# Nunataks and peripheral refugia for alpine plants during quaternary glaciation in the middle part of the Alps

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# Nunataks and peripheral refugia for alpine plants during quaternary glaciation in the middle part of the Alps

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## Abstract

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There is a long-lasting debate about the fate of the mountain flora of the Alps during Quaternary ice ages. Two main possibilities of glacial survival of alpine plant taxa have been discussed, namely (1) total extinction within glaciated areas, survival in peripheral refugia, and subsequent re-immigration into vacant areas after the retreat of glaciers (*tabula rasa* hypothesis) and (2) long-term *in-situ* survival within glaciated regions in ice-free locations above the ice-shield (nunataks) and spread into neighbouring, vegetation-free areas after glaciations (nunatak hypothesis). Based upon floristic and geological biogeographic literature, a map was drawn showing potential peripheral refugia and the according migration routes into the Central Alps, as well as the main high-alpine nunatak areas. This map is proposed to provide a basis for further discussions and investigations on the historical biogeography of alpine plants.

*Key words*: Alpine plants, glacial refugia, historical biogeography, middle part of the Alps, nunataks, postglacial colonisation.

Modern molecular techniques offer the possibility to answer specific biogeographic questions, which can not be investigated by morphological, paleobotanical or floristic means. Recent molecular studies sought to understand the relationship between a plant species' present-day distribution, regional genetic diversities and the history of its populations (Soltis et al. 1997; Taberlet et al. 1998). A major topic of historical biogeography is to evaluate how geological and climatic events have influenced the evolutionary diversification of plants in space (Comes & Kadereit 1998). For instance, exact locations of peripheral glacial refugia of European trees have been determined using molecular techniques (Ferris et al. 1995; Demesure et al. 1995; Petit et al. 1997; Taberlet et al. 1998), but nearly no such investigations were conducted on alpine plant species (the term 'alpine' is used in the sense of occurrence at elevations above timberline). Therefore, there is still a debate about the fate of mountain plants of the Alps during Quaternary glaciations. There are two alternative views how alpine plant species reacted to glaciation, namely (1) total extinction in glaciated areas and survival in peripheral or periglacial refugia, followed by re-immigration into vacant areas after the retreat

of glaciers (*tabula rasa* hypothesis), or (2) long term *in-situ* survival on ice-free mountains within glaciated areas (nunataks) and subsequent spread into neighbouring areas after glaciation (nunatak hypothesis). While some molecular biogeographic studies have been conducted in arctic-alpine plants in Scandinavia (Abbott et al. 1995; Gabrielsen et al. 1997; Tollefsrud et al. 1998), only few such studies were made on mountain plants in the Alps. So far, Bauert et al. (1998) studied a rare glacial relic and Hungerer & Kadereit (1998) were mainly interested in systematic relationships. No general conclusions on the locations of glacial survival can be drawn from these two molecular investigations. The present report summarizes the non-molecular knowledge on the geographic locations of potential peripheral refugia and supraglacial nunataks of alpine plant species during Quaternary glaciations in the middle part (Landolt 1992) of the Alps , mainly the Swiss Alps (without Jura mountains). It thus seeks to give a basis for further studies on the plant biogeography of the Alps.

Investigations on biogeographic questions hitherto mainly relied on distribution patterns of alpine plant species. Locations of glacial survival on nunataks or in peripheral refugia and corresponding migration routes into the Central Alps were in most cases geographically very precisely documented by Chodat & Pampanini (1902), Briquet (1906) and Brockmann-Jerosch & Brockmann-Jerosch (1926). These authors' ideas on the biogeography and evolution of alpine plant species were further developed by Merxmüller (1952, 1953, 1954), Favarger (1958), and Hess et al. (1967), but the main principles remained unchanged. (1) Chodat & Pampanini (1902) and Briquet (1906) proposed the *tabula rasa* hypothesis, i.e. all present-day alpine plant species had to re-immigrate from refugia outside the main glaciated parts of the Alps. For the flora of the middle Alps, Chodat & Pampanini (1902) postulated an east-alpine peripheral refugium in the region between the lakes of Garda and Como, i.e. the Judicaric Alps, and a west-alpine peripheral refugium in the Grajic and Cottic Alps. They thought that species migrated from these refugia along the southern alpine foothills and crossed the high mountain chains via the lowest passes. Accordingly, the Valais in Switzerland was colonised from the Piemont, Valle d'Aosta and Cogne over the passes Great St. Bernard, Ferret, Theodul, Simplon or Nufenen, while the Engadine was colonised from Val Venosta via the passes of Stelvio, Bernina or Ofen. Briquet (1906) postulated additional peripheral refugia. He named one in the southern Lepontic Alps, a jurassic-rhodanic one in the South of Lyon up to southern parts of the Jura mountains and some peripheral, nunatak-like refugia at the edge of the Northern Alps. Chodat & Pampanini (1902) and Briquet (1906) believed that the immigration of plants along main alpine valleys (Rhone valley, Tyrolean Inn valley) was impossible because of the long persistence of slowly retreating glaciers. (2) Brockmann-Jerosch & Brockmann-Jerosch (1926) realized that the present distribution of alpine plant species is often not in accordance with the above migration routes out of peripheral refugia. Brockmann-Jerosch & Brockmann-Jerosch (1926) therefore believed in the existence of high-alpine, supraglacial and seasonally snow-free nunataks. During the Würm glacial maximum (20-18 ky AD) several ice domes existed in the Central Alps, i.e. maximum upper limit of the ice in respective regions, from where the ice surface declined in altitude to all sides. Such ice domes were found for instance in the headwaters of the Rhine river, in the Upper Rhone valley or in the Upper Engadine, where the ice reached a minimum altitude of 2700, 2900 and 3000 m a.s.l., respectively. Supraglacial mountains existed in all mentioned regions (Florineth 1998; Florineth & Schlüchter 1998). Only small mountain tops, ridges or southerly exposed slopes potentially harboured the relic plant populations during glaciation. These habitat patches were potentially snow-free during summer because of their exposition to radiation and extreme wind conditions. Populations surviving on such high-alpine nunataks acted as sources for re-colonisation of vacant areas after glaciation (Brockmann-Jerosch & Brockmann-Jerosch 1926). A major argument in favour of the nunatak hypothesis is that some re-

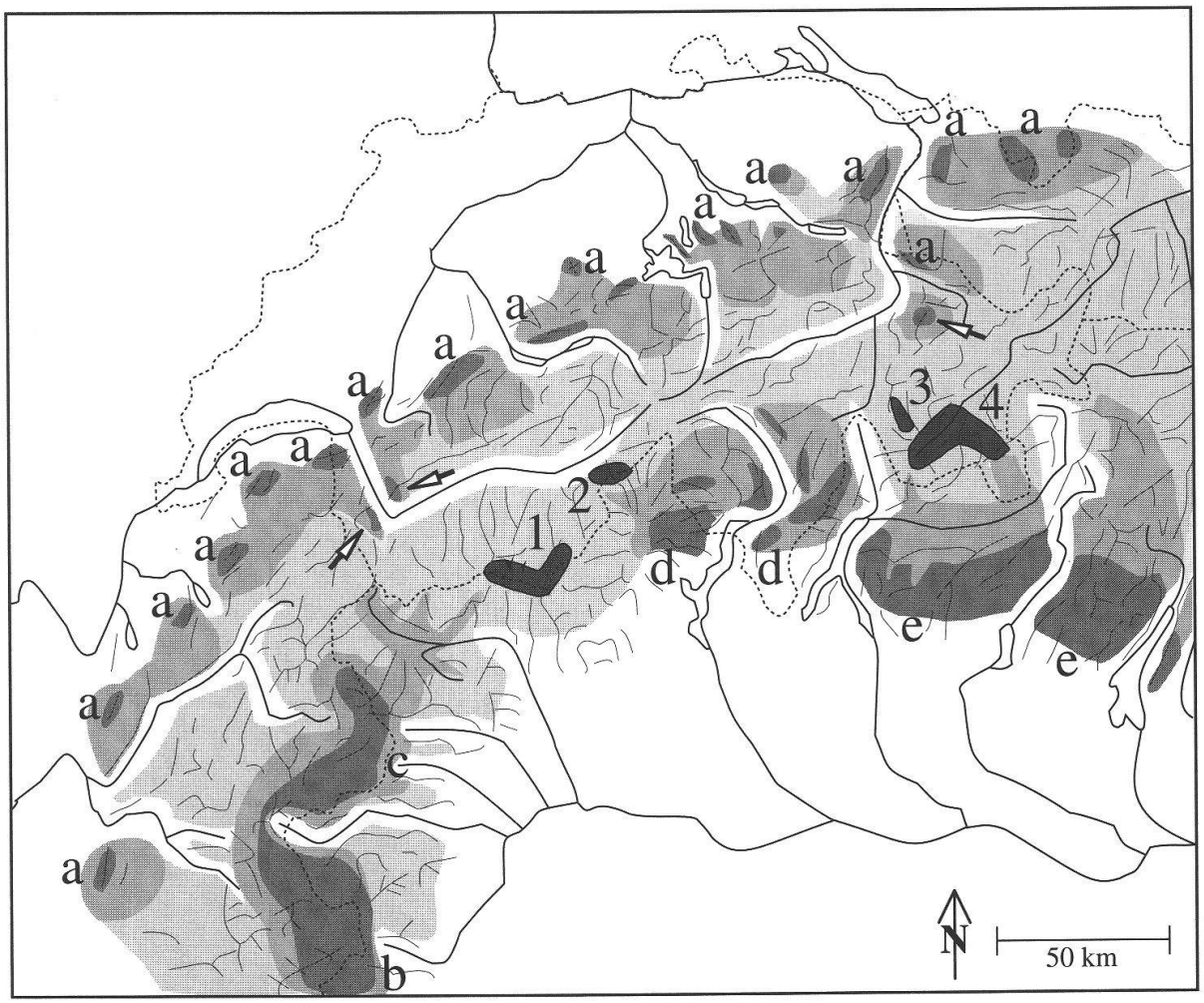


Fig. 1. Postulated nunatak areas and peripheral refugia in the middle part of the Alps during the Pleistocene according to biogeographic literature (Chodat & Pampanini 1902; Briquet 1906; Brockmann-Jerosch & Brockmann-Jerosch 1926; Hess et al. 1967; Hantke & Jäckli 1978). Proposed peripheral refugia are denoted with letters (a – e) and the according migration routes towards the Central Alps with a transgression of shadings from dark grey to light grey. The middle intensity of grey shows the main direction of re-immigration, but does not illustrate a defined postglacial moment. Indicated with black and with numbers (1 – 4) are putative high-alpine nunatak areas within formerly most intensively glaciated regions of the Central Alps. Potential peripheral refugia: (a) northern alpine refugia; (b) Cottic peripheral refugium; (c) Grajic peripheral refugium; (d) Lepontic peripheral refugia; (e) peripheral refugia between the lakes of Como and Garda. Potential nunatak areas: (1) southern valleys of Visp; (2) Simplon; (3) Avers; (4) Upper Engadine. Indicated with arrows are never glaciated areas within the Central Alps, from West to East, Dents du Midi, Dents de Morcle, Rothorn-mountains near Arosa.

gions, which should be migration (sink) areas according to the *tabula rasa* hypothesis, are 'hot-spots' according to species diversities (e.g. valleys of Visp with Zermatt; Becherer 1972; Welten & Sutter 1982). Proposed floristically rich nunatak regions are mountain ranges of the Monte Rosa and of the valleys of Visp, the Simplon, the Rothorn-mountains near Arosa, the Avers, the high mountains of the Engadine and the Bernina (Brockmann-Jerosch & Brockmann-Jerosch 1926).

Additional information on the historic biogeography of alpine plant species could be provided by paleobotanical data. Geographic mapping of radio-dated pollen spectra and macrofossiles has been a powerful tool for evaluating changes in distribution areas and abundance shifts of plant species (Lang 1994; Burga & Perret 1998). However, fossil data are strongly biased towards trees, wind-pollinated plants and wetland species. Fossils of alpine plant species are especially rare because of scarcity of bogs above the timberline (Lang 1994). Moreover, the fossil record is limited in morphological and hence taxonomic resolution and does often not offer the possibility to assign material to species and specific evolutionary lineage (Burga & Perret 1998). Therefore, no specific hypotheses could so far be formulated for exact locations of peripheral refugia or nunataks of non-woody and alpine plant species based on paleobotanical data.

The geographical location of never glaciated areas within ice shields is another possibility to deduce upon refugia (Chodat & Pampanini 1902; Briquet 1906; Hantke & Jäckli 1978; for a critique of the approach see Brockmann-Jerosch & Brockmann-Jerosch 1926). The never glaciated areas within the largest expansion of the ice-shield during Pleistocene (Riss glaciation; 230–130 ky AD) of the middle part of the Alps are shown on a map given in Hess et al. (1967: p. 24). They are mainly situated at the edge of the Northern Calcarious Alps and in the southern Lepontic Alps. Among the never glaciated areas of the Northern Alps are the highest Allgäuer Alps, the Rhaetikon, the mountain ranges of Glarus and around lake Lucerne, including the Pilatus, Schrattenflue and Napf, the mountains north of the lakes of Brienz and Thun, the Prealps of Fribourg, Rochers de Naye, and large parts of the Alps of the Haute-Savoie. Two never glaciated areas within the Central Alps are the Rothorn-mountains near Arosa and the relatively small, isolated Dents de Morcle and Dents du Midi. Among the never glaciated areas in the Lepontic Alps are parts of the Alps of Ticino, the mountains north of Verbania and the mountain chain west of the lake of Como (mountains of Cressem to Camoghé). The northern-most, never glaciated area south of the Alps are parts of the mountain chain between Valle di Leventina and Valle di Blenio (Hess et al. 1967).

Based on all the above given information, a map was drawn showing the potential peripheral refugia, the according migration routes into the central parts of Alps and the postulated high-alpine nunatak areas (Fig. 1). This map is proposed to be a provisional basis of further discussion and for investigations on historical biogeography of alpine plant species (e.g. Stehlik et al. in press). It is open for refinement or fundamental changes.

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## Zusammenfassung

Seit dem Ende des letzten Jahrhunderts wird die Frage, wie und wo Alpenpflanzen die Eiszeiten des Quartärs überlebt haben, kontrovers diskutiert. Zwei alternative Ansichten wurden vertreten, nämlich (1) großflächiges Aussterben in den vereisten Gebieten, gleichzeitiges Überleben in peripheren Refugien und anschließende Einwanderung der heute vorkommenden Alpenpflanzenarten in die vegetationsfreien Flächen der Zentralalpen nach dem Rückzug der Gletscher (*tabula-rasa*-Hypothese), und (2) Überleben der alpinen Pflanzenarten innerhalb der vergletscherten Bereiche der Zentralalpen auf eisfreien Flächen oberhalb des Eisschilds (Nunatakker) und Ausbreitung in benachbarte, vegetationsfreie Gebiete nach der Ver-

eisung (Nunatak-Hypothese). Basierend auf floristischer und geologisch-biogeographischer Literatur wurde eine Karte gezeichnet, worin die potentiellen peripheren Refugien und die entsprechenden Migrationswege daraus in die Zentralalpen, sowie die postulierten hochalpinen Nunatakker-Gebiete enthalten sind. Diese Karte soll als Diskussionsgrundlage für weitere historisch-biogeographische Untersuchungen an alpinen Pflanzenarten dienen.

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