43-66

Veröffentlichungen des Tiroler Landesmuseums Ferdinandeum 86/2006 Innsbruck 2006

# *Rhododendron ponticum* L. var. *sebinense* (SORDELLI) SORDELLI in the Late Pleistocene flora of Hötting, Northern Calcareous Alps: witness of a climate warmer than today?

Thomas Denk

# *Rhododendron ponticum* L. var. *sebinense* (SORDELLI) SORDELLI in der spätpleistozänen Flora von Hötting, Nördliche Kalkalpen: Zeuge eines wärmeren Interglazials als heute?

#### Abstract

The Pleistocene flora of Hötting (Northern Calcareous Alps, Austria) has traditionally been considered an indicator of an interglacial climate warmer than the present one. This was based mainly on the presence of rhododendron leaves and bud scales belonging to the '*Rhododendron ponticum* group'. *Rhododendron ponticum* displays a Euxinian (areas along the southern Black Sea coast) – Iberian (Spain, Portugal) disjunct distribution at present. Based on leaf morphological characteristics the Pleistocene *R. ponticum* var. *sebinense* clearly is more similar to the modern eastern subsp. *ponticum* (Turkish and Caucasian populations) than to the western subsp. *baeticum* (Iberian Peninsula). In view of the Cainozoic occurrence of fossils similar to modern *R. ponticum* in Bulgaria and the Northern Caucasus, the eastern range of the species is suggested to be older and the present disjunction to be of Pleistocene age.

To assess the importance of *R. ponticum* var. *sebinense* for palaeoclimatic considerations, approximate mean annual temperatures were inferred for stands of *R. ponticum* subsp. *ponticum* at high elevations with the moist adiabatic lapse rate (suggesting a temperature decrease of about 5°C/1000 altitudinal metres for humid temperate areas). The inferred mean annual temperatures suggest that the presence of *R. ponticum* var. *sebinense* in the Pleistocene of Hötting does not necessarily point to an interglacial climate warmer than today in this area. Further, the Rossfall-Lahner and the Hungerburg floras representing two distinct lithotypes within the 'Höttinger Breccia' were analysed. Using indicator values for Central European plants shows that the majority of taxa encountered in both floras are classified as 'indifferent' with regard to mean annual temperature requirements or corresponding to the present situation, and that the co-occurrence of "subalpine" and lowland taxa may simply reflect the broad contact zone between such taxa found in alpine environments (such as alpine taxa extending to lower elevations on vertical stripes of scree). Based on the florar loopsition of the Hungerburg and the Rossfall-Lahner assemblages it cannot be ascertained whether the fossiliferous sediments were deposited at the same time or not, nor from which interglacial they were deposited.

Keywords: Rhododendron ponticum var. sebinense – Pleistocene – interglacial – climate – Hötting – Northern Calcareous Alps – Austria

#### Zusammenfassung:

Die pleistozäne Flora Höttingens (Nördliche Kalkalpen, Österreich) wird allgemein als Indiz für ein wärmeres Interglazial als das heutige betrachtet. Ein Hauptgrund dafür ist das Auftreten von Blättern und Knospenschuppen, welche zur *Rhododendron ponticum*-Gruppe gehören. *Rhododendron ponticum* nimmt gegenwärtig ein disjunktes euxinisch (Gebiete entlang der südlichen Schwarzmeerküste) – iberisches (Spanien, Portugal) Areal ein. Aufgrund von blattmorphologischen Merkmalen zeigt die pleistozäne Variante *R. ponticum* var. *sebinense* deutlich grössere Affinität zur modernen Unterart *ponticum* (türkische und kaukasische Populationen) als zur westlichen Unterart *baeticum* (Iberische Halbinsel). Ausgehend vom Auftreten känozoischer Fossilien ähnlich dem modernen *R. ponticum* in Bulgarien und im Nordkaukasus wird angenommen, dass das östliche Areal der Art älter ist und die heutige Disjunktion pleistozänen Ursprungs ist. Unter dieser Vorausgabe konnte die Bedeutung von *R. ponticum* var. *sebinense* für paläoklimatische Überlegungen evaluiert werden. Schätzwerte für mittlere Jahresmitteltemperaturen im Vorkommensgebiet von *R. ponticum* subsp. *ponticum* wurden ermittelt unter der Annahme, dass die Jahresmitteltemperatur pro 1000 Höhenmeter um ca. 5°C abnimmt (moist adiabatic lapse rate). Ausgehend von der erhaltenen Jahresmitteltemperatur kann vermutet werden, dass das Vorkommen von *R. ponticum* var. *sebinense* nicht notwendigerweise auf höhere Temperaturen für das Interglazial von Hötting schliessen lässt. Die Floren von Rossfall-Lahner und Hungerburg wurden analysiert, welche innerhalb der Höttinger Breccie unterschiedliche Lithotypen repräsentieren. Temperaturwerte für zentraleuropäische Pflanzen zeigten, dass ein Grossteil der in beiden Floren vorkommenden Taxa bezüglich ihrer Ansprüche an die Jahresmitteltemperatur als indifferent eingestuft werden oder der heutigen Situation entsprechen. Weiters zeigte sich, dass das gemeinsame Vorkommen subalpiner und Tieflandstaxa die breite Kontaktzone solcher Arten in alpinen Lebensräumen widerspiegelt (beispielsweise alpine Taxa, die in oder entlang von Geröllhalden bis in Tieflagen reichen). Die Artenzusammensetzung der Hungerburg und Rossfall-Lahner Vergesellschaftungen liefert keine Indizien dafür, dass diese Sedimente zur gleichen Zeit oder während unterschiedlicher Phasen des Pleistozäns abgelagert wurden. Daher kann eine präzise zeitliche Einstufung der Höttinger Interglazialflora derzeit nicht gemacht werden.

Keywords: Rhododendron ponticum var. sebinense – Pleistozän – Interglazial – Klima – Hötting – Nördliche Kalkalpen – Österreich

# 1. Introduction

The Cainozoic period (the past 65 million years) is characterized by  $a \pm$  gradual cooling in the northern hemisphere (ZACHOS et al., 2001) that culminated in the Pleistocene cold phases with permanent ice sheets occurring first in the North Atlantic 3.2 to 2.7 million years ago (BAUMANN & HUBER, 1999; THIEDE et al., 1998) and later in the Alps, < 1 million years ago (PENCK & BRÜCKNER, 1909; MUTTONI et al., 2003). In western Eurasia this process was accompanied by the disruption of former homogeneous humid temperate and subtropical biota into the markedly heterogeneous temperate, Mediterranean, and eastern dry continental biota of today. Area disruptions caused the patterns of present disjunct distributions of many plant and animal taxa, one of which is the Euxinian – southwestern European disjunction. Both the Euxinian (Turkish Black Sea coastal areas to Transcaucasia) and southwestern European areas are characterized by mild climates and are largely frost-free during winter at low elevations. Prominent examples among woody flowering plants for such a disjunction are Rhododendron ponticum L. (two subspecies) and Prunus laurocerasus L./P. lusitanica L.; and among amphibians Pelodytes caucasicus BOULANGER/P. punctatus DAUDIN (cf. DENK et al. 2001). Other tree species such as Pterocarva fraxinifolia (POIRET) SPACH that are confined to the Euxinian area today, persisted in Central Europe until the second half of the Middle Pleistocene (REILLE & BEAULIEU, 1995) before they went extinct. The Pleistocene flora of Hötting near Innsbruck and similar floras south of the Alps became famous in

the late 19th century when SORDELLI (1878, 1896) and WETTSTEIN (1888, 1892) recognized remains of *Rhododendron ponticum* in interglacial sediments. Based on the modern distribution of this plant it was concluded that the interglacial of Hötting represents a period warmer than at present in this area (WETTSTEIN, 1992; RYTZ, 1925; MURAWSKI, 1992). Based on its composition WETTSTEIN (1892) considered the flora of Hötting a mixture of central European and Pontic geographical elements. Later authors also suggested a "cool" and a "warm" flora for the Pleistocene of Hötting originating from two lithotypes, the so-called "Red" (Hungerburg) and "White" (Rossfall-Lahner) Breccias (MURR, 1926).

The aims of this paper are, first, to clarify the taxonomic status of *Rhododendron* from the Pleistocene of Hötting and to identify biogeographical patterns for the '*R. ponticum* group'; second, to re-assess the significance of this plant for palaeoclimatic considerations; and third, to evaluate the overall floristic affinities of the Pleistocene flora of Hötting based on a (preliminary) revision and to compare ecological and possible climatic signals from macrofloras and palynofloras. A number of problems related to the dating of Pleistocene floras are discussed as well.

# 2. Material and methods

Fossil material was studied in the following collections: Institute of Geology and Palaeontology, University of Innsbruck (I); Landesmuseum Ferdinandeum, Innsbruck; Museum of Natural History, Vienna (W); Geological Survey, Vienna (GBA); Department of Palaeontology, University of Vienna; Museum of Natural History, Stockholm (S). For comparison, modern plant material was examined at the herbarium Stockholm (S).

Plant bearing sediments have originally been assigned to two lithotypes, the "Red Breccia" and "White Breccia" (WETTSTEIN, 1892). MURR (1926) referred the sediments originating from the Red Breccia collectively as to "Hungerburg Breccia", while those derived from the White Breccia were termed "Ross-fall-Lahner Breccia". Sediments of the White Breccia yielded an absolute age of about 109 ka, while those of the Red Breccia were dated as about 110 ka (cf. SANDERS & OSTERMANN, 2006). Because the two lithotypes are interfingering no conclusion about their stratigraphic position can be made. The Ross-fall-Lahner interval is distinct from the remaining White Breccia by its beds of calciwacke and matrix-supported breccias containing a rich flora including *Rhododendron*. Both MURR (1926) and SANDERS & OSTERMANN (2006) interpret this flora as autochthonous, accumulated in shallow ephemeral ponds as the result of episodic mudflows. SANDERS & OSTERMANN (2006) pointed out that the stratigraphic position of the Rossfall-Lahner interval relative to the Red and White Breccias is unclear, and that the former may have been deposited earlier in the Pleistocene.

The fossils are preserved as impressions, with no organic material left so that no observation of leaf epidermal features is possible. Many leaves show details of venation including, in some cases, areoles formed by highest-order venation. In most entire margined leaves portions of leaf margin are preserved, while in most dentate/serrate leaves no margin is preserved. Larger leaves, in addition, often are fragmentary and/or strongly folded as a consequence of transport and burying in the sediment (mudflows). For the present study no revision of the whole flora was attempted. Despite this, most previously described material has been re-examined and all taxa previously reported for the Hungerburg and Rossfall-Lahner Breccias were classified according to their temperature requirements using indicator values for Central European plants (ELLENBERG, 1992). A number of taxa important for climatic and ecological considerations were then studied in greater detail. The term "warm climate" is used throughout the text. This is meant to indicate a climate warmer than today at the sites from which the Rossfall-Lahner and Hungerburg floras originate.

# 3. Results

# 3.1. Systematic palaeobotany

# 3.1.1. Rhododendron ponticum var. sebinense (Sordelli) Sordelli (Figs. 1-4)

- 1859 Laurinea sp. UNGER in PICHLER: p. 168.
- 1859 Laurus sp. UNGER in PICHLER: p. 168.
- 1859 Persea speciosa auct. (non HEER) UNGER in PICHLER: p. 168.
- 1859 Quercus sp. UNGER in PICHLER: p. 168.
- 1878 Rhododendron sebinense Sordelli: p. 892.
- 1884 Daphne hoettingensis ETTINGSHAUSEN: p. 268 ff., pl. 1, fig. 3, pl. 2, figs 1–5.
- 1886 Actinodaphne hoettingensis STUR: p. 39 ff., pl. 1, figs 2, 3, 5-9.
- 1886 *Cnestis* sp. STUR: p. 49, fig. 17.
- 1888 Rhododendron ponticum L. WETTSTEIN: p. 40 ff., figs 2, 4, 6, 8.
- 1892 Rhododendron ponticum L. WETTSTEIN: p. 497–498, pl. 51, figs 3–6.
- 1896 Rhododendron ponticum var. sebinense Sordelli: p. 239, pl. 43, figs. 6–8.
- 1926 Rhododendron ponticum L. MURR: p. 161, pl. 3 (1), fig. 10.
- 1963 *Rhododendron sordellii* TRALAU: nom. illeg. superfl., p. 106, pl. 1, figs 1–2 (figs 2, 3 as "bud-scales").



Figure 1: *Rhododendron ponticum* var. *sebinense*; Rossfall-Lahner. 1. Leaves from a large block, (S). 2. Leaves preserved in the way they were attached to a twig, woody part of the twig preserved as a mould, (W). Scale bar = 5 cm.



Figure 2: Rhododendron ponticum var. sebinense; Rossfall-Lahner.

**1**, **2**. Leaves preserved in the way they were arranged on the terminal part of a twig. **1**. As *Actinodaphne hoettingensis* (ETTINGSH.) STUR; STUR, 1886, Pl. 1, fig. 9, (1), **2**. (W). **3**. Strongly inflexed leaf; typical feature of modern rhododendron, (S). **4**. Strongly folded leaves, (S). **5**. Imprint of a bud possibly belonging to *R. ponticum*; two bud scales can be distinguished, (S). **6**. Fragment of a large leaf, (S). **7**. Large elliptic-obovate leaf, (W). Scale bar = 1 cm in 5, and 5 cm in the remaining panels.



**Figure 3**: *Rhododendron ponticum* var. *sebinense*; Rossfall-Lahner. **1**, **2**. Fragments of very long and wide leaves, **1**. (S), **2**. (I). Scale bar = 5 cm.

**Description**: Leaves and buds (bud scales?). Leaves petiolate, petiole rarely preserved, 5+ to 10 mm long, lamina elliptic to elliptic-obovate, entire, 81 to 190 mm long, mean 124 mm (130 according to WETTSTEIN, 1888), and 29 to 66 mm wide, mean 45 mm (43 according to WETTSTEIN, 1888); apex bluntly acute, base acute to rounded; primary vein very prominent; secondary veins weak and therefore poorly preserved as imprints, eucamptodromous to brochidodromous, intersecondary veins present but hardly discernible, 5 to 8 secondary veins originating along 5 cm primary vein when no intersecondary veins visible, 8 to 11 veins when secondary and intersecondary veins preserved, density of secondary veins higher in small leaves than in large ones. Imprints of buds broad to narrow ovate with truncate base, 5 to 20+ mm long and 3 to 10 mm wide.

**Remarks**: TRALAU (1963) established the new name *Rhododendron sordellii* TRALAU, which is illegitimate, because the basionym *sebinense* has priority over *sordellii*. *Rhododendron sebinense* SORDELLI was published in 1878 based on Pleistocene leaves from northern Italy and is listed in TRALAU'S synonymy for *R. sordellii*. Even if *R. sebinense* from the Italian localities would turn out to be different from the present material, the basionym *hoettingense* used for these specimens by ETTINGSHAUSEN (1884, *Daphne hoettingensis*) would have priority over *sordellii*.

MURR (1926) suggested that the specimens referred to bud scales of a rhododendron by WETTSTEIN (1892) belong to a fungus of the genus *Xylaria*, similar to the species *X. polymorpha* (PERS.) GREV. native to the Innsbruck area. The fruiting bodies of *Xylaria* grow from the bases of rotten stumps in forests and differ substantially from the present specimens in their irregular size and shape. In contrast, comparisons to modern material of *Rhododendron ponticum* confirm WETTSTEIN'S (1892) interpretation.

Rhododendron ponticum L. var. sebinense (Sordelli) Sordelli



Figure 4: *Rhododendron ponticum* var. *sebinense*; Rossfall-Lahner. 1–6. Small leaves with well-preserved secondary venation. 1–4. (W), 5. As *R. sordellii* TRALAU; TRALAU, 1963 Pl. 1, fig. 2, (S), 6. (I). Scale bar = 5 cm.

# 3.1.2. Systematic position of R. ponticum var. sebinense

TRALAU (1963) argued that *R. ponticum var. sebinense* (syn. *R. sebinense*) should not be included in *Rhododendron ponticum* because of close morphological similarities to other related species such as *R. caucasicum* PALL. and *R. maximum* L. (also noticed by SORDELLI, 1896). Although it is correct that leaf fossils do not provide sufficient characters to establish closer affinities to several modern species related to *R. ponticum* than to any other modern species of the genus. First, a closer relationship to any East Asian or North American modern species than to the western Eurasian *R. ponticum* seems unlikely given the young age of the fossil. Second, among the four western Eurasian species closely similar to the fossil, *Rhododendron ungernii* TRAUTVETTER, *R. smirnowii* TRAUTVETTER, and *R. caucasicum* are geographically restricted endemic species of southwestern Asia, while *R. ponticum*, based on its isolated occurrence on the southern and western Iberian Peninsula, must have had a wider distribution in the past. Based on leaf morphological characteristics *R. ponticum* var. *sebinense* is more similar to the modern eastern subsp. *ponticum* (Turkish and Caucasian populations) than to the western subsp. *baeticum* (BOISSIER & REUTER) HANDEL-MAZZETTI (see **Table 1** for comparative morphology).

	Length of lamina	Width of lamina	Secondary veins per 5 cm	Secondary veins per 5 cm
	(mm)	(mm)	(no intersecondaries counted)	(intersecondaries counted)
Rhododendron ponticum subsp. ponticum(n = 40)	(68) 120 (180)	(18) 36 (65)	(4) 5.7 (9)	(6) 7.9 (12)
Rhododendron ponticum subsp. baeticum (n = 40)	(66) 100 (135)	(21) 30 (40)	(5) 6.6 (10)	(7) 8.9 (13)
Rhododendron ponticum var. sebinense (n = 32)	(81) 124 (190)	(29) 45 (66)	5-8	8–11

Table 1: Comparative morphology of the Rhododendron ponticum group.

# 3.1.3. Biogeography of the R. ponticum group

*Rhododendron ponticum* has a modern disjunct distribution with the subspecies *ponticum* occurring from the southern Black Sea coast to western Georgia, while subsp. baeticum (BOISS. et REUTER) HAND.-MAZZ, has a small and scattered distribution on the southern and western Iberian Peninsula. A third isolated occurrence is known from central Lebanon, where R. ponticum var. brachycarpum BOISS. grows in Pinus pinea L. forests (BROWICZ, 1983). The species belongs to the subgenus Hymenanthes that comprises a group of morphologically similar northern hemispheric species (GOETSCH et al., 2005). Among these are three western Eurasian species that occur sympatrically with R. ponticum in northeastern Turkey and western Georgia (R. caucasicum, R. smirnovii, and R. ungernii; MILNE et al., 1999). The North American species R. maximum and R. catawbiense MICHX. are widely planted in Europe. In Europe, the fossil record of this group may date back to the Palaeocene of England, from where seeds with a morphology as found in the subgenus Hymenanthes have been reported (COLLINSON & CRANE, 1978). Nevertheless, a closer affinity of the fossils to this subgenus cannot be established because seeds of this morphology occur also in other subgenera (for instance subgenus Azalea, R. luteum SwEET). Fossils resembling R. ponticum are extremely scarce throughout the following periods of the Cainozoic. DENK et al. (2005) reported leaves from the Late Miocene of Iceland that are indistinguishable from R. ponticum but also from a number of North American species.



Figure 5: Climate diagrams for stations within the present distribution area of *Rhododendron ponticum* subsp. *ponticum*, and subsp. *baeticum* (diagrams 1 to 5), of naturalized *R. ponticum* in Ireland (6), and for Innsbruck and Bregenz (7, 8) close to the Pleistocene occurrence of *R. ponticum* var. *sebinense*. The Uppsala diagram illustrates the northern limit of cultivated *R. ponticum* in Sweden. Diagrams from LETH et al. (1999).

Despite the scarcity of fossils in the European Neogene, the fossil record suggests that the eastern (Euxinian) area of the *R. ponticum* group is older than the southwestern European (Iberian Peninsula) and possibly the eastern Mediterranean one. KUTUZKINA (1964) described leaves from the upper Middle Miocene of the Northern Caucasus as *Rhododendron* sp. (cf. *R. ponticum*). Fragmentary material from the Pliocene of Bulgaria (STEFANOFF & JORDANOFF, 1935) also appears to belong to *R. ponticum* or a lineage ancestral to it. In contrast, fossil evidence for a westward migration of *R. ponticum* is not older than Pleistocene from which unequivocal leaf and fruit remains are known from southern Central Europe (cf. SORDELLI, 1893; WETTSTEIN, 1888, 1892 etc.). JESSEN et al. (1959) described fruits and seeds from the Hoxnian interglacial (corresponding to the Mindel-Riss Interglacial in the Alps) of Ireland, which they referred to *R. ponticum*. ANDERSSON (1910) reported *R. ponticum* leaves from the Greek island Skyros but did not provide illustrations, and so this record remains somewhat doubtful. Based on current knowledge the modern disjunct distribution of *R. ponticum* appears to be of Pleistocene age.

# 3.1.4. Climatic requirements of modern Rhododendron ponticum

*Rhododendron ponticum* s. l. is found under different climatic conditions, and occupies various ecological niches (cf. ERFMEIER, 2004). Eastern populations occur from sea level to 2200 m a.s.l. (BROWIZC, 1983; DENK et al., 2001). A typical lowland climate along the Black Sea coast of northeastern Turkey is shown in **Fig. 5:1** (Rize, 13.9°C mean annual temperature [MAT]). Further inland and at higher elevations temperatures decrease (**Fig. 5:2**, Bolu, 10.4°C MAT). Due to the absence of meteorological stations MAT for higher elevations in this area of *R. ponticum* can be estimated with the moist adiabatic lapse rate, which is usually near 5°C/1000 altitudinal meters in humid climates (HENDERSON-SELLERS & ROBINSON, 1986). Applying this, MAT would be expected to be about 4.1°C at 2000 m a.s.l., and around 5.5°C at 1500 m a.s.l. At higher elevations in the Pontic Range and the coastal ranges of the eastern Black Sea, substantial snowfall occurs in the winter, often covering the entire shrub layer.

In the western range *Rhododendron ponticum* occurs at mid-altitudes (cf. MEJÍAS et al., 2006). MAT in mountains of southern Spain range from 14.6 to 18.4°C (MEJÍAS et al., 2006) and mean annual precipitation is generally lower than in the eastern range (see **Fig. 5:4, 5**).

In addition, since the 18th century invasive populations that are genetically derived from the western subspecies have spread into natural ecosystems on the British Isles (ERFMEIER, 2004; MILNE & ABBOT, 2000). Here, *Rhododendron ponticum* grows in dense populations in the understorey of deciduous oak forests; but also on sand dunes, heath, and meadows of matgrass (*Nardus stricta* L.). The climate is characterised by even distributions of precipitation throughout the year and mild winter temperatures (see **Fig. 5:6**). *Rhododendron ponticum* individuals planted decades ago in Scandinavia flower and produce seeds (cf. the climate diagram for Uppsala with 5.2°C MAT).

# 3.2. Preliminary analysis of the flora

A great number of identifications made for plant fossils from Hötting date back to the excellent account by WETTSTEIN (1892). WETTSTEIN'S study was revised by MURR (1926), who also considered plant fossils from the Red Breccia (cf. **Figs. 6–8**). A summary of plants recognized by MURR (1926) using currently valid plant names is provided in **Table 2**.

# 3.2.1. Indicator values for taxa reported for the Pleistocene of Hötting

Since all the taxa listed (with the exception of *Rhododendron ponticum*) are found in the modern flora of Central Europe, they were preliminarily classified according to their temperature requirements. For this purpose the so-called "T-value" was utilized. This temperature value was established by ELLENBERG and co-workers (1991) for vascular plants of Central Europe based on the observed ecological amplitude for each taxon. It is important to note that these authors explicitly pointed out that these values are strictly valid only for Central Europe including the Alps. Vertical distributions and their corresponding mean annual temperatures are shown in **Table 3**.

Eight species or 14.8 % of the taxa reported for the Rossfall-Lahner flora are classified as T3 (subalpine)

	Rossfall-Lahner Breccie	T-value (ELLEN- BERG et al. 1992) <sup>b</sup>		Hungerburg Breccie	T-value (ELLEN- BERG et al. 1992)
?	Abies alba MILL.	5	с	Acer platanoides L.	6
с	Acer campestre L.	6	с	Acer pseudoplatanus L.	x
с	Acer pseudoplatanus L.	х	с	Alnus incana L.	4
a	Adenostyles glabra (MILL.) DC.	3	a	Betula pendula ROTH.	x
c?	Alnus alnobetula(EHRH.) C. KOCH	3	?	Calluna vulgaris (L.) HULL.	X
с	Alnus incana L.	4	?	Carex flacca SCHREB.	x
a	Arctostaphylos uva-ursi (L.) SPR.	x	a	Convallaria majalis L.	x
a	Aster bellidiastrum (L.) SCOP.	3	с	Corylus avellana L.	5
?	Carex flacca SCHREB.	х	?	Cystopteris fragilis (L.) BERNH.	х
a	Carex pendula HUDS.	5	?	Dryopteris carthusiana (VILL.) H. P. FUCHS	Х
?	Carex pilosa SCOP.	6	?	Dryopteris filix-mas (L.) SCHOTT	х
с	Convallaria majalis L.	x	?	Equisetum telmateia EHRH.	6
с	Cornus sanguinea L.	5	с	Fragaria vesca L.	x
с	Corylus avellana L.	5	a	Larix decidua MILL.	X
?	Dryopteris filix-mas (L.) SCHOTT	X	a	Malus sylvestris (L.) MILL.	6
с	Fagus sylvatica L.	5	?	Picea abies (L.) KARST.	3
с	Fragaria vesca L.	x	?	Pinus mugo TURRA	3
с	Hedera helix L.	5	с	Pinus sylvestris L.	х
?	Juniperus communis L.	x	?	Populus tremula L.	5
?a	Lathyrus cf. vernus (L.) BERNH.	6 <sup>c</sup>	с	Prunella vulgaris L.	х
с	Maianthemum bifolium (L.) SCHM.	Х	?	Pyrus pyraster (L.) BORKH.	6
?	Orchis sp.		с	Quercus robur L.	6
?	Picea abies (L.) KARST.	3	?	Rubus caesius L.	5
?	Pinus mugo TURRA	3	?	Salix alba L.	6
с	Pinus sylvestris L.	х	?	Salix appendiculata VIL- LARS	3

	Rossfall-Lahner Breccie	T-value (ELLEN- BERG et al. 1992) <sup>b</sup>		Hungerburg Breccie	T-value (ELLEN- BERG et al. 1992)
?	Poa hybrida GAUD.	3	a?	Salix caprea L.	x
с	Polygala chamaebuxus L.	4	с	Salix eleagnos SCOP.	5
с	Populus albaL.	7	а	Salix myrsinifolia SA- LISB.	4
r	Potentilla micrantha RAM.	7	?	Salix purpurea L.	5
с	Prunella grandiflora (L.) JACQ	x	?	Salix triandra L. > S. glabra SCOP.	5
с	Prunella vulgaris L.	х	?	Scirpus sylvaticus L.	5
?	Prunus avium L.	5			
?	Rhamnus catharticus L.	5			
с	Rhamnus frangula L. (incl. hoettingensis WETTST.)	6 <sup>d</sup>			
с	Rhododendron ponticum var. sebinense SORDELLI	-			
?	Ribes alpinum L.	4			
?	Rubus caesius L.	5			
a	Salix myrsinifolia SALISB.	4			
a	Salix appendiculata VILLARS	3			
?	Salix caprea L.	x			
с	Salix eleagnos SCOP.	5			
a?	Salix glabra SCOP.	3			
a?	Salix purpurea L.	5			
a?	Salix triandra L. > S. glabra SCOP.	5			
?	Sorbus aria (L.) CR.	5			
?	Sorbus aucuparia L.	x			
с	Taxus baccata L.	5			
c	Tilia platyphyllos SCOP.	6			
?	Tussilago farfara var. prisca WETTST.	х			
?	Ulmus glabra HUDSON <sup>a</sup>	5			
a	Vaccinium vitis-idaea L.	x			
с	Viburnum lantana L.	5			

#### Rhododendron ponticum L. var. sebinense (SORDELLI) SORDELLI

	Rossfall-Lahner Breccie	T-value (ELLEN- BERG et al. 1992) <sup>b</sup>	Hungerburg Breccie	T-value (ELLEN- BERG et al. 1992)
a	Viola odorata L. (V. pyrenaica RAM.)	5		
r	Vitis vinifera subsp. sylvestris (GMEL.) HEGI	8		

a included are specimens that were ascribed to U. carpinifolia RUPPIUS ex SUCKOW

(= campestris L. em. HUDS.)

<sup>b</sup> see Table 3 for explanation

<sup>c</sup> fairly common until Ångermanland and Jämtland in Sweden. Östersund, 2.6 °C MAT, 496 mm MAP

<sup>d</sup> typical element of forests around Stockholm, fairly common in Norrbotten. Lulea, 1.3 °C MAT, 490 mm MAP

c = confirmed after revision;

a = tentatively accepted but pending revision;

r = rejected after revision or indeterminable;

? = not seen in collections and impossible to decide from illustrations in STUR(1886) and MURR (1926).

Table 2: Plant fossils reported for the Pleistocene of Hötting (after MURR 1926).

taxa. Of these, *Pinus mugo* is uncertain, because its leaves cannot be distinguished from those of *Pinus sylvestris* in the fossil material. *Picea abies* is ecologically very variable and is part of the montane to subalpine vegetation belts. *Alnus alnobetula*, identified by MURR (1926) on the basis of a single leaf impression, typically grows along torrents but also occurs as glacial relict in colline pine forests (*P. sylvestris*). Two species of *Salix, S. appendiculata* and *S. glabra* are typical elements of ravine forests (e.g. Aceri-Fagetum adenostylosum; *S. appendiculata*) and *Pinus sylvestris* forests (*S. glabra*). Both species are also components of *Alnus alnobetula* communities and scree vegetation and talus fans (REISIGL & KELLER, 1989; FISCHER, 2005). Among herbaceous species, *Adenostyles glabra* and *Poa hybrida* are elements of *Alnus alnobetula* communities and/or scree vegetation and may reach down to low elevations along torrents. *Aster bellidiastrum* is not confined to high elevations and displays a vertical range from colline to subalpine. None of the taxa classified as T3 is restricted to the subalpine vegetation belt. Instead, they may reach down to valleys as part of azonal plant communities. Three taxa (9.7 %) of the Hungerburg flora are T3 taxa. All of them are also found in the Rossfall-Lahner flora.

T-value (ELLENBERG et al. 1992)	
Vertical distribution (based on field observations in Germany)	MAT (°C)
T3 indicator of cool conditions, mainly subalpine	(2 -) 3 (- 4)
T4 mainly montane to upper montane	(3.5 -) 4.5 (- 5.5)
T5 indicator of fairly warm conditions from lowland to montane	(5 –) 6 (– 7)
T6 lowland to submontane	(6.5 –) 7.5 (– 8.5)
T7 warmth indicator, warm lowland to colline	(8 -) 9 (- 9.5)
T8 valleys with favourable conditions	(9 -) 10 (- 10.5)
x indifferent	

Table 3: Temperature values and observed vertical distribution for vascular plants in Central Europe and the Alps (from ELLENBERG et al., 1992). MAT = mean annual temperature.



Figure 6: Selection of woody angiosperm taxa from the Pleistocene of Hötting. All specimens stored in (I). 1. *Acer campestre* L. (original to MURR, 1926, Pl. 1, fig. 7), R. 2. *Acer platanoides* L. (original to MURR, 1926, Pl. 2, fig. 23), H. 3. *Acer pseudoplatanus* L., large well-preserved leaf, ?R. 4. *Acer pseudoplatanus* L. (as *A. cf. ponzianum* GAUD., in STUR, 1886, Pl. 2, fig. 9), ?H. 5. *Acer pseudoplatanus* L. (as *Acer sp.*, in STUR, 1886, Pl. 2, fig. 11), ?H. R = Rossfall-Lahner Breccia, H = Hungerburg-Breccia. Scale bar = 3 cm.

Most taxa in the Rossfall-Lahner (35, or 64.8 %) and Hungerburg floras (22, or 70.9 %) are classified as indifferent, T4 (upper montane), or T5 (montane), i.e. their vertical distribution and temperature requirements overlap with the conditions presently found at the fossil sites near Hötting.

Eight or 14.8 % of the taxa reported for the Rossfall-Lahner flora are classified as T6 (five, or 9.26 %), T7 (two, or 3.7 %), and T8 (one, or 1.85 %), i.e. somewhat thermophilous. In the Hungerburg flora, six taxa (19.35 %) are T6 taxa, while higher T values are not found in any taxon (**Table 1**). Among T6 taxa some appear to have a wider ecological amplitude in Scandinavia with a marked area extension into cold areas. The two T7 and the single T8 taxon would appear to suggest climatic conditions warmer than to-day at the site of the Rossfall-Lahner flora. These taxa were selected as "key taxa" and, together with *Rhododendron ponticum*, subjected to further revision.

# 3.2.2. Re-examination of taxa showing 'climatic signal'

# Populus alba L. (Salicaceae)

Two leaf fragments described by MURR (1926) appear to belong to this species (**Fig. 7: 6, 7**). According to the same author the species currently grows at 900 m a.s.l. in the vicinity of the Rossfall-Lahner. "*Potentilla micrantha*" RAM. [cf. *Fragaria vesca*, according to present study]

According to WETTSTEIN (1892) the more frequent branching of the secondary veins in the apical portion of the leaf lamina, and the presence of little dots visible on the lamina and representing hair bases distinguish this species from *Fragaria vesca*. Based on SEM micrographs of the abaxial leaf epidermis of both species (**Fig. 9: 1–4**) the latter character may be encountered in both species. The branching pattern of secondary veins appears to be a better character to distinguish the two species. Nevertheless, it is difficult to use because in rare cases *Fragaria* may show the '*Potentilla* branching pattern' and vice versa. In view of the overlapping patterns of morphological variability encountered for the two species it is difficult to justify the assignment of specimens showing dots on their lamina to *P. micrantha*. According to MURR (1926) the species occurs in the vicinity of the fossil locality.

"Vitis vinifera subsp. sylvestris" (GMEL.) HEGI [indet. according to present study]

This species was not mentioned by WETTSTEIN (1992) but recognized later by MURR (1926) on the basis of two leaf fragments. One specimen was figured by MURR (Pl. 1, fig. 9). Here, the way that the first abmedial vein departs from the lowermost secondary vein resembles the pattern found in *Vitis vinifera*. *Vitis*, however, typically has three to five primary veins (actinodromous venation), of which the two outer ones normally have one or two orders of abmedial veins. This is not the case in the leaf fragment figured. The second leaf assigned to *Vitis* by MURR (1926) is a fragment figured in STUR (1886; Pl. 2, fig. 13). A stout lateral primary vein and densely spaced straight secondary veins originating from the mid vein are not typical of *Vitis vinifera*. On the basis of the scarce and fragmentary material it is impossible to establish closer generic or specific affinities of the fossil specimens; the inclusion within *Vitis vinifera* is not justified by diagnostic morphological features.

# 4. Discussion

# 4.1. Taxonomy and biogeography of the Rhododendron ponticum group

Although the generic identity of the rhododendron leaves from Hötting has been recognized for a long time (WETTSTEIN, 1888), a number of different species names have been applied to them. WETTSTEIN (1888, 1892) assigned the fossils to the modern species *R. ponticum*. It is interesting to note that none of the early accounts on the flora of Hötting (ETTINGSHAUSEN, 1884; STUR, 1886; WETTSTEIN, 1888, 1892) referred to the work of SORDELLI (1878) on the Pleistocene flora of northern Italy including *R. sebinense*. Also MURR (1926) did not mention SORDELLI although by this time the latter had published another account on the Pleistocene rhododendron from northern Italy, in which he had referred to the specimens from Hötting (SORDELLI, 1896). TRALAU (1963), though referring and commenting on the work of SORDELLI established a new name for the plants from Hötting (*R. sordellii*) but treated *R. sebinense* as synonym of his new species ignoring that the basionym *sebinense* had priority over *sordellii*. The cor-



Figure 7: Selection of woody angiosperm taxa from the Pleistocene of Hötting. All specimens stored in (I).
1-3. Alnus incana (L.) MOENCH 1. Small plicate leaf, R. 2, 3. Larger leaves, R. 4. Fagus sylvatica L., only one specimen belonging to this species was found in the collections examined for this study (original to MURR, 1926, Pl. 1, fig. 3), R. 5. Quercus sp., one of two leaf fragments of Quercus found in the collections examined for this study (as Q. robur L. in MURR, 1926, Pl. 2, fig. 21b), H. 6, 7. cf. Populus alba L. 6. Leaf fragment showing higher order venation, R. 7. Fragment of lobed leaf (original to MURR, 1926, Pl. 1, fig. 4), R. 8, 9. Rhamnus frangula L. 8. Larger leaf with typical brochidodromous venation (original to ETTINGSHAUSEN, 1884, Pl. 1, fig. 1), R. 9. Original to STUR, 1886, Pl. 2, fig. 4, R. 10. Viburnum lantana L. (original to Stur, 1886, Pl. 2, fig. 16), R.
R = Rossfall-Lahner Breccia, H = Hungerburg-Breccia. Scale bar = 3 cm.



Figure 8: Selection of woody angiosperm taxa from the Pleistocene of Hötting. All specimens stored in (I). 1-3. Salix spp. 1. Salix myrsinifolia SALISB. (syn. S. nigricans SM.), leaf with well-preserved tertiary venation, R. 2. Salix appendiculata VILLARS (syn. S. grandifolia SERINGE, original to STUR, 1886, Pl. 2, fig. 14), R. 3. Salix eleagnos SCOP. (syn. S. incana SCHRANK), R. R = Rossfall-Lahner Breccia. Scale bar = 3 cm.

rect name for the leaves (and buds, bud scales) of Hötting appears to be *R. ponticum* var. *sebinense*. Despite this, TRALAU'S *R. sordellii* has been used by later authors (e.g. REISIGL & KELLER, 1989).

*Rhododendron ponticum* belongs to the subgenus *Hymenanthes* of *Rhododendron*, which contains more than 200 species. While most species are distributed entirely in southeastern Asia, around ten species are found in western Eurasia, southeastern and western North America, Taiwan, Japan, and South Korea, and extending to northeastern Asia and Siberia (CHAMBERLAIN, 1982). Of the four western Eurasian species *R. caucasicum, R. ponticum, R. smirnovii,* and *R. ungernii,* one appears to belong to a lineage comprising northeastern and southeastern Asian species (*R. smirnovii*; MILNE, 2004; GOETSCH et al., 2005). The remaining species belong to a group of eastern Asian, western Eurasian, and North American species (GOETSCH et al., 2005).

Among the western Eurasian species, *R. ponticum* is the only one that has a Euxinian-Iberian disjunct distribution. This strongly supports the assumption that the Pleistocene fossils from Hötting belong to a lineage of *R. ponticum*. The relatively large size of leaves encountered among the Pleistocene *R. ponticum* var. *sebinense* further appears to preclude a closer affinity to *R. caucasicum* as suggested by TRALAU (1963) and points to a closer relationship between the Euxininan subspecies *ponticum* and the fossil species, than between the Iberian subsp. *baeticum* and the fossil. This and the Cainozoic fossil record suggest that the species or the lineage leading to the modern species originated in or close to its present eastern range.

While *R. ponticum* has repeatedly been used as a typical example of a "Tertiary relict", i.e. a taxon that had a wider distribution during at least some parts of the Tertiary (cf. ROTHMALER, 1955; MILNE, 2004), the present study suggests that the species is a Pleistocene relict rather than a Tertiary relict. Pre-Pleis-

60

tocene fossils possibly belonging to a lineage leading to the modern species are restricted to the modern area of *R. ponticum*, and there is no convincing evidence for a westward expansion prior to the Pleistocene (cf. TRALAU, 1963).

#### 4.2. Floristic affinities of the Pleistocene flora of Hötting

WETTSTEIN (1892), RYTZ (1925), and MURR (1926), among others, emphasised the floristic affinities of the flora of Hötting to the modern "Pontic" and Colchic floras, of northern Turkey and western Georgia. The main reason for this was the presence of R. ponticum in the flora of Hötting. MURR (1926) recognized Vitis sylvestris as another element typical of Pontic forests and pictured a typical beech forest with undergrowth of rhododendron and lianas such as Vitis as a modern analogue for Hötting. The fossils referred to Vitis cannot be assigned to this genus with any confidence and thus are of limited value. The modern Pontic or Euxinian (including also Transcaucasia) flora contains nearly all woody trees and shrubs that are found in Central Europe plus a great number of taxa that went extinct in the Late Cainozoic in Central Europe (Acer cappadocicum GLED., Prunus laurocerasus L., Philadelphus caucasicus KOEHNE, Diospyros lotus L., Smilax excelsa L., Pterocarya fraxinifolia (POIRET) SPACH, Ruscus hypophyllum L., Ouercus pontica C. KOCH, Periploca graeca L., Pteris cretica L., Osmanthus decorus KASAPLIGII, Buxus sempervirens L., Celtis, Zelkova carpinifolia (PALL.) KOCH; cf. DENK et al., 2001). Of these characteristic elements none is present in the flora of Hötting, which therefore should be considered a standard Central European flora with the addition of R. ponticum. At present, another Euxinian element, R. luteum Sweet, shows a similar disjunction with scattered outposts in Poland, Slovenia, and on the Greek island of Lesvos (FISCHER, 2005; YANNITSAROS & BAZOS, unpublished manuscript) indicating a wider distribution of this plant in the past.

#### 4.3. Climatic considerations for the Pleistocene of Hötting

The flora from Hötting has been considered indicative of an interglacial climate that is warmer than today (WETTSTEIN, 1888, 1892; RYTZ, 1925; MURAWSKI, 1992). In contrast, MURR (1926) argued that most elements encountered in the flora of Hötting currently are found close to the fossil locality. To estimate climatic constraints for R. ponticum he suggested considering the range of cultivated R. ponticum instead of the plant's native range. Recent studies on the ecological requirements and strategies of native and invasive populations of *R. ponticum* shed new light on genetic and ecological changes accompanying the area extension of R. ponticum and explain the success of Irish invasive populations (ERFMEIER, 2004). According to ERFMEIER, Georgian and Spanish populations of R. ponticum differ from invasive Irish populations by lower flowering rates and establishment of seedlings. Both native Spanish and invasive Irish populations are characterised by higher plant size and smaller leaf size. The smaller plant size in subsp. ponticum may be linked to the height of the snow cover at high elevations. ERFMEIER (2004) and MILNE & ABBOTT (2000) found that some of these traits are genetically fixed (for instance the larger leaf size in the eastern subsp. *ponticum*) and that in addition the Irish invasive populations are favoured by climatic conditions. Irish populations are derived from Spanish native populations based on genetic studies (MILNE & ABBOTT, 2000). These observations and the fact that native R. ponticum subsp. ponticum occurs from sea level to over 2000 m a.s.l. suggest that the ecological amplitude of this species is wider than that of many other "Tertiary relicts" confined to the Euxinian area at present (cf. 4.2.). While the latter did not survive in any Central European refugia and are absent from Central European (Late) Pleistocene floras, some of them have closely related and derived species in the Mediterranean area (Zelkova, Smilax, Ruscus) or have a disjunct Euxinian-Mediterranean distribution at present (Periploca graeca; cf. DENK et al. 2001). Other species displaying a modern Central European – Scandinavian distribution grow under markedly different climatic conditions in their southern and northern ranges, reflecting most probably different post-glacial histories and different ecological/eco-physiological traits of populations. This is illustrated by T-values for Central European plants that may be much warmer than for the same species growing in Scandinavia (cf. Table 2). Similarly, populations of *R. ponticum* from the Euxinian area may have undergone adaptive changes when they spread towards the west in the course of the Pleistocene. It



**Figure 9**: Comparative leaf morphology, *Fragaria vesca* L. and *Potentilla micrantha* RAM. **1**, **2**, **5**. *Fragaria vesca*, Sandwith 748 (S). **3**, **4**, **6**. *Potentilla micrantha*, Coaz 25/6/1924 (S). **1–4**. SEM micrographs. Abaxial leaf epidermis showing that frequency of trichomes and trichome bases are essentially the same in *F. vesca* and *P. micrantha*. **5**. *Fragaria vesca*, B. Maximov. 1904 (S), leaflets with serrate margin. **6**. *Potentilla micrantha*, E. Julin 5/4/1966 (S). Scale bar = 100 µm in 1–4, and 1 cm in 5, 6.

is difficult to assess the hardiness of planted *R. ponticum* in the cooler parts of Europe because these plants may represent hybrids between closely related species and therefore be more frost resistant (cf. MILNE & ABBOT, 2000; ERFMEIER, 2004). One individual growing in the Botanical Garden of Stockholm has been obtained several decades ago and appears to be from a native stand. It is flowering and producing seeds. Even without considering pronounced ecological shifts for Pleistocene populations of *R. ponticum*, MAT inferred for subalpine stands of *R. ponticum* subsp. *ponticum* ( $\pm$  4°C at 2000 m a.s.l.) suggests that cooladapted populations of this species may easily have been able to cope with climatic conditions as found today in the area of Hötting.

Other warmth indicators (T7 and possibly T8 plants) reported for the flora of Hötting typically are members of azonal communities (riparian stands). Such stands have been extremely negatively influenced by human activities after the last glacial, which may have led to the present reduction of the distribution of *Populus alba* [and *Vitis vinifera* subsp. *sylvestris*] in Central Europe. Elements such as *R. ponticum* subsp. *ponticum* are typical of the zonal vegetation, where they form part of various broadleaved deciduous, conifer, and mixed deciduous-conifer forests (RADDE, 1899). Other elements such as *Quercus robur* (Hungerburg flora) are characteristic of the azonal vegetation, such as riparian stands.

Based on this, there is no convincing evidence for an interglacial climate warmer than today in the area of Hötting. Moreover, the available palaeobotanical data do not necessarily indicate that the two floras of Hötting, the Hungerburg and Rossfall-Lahner floras, were deposited under different climatic conditions. They may simply reflect different taphonomic types of floral assemblages with the autochthonous Rossfall-Lahner flora reflecting a more zonal vegetation, and the allochthonous and badly preserved Hungerburg flora representing azonal vegetation.

#### 4.4. Problems related to the dating of Pleistocene floras

Previous palaeobotanical studies suggested markedly different ages for the fossil flora from Hötting ranging from Late Tertiary (e.g. STUR, 1886) to Pleistocene (ETTINGSHAUSEN, 1884; WETTSTEIN 1892). Geological evidence appears to indicate that the Höttinger Breccia was deposited during the Riss-Würm Interglacial. The White Breccia and the Red Breccia were dated as 109 ± 6.6 ka and 101 ka, respectively (SANDERS & OSTERMANN, 2006). TRALAU (1963) suggested the flora of Hötting to be deposited during the Riss-Würm Interglacial, while the floras of Piánico-Sèllere from northern Italy should be from the Riss-Würm Interglacial. He did not provide further explanations why this should be so. In contrast, GAMS (1954) stated that it cannot be decided to which interglacial floras such as Piánico-Sèllere and Hötting should be assigned. These latter floras have been frequently compared and considered very similar by a number of authors (e.g., GAMS, 1954; EMMERT-STRAUBINGER, 1991) and the richer macroflora from northern Italy could be due to its more southern position. Based on the presence of *Rhinoceros merckii* JAEG., PENCK & BRÜCKNER (1909) and EMMERT -STRAUBINGER (1991) considered the Piánico-Sèllere assemblages to be from the Riss-Würm Interglacial.

MOSCARIELLO et al. (2000) studied the sedimentology and palynology of the basin and found that the succession is overlain by glacial deposits, which they considered to be of Würmian age. Palynological evidence strongly suggested an Eemian (marine isotopic stage MIS 5e) or slightly older age (MIS 7 or 9, 200-320 ka), while the absence of taxa such as *Pterocarya, Carya, Tsuga*, and *Cedrus* excluded an older age. In contrast to studies based on macrofossils alone, however, MOSCARIELLO et al. (2000) reported climatic oscillations in the pollen record of the Piánico sequence suggesting that it includes more than a single interglacial.

All these findings are in stark contrast to a later study by PINTI et al. (2001) who reported a K-Ar dating for a distal tephra from the Piánico-Sèllere basin of ca. 780 ka.

This is interesting for a number of reasons. First, if the dating by PINTI et al. (2001) is correct the correlation of Pleistocene floras based on palynological and macrofossil data appears to be unreliable. A similarly strong discrepancy between age estimates inferred from sequences of pollen floras and absolute dates has been reported by REILLE & BEAULIEU (1995). Furthermore, it raises the question whether or not the Rossfall-Lahner interval of the Höttinger Breccia can be linked to the sedimentation episodes of the Red and White breccias (cf. SANDERS & OSTERMANN, 2006). Macrofossils obtained from the Hungerburg and Rossfall-Lahner floras do not reflect a succession of vegetational changes. As such they are difficult to correlate to other floras. It is not clear from the current palaeobotanical data whether or not the Rossfall-Lahner sequence was deposited earlier than the sediments containing the plants of the "Red" or Hungerburg Breccia. Based on their floral composition the co-occurrence of these two floras is quite possible.

# 5. Acknowledgements

I would like to thank Helga Schmitz (Museum of Natural History, Vienna) for continuous help with literature, and Andreas Kroh (Department of Palaeontology, Museum of Natural History, Vienna), Dietmar Sanders (Institute of Geology and Palaeontology, University of Innsbruck), Wolfgang Neuner, Stefan Heim (Landesmuseum Ferdinandeum, Innsbruck), Barbara Meller (Geological Survey, Vienna), and Reinhard Zetter (Institute of Palaeontology, University of Vienna) for help in the various collections. Norbert Frotzler provided critical feedback.

# 6. References

- ANDERSSON, G. (1910): *Rhododendron ponticum* fossil in the island of Skyros in Greece. A contribution to the knowledge of the extension of a Pontic climate in the west during Quaternary times. – In: ANDERSSON, G. (ed.) Die Veränderungen des Klimas seit dem Maximum der letzten Eiszeit. Stockholm: 144–149.
- BAUMANN, K.-H., HUBER, R. (1999): Sea-surface gradients between the North Atlantic and the Norwegian Sea during the last 3.1. M.Y.: Comparison of sites 982 and 985. – In: RAYMO, M.E., JANSEN, E., BLUM, P. HERBERT, T. D. (eds.) Proc. ODP, Sci. Results, 162: 179–190, College Station, TX (ocean Drilling Program).
- BROWICZ, K. (1983): Chorology of trees and shrubs in south-west Asia and adjacent regions. Vol. 2. Polish Academy of Sciences, Warsaw: 86 pp.
- CHAMBERLAIN, D. F. (1982): A revision of *Rhododendron* II. subgenus *Hymenanthes.* Notes R. Bot. Gard. Edinb. 39: 209–486.
- COLLINSON, M. E., & CRANE, P. R. (1978): *Rhododendron* seeds from the Palaeocene of southern England. Bot. J. Linn. Soc. 76: 195–205.
- DENK, T., FROTZLER, N., DAVITASHVILI, N. (2001): Vegetational patterns and distribution of relict taxa in humid temperate forests and wetlands of Georgia (Transcaucasia). – Biol. J. Linn. Soc. 72: 287–332.
- DENK, T., GRÍMSSON, F., KVAČEK, Z. (2005): The Miocene floras of Icelandand their significance for Late Cainozoic North Atlantic biogeography. – Bot. J. Linn. Soc. 149: 369–417.
- ELLENBERG, H., WEBER, H. E., DÜLL, R., WIRTH, V., WERNER, W., PAULISSEN, D. (1991): Zeigerwerte von Pflanzen in Mitteleuropa. – Scripta Geobotanica 18: 1–258.
- EMMERT-STRAUBINGER, E. (1992): Die Interglazialflora von Piànico (Prov. Bergamo, Italien). In: KOVAR-EDER, J. (ed.) Palaeovegetational development in Europe and regions relevant to its palaeofloristic evolution, Proceedings of the Pan-European Palaeobotanical Conference, Vienna, 19–23 September 1991. Museum of Natural History, Vienna: 15–18.
- ERFMEIER, A. (2004): Ursachen des Invasionserfolges von Rhododendron ponticum L. auf den Britischen Inseln: Einfluss von Habitat und Genotyp. – PhD dissertation, University of Göttingen, Göttingen: 88 pp.
- ETTINGSHAUSEN, C. v. (1884): Über die fossile Flora der Höttinger Breccie. Sitzungsber. Akad. Wissensch. Wien, 1. Abt., 90: 1–16.
- FISCHER, M. A. (ed.) (2005): Exkursionsflora f
  ür Österreich, Liechtenstein und S
  üdtirol. 2nd ed. Land Oberösterreich, Oberösterreichisches Landesmuseum, Biologiezentrum Linz: 1450 pp.
- GAMS, H. (1954): Das Verschwinden von Gehölzen aus den Alpen während des Eiszeitalters. (Festschrift für Erwin Aichinger zum 60. Geburtstag). – Sonderf. Angew. Pflanzensoz. I: 71–76.
- GOETSCH, L., ECKERT, A. J., HALL, B. D. (2005): The molecular systematics of *Rhododendron* (Ericaceae): a phylogeny based upon *RPB2* gene sequences. Syst. Bot. 30: 616–626.

- HENDERSON-SELLERS, A. & ROBINSON, P. J. (1986): Contemporary climatology. Longman Scientific & Technical UK, and John Wiley & Sons, New York: 439 pp.
- JESSEN, K., ANDERSON, S., FARRINGTON, A. (1959): The inter-glacial deposit near Gort, Co. Galaway, Ireland. Proceedings of the Royal Irish Academy, B, 60: 1–177.
- KUTUZKINA, E. F. (1964): The Sarmatian flora of Armavir. In: TAKHTAJAN, A. L. (ed.): Palaeobotanica 5. Russian Academy of Sciences, Moscow: 145–230. (In Russian)
- LIETH, H., BERLEKAMP, J., FUEST, S., RIEDIGER, S. (1999): Climate diagram world atlas. CD-Series: Climate and Biosphere. – Backhuys Publishers, Leiden.
- MEJÍAS, J. A., ARROYO, J., MARAÑÓN, T. (2006): Ecology and biogeography of plant communities associated with a Tertiary relict plant, *Rhododendron ponticum* subsp. *baeticum*, in Southern Spain. – J. Biogeography: in press.
- MILNE, R. I., ABBOTT, R. J., WOLFF, K., CHAMBERLAIN, D. F. (1999): Hybridization among sympatric species of *Rhododendron* (Ericaceae) in Turkey: Morphological and molecular evidence. – Am. J. Bot. 86: 1776–1785.
- MILNE, R. I., ABBOT, R. J. (2000): Origin and evolution of invasive naturalized material of *Rhododendron ponticum* L. in the British Isles. – Mol. Ecol. 9: 541–556.
- MILNE, R. I. (2005): Phylogeny and biogeography of *Rhododendron* subsection *Pontica*, a group with a tertiary relict distribution. – Mol. Phyl. Evol. 33: 389–401.
- MOSCARIELLO, A., RAVAZZI, C., BRAUER, A., MANGILI, C., CHIESA, S., ROSSI, S., BEAULIEU, J.-L., REILLE, M. (2000): A long lacustrine record from the Piánico-Sèllere Basin (Middle-Late Pleistocene, Northern Italy). – Quat. Int. 73/74: 47–68.
- MURAWSKI, H. (1992): Geologisches Wörterbuch. Enke, Stuttgart.
- MURR, J. (1926): Neue Übersicht über die fossile Flora der Höttinger Breccie. Jahrbuch der Geologischen Bundesanstalt 76: 153–170.
- MUTTONI, G., CARCANO, C., GARZANTI, E., GHIELMI, M., PICCIN, A., PINI, R., ROGLEDI, S., SCIUNNACH, D. (2003): Onset of major Pleistocene glaciation in the Alps. – Geology 31: 989–992.
- PENCK, A. & BRÜCKNER, E. (1909): Die Alpen in den Eiszeiten. Tauchnitz, Leipzig.
- PINTI, D. L., QUIDELLEUR, X., CHIESA, S., RAVAZZI, C., GILLOT, P.-Y. (2001): K-Ar dating of an early Middle Pleistocene distal tephra in the interglacial varved succession of Piànico-Sèllere (Southern Alps, Italy). – Earth Planet. Sci. Lett. 188: 1–7.
- RADDE, G. (1899). Die Vegetation der Erde, 3. Grundzüge der Pflanzenverbreitung in the Kaukasusländern. Leipzig, Wilhelm Engelmann.
- REILLE, M. & BEAULIEU, J.-L. (1995): Long Pleistocene pollen records from the Praclaux Crater, South-Central France. – Quat. Res. 44: 205–215.
- REISIGL, H. & KELLER, R. (1989): Lebensraum Bergwald. Alpenpflanzen in Bergwald, Baumgrenze und Zwergstrauchheide. – Gustav Fischer Verlag, Stuttgart: 144 pp.
- ROTHMALER, W. (1955): Allgemeine Taxonomie und Chorologie der Pflanzen (2. Auflage). Willhelm Gronau Verlag, Jena.
- RYTZ, W. (1925): Ueber die Interglazialfloren und Interglazialklimate, mit besonderer Berücksichtigung der Pflanzenreste von Gondiswil-Zell und Pianico-Sellere. – Festschrift Carl Schröter, Veröff. Geobot. Inst. Rübel 3: 540–553.
- SANDERS, D. & OSTERMANN, M. (2006): Sedimentology and depositional setting of the "warm-interglacial" fossil flora of the Höttinger Brekzie (Pleistocene, Northern Calcareous Alps, Austria): a reconstruction. – Veröffentlichungen Tiroler Landesmuseum Ferdinandeum, 86: 91–118.
- SORDELLI, F. (1878): Le filliti della Folla d'Induno presso Varese e di Pontegana tra Chiasso e Balerna nel Canton Ticino paragonate con quelle di altri depositi terziari e posterziari. – Atti della Società Italiana di Scienze Naturali 21: 1–23.
- SORDELLI, F. (1896): Flora fossilis Insubrica. L. F. Gogliati, Milano: 300 pp.
- STEFANOFF, B. & JORDANOFF, D. (1935): Studies upon the Pliocene flora of the Plain of Sofia (Bulgaria). Sofia: 150 pp.
- STUR, D. (1886): Beitrag zur Kenntnis der Flora des Kalktuffes und der Kalktuff-Breccie von Hötting bei Innsbruck. – Abhandl. K.K. Geol. Reichsanst., 12 (2): 31–56.

- THIEDE, J., WINKLER, A., WOLFWELLING, T., ELDHOLM, O., MYHRE, A. M., BAUMANN, K. H., HENRICH, R., STEIN, R. (1998): Late Cenozoic history of the polar North Atlantic – results from ocean drilling. – Quat. Sci. Rev. 17: 185–208.
- TRALAU, H. (1963): Über Rhododendron ponticum und die fossilen Vorkommen des naheverwandten Rhododendron sordellii. – Phyton 10: 103–109

UNGER, F. (1852): Versuch einer Geschichte der Pflanzenwelt. - Wien, Braumüller: 364 pp.

UNGER, F. in PICHLER A. (1859): Beiträge zur Geognosie Tirols. - Ferdinandeums Zeitschrift, 3. Folge, 8. Heft.

WETTSTEIN, R. v. (1888): Rhododendron ponticum L. fossil in den Nordalpen. Sitzungsber. – Akad. Wissensch. Wien, Abt. 1, 97: 37–50.

WETTSTEIN, R. v. (1892): Die fossile Flora der Höttinger Breccie. - Denkschr. Akad. Wissensch. Wien 59: 479-531.

- YANNITSAROS, A. & BAZOS, I. (2002): A brief outline of the flora and vegetation of Lesvos island. Unpublished manuscript.
- ZACHOS, J., PAGANI, M., SLOAN, L., THOMAS, E., BILLUPS, K. (2001): Trends, rhythms, and aberrations in global climate 65 Ma to present. – Science 292: 686–693.

Thomas Denk Department of Palaeobotany Swedish Museum of Natural History Box 50007 104 05 Sweden e-mail: thomas.denk@nrm.se

# **ZOBODAT - www.zobodat.at**

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: Veröffentlichungen des Tiroler Landesmuseums Ferdinandeum

Jahr/Year: 2006

Band/Volume: 86

Autor(en)/Author(s): Denk Thomas

Artikel/Article: <u>Rhododendron ponticum L. var. sebinese (SORDELLI)</u> <u>SORDELLI in the Late Pleistocene flora of Hötting, Northern Calcareous Alps:</u> <u>witness of a climate waremer than today?. 43-66</u>