Short title: Paleogene floras of western Greenland and the Faeroes

Project name: PALEOGENE FLORAS OF WESTERN GREENLAND AND THE FAEROE ISLANDS AND THEIR RELATION TO MODERN MID-LATITUDE FLORAS: TESTING THE ARCTOTERTIARY HYPOTHESIS

1. Project description:

1.1. Project goals

Main objective of the project is to test the validity of Engler's (1882) concept of the "arctotertiary element", that is, to determine whether early Cenozoic high latitude floras were the cradle of tree genera now dominating north-temperate mid latitude forests. Furthermore, the climatic and ecological signals contained in these fossil floras will be used to reconstruct the environment that may have triggered the evolution of the "arctotertiary element".

In order to achieve this
(1) the systematic affinities of pollen and spores from Paleocene (Danian and Selandian) sediments of western Greenland and Eocene (Ypresian) sediments of the Faeroe Islands will be established using modern approaches (light microscopy and scanning electron microscopy) to ensure high taxonomic resolution,
(2) existing museum and university collections containing macrofossils from the above mentioned areas will be studied and this will be complemented by collecting new material.

By combining evidence from the revised palyno- and macrofloras, the phylogenetic affinities of the investigated plant taxa will be established in order to determine the proportion of extinct lineages, distantly related to modern taxa, and co-occurring extant genera, representing the "arctotertiary element" in the studied floras.

1.2. State of the art

In 1882, Adolf Engler, in his classical work "*Versuch einer Entwicklungsgeschichte der Pflanzenwelt*", suggested that many tree genera that are dominating north-temperate mid-latitude forests may have evolved from early Cenozoic plants in Arctic regions. Engler's ideas were fuelled by the monumental work of Oswald Heer, "*Flora fossilis arctica*", in which Heer described numerous plant fossils from Arctic areas such as Arctic North America, Greenland, and Spitsbergen (Heer, 1868-1883). Because of the physiognomic similarities of early Cenozoic plant taxa from the Arctic to younger Cenozoic and modern plants at lower latitudes and the overall taxonomic similarity of the fossil floras, Engler suggested that the former had provided the stock for the latter. He termed these plants the “arctotertiary element” characterized by “numerous conifers and numerous genera of trees and shrubs, which today predominate in North America, in extratropical Asia, and in Europe” (Engler, 1882, p. 327 [own translation]). Examples for such tree genera are, among many others, *Acer, Betula, Corylus, Fagus, Platanus*, *Quercus,* and *Sequoia*. As a consequence of northern hemisphere cooling (Fig. 1), it is believed that these plants migrated towards lower latitudes in the course of the Cenozoic.

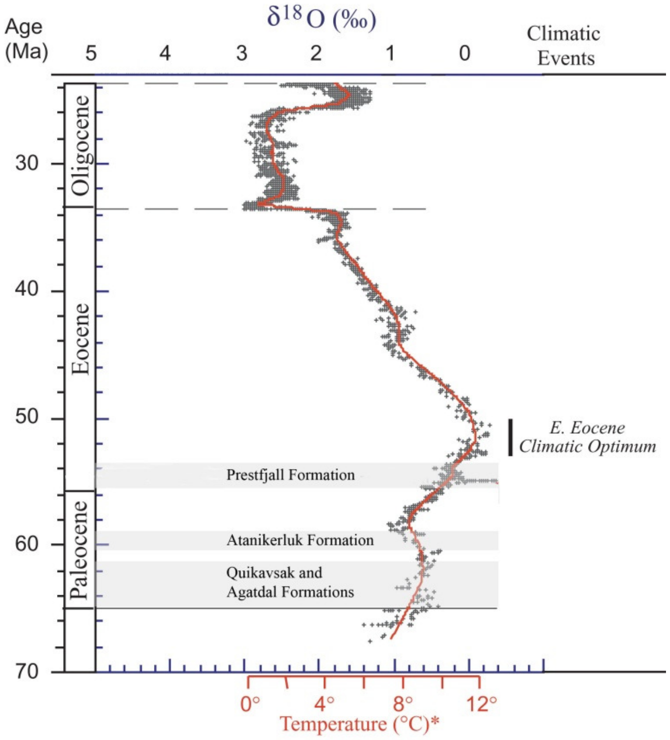

Figure 1: *Global deep-sea oxygen isotope record based on data compiled from DSDP and ODP sites (modified after Zachos et al., 2001). Shaded areas indicate time intervals and Formations in focus (see section* ***1.4.****). The Paleocene formations are situated in western Greenland, the early Eocene Prestfjall Formation on the Faeroe Islands*

Engler’s concept[1] was corroborated later by Hickey et al. (1983), who found that during the Late Cretaceous and early Cenozoic a number of plant and vertebrate taxa appeared in the Canadian High Arctic between 2 to 18 million years before they arrived at mid-latitudes. Hickey et al. (1983) concluded that these taxa probably had their origins in Arctic regions.

More recently, many of the Arctic and northern European early Cenozoic plant taxa have been ascribed to extinct plant genera and the original concept of an arctotertiary element has become unpopular. Boulter & Kvaček (1989) and Kvaček et al. (1994), based mainly on macrofossils, referred most of the plant specimens from the Paleocene of the Isle of Mull (Scotland) and Paleocene to

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[1] The “arctotertiary element” is not equivalent with the “arctotertiary *geoflora*” that was coined by Ralph Chaney in 1959. The arctotertiary geoflora is “a group of plants, which has maintained itself with only minor changes in composition for several epochs or periods of the Earth history” (Chaney, 1959, p. 12). Chaney’s concept was later rejected in several papers by Wolfe (e.g. Wolfe, 1972).

Eocene of Spitsbergen to extinct genera of uncertain systematic affinity. For the Paleocene of Greenland, Koch (1963) assigned most specimens to artificial form-genera. In addition, he listed a number of taxa under the heading "Designs", which means that these taxa are undetermined but somewhat recall taxa previously described from different localities and different ages. Among these are extant genera such as *Alnus*, *Betula*, *Carpinus*, *Cornus*, *Fagus, Magnolia*, and *Quercus*. In a recent monograph on Paleogene plants from Spitsbergen, Budantsev & Golovneva (2009) assigned a large number of woody angiosperms to extant genera, and hence reignited the question about the nature of early Cenozoic high-latitude plant taxa and the relevance of the concept of the arctotertiary element in the sense of Engler (1882) and Hickey et al. (1983).

The aforementioned studies are based on macrofossils. So far, palynological studies focussed on stratigraphic correlation and did not address question whether or not early Cenozoic floras are predominantly composed of extinct genera. Pollen and spores from Ellesmere Island (McIntyre, 1991), Greenland (Croxton, 1978a, b; Hjortkjær, 1991), Spitsbergen (Manum, 1962; Livshits, 1974), and the Faeroe Islands (Laufeld, 1965; Lund, 1983, 1989), have previously been studied. In general, these studies used entirely artificial form-genera and did not aim at assessing the taxonomic (biological) affinities of the recorded pollen and spores. One remarkable exception is the comprehensive study by McIntyre (1991), who recognized numerous extant families and genera among the spores and pollen from the middle Eocene of Axel Heiberg Island. Among these were a large number of genera that are today typical of north-temperate areas in North America, western Eurasia, and East Asia, e.g. *Quercus* Group Quercus (white oaks) and *Fagus*. This would point to an Arctic origin of these genera. However, these records are not the oldest ones for some of the genera. The oldest records of *Fagus*, for instance, are from the early Eocene of western North America (Manchester & Dillhoff, 2004) and possibly from northeastern Asia, indicating a northern North Pacific origin of the genus *Fagus* (Denk & Grimm, 2009b). Hence, it needs to be investigated whether or not these and other taxa were already present in the Paleocene of the older Brito-Arctic Igneous Province floras (Fig. 2). Eventually, all the studies mentioned here are based on light microscopy only and thus their taxonomic resolution is fairly limited. For example, palynologically, intrageneric lineages of *Quercus* can only be distinguished using additional information from SEM (Denk & Grimm, 2009a). The same holds true for the subgenera of *Platanus* (Denk & Tekleva, 2006). Information from high resolution SEM studies of dispersed Miocene pollen enabled Denk et al. (2010) to infer migration routes of particular infrageneric groups of *Quercus*. For the target areas selected for this project, the Faeroe Islands and western Greenland, no study exists that combined results from palynological investigations and evidence from macrofossils.

1.3. Scientific problems addressed

Proportion of modern and extinct plant lineages and taxonomic accuracy

Preliminary studies (own unpublished data; McIntyre, 1991) suggest that in addition to various extinct lineages, several modern genera typical of temperate regions in the northern hemisphere might indeed have been present in the early Cenozoic of the Arctic (*Acer, Aesculus, Alnus, Betula, Carya, Fagus, Quercus, Platanus, Ulmus*); and may partly have originated at high latitudes as suggest by Engler (1882). A detailed palynological study, using the single grain technique, combining light microscopy (LM) and scanning electron microscopy (SEM; Zetter, 1989; see Denk et al., 2011 and Grímsson et al., 2011 for previous such approaches) will provide a taxonomic framework for the palynomorphs encountered in the studied sediments. The combination of LM and SEM will allow for higher taxonomic resolution as compared to previous LM-based studies and recognition of hitherto undetected taxa will lead to a taxon list that depicts more realistically the palaeoflora. For instance, pollen types that are homogeneous when observed under the LM may turn out to belong to various distinct taxa when examined under the SEM (Ferguson et al., 2007; Grímsson et al., 2008; Denk et al., 2010; Grímsson et al., in press; F. Grímsson, D. Ferguson, and R. Zetter, submitted). Small and rare pollen types not considered in conventional LM studies can often be determined when using this approach. For example, a previous LM-based investigation of 10 Ma old sediments from Iceland by Manum (1962) yielded 15 different taxa, whereas Denk et al. (2011), from the same formation reported 90 different pollen taxa. High resolution palynological investigations will address the question, at which point in time and space extant taxa became important elements of Cenozoic high latitude environments. In a second step, the palynological results will be compared to the new and revised macrofossil records. For example, the finding of foliage strongly resembling leaves of *Quercus* in Eocene sediments from Axel Heiberg Island (McIver & Basinger, 1999) may be questioned, because such foliage could have been produced by other plants than oaks. However, additional evidence from the pollen record (McIntyre, 1991 figured pollen unambiguously referable to *Quercus* from the same sediments) lends high credibility to the determination of macrofossils. By this, best possible taxonomic accuracy is ascertained. Two vital questions must be addressed. First, how is the proportion between extinct taxa and taxa representing modern genera? Second, how are taxa belonging to modern genera related to modern taxa? (e.g., are they more closely related to particular modern species, or to infrageneric groups)?

It has repeatedly been argued that modern generic names should not be used for fossil pollen and that the use of form-genera would be less risky and controversial (e.g. Traverse, 2007). In fact, ‘mosaic’ evolution can obscure true relationships of disarticulated plant organs. For example, pollen grains identical to those of a particular modern genus may have been produced by plants very different from the modern genus, and hence come from an extinct, non- or distantly related taxon (Traverse, 2007). We are well aware of this problem. For example, Crane (1989) suggested the possibility that leaves assigned to *Corylus macquarri* Forbes and fruits assigned to the extinct betulaceous genus *Calycites* from the Paleocene of the Isle of Mull (Scotland) were produced by the same plant showing a mosaic of characters found in different extant genera of the Betulaceae. A high-resolution, SEM-supported taxonomic palynological investigation most likely will be able to distinguish pollen types that are intermediary between two or more extant genera of the Betulaceae. Hence, we are confident that possible extinct types are likely to be recognized in the pollen record if the appropriate method is used. The use of artificial, abiological names for dispersed pollen and spores, recommended by Traverse (2007), would be uninformative regarding the objectives of this project. To test the hypothesis of an "arctotertiary element" in the Paleogene Arctic floras requires establishing systematic-phylogenetic (evolutionary) relationships among fossil taxa and between fossil and modern taxa.

Reconstructing biogeographic patterns of extinct plant groups

The extinct Normapolles type pollen with affinities to the Fagales (particularly with Betulaceae, Juglandaceae, Myricaceae, Rhoipteleaceae) had a wide northern hemispheric distribution during the Late Cretaceous and early Cenozoic. While probably absent from the northern North Atlantic during the Cretaceous (cf. Batten, 1981), Manum (1962) figured Normapolles pollen from the early Cenozoic of Spitsbergen. At the same time, according to Lund (1981), no Normapolles pollen occurs in the Eocene of the Faeroe Islands. It is currently unclear whether Normapolles was present in Cretaceous and Cenozoic sediments of western Greenland. Koppelhus & Pedersen (1993) did not encounter any Normapolles pollen in Upper Cretaceous sediments from western Greenland, whereas Ehman et al. (1976) reported *Extratriporopollenites* and *Complexiopollis* from the same formation. To our knowledge, no Normapolles has been reported from the Cenozoic of Greenland. Better insights into the distribution pattern of Normapolles are necessary to understand dynamics of Fagales evolution. Either extinct Normapolles types coexisted with modern members of Fagales, which make up a prominent component of the "arctotertiary element", or a gradual replacement of extinct types with modern types is found. The latter would be indicative of an ancestor-descendant relationship between some of the Normapolles and modern Fagales types.

Reconstruction of biogeographic histories of putative "arctotertiary elements"

In order to understand the origin and evolution of north-temperate woody angiosperms, their biogeographic histories have to be unravelled. Historical biogeography is often understood as the discipline making use of (molecular-based) phylogenetic trees to reconstruct areas of origin for different plant taxa. However, such approaches are based on modern representatives only and areas that are no longer inhabited by a modern plant group are not covered in such studies. For instance, the modern distribution of *Fagus* suggests an East Asian (Chinese) origin of the genus. The incorporation of the fossil record in a holistic evolutionary framework hints towards a high-latitude northern Pacific origin of the genus (Denk & Grimm, 2009).

Similar uncertainties are encountered regarding the origin of other important northern hemispheric tree genera (*Acer; Aesculus; Alnus; Betula; Carya; Fagus; Juglans; Quercus* Group Quercus and Group Lobatae, white oaks and red oaks; *Tilia; Ulmus* etc.) For instance, *Acer arcticum* Heer, found in high-latitude Paleogene floras, may be the oldest known representative of *Acer*, hence, an "arctotertiary element". However, Wolfe & Tanai (1987) questioned its generic identity and regarded it an extinct sister lineage to modern *Acer*. The exact systematic position (in an evolutionary framework) of *Acer arcticum* remains to be determined. The same essentially applies to those specimens from early Cenozoic Arctic sedimentary formations that have been tentatively assigned within genera such as *Alnus, Betula,* etc. (cf. Budantsev & Golovneva, 2009). Because of the modern distribution of temperate tree-genera, the Arctic and subarctic regions bordering the northern North Atlantic have traditionally been underestimated as an important source area for the modern temperate tree flora in the northern hemisphere (but see Denk & Grimm, 2009b). For western Eurasia, in addition to migration from the east after the early Oligocene (because of the closure of the Turgai Seaway), and migration via the North Atlantic (until the latest Miocene, cf. Grímsson & Denk, 2007; Denk et al., 2010, 2011) the Arctic may have played an important role as well.

Evaluating climatic and ecological signals

The floras of the selected key areas were deposited at lower palaeolatitudes than other early Cenozoic Arctic floras (Axel Heiberg and Ellesmere Islands, Spitsbergen, northern Greenland; Smith et al., 2004) but represent a time series from early Paleocene to early Eocene and comprise a period when global temperatures increased culminating in the Early Eocene Climatic Optimum (Fig. 1). It will be evaluated whether the palaeofloras across this time gradient reflect global changes in temperature or whether the generally humid oceanic conditions under which the palaeofloras were deposited compensated for the global change of temperature as inferred from deep sea isotopes (cf. Fig. 1).

Furthermore, the question will be addressed to which degree the palaeofloras from the Faeroe Islands and from western Greenland differ from the higher latitude floras in terms of numbers of deciduous and evergreen taxa. For the floras of the Axel Heiberg and Ellesmere Islands and Spitsbergen monographic studies of both palynomorphs and macrofossils exist and will serve as references for comparison (see McIntyre, 1991 and McIver & Basinger, 1999, for the Axel Heiberg and Ellesmere Islands; Manum, 1962 and Budantsev & Golovneva, 2009, for Spitsbergen). It will be established, whether deciduous plant taxa (*Fagus*, *Quercus* Group Quercus and Group Lobatae, *Acer* etc.) were more prominent elements of the northerly and/or younger palaeofloras or whether they were as well present at the Faeroes and in western Greenland.

Importance of the expected results

The results from the proposed project will be of paramount importance for the understanding of the origin of northern-temperate mid-latitude woody angiosperms (trees and shrubs). Establishing the proportion of true modern genera (the arctotertiary element) in Paleocene and Eocene sediments of the Arctic will have important implications for the understanding of the subsequent (ecological) radiation of these taxa and will shed light on the origin and early evolution of the tree taxa that are among the most important elements of present day temperate forest ecosystems of the northern hemisphere.

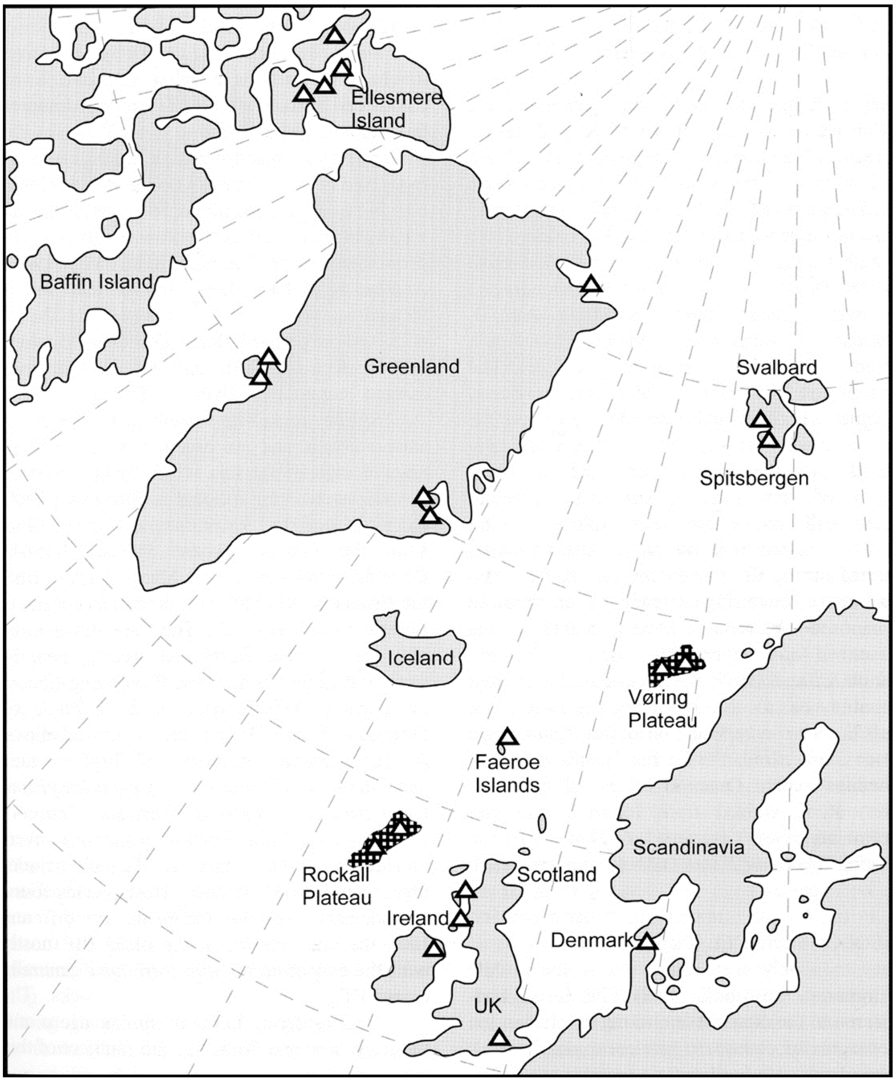


Fig. 2: *Brito-Arctic Igneous province floras in the northern North Atlantic. Localities where Paleocene to Eocene plant fossils have been found, are marked with open triangles, suboceanic localities such as the Rockall and the Vøring Plateaus are outlined with cross-hatching (from Grímsson, 2007).*

In addition, the proposed research project will help better understanding early Cenozoic Arctic and subarctic ecosystems and relationships between North American and European floras of that time. The planned investigation will be the first combined LM and SEM study of early Cenozoic palynomorphs in Arctic areas and the first assessment of the amount of extinct and modern “arctotertiary” genera during this time period at high latitudes.

1.4. Work program

Description of the proposed program

1.4.1. Target areas

The proposed research will focus on two key areas:

(1) Western Greenland, Quikavsak Formation and Agatdal Formation, lower Paleocene, Agatdalen localities and Atanikerluk area; Atanikerluk Formation, middle Paleocene, Atanikerluk area.
(2) The Faeroe Islands, Prestfjall Formation, early Eocene, Suðuroy, Mykines, Vágar, and Tindhólmur islands.

Paleocene sediments in **western Greenland** correspond to the oldest Cenozoic sediments of Brito-Arctic Igneous Province floras (same age as the Paleocene Firkanten Formation in Spitsbergen; Fig. 2). Early Cenozoic sediments of western Greenland have not been subjected to a comprehensive palynological study and previous accounts of the macrofloras are in need of revision. In addition, the early Paleocene locality Atanikerluk of western Greenland has been referred to as the "type-locality" of the "Arctotertiary flora" (Mai, 1991: 29) making it a good candidate for a re-evaluation of Engler's (1882) concept of the arctotertiary element.

Eocene sediments of the **Faeroe Islands** have so far not been comprehensively studied for their palynomorphs and their macrofossils (cf. Rasmussen & Koch, 1963; Lund, 1989). As a matter of fact, only a single species has been described and figured (*Metasequoia occidentalis* (Newb.) Chaney). A previous exploratory field trip to Mykines showed that the composition of macrofossils might be similar to those of other floras of the Brito-Arctic Igneous Province. Also, as mentioned above, the floras of the selected key areas were deposited at lower palaeolatitudes than other early Cenozoic Arctic floras.

1.4.2. Methodology

Stratigraphy and age control

Previous studies on plant-bearing sediments in the early Cenozoic of western Greenland were partly hampered by uncertainties about the correlation between different outcrops. Recently, a comprehensive revision of the lithostratigraphic units and their correlation in the early Cenozoic of western Greenland has been published (Dam et al., 2009). This is crucial, since many formations are part of larger sequences spanning the Cretaceous and early Cenozoic. For example, the name "Atanekerdluk" as used by Heer (1883) may refer to various Upper Cretaceous to lower Cenozoic sediments. Heer's (1883) "Ober- Atanekerdluk A" flora (corresponding to Atanekerdluk I on the map in Heer, 1883, p. 244; Fig. 3a) and "Ober-Atanekerdluk B" flora (Atanekerdluk II on the same map) are distinct parts of the Atanikerluk Formation (Figs 1, 3).

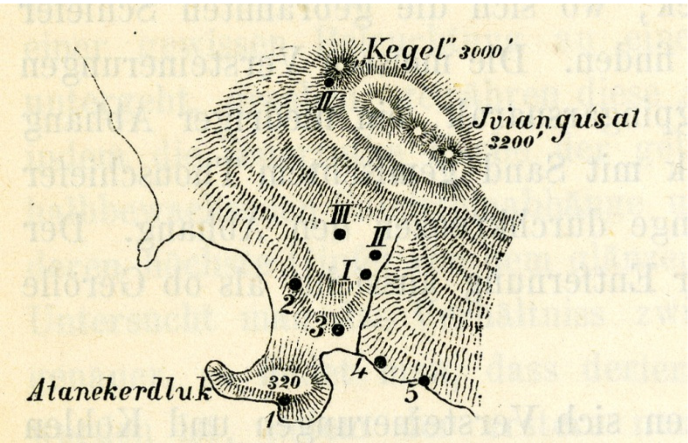
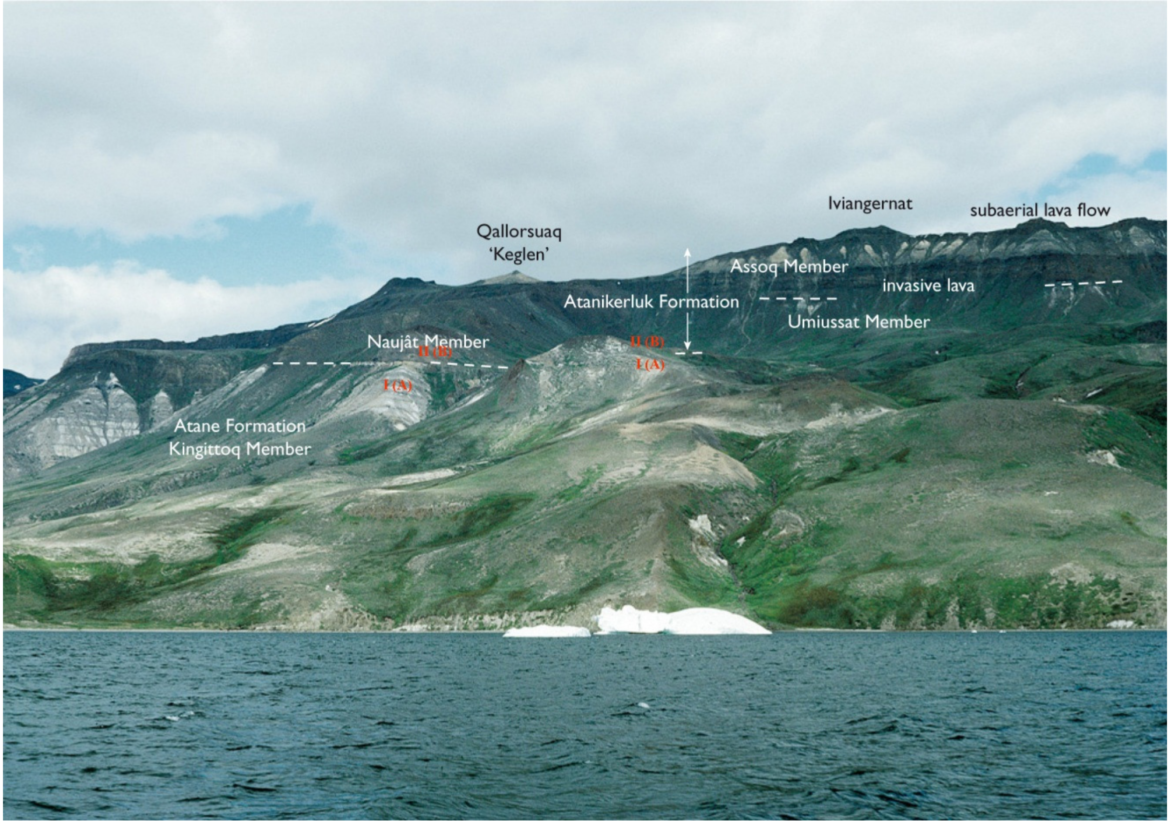


Figure 3: *Lower and middle Paleocene sediments exposed at Atanikerluk ("Atanekerdluk"). **a**. Map by Steenstrup in Heer (1883) indicating the beds I and II (corresponding to Heer's "Ober-Atanekerdluk A and B"). **b**. Photograph showing the same locality. Bed I belongs to the Quikavsak and the Atanikerluk Fm. and bed II to the Atanikerluk Fm.*

a↑ b (from Dam et al., 2009) ↓



Plant-rich localities belonging to the Quikavsak and Agatdal Formations have traditionally been considered to be of different ages (e.g. Heer, 1883; Koch, 1963). Recently, Dam et al. (2009) demonstrated that the Quikavsak and Agatdal Formations are contemporaneous, and are stratigraphically just below the Atanikerluk Formation.

With such a robust stratigraphic framework at hand, it is now possible to correlate several plant-rich outcrops in the region and to determine the exact stratigraphic origin of material in existing museum collections.

The situation on the Faeroe Islands is less complicated than in western Greenland. All plant-bearing sediments belong to the Prestfall Formation (cf. Passey & Jolley, 2009) dated as ca. 54–55 Ma (Fig. 1). This Formation consists of sediments that are bracketed by well-dated basalt below and above.

Palynology

In general, a biological approach to palaeopalynology will be used aiming at assigning dispersed pollen grains to extant families and to extant genera where possible. This is in contrast to the widely used artificial nomenclature for pollen and spores (cf. Traverse, 2007).

Detailed taxonomic studies of palynomorphs will be carried out using a combined LM and SEM investigation. The single-grain technique (Zetter, 1989) allows for investigation of the same grain under the LM and SEM. Furthermore, reliable determinations and a proper taxonomic investigation of dispersed pollen grains can only rely on a combination of LM and SEM (cf. Grímsson et al, 2008; Denk et al., 2010, 2011; Grímsson et al., 2011).

Regarding selection of the palynological samples, see section *1.4.3.*

Macrofossils

Comparative morphological investigations will be carried out. Macrofossils will be compared to coeval fossil taxa and to extant taxa. By this, the amount of taxa will be established that can safely be assigned to modern groups in order to quantify the proportion of "new" arctotertiary elements and old extinct elements. Further, the fossil taxa will be placed into a phylogenetic context to infer possible pathways of evolution leading to the modern taxa that dominate today's north-temperate forest vegetation. This will partly be done by incorporating fossil taxa in morphological phylogenetic analyses (see Denk & Grimm, 2009b) or by establishing closer relationships of fossil taxa to particular modern groups for which (molecular) phylogenies are published.

Taxon lists based on macrofossils and palynological data will be combined in order to reconstruct the palaeoecology and palaeovegtation of the early Cenozoic of western Greenland and the Faeroe Islands.

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