

A monograph of leaf characters
in the genus *Abies*
(Abietoideae, Pinaceae)

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Table of contents

Acknowledgements	3
1 Introduction	7
1.1 Taxonomy and systematics	7
1.2 Biogeography	10
1.3 Morphology and anatomy	10
1.3.1 Habitus	10
1.3.2 Reproductive structures	11
1.3.3 Foliage	11
1.3.3.1 Leaf arrangement	11
1.3.3.2 Leaf color	12
1.3.3.3 Leaf size	12
1.3.3.4 Leaf shape	12
1.3.3.5 Petiole	13
1.3.3.6 Leaf tip	13
1.3.3.7 Leaf base	13
1.3.3.8 Leaf margin	13
1.3.3.9 Midrib	13
1.3.3.10 Stomata	13
1.3.3.11 Cuticle	14
1.3.3.12 Epidermis	14
1.3.3.13 Hypodermis	14
1.3.3.14 Mesophyll	14
1.3.3.15 Vascular bundle	15
1.3.3.16 Endodermis	15
1.3.3.17 Resin ducts	15
2 Material and Methods	22
2.1 Material	22
2.2 Methods	25
3 Species descriptions	26, 71
<i>Abies alba</i> (Sect. <i>Abies</i>)	26, 71
<i>Abies alba</i> (Sect. <i>Abies</i>)	26, 72
<i>Abies alba</i> (Sect. <i>Abies</i>)	26, 73
<i>Abies alba</i> (Sect. <i>Abies</i>)	27, 74
<i>Abies alba</i> (Sect. <i>Abies</i>)	27, 75
<i>Abies alba</i> (Sect. <i>Abies</i>)	28, 76
<i>A. alba</i> , Calabrian Origin (Sect. <i>Abies</i>)	28, 77
<i>A. alba</i> , Montenegrin Origin (Sect. <i>Abies</i>)	29, 78
<i>A. amabilis</i> (Sect. <i>Amabilis</i>)	29, 79
<i>A. balsamea</i> var. <i>balsamea</i> (Sect. <i>Balsamea</i> , Subsect. <i>Laterales</i>)	30, 80
<i>A. balsamea</i> var. <i>phanerolepis</i> (Sect. <i>Balsamea</i> , Subsect. <i>Laterales</i>)	30, 81
<i>A. beshanzenensis</i> (Sect. <i>Momi</i> , Subsect. <i>Firmae</i>)	31, 82
<i>A. bornmuelleriana</i> (Sect. <i>Abies</i>)	31, 83
<i>A. bracteata</i> (Sect. <i>Bracteata</i>)	32, 84
<i>A. cephalonica</i> var. <i>cephalonica</i> (Sect. <i>Abies</i>)	32, 85
<i>A. chengii</i> (Sect. <i>Pseudopicea</i> , Subsect. <i>Delavayanae</i>)	33, 86
<i>A. chensiensis</i> ssp. <i>chensiensis</i> (Sect. <i>Momi</i> , Subsect. <i>Holophyllae</i>)	33, 87
<i>A. chensiensis</i> ssp. <i>salouenensis</i> (Sect. <i>Momi</i> , Subsect. <i>Holophyllae</i>)	34, 88
<i>A. cilicica</i> ssp. <i>cilicica</i> (Sect. <i>Abies</i>)	34, 89
<i>A. colimensis</i> (Sect. <i>Oiamel</i> , Subsect. <i>Religiosae</i>)	35, 90
<i>A. concolor</i> var. <i>concolor</i> (Sect. <i>Grandis</i>)	35, 91
<i>A. concolor</i> var. <i>lowiana</i> (Sect. <i>Grandis</i>)	36, 92
<i>A. delavayi</i> (Sect. <i>Pseudopicea</i> , Subsect. <i>Delavayanae</i>)	36, 93
<i>A. densa</i> (Sect. <i>Pseudopicea</i> , Subsect. <i>Delavayanae</i>)	37, 94
<i>A. durangensis</i> var. <i>coahuilensis</i> (Sect. <i>Grandis</i>)	37, 95
<i>A. durangensis</i> var. <i>durangensis</i> (Sect. <i>Grandis</i>)	38, 96
<i>A. equi-trojani</i> (Sect. <i>Abies</i>)	38, 97
<i>A. ernestii</i> (Sect. <i>Momi</i> , Subsect. <i>Homolepides</i>)	39, 98

<i>A. fabri</i> ssp. <i>fabri</i> (Sect. Pseudopicea, Subsect. Delavayianae)	39, 99
<i>A. fabri</i> var. <i>minensis</i> (Sect. Pseudopicea, Subsect. Delavayianae)	40, 100
<i>A. fanjingshanensis</i> (Sect. Pseudopicea, Subsect. Delavayianae)	40, 101
<i>A. fansipanensis</i> (Sect. Pseudopicea, Subsect. Delavayianae)	41, 102
<i>A. fargesii</i> var. <i>fargesii</i> (Sect. Pseudopicea, Subsect. Delavayianae)	41, 103
<i>A. fargesii</i> var. <i>faxoniana</i> (Sect. Pseudopicea, Subsect. Delavayianae)	42, 104
<i>A. fargesii</i> var. <i>sutchuenensis</i> (Sect. Pseudopicea, Subsect. Delavayianae)	42, 105
<i>A. firma</i> (Sect. Momi, Subsect. Firmae)	43, 106
<i>A. fordei</i> (Sect. Pseudopicea, Subsect. Delavayianae)	43, 107
<i>A. forrestii</i> var. <i>ferreana</i> (Sect. Pseudopicea, Subsect. Delavayianae)	44, 108
<i>A. forrestii</i> var. <i>forrestii</i> (Sect. Pseudopicea, Subsect. Delavayianae)	44, 109
<i>A. forrestii</i> var. <i>georgei</i> (Sect. Pseudopicea, Subsect. Delavayianae)	45, 110
<i>A. fraseri</i> (Sect. Balsamea, Subsect. Medianae)	45, 111
<i>A. gamblei</i> (Sect. Momi, Subsect. Holophyllae)	46, 112
<i>A. grandis</i> (Sect. Grandis)	47, 113
<i>A. guatemalensis</i> var. <i>guatemalensis</i> (Sect. Grandis)	47, 114
<i>A. guatemalensis</i> var. <i>jaliscana</i> (Sect. Grandis)	47, 115
<i>A. hickelii</i> (Sect. Oiamel, Subsect. Hickelianae)	48, 116
<i>A. holophylla</i> (Sect. Momi, Subsect. Holophyllae)	49, 117
<i>A. homolepis</i> var. <i>homolepis</i> (Sect. Momi, Subsect. Homolepides)	49, 118
<i>A. homolepis</i> var. <i>umbellata</i> (Sect. Momi, Subsect. Homolepides)	49, 119
<i>A. kawakamii</i> (Sect. Momi, Subsect. Homolepides)	50, 120
<i>A. koreana</i> (Sect. Balsamea, Subsect. Medianae)	51, 121
<i>A. lasiocarpa</i> var. <i>arizonica</i> (Sect. Balsamea, Subsect. Laterales)	51, 122
<i>A. lasiocarpa</i> var. <i>lasiocarpa</i> (Sect. Balsamea, Subsect. Laterales)	52, 123
<i>A. magnifica</i> var. <i>magnifica</i> (Sect. Nobilis)	52, 124
<i>A. magnifica</i> var. <i>shastensis</i> (Sect. Nobilis)	53, 125
<i>A. mariesii</i> (Sect. Amabilis)	53, 126
<i>A. mexicana</i> (Sect. Oiamel, Subsect. Religiosae)	54, 127
<i>A. nebrodensis</i> (Sect. Abies)	54, 128
<i>A. nephrolepis</i> (Sect. Balsamea, Subsect. Medianae)	55, 129
<i>A. nordmanniana</i> (Sect. Abies)	55, 130
<i>A. nukiangense</i> (Sect. Pseudopicea, Subsect. Delavayianae)	56, 131
<i>A. numidica</i> (Sect. Piceaster)	56, 132
<i>A. oaxacana</i> (Sect. Oiamel, Subsect. Hickelianae)	57, 133
<i>A. pindrow</i> var. <i>pindrow</i> (Sect. Momi, Subsect. Holophyllae)	57, 134
<i>A. pinsapo</i> var. <i>marocana</i> (Sect. Piceaster)	58, 135
<i>A. pinsapo</i> var. <i>pinsapo</i> (Sect. Piceaster)	58, 136
<i>A. pinsapo</i> var. <i>tazaotana</i> (Sect. Piceaster)	59, 137
<i>A. procera</i> (Sect. Nobilis)	59, 138
<i>A. recurvata</i> (Sect. Momi, Subsect. Homolepides)	60, 139
<i>A. religiosa</i> (Sect. Oiamel, Subsect. Religiosae)	60, 140
<i>A. rolii</i> (Sect. Pseudopicea, Subsect. Delavayianae)	61, 141
<i>A. sachalinensis</i> var. <i>mayriana</i> (Sect. Balsamea, Subsect. Medianae)	62, 142
<i>A. sachalinensis</i> var. <i>sachalinensis</i> (Sect. Balsamea, Subsect. Medianae)	62, 143
<i>A. semenovii</i> (Sect. Balsamea, Subsect. Laterales)	63, 144
<i>A. sibirica</i> (Sect. Balsamea, Subsect. Laterales)	63, 145
<i>A. spectabilis</i> (Sect. Pseudopicea, Subsect. Delavayianae)	64, 146
<i>A. squamata</i> (Sect. Pseudopicea, Subsect. Squamatae)	64, 147
<i>A. tamaulipensis</i> (Sect. Grandis)	65, 148
<i>A. veitchii</i> var. <i>olivacea</i> (Sect. Balsamea, Subsect. Medianae)	65, 149
<i>A. veitchii</i> var. <i>veitchii</i> (Sect. Balsamea, Subsect. Medianae)	66, 150
<i>A. vejarii</i> (Sect. Oiamel, Subsect. Religiosae)	66, 151
<i>A. ziyuanensis</i> (Sect. Momi, Subsect. Holophyllae)	67, 152
<i>A. x borisii-regis</i> (<i>A. cephalonica</i> x <i>A. alba</i>)	67, 153
<i>A. x insignis</i> (<i>A. nordmanniana</i> x <i>A. pinsapo</i>)	68, 154
<i>A. x koreocarpa</i> (<i>A. koreana</i> x <i>A. lasiocarpa</i>)	68, 155
<i>A. x masjoanis</i> (<i>A. pinsapo</i> x <i>A. alba</i>)	69, 156
<i>A. x pardei</i> (<i>A. numidica</i> x unknown)	69, 157
<i>A. x vasconcellosiana</i> (<i>A. pindrow</i> x <i>A. pinsapo</i>)	70, 158
<i>A. x vilmorinii</i> (<i>A. cephalonica</i> x <i>A. pinsapo</i>)	70, 159

4 Bibliography 160

5 Index 166

1 Introduction

Like reproductive structures, leaves are also important diagnostic features for identifying plants. While reproductive structures are constant over long periods of time (JAGEL & DÖRKEN 2014, 2015a, b; DÖRKEN & JAGEL 2014; DÖRKEN & NIMSCH 2017; DÖRKEN et al. 2017), because even the smallest changes directly influence reproductive success, leaves, however, are quite variable, because their size, shape and structure are strongly influenced by ecological factors, e.g. aridity, availability of nutrients, light-exposure, etc. Accordingly, leaf adaptation to local habitat changes leads to intraspecific variation in leaf arrangement, size and shape, the density of leaves on a branch, the density of stomata, the formation of trichomes and cuticular waxes, the amount of sclerenchyma, etc. Even within an individual, distinct variations are detectable e.g. sun leaves versus shade leaves (e.g. SPRUGEL et al. 1996; GRASSI & BAGNARESI 2002; ROBAKOWSKI et al. 2003, 2004a, b; ATA 2004; RUETZ 2004; SCHÜTT & LANG 2004b; BUCHER 2004; PERKINS 2004; LICHTENTHALER et al. 2007). However, such variations always occur within a species-specific range, so that an overall leaf structure for each taxon can be recognized. Thus, in identification keys foliar characters can be used as diagnostic features to distinguish conifers (e.g. FULLING, 1934; LIU 1971; KNOPF 2011; KNOPF et al. 2012; ELPE et al. 2017a, b).

In most conifers, especially among scale- and needle-leaved taxa, the leaves appear quite similar to each other at first glance, but they differ significantly from each other especially in their micro-morphology and anatomy. This is also the case in the pinaceous genus *Abies*. Thus, to detect these differences, careful morpho-anatomical investigations using scanning electron microscopy and paraffin technique for leaf sectioning are urgently needed. For needle-leaved conifers, diagnostic features have to cover several external and internal foliar characters like the leaf arrangement at the shoot axis; the leaf size; the leaf shape (incl. the formation of the petiole, base, margin, tip and midrib); the leaf color; the cuticle (present or absent, density and color); the stomata (distribution, arrangement and density); the epidermis (size and shape of epidermal cells); the hypodermis (present or absent; continuous or discontinuous; number of hypodermal layers; size and shape of hypodermal cells); the structure of the mesophyll (monomorphic or dimorphic; size and shape of intercellular spaces); the endodermis (present or absent; size and shape of endodermal cells); the vascular bundle (including division of the vascu-

lar bundle strand; the presence or absence and the position of transfusion tracheids and vascular sclereids) and the resin ducts (size, shape and position).

It has to be taken into account that even within a tree the leaf size, shape and structure can differ significantly (compare ROBAKOWSKI et al. 2004a, b, WYKA 2007). To achieve comparability between different taxa, it is important to compare only similar light-exposed leaves collected from the same parts of the crown. Due to the fact that among most taxa a significant shift from juvenile to mature foliage occurs, it is also necessary to compare leaves collected from individuals which are more or less of the same age. In this work, the exact documentation of all internal and external foliar features is emphasized, which is needed for a serious identification of the species. An identification key based on foliar features is, however, not given, but can be taken from LIU (1971) for a broad spectrum of species and from FULLING (1934) for *Abies* species cultivated in the United States of America. In DE LANGHE (2015) a vegetative identification key, mainly based on foliar features, is given for a large spectrum of species.

1.1 Taxonomy and systematics

The genus *Abies* belongs to the largest coniferous family, the Pinaceae. The genus is placed in the subfamily Abietoideae and shows closest relations to *Keteleeria* (WANG et al. 2000; LISTON 2003). Within the genus *Abies* the systematics and the taxonomy are very complex and both are still controversial (compare e.g. RUSHFORTH 1983, 1984, 1986, 1999, 2008; DEBRECZY & RÁCZ 1995, 2003, 2011; TSUMURA & SUYAMA 1998; PARDUCCI & SZMIDT 1999; AGUIRRE-PLANTER et al. 2000, 2012; SUYAMA et al. 2000; ATA 2004; NIMSCH 2005; XIANG et al. 2009, 2015; SEMERIKOVA and SEMERIKOV 2014; VAZQUEZ-GARCIA et al. 2014), in particular among Mexican *Abies* species e.g. the *A. religiosa-hickellii-guatemalensis* complex (e.g. ANDERSEN et al. 2009) or within several Chinese taxa. The following Chinese taxa should be used as an example to introduce into the problems and the controversies existing within *Abies* taxonomy:

- *A. faxoniana* REHDER & E.H. WILSON

CHENG et al. (1978) described it as a distinct species but LIU (1971), KRÜSSMANN (1983), ECKENWALDER (2009), FARJON (2010) and DEBRECZY & RÁCZ (2011) as a variety of *A. fargesii*, RUSHFORTH (1987) as synonymous to *A. fargesii* and DALLIMORE & JACKSON (1966) as a variety of *A. delavayi*;

- *A. forrestii* COLTM.-ROG.
LIU (1971) regarded it as identical to *A. delavayi* var. *smithii*, CHENG et al. (1978), RUSHFORTH (1987), ECKENWALDER (2009), FARJON (2010) and DEBRECZY & RÁCZ (2011) treated it as *A. forrestii* while DALLIMORE & JACKSON (1966) and KRÜSSMANN (1983), treated it under *A. delavayi* var. *forrestii*;
- *A. ferreana* BORDÈRES & GAUSSEN
LIU (1971) and ECKENWALDER (2009) treated it as *A. fargesii* var. *faxoniana*, KRÜSSMANN (1983) as *A. delavayi* var. *georgei*, RUSHFORTH (1987) as *A. forrestii* ssp. *ferreana*, FARJON (2010) as *A. forrestii* var. *ferreana*, DALLIMORE & JACKSON (1966), CHENG et al. (1978) and DEBRECZY & RÁCZ (2011) described it as a distinct species *A. ferreana*;
- *A. sutchuenensis* (FRANCH.) REHDER & E.H. WILSON
CHENG et al. (1978), RUSHFORTH (1987) and ECKENWALDER (2009) described it as a synonymous to *A. fargesii*, LIU (1971) and FARJON (2010) as a variety of *A. fargesii*, DALLIMORE & JACKSON (1966) and KRÜSSMANN (1983) as the distinct species *A. sutchuenensis*.

Even today new species are found (e.g. HUANG et al. 1984; LI & FU 1997; XIANG 1997) and for several species research material for morpho-anatomical comparisons is hardly or not available. Several taxa are treated as distinct species in China, while outside of China they are hardly known and are mostly not in cultivation. Thus, for botanists and taxonomists outside of China it is often impossible to access material. Accordingly, outside of China several of the local endemic Chinese taxa are degraded to varieties or due to their minor differences they are merged into well-established larger species. Thus, the species status of those taxa remains unknown. Taxa demonstrating these problems best are e.g. *A. beshanzuensis* M.H. WU (1976), *A. chayuenensis* CHENG & L.K. FU (1975), *A. chengii* RUSHFORTH (1987), *A. fanjingshanensis* W.L. HUANG, Y.L. TU & S.Z. FANG (1984), *A. fansipanensis* Q.P. XIANG, L.K. FU & NAN LI (1996), *A. ferreana* BORDÈRES & GAUSSEN (1947), *A. nukiangensis* CHENG & L.K. FU (1975), *A. rollei* BORDÈRES & GAUSSEN (1949), *A. yuana* BORDÈRES & GAUSSEN (1949), *A. yuanbaoshanensis* Y.J. LU. et L.K. FU (1980) and *A. yulongxueshanensis* RUSHFORTH (1987).

This brief discussion above should give a small insight into the existing taxonomic and systematic problems among the genus *Abies*. These contradictions are discussed in NIMSCH (2005) in a broader context.

In addition to low availability of research ma-

terial, several further aspects are responsible for controversies about species concepts in *Abies*. For example, within species covering a large geographical range with different ecological habitats, several ecotypic variations with diverging morpho-anatomical features exist. Thus, it is not surprising that several of them were described as subspecies, varieties or even as hybrids. Accordingly, within *Abies* a high number of infraspecific taxa exist, some of them quite doubtful. Also within a species, certain intraspecific foliar variation is recognizable between plants from different geographic origins (e.g. RUETZ 2004; SCHÜTT & LANG 2004a). In this work, *A. alba*, an European taxon with a large, but disjunct range, is used as an example to illustrate the intraspecific foliar variation among different geographical origins. Thus, leaves of three different origins were compared: a Black Forest origin (Schauinsland mountain, SW-Germany, about 800 m above sea level), a Calabrian origin and a Montenegrin origin (Orjen mountains, about 1450 m above sea level).

Furthermore, a lot of closely related taxa cannot be clearly separated from each other because they are connected by several intermediate forms, e.g. *A. bornmuelleriana*, which's appearance is intermediate between *A. cephalonica* and *A. nordmanniana*.

In addition, natural hybridization is not rare (ATA 2004; BUCHER 2004; PERKINS 2004; ZIEGENHAGEN 2005; XIANG et al. 2015) and can be found within *Abies* worldwide (e.g. MATTFELD 1930; KLAHN & WINIESKI 1962; HAWLEY & DEHAYES 1985; CLAIR & CRITCHFIELD 1988; MIR & KHAN 2007; JANEČEK & KOBLIHA 2007; SEMERIKOVA et al. 2011; KRAJMEROVÁ et al. 2016), which leads to the formation of hybrids showing a morphology which is intermediate between its parents, e.g. *A. cephalonica* × *A. alba* = *A. × borisii-regis* (SCALTSOYIANNES et al. 1999; BELLA et al. 2015).

Due to the problems above it is not surprising that in literature the number of *Abies* species varies significantly: 25 species (NEGER & MÜNCH 1927); 39 species (LIU 1971); 40 species (JACKSON 1948; NEGER & MÜNCH 1952; MELCHIOR & WERDERMANN 1954; KRÜSSMANN 1955, 1983; PILGER 1960; DEN OUDEN & BOOM 1965; PAGE 1990; ROLOFF & BÄRTELS 1996; ECKENWALDER 2009), 46 species (SPORNE 1965; FARJON 1990; MABBERLEY 2009); 47 species (FARJON 2010), 48 species (FARJON 2001; XIANG 2009), 50 species (VAN GELDEREN & van HOEY SMITH 1996), over 50 species (KELLY & HILLIER 2004), 52 species (XIAOGUO et al. 2007), 53 species (ENGELMANN 2013), 55 species (RUSHFORTH 1987), over 60 species (NIMSCH 2005) and 67 species (DEBRECZY & RÁCZ 2011). This highly varying

number of species is because even today new species are being found and because of the varying taxonomic opinions of the different authors. A major problem is the shortage of detailed morpho-anatomical studies dealing with a large spectrum of species exist (e.g. LIU 1971), while molecular-phylogenetic studies including all known species are lacking.

Given its morphological heterogeneity, it is not surprising that the comparatively small genus *Abies* can be divided into numerous sections and subsections and that several different parallel classification systems exist. A detailed overview of previous classification systems is given in LIU (1971) and in FARJON & RUSHFORTH (1989) and so is not discussed here again. Within this work the classification system of the genus *Abies* mainly follows FARJON & RUSHFORTH (1989) which was slightly modified according to the results of XIANG et al. (2004). FARJON and RUSHFORTH (1989) divided *Abies* into 2 subgenera (*Abies* and *Pseudopicea*), 10 sections and 9 subsections. According to their systematic position all taxa treated in this present study are listed below.

1. **Section Abies**
 - A. alba* MILL.
 - A. × borisii-regis* MATTF.
 - A. bornmuelleriana* MATTF.
 - A. cephalonica* LOUD. var. *cephalonica*
 - A. cilicica* (ANT. & KOTSCHY) CARRIÈRE ssp. *cilicica*
 - A. equi-trojani* (ASCH. & SINT. ex BOISS.) MATTF.
 - A. nebrodensis* (LOJAC.) MATTEL
 - A. nordmanniana* (STEVEN) SPACH
2. **Section Piceaster**
 - A. numidica* DE LANNOY ex CARRIÈRE
 - A. pinsapo* BOISS. var. *pinsapo*
 - A. pinsapo* BOISS. var. *marocana* (TRABUT) CEBALLOS & BOLANOS
 - A. pinsapo* BOISS. var. *tazaotana* (H. DEL VILAR) POURTET
3. **Section Bracteata**
 - A. bracteata* (D. DON) D. DON ex POIT.
4. **Section Momi**
 1. **Subsection Homolepides**
 - A. ernestii* REHDER
 - A. homolepis* SIEBOLD & ZUCC. var. *homolepis*
 - A. homolepis* SIEBOLD & ZUCC. var. *umbellata* (MAYR.) WILSON
 - A. kawakamii* (HAYATA) ITO
 - A. recurvata* MAST.
 2. **Subsection Firmae**
 - A. beshanzuensis* M. H. WU
 - A. firma* SIEBOLD & ZUCC.
3. **Subsection Holophyllae**
 - A. chensiensis* VAN TIEGHEM ssp. *chensiensis*
 - A. chensiensis* VAN TIEGHEM ssp. *salouenensis* (BORD. REY & GAUSSEN) RUSHFORTH
 - A. gamblei* HICKEL
 - A. holophylla* MAXIM
 - A. pindrow* ROYLE var. *pindrow*
 - A. ziyuanensis* FU & MO
5. **Section Amabilis**
 - A. amabilis* DOUGL. ex FORBES
 - A. mariesii* MASTERS
6. **Section Pseudopicea**
 4. **Subsection Delavayianae**
 - A. chengii* RUSHFORTH
 - A. delavayi* FRANCH.
 - A. densa* GRIFF.
 - A. fabri* (MASTERS) CRAIB ssp. *fabri*
 - A. fabri* (MASTERS) CRAIB ssp. *minensis* (BORD. REY & GAUSSEN) RUSHFORTH
 - A. fanjingshanensis* HUANG, TU & FANG
 - A. fansipanensis* Q.P. XIANG, L.K. FU & NAN LI
 - A. fargesii* FRANCH. var. *fargesii*
 - A. fargesii* FRANCH. var. *faxoniana* (REHDER & WILSON) LIU
 - A. fargesii* FRANCH. var. *sutchuenensis* FRANCH.
 - A. fordei* RUSHFORTH
 - A. forrestii* C. COLTM.-ROGERS var. *ferreana* (BODERÈRES & GAUSSEN) FARJON & SILBA
 - A. forrestii* C. COLTM.-ROGERS var. *forrestii*
 - A. forrestii* C. COLTM.-ROGERS var. *georgei* (ORR) FARJON
 - A. nukiangensis* CHENG & FU
 - A. rollei* BODERÈRES & GAUSSEN
 - A. spectabilis* (D. DON) SPACH
 5. **Subsection Squamatae**
 - A. squamata* MASTERS
7. **Section Balsamea**
 6. **Subsection Laterales**
 - A. balsamea* (L.) MILL. var. *balsamea*
 - A. balsamea* (L.) MILL. var. *phanerolepis* FERNALD
 - A. lasiocarpa* (FLOOK.) NUTT. var. *arizonica* (MERRIAM) LEMMON
 - A. lasiocarpa* (FLOOK.) NUTT. var. *lasiocarpa*
 - A. semenovii* B. FEDTSCH.
 - A. sibirica* LEDEB.
 7. **Subsection Medianae**
 - A. fraseri* (PURSH) POIR.
 - A. koreana* WILSON
 - A. nephrolepis* (TRAUTV.) MAXIM.
 - A. sachalinensis* (FR. SCHMIDT) MASTERS var.

mayriana MIYABE & KUDO

A. sachalinensis (FR. SCHMIDT) MASTERS var. *sachalinensis*

A. veitchii LINDLEY var. *olivacea* SHIRAS.

A. veitchii LINDLEY var. *veitchii*

8. Section *Grandis*

A. concolor (GORDON & GLEND.) LINDLEY ex HILDEBR. var. *concolor*

A. concolor (GORDON & GLEND.) LINDLEY ex HILDEBR. var. *lowiana* (GORDON) E. MURRAY

A. durangensis MARTINEZ var. *coahuilensis* (I. M. JOHNST.) MARTINEZ

A. durangensis MARTINEZ var. *durangensis*

A. grandis (DOUGL. ex D. DON) LINDLEY

A. guatemalensis REHDER var. *guatemalensis*

A. guatemalensis REHDER var. *jaliscana* MARTINEZ

A. tamaulipensis SILBA

9. Section *Oiamel*

8. Subsection *Religiosae*

A. colimensis RUSHFORTH & NARAVE

A. mexicana MARTINEZ

A. religiosa (H.B.K.) SCHLECHT. & CHAM

A. vejarii MARTINEZ

9. Subsection *Hickelianae*

A. hickelii FLOUS & GAUSSEN

A. oaxacana MARTINEZ

10. Sect. *Nobilis*

A. magnifica ANDR. MURRAY var. *magnifica*

A. magnifica ANDR. MURRAY var. *shastensis* LEMMON

A. procera REHDER

1.2 Biogeography

Data from the fossil record and phylogenetic data suggest an origin of the genus *Abies* in the middle of the Cretaceous at middle and high altitudes of the northern hemisphere (XIAO GUO et al. 2007). Due to the global climate cooling the genus was dispersed southwards in the Eocene and today's distribution ranges appeared in the Quaternary. The current disjunct distribution pattern is a result of several geomorphological events, such as the uplift of the Himalaya, the Alps and the Rocky Mountains (XIAO GUO et al. 2007). In addition, also the occurrence of the Asian Monsoon rains and the Quaternary glaciations had a strong impact on the biogeography and evolution of the genus *Abies* (VENDRAMIN 1999; XIAO GUO et al. 2007; JARAMILLO-CORREA et al. 2008; LINARES 2011; SEMERIKOVA et al. 2011; WANG et al. 2011; PENG et al. 2015; SHAO et al. 2017). The Pleistocene glaciations and warming periods not only had a strong im-

act on the current biogeography of the genus, but also on its genetic diversity and the genetic variation between different populations of the same species, as is still clearly shown by e.g. Mexican *Abies* species (e.g. AGUIRRE-PLANTER et al. 2000; JARAMILLO et al. 2008).

Today the genus *Abies* is restricted to the northern hemisphere and covers a large, disjunct range of different habitats. Most of the taxa are native to temperate or subtropical montane forests. The genus shows its highest diversity in southern Europe, North America and East Asia, where it is also well documented in the fossil record (XIAO GUO et al. 2007). The southernmost *Abies* species is the Mesoamerican *A. guatemalensis*, occurring in montane to alpine habitats in southern Mexico, Honduras and Guatemala (MARTINEZ 1948; RUSHFORTH 1987; ANDERSEN et al. 2006; ECKENWALDER 2009; JARAMILLO et al. 2008; FARJON 2010; DEBRECZY & RÁCZ 2011). The northernmost species is *A. sibirica* which is native even inside the Arctic Circle westwards of the Urals to Western Manchuria, with winter temperatures falling below -50° C (RUSHFORTH 1987). In contrast, *A. kawakamii* straddles the Tropic of Cancer in Taiwan (RUSHFORTH 1987; DEBRECZY & RÁCZ 2011). Taxa like the European *A. alba* covering a huge range are the exception. Most of the others occur in small disjunct populations (e.g. AGUIRRE-PLANTER et al. 2000, 2012; RASMUSSEN et al. 2010).

1.3 Morphology and anatomy

1.3.1 Habitus

The genus *Abies* comprises exclusively evergreen trees mostly with a conical or pyramidal crown (Fig. 1A), in some taxa e.g. *A. alba* or *A. homolepis* var. *homolepis* with a *Cedrus*-like flat top. Some species are large trees reaching up to 70 (-100) m e.g. *A. grandis*, while others are only 12-15 m high (e.g. *A. koreana*). The majority of species are about 30-40 (-50) m high.

The lateral branches of most species are whorled and more or less plagiotropic, spreading from the trunk. The current year's branches vary strongly in color among species, from yellow via reddish to brownish and in the degree of pubescence.

The wood of most species is characterized by the absence of resin pockets, which distinguishes them significantly from other Pinaceae, e.g. *Picea*.

The bark of juvenile trees is quite smooth showing several large resin bladders (Fig. 1B). On mature trees the bark is often strongly vertically fissured (e.g. *A. cephalonica* or *A. cilicica*), or

it breaks up into scales and peels off (e.g. *A. forrestii* var. *forrestii*). The bark of *A. squamata* which is exfoliating in thin papery layers is quite unique among the genus *Abies* and resembles the situation of several species within the angiospermous genus *Betula* (Betulaceae).

1.3.2 Reproductive structures

All *Abies* species are monoecious, male and female reproductive structures are developed on the same tree. They are arranged in compact cones, the male ones are called “pollen cones”, the female ones “seed cones”. In most taxa cones of both gender are developed distantly separated from each other within the crown, pollen cones in lower parts, seed cones in distal parts. This arrangement should help to prevent self-pollination.

On the lower side of last year’s branches numerous pollen cones are inserted abaxially in the distal part. There is always one pollen cone inserted in the axil of a needle-like bract (Fig. 1D). Pollen cones are uniaxial, “flower”-like structures consisting of several helically inserted hyposporangiate microsporangiophores, each of which consists of a central stalk, an adaxial shield-like scutellum and two abaxial microsporangia. The color of the pollen cones varies from mostly yellow (e.g. *A. alba*) to reddish (e.g. *A. pinsapo* var. *pinsapo*). The pollen grains are bisaccate, showing two air sacs (Fig. 1E). All *Abies* species are wind pollinated.

Seed cones, however, are polyaxial, “inflorescence”-like, consisting of several so-called bract scale/seed scale complexes. The bract scale is a leaf. The ovuliferous short shoot, the seed scale, is inserted in the axil of the bract scale. Each seed scale carries two ovules, with a funnel-shaped micropyle pointing downwards. At pollination time the bract scale is mostly significantly larger than the seed scale. After pollination the seed scales get strongly enlarged and close the cone. In some species the bract scales are completely exceeded by the seed scales and are no longer visible externally at maturity (e.g. *A. concolor* ssp. *concolor*). In the majority of species the bract scale remains visible externally as a small tip below each seed scale (e.g. *A. procera*). Bract scales which continue to significantly exceed the seed scales at maturity, as is typical for e.g. *Abies bracteata*, are the exception. Throughout their entire ontogeny, seed cones are in an upright position (Fig. 1C). Interspecifically, mature seed cones vary strongly in size (e.g. *A. koreana*: 3-6 cm long, 2 cm wide; *A. procera*: 20-25 cm long, 6-8 cm wide), in shape (cylindrical via oblong to ovate), and in color: dark brown (e.g.

A. alba), greenish (e.g. *A. pinsapo* var. *pinsapo*), yellow (e.g. *A. firma*), reddish (e.g. *A. pindrow* var. *pindrow*), bluish (e.g. *A. veitchii* var. *veitchii*) or violet (e.g. *A. kawakamii*). At maturity the seed cone axis dries out and shrinks so that the seed cones disintegrate to release the seeds. After that the dry cone axis remains on the shoot for years. The seeds have a distinct wing (Fig. 1F), which is derived from seed scale tissue. The seeds are dispersed by wind.

1.3.3 Foliage

1.3.3.1 Leaf arrangement

Among the genus *Abies* leaves of all species are inserted helically on the shoot axis. There are distinct differences in the leaf arrangement between fertile and sterile shoots axes. But also within sterile shoots distinct differences between orthotropic and plagiotropic shoots exist. On light-exposed orthotropic shoots (Fig. 2A) the leaves either spread radially from the shoot axis or are adpressed and parallel to it.

On light-exposed plagiotropic shoots the situation is, however, much more diverse showing different types of leaf arrangement. Within the majority of species the lower leaves turn upwards so that they get crowded on the upper side of the shoot e.g. *A. squamata* (Fig. 2C), in several species forming a longitudinal U- or V-shaped groove e.g. *A. equi-trojani* (Fig. 2D) or the leaves which are crowded on the upper side are pointing forwards, which leads to a partly strongly overlap of lamina surfaces e.g. *A. pindrow* (Fig. 2E). In addition, among a few species the leaves are radially spreading e.g. *A. pinsapo* var. *marocana* (Fig. 2B). Leaves arranged in two lateral series with recurved leaves as developed in *A. recurvata* (Fig. 2G) are the exception. On shaded plagiotropic shoots, in most species the leaves are arranged in two lateral, more or less two-dimensional flattened series with leaves spreading from the shoot axis (Fig. 2F).

At first glance, the common type of leaf arrangement on light-exposed plagiotropic shoots with crowded leaves on the upper side of the shoot axis with overlapping lamina surfaces seems to be a contradiction to the “typical” arrangement of sun leaves in the “classical” sense. Typical sun leaves show an orientation which ensures optimum light harvest by maximizing light-exposure and preventing self-shading. However, the crowded leaf arrangement on the upper side of a shoot axis in most *Abies* species leads to massive self-shading, particularly, at lower light incident angles. At high light incident angle (e.g. at

zenith, when highest intensities are reached) only the leaf tips are hit by strong direct solar radiation, and the lamina is mostly exposed to less intensive diffuse lateral radiation. Thus, the lamina surface is exposed to direct solar radiation for only a short period each day, mostly at times of low solar altitudes in the morning and in the afternoon, which seems to be unfavorable for sun leaves at first glance. However, the self-shading effect can be regarded as an effective strategy in protecting sun leaves from water loss via the lamina and from damage to chlorophyll from high solar radiation, in particular from an excess of ultraviolet and infrared radiation.

On shaded plagiotropic lateral shoots, leaves are mostly arranged in two flattened lateral series, and a shading of lamina surfaces is prevented by an alternation of short and long needle leaves, which avoids an overlapping of lamina surfaces as is illustrated in Fig. 2F for *A. alba*. It is remarkable that the perfectly alternating long and short leaves are not subsequent members of the same parastichy. They belong to different parastichies and their alternation is achieved by strongly curved petioles. The developmental program that decides which leaf gets elongated and which remains short is not yet understood and needs further ontogenetic investigations. Within a crown the change in the leaf arrangement between light-exposed and shaded shoots is not abrupt. It changes gradually and is accompanied by several transitional forms (e.g. SPRUGEL et al. 1996; CESCATTI & ZORER 2003).

1.3.3.2 Leaf color

The leaf color varies only slightly between the different *Abies* species. In most cases the adaxial side is dark green and often glossy, while the abaxial surface is significantly lighter, mostly light-green to yellow-green. In addition, leaves of some species are covered with a thick whitish, greyish or bluish cuticle.

1.3.3.3 Leaf size

Leaf length of the different *Abies* species varies widely from 1-2 cm (e.g. *A. pinsapo* var. *pinsapo*) up to 7.5 cm (e.g. *A. concolor* ssp. *concolor*). In most species the needle leaves inserted in the middle part of a shoot axis are the largest. The most distal leaves (which are leading towards the outer bud scales) and the most basal leaves (which are representing transitional leaves between the green trophophylls and the inner bud scales) are often significantly smaller. Only in a few taxa are the leaves more or less similar in size and shape all over the entire shoot axis.

However, the leaf size varies not only between the different species but also intraspecifically for several reasons. Leaves of trees growing under xeric conditions are significantly shorter than those developed on trees occurring in moist conditions. Furthermore, with increasing tree age, leaf length decreases, e.g. for *A. alba* (Fig. 11), where needle leaves of a 40-year-old tree are about double the length of those developed on a 150-year-old tree. In addition the position of leaves on a branch has a strong impact on leaf length, for example, if on plagiotropic shoots the lower leaves are turned upwards, the leaves inserted on the upper side are mostly shorter than the lower leaves. In addition, also within the genus *Abies* the light-exposure strongly influences leaf length, as is demonstrated for sun and shade leaves of *A. alba* (Figs. 9 & 10). Leaves inserted on plagiotropic shaded shoots are distichous and can be classified into short and long leaves, with the short leaves about half the size. However, sun leaves of *A. alba* are more or less monomorphic in size and their dimensions correspond well to those of the large sized shade leaves, which is surprising, because in evergreen seed plants occurring under xeric conditions with leaves exposed to high solar radiation a strong leaf reduction which minimizes the loss of water via the lamina is common (THODAY 1931; BLUM & ARKIN 1984; BLUM 1996; BOSABALIDIS & KOFIDIS 2002; PARSONS 2010; SEIDLING et al. 2012; DÖRKEN & PARSONS 2016, 2017, DÖRKEN et al. 2017). Thus, in *A. alba* (Fig. 9) the situation is the complete reverse of that. As described in the chapter about leaf arrangement, the arrangement of sun leaves at the shoot axis leads to self-shading, which reduces the transpiration rates via the lamina and protects the chlorophyll from an excess of UV radiation. If sun leaves were strongly reduced in size the positive self-shading effect gets lost. In consequence most of the lamina surfaces get freely exposed to direct solar radiation, which finally leads to an increase in lamina transpiration rates and in UV-stress for the chlorophyll.

1.3.3.4 Leaf shape

All *Abies* species have narrow, single-veined needle leaves, but their shape varies markedly from species to species. In most cases it is linear (e.g. *A. alba*) to linear-ligulate (e.g. *A. chensiensis* var. *chensiensis*). In addition, also falcate (e.g. *A. squamata*), spatulate-linear (e.g. *A. koreana*) and oblanceolate (e.g. *A. behanzuensis*) leaves can be found. In cross sections the leaf shape varies interspecifically between carinate, avicular, elliptic, rhombic and rarely epsilon-shaped.

1.3.3.5 Petiole

Most *Abies* species have a short, twisted petiole, varying species-specifically from slightly (e.g. *A. alba*) to strongly (e.g. *A. chengii*) twisted. In addition, the petiole of most species is also curved (e.g. *A. nordmanniana* ssp. *nordmanniana*). In some taxa it is adpressed and parallel to the shoot axis (e.g. *A. magnifica* var. *magnifica*, *A. delavayi*).

1.3.3.6 Leaf tip

Among the genus *Abies* four different types of leaf tips can be found – emarginate (Fig. 3A), deeply notched (Fig. 3B), obtuse (Fig. 3C) or acute (Fig. 3D). However, between orthotropic and plagiotropic shoot axes significant differences exist. The tips of leaves inserted on orthotropic shoots are quite uniform in shape – species specifically being either obtuse or acute. On plagiotropic shoots the situation is more diverse and all four possible types of leaf tips can be found, with emarginate (Fig. 3A), deeply notched (Fig. 3B) and obtuse (Fig. 3C) as the most common types, while acute leaf tips (Fig. 3D) are only developed within a few taxa. If the dominating type of leaf tips is obtuse or acute than all leaves of a shoot axis are either obtuse or acute. However, emarginate or notched leaf tips can only be found on leaves inserted in the middle of the shoot axis, while basal- and distalmost leaves are obtuse or even acute. Any one species can show two types of leaf tips but no more.

Because the shape of the leaf tips is species specifically more or less constant, it represents an important and useful diagnostic feature. Diagnostically, only plagiotropic shoots should be used because all four types of leaf tips can be found on them. Also, only leaves from the middle part of a plagiotropic shoot axis should be used, because that is where emarginate and notched types are mostly developed. Accordingly, the leaf tip data (descriptions and images) given in chapter 3 “Species descriptions” describe and illustrate the situation of leaves inserted in the middle part of a plagiotropic shoot axis.

Abies-leaves with an emarginate or notched tip show some morphological and anatomical features similar to cladodes in *Sciadopitys* (Sciadopityaceae) which are however, based on a completely different bauplan (e.g. DICKSON 1866; CARRIÈRE 1868; ENGELMANN 1868; MOHL 1871a, b; STRASBURGER 1872; SCHNEIDER 1913; TROLL 1937; ROTH 1962; TETZLAF 2005; HILLE 2002, 2008; DÖRKEN & STÜTZEL 2010). The *Sciadopitys*-cladode is a fusion-product of two needle leaves which are fused with their adaxial lateral margins to each other (DÖRKEN & STÜTZEL 2011a, b, 2012a, b).

1.3.3.7 Leaf base

Most *Abies* species have a broad disc-shaped or roundish leaf base. *Abies* leaves get abscised as a whole unit, including their leaf base, which leads to the formation of more or less roundish abscission scars at the shoot axis. Thus, leafless shoot axes are quite smooth compared to other Pinaceae, e.g. *Picea*. In *Picea* the leaf bases and the petioles remain on the shoot axes, leading to a “file”-like rough structure after leaf abscission.

1.3.3.8 Leaf margin

The shape of the leaf margin varies strongly interspecifically from flat (e.g. *A. alba*) to strongly revolute (e.g. *A. fordei*), from thick (e.g. *A. sibirica*) to thin (e.g. *A. firma*), and from roundish (e.g. *A. balsamea* var. *balsamea*) via obtuse to acute (e.g. *A. fanjingshanensis*).

1.3.3.9 Midrib

Leaves of all *Abies* species are single-veined and characterized by a well-developed midrib (Fig. 4A). It forms a distinct, abaxial longitudinal ridge, in some species up to $\frac{1}{3}$ of the leaf's width. The midrib separates the two abaxial stomatal bands from each other. Adaxially, above the vascular bundle strand, the midrib is marked by a species-specific shallow (e.g. *A. concolor* ssp. *concolor*) or deep (e.g. *A. mariesii*) longitudinal depression.

1.3.3.10 Stomata

Leaves of most *Abies* species are hypostomatic. However, among basically hypostomatic taxa it is not uncommon that also a few adaxial stomata are irregularly scattered at the tip. Amphistomatic leaves, showing stomata developed on both sides of the leaf in the same density, are the exception and can be found in e.g. *A. concolor* ssp. *concolor* (FADY 2004), *A. pinsapo* ssp. *pinsapo* (PARDOS & PARDOS 2004) and *A. procera* (RUETZ 2004). Epis-tomatic leaves are not found in the genus *Abies*.

The majority of stomata are arranged in two abaxial longitudinal stomatal bands, each band consists of a varying number of stomatal rows. Within a stomatal band the number of stomatal rows varies species-specifically between 4-13. Not only between the different *Abies* species, but also within a tree the number of abaxial stomatal rows per leaf shows some variation, but it is more or less fixed within a species-specific range. In sun leaves (Fig. 9) the number of stomata is always significantly higher than in shade leaves (Fig. 10).

The stomata are varying species-specifically between 20-40 μm in length. Stomata developed at sun leaves are slightly longer than those of

shade leaves. In nearly all species the stomatal pores are all in the same orientation – parallel to the midrib. The stomata are sunken in the epidermis. Within species from xeric habitats they are sunken extremely deeply (e.g. in *A. pinsapo* var. *pinsapo*). Stomata forming crater-like depressions as found in e.g. *A. cilicica*, *A. concolor* ssp. *concolor*, *A. magnifica* var. *magnifica* and *A. nebrodensis* can also be understood as a morphological response to times of seasonal drought to reduce the stomatal water loss. How deeply stomata are sunken in the epidermis, is not exclusively influenced by the local climate, but also correlated to the tree's age, as shown for *A. alba*. In cotyledons (Fig. 6), primary leaves (Fig. 7) and subsequent juvenile leaves (Fig. 8) stomata are only weakly sunken, while in mature leaves collected at a 40-year-old tree (Fig. 9) they are clearly sunken. At a 150-year-old tree (Fig. 11) they are deeply sunken in irregular shaped, crater-like depressions. In addition to the tree's age also the leaf exposure to light has a strong impact on the encryption of stomata. While in sun leaves the stomata are deeply sunken, in shade leaves they are only weakly sunken. Thus, the situation in sun leaves of *A. alba* corresponds well to the situation as found in taxa from xeric habitats, where deeply sunken stomata are needed to reduce the stomatal loss of water, a feature which is not needed in shaded parts of the crown. Thus, this feature is lacking in shade leaves of *A. alba*.

1.3.3.11 Cuticle

In all *Abies* species the epidermis is covered with a cuticle (Fig. 4B). Its thickness varies strongly interspecifically. In most species, the cuticle is only weakly developed adaxial. But the abaxial stomatal bands are covered with a thick cuticle, visible as two whitish stripes. In some taxa both sides of the leaf are covered with a thick, mostly whitish, greyish or glaucous cuticle. In species from xeric habitats the cuticle is thicker, than in species from moist conditions, which reduces water loss from the lamina. Similarly, there is a light-exposure effect where the cuticle on sun leaves is significantly thicker than on shade leaves (SCHÜTT & LANG 2004b) (Figs. 9 & 10).

1.3.3.12 Epidermis

The epidermis consists of one parenchymatic layer of cells varying interspecifically in size and shape (globose, oblong or ovate). The light-exposed adaxial epidermal cells are always significantly larger than those of the shaded abaxial side. In the majority of *Abies* species the epidermis cells are thick walled and the exposed outer

anticlinal walls are thicker than the inner walls (Fig. 4B), a feature which is well-developed in taxa from xeric habitats and absent in taxa occurring under moist conditions.

1.3.3.13 Hypodermis

As in most conifers, in most *Abies* species a well-developed hypodermis consisting of strongly thickened and lignified cells is developed (e.g. FEUSTEL 1921; NAPP-ZINN 1966; LIU 1971; ALVAREZ et al. 1998; GRILL et al. 2004; SANGSTER et al. 2009; BERCU et al. 2010; BERCU 2013; SĘKIEWICZ et al. 2013; GHIMIRE et al. 2015; BORATYŃSKA et al. 2015; DÖRKEN & STÜTZEL 2011a, b, 2012 a, b; DÖRKEN 2015). In most *Abies* species the hypodermis forms a continuous structure that consists of one cell layer (Fig. 4B), which only gets interrupted by the stomatal respiratory chambers. In most species the hypodermal layer ad- and abaxial the vascular bundle and at the leaf margin consists in these parts of more than one layer of cells. In a few species the hypodermis consists occasionally of up to five layers of cells. In other taxa it is developed as a discontinuous layer (e.g. *A. balsamea* var. *balsamea*) or is lacking completely (e.g. *A. ziyuanensis*).

Especially in taxa growing under xeric conditions, the hypodermis is well-developed (e.g. GRILL et al. 2004) which helps to reduce the loss of water via the epidermis and helps the leaves to keep in shape even in times of drought. In addition, the hypodermis represents an important anatomical structure protecting the photosynthetically active mesophyll from an excess of solar radiation, in particular ultraviolet radiation. The strongly lignified, thick-walled hypodermis cells lead to a distinct increase in the path which high solar radiation has to pass before entering the photosynthetically active leaf tissues. Thus, it is not surprising that a well-developed hypodermis is developed in light-exposed sun leaves (Fig. 9), but is absent in shade leaves as shown for *A. alba* (Fig. 10). JORDAN et al. (2005), who investigated the highly scleromorphic foliage within Proteaceae (Angiospermae), suggested high solar radiation as one of the main ecological forces leading to the evolution of highly scleromorphic leaves with large amounts of sclerenchma protecting the photosynthetically active leaf tissues from excess solar radiation.

1.3.3.14 Mesophyll

Leaves of most *Abies* species are bifacial with a distinct dimorphic mesophyll. Towards the adaxial side 1-4 layers of palisade parenchyma are developed. The lower spongy-parenchyma shows

large intercellular spaces (Fig. 4C). On shoots with a radial leaf-arrangement, leaves are isobilateral (= aequifacial) with palisade parenchyma located towards all light-exposed parts, and with an internal spongy parenchyma. While sun leaves are mostly bifacial (Fig. 9), shade leaves are only weakly dimorphic with only a single layer of palisade parenchyma or are more often monomorphic (Fig. 10).

1.3.3.15 Vascular bundle

For gymnosperms, an open dichotomously branched leaf-venation is typical as is distinctly visible within leaves of *Ginkgo* (Ginkgoaceae) (e.g. THOMAS 1864; DAGUILLON 1890; CHAUVEAUD 1923; MARCO 1939; FERRÉ & GAUSSEN 1945; FORSTER & GIFFORD 1974; STEWART & ROTHWELL 1993; BECK 2010; DÖRKEN 2014). Also for Pinaceae it is widely accepted that an open dichotomous leaf-venation is realized (e.g. COULTER & CHAMBERLAIN 1917; MELCHIOR & WERDERMANN 1954; DALLIMORE & JACKSON 1966; MIROV 1967; KRÜSSMANN 1983; LIU 1971; ESAU 1969; FAHN 1982; FARJON 1984; KINDEL 1995; BRESINSKY et al. 2008; ECKENWALDER 2009; TAYLOR et al. 2009). However, in contrast to all other conifers, within leaves of Pinaceae it seems that two vascular bundle strands are surrounded by a common endodermis (= vascular bundle sheath) (Fig. 4D). This feature is unique, because an endodermis is usually a feature of a single vascular bundle strand (DÖRKEN & STÜTZEL 2012a, b; DÖRKEN 2015). However, Pinaceous leaves are supplied by only a single collateral vascular bundle strand, which is surrounded by a more or less distinct endodermis. Within the vascular bundle xylem is located towards the adaxial side and phloem towards the abaxial side. In the middle part of the leaf (Fig. 5C) the vascular bundle strand is divided by several parenchymatic cells into two parts, so that it seems that two separate vascular bundles exist, which are surrounded by a common endodermis. Each of the two parts is divided again by several one-cell broad parenchymatic bands, so that the original roundish vascular bundle strand gets an oval to elliptic shape. At the base (Fig. 5D) and at the tip (Fig. 5B) of the leaf such parenchymatic bands are absent and the vascular bundle is not divided into two parts, as in the middle part of the leaf. Thus, within Pinaceae the general rule that an endodermis is a feature of only a single vascular bundle strand is realized and two apparent vascular bundles are not originated from an open dichotomous branching as it is generally supposed to be.

1.3.3.16 Endodermis

In several conifers the vascular bundle strand is surrounded by a well-developed endodermis (e.g. COULTER & CHAMBERLAIN 1917; FEUSTEL 1921; MELCHIOR & WERDERMANN 1954; NAPP-ZINN 1966; MIROV 1967; LIU 1971; ESAU 1969; FAHN 1982; TAYLOR et al. 2009; DÖRKEN & STÜTZEL 2012 a, b; DÖRKEN 2013a). The endodermis controls the exchange of water and nutrients between the vascular bundle and the mesophyll (e.g. SCHREIBER et al. 1994; WAGENITZ 2003; SACK & HOLBROOK 2006; LIESCHE et al. 2011; GRIFFITHS et al. 2013; SACK & SCOFFONI 2013; DÖRKEN 2013a). Thus, it is an effective structure to avoid undesirable water loss resulting from an uncontrolled exchange between the bundle and the surrounding tissue. Within the genus *Abies* the endodermis consists of parenchymatic cells, in most species varying strongly in size and shape (Fig. 4D). In some species (e.g. *A. densa*) the endodermis is weakly developed forming an incompletely closed annular structure.

1.3.3.17 Resin ducts

Within the leaves of all *Abies* species resin ducts occur (Fig. 4F). Their number varies interspecifically but is mostly constant within a taxon. In the majority of species typically two resin ducts are developed, which are characterized by a thick walled, but not lignified, single-layered, distinct sheath and an inner single layered, and thin-walled epithelium (Fig. 4F). Only among a small spectrum of species the number of ducts per leaf is significantly increased, e.g. *A. hickelii*: 4-12, *A. hidalgensis*: 4-5 (-7), *A. oaxacana*: 8-12 and *A. zapotekensis*: up to 4. In taxa like *A. firma*, *A. fabri* and *A. bracteata* occasionally 4 resin ducts per leaf occur (DALLIMORE & JACKSON 1966; REHDER 1967; LIU 1971; KRÜSSMANN 1983; PANETSOS 1992; DEBRECZY & RÁCZ 1995, 2011; FARJON 1990, 2010; WU & HU 1997; ANDERSEN et al. 2006; ENGELMANN 2013). This high number of resin ducts distinguishes these species significantly from all others and is therefore an important diagnostic feature. The evolutionary and ecological reasons leading to the increased number of resin ducts per leaf and their taxonomic and phylogenetic relevance is still controversial. DEBRECZY & RÁCZ (1995) suspected that an increased number per leaf could be regarded either as representing a primitive, ancestral feature or maybe a consequence of rapid climatic changes occurred during the evolutionary history of the respective taxon. Their first hypothesis is supported by the fact that among several taxa of ancient coniferous groups, e.g. Podocarpaceae s.l., up to 10 median resin ducts per leaf can be developed (DEBRECZY & RÁCZ 1995).

The position of resin ducts within a leaf varies markedly interspecifically (e.g. PANETSOS 1992; FADY 2004; DEBRECZY & RÁCZ 2011; EO & HYUN 2013). In some species the resin ducts are median in the mesophyll (e.g. *A. fraseri*), in other cases they are adjacent to the abaxial hypodermis (e.g. *A. alba*). Investigations on the foliar shift in *A. alba* from juvenile to mature foliage show, that the position of resin ducts in cotyledons (Fig. 6), primary leaves (Fig. 7), subsequent juvenile leaves (Fig. 8) and mature leaves from a 40-year-old-tree (Fig. 9) is similar – always adjacent to the abaxial hypodermis. But in leaves from 150-year-old trees (Fig. 11) the resin ducts are median. In addition to the age of a tree, also the position of leaves in the crown plays an important role in the position of resin ducts. In leaves developed in basal parts of the crown the resin ducts are more or less marginal, while in distal parts of the crown their position changes to median. These observations fit quite well with those of GAUSSEN (1964), ROLLER (1966), PANETSOS (1992), FADY (2004) and DEBRECZY &

RÁCZ (2011). ROLLER (1966), who investigated the position of resin ducts in leaves of *A. balsamea*, *A. lasiocarpa* and *A. fraseri*, concluded that their position is not affected by elevation and latitude and also not by the change in microclimatic conditions between shaded basal and sun exposed distal parts of the crown. ROLLER suggested that the position changes relate to tree age, rather than to ecological factors being different between juvenile and adult trees. In adults of all the taxa he investigated, in trees of the same taxon, duct position was always more or less similar.

This dislocation of resin ducts occurring within increasing age of an individual clearly demonstrates the importance that when the position of resin ducts is used as a taxonomic or diagnostic feature only leaves of same-aged trees collected in more or less the same parts of a crown should be compared to each other.

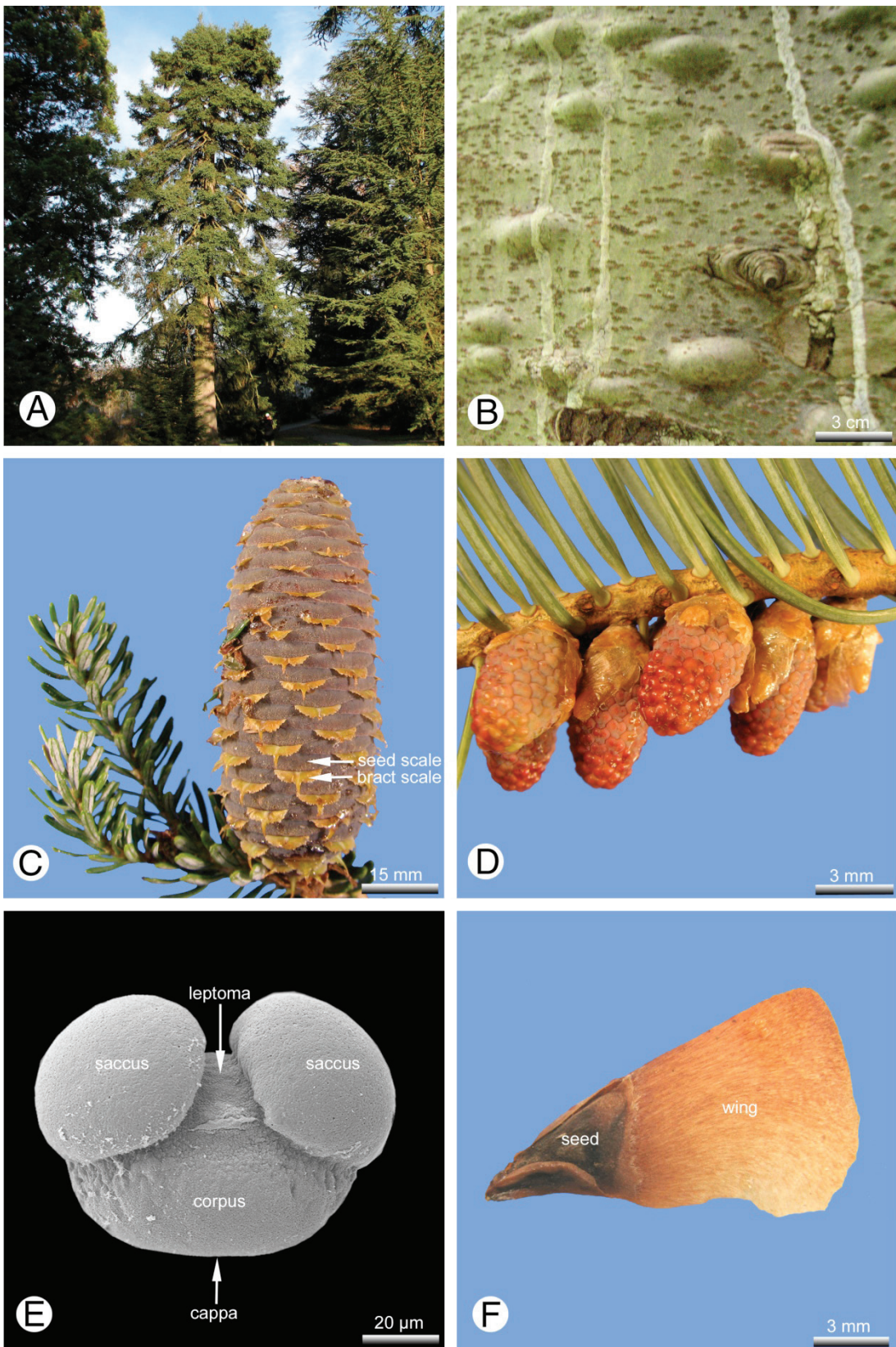


Fig. 1: Morphology of *Abies*; **A:** *A. pinsapo* var. *pinsapo*, habitus; **B:** *A. amabilis*, trunk with several resin bladders; **C:** *A. koreana*, mature seed cone; **D:** *A. concolor* ssp. *concolor*, mature pollen cones; **E:** *A. pinsapo* var. *pinsapo*, bisaccated pollen grain; **F:** *A. alba*, winged seed.

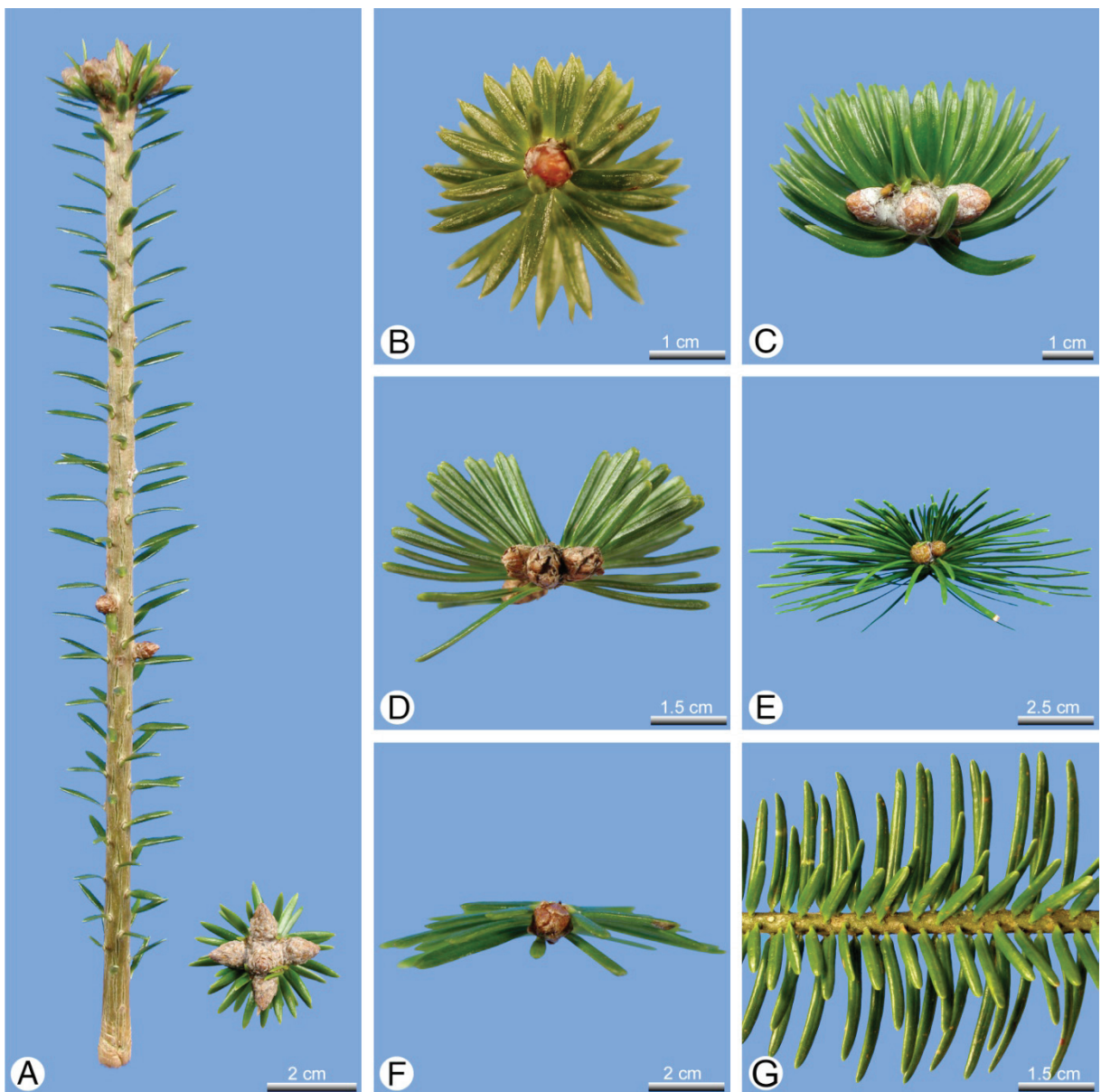


Fig. 2: Leaf arrangement on orthotropic (A) and plagiotropic (B-G) shoots of *Abies*; on orthotropic shoots leaves always radial spreading; on plagiotropic shoots different types of leaf arrangements can be found: radial (B); lower leaves turn upwards and are crowded on the upper side of the shoot axis (C); lower leaves turn upwards, crowded on the upper side of the shoot axis but forming a longitudinal, U-shaped groove (D); lower leaves turn upwards, crowded on the upper side of the shoot axis but pointing forwards (E); leaves arranged in two lateral series, leaves spreading from the shoot axis (F); leaves arranged in two lateral series, upper leaves recurved (G); **A:** *Abies alba*; **B:** *A. pinsapo* var. *marocana*, sun-leaves; **C:** *A. squamata*, sun-leaves; **D:** *A. equi-trojani*, sun-leaves; **E:** *A. pindrow*, sun-leaves; **F:** *A. alba*, shade-leaves; **G:** *A. recurvata*, sun-leaves.

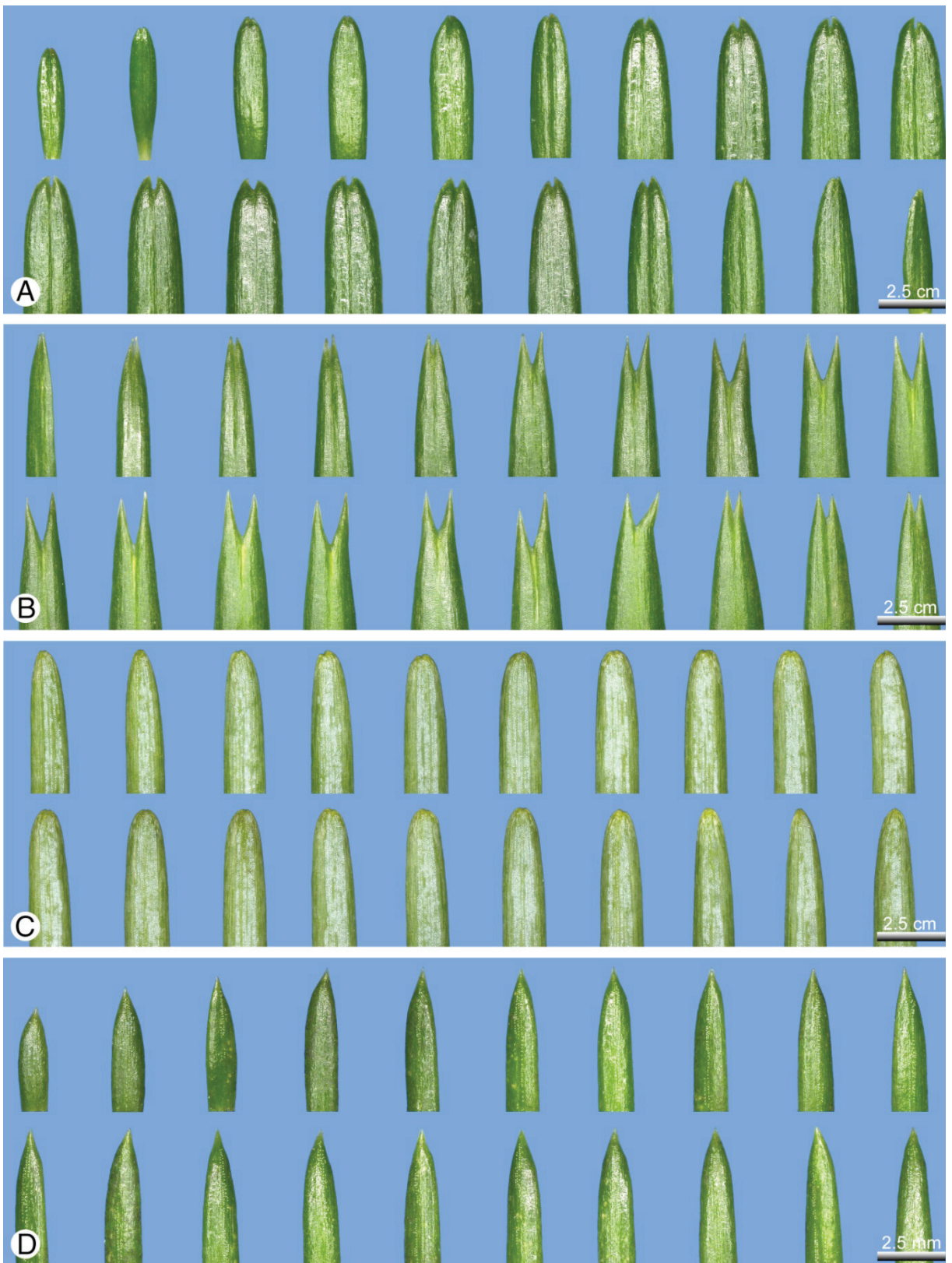


Fig. 3: Leaf tips occurring in the genus *Abies*; four major types leaf tips exist: emarginate (A), deeply notched (B), obtuse (C) and acute (D); the illustrated leaf tips represent an entire transitional series from distal to basal leaves of a plagiotropic shoot axis; emarginate or notched leaf tips are only developed in the middle part of a shoot axis, the basalmost and distalmost leaves are obtuse to acute; **A:** *A. alba* (emarginate); **B:** *A. firma* (notched); **C:** *A. concolor* ssp. *concolor* (obtuse); **D:** *A. pinsapo* var. *marocana*, juvenile leaf type (acute).

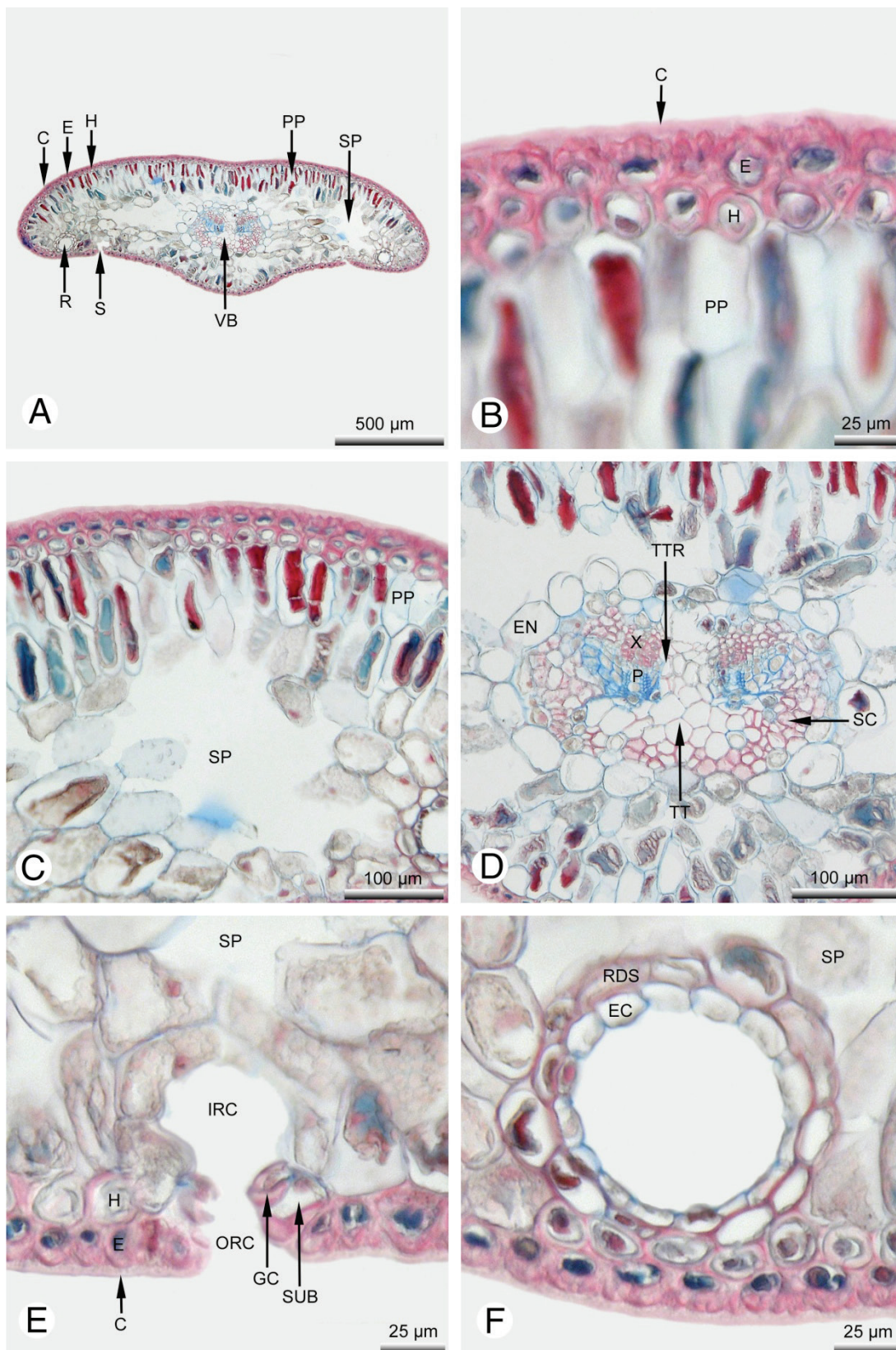


Fig. 4: Anatomy of leaves in *Abies* using the example of *A. cephalonica*; **A:** Cross section of a leaf; **B:** Detail of the upper surface; epidermis with a thick cuticle; hypodermis well developed; **C:** Dimorphic mesophyll, abaxial palisade parenchyma and abaxial spongy parenchyma; **D:** Vascular bundle; **E:** Stoma; **F:** Resin duct. (C = cuticle; E = epidermis; EC = epithelial cells; EN = endodermis; GC = guard cell; H = hypodermis; IRC = inner respiratory chamber; ORC = outer respiratory chamber; PP = palisade parenchyma; R = resin duct; RDS = resin duct sheath; S = stoma; SC = sclerenchyma; SUB = subsidiary cells; SP = spongy parenchyma; P = phloem; TT = transfusion tissue; TTR = transfusion tracheids; VB = vascular bundle; X = xylem.

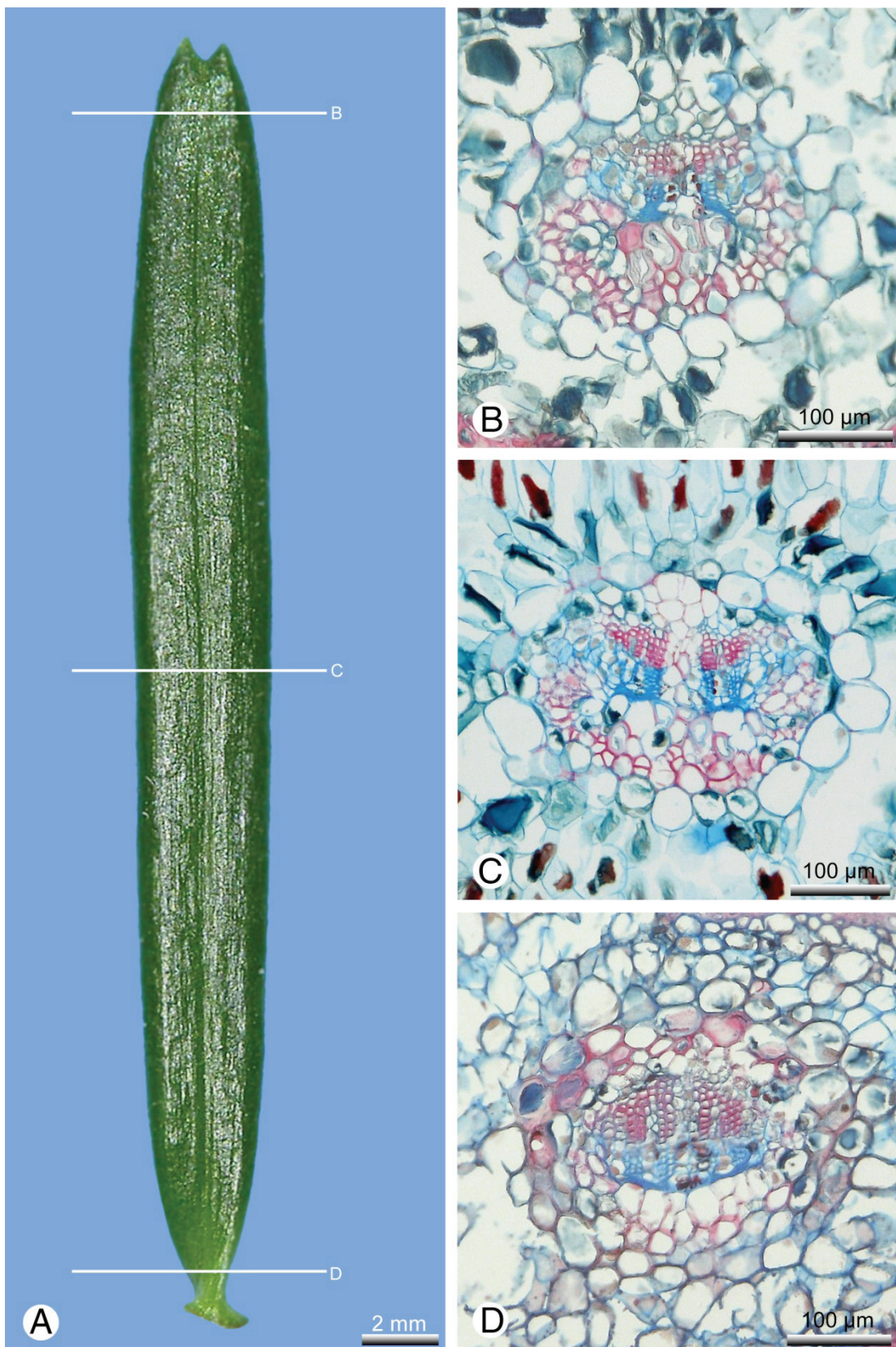


Fig. 5: Vasculature in leaves of *Abies* using the example of *A. alba*; **A:** needle leaf used for sectioning; **B:** Cross section in distal parts of the leaf; vascular bundle only weakly divided into two parts, each part also weakly divided by some one-cell broad parenchymatic bands; **C:** Cross section in the middle of the leaf; the vascular bundle strongly divided by 2-4 layers of parenchymatic cells into two parts; each part also weakly divided by some one-cell broad parenchymatic bands; **D:** Cross section in basal parts of the leaf; vascular bundle not divided into two parts but weakly divided by some one-cell broad parenchymatic bands.

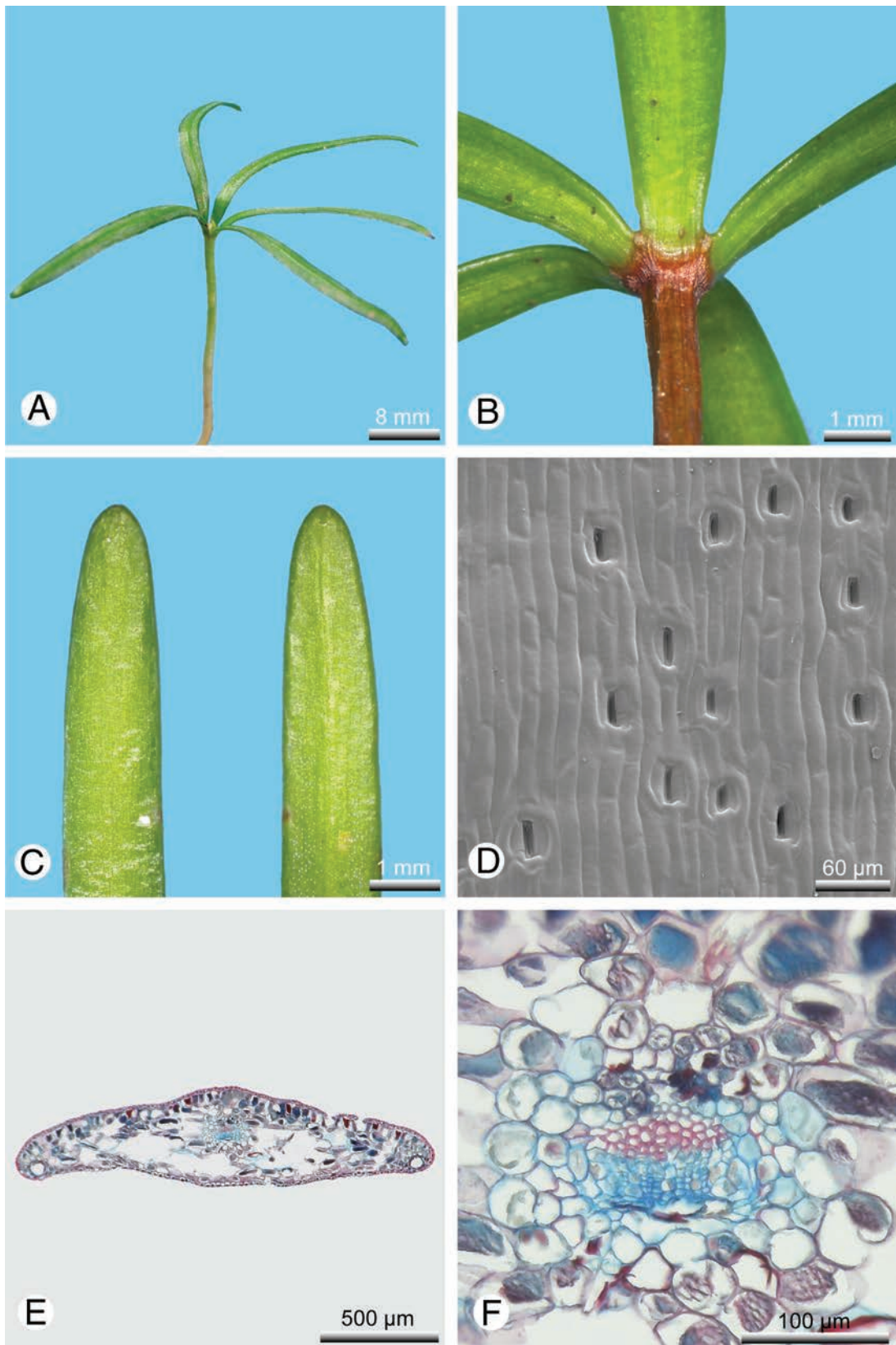


Fig. 6: *A. alba* (Sect. *Abies*), cotyledons, Black Forest origin; **A:** Seedling with 5 cotyledons; **B:** Detail leaf bases; **C:** Detail leaf tip; **D:** Abaxial stomatal detail (SEM-image); **E:** Cross section of a cotyledon; **F:** Detail of a vascular bundle.