Buellia centralis and chemotypes of Dimelaena oreina in Tibet and other Central-Asian regions

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15 specimens of *Buellia centralis* and 106 specimens of *Dimelaena oreina* from Tibet and other Central Asian regions have been studied chemically. *Buellia centralis* contains rhizocarpic, hypoprotocetraric and nornotatic acid. Molecular analyses revealed its taxonomic position within the core group of *Buellia*. Except for chemotype IV (gyrophoric acid and fumarprotocetraric acid) and VI (sphaerophorin and gyrophoric acid), all hitherto known chemotypes of *Dimelaena oreina* are present in the study area. Due to the occurrence of hypostictic acid (accompanied by stictic acid) as a major compound in *Dimelaena oreina*, a new chemotype (Vb) is defined. The use of just a single areola for TLC-investigations confirmed this new chemotype as well as the existence of chemotypes IV (gyrophoric acid and fumarprotocetraric acid), chemotype VII (stictic acid and gyrophoric acid), and the newly recognised (sub-)chemotypes of chemotype II (chemotype IIa with gyrophoric acid and chemotype IIb with ovoic acid in addition to gyrophoric acid).

Key words: chemistry, distribution, lichenized fungi, phylogeny.

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Introduction

To date, the scientific results of two expeditions by the first author to the Tibetan region (1994 and 2000), based on collections of lichens (and their lichenicolous fungi), have been published in approximately 30 papers (compiled in Obermayer 2004). In continuation of these publications, the present contribution deals with *Buellia centralis* and *Dimelaena oreina*, both representing saxicolous species of the lichen family Physciaceae, characterized by a crustose yellowish thallus with radiate-plicate margins and brown coloured, two-celled spores without wall-thickenings.

The aim of the present paper is to provide new data on the chemotypes of Central-Asian specimens of *Dimelaena oreina*, as well as on the chemistry, anatomy and distribution of *Buellia centralis*. The generic position of the latter and its supposed relation to some similar members of the Physciaceae is discussed on a mtSSU-based, phylogenetic approach.

Material and methods

The study is based on material collected on field trips to Tibet and adjacent areas in 1994 and 2000, and on further specimens from the following herbaria: GZU, H, M, S, TAD and UPS. Unless otherwise stated, the specimens are housed in GZU.

Standard light microscopic techniques were employed for the examination of specimens. Habit photographs were taken through a Wild M3B microscope using a Nikon Coolpix 5000 digital camera. For the identification of lichen substances, standardized methods for thin layer chromatogra-

Table 1. Specimens tested by means of "one-areola-TLC" for confirmation of chemotypes, all in GZU.

Specimens tested	No. of areoles	Chemotype
Austria, Hafellner 2856a	5	IV
Austria, Hafellner 2856b	1+1	IV+IIa
Austria, Mayrhofer & Poelt s.n.	2	IV
Austria, Mayrhofer 13558	3	IV
Austria, Mayrhofer 13265	3	IV
Austria, Türk 32431	2	IV
Austria, Mayrhofer 15294	1+2+1	I+IV+V
USA, Hafellner 36961	1	VII
Austria, Mayrhofer 15296	5+6	I+V
Austria, Mayrhofer 15294 & Lambauer	1+2+1	I+IV+V

phy (TLC) were used following Culberson & Ammann (1979) and Elix et al. (1987). For a better resolution of the spots, plates were let run up to 15 cm height. In many cases, a single areola (c. 0.6–1.5 mm in diam.) was removed from *Dimelaena*-specimens in order to avoid ambiguous ("mixed") results due to obviously intermixed thalli. In these cases, only solvent B was used in order to get more concentrated spots. The depsidone hypostictic acid can be easily separated from norstictic acid (with a similar Rf in B), because it quickly develops a red spot during the heating of the plate, whereas norstictic acid becomes brownish-yellow.

A number of specimens from Central Europe and USA (Table 1) were tested by means of "one-areola-TLC" in order to confirm the occurrence of chemotype IV (usnic acid, gyrophoric acid [never with ovoic acid], fumarprotocetraric acid), chemotype VII (usnic acid, stictic acid, gyrophoric acid) and a supposed (but then not confirmed) new chemotype with stictic acid and fumarprotocetraric acid (see specimen "Mayrhofer 15296"). Note that this and other "unusual" combinations of compounds are probably due to mixed thalli and have been cited in several earlier publications, e.g. Leuckert et al. (1975).

PCR amplification and sequencing. The thalli and apothecia were first checked for contaminations such as lichenicolous fungi. Uninfected apothecia were used for direct PCR. The carbonized epihymenium was removed from the apothecium using a razor-blade. A single piece of the hymenium (c. $50 \times 50 \times 15$ µm) was then cut out and placed in a PCR tube with the appropriate amount of water. The other chemicals for the PCR reactions were then added. The amplification included the mitochondrial SSU rDNA. Primers for amplification were mtSSU1 and mtSSU3R (Zoller et al. 1999). 50 µl PCR mix (10 mM Tris pH 8.3/50 mM KCl/1.5 mM $MgCl_2$/50 µg gelatine) contained 1.25 units of Taq polymerase (Amersham), 0.2 mM of each of the four dNTPs and 0.5 µM of each primer. Annealing conditions were 55°C or alternatively 56°C–50°C touchdown during the first 6 cycles, followed by 30 cycles with 50°C annealing temperature. Products were either PEG precipitated or cleaned using QIAGEN quick spin columns (Qiagen, Vienna). Both complementary strands were sequenced using the BigDye Terminator Cycle Sequencing Ready Reaction Kit (ABI, Vienna) according to the manufacturers instructions. Sequences were run on an ABI310 automated sequencer (ABI).

Sequence alignment and analyses. The mtSSU sequences were assembled using the BioEdit software (BioEdit 5.0.9; Hall 1999) and aligned using ClustalW as embedded in BioEdit. The mtSSU dataset was the subject to a phylogenetic analysis using MrBayes Version 3 (http://morphbank.ebc.uu.se/mrbayes/). The general time reversible substitution model with among-site variation (GTR + Γ rates for variable site were drawn from a gamma distribution with 4 discrete categories) was used for likelihood calculations. The nucleotide substi-

Table 2. The species sequenced for this study with their collector and Genbank accession numbers for mtSSU (sequences of species without collecting data were retrieved from Genbank for comparison).

Species	Vuocher specimen (herbarium)	GenBank no.
Buellia aethalea	Austria, Hafellner 58173 (GZU)	AY640585
Buellia centralis	Tibet, Obermayer 05264 (GZU)	AY640586
Dimelaena oreina	Tibet, Obermayer 05335 (GZU)	AY640587
Dimelaena radiata	Canary Islands, Hafellner 53407 (GZU)	AY640588
Buellia dijiana	Retrieved from GenBank	AY143416
Buellia disciformis	Retrieved from GenBank	AY143401
Buellia elegans	Retrieved from GenBank	AY143417
Buellia epigaea	Retrieved from GenBank	AY143418
Buellia schaereri	Retrieved from GenBank	AY143420
Rinodina plana	Retrieved from GenBank	AY143425
Rinodina sophodes	Retrieved from GenBank	AY143426

tution model was selected using a likelihood ratio test (Huelsenbeck & Crandall 1997) with the program MrModeltest (Nylander 2002), a simplified version of Modeltest v3.06 (Posada & Crandall 1998) following the Akaike Information Criterion (AIC). The Markov Chain Monte Carlo (MCMC) analysis was run for 2 000 000 generations, with 10 chains starting from a random tree, and using the default temperature of 0.2. Every 100th tree was sampled, and the first 100 000 generations were discarded as burn-in. The likelihood parameters in the sample had the following average values (± one standard deviation): rate matrix r(GT) = 1.000 (± 0), r(CT) = 2.952 (± 0.610), r(CG) = 0.441 (± 0.059), r(AT) = 1.161 (± 0.094), r(AG) = 2.086 (± 0.257), r(AC) = 0.617 (± 0.055), base frequencies π(A) = 0.331 (± 0), π(C) = 0.155 (± 0),π (G) = 0.219 (± 0), π(T) = 0.295 (± 0) and the gamma shape parameter α = 0.405 (± 0.007). A consensus phylogram showing mean branch lengths was calculated with the sumt command in MrBayes.

The tree with posterior probabilities of topologies higher than 50% is presented (Fig. 3). Two species of *Rinodina* (*R. plana* and *R. sophodes*) were used as outgroup taxa. We produced 4 new mtSSU rDNA sequences (Table 2). Regarding *B. centralis* we got another identical sequence from the same locality (Obermayer 5245, in UPS, data not shown). The sequences are submitted to EMBL/GenBank (http://www.ncbi.nlm.nih. gov/) and a list of sequenced taxa together with their genbank accession numbers is presented in Table 2. A number of sequences were retrieved from Genbank for comparison (Table 2).

The species

Buellia centralis H.Magn.

Lichens from Central Asia: 147 (1940). – Type: China occidentalis, prov. Kansu, Yü-erh-hung, 2680-2830 m, in jugo montium, 30.I.1932, Birger Bohlin 79 (S! holotype, UPS! isotype).

ILLUSTRATIONS. Magnusson 1940: plate XII, Fig. 1; Golubkova 1983: 58, Fig. 1; this paper: Figs 1 & 2.

Thallus saxicolous, crustose, deeply cracked and soon becoming separated into single areolae, with marginally radiating lobes (Fig. 1A); cortex yellowish (more intensive at lobe tips), partly pruinose; medulla white, with calcium oxalate-crystals. **Apothecia** black, 0.3–1 mm in diam., roundish when young to rhomboid, mainly marginally immersed in the areolae (up to thallus level) and surrounded by deep cracks (Fig. 1B), sometimes deeply cracked and one apothecium divided into portions or with a few apothecia arranged together, of the *Aethalea*-type (see Scheidegger 1993: 324) with an almost invisible, lecideine margin and plane to slightly convex, often slightly whitish pruinose disc; pruina dark orange-red under long wave UV; hymenium 70–90 µm high; epihy-

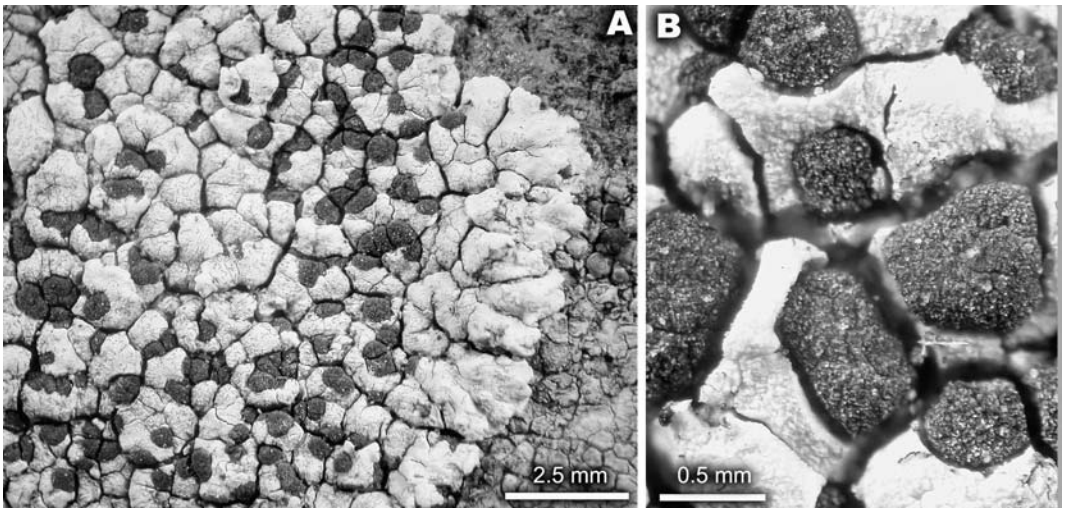

Figure 1. *Buellia centralis* (Obermayer 05264, GZU). A. Thallus with apothecia and marginally radiating lobes. B. Slightly pruinose apothecia sunken into the cracked thallus.

menium brownish (HNO_3 –), with yellow crystals; paraphyses at base 2 µm wide, with apices swollen and with a dark brown pigmented cap up to 5 µm wide; hypothecium dark brown. **Asci** of the *Bacidia*-type (see Figs 2A, 2B and Rambold et al. 1994). **Spores** 1-septate, colourless when very young, brownish-grey when mature, dark brown when old, 13–15 × 6–7.5 µm; spore wall up to 1 µm wide, very faintly sculptured, uniformly thickened, of the *Buellia*-type (see Scheidegger 1993: 334); spore septum and apical parts not thickening during development (ontogeny of type A; Giralt & Mayrhofer 1995); septal pore canal visible in young stages, 0.5 µm wide (cf. Figs 2C, 2F and Bungartz & Nash III 2004: 53, Fig. 9). **Pycnidia** dispersed, immersed, globose, with ostiolum colourless, later pale brownish. **Conidia** bacilliform to subelliptical (rarely clavate or slightly fusiform or even bifusiform), 4–4.5 × 1.5–2 µm (Fig. 2G).

Chemistry. Cortex and medulla K–, C–, PD–, I–; contains rhizocarpic acid in the cortex and hypoprotocetraric acid and nornotatic acid in the medulla.

Distribution. *Buellia centralis* was known from the Chinese provinces Gansu (type locality) and Neimongol (Magnusson 1944), from Tajikistan (Golubkova 1973, Kudratov & Mayrhofer 2002) and from Mongolia (Golubkova 1981, Cogt 1995). All localities cited in these papers, in addition to the new records (see below) from the Karakorum range (Pakistan/China), the Kali-Gandaki area in Nepal and the headwater region of the Subansiri river in South East Tibet, indicate that this taxon has an Arid Central Asian distribution (Fig. 4).

Remarks. In contrast to the chemically well-known *Dimelaena oreina* (see below), no information was available on the lichen substances of the similarly yellow-coloured *Buellia centralis*. HPLC and TLC studies revealed the uncoloured depsidones, hypoprotocetraric acid and nornotatic acid, and the yellow pulvinic acid derivative rhizocarpic acid in the cortex. The latter is a very rare substance in members of the family Physciaceae. It is found only in *Dermatiscum thunbergii* (Harper & Letcher 1966) and, in the course of the present studies, in an unnamed epiphytic *Buellia* species of the Tibetan area (e.g. Obermayer 07287, 07435). Note that the rhizocarpic acid containing *Buellia saurina* W.A.Weber has been recently transferred to the genus *Rhizocarpon* (Bungartz & Fryday 2004). Calycin, a further yellow pulvinic acid derivative has been reported from *Buellia rhodesiaca* (Harper & Letcher 1966).

There are other yellowish lichen substances that

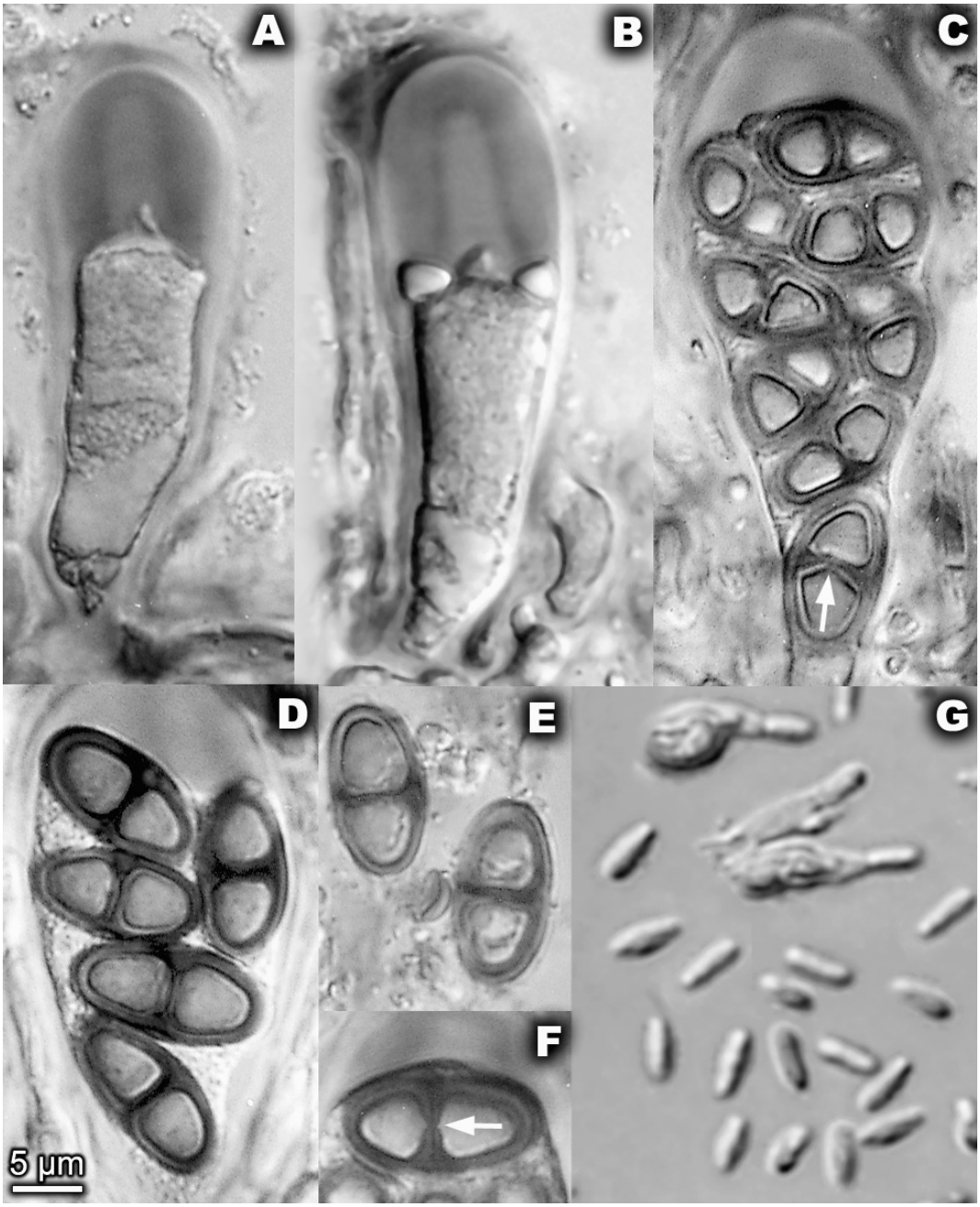

Figure 2. *Buellia centralis* (Obermayer 05264, GZU). A–B. Young asci (without spores) with typical *Bacidia*-Type ascus-apex. C. Ascus with young spores. D–F. Spores. White arrows in C and F point at the septal pore canal. G. Conidia. A–F. In Lugols solution (pretreated with HNO_3).

are known from some crustose genera of the family Physciaceae: usnic acid (a dibenzofurane) in *Dimelaena oreina* (first reported by Zopf 1907) and *Buellia cedricola* (Nordin 2000), as well as some yellowish xanthones and related substances in *Buellia*, *Dimelaena*, *Diploicia* and *Rinodina* species (e.g. Leuckert & Mathey 1975, Singh & Awasthi 1981, Leuckert & Mayrhofer 1984, Elix et al. 1987, Scheidegger & Ruef 1988, Mayrhofer et al. 1996, Matzer et al. 1997, Kalb & Elix 1998, Elix & Tønsberg 1999, Trinkaus et al. 2000).

Because of its radiate-plicate thallus, Magnusson (1940) placed his new species *Buellia centralis* within section *Diploicia* (A.Massal.) Stizenb. In addition to this section, Zahlbruckner (1926) also recognized two further sections in the genus *Buellia*, namely *Eubuellia* and *Diplotomma*. More recently, *Diploicia* and *Diplotomma* have been treated at generic rank by various authors.

Molecular studies by Molina et al. (2002), based on an nITS rDNA data set, showed that *Diploicia* and *Diplotomma* form a well supported monophyletic group consisting of two separate monophyletic clades. Therefore they suggested that both genera be united under the older name *Diplotomma*. Nevertheless, they have recommended multigenic studies to confirm the congenerity.

From a morphological point of view, *Diploicia* is well separated from *Buellia centralis* by its spores with internal wall-thickenings and an ontogeny of type B (Matzer et al. 1997); the latter show no internal sporewall-thickenings and an ontogeny of type A (Giralt & Mayrhofer 1995). *Diplotomma* differs from *Buellia centralis* by its pluriseptate spores and a marginal thalline rim surrounding the apothecia (see e.g. Nordin 1996: 346, Fig. 10). The marginally radiating thallus, the bacilliform conidia, and some basic spore characters of *Buellia centralis* suggested a closer relationship with *Dimelaena*.

In order to confirm these anatomical observations and their resulting taxonomical conclusions, we applied molecular methods. The phylogeny of several crustose members of the Physciaceae was previously analyzed by Grube & Arup (2001). Their study, based on nITS rDNA, supported the informal division of the family into two groups (the *Buellia*-group and the *Physcia*-group) according to the system of Rambold et al. (1994) based on ascus characters. Grube & Arup (2001) also demonstrated the heterogeneity of the *Buellia*-group, confirmed by low bootstrap values in the topology of its constituent clades. To improve the resolution within the phylogeny of Physciaceae and Caliciaceae, Wedin et al. (2002) combined nITS rDNA and mtSSU rDNA, and likewise confirmed two major groups. Helms (2003) divided the two groups in subclades, based on nSSU and nITS datasets. The genus *Buellia* was, with one exception, restricted to one subclade (subclade IV). The support for a monophyletic origin of this subclade, equivalent to the genus *Buellia* as currently understood, was consistently low in various analyses and, within the subclade, the relationships remain poorly resolved. Because of the heterogeneity in the nITS rDNA in the *Buellia*-group, resulting in substantial ambiguities in the alignment, we used the more conserved mtSSU rDNA, which proved to be an interesting alternative for exploring phylogenetic questions at family or genus rank in lichens (e.g. Zoller et al. 1999, Crespo et al. 2001). Although we repeatedly tried to obtain mtSSU rDNA data from *Diploicia canescens* (both from sterile material and from apothecia) we unfortunately got no results.

The results of the present phylogenetic studies (see Fig. 3) show two clades. Clade A includes the type species of *Buellia* (*B. disciformis*), members of the *B. epigaea* group, other *Buellia* species (*B. aethalea*, *B. schaereri*) and *B. centralis*. Clade B represents the genus *Dimelaena* with *D. oreina* and *D. radiata*. Thus, the present analyses support both the status of *Dimelaena* as a distinct genus and the fact that, due to its placement within the core group of *Buellia*, *B. centralis* is not closely related to the genus *Dimelaena,* which was primarily supposed.

Additional specimens examined. **China**. *Xinjiang*: Karakorum, Aghil Range, Sukuwat-valley, way from Yarkand valley to Aghill pass, lower part of the gorge-like valley, 36°17'N, 76°35'E, 3880 m, 1989, Dickoré F4. Tibet, *Xizang*: Himalaya Range, 210 km SE of Lhasa, 15 km ESE of Lhüntse, way to Qayü, dry-valley of Subansiri,

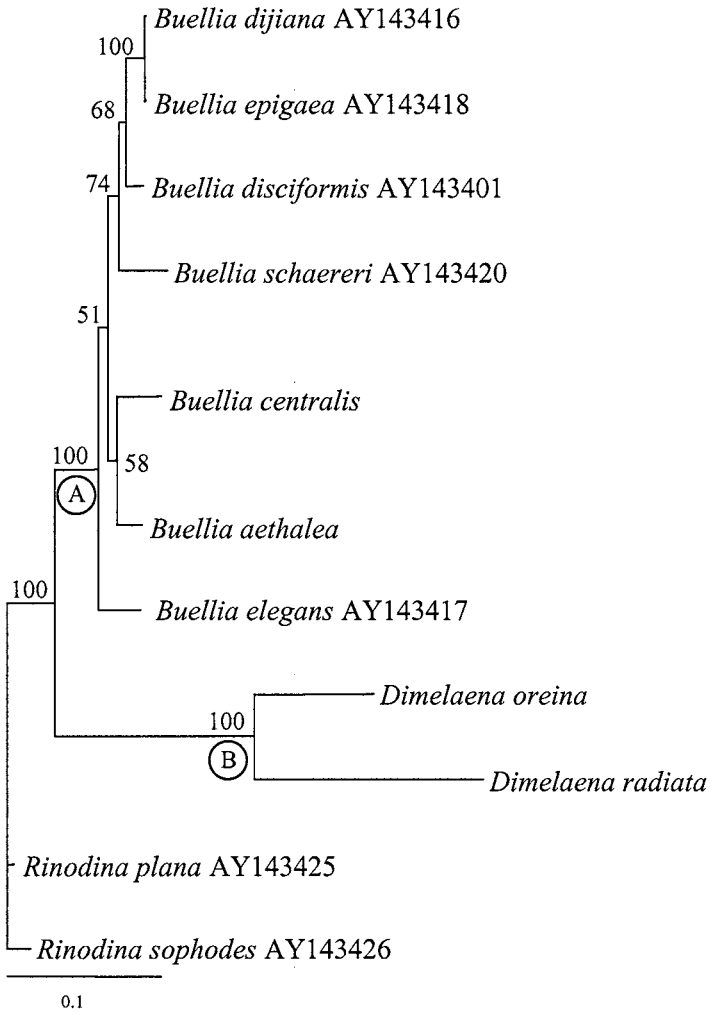

Figure 3. 50% Majority rule consensus tree based on mtSSU rDNA. Bayesian posterior probability supports are indicated at branches; branch lengths are proportionate to character state (nucleotide) changes. Clade A indicates the "*Buellia*-core-group" and clade B the monophyletic clade of the genus *Dimelaena*.

28°24'N, 92°37'E, 4100–4200 m, 1994, Obermayer 05264, 05245 (UPS). **Mongolia**. Gobiiskii Altai, Dundu-Saikhan ridge, 2825 m, in mountain steppe, 1970, Golubkova & Zogt 808 (M, together with *Dimelaena oreina* chemotype IIa, this locality is also cited in Golubkova 1981: 169); Gobi Altaj, Ich-Nomogon-Ula mountains, 1850 m, 1970, Golubkova & Zogt 897 (H). **Nepal**. Kali-Gandaki-area, slightly NW of Tukuche, path to Podasedanda, windexposed S-facing slopes with a few stunted trees, 3500 m, 1979, Kirschbaum (s.n.7; including *Dimelaena oreina* chemotype Vb). **Pakistan**. Karakorum, Baltistan, Haramosh Range, "Alm" Matumdus, NW of Chutren, 35°42'N, 75°23'E, 3620 m, *Betula-Salix* forest, rocky slopes, 1991, Poelt K91-80, K91-81; Karakorum, Gilgit, Rakaposhi Range, Baghrot, rocky slopes opposite to Hinarche Glacier, near Gussoner (=Gassunar), 36°03'N, 74°34'E, 2450 m, 1991, Poelt K91-92; Karakorum, Shimshal Gorge, below Dut, 2750 m, arid gorge, 1991, G. & S. Miehe 6387a. **Tajikistan**. Southern slope of Turkestan mountain Range, Gornaj (Mountain) Matcha, canyon Soikalachona, 2100 m, 1990, Kudratov 12611 (TAD); ibid., 2400 m, 1990, Kudratov 12635 (TAD); ibid., village Padask, canyon Takob, 2400–2500 m, 1990, Kudratov 12507 (TAD).

Dimelaena oreina (Ach.) Norman

Nytt Magasin for Naturvidenskapene 7: 132 (1852).

Synonyms (relevant for Asian specimens); *Rinodina altissima* H.Magn., *Rinodina altissima* var. *exalbescens* H.Magn., *Dimelaena oreina* var. *exalbescens* (H.Magn.)

Figure 4. Known distribution of *Buellia centralis* and chemotype Vb of *Dimelaena oreina*. ○ = investigated material of *Buellia centralis*. ○ = localities of *Buellia centralis* cited in literature. ◉ = investigated material of *Dimaelaena oreina* chemotype Vb.

Wei, *Rinodina oreina* var. *griseoviridis* H.Magn., *Rinodina pallido-ochracea* Räsänen. For further synonyms see Sheard & Ahti (1975).

For descriptions, see Hale (1952), Sheard (1974), Sheard & Ahti (1975) and Mayrhofer et al. (1996).

Chemistry. In addition to the hitherto known concept of chemotypes (for the latest summary see Calatayud & Rico 1999), chemotype II and chemotype V are each divided into two subtypes (IIa, IIb, Va and Vb). Vb contains the compound hypostictic acid (new for *Dimelaena*; Table 3). TLC investigations based on a single areola (see Material and methods) have been applied to many cited specimens to avoid mixed results.

Distribution. *Dimelaena oreina* is distributed worldwide with its centre of chemical diversity in the northern hemisphere. Only one chemotype (II) has been reported for the southern hemisphere (Mayrhofer et al. 1996). Except chemotype VI (with sphaerophorin), which has been described from western North America (Culberson et al. 1984), all the chemotypes are present in the Eurasian region.

A number of papers have given reports and/or overviews of *Dimelaena oreina* from different Central-Asian regions; for example, from Afghanistan (Poelt & Wirth 1968), Mongolia (Cogt 1995, Biazrov 2003), Nepal (Poelt 1990), Tajikistan (Kudratov & Mayrhofer 2002), Sikkim (Sheard 1977), Tibet (Paulson 1925), the whole China (Wei 1991), and from the Chinese province Xinjiang (Abbas & Wu 1998, Abbas et al. 2001). Based on collections mainly from Mongolia, Sheard & Ahti

Table 3. Chemotypes and their composition of lichen products in *Dimelaena oreina*. The major distinguishing chemical compounds in bold.

Chemotype	Chemical compounds
I	usnic acid, **fumarprotocetraric acid**, protocetraric acid (trace)
IIa	usnic acid, **gyrophoric acid**, lecanoric acid (trace)
IIb	usnic acid, **gyrophoric acid**, **ovoic acid**, lecanoric acid (trace)
III	**usnic acid** [no further substances]
IV	usnic acid, **fumarprotocetraric acid**, **gyrophoric acid** [no ovoic acid] – chemotype not found in Central-Asian material
Va	usnic acid, **stictic acid**, norstictic acid (minor, trace), menegazziaic acid (trace), cryptostictic acid (trace), constictic acid (trace)
Vb (new)	usnic acid, **stictic acid**, **hypostictic acid**, [no norstictic acid], menegazziaic acid (trace), cryptostictic acid (trace), constictic acid (trace), hypoconstictic acid (trace)
VI	usnic acid, **sphaerophorin**, gyrophoric acid (trace) – chemotype not found in Central-Asian material
VII	usnic acid, **gyrophoric acid**, **stictic acid**

(1975) presented a first overview on "chemical races" of *Dimelaena oreina* in East Central Asia. They reported chemotype II (with gyrophoric acid), chemotype III (with usnic acid only), and chemotype V (with stictic acid complex) for the area, the latter regarded as the most widspread one.

Leuckert et al. (1981) reported a well defined correlation between chemistry and elevation (700–2700 m) in a dry valley of the Central European Alps. The stictic acid chemotype (V) was shown to be the dominant one (60–80%) in the lower regions whereas chemotype I (with fumarprotocetraric acid) and chemotype IV (with fumarprotocetraric + gyrophoric acid) were the only two found at higher altitudes with a frequency of ca 70–80 and 20–30% respectively.

In the Himalayan-Tibetan Area, similar correlations are not evident. Within this region, where *Dimelaena oreina* ranges from 3300 to 5780 m altitude, both lowest and highest records belong to chemotype IIb (gyrophoric + ovoic acid). This chemotype (33 specimens) is, together with chemotype Va (32 specimens, 3600–5540 m), the most abundant one in the whole study area, whereas chemotypes I (9 specimens, 3900–5100 m), IIa (8 specimens, 4780–5280 m), III (10 specimens, 4000–5000 m), Vb (12 specimens, 3500–4700 m) and VII (7 specimens, none from Tibet) can be regarded as relatively rare. Chemotype IV (gyrophoric acid, fumarprotocetraric acid) occurs in European specimens (see Material and methods) but has not been found among the Central Asian material.

It is remarkable that only about 10% of the investigated thalli belong to chemotype III (usnic acid only). This chemotype, reported for Greenland by Leuckert & Poelt (1978) and Leuckert et al. (1987), was regarded by the latter authors as being dominant in the "climatically unfavourable northern region".

The new chemotype Vb (with hypostictic acid) is known only from the Central and Southeastern Himalayas and from the Southeast Tibetan Fringe Mountains (Fig. 4). There are also two reports from Mongolia (Huneck et al. 1984; Cogt 1993) in which specimens of chemotype V containing usnic acid and norstictic acid (including constictic acid, but lacking stictic acid) are cited. It was not possible to verify whether this "new" chemotype really exists. However, in herbarium GZU, there are three specimens of *Dimelaena oreina*, which are probably duplicates of the samples cited by Huneck et al. (1984). All three specimens (MVR 38, MVR 187, MVR 226) belong to chemotype Va (with stictic and norstictic acid).

Remarks. The genus *Dimelaena* was introduced by Norman (1852) with *D. oreina* as the type species. The new genus was accepted by only some authors (e.g. Beltramini 1858, Fries 1861, Arnold

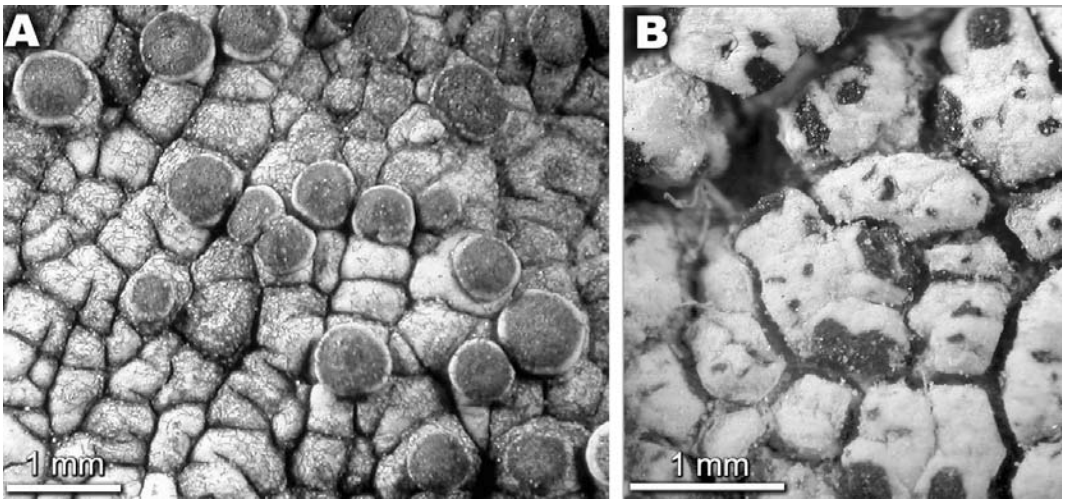

Figure 5. Morphological variability of apothecia in *Dimelaena oreina*. A. Lecanoroid apothecia (Obermayer 05335, GZU). B. Aspicilioid (totally immersed) apothecia with marginal position, "*Rinodina altissima*"-like (Steiner Ste36/5, M).

1873), whereas others (e.g. Fries 1871, Jatta 1889, Zahlbruckner 1926) followed Massalongo (1852) who placed the taxon in *Rinodina*. Since Poelt (1969), the genus *Dimelaena* is generally accepted. Sheard (1974) redefined the limits of the genus to include only those species with an unthickened spore wall and a radiate-plicate thallus margin. He accepted five species (*D. californica, D. diffractella = D. tenuis, D. oreina, D. radiata, D. thysanota*). Two new taxa (*D. australiensis, D. weberi*) were added by Sheard & Mayrhofer (1984) and since then, another species (*D. elevata*) has been described by Mayrhofer et al. (1996).

Within the genus *Dimelaena*, *D. oreina* is the only species characterized primarily by the presence of usnic acid and additional compounds that lead to the recognition of seven distinct chemotypes (Leuckert et al. 1975, Sheard 1977, Culberson et al. 1984, Calatayud & Rico 1999).

Due to the very broad spectrum of morphological features (Figs 5A, 5B), some distinct taxa have been described in the past. For instance, Brodo et al. (2001) consider *D. suboreina* as a distinct species because of its strongly pruinose apothecia and areolae. Another example is *Rinodina altissima,* which has been separated from *D. oreina* both by Magnusson (1940) because of its "smaller, always immersed, immarginate apothecia" and by Sheard & Ahti (1975) mainly because of the marginal position of the apothecia (see also Fig. 5B in the present paper).

Because morphological characters do not correlate with chemical ones, we followed other authors who have subsumed several chemotypes within one species. But the question arises, whether there are indeed morphologically distinct taxa or sibling species in the sense of Culberson (1986), each with the ability to express more than one chemotype, perhaps as a result of the ageing process, microclimatic conditions or ancestral polymorphism. Regarding the species complex of *Dimelaena oreina,* Grube & Kroken (2000) conjectured that "the presence of pairwise combinations of characters could represent the result of genetic recombination within one species". However, among all possibilities, the process of gene flow, excellently demonstrated for the *Cladonia chlorophaea* complex by Culberson & al. (1988), might be the best explanation for the occurrence of all those existing morpho- and chemotypes.

Thus, the obviously intermixed growth of chemically different areolae within a few millimeters (which has been observed several times during this study) can be explained by the ability of the

fungus to produce and disperse spores with different chemical capability from the one single ascus. Molecular based studies in connection with single-spore cultures on supposedly interbreeding populations of *Dimelaena oreina* would help to solve those questions.

SPECIMENS EXAMINED. Only the major chemical compounds are cited after the chemotype; specimens on which one-single-areola TLC has been applied are marked with an asterisk (*) before the collection number:

Chemotype I (usnic acid, fumarprotocetraric acid, protocetraric acid): **China**. Tibet, *Sichuan*: Tibetan fringe mountains (=Hengduan Shan), Shaluli Shan, 58 km NE of Batang, 30°19'20"N 99°34'02"E, 4710 m, W-exposed alpine mats with outcrops, 2000, Obermayer 08411a (together with chemotype Va). *Xizang*: Himalaya Range, 140 km S of Lhasa, canyon of Kuru river, 28°21'N, 90°53'E, 3900 m, E-facing steep slopes, 30 m above the river, 1994, Obermayer 04451 (together with chemotype Vb), 04453; way from Quamdo (=Changtu) to Nagqu (=Nakchu), 31°10'N, 96°10'E, 4500–4700 m, pass-area, 1994, Obermayer 04098a. **Nepal**. East-Nepal, Khumbakarna-Himal, Dhankuta Distr., Barun, Glacier-Valley, 5100 m, 1972, Wraber *s.n.1, *s.n.2; Langtang Area, Chisedang Lekh, Palpa (Papal), 3500 m, 1986, Poelt N86-L612; Langtang Area, N-exposed slopes towards Langshisa Glacier, SE of Langshisa Kharka, 4300–4400 m, 1986, Poelt *N86-L1342 (together with chemotype V); Mahalangur Himal, Khumbu, morains of the Khumbu-glacier, 5000 m, 1962, Poelt L948 (M).

Chemotype IIa (usnic acid, gyrophoric acid): **China**. *Jilin*: Yanbian, Chaoxianzu Zizhizhou, Changbai Shan (border mountains to N-Korea), Nature Reserve "Changbai Shan", South of Songjiang (=Antu), 42°N, 128°E, 2450 m, 1980, Hertel 22620 (M), 22625 (M). *Xinjiang*: Karakorum, E of the K2-glacier, above the confluence of the Siangkiang-glacier, 35°58'N, 76°28'E, 4900 m, 1986, Dickoré *F24a. S-Tibet, *Xizang*: Tibetan Himalaya, Everest E, head of Kangchung Glacier, 13 km E of Everest top (Camp Ev8), 28°59'N, 87°02'E, 5280 m, open windblown moraine shoulder, 1989, Dickoré K-60-7, K-61-5; Himalaya Range, 90 km SW of Lhasa, 15 km NNE of Nagarzê, SE-exposed rocks at the shore of Yamzho Yumco (=Yamdok Tso), 29°04'N, 90°23'E, 4400 m, 1994, Obermayer *04214 (together with chemotype V). **Mongolia**. Gobiiskii Altai, Dundu-Saikhan ridge, 2825 m, mountain steppe, 1970, Golubkova & Zogt 808 (M, together with *Buellia centralis*). **Nepal**. Langtang Area, Yala, 4980 m, succession on moraine W-exposed, 1986, G. & S. Miehe 4841a. **Nepal/China**. W-central Himalaya, Nepal/Tibet border, below Burang, 30°09'N, 81°16'E, 4780 m, wind-blown quartzitic cliffs, 1993, G. & S. Miehe 9606a (together with chemotype V). **Russia**. Siberia, Altai Mountains, vicinity of the village Mujuta, at the mountain Túrko?, 28.VI.1927, M. Lauran? s.n. (M, together with chemotype V). **Tajikistan**. in declivib. boreal, M. Zaravschansk distr. Staro-Mattschinsk, prope pagum Padask, 2200 m, 1975, Kudratov 2505.

Chemotype IIb (usnic acid, gyrophoric acid, ovoic acid): Note. One-single-areola-TLC did not show a chemotype with ovoic acid only. **Afghanistan**. *Kabul*: Paghman-Mountain, above the village Paghman, near the junction of the valleys Chap-Darrah and Rast-Darrah, left side of the valley, 34°37'N, 68°56'E, 2550 m, 1970, Steiner *Ste36/5 (M), *Ste36/5a (together with chemotype VII); ibid., right side of the valley, 34°37'N, 68°56'E, 2550 m, 1970, Steiner Ste59/6a, *Ste59/6b (both specimens together with chemotype VII); ibid., 4 km above the village Paghman, 34°37'N, 68°55'E, 2450 m, 1970, Steiner Ste2a, Ste2b. *Wakhan*: Eastern-Hindukusch, Quazi-deh-valley, 3200 m, 1964, Roemer F107 (M). **Bhutan**. *Thimphu*: Thimphu valley below Tango Gonpa, 27°35.6'N, 89°38.3'E, temperate oak forest with *Rhododendron*, 1998, Søchting *US 8410-dupl. **China**. *Qinghai*: Central Tibet, N.Central Tangula Shan (Yangtse sources, Gar Qu), SE of Geladandong glacier-snout, 33°27'N, 91°13'E, 5380 m, N-facing landslide, large boulders (Quarzite, Granite, Gabbro), 1989, Dickoré *L-08b. *Xinjiang*: Karakorum, E of the K2-glacier, above the confluence of the Siangkiang-Glacier, 35°58'N, 76°28'E, 4900 m, 1986, Dickoré *F24a (together with chemotype IIa), F24b; ibid., 35°59'N, 76°28'E, 4750 m, alpine meadows, 1986, Dickoré F5, F6; Karakorum, W of the K2-Glacier, between the advanced Basecamp and the "Italienercamp", (flat area), 36°01'N, 76°27'E, 4450 m, steep, N-exposed rockside (gneiss with quartzit), alpine flora in rock crevices, 1986, Dickoré F31; western central Kunlun Shan (north-facing slopes), at the confluece of the right branch of the valley of Kodi, 25 km NE of Mazar, 36°38'N, 77°09'E, 4250 m, 1986, Dickoré F47a, F47b. Tibet, *Xizang*: Himalaya Range, 170 km SE of Lhasa, Tsangpo valley, in the village Gyaca, 29°06'N, 92°40'E, 3300 m, 1994, Obermayer 05335; Himalaya Range, 170–175 km S of Lhasa, between Lhozhag and Lhakhang Dzong, slopes W of the Kuru river valley, 28°18'N, 90°57'E, 3900 m, 1994, Obermayer *04679; Himalaya Range, 130 km SSW of Lhasa, eastside of Puma Yumco (=Pomo Tso), way to the nearest mountain east of Pomo Tso, 28°31'N, 90°37'E, 5770–5784 m, little summit, 1994, Obermayer 04296; Nyainqêntanglha Shan, 120 km E of Lhasa, "Mila-Pass" between Lhasa and Gongbo Gyamda, 29°51'N, 92°21'E, 4950 m, alpine meadows, 1994, Obermayer 07667. **India**. Himalaya or., Almora, Khoti to Dhakuri, 8000 ft, ad saxa quartzica prope viam ad glac. Pindari, 1950, D.D. & A.M. Awasthi 692 (H, holotype of *Rinodina pallido-ochracea*). **Iran**. Montes Elburs centr., in jugo Kandawan, in declivibus borealibus, 2700–3000 m, 1937,

Rechinger 2225 (M). **Kyrgyzstan**. Central-Tian Schan, basin of Sazy-Dzhaz river, Canyon of Molo river, alpine zone, rock outcrops, 42°N, 79–80°E, 3200 m, 1975, Baibulatova 242 (together with chemotype VII). **Nepal**. Kali-Gandaki-area, slightly NW of Tukuche, path to Podassedanda, windexposed southern slope with single stunted trees, 3500 m, 1979, Kirschbaum *s.n. (together with chemotypes Va and Vb); Langtang Area, way Khangjung to Sangsa (E of Khangjung), towards Pang Sang Lekh, pastures, rocks, open woods, 2500–2700 m, 1986, Poelt N86-L1273; Mahalangur Himal, Khumbu, rocky slopes south of Khumzung, 3900–4000 m, 1962, Poelt L930 (M), L933 (M). **Pakistan**. Hindukusch, Bar, 36°23'N, 74°17'E, 2500 m, 1959, Lobbichler 825 (M), 827 (M); Karakorum, Shinghai Gah, 35°48'N, 74°10'E, 3920 m, 1990, G. & S. Miehe 907; Northern Areas, Karakorum, Baltistan, Haramosh Range, Tormik Valley above Dasu, to "Alm" Pakora, 35°41'N, 75°21'E, 2850 m, small rivulet, pasture, rocky slopes, 1991, Poelt K91/496; Northern Areas, Northwestern Himalaya, Baltistan, eastern Deosai Plateau, 35°05'N, 75°34'E, 4100 m, small rivulet, pasture, rocky slopes, 1991, Poelt K91/316; ibid., 4000 m, small rivulet, pasture, rocky slopes, 1991, Poelt K91/487, K91/772; Swat, Kalam, 1963, Ahmad *505.

Chemotype III (usnic acid only): **China**. Tibet, *Sichuan*: Tibetan fringe mountains (=Hengduan Shan), Shaluli Shan, 50 km S of Litang, road from Cogsum to Sumdo, 29°34'15"N, 100°18'55"E, 4250 m, boulder field, big siliceous rocks, 2000, Obermayer 09603; ibid., 29°33'05"N, 100°17'25"E, 4330 m, boulder field, big siliceous rocks, 2000, Obermayer 09753; ibid., 58 km NE of Batang, 30°19'20"N, 99°34'02"E, 4710 m, W-exposed alpine mats with outcrops, 2000, Obermayer 08411b, 08412. *Xizang*: Himalaya Range, 190 km SSE of Lhasa, 125 km S of Tsetang (Nedong), 20 km S of Nera Tso (=Ni la Hu), way to Cona (=Tsona), 28°07'N, 91°55'E, 4650–4800 m, alpine meadows, 1994, Obermayer 05064b; way from Quamdo (=Changtu) to Nagqu (=Nakchu), 31°10'N, 96°10'E, 4500–4700 m, pass-area, 1994, Obermayer 04093. **Nepal**. Langtang Area, Yala, 4980 m, succession on moraine, W-exposed, 1986, G. & S. Miehe 4841b; Mahalangur Himal, Khumbu, outcrop N of Lobuche, 5000 m, 1962, Poelt L941 (M). **Nepal/China**. W-central Himalaya, Nepal/Tibet border, below Burang, 30°09'N, 81°16'E, 4780 m, wind-blown quartzitic cliffs, 1993, G. & S. Miehe 9606b. **Pakistan**. Northern Areas, Northwestern Himalaya, Baltistan, eastern Deosai Plateau, 35°05'N, 75°34'E, 4000 m, small rivulet, pasture, rocky slopes, 1991, Poelt K91-326.

Chemotype IV (usnic acid, gyrophoric acid, fumarprotocetraric acid): No specimens of chemotype IV were found in Central-Asian collections.

Chemotype Va (usnic acid, stictic acid, norstictic acid [minor, trace]): **Bhutan**. *Thimphu*: between Sim Kotaa Lake and Gigme Lang tsho, 27°32'N, 89°31'E, 3900–4100 m, alpine meadow with rocky outcrops, 1998, Søchting *US 9134-dupl. **China**. Tibet, *Sichuan*: Tibetan fringe mountains (=Hengduan Shan), Shaluli Shan, 50 km S of Litang, road from Cogsum to Sumdo, 29°33'05"N, 100°17'25"E, 4330 m, boulder field (big siliceous rocks), 2000, Obermayer 09525; Shalui Shan Mts, 30 km NNE of Batang, SSE of Yidun, 30°16'N, 99°25'E, 4000–4150 m, S-facing slope, 1994, Obermayer *03361 (together with chemotype Vb); Tibetan fringe mountains (=Hengduan Shan), Shaluli Shan, 58 km NE of Batang, 30°19'20"N, 99°34'02"E, 4710 m, W-exposed alpine mats with outcrops, 2000, Obermayer *08411a (together with chemotype I); Shalui Shan Mts., 35 km NNE of Batang, SE of Yidun, 30°16'N 99°28'E, 4200–4300 m, pasture with schist outcrops, 1994, Obermayer 03451. Tibet, *Xizang*: Himalaya Range, 170 km S of Lhasa, between Lhozhag and Lhakhang Dzong, Kuru river valley, 28°12'N, 91°00'E, 3600 m, pass area, 1994, Obermayer *04538; Himalaya Range, 170 km SE of Lhasa, 110 km SSE of Tsetang (Nedong), 28°35'N, 92°23'E, 4700 m, alpine meadows, 1994, Obermayer 04970; Himalaya Range, 190 km SSE of Lhasa, 125 km S of Tsetang (Nedong), 20 km S of Nera Tso (=Ni la Hu), way to Cona (=Tsona), 28°07'N, 91°55'E, 4650–4800 m, alpine meadows, 1994, Obermayer 05064a; Himalaya Range, 160 km S of Lhasa, dry valley of Kuru river, 10 km NW of Lhozhag (=Lhodak=Locha), 28°24'N, 90°39'E, 4230 m, N-exposed steep rocks in a glen, 1994, Obermayer *04363 (together with chemotype Vb); Himalaya Range, 90 km SW of Lhasa, 15 km NNE of Nagarzê, SE-exposed rocks at the shore of Yamzho Yumco (=Yamdok Tso), 29°04'N, 90°23'E, 4400 m, 1994, Obermayer *04214 (together with chemotype IIa); Himalaya, Sunkosi valley, above Zhang Mu, 27°59'N, 85°58'E, 5200 m, 2000, Tichy (ex herbarium Türk 29489b); Tanggula Shan, way from Quamdo (=Changtu) to Nagqu (=Nakchu), 31°30'N, 95°00'E, 3700 m, 1994, Obermayer 04116; way from Bamda to Quamdo (=Changtu), 30°41'N, 97°08'E, 4400 m, 1994, Obermayer 04005; way from Quamdo (=Changtu) to Nagqu (=Nakchu), 31°52'N, 93°55'E, 4000 m, 1994, Obermayer 04152. **Kazakhstan**. Vost. Kazakhstankaja, N of the road SE of Karatogay, 48°15'N, 84°36'E, 610 m, dry sandy area close to a mountain ridge, 1993, Moberg & Nordin K16:20 (M). **Mongolia**. 25 km W of Ulan-Bator schist rocks in mountain steppe, 1978, Huneck MVR226; near Soutschina, 25 km W von Ulan Bator, 1300 m, 1978, Huneck MVR38; Eastern Aimak, valley of the Uldz-Gol, Ulz-Saikhan-Ula ridge, Sogot-Ula hill, 1228 m, mountain steppe, 1974, Golubkova & Zogt *1512 (M); Tarbagatai, 2400 m, 1978, Huneck MVR187; Western Mongolia, Chovd Aimak, Chovd Sum, Ougozny Ulaan and Ulaaniar-rocks, 1974, Hilbig & Schamsran s.n. **Nepal**. Kali-Gandaki-Gebiet, slightly NW of Tukuche, path to Podassedanda, wind exposed south-facing slopes, 3500 m, 1979, Kirschbaum *s.n.

(together with chemotypes IIb and Vb); Langtang Area, Chisedang Lekh, Palpa (Papal), 3500 m, 1986, Poelt N86-L1162; Langtang Area, N-exposed slopes towards Langshisa Glacier, SE of Langshisa Kharka, 4300–4400 m, 1986, Poelt *N86-L1342 (together with chemotype I); Langtang Area, way Khangjung to Sangsa, E of Khangjung, towards Pang Sang Lekh, pastures, rocks, open woods, 2700 m, 1986, Poelt N86-L1161; Mahalangur Himal, Khumbu, Bibre, 4500–4700 m, 1962, Poelt L1530 (M), L1632 (M); Mahalangur Himal, Khumbu, Dingpoche, windblown rock at a Tschorten, 4340 m, 1962, Poelt *L953 (M); Mahalangur Himal, Khumbu, ridge west of Gorak Shep, 5540 m, 1962, Poelt *L956 (M); Thak Khola, N of Dzong, near Muktinath, 4000 m, exposed cliffs, 1986, G. & S. Miehe 16898 (together with chemotype Vb). **Nepal/China**. W-central Himalaya, Nepal/Tibet border, below Burang, 30°09'N, 81°16'E, 4780 m, wind-blown quartzitic cliffs, 1993, G. & S. Miehe 9606a (together with chemotype IIa), 9606c. **Pakistan**. Northern Areas, Northwestern Himalaya, Baltistan, eastern Deosai Plateau, 35°05'N, 75°34'E, 3950–4000 m, small rivulet, pasture, rocky slopes, 1991, Poelt *K91-286. **Russia**. Siberia, Altai-Mountains, vicinity of the village Mujuta, at the mountain Túrko?, 1927, M. Lauran? s.n. (M, together with chemotype IIa); Yakutia, Ojmyakonskii region, along the river Indigirka, 8 km NNE of Ust'-Nera, 64°38'N, 143°20'E, 550–600 m, 1992, Zhurbenko 92385.

Chemotype Vb (usnic acid, stictic acid, hypostictic acid): **China**. Tibet, *Sichuan*: Shalui Shan Mts., 30 km NNE of Batang, SSE of Yidun, 30°16'N, 99°25'E, 4000–4150 m, S-facing slope, 1994, Obermayer *03361 (together with chemotype Va). *Xizang*: Himalaya Range, 140 km S of Lhasa, canyon of Kuru river, 28°21'N, 90°53'E, 3900 m, E-facing steep slopes, 30 m above the river, 1994, Obermayer *04450; Himalaya Range, 160 km S of Lhasa, dry valley of Kuru river, 10 km NW of Lhozhag (=Lhodak=Locha), 28°24'N, 90°39'E, 4230 m, N-exposed steep rocks in a glen, 1994, Obermayer 04363 (together with chemotype Va); ibid., 165 km SSE of Lhasa, 40 km W of Lhünze, little village on way to Nera Tso (=Ni La Hu), 28°23'N, 92°05'E, 4300–4400 m, 1994, Obermayer 05303; ibid., 170–175 km S of Lhasa, between Lhozhag and Lhakhang Dzong, slopes W of the Kuru river valley, 28°18'N, 90°57'E, 3900 m, 1994, Obermayer 04676; ibid., 1994, Obermayer 04679 (together with chemotype IIb); ibid., 4100 m, 1994, Obermayer 04794; ibid., 170 km S of Lhasa, between Lhozag and Lhakhang Dzong, W-facing slopes of Dhalari mountain, 28°20'N, 90°58'E, 4150–4300 m, 1994, Obermayer 04469, *04476; ibid., 4300 m, NNW-exposed overhang, 1994, Obermayer *04492; way from Quamdo (=Changtu) to Nagqu (=Nakchu), 31°10'N, 96°10'E, 4500–4700 m, pass-area, 1994, Obermayer 04098b. **Nepal**. Kali-Gandaki-Area, slightly NW of Tukuche, path to Podassedanda, wind exposed south-facing slopes, 3500 m, 1979, Kirschbaum *s.n. (together with chemotype IIb and Va); ibid., Kirschbaum *s.n. (together with *Buellia centralis*); Thak Khola, N of Dzong, near Muktinath, 4000 m, exposed cliffs, 1986, G. & S. Miehe 16898 (together with chemotype Va).

Chemotype VI (usnic acid, sphaerophorin, gyrophoric acid): No specimens of chemotype VI were found in Central-Asian collections.

Chemotype VII (usnic acid, stictic acid, gyrophoric acid): **Afghanistan**. *Kabul*: Paghman-Mountains, above the village Paghman, near the junction of the valleys Chap-Darrah and Rast-Darrah, right side of the valley, 34°37'N, 68°56'E, 2550 m, 1970, Steiner *Ste36/5a (together with chemotype IIb), *Ste36/5b, Ste59/6 (M), Ste59/6a, *Ste59/6b (the latter two together with chemotype IIb). **Kyrgyzstan**. Central-Tian Shan, basin of Sazy-Dzhaz river, canyon of Molo river, alpine zone, rock outcrops, 42°N, 79–80°E, 3200 m, 1975, Baibulatova *242 (together with chemotype IIb). **Nepal**. Khumbu, rocky slopes south of Khumzung, 3900–4000 m, 1962, Poelt L935 (M).

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