

Fossil leaves as palaeoclimate proxies in the Palaeogene of Spitsbergen (Svalbard)

DIETER UHL^{1*}, CHRISTOFER TRAISSER², URSEL GRIESSER² and THOMAS DENK³

¹Palaeoecology, Institute for Environmental Biology, Faculty of Sciences, Utrecht University, Laboratory of Palaeobotany and Palynology, Budapestlaan 4, 3584 CD Utrecht, The Netherlands; Institut für Geowissenschaften, Universität Tübingen, Sigwartstrasse 10, D-72076 Tübingen, Germany; e-mail: dieter.uhl@gmx.de

*Present address: Villenstraße 13, 67433 Neustadt an der Weinstraße, Germany

²Institut für Geowissenschaften, Universität Tübingen, Sigwartstrasse 10, D-72076 Tübingen, Germany; e-mail: christopher.traisser@uni-tuebingen.de

³Department of Palaeobotany, Swedish Museum of Natural History, P.O. Box 50007, S-10405 Stockholm, Sweden; e-mail: thomas.denk@nrm.se

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ABSTRACT. Since modern Arctic regions are characterized by an icehouse climate no modern vegetation type exists that is comparable to the early Cainozoic vegetation of high latitudes. In addition, many of the plant taxa reported from the early Cainozoic of Arctic areas cannot currently be placed within extant taxa below the rank of families. This makes it difficult to estimate various aspects of palaeoclimate using quantitative approaches. In the present paper four different quantitative palaeobotanical methods are used to estimate palaeoclimate parameters for three floras from the early Palaeocene and the middle Eocene–early Oligocene of Spitsbergen. The methods used are: 1) the Coexistence Approach based on the nearest living relative (NLR) method, 2) leaf margin analysis, 3) the multivariate Climate-Leaf Analysis Multivariate Program (CLAMP) based on leaf physiognomy of modern vegetation mainly from North America and East Asia, and, 4) a recently developed multivariate leaf-physiognomical approach based on modern European vegetation.

Because most NLRs could only be determined with a low taxonomic resolution the Coexistence Approach estimated rather wide ranges for temperature and precipitation for most of the floras investigated. Leaf margin analysis for the Lower Paleocene Firkanten Formation produced an estimate for mean annual temperature (MAT), which is in agreement with other proxies and previous interpretations, but estimates for both Eocene formations appear to be too low. CLAMP produced temperature estimates that are in fairly good agreement with previous palaeoclimatic interpretations for the Palaeogene of the Arctic, as well as most CA estimates. Although estimates for the length of the growing season (GSL) are more or less in accordance with what can be expected for polar regions, estimates for growing season precipitation (GSP) may be slightly too low, especially for the Eocene – Oligocene floras. The European leaf physiognomic approach (ELPA) produced temperature estimates that are consistently lower than all other methods, as well as independent proxies. Accordingly, GSL estimates are rather low and GSP estimates are even lower than those obtained with CLAMP. All methods point to a cooling trend from the Paleocene to the middle/late Eocene – early Oligocene. Such a cooling trend is in agreement with independent data on global and regional climate development during the Palaeogene. In general, leaf physiognomic methods may be taphonomically biased towards specific leaf types and several authors have argued against the use of leaf physiognomic methods calibrated with data from modern vegetation, which cannot be considered a potential analogue for polar forests from the Palaeogene of the Arctic. Nevertheless, our results indicate that only CLAMP, and with some restrictions also CA, seem to be able to produce quantitative estimates for selected palaeoclimate parameters for the Palaeogene of Spitsbergen.

KEY WORDS: leaf physiognomy, Coexistence Approach, palaeoclimate, Palaeogene, Spitsbergen, Arctic

INTRODUCTION

During the early Palaeogene warm climates at high latitudes allowed broad-leaved, deciduous forests to flourish poleward of the Arctic

Circle (Heer 1868, 1870, 1876, Budantsev 1983, Boyd 1990, McIver & Basinger 1999). Because these ecosystems have no living ana-

logue, it is not yet clear how plants and animals inhabiting these forests could cope with the extreme seasonality (i.e. light conditions) at these latitudes (e.g. Royer et al. 2003). Furthermore, most of the plants that occurred on Spitsbergen and other Arctic areas during the Palaeogene appear to represent extinct genera (Kvaček et al. 1994). Because Palaeogene Arctic forests grew under climatic conditions that are so different from present ones, and because their taxonomic similarity to modern plants is low, it is unclear which methods, if any, are best for making quantitative estimates of palaeoclimate parameters (Spicer & Parrish 1990, Boyd 1990, 1994, Basinger et al. 1994, Herman & Spicer 1997, McIver & Basinger 1999, Golovneva 2000a, b). Here, we evaluate some of the advantages and disadvantages of different quantitative techniques for estimating the palaeoclimate of the Palaeogene of Spitsbergen.

At least since the Late Cretaceous Spitsbergen, the largest island of the Svalbard archipelago, has been continuously located at a palaeolatitude north of the Arctic Circle (Harland 1997). Palaeogene fossil floras from Spitsbergen are among the richest from the Arctic (Kvaček & Manum 1997). These floras were initially described by Heer (1868, 1870, 1876), who recognized more than 120 taxa of higher plants, which he assigned to about 35 families. Subsequent taxonomic revisions reduced the number of recognized taxa significantly (Schloemer-Jäger 1958, Schweitzer 1974, Zastawniak 1981, Budantsev 1983, Kvaček & Manum 1993, Kvaček et al. 1994, Golovneva 1997, 2000a, 2002, Birkenmajer & Zastawniak 2005). A comprehensive modern revision of the Palaeogene floras from Spitsbergen, however, has not been published. A planned monograph on the Spitsbergen flora by Budantsev and Golovneva (cf. Kvaček & Manum 1997, Golovneva pers. comm.) has not yet been published.

Based on superficial similarities of the Spitsbergen flora to Neogene floras from Central Europe, Heer (1868, 1870, 1876) assigned a Miocene age to these floras. However, more recent investigations using marine invertebrates and palynomorphs have revealed a Palaeogene age for the plant bearing deposits (Ravn 1922, Manum & Thronsdén 1986). Fossil plants occur in two formations in the Central Basin, as well as some localities

located in the foldbelt at the western margin of Spitsbergen (Fig. 1). The Firkanten Formation (Fig. 2), unconformably overlying mid-Cretaceous rocks, is most probably of early Paleocene age (Manum & Thronsdén 1986, Dallmann et al. 1999). Several authors suggested an Early Eocene age for the Aspelintoppen Formation on the basis of micro- and macro-palaeobotanical data (Head 1989, Kvaček et al. 1994), whereas others suggested a middle Eocene – Early Oligocene age, based on micro- and macro-palaeobotanical data (Manum & Thronsdén 1986, Dallmann et al. 1999).

Plant-bearing localities are also known from the Tertiary foldbelt, west of the Central Basin. Here the most important collections come from Ny Ålesund and Renardodden (Fig. 1). The age of the Tertiary strata from Ny Ålesund is not well constrained. Kvaček et al. (1994) suggested a possible correla-

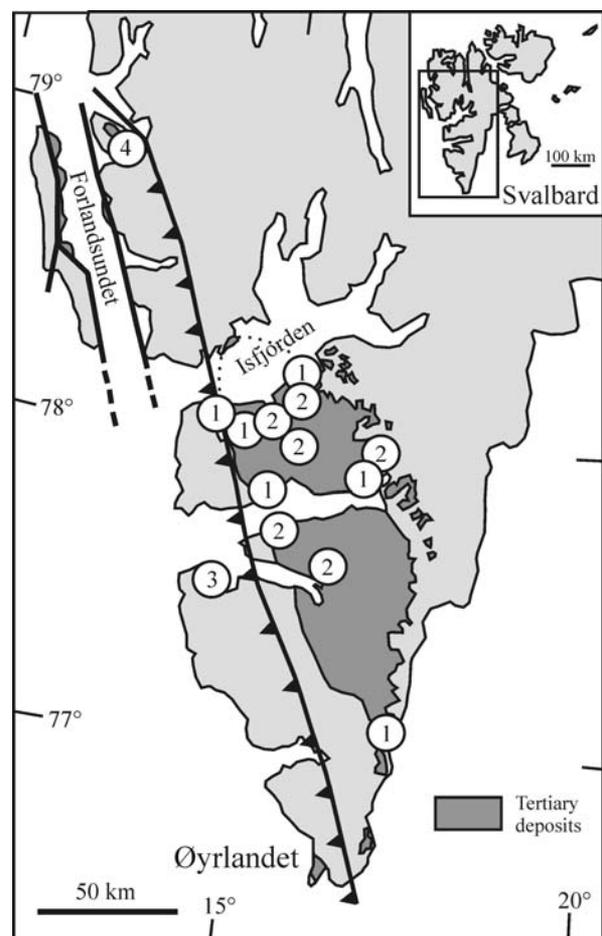


Fig. 1. Simplified geological map of the southern part of Spitsbergen, showing the area of Tertiary deposits in the Central Basin and the outcrops in the foldbelt. Numbers 1–4 refer to the stratigraphic position of the plant bearing localities (1 – Firkanten Formation, 2 – Aspelintoppen Formation, 3 – Renardodden Formation, 4 – Ny Ålesund; cf. Fig. 2). After Denk et al. (1999) modified

tion with the Aspelintoppen Formation based on macroscopic plant remains similarities, whereas most other authors favour a Palaeocene age based on lithostratigraphic correlations (Dallmann et al. 1999). In contrast, the age of the Renardodden Formation has reasonably well been determined as late Eocene–early Oligocene based on dinoflagellates (Head 1984, Dallmann et al. 1999) suggesting an overlap with the upper part of the Aspelintoppen Formation (Fig. 2).

According to Schweitzer (1980), plants from the Firkanten Formation are of paralic origin and grew in coastal bogs. This author distinguished three different plant associations within this formation: 1) marshes fringing large lakes, 2) *Taxodium* swamps, and 3) *Sequoia*, *Ginkgo*, angiosperm mixed forests. For the Aspelintoppen Formation Schweitzer (1980) assumed more continental (limnic) conditions. Here plants are thought to have originated from the borders of big, shallow inland lakes with large meadows of *Equisetum*, fol-

lowed by a succession of *Osmunda* – Fagales-bog forest and a species-rich deciduous forest with abundant *Metasequoia*. In both cases, Schweitzer (1980) assumed that the drier slopes of adjacent mountains were probably inhabited by coniferous forests with *Pinus*, *Picea*, *Tsuga*, and *Pseudolarix*. According to Kvaček et al. (1994) a deciduous habit for all of the floras from the Palaeogene of Spitsbergen is clearly indicated by the physiognomy of the angiosperm foliage and none of the taxa suggests an evergreen habit. This overall impression is furthermore supported by the dominance of remains of *Metasequoia* among the conifers.

In his initial studies of Cainozoic plants from Spitsbergen Heer (1868, 1870) suggested a moderately temperate climate based on comparisons with nearest living relatives (NLRs), which he believed to be comparable to his fossil taxa. In the most detailed study so far on the environment and climate in the Palaeogene of Spitsbergen, Schweitzer (1980)

Age	Bellsund	Kongsfjorden	N	Central Tertiary Basin	S
Oligocene	?				
	Renardodden Formation				
Eocene	?				
	Skilvika Formation				
	?				
				Aspelintoppen Formation	
Paleocene				Battfjellet Formation	
				Frysjaodden Formation	
				Hollandardalen Formation	
				Grumantbyen Formation	
				Basilika Formation	
				Firkanten Formation	
Group	Calypsostranda Group		Van Mijenfjorden Group		

Fig. 2. Stratigraphy of the Palaeogene Calypsostranda and Van Mijenfjorden Groups on Spitsbergen. The plant bearing formations considered in this study are highlighted in grey. from After Dallmann et al. (1999), modified

concluded that the fossil angiosperms from Spitsbergen provide little information about climate. According to this author most of the taxa belong to long extinct groups and can not be assigned with certainty to modern families, a view not in accordance with the interpretations of subsequent authors (Budantsev 1983, Kvaček & Manum 1993, 1997, Kvaček et al. 1994, Denk et al. 1999, Golovneva 2000a, b). Nevertheless Schweitzer (1980) also suggested that those angiosperms, which are assignable to modern genera have NLRs with a warm temperate to cool temperate distribution. Only some alleged coryphoid palm fruits reported by Schweitzer (1980) and Golovneva (2000b) from the Aspelintoppen Formation have been interpreted as being indicative of an even warmer climate. However, this material could not be located in the Schweitzer collection, currently stored at Jena University (Thuringia, Germany; Arndt pers. comm.), and its determination could therefore not be confirmed. There are no coryphoid remains from Spitsbergen in the Stockholm collection (Denk et al. 1999), and the St. Petersburg collection (Budantsev, pers. comm.). Hence, the occurrence of these palms must remain doubtful at the moment and therefore we did not consider this group for our palaeoclimatic interpretation.

In contrast to angiosperms, Schweitzer (1980) considered the conifers from the Palaeogene of Spitsbergen to be excellent climatic indicators. In an earlier work, this author (Schweitzer 1974) determined 15 taxa, which have very close NLRs pointing to a warm temperate climate (MAT about 15–18°C, frosts very rare or absent). Schweitzer (1980) also interpreted distinct growth rings in conifer wood and the high amount of deciduous taxa as indicative of pronounced seasonality of precipitation. However, the distinct growth rings could also reflect potential influences of the seasonal light regimes experienced by these plants. In addition, the conifer taxa chosen as NLR may not provide representative climate data due to their highly relictual modern distributions, as pointed out by Wolfe (1980).

Other investigations, based mainly on conifers and angiosperms, produced palaeoclimate estimates which range from warm temperate (Schloemer-Jäger 1958, Golovneva 2000b) to moderately temperate (Manum 1962), and almost cool temperate (Golovneva 2000b). The latter author's assumptions are not only

based on comparisons with NLRs, but also on a multivariate leaf physiognomic analysis – Climate Leaf Analysis Multivariate Program (CLAMP). Golovneva's results, which are based on the extensive Spitsbergen collections housed at the Swedish Museum of Natural History, Stockholm, as well as the Komarov Botanical Institute in St. Petersburg (Russia), suggested a significant drop in mean annual temperatures (MAT for Firkanten Fm. 12.6°C; Aspelintoppen Fm. 9.5°C; Renardodden Fm. 8.4°C), and in the mean temperatures of the coldest month (CMMT for Firkanten Fm. 6.5°C; Aspelintoppen Fm. 1.5°C; Renardodden Fm. –1.0°C) between the early Paleocene and the middle/late Eocene. In contrast Manum (1994) came to the conclusion that the Palaeogene floras from Spitsbergen do not signal major climatic changes.

Although several palaeoclimate estimates exist for the Palaeogene of Spitsbergen only the CLAMP estimates of Golovneva (2000b) can be regarded as true quantitative estimates, although several investigations have questioned the usability of leaf physiognomy as a reliable quantitative proxy for palaeoclimate parameters in this region (Boyd 1990, 1994, 2000, Basinger et al. 1994). All in all, it is difficult to estimate how reliable all quantitative palaeobotanical methods, not only leaf physiognomic approaches, will work under the non-analogue conditions of the Palaeogene of the High Arctic.

Here we use different quantitative palaeobotanical methods for three Palaeogene floras from Spitsbergen. These methods are based on leaf physiognomy and the NLR approach, and have previously been used for estimating palaeoclimate parameters of fossil floras from the Tertiary of mid-latitude regions (Wing & Greenwood 1993, Wolfe 1993, Wilf 1997, Pross et al. 1998, Utescher et al. 2000, Wing et al. 2000, Uhl et al. 2003, 2006, Liang et al. 2003, Mosbrugger et al. 2005), as well as the Late Cretaceous and Early Palaeogene of Antarctica (Poole et al. 2005).

MATERIAL AND METHODS

MATERIAL

This study is based on the extensive collection of Palaeogene leaves from Spitsbergen, housed at the Swedish Museum of Natural History (S) in Stockholm,

Sweden. The material considered here comes from the Lower Paleocene Firkanten Formation (2510 specimens), the Middle Eocene – Lower Oligocene Aspelintoppen Formation (823 specimens), and 1054 specimens from the Upper Eocene – Lower Oligocene Renardodden Formation (Figs 1, 2). More than 4000 specimens were collected by several Swedish expeditions during the second half of the 19th century and the first decades of the 20th century. Parts of this material have been published by various authors (Heer 1868, 1870, 1876, Schweitzer 1974, Kvaček & Manum 1993, 1997, Kvaček et al. 1994 – for a complete list of publications see: Denk et al. 1999), but the greater part of the Stockholm collection still remains unpublished (Denk et al. 1999).

In this work we follow the (preliminary) taxonomic approach outlined in Kvaček et al. (1994) and Kvaček and Manum (1997). This implies that in many cases leaves have been assigned to form genera, because they cannot be placed within particular modern genera based on leaf morphological characters only. Some characteristic taxa from the Palaeogene of Spitsbergen and their corresponding leaf physiognomy are shown in Figure 3 and Plates 1 and 2.

A state of the art overview of the taxonomy and stratigraphic distribution of the material housed in the Stockholm collections has recently been published by Denk et al. (1999). A list of the taxa used for this study, their occurrence in the different formations, and their assumed NLRs is presented in Table 1. For our purposes we combined all taxa from the individual sampling localities within each of the three formations considered here. Although this procedure combines floras of quite different age, especially in the case of the Aspelintoppen Formation, we gain the advantage of combining plants found in different depositional environments. This gives a more complete picture of the source vegetation than can be obtained from a single locality or facies, and increases the number of species, and therefore the robustness, of palaeoclimatic estimates (although the number of taxa that could be

used for the leaf physiognomic analysis is still rather low for the individual formations).

METHODS

We compared the results of three widely used techniques of palaeoclimatic analysis: 1) the Coexistence Approach (CA) which is based on the nearest living relative (NLR) concept (Mosbrugger & Utescher 1997), 2) leaf margin analysis (LMA) after Wolfe (1979) and Wilf (1997), and, 3) CLAMP, a multivariate method using leaf physiognomy, based on a modern calibration data set covering mainly North America and East Asia (Wolfe 1993, 1995, Wolfe & Spicer 1999). Additionally, we used a recently developed alternative multivariate approach, which uses a calibration data set compiled from European woody angiosperms (Traiser 2004, Traiser et al. 2005, Uhl et al. 2006). We only reconstructed climate features that can be obtained from more than one of the methods we seek to compare: mean annual temperature (MAT), mean temperature of the warmest month (WMMT), mean temperature of the coldest month (CMMT), mean annual precipitation (MAP), length of the growing season (GSL), growing season precipitation (GSP).

Coexistence Approach

The Coexistence Approach (CA) is a largely computer-based modification of the NLR-approach. CA compares, for a given climatic parameter (e.g., MAT), the ranges of as many as possible NLRs of an individual fossil flora and determines the interval in which most of the NLRs should theoretically be able to coexist. This interval is then assumed to represent a range of the chosen climatic parameter in which the fossil plants may have been able to coexist. The advantages and disadvantages of this method have been discussed repeatedly (Mosbrugger & Utescher 1997, Uhl et al. 2003), and it has been used by various authors to estimate selected palaeoclimatic parameters from

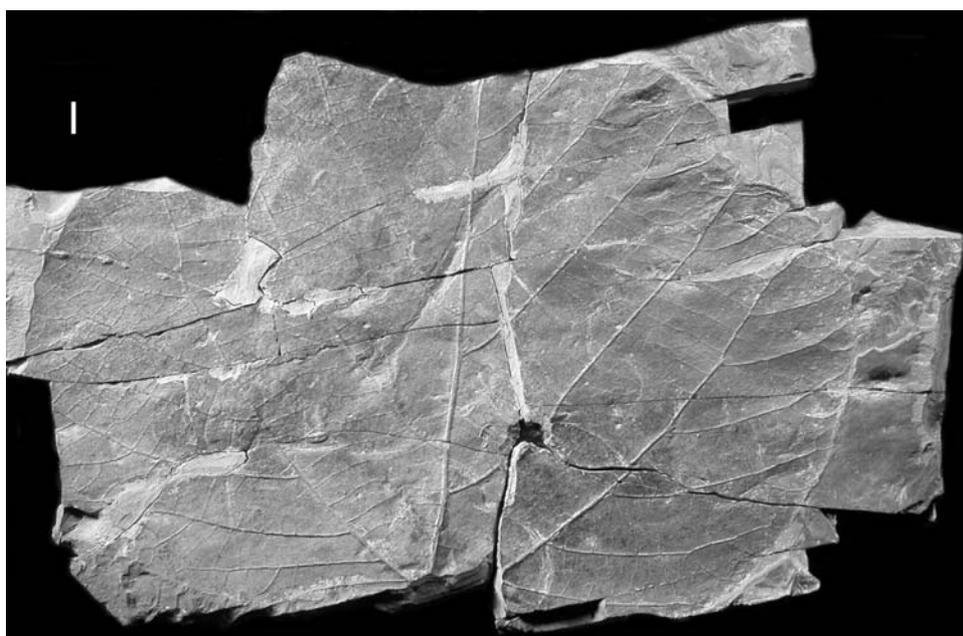


Fig. 3. Very large leaf of unknown taxonomic affinity, S051799, Kolfjellet, Firkanten Formation. Scale bar – 1 cm

European Tertiary floras (Mosbrugger & Utescher 1997, Pross et al. 1998, Utescher et al. 2000, Uhl et al. 2003, 2006, Mosbrugger et al. 2005), East Asian Neogene floras (e.g. Liang et al. 2003), and Late Cretaceous and Early Palaeogene floras from Antarctica (Poole et al. 2005).

Climatic parameters for the individual NLRs were taken from the CLIMBOT database on which the CA is based (cf. Mosbrugger & Utescher 1997). A number of fossil taxa were not included into the CA analysis because their taxonomic affinities are not sufficiently resolved (*Celastrinites*, *Elatocladus*, among others). Others can be compared to modern taxa at the genus or family level, and, in case of some conifers, at the species level (cf. Table 1). In case of *Aesculus* we did

not follow Kvaček et al. (1994) but considered the fossil species to belong to the modern genus based on the presence of entire palmate leaves in the St. Petersburg collection (cf. Golovneva 2000a). Also in case of *Ulmites ulmifolius* we did not follow Kvaček et al. (1994) but rather Nathorst (1910) and Budantsev (1983) considering these leaf remains to belong to the modern genus *Ulmus*. Similar leaves have been reported in association with *Ulmus* fruits from the middle Eocene of western North America (Denk & Dillhoff 2005). The modern range of *Cercidiphyllum* clearly reflects a relict distribution and we are aware of the potential pitfalls using relict taxa as NLR. Despite this, *Cercidiphyllum* was used as NLR for *Trochodendroides*, since today the family Cercidiphyllaceae is monotypic

Table 1. List of identified taxa from the Palaeogene of Spitsbergen housed in the collections of the Swedish Museum of Natural History and their occurrence in the individual stratigraphic horizons, together with their corresponding NLRs. (NLRs used for the CA in **bold**. In case of taxa which are nowadays monospecific and therefore have probably very restricted climatic requirements, as compared to their fossil counterparts, the corresponding family has been used for CA instead of this taxon. F.-Fm. – Firkanten Formation, A.-Fm. – Aspelintoppen Formation, R.-Fm. – Renardodden Formation)

Fossil taxon	F.-Fm.	A.-Fm.	R.-Fm.	NLR
<i>Acer arcticum</i> Heer	X	X	X	Acer
<i>Aesculus longipedunculus</i> Schloem.-Jäg.		X		Aesculus
“ <i>Betula</i> ” sp.		X		? <i>Betula</i>
<i>Celastrinites septentrionalis</i> (Krysht.) Golovn.	X	X	X	indet.
<i>Coniopteris blomstrandii</i> (Heer) Kvac. & Man.		X		indet.
“ <i>Cornus</i> “ <i>hyperborea</i> Heer			X	indet.
<i>Corylites hebridicus</i> Sew. & Holt.	X	X	X	Betulaceae
<i>Craspedodromophyllum malmgreeni</i> (Heer) Golovn.	X	X	X	? Betulaceae
<i>Craspedodromophyllum</i> sp. div.	X	X	X	? Betulaceae
<i>Cupressinocladus interruptus</i> (Newb.) Schweit.	X			Cupressaceae
cf. <i>Dombeyopsis</i> sp.		X		? Sterculiaceae
<i>Elatocladus olriki</i> (Heer) Bell	X			indet.
<i>Equisetum arcticum</i> Heer complex	X	X	X	<i>Equisetum</i>
Fagales indet.	X	X	X	Fagales
<i>Ginkgo spitsbergensis</i> Man.	X	X		<i>Ginkgo biloba</i>
<i>Glyptostrobus nordenskiöldii</i> (Heer) Br.	X		X	<i>Glyptostrobus lineatus</i> (Taxodiaceae)
<i>Grewiopsis pterospermoides</i> Budantsev	X	X		indet.
<i>Haemantophyllum nordenskiöldii</i> (Heer) Boul. & Kvac.			X	Alismataceae
? Juglandaceae gen. et sp.			X	? Juglandaceae
<i>Koelreuteria borealis</i> Heer			X	Koelreuteria
<i>Macclintockia dentata</i> Heer		X		monocot foliage
“ <i>Macclintockia</i> “ <i>tenera</i> Heer			X	monocot foliage
“ <i>Majanthemophyllum</i> “ <i>boreale</i> Heer	X			indet.
<i>Metasequoia occidentalis</i> (Newb.) Chan.	X	X	X	<i>Metasequoia glyptostroboides</i> (Taxodiaceae)
<i>Nordenskiöldia borealis</i> Heer	X	X	X	Trochodendraceae
<i>Nyssidium arcticum</i> (Heer) Ilj.	X		X	Cercidiphyllaceae
<i>Nyssidium ekmannii</i> Heer	X		X	Cercidiphyllaceae
<i>Osmunda macrophylla</i> Penh.		X		Osmunda regalis
<i>Parataxodium wigginsii</i> Anl. & Louth.	X		X	? Taxodiaceae
<i>Platanus</i> sp.	X	X	X	Platanus
<i>Pseudolarix septentrionalis</i> Schloem.-Jäg.	X			Pseudolarix
<i>Sequoia langsdorfii</i> (Brgn.) Heer	X		X	<i>Sequoia sempervirens</i> (Taxodiaceae)
<i>Taxodium dubium</i> (Sternb.) Heer	X	X	X	<i>Taxodium distichum</i> (Taxodiaceae)
<i>Trochodendroides crenulata</i> (Heer) Boul. & Kvac.	X		X	Cercidiphyllum
<i>Trochodendroides richardsonii</i> (Heer) Krysht.	X	X	X	Cercidiphyllum
<i>Ulmites ulmifolius</i> (Schloem.-Jäg.) Kvac. Man. & Boul.	X	X	X	Ulmus
<i>Ushia olafsenii</i> (Heer) Boul. & Kvac.	X	X		Fagales
<i>Zizyphoides flabellum</i> (Newb.) Crane, Manch. & Dilch.	X			<i>Trochodendron</i>

and given the wide ecological range of the two living species we do not think that the climate range for this NLR is substantially biased (for instance, the natural climatic range of the two living species comprises the climate conditions found in Stockholm where *Cercidiphyllum* is frequently planted producing fertile seeds; Denk pers. observation).

Leaf margin analysis

Bailey and Sinnott (1915, 1916) were the first to observe a direct correlation between the proportion of dicot woody species with entire margined leaves and MAT in extant vegetation. Subsequently, different modern calibration data-sets have been developed that allow quantitative estimation of MAT values from fossil dicot leaves (Wolfe 1979, Wilf 1997, Kowalski 2002). Here we used a regression equation based on a modern dataset from mesic forests of East Asia (Wolfe 1979, Wing & Greenwood 1993) that describes the correlation between the proportion of woody species with entire-margined leaves in a flora (P) and mean annual temperature (MAT):

$$\text{MAT} = 30.6P + 1.14$$

The regression error of this equation is $\pm 0.78^\circ\text{C}$ (Wing & Greenwood 1993), but here we report the (generally larger) error due to binomial sampling as calculated by Wilf (1997; his equation 4):

$$\sigma_{\text{MAT}} = c \sqrt{\frac{P(1-P)}{r}}$$

where P represents the proportion of leaf species with entire margins, r the total number of species in the flora, and c the constant in the regression equation (here 30.6).

CLAMP

CLAMP (Climate Leaf Analysis Multivariate Program) was introduced by Wolfe (1993) and since then has been developed further by a number of authors (Wolfe 1995, Kovach & Spicer 1996, Wolfe & Spicer 1999). In contrast to leaf margin analysis CLAMP uses up to 31 physiognomic characters simultaneously (e.g. leaf margin type, details of tooth morphology, leaf size, leaf length:width ratio, leaf shape). The multivariate physiognomic data set is analysed by Canonical Correspondence Analysis, a direct ordination method, widely used in plant ecology (Ter Braak 1986). The current version of the modern data set (CLAMP3) consists of 173 (CLAMP3A) or 144 (CLAMP3B) leaf samples respectively, mainly from North America and East Asia. The slightly larger CLAMP3A subset includes a well-defined, so-called, subalpine nest of floras from high altitudes or latitudes with leaf physiognomies adapted to freeze-induced drought (Wolfe & Spicer 1999). Although inclusion of the subalpine sites may be important for studies of Tertiary elevation changes (Povey et al. 1994, Wolfe et al. 1998), and high-latitude Neogene floras (Wolfe 1994), the almost frost-free conditions in the High Arctic during the Palaeogene (Schweitzer 1980, Wing & Greenwood 1993, Markwick 1998) suggest that the subalpine sites should be excluded from the modern calibration set for this study. Nevertheless we performed our CLAMP analysis with both calibration data-sets.

All calculations for CLAMP were performed with the software-package CANOCO 4.02 for Windows and the pre-programmed spreadsheet-files provided by R.A. Spicer at the CLAMP web-site (<http://tabitha.open.ac.uk/spicer/CLAMP/Clampset1.html>).

European Leaf Physiognomic Approach (ELPA)

This method uses a grid-based (0.5° lat – 0.5° long) calibration dataset that, at the moment, comprises 1835 synthetic floras (Traiser et al. 2005). A synthetic flora at a specific geographical coordinate is defined by the list of taxa whose distribution maps cover that locality (Klotz 1999, Klotz et al. 2003). These synthetic floras have been generated with the aid of distribution maps of 108 woody angiosperm taxa, which have been physiognomically characterized based on floristic manuals. Synthetic floras included in the actual calibration dataset are restricted to grid-cells with more than 25 taxa and an elevation between 0 and 400 m above sea-level. Details of this data-set are discussed in Traiser et al. (2005). Physiognomic data and climatic data (from New et al. 1999) are processed with Redundancy Analysis (RDA), an alternative direct ordination technique, using CANOCO 4.02 for Windows in analogy to the CLAMP-procedure (Traiser 2004, Traiser et al. 2007).

This method has already been applied successfully to palaeofloras from the European Tertiary (Traiser 2004, Uhl et al. 2006), and we included this approach to get an idea about its applicability of the underlying calibration dataset under the non-analogous conditions represented by Palaeogene floras in the High Arctic.

The leaf physiognomic characterization of the individual floras used for all three physiognomic approaches is given in Table 2.

RESULTS

COEXISTENCE APPROACH

Potential NLRs for most of the fossil taxa from the Palaeogene of Spitsbergen could only be determined with a low taxonomic resolution (cf. Tab. 1). Looking at the taxa, which are responsible for the upper and lower limits of the intervals of coexistence for the individual palaeoclimate parameters and flora, we see that only a few taxa are limiting (Tab. 4). CA estimates for WMMT have a rather wide range for all three floras (Tab. 3; Fig. 4). Lower limits for MAT, CMMT, and MAP are significantly higher for the Firkanten Formation than for both other floras, whereas the upper limits do not differ except for WMMT. The warmer lower limits for MAT and CMMT at the Firkanten Formation are due to the presence of *Pseudolarix* in this flora. If this taxon would be omitted from our analysis the lower limits

Table 2. Leaf physiognomic characterization for the three investigated palaeofloras from the Palaeogene of Spitsbergen. For definition of the individual characters see Wolfe (1993, 1995), Traiser (2004), and Traiser et al. (2005)

Physiognomy	Firkanten Formation	Aspelintoppen Formation	Renardodden Formation
Lobed	5.0	7.1	1.9
No Teeth	44.4	15.8	18.2
Teeth Regular	52.8	63.2	50.0
Teeth Close	33.3	57.9	59.1
Teeth Round	58.3	39.5	45.5
Teeth Acute	33.3	44.7	45.5
Teeth Compound	16.7	26.3	13.6
Nanophyll	0.0	0.0	0.0
Leptophyll I	0.0	0.0	0.0
Leptophyll II	0.0	0.7	0.0
Microphyll I	0.0	0.7	4.8
Microphyll II	21.5	17.5	28.4
Microphyll III	32.0	29.4	34.5
Mesophyll I	17.1	19.1	15.2
Mesophyll II	10.1	14.4	7.2
Mesophyll III	19.3	18.0	9.8
Apex Emarginate	0.0	0.0	0.0
Apex Round	23.1	29.4	40.6
Apex Acute	76.9	67.6	59.4
Apex Attenuate.	0.0	2.9	0.0
Base Cordate	40.0	31.6	52.4
Base Round	50.0	60.5	42.9
Base Acute	10.0	13.2	4.8
L:W<1:1	9.4	20.0	13.6
L:W 1-2:1	62.5	65.0	75.0
L:W 2-3:1	21.9	12.5	6.8
L:W 3-4:1	6.3	2.5	4.5
L:W>4:1	0.0	0.0	0.0
Shape obovate	0.0	2.6	1.9
Shape elliptic	53.1	68.4	66.6
Shape ovate	46.9	34.2	31.4
Leaf simple ^{1*}	95.0	95.2	100.0

^{1*} Only used for ELPA

Table 3. Palaeoclimate estimates obtained with the CA for the three investigated palaeofloras from the Palaeogene of Spitsbergen

	Firkanten Formation	Aspelintoppen Formation	Renardodden Formation
MAT min (°C)	15.7	9.1	10.0
MAT max (°C)	17.0	17.0	17.0
WMMT min (°C)	21.7	21.7	21.7
WMMT max (°C)	28.6	27.9	27.9
CMMT min (°C)	2.2	-2.7	-2.7
CMMT max (°C)	6.2	6.2	6.2
MAP min (mm)	979	578	578
MAP max (mm)	1520	1520	1520

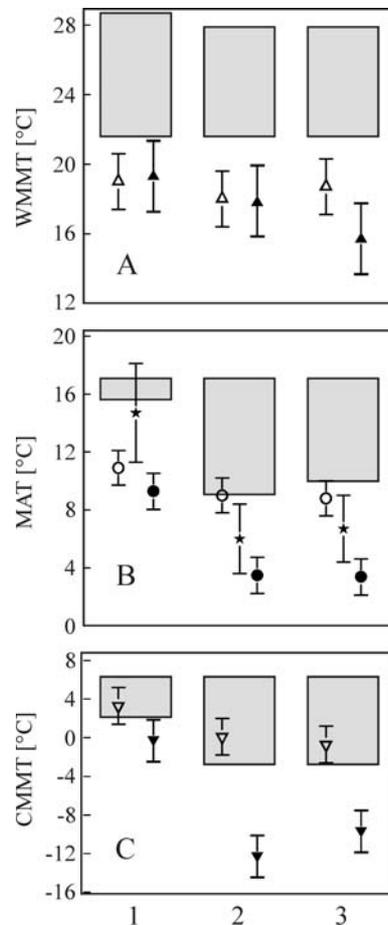


Fig. 4. Graphical comparison of the results for WMMT (A), MAT (B) and CMMT (C) obtained with the different methods. * – LMA, open symbols (Δ , \circ , ∇) – CLAMP3B, solid symbols (\blacktriangle , \bullet , \blacktriangledown) – ELPA, grey boxes – CA. 1 – Firkanten Formation, 2 – Aspelintoppen Formation, 3 – Renardodden Formation. (cf. Tabs 2, 4–6)

of both parameters would be the same as in the Aspelintoppen and Renardodden formations. CA estimates for the Aspelintoppen and Renardodden formations do not differ significantly from each other, only the lower limit of MAT is slightly higher for the Renardodden Formation (<1°C difference). WMMT estimates from CA are significantly warmer than any estimates obtained by the physiognomic methods used in the present study.

It should be noted that by excluding the relictual *Cercidiphyllum* as a potential NLR from the CA analysis the intervals of coexistence for all parameters where this taxon defines the upper or lower limits become wider obscuring any differences between the individual floras.

LEAF MARGIN ANALYSIS

LMA provides only estimates of MAT (Tab. 5; Fig. 4). Our results indicate a significant drop of MAT from the Lower Paleocene

Table 4. List of the taxa which set the limits of the intervals of coexistence for the three floras from the Palaeogene of Spitsbergen

Firkanten Formation	NLR taxa	
	lower limit	upper limit
MAT	<i>Pseudolarix</i>	<i>Cercidiphyllum</i>
WMMT	<i>Cercidiphyllum</i>	<i>Acer</i>
CMMT	<i>Pseudolarix</i>	<i>Cercidiphyllum</i>
MAP	<i>Pseudolarix</i>	Taxodiaceae
Aspelintoppen Formation	NLR taxa	
	lower limit	upper limit
MAT	Taxodiaceae	<i>Cercidiphyllum</i>
WMMT	<i>Cercidiphyllum</i>	<i>Cercidiphyllum</i>
CMMT	Taxodiaceae	<i>Cercidiphyllum</i>
MAP	<i>Cercidiphyllum</i>	Taxodiaceae
Renardodden Formation	NLR taxa	
	lower limit	upper limit
MAT	<i>Koelreuteria</i>	<i>Cercidiphyllum</i>
WMMT	<i>Cercidiphyllum</i>	<i>Cercidiphyllum</i>
CMMT	Taxodiaceae	<i>Cercidiphyllum</i>
MAP	<i>Cercidiphyllum</i>	Taxodiaceae

Table 5. Palaeoclimate estimates obtained with LMA for the three investigated palaeofloras from the Palaeogene of Spitsbergen

	Firkanten Formation	Aspelintoppen Formation	Renardodden Formation
MAT [°C]	14.7	6.0	6.7
Stand. dev. [°C]	3.4	2.4	2.3

Firkanten Formation (warm temperate) to the middle Eocene – Lower Oligocene Aspelintoppen Formation (cool temperate) and no great differences between the Aspelintoppen Formation and the Upper Eocene – Lower Oligocene Renardodden Formation. The standard deviation of the MAT estimate from LMA overlaps with the MAT estimate from CA for the Firkanten Formation, but for the other two formations the LMA estimate is slightly colder than the CA estimate of MAT.

CLAMP

Results obtained with CLAMP calibration sets with and without the subalpine sites are in good agreement with each other (Tab. 6). Except for the Firkanten Formation, CLAMP3B estimates for MAT are in good agreement with the lower boundaries of the estimates obtained from the CA (Tab. 3, Fig. 4). CLAMP3A estimates are slightly lower than CA estimates. CLAMP-based estimates of MAT from the

Table 6. Palaeoclimate estimates obtained with CLAMP3B for the three investigated palaeofloras from the Palaeogene of Spitsbergen

	Stand. dev.	Firkanten Formation	Aspelintoppen Formation	Renardodden Formation
MAT (°C)	1.2	10.9	9.0	8.8
WMMT (°C)	1.6	19.0	18.0	18.7
CMMT (°C)	1.9	3.3	0.1	-0.7
GSL (month)	0.7	6.4	5.4	5.4
GSP (mm)	336	618	357	310

Firkanten Formation are significantly lower. CMMT estimates from CLAMP3B are in good agreement with CA estimates for all three floras. As in the CA and LMA, CLAMP shows a slight reduction of MAT and CMMT from the Firkanten Formation to the Aspelintoppen Formation, and no significant differences can be seen between the two younger assemblages. CLAMP3A estimates for WMMT are slightly lower and CMMT estimates slightly higher, than the CLAMP3B estimates. GSL is estimated to be somewhat longer for the Firkanten Formation than for the other two formations, with slightly shorter estimates obtained with CLAMP3A. The same trend as for GSL can be seen for GSP (also lower for CLAMP3A), however, in this case errors are rather high and overlap markedly.

ELPA

Estimates for MAT and CMMT based on ELPA (Tab. 7) are consistently lower than those from all other methods used here, but WMMT values overlap with CA and CLAMP values (Firkanten Fm., Aspelintoppen Fm.) or only CLAMP values (Renardodden Fm.). Despite the differences in absolute values, ELPA estimates for MAT and CMMT also show a decrease between the Firkanten Formation and the Aspelintoppen Formation, with CMMT values dropping significantly below

Table 7. Palaeoclimate estimates obtained with ELPA for the three investigated palaeofloras from the Palaeogene of Spitsbergen

	SE	Firkanten Formation	Aspelintoppen Formation	Renardodden Formation
MAT (°C)	1.1	9.2	3.5	3.4
CMMT (°C)	2.2	-0.2	-12.2	-9.6
WMMT (°C)	2.1	18.2	17.8	15.7
GSL (month)	0.7	5.6	4.5	3.9
GSP (mm)	81.1	356.8	260.8	247.8

freezing point. GSL decreases also between the Firkanten Formation and the Aspelintoppen Formation, with another slight reduction in the Renardodden Formation. Consistent with the lower temperature estimates, the GSL values are below the estimates obtained with CLAMP. Also the GSP for the individual floras is significantly lower than estimated with CLAMP. ELPA estimates of GSP are slightly lower in both Eocene – Oligocene floras, a trend also seen in the CLAMP estimates. However, the decrease in GSP is less pronounced for the ELPA estimates.

DISCUSSION

Our CA estimates for all three floras from the Palaeogene of Spitsbergen overlap, but the differences in the lower limits of MAT and CMMT between the Firkanten Formation and the other floras, as well as corresponding estimates from all leaf physiognomic methods, point to a cooling after deposition of the Firkanten Formation. This is in contrast to Manum (1994) and Denk et al. (1999), who concluded, based on taxonomic investigations of these floras, that the taxonomic composition does not signal major climatic changes. Nevertheless, comparable cooler temperatures for the middle Eocene to early Oligocene, as compared to the early Paleocene, have been reconstructed not only on a global scale (Zachos et al. 2001), but also on a regional scale (Moran et al. 2006). There are no significant differences within the individual methods between the climate estimates for the stratigraphically overlapping and therefore at least partly contemporaneous Aspelintoppen and Renardodden formations.

Our climatic interpretations based on CA and CLAMP generally are in good agreement with the results of previous investigations on Arctic palaeoclimates (Schloemer-Jäger 1958, Vonderbank 1970, Schweitzer 1974, 1980, Basinger et al. 1994, Manum 1994, Golovneva 2000a, b, Tripathi et al. 2001), although our CLAMP estimates are slightly colder. For the early Palaeogene (middle Eocene) of the Canadian High Arctic Basinger et al. (1994) estimated CMMT as 0–4°C, WMMT >25°C, and MAT as 12–15°C, based on selected NLRs and other proxies (e.g. crocodylians). According to McIver and Basinger (1999) this estimate for CMMT may be even slightly too cold. This

view is better in agreement with interpretations about the palaeoclimatic relevance of fossil crocodylians (Markwick 1998). *Alligator* sp., as the most cold-insensitive extant crocodylian, has a lower limit for CMMT about 5°C (Neill 1971, Markwick 1998) and there is no evidence that crocodylian populations can survive longer frost periods (Hutchinson 1982, Markwick 1998). The occurrence of fossil crocodylian remains on Ellesmere Island also implies that MAT has to be at least 14.2°C or even warmer in this area (Markwick 1998). However, so far no crocodylians remains have been discovered from Svalbard, which could corroborate such an interpretation for this archipelago. According to Basinger et al. (1994) also summer growing conditions in the Canadian High Arctic seem to have been mild and moist during the early Palaeogene, a view, which is also supported by the width and uniformity of annual growth rings.

There is still a debate whether or not physiognomic methods are meaningful in case of Palaeogene floras from the Arctic (Boyd 1990, 1994, 2000, Basinger et al. 1994, Golovneva 2000a, b). Previous results suggested that the use of leaf physiognomy for determining the Arctic palaeoclimates may be erroneous due to the possible adaptations of species and leaves to low light levels in the Arctic (Boyd 1990, 1994). Basinger et al. (1994) also considered leaf physiognomy not to be useful for Palaeogene vegetation of the Arctic because no living analogue of the corresponding ecosystem exists and therefore the overall physiognomic composition of this ecosystems is not represented by modern calibration datasets.

The angiosperms within the palaeofloras from the Palaeogene of Spitsbergen are dominated by non-entire leaves, both quantitatively and with regard to taxonomic composition; entire-margined taxa are only represented by a few specimens, which are difficult to classify (Kvaček et al. 1994). These authors also suggested that a deciduous habit for all of the floras from the Palaeogene of Spitsbergen is clearly indicated by the physiognomy of the angiosperm vegetation and that none of the taxa would suggest an evergreen habit. A noteworthy exception are the alleged coryphoid palms mentioned by Schweitzer (1980) from the Aspelintoppen Formation. However, as stated above the occurrence of these palms remains doubtful at the moment.

A possible reason for the dominance of

deciduous taxa could be that the plants from the Palaeogene of the High Arctic were deciduous to minimize carbon loss by respiration in the polar night (Spicer & Chapman 1990). However, such an interpretation is not unchallenged. In a study combining the investigation of modern taxa grown under controlled conditions and ecological modeling, Royer et al. (2003) showed that the quantity of carbon loss by annual shedding of leaves is significantly greater than that lost by evergreen trees through respiration during winter, at least for the living taxa considered (i.e. *Metasequoia glyptostroboides*, *Taxodium distichum*, *Ginkgo biloba*, *Sequoia sempervirens*, and *Nothofagus cunninghamii*; the latter genus has a good fossil record from Antarctica). This implies that a deciduous habit could be a metabolic disadvantage under the temperature and light conditions assumed for early Palaeogene and late Cretaceous floras from the Arctic. The question remains in what way these results, obtained from modern plants, can be applied to their Palaeogene precursors.

Another question is, whether all taxa from the Palaeogene of Spitsbergen believed to have been deciduous were in fact deciduous or not. As we do not know the exact taxonomic affinities of most angiosperm taxa from Spitsbergen the interpretation that (almost) all are deciduous is primarily based on the fact that deciduous leaves tend to be non-entire margined (Givnish 1979, Wolfe & Upchurch 1987, Uhl et al. 2003). However, already Givnish (1979) pointed out that in the tropics many understorey plants, experiencing low light levels, are non-entire even though the leaves of the canopy species are entire margined (see also Richards 1952). This may suggest a leaf physiognomical response to low light levels and may also explain the dominance of taxa with non-entire margined leaves in the early Tertiary Arctic floras. However, Howard (1969) showed that thin evergreen leaves in the tropics, have also a tendency to be non-entire. This results may indicate that more fossil leaves as currently believed, based on leaf texture and margin types, have probably been evergreen, not only from the Palaeogene of the Arctic (Boyd 1990). Obviously other factors than temperature and deciduousness can play an important role in shaping the physiognomic appearance of leaves. In the modern world, deciduousness, as a response to cold tempera-

tures, is apparently correlated with the same physiognomic signatures as deciduousness induced by high-latitude winter darkness in the past (McIver & Basinger 1999). This could in fact imply that most (if not all) leaf physiognomic methods, which are calibrated with extant non-analogous floras can probably not be used for deriving reliable quantitative palaeoclimatic estimates with these floras. CLAMP maybe represents an exception from this rule, as this method is the only leaf physiognomic method used in the present study that seems to produce palaeoclimate estimates that are more or less in agreement with other palaeoclimatic evidence for the Palaeogene of the High Arctic.

By accepting the potential interpretation that it would not be possible to use most of the existing leaf physiognomic methods for deriving reliable quantitative palaeoclimatic estimates the problem remains how to interpret the observation that all physiognomic methods, including the work done by Golovneva (2000b), point to a potential cooling between the early Paleocene and the Eocene. One possible explanation could be that although leaf physiognomy of Palaeogene floras from the Arctic is primarily adapted to the special light conditions and only secondarily to climatic conditions, changes in the climate could still have affected the overall leaf physiognomy. In this case the changes in the leaf physiognomic compositions of the floras would in fact reflect climatic changes, although no reliable quantitative interpretation of the changes would be possible at the moment.

However, there is also the possibility that the leaf physiognomic differences between the different floras are mainly caused by taphonomic influences, as suggested by Denk et al. (1999) for the taxonomic differences. Wilf (1997) pointed out that even in the CLAMP calibration data-set the temperature signal is dominated by leaf margin type. As Uhl et al. (2003) could demonstrate, the percentage of taxa with entire margined leaves within a flora can be strongly influenced by taphonomic biases. Given the overall low number of taxa with entire margins in the three floras from the Palaeogene of Spitsbergen a possible taphonomic bias could have severe effects on any estimate based on leaf physiognomy. In all three stratigraphic levels entire-margined taxa are in fact only represented by a few specimens

in the Stockholm collections (Kvaček et al. 1994). Nevertheless, the absence or presence of a few entire margined leaves could lead to conspicuously different estimates based on leaf physiognomy. Uhl et al. (2003) showed that at two localities from the Upper Oligocene and Middle Miocene of Germany the absence or presence of a few entire margined taxa can lead to differences of up to 12°C for MAT estimates based on LMA. The observed decrease of MAT between the Firkanten Formation and the Aspelintoppen Formation is well within this range of error due to taphonomic disturbance. However, it is not yet clear whether the observations by Uhl et al. (2003), obtained for only two individual floras, can be generalized or not, but it is very likely that a multivariate approach such as CLAMP is less affected by taphonomy (Uhl et al. 2003, 2006, Spicer et al. 2005). CLAMP results suggest a less pronounced cooling between the Firkanten Formation and the Aspelintoppen Formation than LMA. It seems possible that the smaller differences between the Firkanten Formation and the Aspelintoppen Formation, as compared to LMA values, can also be explained by the smaller susceptibility of CLAMP towards taphonomic influences (Uhl et al. 2006). However, it should also be expected that ELPA, another multivariate method, would also be less susceptible towards taphonomy, resulting in smaller differences between the Firkanten Formation and the Aspelintoppen Formation. The latter is not the case.

Golovneva (2000b), using CLAMP, did also find a reduction of temperatures between the Firkanten Formation and the Aspelintoppen Formation, although she based her analysis not only on the material from Stockholm, but also on the large collections in St. Petersburg. This indicates that both collections are representative and do not contain different proportions of entire margined leaf fossils. As Wilf (1997) suggested, taphonomic effects on leaf physiognomic methods in general can largely be overcome by collecting as many species as possible, from different facies types and the largest number of sites per stratigraphical level. By combining data from different collections Golovneva (2000b) followed such an approach, but her results are almost the same as our results, which are based on a different data-set, indicating that the Stockholm collection represents almost the same leaf physiog-

nom character space as the combined Stockholm and St. Petersburg collections.

Considering the overall low number of taxa available, even for entire formations, all climate estimates derived from leaf physiognomic methods have to be interpreted with great caution. Although the possibility of taphonomic biases remains, it seems very likely that the methods used here and by Golovneva (2000b) really depict a change of climatic conditions between the Lower Paleocene Firkanten Formation and the younger formations. However, at the moment nothing can be said about a realistic degree of such a temperature decrease, although CLAMP produced temperature estimates that are in rather good agreement with previous palaeoclimatic interpretations. Nevertheless, the CLAMP estimates may be slightly too cold as compared to other evidence. The CA produced estimates which probably enclose the real values, but are mostly too wide to provide reasonable information. LMA and ELPA produced estimates, at least for the two Eocene – Oligocene formations, which are rather too cold as compared to other evidence.

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PLATES

Plate 1

Plant remains from the Palaeogene of Spitsbergen. Scale bar – 1 cm

1. *Equisetum arcticum* Heer, S052231, Nordenskiöldsfjellet, Aspelintoppen Formation
2. *Equisetum arcticum* Heer, S052113, Nordenskiöldsfjellet, Aspelintoppen Formation
3. *Osmunda macrophylla* Penh., S052413, Nordenskiöldsfjellet, Aspelintoppen Formation
4. *Metasequoia occidentalis* (Newb.) Chan., S020261, Cap Lyell, Renardodden Formation
5. *Corylites* sp., S051041, Cap Lyell, Renardodden Formation
6. *Zizyphoides flabellum* (Newb.) Crane, Manch. & Dilch., S051659, Kolfjellet, Firkanten Formation
7. *Trochodendroides* sp. (part and counterpart), S051655, Kolfjellet, Firkanten Formation
8. “*Betula*” sp., S052258, Nordenskiöldsfjellet, Aspelintoppen Formation

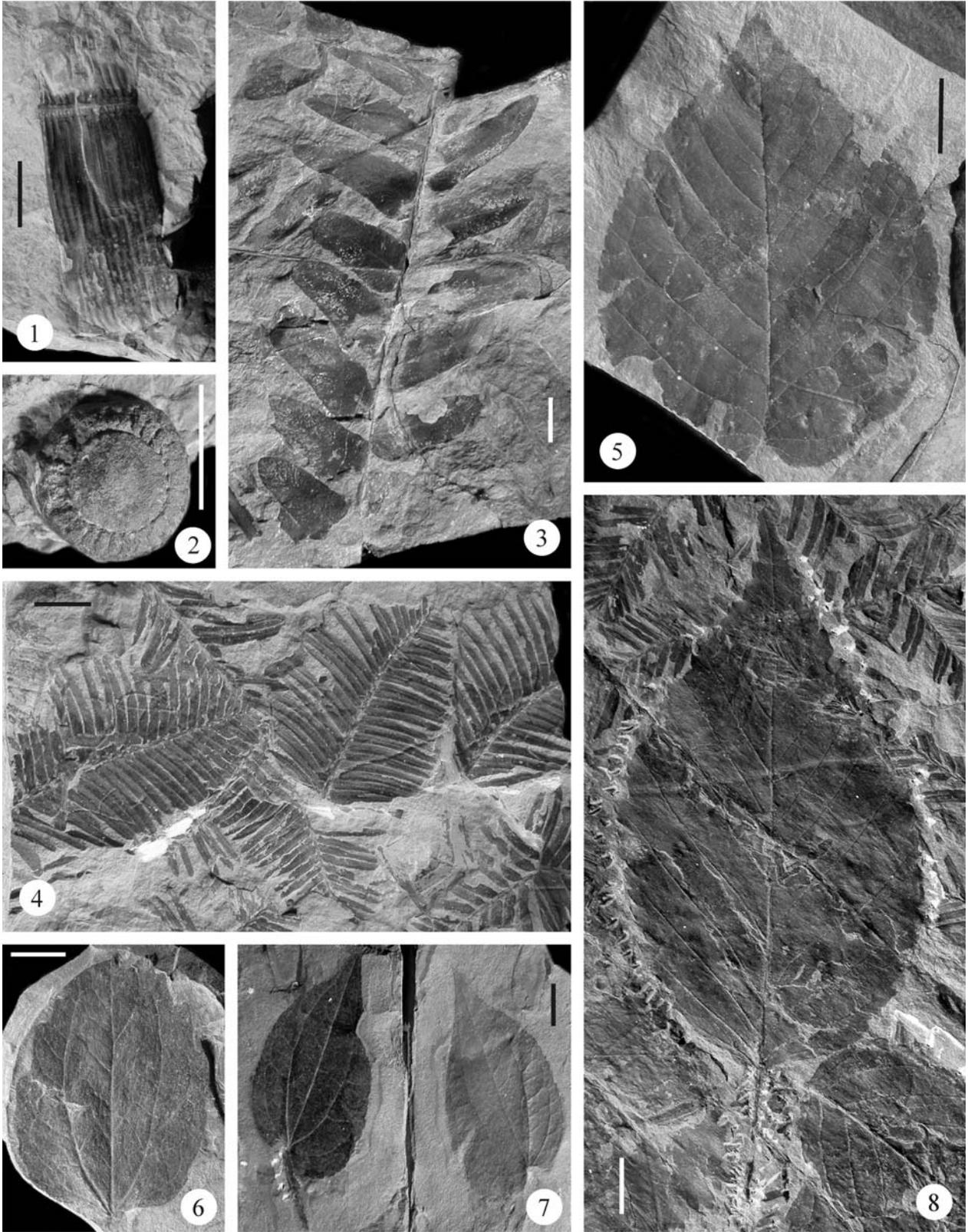


Plate 2

Plant remains from the Palaeogene of Spitsbergen. Scale bar – 1 cm

1. *Zizyphoides flabellum* (Newb.) Crane, Manch. & Dilch. (bottom, left), *Metasequoia occidentalis* (Newb.) Chan. (top, right), S052147, Nordenskiöldsfjellet, Aspelintoppen Formation
2. *Aesculus longipedunculus* Schloem.-Jäg., S052399, Nordenskiöldsfjellet, Aspelintoppen Formation
3. *Celastrinites septentrionalis* (Krysht.) Golovn., S051638, Kolbjellet, Firkanten Formation
4. *Ulmites ulmifolius* (Schloem.-Jäg.) Kvač., Man. & Boul., S052651, Liljewalchfjellet, Aspelintoppen Formation
5. *Acer arcticum* Heer, S050861, Cap Lyell, Renardodden Formation
6. *Acer arcticum* Heer, samara, S050858, Cap Lyell, Renardodden Formation
7. *Trochodendroides richardsonii* (Heer) Krysht., S052402, Nordenskiöldsfjellet, Aspelintoppen Formation
8. cf. *Dombeyopsis* sp., S052466, Lars Hiertaafjellet, Aspelintoppen Formation
9. *Ushia olafsenii* (Heer) Boul. & Kvač., S052416, Nordenskiöldsfjellet, Aspelintoppen Formation

