland*, *J.W.Bjerke* & *L. Nilsen* (TROM); Austfjorden: N side of the mouth of Simledalen, 79°05'N, 16°01'E, *A. Elvebakk* 01:157 (TROM); N side of the mouth of Zeipeldalen, 78°56'N, 16°12'E, *A. Elvebakk* 01:145 (TROM); the Austbothytta area, 78°59'–79°00', 16°21'–22'E, *A. Elvebakk* 02:027, 02:088, *A. Elvebakk* 02:105 & *L. Nilsen* (TROM); ESE of Einsteinodden, 79°02'N, 16°22'E, *A. Elvebakk* 02:010, *L. Nilsen* & *T. Tønsberg* (TROM); NW slope of Einsteinfjellet, 79°05'N, 16°18'E, *A. Elvebakk* 02:012, *L. Nilsen* & *T. Tønsberg* (TROM); Austfjordneshytta, 79°07'N, 16°10'E, *A. Elvebakk* 02:118 (TROM). **Canada:** Nunavut, between Hedley Bay and Cambridge Bay, 70°45'N, 109°01'W, 150 m, *A. Elvebakk* 99:386 (TROM).

Discussion

Allocetraria madreporiformis has its only known localities within the Nordic countries and Greenland in the Inner Wijdefjorden National Park, and this peculiar distribution calls for a discussion. What is very striking is that it thrives in areas where widespread, fruticose ridge lichens like *Flavocetraria cucullata* (Bellardi) Kärnefelt & A. Thell, *F. nivalis* (L.) Kärnefelt & A. Thell, *Alectoria nigricans* (Ach.) Nyl., *Thamnotia vermicularis*, *Cetraria aculeata*, and *C. islandica* (L.) Ach. are very rare or completely lacking.

Heavy reindeer grazing is very detrimental to the cover of fruticose lichens. On the western side of the main fjord and in Vestfjorden there are very few reindeer, but the reindeer population is quite large on the eastern side (own unpublished observations). However, the ridge lichens are also absent from protected crevices between rocks, where they normally find refuges in otherwise heavily grazed areas, in addition to occurrences as small, scattered specimens elsewhere. The lack of these common ridge lichens and the contrasting presence of *Allocetraria madreporiformis* can therefore not primarily be explained by reindeer grazing. Lichens of arctic and alpine ridges obviously tolerate desiccation and wind erosion, also from ice crystals during frequent snow-free winter situations. However, their habitats are normally stabilized by pebbles, rocks or outcrops of variable chemical compositions. The ridges of the study area differ ecologically by their saline soils, the arid climate, and the frequently deposited and thick covers of wind-transported, fine-grained soils. Fine-grained soil deposition and aridity probably explain the presence of *A. madreporiformis* and the absence of ubiquitous fruticose ridge lichen species otherwise hardly lacking from any arctic or alpine ridge.

The regression curve shows that *A. madreporiformis* has a significant preference for slightly alkaline soil, with a peak at pH 7.8 (Fig. 2). However, the correlation coefficient is rather low, which is due to several locations with such pH levels, but without *A. madreporiformis*. Nevertheless, this should reflect true conditions, and not just a normal distribution over a standard

calcareous soil gradient which would be in the pH range 7–8, as shown for many Svalbard species by Elvebakk (1982), who also indicated that when applied to purely mineral soil samples, pH values alone are good environmental indicators.

Allocetraria madreporiformis avoids saline crusts, but prefers bare surfaces of fine-textured mineral soil. Surface instability is probably important in explaining the distribution of *A. madreporiformis*, and it represents a habitat with low competitive stress. However, the species is absent from other instable alkaline areas affected by cryoturbation in more humid and cooler parts of Svalbard. Thus, it probably requires, for Svalbard, relatively high growing season temperature. It also avoids liquid water except for a short freeze-thaw period during spring, associated with substrate instability, and also tolerates the substrate instability from soil desiccation and aeolian soil transport later during the season, factors preventing the establishment of a soil crust and other fruticose lichens.

In Central Europe, *A. madreporiformis* has been recorded from young glacier forefields (Bilovitz et al. 2014) that consist of open, instable calcareous soil. Poelt (1969) stated that it prefers wind-exposed sites of calcareous schists, which agrees with its absence from the most strongly alkaline sites, like in Wijdefjorden.

The habitat ecology of the two other members of the ‘exclusive trio’ of the high-arctic Svalbard species is entirely different. *Dactylina arctica* always grows in closed and stable vegetation with *Cassiope tetragona* and *Racomitrium lanuginosum* on siliceous substrates stabilized by presence of rocks and boulders, whereas *Dactylina ramulosa* grows on siliceous substrates, but with a subneutral chemistry and in moderate snowbeds, often with smaller stones and pebbles (Øvstedal et al. 2009, own unpublished observations).

The genus *Allocetraria* was reviewed by Wang et al. (2015a; b), who concluded that it includes 11 species, all present in the western provinces of China. After the transfer of one species to the monotypic genus *Usnocetraria* (see Divakar et al. 2015), only *A. madreporiformis* and *A. stracheyi* (Bab.) Kurok. & M.J. Lai have wider distributions (Randlane et al. 2001, Wang et al. 2015b).

The Qinghai-Tibetan Plateau, the obvious evolutionary centre of the *Allocetraria* clade based on the distribution data cited above, has received much attention lately. A review article by Wen et al. (2014), shows how the dramatic uplifts here during four major periods from 25 to 1.6 Ma operated as a driving force in evolution. New major habitats developed, like high-alpine mountains, moist habitats towards the south as a response to the new monsoon climate, and steppes and deserts in the northern rain shadow areas. There is an increasing body of evidence showing how the Qinghai-Tibetan Plateau (QTP) was a source area of alpine plant evolution with subsequent dispersal to other areas in the Northern Hemisphere, parallel to the pattern in *Allocetraria*. The genus *Meconopsis*, with c. 80 species, arose at c. 16 Ma (Xie et al. 2014), but remained in its core area, whereas its sister group, the arctic-alpine poppies (*Papaver*, section *Meconella*) diversified in arctic and northern, alpine areas. *Rhodiola*, with c. 90 species, with estimated age 12 Ma. (Zhang et al. 2014), has most of its species in the QTP area, but has migrated to other areas of the Northern Hemisphere. *Saussurea* originated during the third QTP uplift period at 6.7–8 Ma and has diverged into no less than 450 species (Wang et al. 2009), the majority restricted to the QTP, and the bulk of the remaining ones to adjacent areas of Asia. Favre et al. (2016) showed how *Gentiana* diversified and radiated from a centre in the QTP at 14 – 7 Ma, while Jia et al. (2012) showed how *Hippophae* migrated to Europe and other parts of Asia from a centre in the same area. There are additional spectacular examples of rapid evolution in this area, like *Pedicularis*, *Primula*, *Rheum*, *Rhododendron*, *Saxifraga* and many Asteraceae groups (Wen et al. 2014).



Figure 3. *Allocetraria madreporiformis*. The specimen Elvebakk 01:145 photographed in the field.

The very strong concentration of *Allocetraria* species to the Sino-Himalayan area and its estimated age of 7.5 Ma (Divakar et al. 2017) indicate that it also represented an evolutionary response to the formation of these large new habitats. Most species are adapted to terricolous, high-alpine habitats, up to altitudes of 5800 m; one species is primarily saxicolous, while another species grows on *Rhododendron* twigs near the treeline (Randlane et al. 2001, Wang et al. 2015b). On the other hand, *A. madreporiformis* appears to be primarily associated with steppe-like environments in this area, with secondary migrations to other dry and cold parts of the Northern Hemisphere. It is known from dry areas of China, such as Xinjiang, Qinghai and Tibet, and from Turkestan, Kyrgyzstan and Mongolia. In Europe it is even known from the alpine region of Sicily (Randlane et al. 2001). In North America, it is widely distributed in dry alpine and arctic areas, extending southwards to New Mexico (Thomson & Bird 1978, Brodo et al. 2001).

Its particular ecological requirements on Svalbard, reported here, might therefore reflect its evolutionary origin in dry areas of the QTP. The Svalbard localities are both geographically and ecologically isolated, and may have been established in the early Holocene by westward dispersion, as quite a number of localities are known from Novaya Zemlya (Lyngø 1933). Although it is not known from Greenland, it is present in the neighbouring Ellesmere Island region (Kristinsson et al. 2010). A migration to Svalbard from the west cannot be ruled out either, and large exposed sea floor areas during the early Post-Glacial (Wohlfarth et al. 2008) might have represented migration areas different from those of today. Even more important, the continuous sea ice is a primary long-

distance dispersal vector, facilitating east-west migration to Svalbard, as shown for vascular plants (Alsos et al. 2007).

The two primary studies on cetrarioid phylogeny are those of Thell et al. (2009) and Nelsen et al. (2011), whereas a reduced number of the samples used by the latter study were re-analyzed with two additional genetic markers and some additional samples in the temporal approach by Divakar et al. (2017). The two latter studies have many clades and ‘orphans’ represented by only one or two sequences, and with a resulting non-monophyly of many genera. The study by Thell et al. (2009) had more samples analyzed, and no less than 65 among the 90 cetrarioid species accepted then were included. However, the numbers of successfully obtained sequences were very incomplete for the genetic markers except ITS. Consequently, the molecular support for many of the clades of genera and potential genera accepted prior to the study by Divakar et al. (2017) was poor. Still, Nelsen et al. (2011) showed that the genetic distances between clades representing genera were in the same range for cetrarioids (except *Kaernefeltia*, *Arctocetraria* and *Tuckermanella*) as for other well-established Parmeliaceae genera, e.g. *Menegazzia*, *Bryoria* and *Brodoa*.

The cetrarioid clades appear to have developed either in the QTP, with neighbouring areas, in North America, or on a broad circumpolar scale in the Northern Hemisphere, with weaker speciation having occurred in Europe and in the amphi-Beringian area. Furthermore, most groups are adapted to cool habitats at high latitudes and/or altitudes. We believe that increased sampling with a broad molecular approach should investigate this pattern further, particular in the light of numerous recent findings that the QTP uplift episodes have played a major role in the evolution of and within alpine plant genera (Wen et al. 2014, Favre et al. 2016). Moreover, sampling of widely distributed cetrarioid genera should also cover the QTP area.

The introduction of a 28–32 Ma age threshold for acceptance of genera as proposed by Divakar et al. (2017), would exclude a priori all QTP uplift processes as being irrelevant for evolution at generic level. Moreover, with the current lack of cetrarioid fossils, a temporary approach model ignores possibly increased evolutionary radiation rates in groups of organisms triggered by such uplift processes.

Allocetraria has a similar age estimate and geography pattern, when compared to the amazing evolution shown by the genus *Saussurea* (Wang et al. 2009), with its similar centre in the QTP area, and with weaker diversification to other parts of the Northern Hemisphere, both in moist and steppe-like habitats. Therefore, we would prefer a model of 13 imperfectly defined cetrarioid core genera in addition to ‘orphaned’ species, over an alternative of only two widely defined ones, as a starting point for further phylogenetic studies. Such improved studies will add a focus on evolutionary patterns, even if clade names at generic level will continue to change, and some might eventually deserve subgeneric level. It is our hope, that the hypothesis presented here on the origin of the isolated *A. madreporiformis* population on Svalbard will stimulate future phylogenetic studies to also address the role of the QTP uplift on the evolution of cetrarioid lichens. Finally, we recommend that the populations of this character species of the exclusive high-arctic steppes of Inner Wijdefjorden National Park need to be properly monitored under the dramatically changing Svalbard climate.

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