

**A Revision of the European Representatives of
the Microlepidopteran
Genus *Dioryctria* ZELLER, 1846**

(Insecta: Lepidoptera: Pyralidae: Phycitinae)

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Hinweis:

Alle nomenklatorisch relevanten Handlungen in dieser Arbeit gelten im Sinne von Artikel 8.2 des Internationalen Codes für Zoologische Nomenklatur als unpubliziert (ICZN 2000).

Disclaimer:

All nomenclatorically relevant acts in this thesis have to be regarded as unpublished according to Article 8.2 of the International Code of Zoological Nomenclature (ICZN 2000).

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I. Introduction

When referring to small moths, the common association is pest species, such as clothes moths or infestations of stored goods like flour or dried fruits. However, many more ecological adjustments are known in Microlepidoptera. The Lepidopteran suprafamily of Pyraloidea alone, comprising the families Crambidae and Pyralidae, contains approximately 16 000 known species worldwide (Heppner 1991) and roughly the same number is expected to be discovered (Munroe & Solis 1998).

Pyraloidea generally are quite versatile in their larval ecology with their feeding preferences ranging from stored produce and other dried organic materials to all parts of living plants (Goater 1986, Goater et al. 2005). The larvae of the genus *Dioryctria* ZELLER, 1846 are generally dependant in this respect on Gymnosperm host plants. Consequently, the genus is restricted to the northern hemisphere (Earle 2006). To date, it contains 79 recognized conifer feeding species worldwide, with the species status of at least *D. simplicella*¹ and *D. mutarella* regarded as unclear (for the most recent catalogue, see GlobIZ 2006). Most *Dioryctria* species have been reported as serious pests on coniferous trees (Hannemann 1964, Hedlin 1980, Johnson 1967, Perny 2005, Schwenke 1978). Depending on the species, the larvae attack cones, shoots, twigs, buds, boles, wounds, galls, and rust cankers of either a broad or a narrow spectrum of host plants (Hedlin et al. 1980). For example, *D. abietella* has been identified as a main pest species on *Abies*² cones (Patočka 1960), at times causing tree top damage of up to 15%; on a variety of crops other than *Abies*, even complete seed destruction was observed (Schwenke 1978). Scientists commissioned to monitor developments in forest ecology and pest management have recently noticed an increase of damage on Norway Spruce *Picea abies* caused by *D. abietella* in Austria (Perny 2005). While *D. abietella* is particularly perilous among monocultures, such as Christmas tree plantations, seed orchards, and tree nurseries, *D. sylvestrella* was observed to be destructive in forests, especially when the host was already weakened. *D. mendacella* has been registered as causing local seed loss of up to 50% (Schwenke 1978).

Based on shared morphological features, Mutuura & Munroe (1972) introduced seven species groups, which have since been expanded to 11 (Mutuura & Munroe 1974, Wang & Sung 1982, Neunzig 2003). In a recently published morphological and molecular study, the phylogenetic framework of *Dioryctria* was investigated for 14 species, mostly nearctic, belonging to seven species groups (Du et al. 2005). The results suggest that most of those classical species groups

¹ complete zoological taxonomic citations for *Dioryctria* and outgroup species are given in appendix 1

² complete botanical taxonomic citations are given in appendix 7

represent monophyletic lineages.

In Europe, 11 *Dioryctria* species are known, eight of which belong to the *abietella*³-group (Mutuura & Munroe 1974), named after the type species of the genus, *D. abietella*. Members of this group cause the majority of taxonomic confusion and identification challenges in this region of the world. The most outstanding unresolved problem from the taxonomic point of view regards a flock of morphologically virtually indistinguishable taxa around *D. simplicella*, also including *D. mutata*, *D. aulloi*, and *D. resiniphila*, and together addressed as the "*simplicella*-species-complex" in this thesis.

In general, safe identification in the genus still remains problematic in many cases due to a lack of reliable, readily recognisable morphological characters, leading to considerable confusion and misinterpretation. The difficulties of dependable species determination leaves foresters and applied entomologists alike, hampered in their recognition of the infesting *Dioryctria* species. In fact, the *simplicella*-species-complex provides an example of validly described species, better characterised in terms of ecology (larval biology, feeding habit, host plant) than by morphology (e.g. Seegerer & Pröse 1997).

The former example makes it quite evident that established criteria for identification are required and are crucial in the prevention of ongoing and future outbreaks. The example of the horse chestnut leaf miner (*Cameraria ohridella* DESCHKA & DIMIC, 1985) shows quite drastically the consequences of a species, possibly introduced from Asia, spreading rapidly over almost all of Europe in less than two decades. First found and described from Macedonia, it had reached central Germany in 1996 via Austria. Since, it has spread with a rate of 50-100km per year. It is now found throughout Europe from Greece to France and eastern Spain, reaching as far north as Denmark, Sweden, and even England. Meanwhile, half the area of the Ukraine is affected as well (Buchsbäum & Schönitzer 2000, Šefrová & Laštůvka 2001, Heitland et al. 2005, Avtzis & Avtzis 2006). Although such a case has not yet been recorded for *Dioryctria* the increase of international trade in the course of globalization bears a growing risk of introducing neobiota, including harmful pest species, thereby adding a new dimension to the problem. The economic aspects alone (the *Cameraria*-case for example has resulted in at least two major monitoring and pest control research projects, one by the European Union and the other by the city of Hamburg/Germany) make a strong case for the need to clarify the taxonomic status of the genus *Dioryctria* and to gather characters for safe identification.

Regardless of the taxonomic literature available, a phylogenetic treatment that includes the

³ the format of the group names follow previous publications (e.g. Neunzig 2003) and therefore contain only the species epithet and lack the genus name.

European species is still missing, so this study was designed to illuminate various aspects concerning their status by means of morphological, molecular, statistical, and ecological approaches. In the course of the taxonomic revision part, all European species were morphologically investigated, including the *simplicella*-species-complex. In order to obtain a solid base for phylogenetic investigation, the species are morphologically re-described, since the original descriptions are sparse and lack detail especially with genitalia investigations unavailable for the majority of type specimens for most of the species found in Europe.

It is a known fact that within *Dioryctria* there are several problematic species, as with the above-mentioned species associated with *D. simplicella*. Thus, the examinations of the species included in this study were expanded by sequence analysis of the mitochondrial cytochrome oxidase I gene (COI). This gene is present in a sufficient number of copies and has been proven capable of resolving close inter-specific (Brown et al. 1994, Sperling & Hickey 1994a) and even intra-specific (Bogdanowicz et al. 1993, Brower 1994) relationships within Lepidopteran genera. This combined approach aims to clarify the identities of species and their phylogenetic relationships. The challenge encountered in obtaining suitable DNA, which could allow for complete COI generation from set and older specimens without serious damage to vouchers, called for an innovative approach to DNA extraction. Such a method was developed and published in the course of the work presented here and is the foundation of the molecular part of this study (Knölke et al. 2005).

Aside from the attempt to resolve the controversy surrounding the taxonomic status of *D. simplicella* and *D. mutarella*, as well as their relations to the other members of the *simplicella*-species-complex, characters were sought after that would allow for accurate identification of the European taxa. To provide a clear reference in this paper, specimens with blackish obscured forewing patterns are referred to as *D. simplicella* auct., and light-grey specimens clearly displaying the "*Dioryctria*"-patterns of forewings are referred to as *D. mutarella* auct., regardless of the phylogenetic identity of the taxa. Furthermore, the placement of some species was reassessed. First, *D. nivaliensis* was assigned to a species-group, and second, the placement of *D. robiniella* into the genus by Speidel and Asselbergs (2000) was reviewed. On a wider scope, the relationships between the European species and species-groups were addressed, in particular how the phylogenetic results for the European species correspond to the findings of Du et al. (2005). Evolutionary aspects were considered in the light of the ecology and feeding habits of the larvae. The question if larval ecology correlates with morphological and molecular results and whether this turns out to be a valid trait to facilitate the determination of species has also been considered.

II. Material and Methods

2.1. Taxon Sampling for Molecular, Morphological, and Ecological Investigation

Male and female specimens from all known European, two Japanese, and selected other non-European *Dioryctria* species were morphologically investigated for external and internal (i.e. genitalia) characters. To provide an overview of the genus, a compilation of all known species worldwide, including the species group assignments, is listed in appendix 1 for the first time.

Complete morphological datasets could be assembled for at least one male and one female specimen of each European species and one of the two Japanese species. For the investigation of morphological traits and of collecting data¹, the numbers of specimens of each species given in table 2.1 were consulted.

Eligible specimens from each species of the European and Japanese material were selected for sequencing (for criteria see Knölke et al. 2005). To account for possible genetic and morphological variation, specimens from as many different regions of Europe as possible were examined. However, practical limitations were encountered due to the need of reasonably fresh material for genetic analyses and as a result of low population numbers of certain species, sometimes combined with their geographically restricted distribution. This was especially true for the "rare" taxa (*D. aulloi*, *D. resiniphila*, *D. simplicella* auct., and *D. robiniella*). Rare in this case refers to the presence in collections and might not reflect the real situation in the field. Regardless, DNA isolation and obtaining sequences was possible for fair amount of specimens. For example *D. mutarella* auct. was sequenced from as many locations as possible to gain an overview of the possible influence of origin on sequence variation.

In addition, further non-European species were included, adding more species to the groups represented by European species and also expanding the dataset by two more *Dioryctria* species-groups (*zimmermani*-, and *baumhoferi*-group) (see table 2.1). Thus a broader base was created by adding further European taxa in order to test the stability of the phylogenetic framework proposed by Du et al. (2005). Also it enabled the testing of whether newly added species can be conclusively positioned in the resulting phylogenies. Ultimately this should also illuminate the relationships between the European and non-European species, and possibly enable the isolation of patterns with respect to the different larval feeding habits, or rather to their possible evolutionary implications. In addition to the European and Japanese species, the *Dioryctria*

¹ collecting data are given in appendix 6

species analysed by Du et al. (2005) had to be morphologically re-examined (exception: *D. ponderosae*, for which no adequate data was accessible), in order to draw up characters useful for discerning the species at hand. Many of those characters were previously unused in parsimony analyses.

This subsequently enabled the comparisons between molecular, morphological/ecological and combined datasets. The morphological characters included in phylogenetic analyses are assembled and specified in appendix 4.

Table 2.1: List of previously described species available for investigation²:

<i>Dioryctria</i> Species Groups	Species ³	No. of Specimens Examined
<i>abietella</i> -group	<i>Dioryctria abietella</i>	431
	<i>Dioryctria abietivorella</i>	3
	<i>Dioryctria aulloi</i>	4
	<i>Dioryctria mendacella</i>	119
	<i>Dioryctria nivaliensis</i> *	14
	<i>Dioryctria pineae</i>	60
	<i>Dioryctria resiniphila</i>	99
	<i>Dioryctria simplicella</i> auct. = <i>Dioryctria mutata</i> auct.	36 271
<i>schuetzeella</i> -group	<i>Dioryctria schuetzeella</i>	46
	<i>Dioryctria reniculleloides</i> #	2
<i>sylvestrella</i> -group	<i>Dioryctria magnifica</i> #	6
	<i>Dioryctria rubella</i>	3
	<i>Dioryctria sylvestrella</i>	101
<i>taiella</i> -group	<i>Dioryctria robiniella</i>	2
<i>auranticella</i> -group	<i>Dioryctria auranticella</i> #	1
	<i>Dioryctria juniperella</i>	9
	<i>Dioryctria okui</i>	3
	<i>Dioryctria yiai</i> #	1
<i>zimmermani</i> -group	<i>Dioryctria taedivorella</i> #	1
	<i>Dioryctria tumicoella</i> #	2
	<i>Dioryctria zimmermanni</i> #	3
<i>baumhoferi</i> -group	<i>Dioryctria clarioralis</i> #	4
Outgroup species	<i>Oncocera faecella</i> (Zeller, 1839) #	2
	<i>Ceroprepes ophthalmicella</i> (Christoph, 1881) #	--
	<i>Aphomia sociella</i> (Linnaeus, 1758)	2
	<i>Chamaesphexia tenthrediniformis</i> (Denis & Schiffermüller, 1775) #	--
	<i>Choristoneura fumiferana</i> (Clemens, 1865) #	--

² Tables, figures, and plates are numbered according to chapters.

³ bold: European species; *: newly assigned to group; #: sequence from GenBank;

The COI sequences of most non-European *Dioryctria* species and those of all outgroup species, with the exception of *A. sociella*, were retrieved from GenBank. Accession numbers and individual data for all specimens included in tree-calculating analyses are given in appendix 2, sequences not submitted to GenBank are compiled in appendix 3. There are four additional species groups established in *Dioryctria* (*erythropasa*-, *mongolicella*-, *ponderosae*- and *pygmaeella*-group) for which no adequate material was available (see appendix 1).

The outgroup species *O. faecella* was selected in accordance with the species chosen by Du et al. (2005) to aim for comparable tree results. *C. ophthalmicella* was omitted for morphological and combined analyses, as a number of the selected characters, both morphological and ecological, could not be scored due to unavailable material and unknown ecology. In the course of finding a tree based on molecular data exclusively, it became clear that more (and more distantly related) outgroup species were required to obtain meaningful results, so *C. ophthalmicella* was kept and *A. sociella*, *C. tenthrediniformis*, and *C. fumiferana* were additionally included in various combinations in selected runs.

Abbreviations of collections and institutions that kindly provided material are assembled in appendix 6, the abbreviations of the ones that hold type specimens in appendix 1.

2.2. Preparation of Specimens and DNA-Extraction

2.2.1 Preparation and Investigation of Antennae

Antennae of male specimens were removed under a stereomicroscope Wild M3Z (Wild, Heersbrugg, Switzerland) at 40X magnification, generally used for magnification. Removal was facilitated by applying a droplet of Barber's relax liquid (alcohol 95% 53ml; aqua dest. 49 ml; ethylacetate 19ml; benzene 7ml) to the base of the antenna. This fluid, until evaporated, causes the membranes and tissues of dried specimens to regain flexibility within 10-20 seconds and reduces the risk of breaking the flagellum upon removal. Scales covering areas of interest were removed from dry antennae using a thin brush. Antennae were then mounted on an aluminium specimen stub (Agar Scientific Ltd., UK) with a self-adhesive conductor tab (Plano GmbH, Wetzlar, FRG), coated with gold (135s, 2.4V, 20 mA; Polaron SEM coating system, Polaron, GaLa GmbH, FRG), and finally investigated using a SEM (Leo 1430VP, Leo Elektronenmikroskopie GmbH, FRG). For light microscopy, antennae were macerated in boiling KOH (10%), carefully cleaned, then dehydrated in 98% alcohol, and embedded in Euparal (Roth, Karlsruhe, FRG) on the glass slides (= "genitalia slides").

2.2.2. Preparation of Specimens for Molecular Analyses and Genitalia Investigation

DNA was extracted according to the procedure of Knölke et al. (2005), established in the course of the laboratory work of this study. The specimens and remnant DNA are stored at ZSM, unless otherwise noted. A list of DNA voucher specimens included in this study is given in appendix 2. The sclerotised parts of the abdomens, including terminalia, of specimens designated for sequence analysis were recovered for preparation of genitalia slides. Abdomens of all other specimens were macerated in boiling KOH (10%) for 15-20 minutes. Subsequently, genitalia slides were prepared following standard protocols of Robinson (1976) and Brown (1997). One male and one female genital respectively are illustrated for each European species (plates III.1 & III.2).

2.2.3. Photography and Imaging

Microscopic Photographs of genitalia were taken with a setup of a DMR compound stereomicroscope (Leika, Leitz DMRD/DMRBE, Leika Mikroskopie & Systeme GmbH, Wetzlar, FRG), a CCD camera (Spot Insight Color, Vistron Systems GmbH, Puchheim, FRG), and Spot Advanced software (version 4.0.9, Diagnostic Instruments, Inc., Sterling Heights, Michigan, USA). Altering the setup, magnified images of specimens were taken by replacing the stereomicroscope with a macro lens 10-108mm F/2.5 (Navitar TV Zoom 7000, Japan) and placing the specimen in a circum-lit box.

Drawings were traced from enlarged image printouts by steel pen or technical ink pen, subsequently scanned (Epson Perfection 1200U), and like all images further processed in Photoshop CS2 (Adobe Systems Inc., USA).

2.3. Morphological Data, Measurements, and Ecology

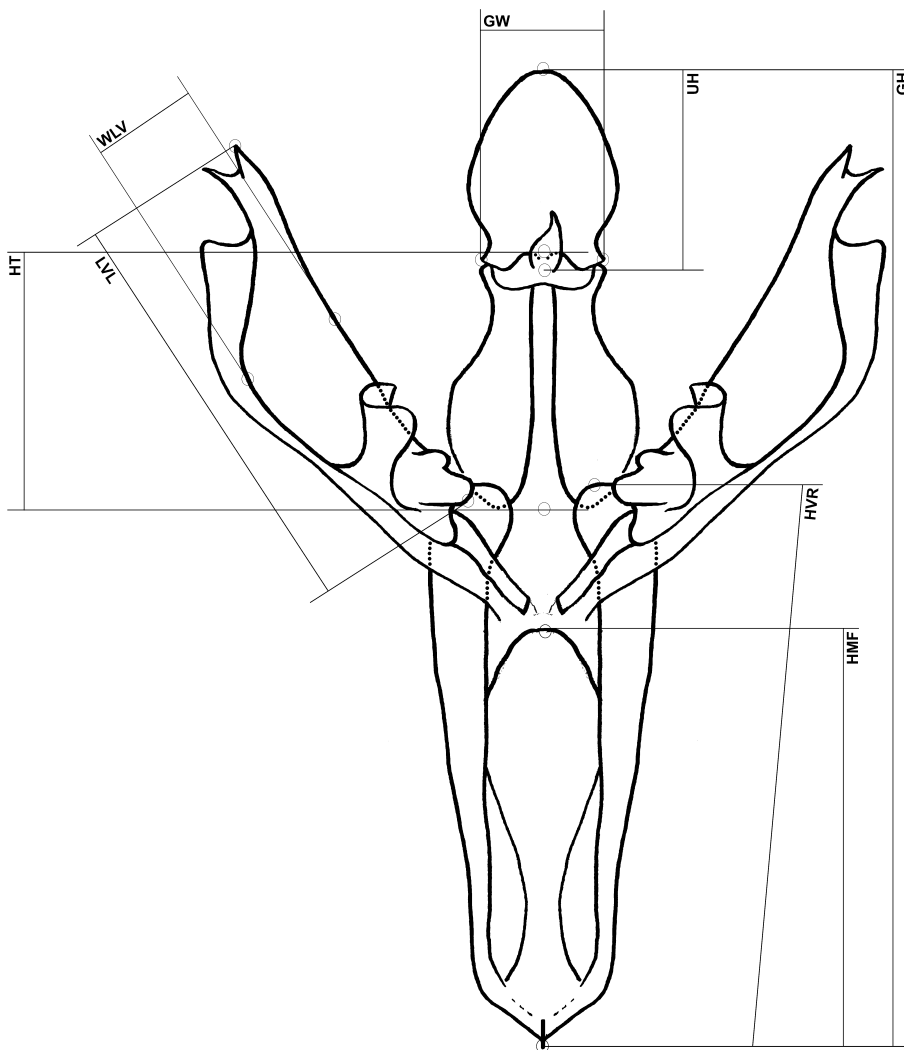
2.3.1. Measurements and Morphological Characters

A number of measurements were taken from wings and terminalia in order to trace potential taxonomically distinctive features. Wings were measured utilizing a sliding calliper. All genitalia measurements were obtained from photographs of the genital slides using the Photoshop measuring tool with an accuracy of 0.1 and 0.01mm. The morphometric analysis (SPCA) was based on measurements taken from male genitalia exclusively (see fig. 2.3).

The character states found in the morphological character-matrix (appendix 5) were generally

drawn up directly from the specimens. Only if these were unavailable, the data was adopted from preferably original descriptions or from other literature (e.g. Du et al. 2005, Heinrich 1956, Neunzig 2003). The consecutive numbers refer to the character numbers in the morphological matrix (see appendix 4). Selected Du et al. (2005) data were retained and adjusted to suit the requirements of resolving the relationships between the European species. Deviations from the study by Du et al. (2005) regarding character definition and character coding are commented. To enable cross referencing, the original character numbers assigned by Du et al. (2005) are given in brackets, following the character numbers assigned here. For specifics regarding the character codings, see appendix 4. Most ecological data were adopted from literature, some from specimen labels or from personal observations.

Figure 2.3: Measurements on male genitalia:



GH: Genital height; measured from apex of uncus to anterior tip of vinculum.
UH: Height of uncus; measured from apex of uncus to anterior most expansion of gnathos arms. **GW:** Gnathos width; measured as laterally widest expansion of gnathos arms. **HT:** Height of tectum; measured from anterior to posterior most points of length. **HMF:** Height of medial weaker sclerotised field in vinculum; measured from anterior tip of vinculum to posterior most margin of area. **HVL:** Height of vinculum left; measured from anterior tip of vinculum to posterior most left process near articulation area of left valve. **HVR:** Height of vinculum right; see above. **LVL:** Length of left valve; measured from tip/spine at apex of costa to medial-most articulate caput of valve. **LVR:** Length of right valve; see above. **WVL:** Width of left valve; measured as the longest perpendicular dropped on the line defined by length of valve. **WVR:** Width of right valve; see above.

LP: Length of phallus; measurement taken from sclerotised tube of uneverted phallus **DP:** Diameter of phallus; measurement taken from sclerotised tube of uneverted phallus.

2.3.2 Sheared Principal Component Analysis (SPCA)

As an advancement of ordinary principal component analysis (PCA), the SPCA method was designed to detect possible shape differences between homologous landmarks (Humphries et al. 1981). It is a multivariate method that aims to transform, step-by step, the bulk of the observed variance in a matrix into the least number of mutually independent components. Other than ordinary PCA, the second, third, and consecutive components are regressed (sheared) against the first component to eliminate size effects, as this first component - which is strongly correlated with size - explains most of the variation in the dataset. While ordinary PCA calculates the overall inter-group variance only, SPCA calculates an intra-group size-variance score for any defined group of specimens within the entire dataset. Based on the assumption that overall size effects resemble intra-group size effects, and hence can be regressed, the size-variance is sheared against the whole of the intergroup variance of the complete dataset. Whereas the shape related components (PCII, PCIII, etc.) may have values that are positive or zero with diverse variables (Rohlf & Bookstein 1987), size related PCI values display positive loadings exclusively. The degree of correlation for a character between subsequent PC loadings indicates the fraction of observed variance of one component that is explained by single variables. "Sheared" PCA assumes that the observed variance within groups may differ according to size and shape, whereas in normal PCA, loadings resemble overall co-variances. Therefore, loadings are equal to covariance, controlling for group only. In the final steps of the shearing procedure, the remaining overall variance in the dataset contains the informative intra-group shape variance, which is regressed in subsequent steps. As a result, PCII and PCIII represent shape effects that are corrected for overall size effects much more efficiently than in ordinary PCA. Identical to PCA, the first principal component (PCI) integrates most variation observed within the data set, which is assumed to be only size related; in contrast, PCII, PCIII, and further sequential components account for the variation that is not explained by PCI and are therefore considered to be corrected for size effects.

SPCA should enable the objective distinction of the morphologically hard to pinpoint species, as "principal component...analyses do not presume multiple groups and thus allow for their discovery" (Humphries et al. 1981). Therefore, it was engaged in order to attempt to illustrate shape differences of the male genitalia that are not immediately obvious upon visual as well as metric investigation among the species of the morphologically virtually indistinguishable *simplicella*-species-complex.

SPCA analysis requires a priori grouping which was achieved through morphological and

geographical determination of the subjected specimens into the five species mentioned next (i.e. groups).

In this study, a total of 65 male specimens including all species from the *simplicella*-species-complex (*D. simplicella* auct. n=6, *D. mutata* auct. n=23, *D. aulloi* n=2, *D. resiniphila* n=13), and 21 *D. abietella* specimens were analysed, with 12 measurements taken from each specimen. Measurements were obtained from photographs of the male genitalia slides using the Photoshop measuring tool (PS CS2 Adobe) with an accuracy of 0.01 mm (see fig. 2.3). Log-transforming the readings was unnecessary, since the margin of error when measuring with high magnification photographs is negligible (from 50x depending on zoom in Photoshop). These species resemble the five groups subjected to SPCA analyses. Subsequently, taxa were included into several runs to observe their influence on the overall dataset. This was the first attempt to use a set of genitalia measurements to investigate inter-specific relationships in this genus. Computation was performed utilizing the SHEAR program on DOS operating interface (McLeod 1990). The following is the current source (as of October 2007) for download of the program: http://www.nhm.ac.uk/hosted_sites/paleonet/ftp/ftp.htm.

Results of the SPCA analysis were illustrated using Excel 97 (Microsoft®).

2.4. Molecular Data

2.4.1. DNA Sources and a New Method of Extraction

A total of 54 specimens, preserved partly in ethanol (98%), but most of them dried, yielded sufficient DNA to obtain complete COI sequence (listed in appendix 2).

A new procedure of DNA extraction for Lepidoptera was established at the beginning of the work. With this new method, DNA can be extracted from Lepidopteran abdomens without any more damage to the specimen than is already standard for species identification when genitalia slides are prepared. For detailed description of the method see Knölke et al. (2005).

2.4.2. Selection of Molecular Marker

For molecular analysis, the mitochondrial cytochrome oxidase I (COI) gene was chosen. Not only is it a mitochondrial marker, present in a sufficient amount of copies, which was inevitable, since most of the material accessible was dried museum specimens where DNA is prone to degradation; but also, this gene has been proven suitable to resolve relations on species level in Lepidoptera and other insect taxa (Simon et al. 1994, Sperling et al. 1994a). Hebert et al. (2003) demonstrated the capability of identifying species in Lepidopterans with excellent accuracy by

employing even a small fraction of this gene.

2.4.3. PCR Amplification, Primers, and Sequencing

A 1536 bp fragment of mitochondrial genome resembling the complete COI gene was obtained by producing a number of overlapping fragments of various lengths, dependent on DNA quality. New primers were designed to suit the requirements of the species sequenced. All primers used are assembled in table 2.4. Nomenclature of new primers follows the standard of Simon et al. (1994).

Table 2.4: PCR primers:

Primer	Designation	oligo (5'-3')	Reference
4	TY-J-1460	TAC AAT TTA TCG CCT AAA CTT CAG CC	Sperling et al. 1994 a & b
7rev	C1-N-1729	GGC AAW GCT ATA TCW GGT GCT CC	New/DNATAX lab
7neu	C1-J-1744	TTT AAT GTT AGG AGC ACC AGA TAT AG	New
6	C1-J-1718	GGA GGA TTT GGA AAT TGA TTA GTT CC	Farrell in Simon et al. 1994
6 Apho	C1-J-1716	TTG GAG GTT TTG GTA ATT GAC TT	New
9	C1-N-2191	CCC GGT AAA ATT AAA ATA TAA ACT TC	Harrison in Simon et al. 1994
9 Apho	C1-N-2188	TGT CCA AAA AAT CAA AAT AAA TGT	New
8	C1-J-2183	CAA CAT TTA TTT TGA TTT TTT GG	Simon et al. 1994
10	C1-J-2195	TTG ATT TTT TGG TCA TCC AGA AGT	Roehrdanz 1993
11neu	C1-N-2393	TTC CTG TAG GTA CTG CAA TAA TTA TAG	New
1026rev	C1-N-2500	AAT CCT CCA ACA GTA AAT AAA AAA AC	New
1026fwd	C1-J-2526	GTT TTT TTA TTT ACT GTT GGA GGA TTA	New
1261rev	C1-N-2735	AAG AAA TGT TGA GGA AAA AAT GTT A	New
1263fwd	C1-J-2761	ACA TTT TTT CCT CAA CAT TTC TTA G	New
1352fwd	C1-J-2853	CTC TTC TTT AGG ATC TTA TAT TTC TTT A	New
1495rev	C1-N-2849	GCT GGG GGA AGA TTT TGA TAT	New
12	TL2-N-3014	TCC AAT GCA CTA ATC TGC CAT ATT A	Harrison in Simon et al. 1994

PCR amplifications were performed in 25µl preparations consisting of 16.5µl molecular biology grade water, 2.5µl Expand High Fidelity buffer 10x with 15mM/ml MgCl₂ (Roche), 0.5µl MgCl₂ stock solution (25mM/ml) (Roche), 2.5µl dNTP (2 mM each), 0.38µl per primer (20pM/µl), 0.87U (0.25µl) Expand High Fidelity TaqPolymerase (Roche), and 100ng (2µl, 50ng/µl) DNA (all Roche chemicals from Expand High Fidelity PCR system, Roche Diagnostics GmbH, Mannheim, FRG). Amplification routine utilizing a Dyad DNA engine Peltier thermal cycler (M.J. Research Inc., Waltham, MA, USA) was as follows: one cycle of 4 min at 94°C, 45 cycles at 94°C for 1:30 min, 48°C for 1:00 min, 72°C for 1:30 min, and one final cycle at 72°C for 3 min. PCR products were cleansed using MinElute PCR Purification Kit (Qiagen, Hilden, FRG). The ABI Prism BigDye Terminator Cycle Sequencing Ready Reaction Kit (V1.1) (Applied Biosystems, Foster City, CA, U.S.A) was used for cycle sequencing. In the 10µl reaction volumes, the BigDye stock was diluted by 2 volumes of Big Dye Terminator V1.1, V3.1 5x sequencing buffer. The 10µl reaction volume was composed as follows: 5.25µl molecular

biology grade water, 1.5µl Big Dye, 1.25µl primer (20pM/µl), and 200ng (2µl, 100ng/µl) DNA. Cycle sequencing parameters were as follows: one cycle at 94°C for 2 min, 35 cycles at 94°C for 0:20 min, 48°C for 0:15 min, and one cycle at 60°C for 4:00 min. Products were purified with Sephadex G-50 fine (Fluka, Seelze, FRG) before analysed on an ABI Prism 377 DNA Sequencing Unit. Sequence fragments were aligned in GenTool (V1.0) (BioTools Inc. 1999). Results were proofread by eye.

2.5. Data Analysis/Tree Constructions

2.5.1. PAUP Analyses

Four final PAUP 4b10 (Swofford 1997) runs were performed: the morphological and molecular datasets separately, a combined run including both, and one combined data neighbour joining tree (NJ). For all runs, 22 species of the genus *Dioryctria* were placed in ingroup (see table 2.1). The character settings were single state, unordered, and of equal weight. The tree search algorithms were parsimony, heuristic search, swapping algorithm=TBR, nchuck=10, chuckscore=1, and random addition sequence. Branch stability of resulting trees was investigated by bootstrapping with 100 addition sequence replicates and 100 or 1000 bootstrap replicates. *Oncocera faecella* was set as outgroup for morphological and combined analyses. The morphological dataset includes 47 characters as specified in appendix 4. To the molecular dataset (1536 bases, complete COI sequence), *C. ophthalmicella* and *A. sociella* were added as outgroup species to improve resolution and support of ingroup. Bootstrap values were plotted on strict consensus trees.

2.5.2. Bayesian Analyses

Bayesian analyses were performed using MrBayes (Ronquist et al. 2003), for the method provides a rapid approach and offers trees obtained through an alternative algorithm. It also gives node support-values immediately without extra calculation required.

The parameters for the runs were set as follows: Mcmc nchains = 4, ngen = 1000000, samplefreq = 1000; printfreq = 100; Prset statefreqpr = dirichlet (1,1,1,1); Lset nst = 6, rates = invgamma. The topologies of these trees were compared to those trees that were obtained using PAUP parsimony analyses.

III. Results

3.1. Taxonomy of European Species

Most of the European species of *Dioryctria* were originally described when detailed genitalia investigation was still uncommon, and even descriptions of outer characters are sometimes quite meagre, so that no thorough morphological treatment is available. *D. nivaliensis* represents such a case. The ignorance of genitalia morphology led Rebel in his original description in 1892 to place *D. nivaliensis* near *D. sylvestrella*. This error is understandable considering his observations of these type specimens' outer appearance alone. Once genital slides are consulted, the incorrect placement becomes evident. For the first time, this species is placed into a species-group in this paper. Detailed attention to new species group assignments is given in chapter 3.3. In fact, a number of identifications found in literature are doubtful due to the difficulties of reliable recognition of species in general. These misconceptions seriously compromise the validity of statements in many published records on ecology, biogeographical distribution, and interspecies relations. Therefore, the author was rather careful in assessing the credibility of sources.

The great likenesses among certain other species led to more comparable examples throughout the genus. *D. abietella*, to mention just one European case, has for a long time been confused with *D. mutatella* (Fuchs 1903) and *D. sylvestrella* (Parsons & Clancy 2002). Other species like *D. schuetzeella* have mistakenly been placed near *D. abietella* (Fuchs 1899). And even the North American species *D. abietivorella* was not recognized as different from *D. abietella* by both Heinrich (1956), in his treatment of North American *Dioryctria*, and by Zocchi (1961), who dealt in great detail with the species *D. abietella*, *D. mendacella*, *D. pineae*, *D. mutatella*, *D. schuetzeella*, and *D. sylvestrella*, all found in Italy.

Hitherto, no compilation of all known European representatives of the genus *Dioryctria* exists. Therefore, a comparative re-description for each of the European species deduced from a firm base of investigated material is given in this chapter (for number of investigated specimens see table 2.1 in material and methods section). Host plant associations are addressed in greater detail in a separate chapter (3.6.).

The species-groups of the genus *Dioryctria* and information on their respective species assignments were assembled in appendix 1. It also includes all available information on type locality and institutions holding the holotype specimens for all species worldwide.

The species-groups and species that follow here are given in alphabetical order.

3.1.1. Description of the Genus *Dioryctria*

Dioryctria ZELLER, 1846 b: 732

Type species: *Tinea abietella* [DENIS & SCHIFFERMÜLLER], 1775, by subsequent designation by Ragonot, 1893, in Romanoff, Mém. Lépid. 7: 188

= *Dioryctriodes* MUTUURA & MUNROE, 1974: 937

type species: *Dioryctriodes daelei* MUTUURA & MUNROE, 1974, by original designation Speidel & Asselbergs 2000: 144 (syn.)

= *Ocrisia* RAGONOT, 1893: 525

type species: *Myelois robiniella* MILLIÈRE, 1865, by monotypy

Speidel & Asselbergs 2000: 144 (syn.)

= *Pinipestis* GROTE, 1878: 19

type species: *Nephopterix zimmermani* GROTE, 1877, by monotypy Ragonot 1893: 189 (syn.)

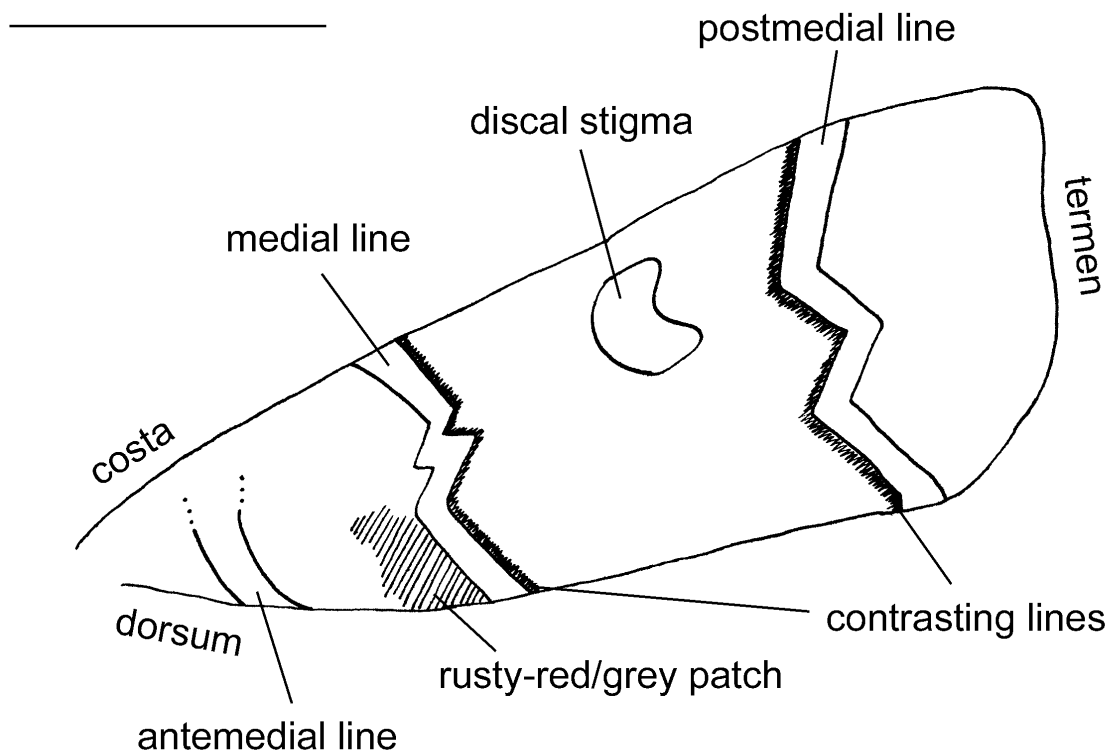
The autapomorphies for the genus *Dioryctria* are hard to pinpoint, as there are exceptions found for even those characters that appear most obvious at first, and have been mentioned frequently in literature (e.g. Heinrich 1956, Neunzig 2003). Due to the unresolved phylogenetic relations in the Phycitidae in general, no hypothesis regarding possible sister taxa exist to date. The high degree of resemblance within the genus was summarized aptly by Heinrich (1956): "*Dioryctria* is one of the most, if not the most, distinct and sharply defined genus in the Phycitidae; ... Its male and female genitalia have a characteristic habitus, difficult to describe, but easily observed in slides or figures." The light discal stigma on the forewings is a character exclusively found in most *Dioryctria*, while other genera display two smaller dark dots never found in *Dioryctria*. Therefore, confusion with other genera is unlikely when the following characteristic traits of the adult specimens are considered. Annotations are made when departures are encountered.

Head. Proboscis well developed. Antennae in males with a slight sinus at base formed by 2-5 modified flagellomers, usually covered by a moderately to strongly developed scale tuft. The scale tuft covers up to five flagellomers, distally modified by an anterio-dorsal process; the processes gain prominence from proximal to distal. Flagellomers 1 and 2 are entirely fused, 2 and 3 fused in ventral half, all following flagellomers separated. The number of processes varies within a species; the 7th flagellomer is the last one possibly modified. Labial palpus upturned in all species but *D. robiniella*. Maxillary palpus small.

Thorax. Forewings (see fig. 3.1.1) narrow, maculation is characteristic for the majority of the genus. The diagnostic dentate course of the usually well contrasted postmedial and medial lines are good characters for most species. However, the two known species of the *taiella*-group display unusual uniformity of colouration throughout the forewing, and the course of these fasciae is to be ascertained only by very close investigation. While finding the

postmedial line in these species is facilitated by its proximal contrasting line, which is dark and becomes the predominant maculation feature of the forewing, together with a broad dark streak situated proximo-costal, the detection of the antemedial line is by far more difficult. Nevertheless, both lines are present. The white to light grey discal stigma, generally a good character, can be seen in the *taiella*-group only under magnification and seems to be more a result of slightly different orientation of the scales in that area than of the minute colouration differences in the area of its expected presence. In *D. clarioralis* it even seems to be entirely obscured.

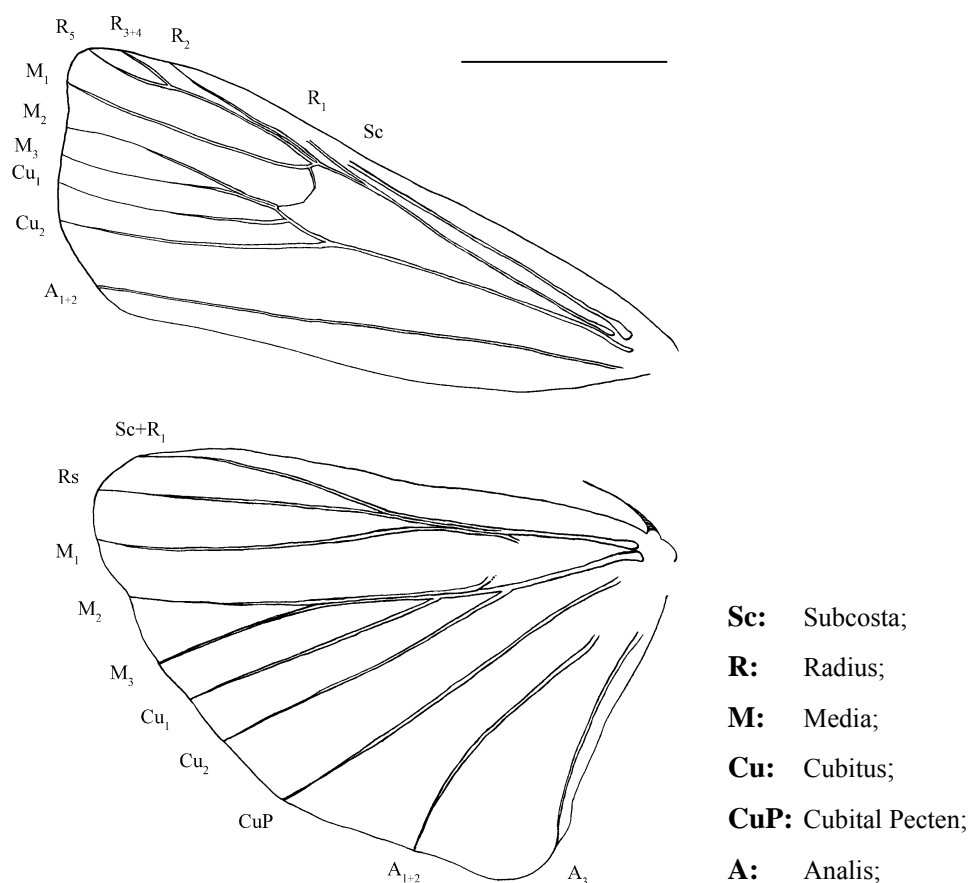
Figure 3.1.1: Schematic pattern of forewing, scale 0.5 cm:



Venation (see fig. 3.1.2): Nomenclature of veins follows Comstock as cited in Forster & Wohlfahrt (1977) and Goater et al. (2005). Forewing with 11 veins; R_{3+4} stalked with R_5 ; M_1 originating from ventro-distal angle of cubital cell, M_2 and M_3 from dorso-distal angle of cell, both parallel and close together for approximately $\frac{1}{4}$ of their length before diverging. Cu_1 from slightly proximad of dorso-distal angle of cell; insertion of Cu_2 well shifted proximally. Hindwing light grey, darkening towards the costa and latero-caudal seam and slightly along the veins, postmedial line inconspicuous, usually more obvious on underside of wing. With eight veins; S_c+R_1 closely approximate for up to $\frac{1}{2}$ of their length distad of cell M_2 and M_3 parallel or

stalked for more than $\frac{1}{2}$ of their length distad of cell. Cu_1 from dorso-distal angle of cell; insertion of Cu_2 well situated proximally.

Figure 3.1.2: Wing venations; left forewing and hindwing of *D. nivaliensis* DNATA02797, scale 0.5 cm:

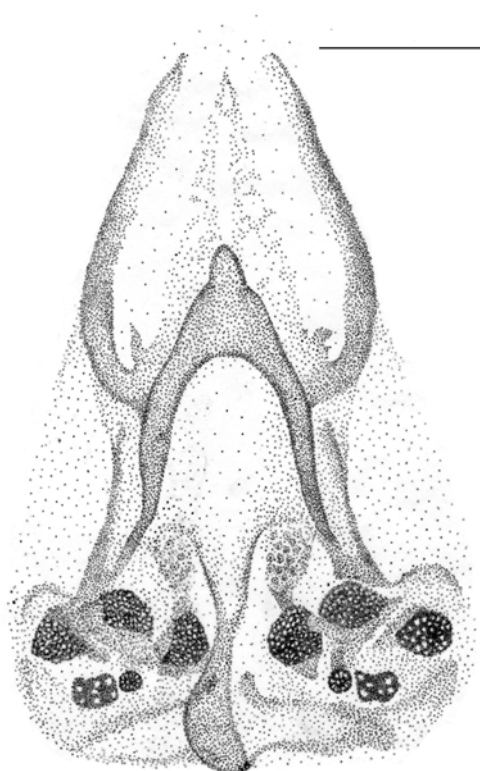


Male pregenital abdomen. T8 funnel-like enlarged posteriorly; posterior rim medially drawn in. S VIII (see fig. 3.1.3) elongated triangular with a W-shaped sclerotisation, possibly resembling the median plate sensu Roesler (1973), composed of a bifid sclerotised ridge in the central third of sternite, well produced at apex (not in *D. robiniella*), and two strongly sclerotised curved margins circumscribing a weakly sclerotised area covering approximately the caudal half of the sternite, their ends pointing medially. Two pairs of five highly derived scale-tufts, anteriorly arising from strongly sclerotised well defined plates.

Male terminalia. (plate III.1) Transtilla inconspicuous. Tegumen with median ridge deeply inverted; ventral edges strongly sclerotised. Gnathos arms anastomosed with ventral edges of tegumen, posteriorly round enlarged, supporting the median gnathos shield, the latter bearing a hooked processes dorsally. Uncus longer than wide. Anal cone ventrally slightly sclerotised. Valve dorsally strongly sclerotised, outlines and surface smooth; at ventro-basal edge of the sclerotised part arises a sclerotised slightly concave shield (=sella). The ventral part

of valve is membranous, slightly rolled longitudinally, strongly setose, and ventro-basally with coremata at least as long as valve. Juxta U-shaped, ventrally weakly sclerotised, dorsally bearing elongated lateral lobes. Vinculum V-shaped, dorso-ventrally flattened, forming a groove, reaching far anteriorly, almost doubling the length from apex of uncus to insertion point of valve. Phallus straight, elongated; ovate, dorso-ventrally slightly compressed in diameter; opening for ductus ejaculatorius anteriorly; inside the phallus variable numbers and arrangements of cornuti.

Figure 3.1.3: Sternite VIII of *D. abietella* with scaletufts removed, scale 0.5 mm:



Female terminalia. Ovipositor short, tapered. Apophyses posteriores longer than anterior ones. Apophyses anteriores can be curved more or less inward at tip. Segment VIII longer than wide, a sclerotised ring ventrally interrupted by a membranous narrow band. Genital opening simple. Antrum membranous, short. Ductus bursae from twice to five times as long as wide, flattened dorso-ventrally, strongly sclerotised terminating just before genital opening; anteriorly with a strong dorso-ventral double kink. Corpus bursae weakly sclerotised, lacking sculpture. Signum a band of spines. Ductus seminalis originating left lateral from posterior third close to signum.

Life history. The distribution is holarctic, host plants are predominantly gymnosperms; the majority of species are endophagous.

3.1.2. General Description of European *Dioryctria*

For practical reasons and to facilitate the recognition of species here summarized, morphological characteristics generally found in all European species are provided. If single species display exceptions, they are addressed separately in the description of the species.

Head. Colour mottled grey, with individual scales bicoloured dark grey with light grey tips. Labial palpus length of 3rd segment $\frac{1}{4}$ - $\frac{1}{3}$ of the length of 2nd segment. Maxillary palpus small, squamous, sclerotised distal segment narrows at tip.

Thorax. Colour mottled grey. Forewings smoothly scaled, areas of raised scales missing; basic colouration greyish brown. Transverse fasciae and discal stigma whitish grey; medial and postmedial line jagged; medial line jagged with two strong dentations pointing basally, discharging into costa pointing basally, into dorsum pointing distally; postmedial line contrasted by a black line as wide as postmedial line proximally. A whitish grey blotch, variable in shape and size, attached distally between veins Cu and Ax₁.

Abdomen. Colour grey; posterior ends of tergites distinctly paler, sternites pale grey mottled fuscous.

Male pregenital abdomen. Colour grey; posterior ends of tergites and sternites distinctly paler; sternites pale grey mottled fuscous. S VIII with scale tufts on sclerotised bases that are arranged in two pairs; each pair is arranged in two groups; group I is situated laterally and composed of three tufts, group II is situated close to the middle of sternum and is composed of two tufts; group I: tuft I is close-fitting to the segment along the lateral sclerotisation, distally forming a hook which holds the second bifurcated part of this tuft; tuft II is the shortest of this group and slightly C-shaped; tuft III covers the other two tufts of this group ventrally, is slightly bent and exceed all other tufts posteriorly; group II: tuft IV covers all other tufts ventrally and turns laterally and upwards to end as the most lateral tip; tuft V, the innermost tuft is bent S-like, the tips of these scales are broad spatulate; the entire complex is very compact. A semicircular, longitudinal crest located baso-medially on the interior side of the sternite.

Female terminalia. Ductus bursae long; Colliculum elongated, forming a pair of longitudinally corrugated, dorso-lateral sclerotisation at posterior end, sclerotisation stronger and appear laterally concentrated posterior; strongly sclerotised ridges forming the columella. Corpus bursae oval shaped widening into a dorso-caudal bulging; base of bulging girdled by a band of strong, slender spines forming signum.

3.1.3. Description *abietella*-group:

Male pregenital abdomen. Apex of medial plate of S VIII produced (fig. 3.1.3).

Male terminalia. Apex of uncus broadly to mediocly rounded overall appearance eggshaped. Terminal area of costa of valve smooth; displaying an acute preapical spine on costa; preapical costal area reminiscent of a bottleneck; dorsal and ventral costal margins not parallel, diverging distally up to $\frac{2}{3}$ from base; sacculus elongated slightly cone shaped. Vinculum length considerably longer than 0.5x total genital length. Phallus with small, sturdy cornuti and one, rarely two, large cornuti; number of small cornuti from 10 to 35.

Female terminalia. Ductus bursae anteriorly expanded; anterior adjacent to sclerotised part of ductus bursae a cluster of spines; posterior margins of ductus bursae ventrally infolded.

3.1.3.1. *Dioryctria abietella* (DENIS & SCHIFFERMÜLLER, 1775: 138) (Tinea)

Type locality: [Austria] Wienergegend

ZELLER 1846 b: 734 (*Dioryctria*)

= [*Tinea*] *decuriella* HÜBNER, 1796 e: pl. 11 fig. 74

type locality: Germany

ZELLER 1846 b: 734 (*Dioryctria*)

Material examined.

123♂♂, 308♀♀ no type material available.

Description. (plate III.3a)

Measurements. Forewing length ♂♂: 11.9–14.9mm (n=44); ♀♀: 11.9–15.2mm (n=72). Length of antennae: 8–11mm.

Head. Antennae filiform, in males slightly serrate with a moderately developed scaletuft covering four to five modified flagellomers. Labial palpus 3rd segment $\frac{1}{3}$ of length of 2nd segment.

Thorax. Forewing greyish with scattered black, whitish grey and rusty-red scales. Antemedial line most prominent towards dorsum, sometimes obsolete, distally contrasted by a thick black line; the area between antemedial and medial line filled with dull rusty-red scaling, which appears most prominent dorsally. Medial line contrasted distally by a black line approximately as wide as medial line. Discal stigma reniform, whitish, adjacent to a median shade. The area distal to median shade mottled whitish grey; an area of rusty-red scales between lower, proximal end of discal stigma and dorsum, variable in size and inconspicuous, but usually clearly visible under stereomicroscopic magnification. Postmedial line

distinctly dentate, stronger so in dorsal half, discharging into costa in an acute angle, contrasted by a brownish suffusion distally. A fine black terminal line usually interrupted by greyish white scaling. Cilia brownish grey, with inconspicuous cilia line. Hindwing light beige coloured. Cilia light grey, cilia line dark brown proximally contrasted by a cream-coloured fine line.

Male pregenital abdomen. Apex of medial plate of S VIII well produced.

Male terminalia. Apex of uncus broadly rounded, overall appearance eggshaped; lateral margin convex. Costa of valve longer than setiferous region of valve; preapical spine on costa close to apex; tip of apex broad and blunt. Phallus with one large cornutus of $\frac{1}{4}$ of length of phallus and a cluster of 20 to 35 smaller cornuti.

Female terminalia. Length of ductus bursae greater than 5x width; posterior medial lobe on ductus bursae present; ductus bursae curved, strongly sclerotised leaving a narrow membranous longitudinal stripe in the central third; colliculum restricted to posterior $\frac{2}{3}$ of ductus bursae; anterior cluster of spines not sitting on a specific sclerotisation; lateral anterior process of ductus bursae on the right.

Diagnosis.

D. abietella is very similar to *D. sylvestrella*. Externally, it differs mainly in the course of the postmedial line. In *D. abietella*, it discharges into costa at an acute angle and the line has a notably uneven appearance. The male genitalia differ predominantly and obviously in the shape of the valves (see plate III.1a & j).

D. mutata auct. can be discerned by the lack of the rusty red baso-dorsal patch adjacent to the medial line in the forewing and the difference of the tip of the valve in the male genitalia. The same is true for *D. resiniphila* that additionally differs in range of distribution, as it is confined to the eastern Mediterranean.

Distribution.

Europe (Karsholt & Razowski 1996) eastwards to Caucasia. Records from south-eastern European and Asian countries may refer to similar species and require confirmation.

Records of *D. abietella* from North America (e.g., Sinev 1986) are the result of misidentifications of nearctic species. *D. abietella* is neither native in, nor known to have been introduced to North America.

Remarks.

The type specimens of Denis and Schiffermüller became lost during a fire in Vienna in 1848 (Horn et al. 1990).

There is considerable variation of specimens in size and in the development of certain characters of the wing pattern. In particular, the amount of reddish and whitish scaling can be reduced, and the development and number of angles in the lines can be varied, especially regarding the exact course of the postmedial line. Small, greyish specimens can resemble *D. mutata* auct., while extreme forms even can externally closely resemble Mediterranean *D. resiniphila* (Segeer personal communication).

3.1.3.2. *Dioryctria aulloi* BARBEY, 1930: 69

Type locality: Spain: Malaga: Ronda

Material examined.

2♂♂, 2♀♀ including ♂ lectotype specimen and holotype genital slide.

Description. (plate III.3b)

Measurements. Forewing length ♂♂: 11.7-13.5mm (n=2); ♀♀: 13mm (n=1). Length of antennae: 10-11mm.

Head. Antennae filiform, in males serrate with a moderately developed scaletuft covering four modified flagellomers. Labial palpus 3rd segment $\frac{1}{4}$ of length of 2nd segment.

Thorax. Forewing rather uniformly dark grey. Antemedial line jagged, proximally and distally evenly contrasted by a thin black line. The area proximally of medial line mottled dark grey; proximally adjacent to medial line a thick black band-like suffusion reaching costa in full width; dorsally surrounding a light grey elongated blotch. Medial line jagged with two strong dentations pointing basally, of even width over entire length, discharging into dorsum pointing distally, contrasted distally by a narrow black line; a whitish grey blotch, variable in shape and size, attached distally between veins Cu and Ax₁; distally a black suffusion on a imagined diagonal line between distal discal stigma and dorsal end of medial line, reaching dorsum and sometimes dorsal end of medial line but not reaching medial line between veins Cu and Ax₁. Discal stigma reniform; entire area around discal stigma uniformly dark grey. Postmedial line with one distinct denture approximately at $\frac{1}{3}$ from costa, the line thus forming two angled arches, discharging into dorsum pointing distally, discharging into costa in an approximately 60° angle, contrasted black proximally and sometimes by a slightly lighter suffusion distally. A fine black terminal line usually interrupted by greyish white scaling. Cilia mottled grey, with inconspicuous cilia line. Hindwing light grey coloured, cilia mottled grey, cilia line dark brown proximally contrasted by a fine white line.

Male pregenital abdomen. Apex of medial plate of S VIII well produced.

Male terminalia. Apex of uncus mediocly rounded; overall appearance eggshaped; lateral

margin convex. Costa of valve longer than setiferous region of valve; preapical spine on costa close to apex; tip of apex narrowed and acute.

Female terminalia. Length of ductus bursae greater than 5x width, posterior medial lobe on ductus bursae present; ductus bursae straight, strongly sclerotised leaving a narrow less membranous longitudinal stripe in the central third. Colliculum restricted to posterior $\frac{2}{3}$ of ductus bursae; anterior cluster of spines not sitting on a specific sclerotisation; lateral anterior process of ductus bursae on the right.

Diagnosis.

D. aulloi belongs to the *simplicella*-species-complex, and is therefore morphologically very hard to set apart from both *D. mutarella* auct. and *D. resiniphila*. The only reliable outer character seems to be the morphology of the flagellomeres or the male antennae, as they are cylindrical in *D. mutarella* auct, serrate in *D. resiniphila*, and extensively serrate in *D. aulloi* (plate III.81). However, this character can only safely be assessed under comparatively high magnification. The restricted range of *D. aulloi* in southern Spain and the distribution of *D. resiniphila* in Greece might even be a diagnostic trait.

Distribution.

Europe: Spain, Andalusia.

Remarks.

D. aulloi was originally described from *Abies pinsapo* (Barbey 1930) and no further host plants have been recorded to date. The tree is "indigenous only in a limited and disjoint range in the Sierra de Ronda (Part of the Cordillera Penibetica)" (Earle 2006) in southern Spain. If *D. aulloi* is indeed linked to this host exclusively, it would be endemic to the area. Consequently, the statement of Mutuura (1971) that *D. aulloi* was found in Algeria requires confirmation, as the host plant species' range is not consistent with that record.

3.1.3.3. *Dioryctria mendacella* (STAUDINGER, 1859: 222-223) (*Nephoptyx* [sic])

Type locality: Spain: Chiclana

= *Euzophera maritanella* MILLIÈRE, 1875: 264, pl. 2: fig. 14

type locality: France: Cannes

Material examined.

47♂♂, 72♀♀ including holotype.

Description. (plate III.3c)

Measurements. Forewing length ♂♂: 11.5-15.5mm (n=46); ♀♀: 10.5-16mm (n=60). Length of antennae: 7-10mm.

Head. Antennae in males unipectinate, pectina gradually shorter towards base and midpoint of flagellum; scaletuft absent; at base of antenna four modified flagellomers; in females filiform. Labial palpus 3rd segment $\frac{1}{3}$ of length of 2nd segment.

Thorax. Forewing light grey with sporadically scattered black scales. Antemedial line cuneiform widening towards costa usually not reaching dorsum, distally contrasted by a thick black line widening towards dorsum; the area between antemedial and medial line light grey, proximally of medial line a bar like suffusion of black scales. Sometimes the area that displays rusty-red scaling in *D. abietella* is medium grey. Medial line more or less straight, discharging into dorsum pointing distally, widening towards costa, contrasted distally by a black line approximately half as wide as medial line. Distally disjoint from medial line between veins Cu and Ax₁ a dark rectangular suffusion situated at midpoint on an imagined diagonal line between discal stigma and dorsal end of medial line not reaching dorsum. Discal stigma reniform, with more or less obvious dark shades proximally and distally but not reaching the postmedial line. Postmedial line with one distinct denture at midpoint, the line thus forming two curved arches, discharging into costa in an almost 90° angle, contrasted black proximally and by a lighter suffusion distally. A fine black terminal line, usually uninterrupted or if then only sporadically interrupted by fine light grey lines. Cilia brownish grey, with inconspicuous cilia line. Hindwing cream coloured, cilia white, cilia line brown contrasted proximally by a fine cream-coloured line.

Male pregenital abdomen. Apex of medial plate of S VIII well produced.

Male terminalia. Apex of uncus broadly rounded; overall appearance eggshaped; lateral margin convex. Costa of valve longer than setiferous region of valve; preapical spine on costa close to apex and shifted inwardly from margin; tip of apex narrowed and acute.

Female terminalia. Length of ductus bursae approximately 7x width; posterior medial lobe on ductus bursae absent; ductus bursae straight, strongly sclerotised leaving a narrow less sclerotised longitudinal stripe in the central third; colliculum restricted mainly to posterior third of ductus bursae, laterally condensed; anterior cluster of spines not sitting on a specific sclerotisation; lateral anterior process of ductus bursae on the right; no posterior medial lobe on ductus bursae.

Diagnosis.

D. mendacella is readily recognized by its grey colouration, macroscopically lacking reddish scales. The predominant external traits that separate it from the species of the "*simplicella*-species-complex" are unipectinate antennae in males as well as the larger overall size of the specimens. The pectina are decidedly shorter than in *D. pineae* and *D. nivaliensis* and macroscopically reach only to about the midpoint of antennae. The transverse fasciae are broader, the postmedial line discharges into costa at nearly a 90° angle, rather than an acute angle; it is also less dentate. The male genital differs only slightly in the position of the preapical spine on valval costa, which is located further inward in relation to the costal margin.

Distribution.

The species occurs around the zoogeographical region of the Mediterranean where Mediterranean forests are found.

3.1.3.4. *Dioryctria nivaliensis* REBEL, 1892: 256-257, pl. XVII fig. 10

Type locality: [Spain: Canary Islands]: Tenerife

Material examined.

2♂♂, 12♀♀ including holotype.

Description. (plate III.3d)

Measurements. Forewing length ♂♂: 15-17mm (n=3); ♀♀: 13.5-17mm (n=13). Length of antennae: 9.5-11mm.

Head. Antennae in males unipectinate, pecten gradually shorter towards base and tip of flagellum; at base five modified flagellomers, scaletuft absent, in females filiform. Labial palpus 3rd segment $\frac{1}{3}$ of length of 2nd segment.

Thorax. Forewing dull reddish grey with scattered black, whitish grey and rusty-red scales. Antemedial line most prominent towards costa, sometimes blurred, distally contrasted by a thick black to rusty-red line; the area between antemedial and medial line filled with dull rusty-red scaling, which appears most prominent dorsally. Medial line contrasted distally by a black to rusty-red line approximately as wide as medial line. Discal stigma reniform, very light grey to white, adjacent to a median blackish reddish shade. The area distal to median shade mottled whitish-grey. Postmedial line distinctly dentate, stronger so in dorsal half, discharging into costa in an acute angle, contrasted black to rusty-red proximally and by a rusty-red to black suffusion distally. A fine black terminal line usually uninterrupted not always spanning the entire distance from dorsum to costa. Cilia brownish grey, with inconspicuous

cilia line. Hind wing light beige, cilia beige, cilia line dark brown proximally contrasted by a cream-coloured line.

Male pregenital abdomen. Apical process of medial plate on S VIII slender and elongated.

Male terminalia. Apex of uncus broadly rounded; overall appearance eggshaped; lateral margin convex. Costa of valve longer than setiferous region of valve; preapical spine on costa antero-dorsally disconnected from apex; tip of apex narrowed and acute.

Female terminalia. Length of ductus bursae greater than 7x width; posterior medial lobe on ductus bursae absent; ductus bursae straight; colliculum restricted mainly to posterior third of ductus bursae, anterior cluster of spines not sitting on a specific sclerotisation; laterally condensed; lateral anterior process of ductus bursae absent.

Diagnosis.

D. nivaliensis is larger than most *Dioryctria*. In Europe it can be distinguished from the three species, *D. abietella*, *D. schuetzeella*, and *D. sylvestrella*, which also display reddish scaling, by the following features: The distinctly darker wing coloration, the more widely spread dark reddish scaling, as well as the size and the male antennae, which are unipectinate versus serrate. The male genital is characteristic in apical valval morphology.

Distribution.

The species seems to be endemic to the Canary Island of Tenerife.

Remarks.

D. nivaliensis belongs to the *abietella*-group. The characters that justified the assignment of the species to the *abietella*-group are treated in detail in chapter 3.3.1.1.

3.1.3.5. *Dioryctria pineae* (STAUDINGER, 1859: 222) (*Nephopteryx* [sic])

Type locality: Spain: Chiclana

type: MNHU

Material examined.

33♂♂, 27♀♀ including holotype.

Description. (plate III.3e)

Measurements. Forewing length ♂♂: 14-17.5mm (n=29); ♀♀: 15-18.5mm (n=24). Length of antennae: 10-14mm.

Head. Antennae in males unipectinate, pecten gradually shorter towards base and tip of flagellum; with five modified flagellomers at base, scaletuft absent; in females filiform. Labial palpus 3rd segment 1/3 of length of 2nd segment. Labial palpus upturned.

Thorax. Forewing light to medium grey with sporadically scattered dark grey and rusty-red scales, the latter being obvious under magnification; light wing markings of notably low contrast with ground colour. Antemedial line blurred in quite a few specimens to the point of absence. Medial line broadens slightly towards costa, contrasted distally by a black line approximately half as wide as medial line; the area proximal of medial line light grey; proximally adjacent to medial line a thick brown band-like suffusion fading towards and barely reaching costa; dorsally sometimes encircling a light grey elongated blotch; distally removed from medial line between veins Cu and Ax₁ a dark rectangular suffusion consisting of a black and distally a rusty-red stripe situated at midpoint on an imagined diagonal line between distal discal stigma and dorsal end of medial line reaching dorsum varying in size and intensity, but clearly visible under magnification. Discal stigma reniform or rhombic, faintly contrasted proximally and distally by rusty-red or black scales. Postmedial line with one distinct denture at midpoint, the line thus forming two curved arches, discharging into costa in an angle of ~60°, contrasted by a medium dark, sometimes pale rusty-reddish suffusion distally; a fine black terminal line usually interrupted by greyish white scaling. Cilia mottled grey, with inconspicuous cilia line. Hindwing light grey coloured, cilia white, cilia line dark brown proximally contrasted by a fine white line.

Male pregenital abdomen. Process at central apex of medial plate on S VIII distinctly slender and elongated.

Male terminalia. Apex of uncus mediocly rounded, overall appearance eggshaped; lateral margin convex. Costa of valve longer than setiferous region of valve; preapical spine on costa antero-dorsally removed from apex; tip of apex broad and blunt. Phallus with one large cornutus of approximately 1/3 of phallus length and a cluster of ca. 35 smaller cornuti.

Female terminalia. Length of ductus bursae greater than 5x width; posterior medial lobe on ductus bursae absent; ductus bursae straight, strongly sclerotised leaving a narrow less sclerotised longitudinal stripe in central third; colliculum restricted mainly to posterior third of ductus bursae, laterally condensed; anterior cluster of spines not sitting on a specific sclerotisation; lateral anterior process of ductus bursae on the right.

Diagnosis.

The process at apex of medial plate is distinctly elongated in *D. pineae*. The specimens are rather large, comparable only to *D. nivaliensis* in Europe, which also possess unipectinate male antennae and an elongated apical process on S VIII. However, misidentification is unlikely due to the light colouration and conspicuously blurred forewing pattern in many *D. pineae*

specimens. The larger size and longer pectination of male antennae, along with different forewing patterns, make a distinction from *D. mendacella* easily possible by outer characters. In male genitalia, the tip of the valval costa is broadly rounded in *D. pineae*, unlike in the other two species with unipectinate male antennae, *D. nivaliensis* and *D. mendacella*.

Distribution.

The species is known from southern Europe.

3.1.3.6. *Dioryctria resiniphila* SEGERER & PRÖSE, 1997: 58, fig. 1-3

Type locality: Greece, Kefalliniá, Mt. Ainos Oros, 1200 m

Material examined.

37♂♂, 62♀♀ including holotype.

Description. (plate III.3f)

Measurements. Forewing length ♂♂: 12.5-14.5mm (n=17); ♀♀ 11.5-15mm (n=21). Length of antennae: 7-10mm.

Head. Antennae filiform, in males serrate with a moderately developed scaletuft covering four to five modified flagellomers. Labial palpus 3rd segment 1/3 of length of 2nd segment.

Thorax. Forewing greyish with scattered black scales, singular whitish grey, rusty-red and yellow scales can be found under magnification in some specimens. Antemedial line jagged, proximally and distally evenly contrasted by a thin black line. Medial line jagged with two strong dentations pointing basally, of even width over entire length, discharging into dorsum pointing distally, contrasted distally by a narrow black line; proximally adjacent to medial line a thick black band-like suffusion reaching costa in full width; dorsally surrounding a light grey elongated blotch; a whitish-grey blotch, variable in shape and size, attached distally between veins Cu and Ax₁; distally removed from medial line between veins Cu and Ax₁ a dark rectangular suffusion consisting of black and dispersed rusty-red scales situated at midpoint on a imagined diagonal line between distal discal stigma and dorsal end of medial line, reaching dorsum. Discal stigma reniform; contrasted proximally and distally by black scales; no significant dark suffusion connecting discal stigma and postmedial line. Postmedial line with one distinct denture at midpoint, the line thus forming two angled arches, discharging into costa in an approximately 60° angle, a second smaller kink close to dorsum, contrasted black proximally and by a lighter sometimes rusty-reddish suffusion distally; a fine black terminal usually uninterrupted line. Cilia mottled grey, with inconspicuous cilia line. Hindwing light grey coloured, cilia white, cilia line dark brown proximally contrasted by a white line.

Male pregenital abdomen. Apex of medial plate of S VIII well produced.

Male terminalia. Apex of uncus mediocly rounded; overall appearance eggshaped; lateral margin convex. Costa of valve longer than setiferous region of valve; preapical spine on costa close to apex; tip of apex narrowed and acute.

Female terminalia. Length of ductus bursae greater than 6x width; posterior medial lobe on ductus bursae present; ductus bursae curved, strongly sclerotised leaving a narrow less sclerotised longitudinal stripe in the central third; colliculum restricted to posterior $\frac{2}{3}$ of ductus bursae; anterior cluster of spines not sitting on a specific sclerotisation; lateral anterior process of ductus bursae on the right.

Diagnosis.

Along with *D. simplicella* auct. and *D. aulloi*, *D. resiniphila* belongs to the *simplicella*-species-complex. The external character that differs in these three species is the morphology of the male antennal flagellomers, visible under 40X magnification, being cylindrical in *D. simplicella* auct. and stronger serrate in *D. aulloi*. In some specimens, if well preserved, a slightly yellowish to reddish tint can occur at the grey blotch situated baso-dorsally at the medial line.

Distribution.

The species is known only from Greece; therefore, the distribution might also be a diagnostic trait.

3.1.3.7. *Dioryctria simplicella* HEINEMANN, 1865: 148–149

Type locality: ‘Gegend von Frankfurt a. M.’

Roesler (sp.)

= *Dior.[yctria] abietella* var. *mutatella* FUCHS, 1903: 233

Type locality: Germany: Brandenburg

Dior.[yctria] abietella var. *mutatella* FUCHS, 1903: 233, **syn. rev.** Type locality: Germany: Brandenburg.

Material examined.

109♂♂, 160♀♀ greyish form (*D. mutatella* auct.) no type material available.

7♂♂, 29♀♀ blackish form (*D. simplicella* auct.) no type material available.

Description. (plate III.4) Greyish form (*D. mutatella* auct.) and blackish form (*D. simplicella* auct.):

Measurements. Forewing length ♂♂: 10-14.5mm (n=52); ♀♀: 8.5-13mm (n=184). Length of antennae: 9.5mm.

Head. Antennae filiform in both genders, flagellomers in males cylindrical with a moderately developed scaletuft. Labial palpus 3rd segment $\frac{1}{3}$ of length of 2nd segment.

Male pregenital abdomen. Apex of medial plate of S VIII well produced.

Male terminalia. Apex of uncus broadly rounded, overall appearance eggshaped; lateral margin convex. Costa of valve longer than setiferous region of valve; preapical spine on costa close to apex; tip of apex narrowed and acute.

Female terminalia. Length of ductus bursae greater than 6.5x width; posterior medial lobe on ductus bursae present; ductus bursae straight, strongly sclerotised leaving a narrow less sclerotised longitudinal stripe in the central third; colliculum restricted to posterior $\frac{2}{3}$ of ductus bursae. The strongly sclerotised ridges forming the columella bear a number of prominent inward protruding spines. Although variable in number and intensity they are always present, anterior cluster of spines not sitting on a specific sclerotisation; lateral anterior process of ductus bursae on the right.

Description. (plate III.4f) Greyish form (*D. mutarella* auct.):

Measurements. Forewing length ♂♂: 10–14.5mm (n=45); ♀♀: 8.5–13mm (n=156).

Thorax. Forewing grey, mottled with black and whitish grey scales, singular rusty-red and yellow scales can be found under magnification in some specimens. Antemedial line jagged, proximally and distally contrasted by a dark suffusion and a thin black line respectively. Medial line contrasted distally by a black line as wide as medial line; proximally adjacent to medial line a thick black mottled grey band-like suffusion reaching costa in full width; dorsally encircling a light grey blotch; all these patterns more or less blurred; medial line of even width over entire length, the part costal wards of first kink not uniform light grey but mottled black to different extents; distally removed from medial line between veins Cu and Ax₁ a dark suffusion consisting of black scales connecting in a diagonal line distal discal stigma and dorsal end of medial line, reaching dorsum. Distal discal stigma reniform, greyish; contrasted proximally and distally by black scales. Postmedial line jagged, with one distinct denture at midpoint, the line thus forming one angled arch costal-wards and a slightly dentate arch towards dorsum, discharging into costa in an angle of ~60° angle or more, contrasted by a mottled grey slightly darkened suffusion distally. A fine black terminal line usually unevenly interrupted by greyish white scaling. Cilia mottled grey, with inconspicuous cilia line. Hindwing light grey coloured, cilia white, cilia line dark grey proximally contrasted by a white line.

Description. (plate III.4a) Blackish form (*D. simplicella* auct.):

Measurements. Forewing length ♂♂: 10–12.5mm (n=7); ♀♀: 9–12mm (n=28).

Thorax. Forewing predominantly black, at dorso-proximal position relative to medial line where a large brown patch is situated in some species (e.g. *D. abietella*, *D. sylvestrella*) in most specimens a light patch, sometimes however even there completely darkened. Postmedial line and distal discal stigma hardly visible, if there, slightly lighter than wing colouration. Fringe light beige; terminal line black. Intermediate stages between this darkened form and the common greyish as well as the rare black forms are illustrated in plate III.4.

Diagnosis.

Both in collections and in the field the grey form is notably more frequently represented than the black form or even its intermediates. The black form is easily recognized due to the obvious differences in forewing colouration. If identification seems uncertain, genitalia investigation should clear all doubts. Since the distribution of the grey form is more widespread than the other two species of the "*simplicella*-species-complex" throughout Europe, geographical and ecological information require consideration for identification. The only external character that seems diagnostic is the cylindrical shape of the male antennal flagellomeres, however, only detectable through magnification.

Distribution.

Own attempts to obtain black *D. simplicella* auct. specimens both in the field and from collections first seemed to confirm Hassler & Speidel (1986), who reported it as known only from Germany (see appendix 6). However, thorough literature research suggests a broader range of these animals. Parsons and Clancy (2002) show images of one female from Windsor Forest, Berkshire [21.vii.1995, leg. B. Skinner], and one female from Blackheath, Surrey [20.vii.1987, leg. B. Skinner], plus one specimen from Kent, Orlestone [23.vii.1993, leg. S.P. Clancy].

Wieser et. al. (2004) report specimens from Carinthia (Kärnten), Bezirk Völkermarkt, Griffner Schoßberg 46°42'N 14°43'E, 484-616m. Palm (1986) lists black *D. simplicella* auct. as common in Europe, certainly from Belgium, Netherlands, Great Britain, Germany, Lithuanian, Latvia (common, widespread), Finland (even in the north), Sweden, Norway (common), Denmark in the Dunes of Jylland's west coast, and at Sjælland's north coast (common in some places numerous); in the rest of the country they are, however, rather rare. Karsholt & Ratzowski (1996) neglected to specify the morphotype, yet they list the species from all over Europe: Austria, Belgium, Denmark, Czech Republic, Eastern Europe, England, Estonia, Finland, France, Germany, Hungary, Latvia, Lithuania, Luxembourg, Netherlands, Norway, Romania, Slovakia, Sweden, and Switzerland.

Remarks.

The type of *D. simplicella* from the "Frankfurter Gegend" is believed to be lost (Heuser et al. 1971, Hassler & Speidel 1986). Adults have been caught in open habitats with sandy dunes. In literature it is assumed that the larvae feed inside green cones, annual twigs, and buds of *Pinus sylvestris*, as well as in annual twigs and buds of *Picea glauca* (Hassler & Speidel 1986, Petersen & Gaedike 1980).

The type of *D. mutarella* was lost along with the collection of Fuchs (Horn et al. 1990).

3.1.3.8. *Dioryctria SK1* sp. nov. - a new Species from La Palma – plate III.5

Type locality: [Spain: Canary Islands:] La Palma, 800m, Umg. Los Canarios, 07.-08.04.1973

Material examined.

1♂ **Holotype**, Spain, La Palma, 800m, Umg. Los Canarios, 07.-08.04.1973

1♀ **Paratype**, Spain, La Palma, 800m, Umg. El Paso, 03.-08.04.1973

Description. (plate III.5a & f)

Measurements. Forewing length ♂: 16.4mm (n=1); ♀: 17.5mm (n=1). Length of antennae: 11mm.

Head. Frons mottled light grey. Antennae in females filiform in males unipectinate with an only weakly developed basal kink, scaletuft absent. Labial palpus light grey with scattered dark grey scales, upturned, 3rd segment fusiform $\frac{1}{3}$ of length of 2nd segment.

Thorax. Forewing dark brownish grey, the male quite blurred, the female with clearer pattern; under stereomicroscopic magnification with scattered black, pale orange and fewer whitish grey scales. All transverse lines not displaying white or light grey scales exclusively, but sprinkled with pale orange and some dark grey scales. Antemedial line white, rather narrow not exceeding midpoint of width of forewing, quite blurred in the male specimen, distally adjacent to an area of blackish grey scales; the area between antemedial and medial line displays a white blotch centrally, and only faint indications of accumulations of pale orange scales. Medial line not clearly defined, composed of white and some pale orange scales, hardly reaching dorsum, most prominent and wide at costa, distally contrasted by a black to rusty-red scaling most clearly so between medial line costa and distal discal stigma, blurring towards dorsum. Discal stigma rectangular to almost rhombic, very light grey to white; the rest of the area between medial and postmedial lines mottled whitish-grey dusted with few pale orange scales. Dentation of postmedial line reminiscent of that of *D. sylvestrella*, with the dorsal

half only slightly curved proximally discharging into dorsum at nearly a 90° angle, at $\frac{2}{3}$ a sudden inward kink followed by an distal-ward kink, line then discharging into costa at an acute angle of approximately 45°; the fascia contrasted black with some pale orange scales only visible under magnification proximally and distally, with the distally shade threefold the width of the proximal one and fading distally through accumulation of light grey scales. The terminal line almost entirely faded in the male specimen, in the female specimen distinct and practically uninterrupted. Cilia brownish grey, with dark grey ciliar line. Hindwing quite heavily dusted with dark grey scales, distally more intensely so than proximally; cilia brownish grey; ciliar line dark brown, proximally contrasted by a cream-coloured fine line. A postmedial line faintly visible on underside of hindwing in the female.

Male pregenital abdomen. Apex of medial plate of S VIII distinctly elongated.

Male terminalia. Apex of uncus broadly rounded, appears cut off; overall appearance eggshaped; lateral margin convex. Costa of valve longer than setiferous region of valve; margins in medial third almost parallel; ventrally proximal of junction of setiferous part of valve with costa a strong kink; apical region of costa dorsally with a bulge proximal of narrowed and acute tip of apex, distal costal region with two indentions separated by the large, acute, anterior-dorsally shifted preapical spine. Phallus with one large cornutus and a cluster of 21 smaller cornuti.

Female terminalia. Length of ductus bursae 4.4x width; posterior medial lobe on ductus bursae absent; ductus bursae straight, colliculum restricted mainly to posterior third of ductus bursae, laterally condensed; lateral anterior process of ductus bursae missing; longitudinal membranous area of ductus bursae absent. The anteriorly of sclerotised part of ductus bursae situated cluster of spines associated with a sclerotised latero-ventral plate on the right. Girdle forming signum very well developed with a second row on the left.

Diagnosis.

The new species, *D. SKI*, is one of the few species of the genus that display unipectinate antennae. In Europe, there are only *D. mendacella*, *D. pineae*, and *D. nivaliensis*. *D. mendacella* is distinctly smaller and the male genital characters differ in the shape of the apical region of the valves. *D. pineae* is unique in the male genital shape of the costal apex, as the costal margins clearly diverging distad and the costal apical spine is missing. The margins of costa of valve in this new species are nearly parallel.

D. nivaliensis, externally the closest match, differs mainly in the shape of the distal region of costa. While in *D. nivaliensis*, the terminal margin forms a straight line from junction with the

dorsal margin to the costal apex, in the new species this area differs considerably: the region below the costal apex is indented twice: first, from the costal apex to the preapical spine; and second, from the preapical spine to the posterior end of the dorsal margin. The female genitalia are unique in the presence of a sclerotised plate anterior of ductus bursae.

Distribution.

So far, the species is only known from the Canary Island of La Palma.

Remark.

This new species belongs to the *abietella*-group. This placement is established in detail in chapter 3.3.1.4.

The species was not included in tree calculations, since it failed to yield suitable DNA due to the age of the set specimens. The wing pattern was described using the female paratype, as the male specimen is faded and worn to an extent that obscures the wing pattern.

The host plant is unknown, but it is likely to be *Pinus canariensis*, since it is native to the Canary Islands and abundant on La Palma island (Mirov 1967). This new species will be validly published in an appropriate journal later.

3.1.4. Description *schuetzeella*-group:

Thorax. Forewing proximal of postmedial line a dark contrasting line at Cu₂ interrupted and following Cu₂ in proximal direction for approximately 1-1.5mm then fading.

Male terminalia. Apex of uncus narrowly rounded, hairpin-like, general shape elongated triangular; lateral margin linear or slightly convex. Terminal area of costa of valve smooth; displaying a blunt preapical spine on costa; costal apex straightly elongated; dorsal and ventral costal margins parallel. Vinculum length 0.5x or slightly longer than 0.5x total genital length. Phallus with small cornuti intermediate in diameter but lacking large cornuti; number of small cornuti between 45 and 65.

Female terminalia. Ductus bursae almost parallel to anteriorly slightly expanded; posterior medial lobe on ductus bursae absent; on the anterior left of ductus bursae a lateral process. Anteriorly adjacent to ductus bursae no conspicuous structure.

3.1.4.1. *Dioryctria schuetzeella* FUCHS, 1899: 180-183

Type locality: Deutschland [Germany], Rachlau

Material examined.

29♂♂, 17♀♀ no type material available.

Description. (plate III.3h)

Measurements. Forewing length ♂♂: 10-11.5mm (n=14); ♀♀: 9.5-12mm (n=9). Length of antennae: 6-8 mm.

Head. Antennae filiform, in males smooth with a moderately developed scaletuft covering 5 modified flagellomers. Labial palpus 3rd segment $\frac{1}{3}$ of length of 2nd segment.

Thorax. Forewing strongly mottled grey with scattered black, whitish grey and very few pale orange scales; wing pattern in general of notably high contrast, all transverse lines and discal stigma white. Antemedial line blurred, sometimes obsolete, distally contrasted by a thick black line; the area between antemedial and medial line filled with black and pale orange scaling, which dominates dorsally. Medial line contrasted distally by a black line at least as wide as medial line; the whitish-grey blotch, between veins Cu and Ax1 missing in most specimens. Discal stigma reniform, a conspicuous dark suffusion connecting discal stigma and postmedial line; an area of pale orange scales between lower, proximal end of discal stigma and dorsum, variable in size and sometimes inconspicuous, but usually clearly visible under magnification. Postmedial line strongly dentate, especially in dorsal half, discharging into costa in an angle of $\sim 45^\circ$, contrasted by a brownish suffusion distally; a fine black terminal line usually interrupted by greyish white scaling. Cilia mottled brown and grey, with inconspicuous cilia line. Hindwing rather evenly grey coloured, the inconspicuous postmedial line forming a faint characteristic light spot of the size of discal stigma at middle in the majority of specimens. Cilia white, ciliar line beige contrasted by a fine, cream-coloured line.

Male pregenital abdomen. Apex of medial plate on S VIII elongated, not shouldered.

Male terminalia. Apex of uncus narrowly rounded, hairpin-like, general shape elongated triangular; lateral margin linear or slightly convex. Costa of valve longer than setiferous region of valve; preapical spine on costa anterio-dorsally removed from apex; tip of apex narrowed and acute; sacculus ampulla shaped; with a curved sclerotised ridge running anterio-caudally.

Female terminalia. Length of ductus bursae approximately 6x width; posterior medial lobe on ductus bursae present; medial partly transverse wrinkles in posterior part of ductus bursae; ductus bursae straight, colliculum extensively longitudinally wrinkled throughout entire length of ductus bursae.

Diagnosis.

Among *D. schuetzeella*, the termen of the forewing meets the costa at a more acute angle than in other European species. Its distinction from *D. abietella* and *D. sylvestrella* is easily possible due

to its smaller size and due to an overall higher contrast in the forewing pattern, yet the rusty-red mark situated dorso-basally to the medial line is usually paler.

Distribution.

D. schuetzeella is found throughout Europe in temperate climates.

Remarks.

D. schuetzeella is the only European species known to feed externally on the foliage of *Picea* and *Abies* species.

3.1.5. Description *sylvestrella*-group:

Male pregenital abdomen. Apex of medial plate of S VIII bears a short process shouldered by a groove.

Male terminalia. Apex of uncus cut off or slightly concave, all-over appearance rectangular with corners rounded. Ridges in terminal area of costa of valve; no preapical spine on costa; costal apex hooked elongated; dorsal and ventral costal margins not parallel, diverging distally; sacculus ampulla shaped. Vinculum length considerably longer than 0.5x total genital length. Phallus with small, thin cornuti but lacking large cornuti; number of small cornuti exceeding 60.

Female terminalia. Length of ductus bursae greater than 5x width; posterior medial lobe on ductus bursae present; no lateral anterior process of ductus bursae; anteriorly adjacent to ductus bursae no conspicuous structure.

3.1.5.1. *Dioryctria sylvestrella* (RATZEBURG, 1840: 242, pl. XV fig. 1) (*Ph.[alaena]* *T.[inea]* (*Phycis*))

= *Nephoteryx* [sic] *splendidella* HERRICH-SCHÄFFER, 1848 (vol. 4): 79 (line 24); 1847 (vol. 5): pl. 7 fig. 43

Type locality: [Germany, central Bavaria:] Regensburg

Ragonot 1885 a: 52 (syn.)

Material examined.

58♂♂, 43♀♀ no type material available.

Description. (plate III.3i)

Measurements. Forewing length ♂♂: 12-15.5mm (n=24); ♀♀: 13-16mm (n=12). Length of antennae: 8-11mm.

Head. Antennae filiform, in males serrate, with a moderately developed scaletuft covering 4

modified flagellomers. The most distad of the row of spines rather long. Labial palpus 3rd segment $\frac{1}{3}$ of length of 2nd segment.

Thorax. Forewing greyish with scattered black, whitish grey and rusty-red scales. Antemedial line most prominent towards dorsum, not reaching costa, distally contrasted by a black line not as wide as antemedial line; the dorsal half between antemedial and medial line conspicuously filled with bright rusty-red scaling. Medial line contrasted distally by a black line approximately as wide as medial line; the whitish grey blotch, between veins Cu and Ax₁, sometimes displacing the contrasting black line or even touching medial line. Discal stigma reniform, a black suffusion on an imagined diagonal line between discal stigma and dorsal end of medial line, reaching dorsum and sometimes dorsal end of medial line; discal stigma whitish, slightly darker contrasted. Postmedial line with one distinct denture at midpoint, the line thus forming two angled arches, discharging into costa in an angle of $>60^\circ$, contrasted by a black to mottled brownish suffusion distally. A fine black terminal line usually interrupted by greyish white scaling. Cilia brownish grey, with inconspicuous cilia line. Hindwing light beige coloured. Cilia light grey, cilia line dark brown proximally contrasted by a cream-coloured line.

Male terminalia. Apex of uncus cut off or slightly concave all over appearance rectangular with corners rounded, lateral margin convex; costa of valve as long as setiferous region of valve, with terminal ridges; apex tip narrowed and acute.

Female terminalia. Length of ductus bursae greater than 5x width; posterior medial lobe on ductus bursae present; ductus bursae straight, colliculum extensively longitudinally wrinkled throughout entire length of ductus bursae; ductus bursae anteriorly expanded. Posterior a medial lobe on ductus bursae.

Diagnosis.

Despite the similarity to *D. abietella*, *D. sylvestrella* differs externally in some aspects of the postmedial line. Mainly, the course of the postmedial line, which discharges into costa at a blunt angle and has smooth outlines. In contrast, the postmedial line in *D. abietella* discharges into the costa at an acute angle and the line has a more frazzled appearance. The male genitalia differ predominantly and obviously in the shape of the valves (see plate III.1a & j).

3.1.6. Description *taiella*-group:

Head. Male antennae with a strongly developed scale tuft.

Thorax. Colour light grey to beige. Forewings general coloration rather uniformly light

ash grey, with few black scales widely scattered more densely so toward costa; lack the pattern typical in *Dioryctria*. Antemedial line missing; at costa in the area where in other *Dioryctria* forewings the antemedial line is situated, a dark brown streak discharging into costa in an acute angle, ending medio-distally at about midpoint of a faintly visible slightly lighter than ground colour medial line. Medial line sometimes vanished. Discal stigma missing. Postmedial line fine, black, extremely dentate discharging into costa at an acute angle, running from costa near apex baso-medially to where M_1 meets discal cell very faintly visible following M_2 distal-ward, buckling basal-ward again to Cu_2 , following that vein fading quickly not reaching the dorsum. A fine black terminal line interrupted by light ash grey scaling. Cilia light grey, with inconspicuous cilia line.

Male terminalia. Apex of uncus mediocly rounded; general shape elongated triangular; lateral margin linear or slightly convex; costa of valve longer than setiferous region of valve; no preapical spine on costa; Terminal area of costa of valve smooth. Apex tip narrowed and acute; sacculus ampulla shaped. Phallus with one big cornutus and from 20 to 35 small cornuti.

Female terminalia. Ovipositor bigger than in other *Dioryctria*. Papillae anales apically and laterally broadly rounded. S VIII rather short, nearly as wide as long. Ductus bursae with a sclerotised posterior medial lobe; laterally margins of ductus bursae conspicuously swollen. Longitudinal membranous area of ductus bursae missing; adjacent to anterior end of ductus bursae a cluster of spines.

3.1.6.1. *Dioryctria robiniella* (MILLIÈRE, 1865: 87, 99, pl. 61 fig. 8-11) (*Myelois*)

Speidel & Asselbergs 2000: 144 (*Dioryctria*)

= *Dioryctriodes daelei* MUTUURA & MUNROE, 1974: 939, fig. 1, 2

Type locality: Italy: Alpi Maritimi: Diano-Castello

Speidel & Asselbergs 2000: 144 (syn.)

Material examined.

1♂, 1♀ no type material available.

Description. (plate III.3g)

Measurements. Forewing length ♂: 12mm (n=1); ♀: 10.6mm (n=1). Length of antennae: 6.3-6.5mm.

Head. Antennae filiform, in males slightly serrate with a strongly developed scaletuft covering 3 modified flagellomers. Labial palpus porrect, 3rd segment more than 0.5x length

of 2nd segment.

Thorax. Forewing in distal area of discal cell a black spindle-shaped streak.

Male pregenital abdomen. Process at central apex medial plate of S VIII missing, instead a slight indentation.

Male terminalia. Dorsal and ventral costal margins not parallel, diverging distally. Costal apex hooked elongated. Vinculum length approximately 0.5 x total genital length.

Female terminalia. Length of ductus bursae 3.8x width; ductus bursae slightly curved, strongly sclerotised; colliculum restricted to posterior $\frac{2}{3}$ of ductus bursae.

Diagnosis.

D. robiniella is very different from all other European species in all aspects specified in the description of the *taiella*-group above. Worldwide, it is possibly confused only with *D. taiella* from Afghanistan. However, it is readily discernable from that species externally by the black spindle-shaped streak in the forewing found in the distal area of the discal cell that is absent in *D. taiella*.

Distribution.

D. robiniella occurs in the Mediterranean, and is known from Spain, France, Italy, Croatia, Morocco, and Algeria (Speidel & Asselbergs 2000).

Remarks.

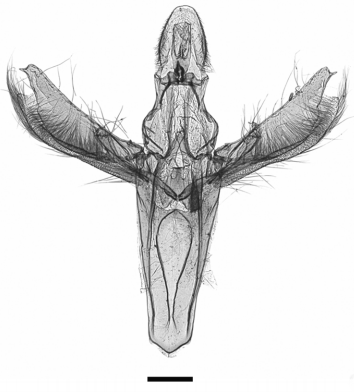
Life history. The larvae feed on *Cupressus sempervivens* (Siépi 1909, Speidel & Asselbergs 2000).

Plate III.1: Male Genitalia

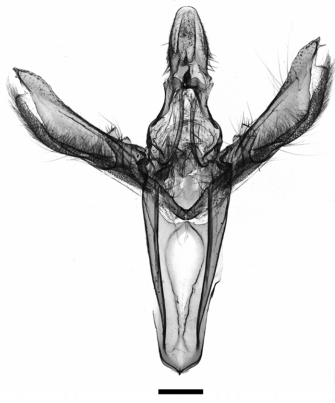
scalebars = 500µm

- a** = *D. abietella*
- b** = *D. aulloi*
- c** = *D. mendacella* **holotype**
- d** = *D. nivaliensis*
- e** = *D. pineae*
- f** = *D. resiniphila*
- g** = *D. robiniella*
- h** = *D. schuetzeella*
- i** = *D. simplicella* auct.
- j** = *D. sylvestrella*

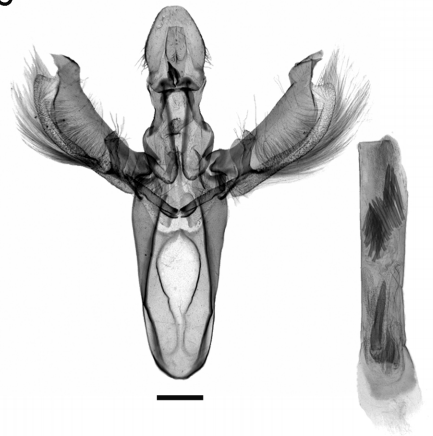
a



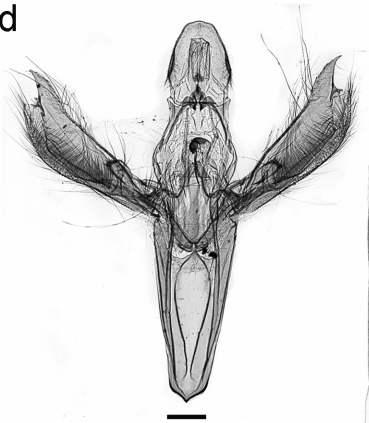
b



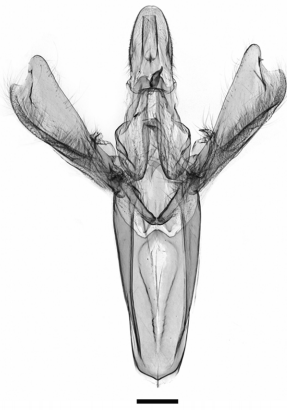
c



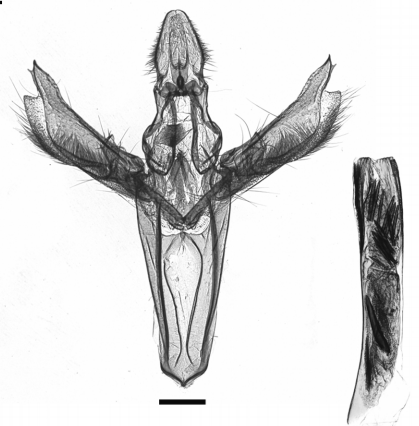
d



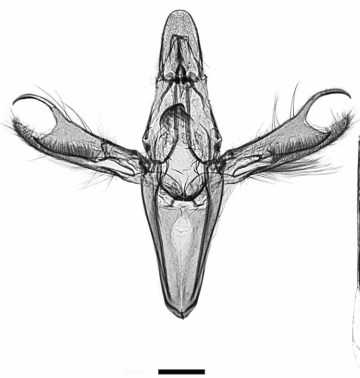
e



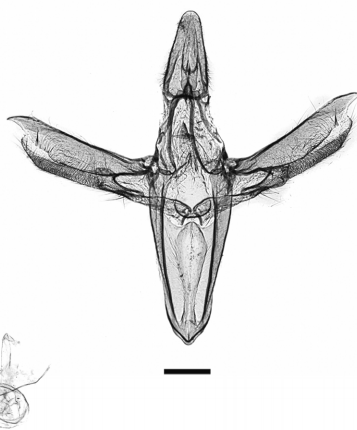
f



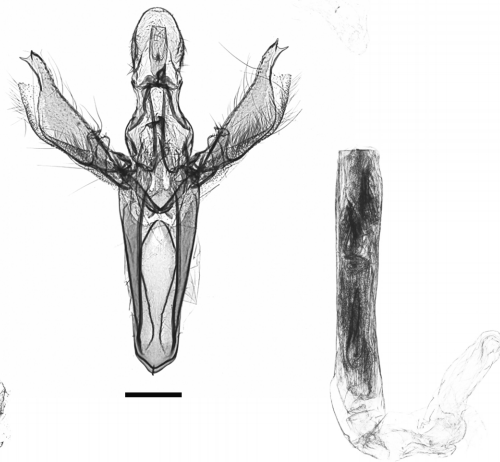
g



h



i



j

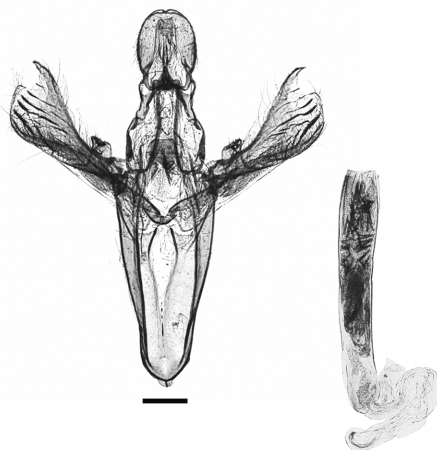


Plate III.2: Female Genitalia

scalebars = 500µm

- a** = *D. abietella*
- b** = *D. aulloi*
- c** = *D. mendacella*
- d** = *D. nivaliensis* **holotype**
- e** = *D. pineae*
- f** = *D. resiniphila*
- g** = *D. robiniella*
- h** = *D. schuetzeella*
- i** = *D. simplicella* auct.
- j** = *D. sylvestrella*

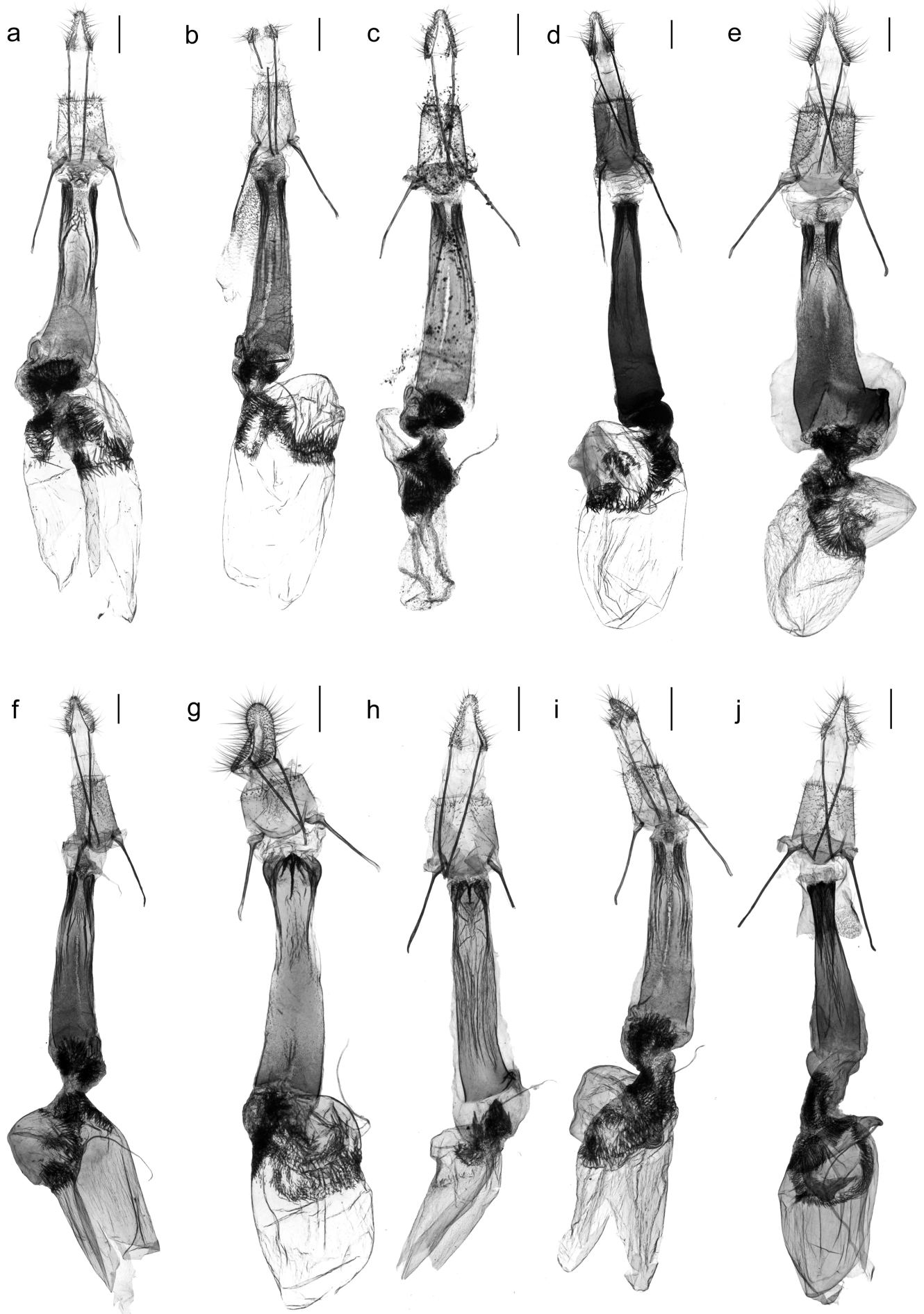


Plate III.2

Plate III.3: Specimens

scalebars = 1cm

- a** = *D. abietella* ♂
- b** = *D. aulloi* ♂ lectotype
- c** = *D. mendacella* ♀
- d** = *D. nivaliensis* ♀
- e** = *D. pineae* ♂
- f** = *D. resiniphila* ♂
- g** = *D. robiniella* ♂
- h** = *D. schuetzeella* ♀
- i** = *D. sylvestrella* ♂



a



b



c



d



e



f



g



h



i

Plate III.4: *Dioryctria simplicella* Specimens

scalebars = 1cm

a = *D. simplicella* auct.

b = *D. simplicella* intermediate

c = *D. simplicella* intermediate

d = *D. simplicella* intermediate

e = *D. simplicella* intermediate

f = *D. mutarella* auct.



a



b



c



d



e



f

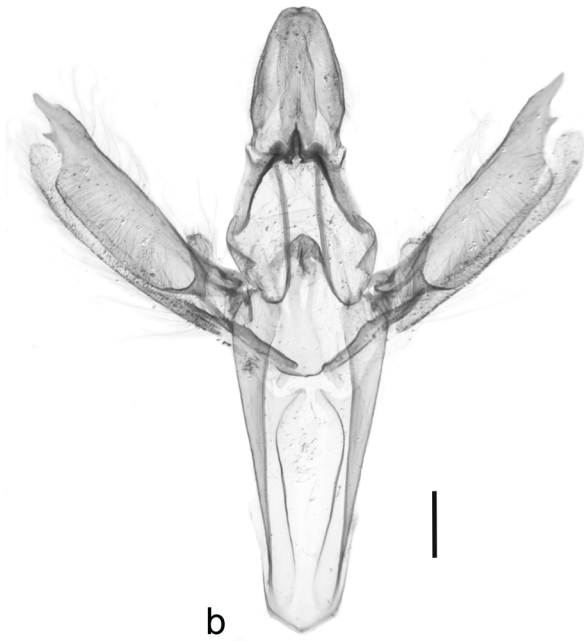


Plate III.4

Plate III.5: *Dioryctria SK1 sp. nov.*

scalebars = 500 μ m on genitalia
1cm on specimens

- a** = male type specimen
- b** = male genital
- c** = phallus
- d** = S VIII
- e** = female genital
- f** = female type specimen



3.2 Key to the European *Dioryctria* Species

Despite the existence of keys to selected species by Zocchi (1961) and Petersen & Gaedike (1980), no key including all European *Dioryctria* species was assembled to date. As mentioned before, safe identification remains a problem to this day, so the key given here is intended to provide essential characters that allow for the accurate discrimination between the European species. A detailed description of each species is given in chapter III.1.

Note that grey colouration yellows in collections over time so that light grey in a freshly caught specimen, for example, will change to light beige. Additionally, the wing pattern can be more or less blurred in male specimens.

- | | | |
|---|---|------------------------|
| 1 | Forewings display pattern characteristic for the genus | 3 |
| — | Forewings lack pattern characteristic for the genus | 2 |
| 2 | Forewings black or conspicuously darkened, thus wing pattern partly or entirely obscured; forewing length 8.5-14.5mm | <i>D. simplicella</i> |
| — | Forewing ground colour uniformly light grey; in central distal area of discal cell a black spindle-shaped proximo-distally oriented streak, discal stigma macroscopically not visible; maxillary palps porrect | <i>D. robiniella</i> |
| 3 | Forewings dorsal half between antemedial and medial line filled with rusty-red scales, forming a patch | 4 |
| — | The same area without a rusty-red patch | 8 |
| 4 | Discal stigma connected to postmedial line by a conspicuous dark suffusion; the proximal dark contrasting line of postmedial line interrupted at Cu ₂ following that vein proximally for 1-1.5mm | <i>D. schuetzeella</i> |
| — | Discal stigma not connected to postmedial line | 5 |
| 5 | Postmedial line discharging into costa at 60° angle or less | 6 |
| — | Postmedial line discharging into costa at an approximately 90° angle; postmedial line with two dentations | <i>D. sylvestrella</i> |

- 6 **Postmedial line** discharging into costa at an angle of up to 45°; **male antennae** filiform, flagellomers lamellate *D. abietella*
- **Postmedial line** discharging into costa at an angle of approximately 60°; **male antennae** unipectinate 7
- 7 **Forewing length** 13.5-17mm; termen of **valve** appears cut off; **distribution:** exclusively known from Tenerife, Canary Islands, Spain *D. nivaliensis*
- **Forewing length** 16.4-17.5mm; termen of **valve** twice curved inwards; a **sclerotised plate** associated with cluster of spines adjacent anteriorly to ductus bursae; **distribution:** type locality La Palma, Canary Islands, Spain ... *D. SKI sp. nov.*
- 8 **Postmedial line** discharging into costa at an approximately 90° angle; postmedial line with two dentations; **forewing** ground colour uniformly medium grey; **male antennae** unipectinate *D. mendacella*
- **Postmedial line** discharging into costa at an angle of approximately 60°; **male antennae** filiform 9
- 9 **Forewing** ground colour rather uniformly light grey; pattern more or less blurred; wing length 14-18.5mm; **male antennae** unipectinate; in **male genital** apex of valve rounded *D. pineae*
- **Forewing** ground colour rather medium grey, pattern clear with high contrast; **male antennae** filiform, flagellomers serrate 10
- 10 Serration of male **flagellomers** distinct; **distribution:** eastern Mediterranean, confirmed from Greek mainland and isles *D. resiniphila*
- Male **flagellomers** prominently serrate; **distribution:** likely to be endemic to southern Spain *D. aulloi*
- Male **flagellomers** cylindrical; **distribution:** all over Europe *D. simplicella*

3.3. New Assignments to Species-Groups

Of the 79 validly described *Dioryctria* species to date, seven have not been assigned to any species group. Two species should be excluded from the total count. These are *D. mutata* auct., since it is a synonym of *D. simplicella* auct. as a result of this study, and *D. symphoniella*. During compilation of the species of the genus *Dioryctria* and the study of the original descriptions, attention was drawn to *D. symphoniella* by a peculiar statement in the original description. It seems doubtful that the species should belong into the genus, because Hampson (1899) claims the specimen to possess two black spots at the position of the discal stigma, a trait not found in any *Dioryctria*. Genitalia investigation of the type specimen will be required to newly place the species.

The two species *D. okui* and *D. juniperella* were placed in a new species group, the *okui*-group, as treated in detail in chapter 3.3.2. The new species *D. SK1* is additionally treated.

3.3.1. New Assignments to *abietella*-group

All four species that follow display pectinate male antennae, even if allegedly weakly developed in *D. postmajorella*. This feature is exclusively known from the *abietella*-group and is a strong, easily accessible external indicator that a species might belong into said morpho-group. Genitalia traits and outer appearance were considered to safely place the following species into this group.

3.3.1.1. Assignment *Dioryctria nivaliensis*

The wing pattern is reminiscent of *D. abietella*, yet it is darker with more of a reddish-brown hue. The broadly rounded uncus, the shape of the apical region of the valve, and the presence of a preapical spine combined with the composition of cornuti in the phallus in males mainly indicate that the species belongs to the *abietella*-group. The female genitalia traits that support the placement is a long ductus bursae which expands anteriorly.

These findings are supported by the position of *D. nivaliensis* in the phylogenetic trees. It always clusters with the species of the *abietella*-group investigated in this study.

3.3.1.2. Assignment *Dioryctria peltieri*

De Joannis (1908) in the original description of *D. peltieri* states that the species seems to be somewhat intermediate between *D. abietella* and *D. pineae*, regarding clarity of wingpattern and the length of antennal pecten in males.

The fact that the antennae display pectination, along with the strong dentation of the postmedial line (de Joannis 1908), are good indications for the affiliation of the species to the *abietella*-group.

Confirmation by genitalia investigation remains to be produced as specimens were not available and the placement was deduced from the original description alone.

3.3.1.3. Assignment *Dioryctria postmajorella*

Neunzig (1996) claims in his original description that the species is closely related to *D. majorella*. The latter has been placed into the *abietella*-group by Mutuura and Neunzig in 1986. The male antennae are strongly serrate to unipectinate.

The general appearance of the male genital armature as well as that of female genitalia is peculiarly reminiscent of those of *D. pineae*. In the male especially, the broadly rounded apex of the valve and the acute preapical spine along with the shape of the uncus are very much like those of *D. pineae*. The same is true for the composition of cornuti in the phallus.

The female genitalia features resemble very closely those of *D. pineae*. All characters included in this study for phylogenetic analyses display the same character states in both species.

3.3.1.4. Assignment *Dioryctria SKI sp. nov.*

The assignment is based not only on the unipectinate male antennae, since this species also shares the following traits characteristic for the group as a whole. First, the apex of the medial plate of SVIII is produced and quite elongated, as can be found in *D. pineae* and *D. nivaliensis*. Second, the uncus appears eggshaped with a rounded apex. Third, the terminal costal margins of the valves lack longitudinal prominent ridges, as diagnostic for the *sylvestrella*-group, but are smooth with the exception of an acute preapical spine. Additionally, the sacculus is approximately cylindrical at base and the vinculum is more than half the length of total genital length. The phallus displays small, sturdy cornuti as well as one large cornutus, and with the 21 small cornuti found in the male specimen, it falls well within the range from 10 to 35 characteristic for the group. Finally, the ductus bursae, with ventrally infolded margins, in females expands anteriorly and carries a cluster of spines anteriorly adjacent to the sclerotised part of the ductus bursae.

3.3.2. *okui*-group – a New Morphogroup

In the course of this study, two Japanese species, *D. okui* and *D. juniperella*, were investigated to broaden the database and to possibly contribute to the solution of the problems pointed out by

Du et al (2005) regarding the *auranticella*-group, into which both have been formerly placed (Mutuura & Munroe 1972). Quite unexpectedly the inclusion of the two species in the analyses failed to improve the situation regarding the *auranticella*-group. They were even found to form a separate group.

Both species seemed to fit quite well into the *auranticella*-group at first glance, predominantly based on their genitalia morphology, and even retained that impression when morphological characters were used to create a parsimonious tree (see chapter 3.4.). Upon addition and analysis of the molecular data, however, it became obvious that both species are clearly set apart from the *auranticella*-group, or rather *D. auranticella*, as it became clear that the entity of that group requires re-evaluation. Moreover, in all runs that included molecular data, illustrated in chapter 3.4. as well as in trial runs (not shown), *D. okui* and *D. juniperella* cluster together, distinctly removed from both *D. auranticella* and *D. yiai* in the tree topologies. These outcomes gave rise to a close re-investigation of morphological traits, which subsequently justify the following definition of a new morphogroup - the *okui*-group - comprising *D. okui* and *D. juniperella*.

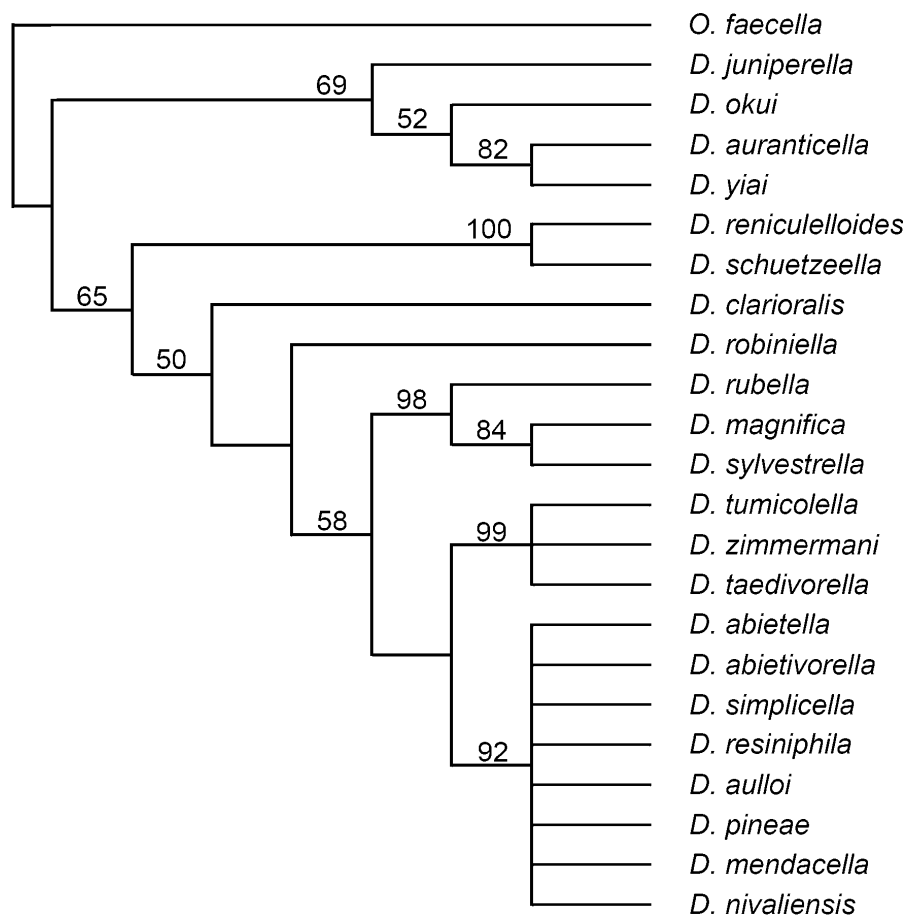
This new group is defined not only by morphological resemblance, but also by ecology, since larvae of both species are external foliage feeders (Mutuura 1958, Mutuura & Munroe 1972, Yamanaka 1990). This distinguishes them from both *D. auranticella* and *D. yiai* and, in fact, from the majority of the genus. The host plant shift observed for *D. juniperella*, feeding on *Juniperus chinensis* (Yamanaka 1990), is likely to be a derived feature, so *D. okui* was chosen as the eponymous species. The morphological traits discerning both species from *auranticella*-group species are as follows, with character states in brackets referring to *auranticella*-group: lamellate male flagellomers (vs. cylindrical), a dark (vs. reddish) forewing colouration, an acute preapical spine (vs. blunt) on male costa, the shape of costal apex as narrowed and acute (vs. blunt), and a medial sclerotised lobe (vs. none) located on the posterior of the ductus bursae. In addition, their biogeography seems to confine both species to Hokkaido Island of Japan. The rather low bootstrap value in parsimony analyses is alleviated by the fact that, with exception of the morphological/ecological tree, they always form a distinct clade, even if situated disjoint from the base of the *abietella*-group in the NJ tree.

3.4. Phylogenetic Analyses

3.4.1 Trees Based on Morphological and Ecological Data

The PAUP run conducted from 45 morphological and two ecological characters (see appendices 4 & 5; plates III.6 & III.7), with the settings specified above, and 1000 heuristic search replicates, yielded 18 most parsimonious trees of length (l) = 156. The trees differ mainly in the relations within the *abietella*-group, thus confirming the close morphological resemblance in this group. *D. aulloi* and *D. resiniphila* cluster together in 12 of the 18 trees. The same is true for the situation of *D. nivaliensis* at the base of the *abietella*-group. In 11 trees, *D. zimmermani* and *D. tumicolella* form a cluster. Bootstrap support was calculated with 1000 replicates. The strict consensus tree is given in fig. 3.4.1 with bootstrap support values plotted on. Two major lineages, albeit not strongly supported, became evident. One is composed of species that have been assigned to the *auranticella*-group (Mutuura & Munroe 1972, Yamanaka 1990); the other includes the rest of the ingroup species.

Figure 3.4.1: Consensus tree of the 18 most parsimonious trees from morphological/ecological dataset, bootstrap values of 1000 replicates plotted on:



3.4.1.1. Group Supports

All species groups represented by more than one species were found as monophyletic clades in the tree. A very robust support was observed for the members of the *schuetzeella*-(100%), *zimmermani*-(99%), *sylvestrella*-(98%), and *abietella*-(92%) groups, each forming a well-defined monophylum.

The results of Du et al. (2005) exhibiting the monophyly of *zimmermani*-, *sylvestrella*-, and *abietella*-groups can thus be regarded as validated, even with slightly improved bootstrap values for the *sylvestrella*-group and the considerably enlarged *abietella*-group. Upon the addition of the eponymous species *D. schuetzeella* to the *schuetzeella*-group, two of the three known representatives of the group are now included and consequently the monophyly of the *schuetzeella*-group could be clearly demonstrated, even based on the morphological data alone. The species groups represented by a single species (*D. clarioralis*, *D. robiniella*) in this analysis formed distinct lineages. Where applicable, these results were consistent with the findings of Du et al. (2005). Thus the presented tree of Du et al. (2005) withstood the expansion of the dataset by 10 species to 22 representatives of the genus, as well as the modification of the morphological dataset and the addition of ecological data.

3.4.1.2. The *auranticella*-group

The *auranticella*-group at the moment comprises of eight species from North America and Asia. It was originally defined by Mutuura & Munroe (1972), later expanded by Yamanaka (1990) and re-defined for the American species by Neunzig in 2003 (for more details, see discussion section). For the analyses in this thesis, four species of this morpho-group (*D. auranticella*, *D. yiai*, *D. juniperella*, and *D. okui*) were investigated. Within the *auranticella*-group, only the branch of *D. yiai* and *D. auranticella* was moderately well supported, while the topology for the two Japanese species, *D. okui* and *D. juniperella*, was not. This can be taken as an indication that the doubts voiced by Du et al. (2005) about the monophyly of the group, based on the investigation of *D. auranticella* and *D. yiai* alone, can be supported by the results of this study.

Subsequent close morphological reinvestigation of *D. okui* and *D. juniperella* resulted in the discovery and definition of the newly described *okui*-morphogroup based on the characters specified in chapter 3.3.2. The characters that enabled the definition of the *okui*-group were all included into the morphological dataset. The signal of those five characters in the dataset, however, was not strong enough to group the two species *D. juniperella* and *D. okui* as a separate cluster in the resulting trees based on morphological and ecological data alone. The additional investigation of molecular data verified the morphological findings by separating the

four species *D. auranticella*, *D. yiai*, *D. juniperella*, and *D. okui* into two separate clusters (see below).

3.4.2. Trees Based on Molecular Data

3.4.2.1. Parsimony Analysis

The molecular dataset consisting of 1536 base pairs had the following properties: 1065 nucleotide sites were constant, 156 variable sites were parsimony uninformative, and 315 were parsimony informative. The PAUP analysis resulted in three most parsimonious trees ($l=1123$, $ci=0.5450$, $hi=0.4450$, $ri=0.5587$, $rc=0.3045$).

The three trees differ with respect to the placement of *D. auranticella*, which either forms an isolated lineage basally of the *schuetzeella*-group, or clusters with the same. The *auranticella*-group can not be maintained in its current composition, as the position of the included species in the tree is disjoint and indicates paraphyly. *D. yiai* is found at the base of the tree. The Japanese species *D. okui* and *D. juniperella* cluster and form a group basally of the *abietella*-group. Furthermore, the position of *D. robiniella* alternates between clustering basally with the *zimmermani*-group (once) and adhering basally to *D. clarioralis* (twice). Regardless, it forms an isolated, distinct lineage well within *Dioryctria*, thus confirming the placement into the genus by Speidel & Asselbergs (2000). Finally, the *sylvestrella*-group forms a clade with the *zimmermani*-group twice and is found once as a separate lineage.

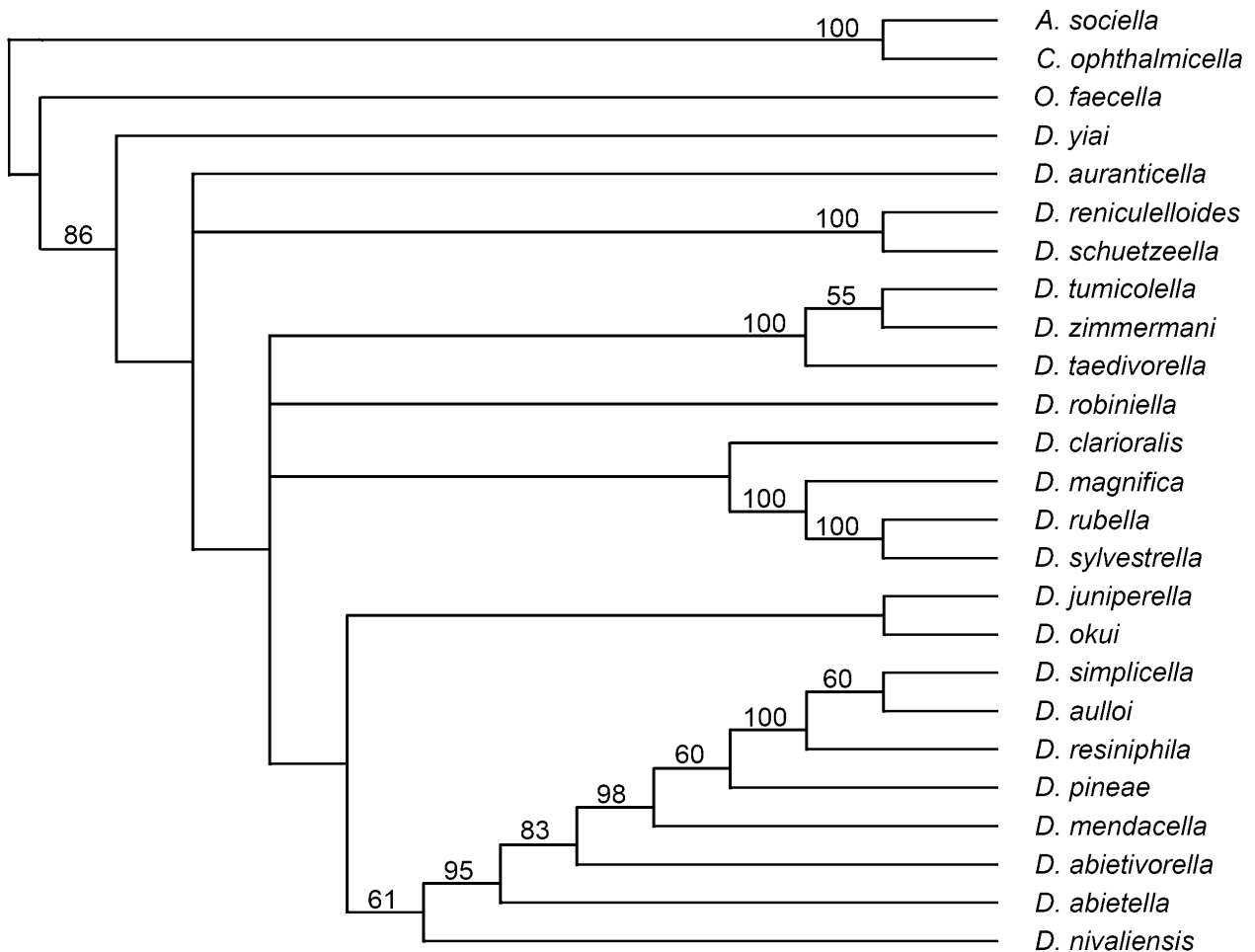
The strict consensus tree (fig. 3.4.2) confirms the monophyly of the genus *Dioryctria*. Upon addition of an extra outgroup species, *Aphomia sociella* (LINNAEUS, 1758) (Pyralidae: Galleriinae), a sufficient ingroup support of 86% could be obtained.

While the relationships among species-groups are generally poorly supported and frequently fall into polytomies, all species-groups but the *auranticella*-group, as mentioned above, form distinct and well-supported monophyla. The respective monophylies of the *sylvestrella*-, *zimmermani*-, and *schuetzeella*-groups are each supported by 100% bootstrap value.

The branching order within the *abietella*-group remains stable and well supported, even in trial runs with modified datasets (trees not shown). *D. nivaliensis* branches off the base of the *abietella*-group, the monophyly of which, as a whole, is moderately supported. *D. abietivorella*, the only Nearctic group member analysed so far, is embedded in the European species. The three species noticed for having unipectinate male antennae (*D. nivaliensis*, *D. pineae*, and *D. mendacella*) do not form a monophyletic clade. The externally extremely similar species of the *simplicella*-species-complex (*D. simplicella* auct., *D. aulloi*, and *D. resiniphila*) consistently

occur as distinct but closely related lineages, with *D. simplicella* auct. and *D. aulloi* as sister species.

Figure 3.4.2: Consensus tree of three most parsimonious trees from molecular data, bootstrap values of 100 replicates plotted on:



3.4.2.2. Similarities and Differences Between Morphological and Molecular Parsimony Trees

In general, trees of better resolution were extracted from the molecular data set, if only for the species within the species-groups. Support of the inter-group relationships was poor in all cases and varied among different parsimony trees. Consistent and well-supported monophylies were found in both analyses for the *schuetzeella*-, *zimmermani*-, *sylvestrella*-, and *abietella*-groups.

D. robiniella consistently formed an isolated lineage well within *Dioryctria*. *D. nivaliensis* was always found to be a member of the *abietella*-group. The *simplicella*-species-complex is resolved in the molecular tree. However, the sister-species relation differs from the impression that one might get from the morphological trees regarding the affinity of *D. aulloi* towards *D. simplicella* auct. or *D. resiniphila* respectively. The most obvious difference between the trees

is the integrity of the *auranticella*-group, which formed a monophylum with respect to the morphomatrix, but a paraphylum with respect to the molecular data set. This phenomenon is in addressed in detail both in chapter 3.3.2. and the discussion section.

3.4.3 Trees Based on Combined Datasets

3.4.3.1. PAUP Tree from Combined Datasets

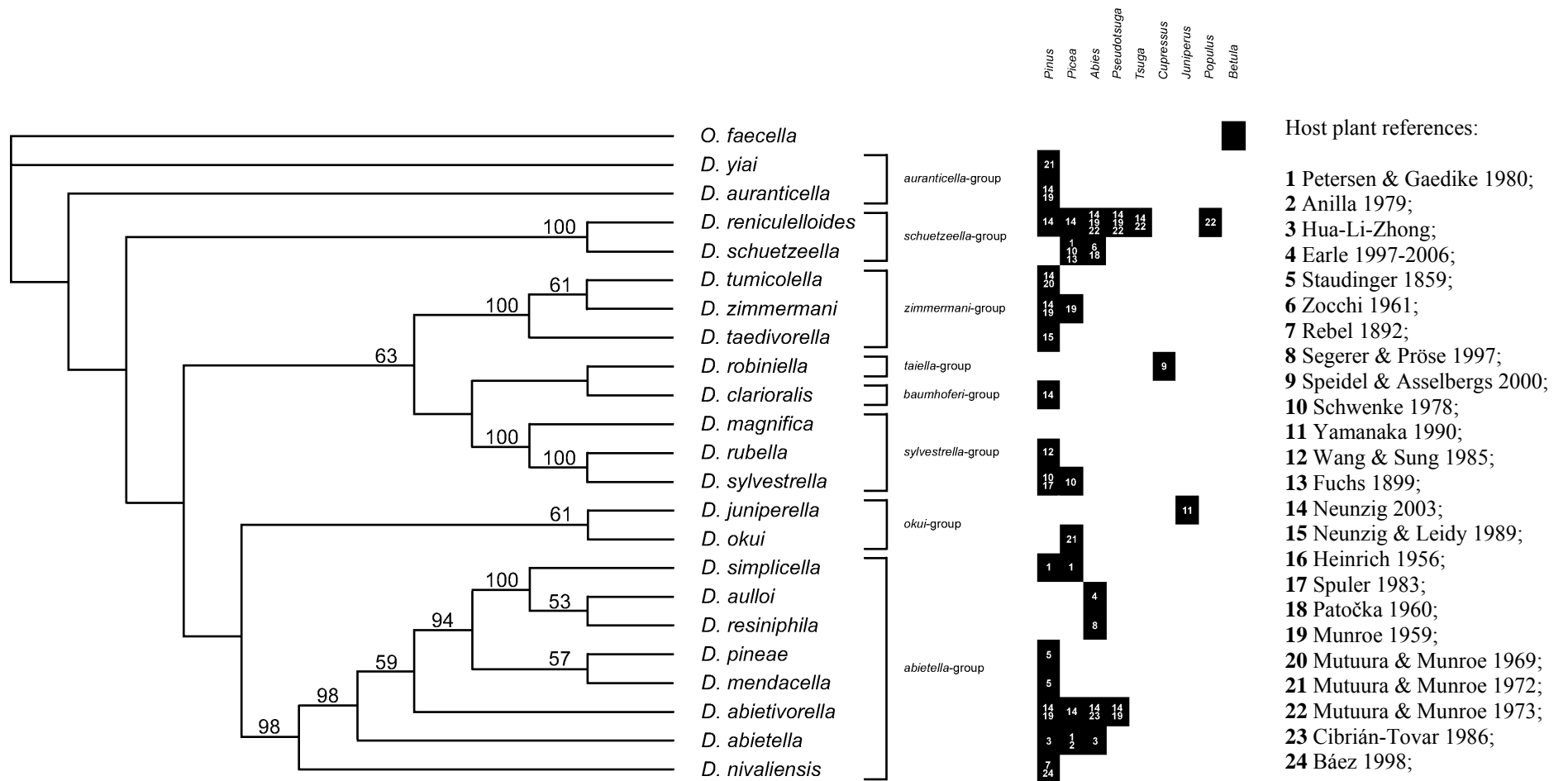
Combined PAUP analysis yielded a single most parsimonious tree (fig. 3.4.3) with a length of 1091 (CI=0.5527, HI= 0.4473, RI= 0.6096, RC=0.3369). Of the grand total of 1583 characters, 1126 were constant, 139 variable but parsimony-uninformative, and 318 parsimony-informative. *D. yiai* was the basal most species in this fully resolved tree. The support of the nodes seemed satisfactory enough to draw some conclusions regarding the ecology and biogeography of the included representatives of the genus (see host plant and discussion sections). Despite the fact that in the combined analysis the resolution of the tree was clearly improved, the relationships among species groups still lack satisfactory statistical support.

Four out of five morpho-groups were well-supported: *schuetzeella*-, *zimmermani*-, and *sylvestrella*-group with 100% each, as in the molecular tree, and *abietella*-group with 98% including *D. nivaliensis* as the basal branch. Like in the molecular tree, the *auranticella*-group remained paraphyletic. The major lineages apparent in the tree were: (i) *D. yiai* as the most basal ingroup taxa, (ii) *D. auranticella*, (iii) the *schuetzeella*-group, (iv) the *abietella*-group together with the *okui*-group, and (v) a clade composed of representatives of the remaining species groups which, in general, maintain their monophyletic character with high support.

As a major difference to the molecular tree, *D. robiniella* and *D. clarioralis* displayed affinity to the *sylvestrella*-group. The two Mediterranean species *D. mendacella* and *D. pineae*, other than in the molecular tree, clustered as sister-species, forming the sister-clade of the *simplicella*-species-complex. This result was plausible, as they both display unipectinate antennae in the male and were originally described from the same mountainous area of Andalusia/Spain by Staudinger in 1859. Finally, the problematic *simplicella*-species-complex displayed the highest support value within the group (100%). However, the relationships have shifted so that in this run there was a better chance that *D. resiniphila* and *D. aulloi* could be sister species, as already indicated in 2/3 of the morphological trees.

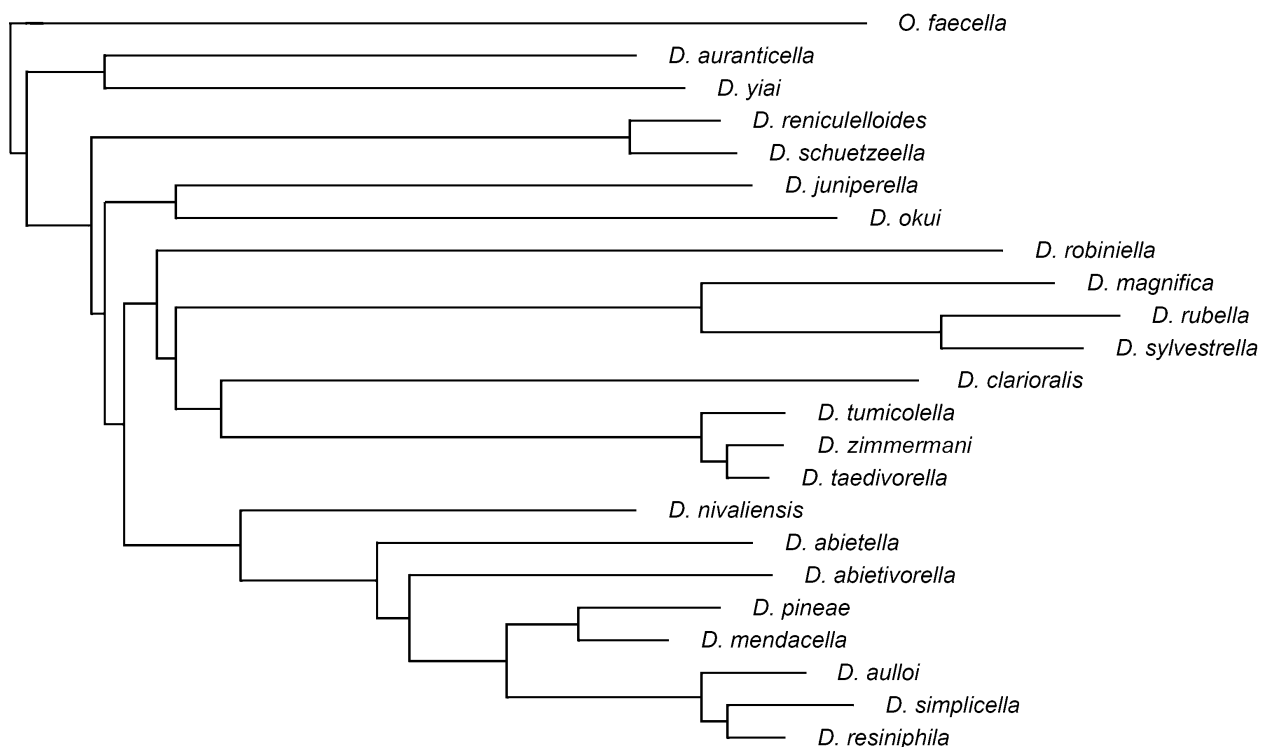
A neighbour joining (NJ) tree (fig. 3.4.4.) calculated from the same combined dataset also supported all major clades that were found to be well supported in the former analyses.

Fig. 3.4.3: Single most parsimonious tree from combined datasets of 1000 heuristic search replicates, bootstrap values of 100 bootstrap replicates and host plant genera plotted on:



The branching order within the *abietella*-group basically resembled that of the parsimonious tree. One exception, however, was the third alternative of the possible sibling species association within the *simplicella*-species-complex. *D. simplicella* auct. and *D. aulloi* were sister species in this tree topology. In this illustration, the differences between those three species became visible as individual terminal branch lengths. The *okui*-group was removed from the *abietella*-group but remained distinct from the remnant two species of the *auranticella*-group, from which it was separated by the *schuetzeella*-group. *D. robiniella* and *D. clarioralis* were separated by the interjacent *sylvestrella*-group.

Fig. 3.4.4: NJ tree from combined datasets:



3.4.3.2. Trees from Bayesian Analyses

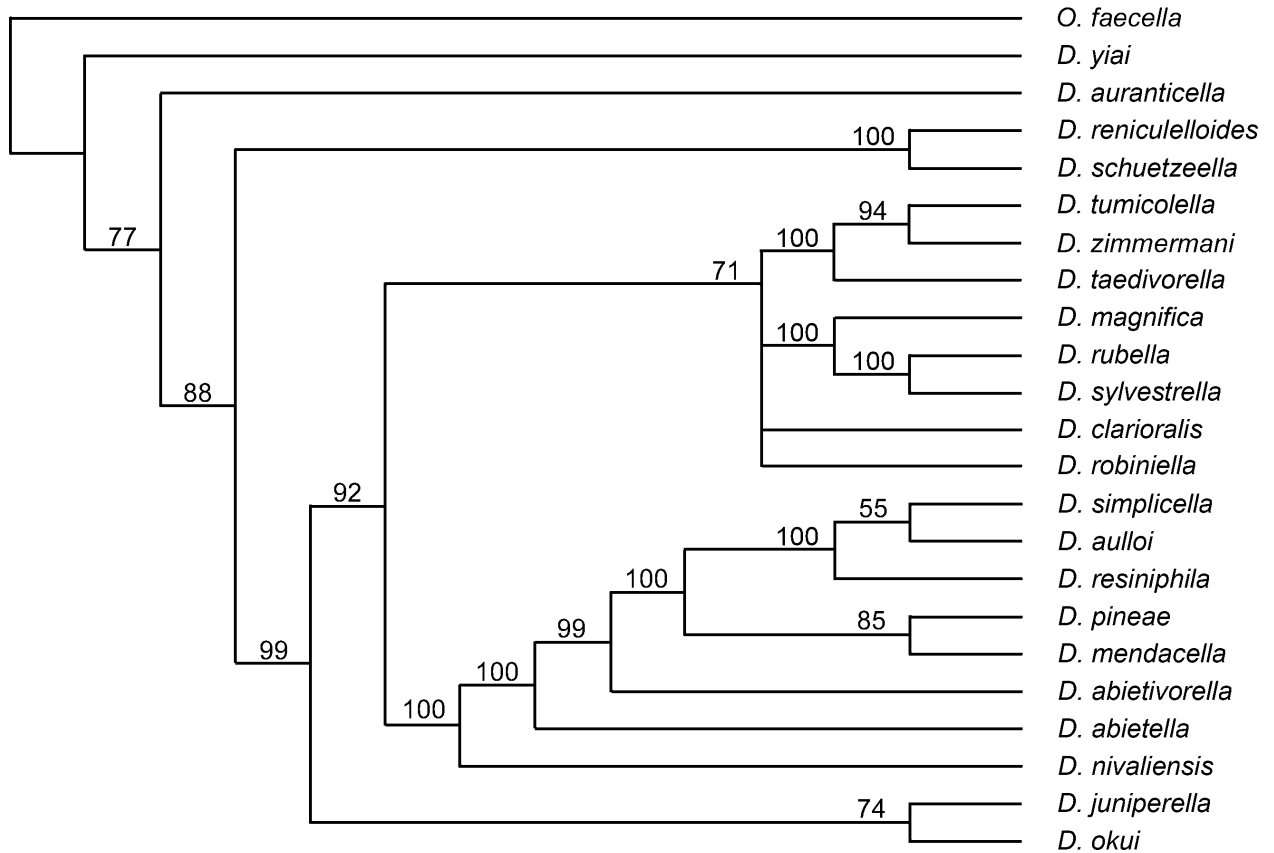
Two Bayesian analyses were performed with the molecular and combined data sets. The tree obtained from the unchanged combined data set, already used for PAUP analyses, was not fully resolved (fig. 3.4.5).

Optimal support for the *schuetzeella*-, *zimmermani*-, *sylvestrella*- and *abietella*-groups (100%) and moderately well support for the *okui*-group (74%) were observed.

Consistent with the PAUP analyses and the Bayesian molecular tree, *D. yiai* and *D. auranticella* were the basal most species. It followed the *schuetzeella*-group and an isolated branch comprised of the *okui*-group. A clade forming a polytomy that included the four species-groups,

sylvestrella-, *zimmermani*-, *baumhoferi*-, and *taiella*-group, formed the adjacent neighbour to the *abietella*-group. The topology of the *abietella*-group was highly consistent with all other trees.

Fig. 3.4.5: Bayesian tree from combined datasets:



In the molecular tree (fig 3.4.6), calculated from the same data set as in the corresponding PAUP run with three outgroup species, the ingroup genus *Dioryctria* was strongly supported as monophyletic, with *O. faecella* as its closest relative of all the outgroup species.

As could be expected, the *auranticella*-group has disintegrated. *D. okui* and *D. juniperella* were found as individual lineages, likewise *D. robiniella*. All other species-groups were maintained and, if comprised of several species, resolved with 100% support.

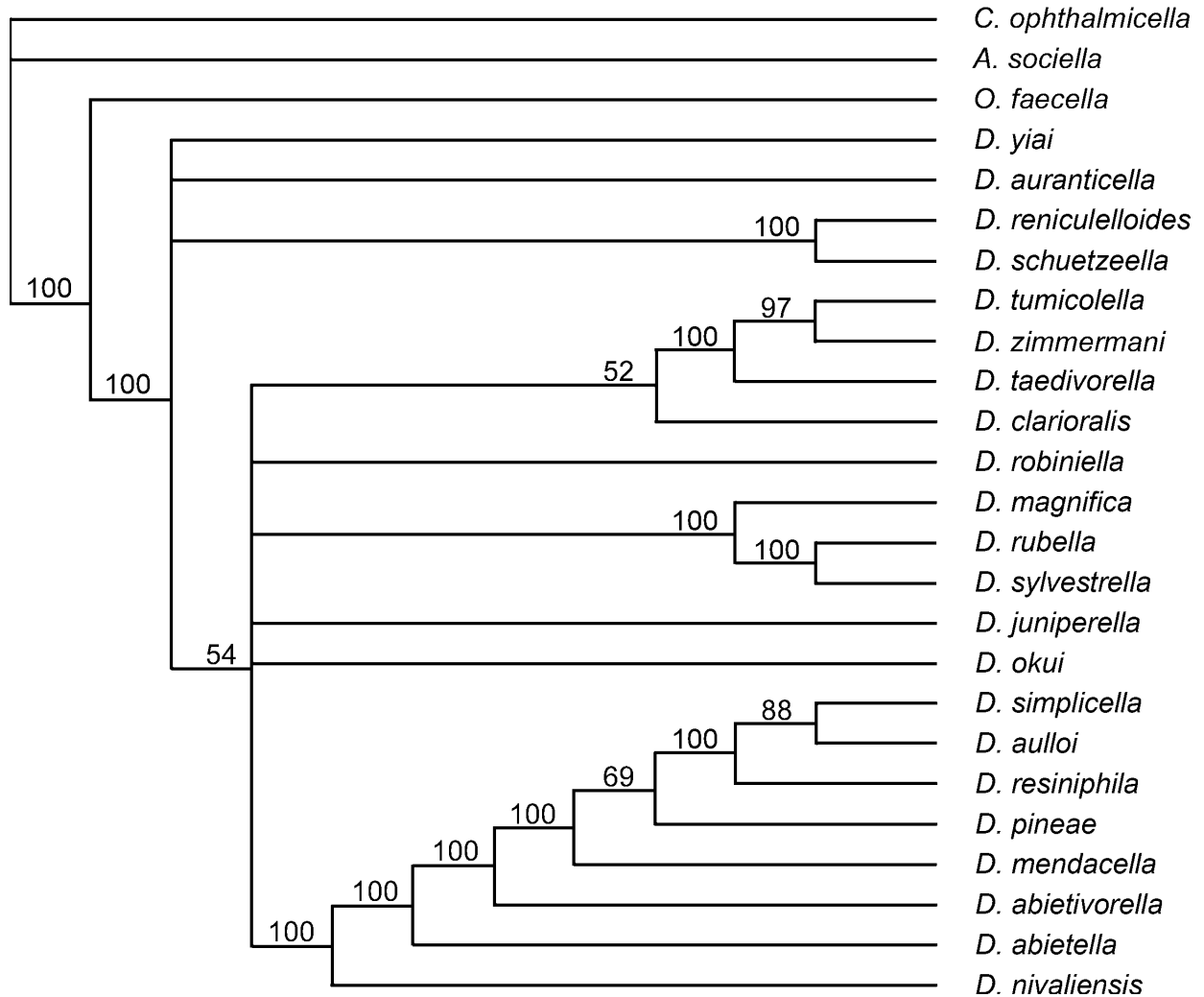
The relationship among the species groups remained an unresolved polytomy. Only the *schuetzeella*-group, *D. auranticella*, and *D. yiai* are well supported in their placement basally of the other species of the ingroup. Therein, the *abietella*-group as composed in the PAUP-trees, the *zimmermani*-group with *D. clarioralis*, the *sylvestrella*-group, *D. robiniella*, *D. okui*, and *D. juniperella* were found.

Complete very well supported resolution, perfectly consistent with the results from the PAUP run, was obtained for the *abietella*-group.

Experimenting with the two additional outgroup species, *C. tenthrediniformis* and *C. fumiferana*

(trees not shown), only slightly improved resolution. The addition of those outgroup species pulled together the *sylvestrella*- and the *zimmermanni*-groups, along with *D. clarioralis* and *D. robiniella*, into a polytomous clade, situated opposite the *abietella*-group. In that group *D. pineae* and *D. mendacella* were sister species once more. The one remarkable difference was the re-appearance of the *okui*-group.

Fig. 3.4.6: Bayesian tree from molecular dataset:



3.4.3.3. Genetic Variability

Average intra-species distances of COI gene were determined if complete sequences could be obtained from more than one specimen (see table 3.4). A similar comparison among the different species groups of *Dioryctria* was rescinded, since no species group is yet completely represented.

Average intra-species variation ranged from 0 to 0.46%, with species of the *abietella*-group being the most conservative and those of the *sylvestrella*-group the most variable. For

comparison, the closest value among different species was 0.651% between *D. aulloi* and *D. resiniphila*.

The intraspecific values were statistically most informative for *D. abietella* and *D. simplicella* auct., as quite a lot of specimens (12 and 16, respectively) yielded complete sequences, including specimens from different Palearctic regions. For the reasons outlined in the next chapter in great detail, *D. simplicella* auct. and *D. mutatella* auct. are considered conspecific.

D. abietella is a wide spread species, ranging all across the Palearctic from western Europe to eastern China. Comparison of the published sequence from a Chinese specimen (Du et al. 2005) with those from Germany, Italy, and USSR made it clear that this species maintains a high level of genetic integrity over the greater part of its distribution range.

Table 3.4: Sequence divergence of complete COI, in % as uncorrected average pairwise distances:

species	% sequence divergence
<i>D. abietella</i>	0.26 (12)
<i>D. abietivorella</i>	0.0 (3)
<i>D. aulloi</i>	0.0 (2)
<i>D. mendacella</i>	0.013 (2 from Spain)
<i>D. resiniphila</i>	0.065 (4)
<i>D. simplicella</i> auct.	0.13 (5)
= <i>D. mutatella</i> auct.	0.13 (11)
<i>D. schuetzeella</i>	0.26 (2)
<i>D. magnifica</i>	0.326 (2)
<i>D. sylvestrella</i>	0.456 (7)

Plate III.6: Male Genitalia Character States

scalebar = 500µm on genitalia

complete male armature: *D. pineae*

15(0) *D. clarioralis*; 15(1) *D. schuetzeella*;
15(2) *D. abietella*; 15(3) *D. sylvestrella*;

16(0) *D. schuetzeella*; 16(1) *D. nivaliensis*;
16(2) *D. sylvestrella*;

17(0) *D. schuetzeella*; 17(1) *D. abietella*;
17(2) *D. taedivorella*;

18(0) *D. mendacella*; 18(1) *D. robiniella*;

21(0) *D. resiniphila*; 21(1) *D. sylvestrella*;

22(0) *D. sylvestrella*; 22(1) *D. resiniphila*;

23(0) *D. mendacella*; 23(1) *D. nivaliensis*;
23(2) *D. schuetzeella*;

25(0) *D. juniperella*; 25(1) *D. abietella*;
25(2) *D. robiniella*;

26(0) *D. robiniella*; 26(1) *D. sylvestrella*;

27(0) *D. juniperella*; 27(1) *D. robiniella*;

28(0) *D. auranticella*; 28(1) *D. abietella*;
28(2) *D. sylvestrella*;

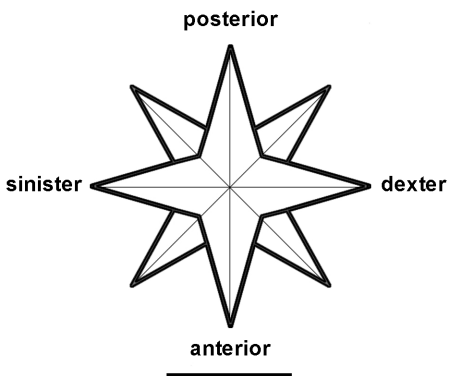
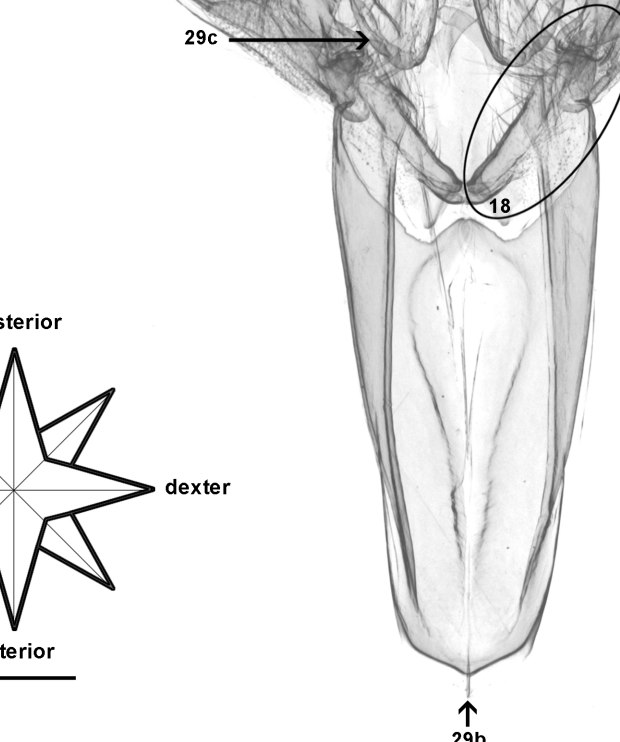
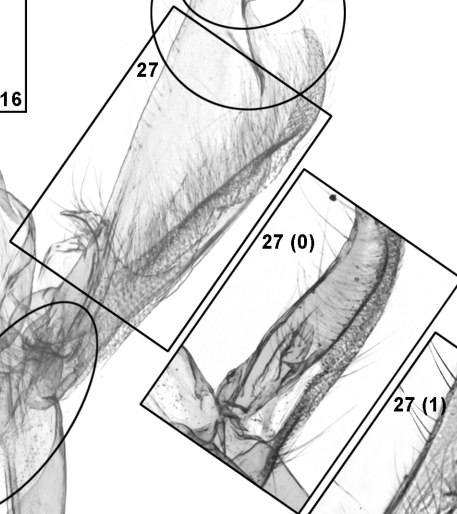
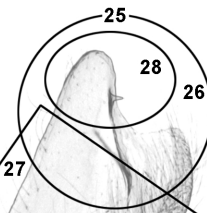
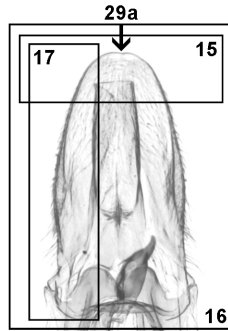
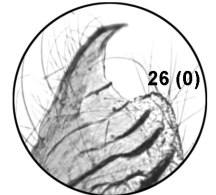
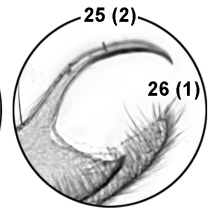
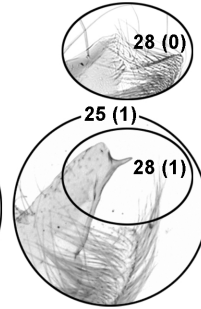
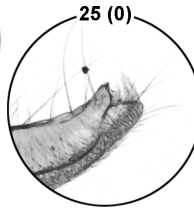
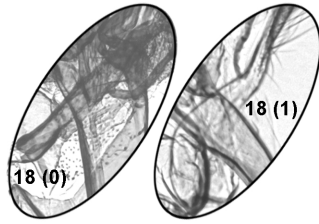
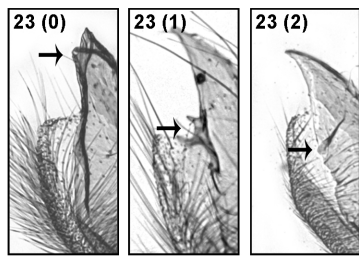
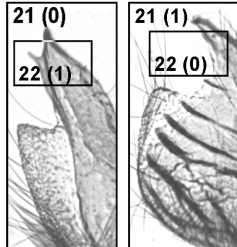
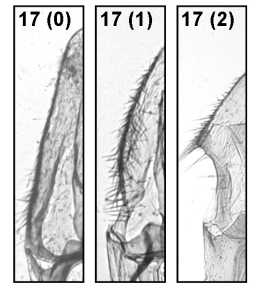
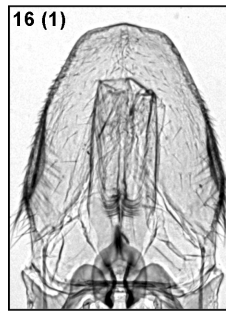
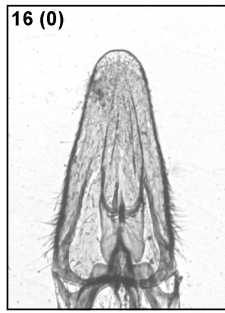
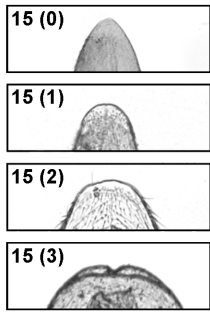


Plate III.6

Plate III.7: Female Genitalia Character States

scalebar = 500µm on genitalia

complete female armature: *D. pineae*

36 *D. pineae*

37(0) *D. mendacella*; 37(1) *D. robiniella*;

38(0) *D. sylvestrella*; 38(1) *D. resiniphila*;

39(0) *D. resiniphila*; 39(1) *D. schuetzeella*;

40(0) *D. sylvestrella*; 40(1) *D. resiniphila*;

41(0) *D. juniperella*; 41(1) *D. sylvestrella*;

41(2) *D. resiniphila*; 41(3) *D. schuetzeella*;

42(0) *D. juniperella*; 42(1) *D. sylvestrella*;

42(2) *D. robiniella*;

43(0) *D. robiniella*; 43(1) *D. aulloi*

43(2) *D. schuetzeella*;

44(0) *D. sylvestrella*; 44(1) *D. resiniphila*;

45(1) *D. sylvestrella*; 45(2) *D. juniperella*;

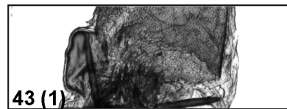
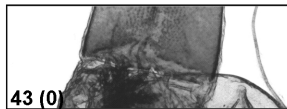
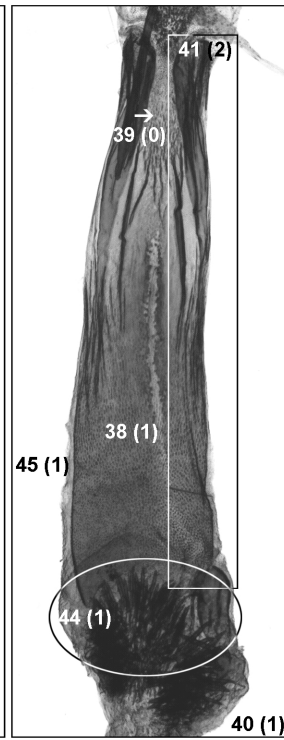
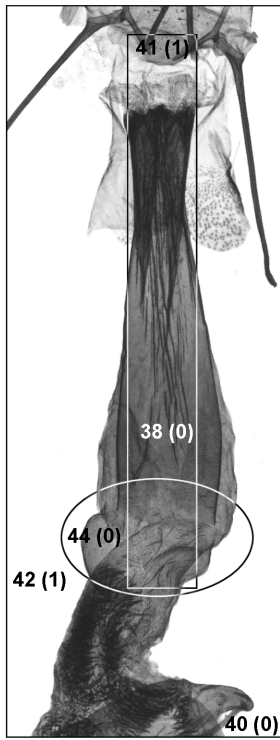
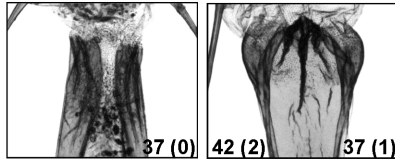
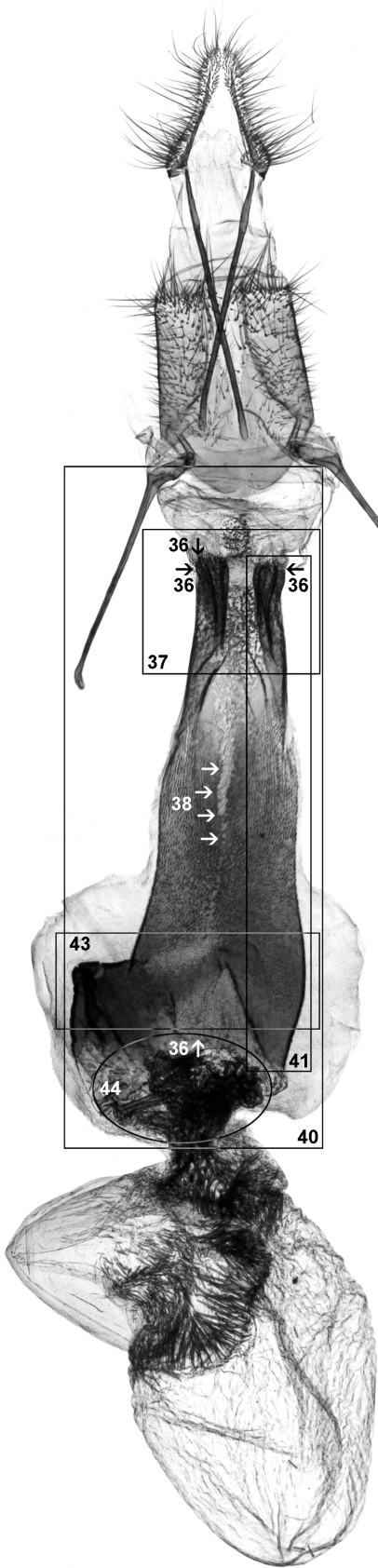
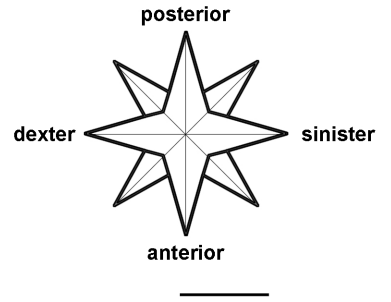


Plate III.7

3.5. The *simplicella*-Species-Complex

This species flock, as defined in the introduction, is an example of a species-complex found in Europe, the members of which are hard to distinguish. In fact, they are better characterised by larval biology and feeding habit than by external features and the morphology of the terminalia. Foremost, the identities of the taxa *Dioryctria simplicella* auct. and *D. mutatella* auct. are in need of clarification. Types of both species have unfortunately been lost, so the designation of neotypes is desirable in a future publication in an appropriate journal. The focus of the work conducted here was to clarify the relationships of taxa in this group. To achieve this, morphology, ecology, and genetic divergence were studied.

3.5.1. The Current Species Status of *Dioryctria simplicella* auct. and *Dioryctria mutatella* auct.

The identity of *D. simplicella* auct. and of *D. mutatella* auct. has been one of the more extensively debated *Dioryctria* related topics for more than a century. The fact that types of both had been lost further complicated the matter and caused considerable speculation and confusion. In 1901, Rebel removed *D. simplicella* HEINEMANN, 1865 from the genus and declared it synonymous to *Salebriopsis albicilla* (HERRICH-SCHÄFFER, 1849). More than six decades later, in 1968, Roesler restored its status as a valid species of the genus *Dioryctria*. Petersen & Gaedike (1980) regarded both species as synonymous, with reservations as to the identity of the species from Heinemanns original description. For more detailed attention to the history of the taxonomic status of both species, see discussion section.

In the course of this revision of the European taxa, attempts to resolve the issue were resumed, this time adding sequence analysis of the mitochondrial COI gene to the classical morphological approach.

To account for the historic names and to avoid confusion throughout this thesis, as mentioned in the introduction, *D. simplicella* and *D. mutatella* were referred to as *D. simplicella* auct. and *D. mutatella* auct. respectively, unless a specific citation was given along with the species names.

All results presented here indicate that the appearance of *D. simplicella* auct. might be nothing else but a melanistic form, and consequently, *D. simplicella* auct. and *D. mutatella* auct. should be synonymous.

3.5.2. Re-evaluation of Traits Allegedly Useful to Distinguish *D. simplicella* auct. and *D. mutarella* auct.

As a base for investigation and discussion, all characters found in literature that were claimed by the cited authors to discriminate between *D. simplicella* auct. and *D. mutarella* auct. were assembled in the following table (3.5.1). Rebel was deliberately neglected, as it is doubtlessly evident that all specimens in question that were investigated by the authors cited here, as well as the individuals examined in this study, belong in the genus *Dioryctria*. To critically assess the validity of the statements previously made, these characters were carefully re-evaluated with respect to their reproducibility and to their suitability to clearly separate both taxa. Genitalia slides of six male and 25 female *D. simplicella* auct. and of 26 male and 25 female *D. mutarella* auct. specimens were compared.

Table 3.5.1: Features allegedly diagnostic for discriminating between *D. simplicella* auct. and *D. mutarella* auct.:

Character	<i>D. simplicella</i> auct.	<i>D. mutarella</i> auct.
1. Forewing pattern	Reddish brown-grey, glossy, no pattern (Heinemann 1865); reduction of forewing pattern, showing an exceptionally strong dark blackish-brown suffusion (Roesler 1968)	Grey, with pale discal stigma and zigzag lines, as characteristic for most <i>Dioryctria</i> spp. (Fuchs 1899, Heinrich 1956)
2. Male terminalia: Costa of valve and sella	Mid part of costa broader than in <i>D. mutarella</i> , subapically slightly constricted; sella broad at base, tapered, not exceeding costal margin (Roesler 1968)	Mid part of costa less broad than in <i>D. simplicella</i> , subapically not constricted; sella broad at base, not tapered, slightly exceeding costal margin (Roesler 1968)
3. Female terminalia: sclerotisation of anterior end of ductus bursae	Area strongly sclerotised (Roesler 1968, Hassler & Speidel 1986)	Weaker sclerotised than in <i>D. simplicella</i> (Roesler 1968, Hassler & Speidel 1986)
4. Female terminalia: arrangement of spines in anterior end of ductus bursae	A few spines only, forming a circular signum (Roesler 1968)	Spines without regular pattern (Roesler 1968)
5. Habitat and distribution	In warm sandy wind blown habitats with pine bushes and trees, in W Germany only, occurring sympatrically with <i>D. mutarella</i> (Hassler & Speidel 1986)	Widely spread in pine forests from throughout Europe, predominantly in temperate and northern climate zones (Nuss et al. 2004 and results in this paper)

3.5.2.1. Forewing pattern (plate III.4)

Upon close inspection of the 31 accessible specimens of *D. simplicella* auct., the forewings turned out to be quite variable in their intensity and distribution of blackish scaling. In most cases, the forewings are almost entirely black without any obvious pattern, except for a light greyish patch found towards the dorsal margin. The position of that patch corresponds with the position of the occasionally present rusty red patch which is situated baso-dorsally of the medial line in *Dioryctria* with wing pattern characteristic of the genus.

More rarely, a light discal stigma is visible as well (plate III.4c & d). However, specimens with completely obscured forewings do occur (plate III.4a), as well as suffused forms with clearly visible patterns strongly reminiscent of darkened *D. mutarella* auct. (plate III.4d). In addition, specimens showing a greyish pattern, as usually present in *D. mutarella* auct. but with an obscured area between medial and postmedial line (plate III.4e), were found.

Thus, these results, as well as reviewed literature (Parson & Clancy 2002), yielded a number of transitional forms ranging from completely black *D. simplicella* auct. (plate III.4a) to grey *D. mutarella* auct. (plate III.4f). Hassler & Speidel (1986) were therefore mistaken in assuming that no intermediates exist.

3.5.2.2. Male Terminalia: Costa of Valve and Sella

Genitalia slides of two series of six male *D. simplicella* auct. and 26 male *D. mutarella* auct. were compared. Specimens with darkened forewings were readily recognized by their external appearance; grey individuals were determined by genitalia slides and geographical information. For selected specimens, COI sequences were also available.

The shape of the tip of the valve was compared for 32 specimens, including the black specimens. Plate III.9 gives an overview of the variety encountered: 47% of specimens displayed an acute valval tip plus a pointy preapical spine, as illustrated for example in plate III.9a-e; 47% had a more or less rounded apical tip (plate III.f-o); and 6% (i.e. one specimen of each morphotype) yielded quite different shapes of the valval tip, with both dentures almost completely rounded (plate III.9n & o). The specimen of plate III.9e bears an additional tiny denture proximally of the tip of the valve. For the investigation of the shape of the tip of the valve, the left side was chosen, as this was intact on all slides.

Contrary to the results published earlier by Roesler (1968), a subapical constriction was lacking in a number of *D. simplicella* auct. specimens (plate III.9m, o). On the other hand, this feature could occasionally be found in *D. mutarella* auct. specimens (plate III.9b, h). Hence, the specific differences described by Roesler (1968) could not be reproduced. Rather, a substantial amount of variation was observed in both taxa in the shape of the valves, including asymmetries, thus confirming earlier results for species of the *abietella*-group from Germany examined by Petersen & Gaedike (1980).

The sella is very likely to form artefacts when embedded. Due to its more or less membranous consistency, it can easily be buckled or squeezed. Therefore, features like the shape and the length of the sella per se, as well as its relation to the valve, turned out to be unsuitable for comparison.

Once again, the findings of Roesler (1968) could not be reproduced. Rather, by examination of Roesler's original slides, the quality of which does not meet modern standards, the artificial nature of the reported "differences" became obvious. Length and shape of the sella were obviously preparation artefacts. For detailed assessment of Roesler's findings, see discussion section.

3.5.2.3 Female Terminalia

Investigations were performed on loose genitalia kept in glycerol to preserve their three-dimensional character.

The strength of sclerotisation of the ductus bursae turned out to be variable and did not correlate with the taxa assignments as described by Roesler (1968) and by Hassler & Speidel (1986).

The anterior region of the ductus bursae carries a dense rhombal shaped cluster of spines. Both the degree of sclerotisation and the arrangement of spines in this region turned out to be individually variable in both taxa. Furthermore, embedding artefacts can cause variation in the appearance of the spine cluster. This is due to a double kink in the ductus bursae posteriorly of these spines, which is more or less forced into two dimensions by application of the cover glass. The result is a distortion of the structures, consequently resulting in apparent difference in shapes of the spine field in different slides, depending on the degree of "flattening." Again, it was impossible to correlate the species specific traits sensu Roesler (1968) with the actual morphotypes investigated.

3.5.2.4. Distribution

D. simplicella HEINEMANN, 1865 was originally described from, and is still predominantly found in, south-western Germany. In addition to published reports (Roesler 1968, Hassler & Speidel 1986), two specimens from Saarland were collected by A. Werno.

However, there are sporadic findings outside south-western Germany as well, as is proved by the examined specimens from north-western Germany (Lower Saxony, Northrhine-Westphalia) and from easternmost Germany (Brandenburg, Jänschwalde Ost). Moreover, Parsons and Clancy (2002) report *D. simplicella* auct. from Great Britain, where individual populations can evidently be comprised of up to 25% of the blackish form. Thus, in contrast to the statement of Hassler and Speidel (1986), *D. simplicella* auct. specimens are by no means endemic to south-western Germany, but do occur elsewhere.

3.5.3. General Investigation of all Members of the *simplicella*-Species-Complex

The search for further distinctive morphological characters for the *simplicella*-species-complex yielded the shape of male flagellomers of the antennae (plate III.8) as the most reliable external feature for identification of *D. aulloi*, *D. resiniphila*, and *D. simplicella* auct./*D. mutatella* auct. Unfortunately, this trait is only detectable under magnification, preferably using the scanning electron microscope SEM. This is the only external physical trait, unrecognized in the past, that was found useful in the course of this study to discern species in the *simplicella*-species-complex, apart from the fact that black-winged specimens doubtlessly can be determined as *D. simplicella* auct. No significant differences between *D. simplicella* auct. and *D. mutatella* auct. could be found in the male antennae, although there are evident differences among the shape of flagellomers of *D. abietella*, *D. aulloi*, and *D. resiniphila*. Moreover, the shape of each of these flagellomers is distinct from the ones of *D. simplicella* auct. and *D. mutatella* auct.

A search for additional morphological traits was conducted to enable the determination of the Mediterranean sister species *D. aulloi*, endemic to Spain, and *D. resiniphila*, endemic to Greece. Also *D. abietella* from the same morpho-group, but representing a more distantly related species, not belonging to the *simplicella*-species-complex was included in the considerations to enable the assessment of variation. Special attention was given to both male and female genitalia structures with the following results:

In the distal part of the columella, sturdy and slightly hooked spines are present in *D. abietella* as well as in *D. resiniphila*. In *D. resiniphila*, a high degree of variation was observed. These spines are lacking in the specimen of *D. aulloi*. Since it was only possible to examine a single female, one has to bear in mind that this may in the future turn out to be either an individual abnormality or may lie well within a range of variation.

To pinpoint possible differences in the shape of male genital features in the *simplicella*-species-complex that are not readily obvious from the comparison of measurements alone, SPCA analyses were performed.

3.5.3.1. Sheared Principal Component Analysis (SPCA) of Five *Dioryctria* Species.

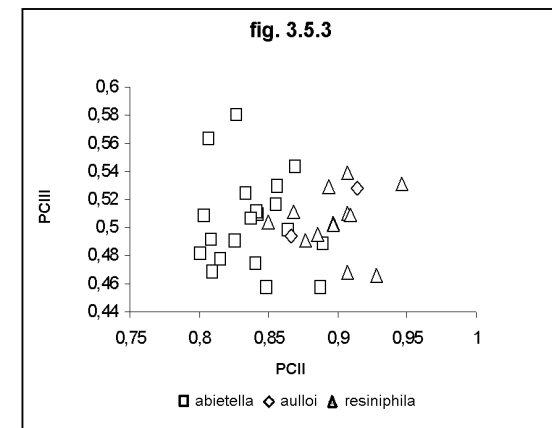
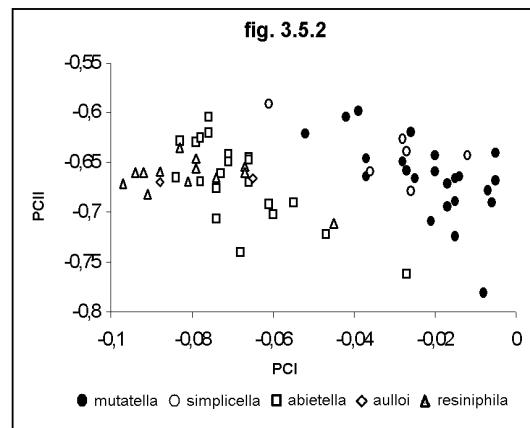
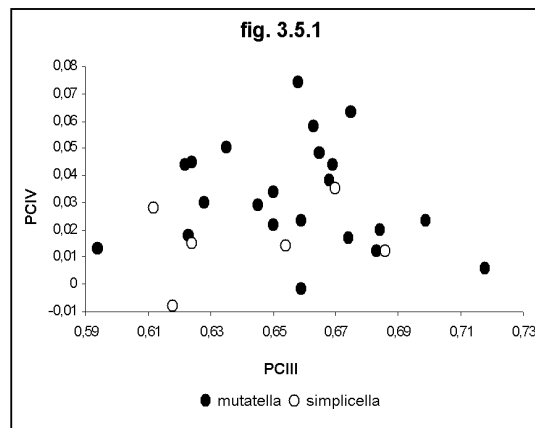
This is the first effort to utilise a set of male genitalia measurements as an approach to the problem of discriminating between the species of the *simplicella*-species-complex.

Attempts were made to ascertain whether morphometric data of the male genital are capable of clustering the five taxa in accordance to the species (SPCA-groups) included in the run, and more specifically, if *D. simplicella* auct. and *D. mutatella* auct. would form distinct clusters. The

Table 3.5: Loadings of first four sheared principal components of pooled covariance matrix of figs. 3.5.1, 3.5.2, and 3.5.3:

Measurement	Component											
	fig. 3.5.1				fig.3.5.2				fig.3.5.3			
	I	II	III	IV	I	II	III	IV	I	II	III	IV
GH	0.261213	0.082352	0.176726	-0.029762	0.299467	-0.154772	0.023983	-0.069429	0.266348	0.046506	0.110912	-0.040669
UH	0.284381	0.383026	-0.227168	0.122749	0.300370	0.091805	0.003757	-0.394318	0.327298	-0.199348	-0.218536	0.068886
GW	0.149455	-0.733147	0.428448	-0.017803	0.255688	-0.278404	-0.790496	0.361094	0.166270	-0.645675	0.609697	0.165512
LVL	0.243435	0.220498	0.144278	0.110551	0.245917	0.111868	0.361370	0.402006	0.323963	0.305521	0.014479	0.368984
LVR	0.235000	0.154282	0.132824	0.111141	0.248424	0.113392	0.341498	0.428148	0.313282	0.316667	0.018564	0.364915
WVL	0.399230	-0.273281	-0.613921	-0.081913	0.295077	0.608517	-0.177429	-0.127061	0.390309	-0.317167	-0.493666	-0.113021
WVR	0.434605	-0.305256	-0.307242	0.147962	0.292348	0.524254	-0.150879	0.046120	0.330629	-0.239447	-0.359662	0.023057
LP	0.162004	-0.008762	0.273888	0.761966	0.307231	-0.255268	0.171059	0.291905	0.241543	0.273554	0.210752	0.041031
HVL	0.286276	0.122210	0.233335	-0.255860	0.333238	-0.232660	0.088711	-0.077782	0.292831	0.139985	0.182521	-0.018128
HVR	0.299834	0.121574	0.145513	-0.326589	0.328934	-0.215338	0.094102	-0.135203	0.279920	0.158005	0.178113	-0.031944
HMF	0.347814	0.116931	0.271690	-0.335372	0.333535	-0.230608	0.088466	-0.484509	0.299092	0.144461	0.196935	-0.819317
HT	0.216180	0.158434	-0.020026	0.255661	0.187381	0.027539	-0.138782	0.042716	0.132784	-0.222234	0.215304	0.096314
Eigenvalue	0.007	0.001	0.001	0.000	0.025	0.001	0.001	0.001	0.005	0.001	0.001	0.001
Variance explained [%]	69.514	9.012	8.113	3.756	85.454	4.783	3.544	1.864	54.856	16.307	8.959	7.535

GH genital height; UH uncus height; GW gnathos width; LVL/R length valve left/right; WVL/R width valve left/right; LP length phallus; HVL/R height vinculum left/right; HMF height membranous field; HT height tectum



required a priori grouping according to species made accurate determination of species necessary. For *D. simplicella* auct., the darkened forewings were taken as a reliable trait for identification. One of the *D. aulloi* specimens included is the lectotype, an additional one was included as it belongs to the species based on its geographical and sequence data, as well as its morphology of the male antennae. *D. resiniphila* individuals all originated from Greece and partly yielded sequence during molecular investigations. Identification of *D. abietella* was unproblematic.

As mentioned before, meaningful measurements were limited in this specific case. First, the many three-dimensional structures of the terminalia (e.g. uncus, vinculum, tectum) are forced into two dimensions when embedded. This causes artefacts, yielding incomparable measurements (e.g. width of uncus). Consequently, only a limited number of measurable morphological traits were found to be useful for comparative analysis (table 3.5). Second, significant distinctions based on measurements were nearly impossible to grasp in any classical statistical manner, for the overlap regarding individual types of measurements (e.g. height of genital) is quite large. Third, not only *D. simplicella* auct., but even more so *D. aulloi*, was available in sparse numbers only, which alone ruled out the application of any more common classical statistical approach. Therefore, a method considering the entirety of available measurements simultaneously, independent of the number of specimens, seemed the only alternative. The attributes of SPCA make it possible to subject a smaller number of specimens per species to the analysis than is required in ordinary statistical practices while still obtaining informative results. This was especially expedient in the case at hand. Unfortunately, the potential number of specimens included into SPCA analyses was further limited, owing to the fact that the damage of the specimens prevented the assembly of a complete dataset for every single specimen, as required for SPCA.

The results of two revealing SPCA runs were illustrated. The first run included *D. simplicella* auct. and *D. mutarella* auct. specimens exclusively (fig. 3.5.1); the second, all four species of this species flock plus *D. abietella* (fig. 3.5.2). Principal component loadings are given in table 3.5.

When evaluating the results for *D. simplicella* auct. and *D. mutarella* auct. for selected combinations of principal components (=PC), (PC II/PC III, PC II/PC IV, PC V/PC VI; results not illustrated, and PC III/PC IV; fig. 3.5.1), no distinct clustering of groups was observed in any of them. Instead, they form one inseparable cloud. The larger variance of the *D. mutarella* auct. specimens in PC IV is influenced mainly by the character “length of phallus,” evident in the PC loading chart (table 3.5.) from the highest loading norm (0.761966). In a following step, the dataset was expanded to five species. As illustrated in fig 3.5.2, it can be observed that a

D. simplicella auct./*D. mutabella* auct. cluster is obviously set apart from the other three included species. Once more, even in a different combination of principal components (PCI/PCII), no significant distinction between *D. simplicella* auct. and *D. mutabella* auct. is detectable. Therefore, the SPCA results for *D. simplicella* auct. and *D. mutabella* auct. supported the statements claiming them to be con-specific as detailed above, and these results are also consistent with molecular findings explained in detail below. To a certain degree, SPCA seems to possess the valuable advantage, unknown among other statistic methods, to allow for demonstration of likeness in a dataset.

The remaining three species are clearly set apart from the *D. simplicella* auct./*D. mutabella* auct. cluster and show no overlap or contact zone with the latter. Therefore, neither combination of included groups, nor combinations of PCs, yielded any support for the assumption that *D. simplicella* auct. as well as *D. mutabella* auct. can be discriminated based on the male genital features investigated here.

Unfortunately, the three remaining species, though distinct from *D. simplicella* auct./*D. mutabella* auct., do not form isolated clusters, but are overlapping for the majority of included specimens.

The data sets of *D. simplicella* auct. and *D. mutabella* auct. were removed for the run illustrated in fig 3.4.3. This run then included the three unresolved species from the previous run only, to test whether the addition of *D. simplicella* auct./*D. mutabella* auct. caused any concealment of possible information in the dataset that might prove useful for tracing minute differences between *D. abietella*, *D. aulloi* and *D. resiniphila*. Although, the illustration (fig. 3.5.3) shows that *D. abietella* and *D. resiniphila* still share a zone of overlap, the formation of better defined clusters can nevertheless be observed. As the two species *D. abietella* and *D. resiniphila* can be discriminated based on other features, this result should not cause any problems, yet it stresses once more the great overall similarity of male genitalia in the group.

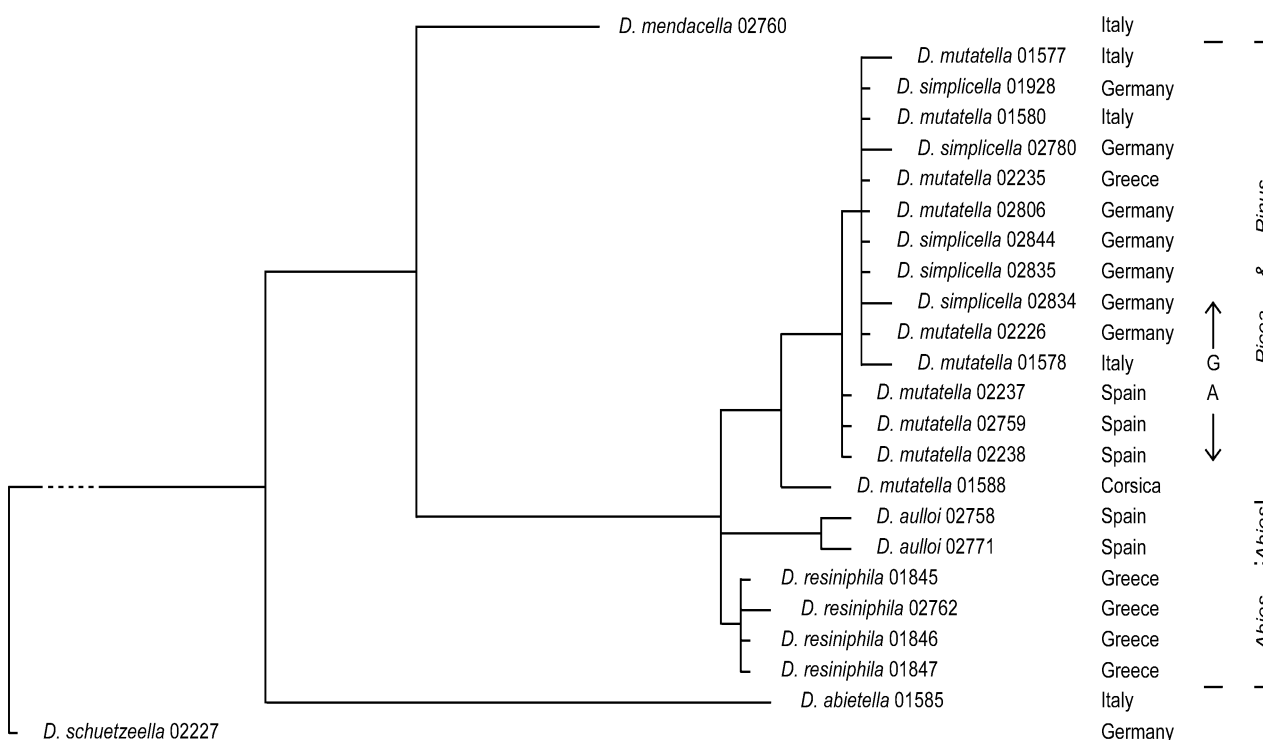
The two specimen of *D. aulloi* fall well into the range of *D. resiniphila* and, again, seem indistinguishable. The addition of further specimens for the underrepresented *D. aulloi* might yield a cluster that overlaps but differs from the one formed by the *D. resiniphila* specimens.

3.5.3.2. COI Sequence Analyses for *D. simplicella* auct and *D. mutabella* auct.

Cladistic analysis of the COI gene was performed in order to test whether molecular data support the conclusions drawn from morphological investigations that *D. simplicella* auct. and *D. mutabella* auct. are indeed synonymous.

Since much of the material investigated was aged or otherwise treated inadequately, only five *D. simplicella* auct., caught between 2001 and 2004, and 10 *D. mutarella* auct. yielded complete COI sequences, and could be subjected to a PAUP run (fig. 3.5.1).

Fig. 3.5.1: Neighbour Joining (NJ) tree of complete COI sequences:



Cladistical analysis

In order to obtain a meaningful cladogram, COI sequences of *D. abietella* (n=1), *D. mendacella* (n=1), *D. aulloi* (n=2), *D. resiniphila* (n=4), and *D. schuetzeella* (n=1), were additionally included. All species, except *D. schuetzeella* representing the *schuetzeella*-group, belong to the *abietella*-group. *D. schuetzeella* was designated as outgroup. The species qualifies as a suitable outgroup, for it is situated basally of the *abietella*-group in all trees calculated from various datasets in this thesis (compare chapter III.4).

A neighbour joining tree (NJ) was obtained (fig.3.5.1) in which all *D. simplicella* auct. and *D. mutarella* auct., except the specimens from Spain (DNATAX-02759, DNATAX-02237 and DNATAX-02238) and one specimen from Corsica (DNATAX-01588), form a terminal polytomy. No sorting of morphotypes was observed, as would be expected for a single species.

The specimens of both *D. resiniphila* and *D. aulloi* cluster separately. In this analysis the branches towards the *D. simplicella* auct./*D. mutarella* auct.-, *D. aulloi*-, and *D. resiniphila*-clusters were unresolved. The pattern of arrangement in the tree confirms again their status as separate species.

*Sequence variation**Variation within the D. simplicella auct. and D. mutabella auct.:*

Nine of the 16 examined *D. simplicella* auct. and *D. mutabella* auct. exhibited identical COI-sequences. Each of the remaining *D. simplicella* auct. and *D. mutabella* auct. specimens exhibited a single point mutation; specimen DNATAX-01588 from Corsica carries seven. As the mutations are not consistent with the two morphotypes, no sequence autapomorphy of any of the two "taxa" could be traced.

The mutations in specimens DNATAX-01578 (pos. 708 A→G) and DNATAX-02834 (position 120 C→T) are silent, individual but different from each other, and of the transition type. The transition type base change in the specimen DNATAX-02780 (position 1504 T→C) results in a replacement mutation leading to an aminoacid substitution from Tyrosine (Y) to Histidine (H).

All these mutations could either be interpreted as individual (as is probable for *D. mutabella* auct. DNATAX-01578), since the two others with the same collecting data lack the mutation), or as a special trait of the local population. This possibility, however, could not be further investigated, because the *D. simplicella* auct. morphotype is very rare, both in collections and in the field.

The three *D. mutabella* auct. specimens from Spain, DNATAX-02237, DNATAX-02238, and DNATAX-02759, are set apart basal-wards in the tree from all other *D. simplicella* auct. and *D. mutabella* auct. specimens investigated. At position 60 of the COI gene, these specimens share, character state "A" instead of "G".

Adenine in position 60 seems to be the plesiomorphic character state, as it is present in all other *Dioryctria* specimens in this study, including those originating deeper in the tree. Although specimen DNATAX-02836 (also from Spain) yielded incomplete sequence (total of 1460 bp in two contingents) and was therefore not included into PAUP analysis, the obtained partial sequence, including position 60, was similar to specimen DNATAX-02759.

Consequently, all investigated specimens from the Iberian Peninsula share the trait "A" with all investigated *D. aulloi*, *D. resiniphila*, and in fact with all known European sequences obtained in this study, whereas all other *D. simplicella* auct. and *D. mutabella* auct. share a character state "G", likely to be derived. Therefore, the fact that all *D. simplicella* auct. and all *D. mutabella* auct. outside Spain and Corsica share the derived character state "G" further hints towards common genetic identity of *D. simplicella* auct. and *D. mutabella* auct.

These results suggest that the sequence differences between *D. simplicella* auct. and *D. mutabella* auct. are caused by intraspecific variation and are not of any taxonomic value. This interpretation is further supported by the fact that the mutation in *D. mutabella* auct. specimen DNATAX-01578 (position 708 A→G) seems to be an individual occurrence, as three additional

D. mutabella auct. specimens with the same collecting data (DNATAX-01576, DNATAX-01577, and DNATAX-01580), lack this transversion.

The three point mutations in specimens DNATAX-01577, DNATAX-01578, DNATAX-02780, and DNATAX02834 result in longer terminal branches.

The accumulation of mutations in specimen DNATAX-01588 is likely to be a result of its geographic isolation as an island inhabitant on Corsica.

The sequence diversion deviation among the two “taxa” of interest amounts to 0.130% at most, whereas the sequence difference between the two representatives of the closely related but distinct species, *D. pineae* and *D. mendacella* (both from Spain), add up to 1.302%. This is tenfold the percentage of the variation between *D. simplicella* auct. and *D. mutabella* auct.

The fact that all *D. simplicella* auct. and all other *D. mutabella* auct. from central Europe share the derived character state “G” further strengthened the concept of *D. simplicella* auct. and *D. mutabella* auct. as being synonymous. In summary, neither morphological traits nor molecular data separated the two taxa *D. simplicella* auct. and *D. mutabella* auct. Therefore, both the morphological and the molecular data show that the former species *D. simplicella* auct. and *Dioryctria mutabella* auct. are indeed morphotypes of the same species.

Even though the statement of Petersen & Gaedike (1980) that *D. simplicella* was a darker variety of *D. mutabella* could be confirmed, *D. simplicella* HEINEMANN, 1865 is the older and therefore valid taxon name.

D. aulloi and *D. resiniphila*

D. aulloi is endemic to Spain and carries six mutations, which are autapomorphic for the species (n=2) (position 72 T→A, position 153 T→C, position 237 A→G, position 996 T→C, position 1164 A→G and position 1182 C→T). The sequence divergence to *D. simplicella* auct. ranges from 0.846% to 1.107%; the sequence divergence to the very similar *D. resiniphila* between 0.651%-0.716%. *D. simplicella* auct. and *D. resiniphila* are separated by a 0.781%-0.911% sequence difference. In position 60, both species carry the plesiomorph character state A.

Morphological traits, larval biology, and distribution in *D. aulloi* support its status as distinct species regardless of the rather small genetic divergence of 1.04% towards *D. simplicella* auct. For example, the shape of the antennal flagellomers differs as they appear extremely serrate (see plate III.81). The possibility that *D. aulloi* and *D. resiniphila* might be subspecies of *D. simplicella* auct. was considered unlikely, since in addition to geographical and genetic properties of the species, the host plants differ on the genus level (*Picea* and *Pinus* for *D. simplicella* auct.; two different species of *Abies* for *D. aulloi* and *D. resiniphila*).

Plate III.8: Male Antennae

scalebars a-c = 1cm
scalebars d-g = 50µm
scalebars h-m = 20µm

- a = scaletuft *D. mendacella* 1(0)
- b = scaletuft *D. abietella* 1(1)
- c = scaletuft *D. robiniella* 1(2)
- d = antennal flagellum *D. schuetzeella*
- e = antennal flagellum *D. aulloi*
- f = antennal flagellum *D. mendacella*
- g = antennal flagellum *D. nivaliensis*
- h = SEM flagellomers *D. abietella*
- i = SEM flagellomers *D. schuetzeella*
- j = SEM flagellomers *D. simplicella* auct.
- k = SEM flagellomers *D. resiniphila*
- l = SEM flagellomers *D. aulloi*
- m = SEM flagellomers *D. mendacella*

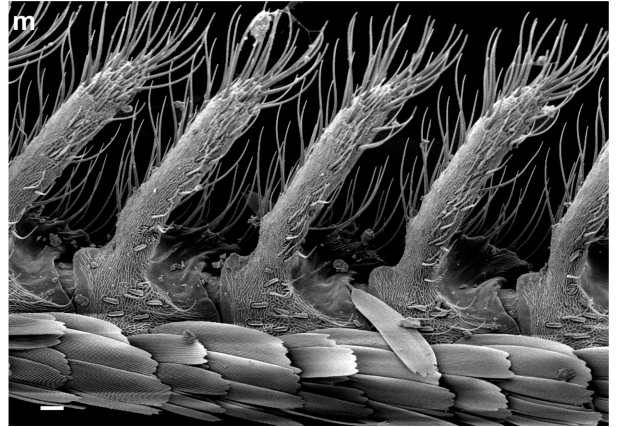
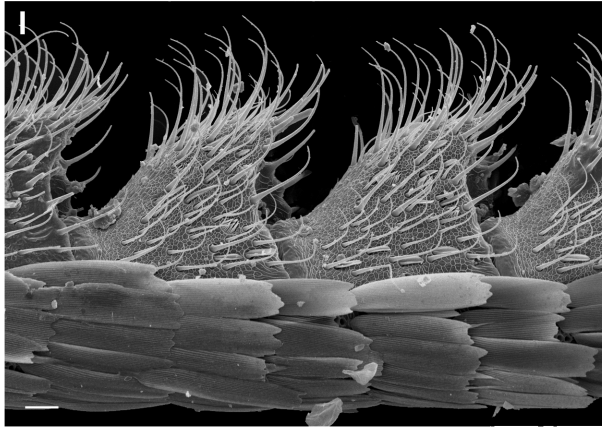
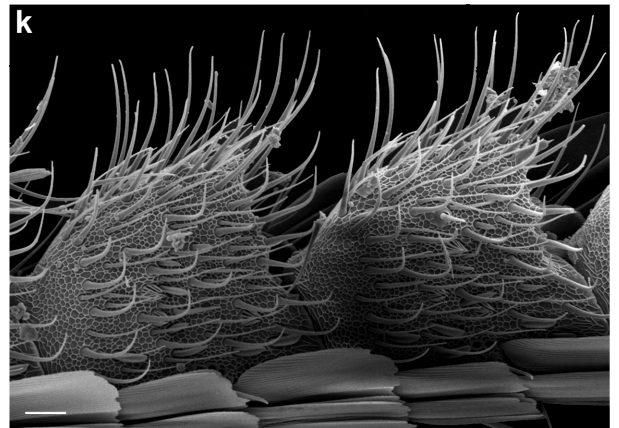
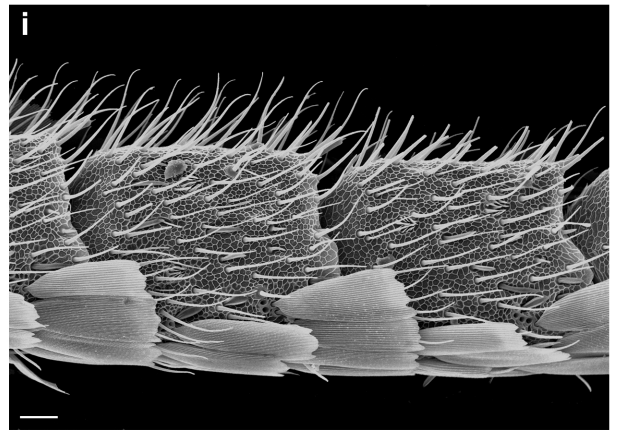
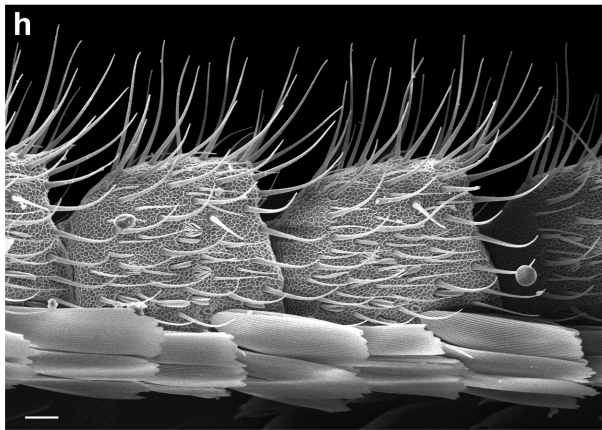
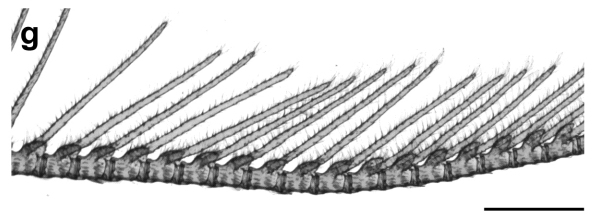
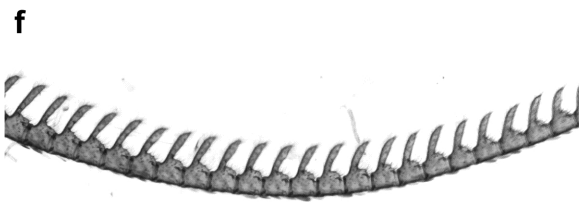
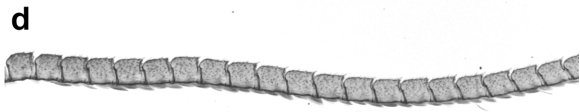
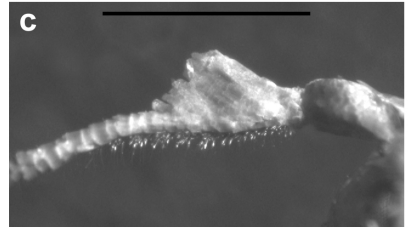
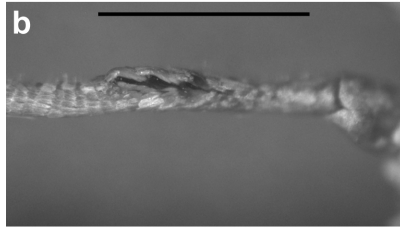
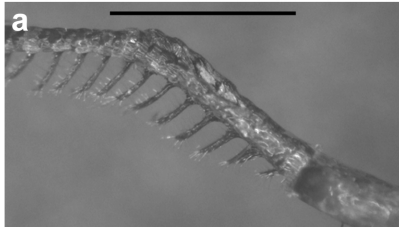


Plate III.9: Apex of Left Valve of *D. simplicella* auct. and *D. mutatella* auct.

● = black specimens (*D. simplicella* auct.);

○ = grey specimens (*D. mutatella* auct.);

scalebar = 100µm

a = *D. mutatella* auct. 10

b = *D. mutatella* auct. 128

c = *D. simplicella* auct. DNATAX01928

d = *D. simplicella* auct. 5291 (Roesler)

e = *D. mutatella* auct. 62

f = *D. simplicella* auct. 28

g = *D. simplicella* auct. 29

h = *D. mutatella* auct. 3

i = *D. mutatella* auct. 55

j = *D. mutatella* auct. 8

k = *D. mutatella* auct. 1

l = *D. mutatella* auct. DNATAX02765

m = *D. simplicella* auct. DNATAX02835

n = *D. mutatella* auct. 77

o = *D. simplicella* auct. DNATAX01929

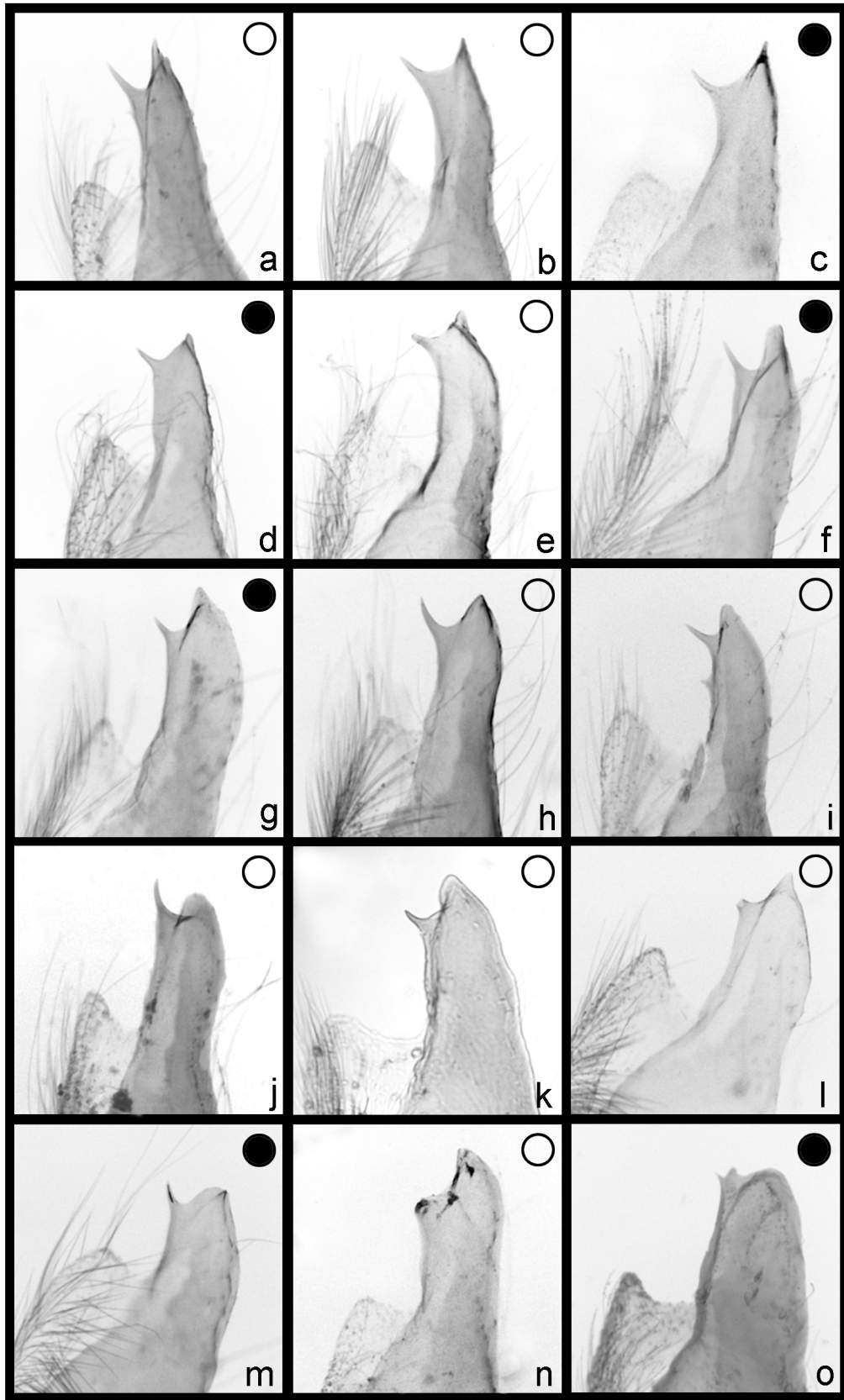


Plate III.9

3.6. Larval Host Plants

To enable meaningful implications regarding larval host plant association, it became obvious that host plant records for all species worldwide required assembling in a first step (see appendix 7).

While the host plant association of the species is reasonably well documented for Europe, no such data was obtainable for 10 of the non-European species.

The overwhelming majority of 56 species dwells in 49 different *Pinus* species. Additional hostplant species are found both inside the Pinaceae (*Abies*, *Tsuga*, *Pseudotsuga*, and *Larix*) and Cupressaceae (*Cupressus*, *Juniperus*, and *Taxodium*). Records of non-gymnosperm hosts include a member of the Fagaceae, *Betula* and the Salicaceae, *Populus*, respectively. In addition to their *Pinus* hosts eight species feed additionally on *Picea*. Seven species feed on *Abies* hosts and *Pinus*.

Two North American species (*D. abietivorella* and *D. reniculleloides*), both polyphagous on number of hosts (see appendix 7), are the only species known to feed on *Larix*. Five species feed on *Pseudotsuga* none of these, however, do so exclusively. Of the species of the *schuetzeella*-group only, *D. reniculleloides* is known from *Pinus*. Both American representatives of the morpho-group are the only ones reported from *Tsuga*. *D. peltieri* and *D. peyerimhoffi* are both monophagous on *Cedrus*. *D. okui* is so far known as oligphagous from three *Picea* species only, while *D. resiniphila* seems monophagous on *Abies cephalonica*. *D. robiniella* is believed to live on *Cupressus*. Should it do so exclusively, it is one of two species that have performed a complete host plant shift into another gymnosperm family, the Cupressaceae. The second species on Cupressaceae is *D. juniperella* on *Juniperus chinensis*.

Range of Pinaceae

An overview of geographical distribution of the genus *Pinus* is given in Mirov (1967). It shows that *Pinus* is essentially restricted to the northern hemisphere. Its range is limited in the North by the arctic regions and in the South by the equator. Only one species *Pinus merkusii* DEVRIES, as an exception, crosses the equator and reaches into the southern hemisphere in south-eastern Asia in one location on Sumatra.

Pinaceae dominate the vegetation of vast tracts of land including forests of the boreal and Pacific regions in North America, the western mountains, the south-eastern coastal plain, and in fact also in the temperate regions of Europe and Asia. Various species, most commonly *Pinus radiata*, have been widely introduced for timber production in sub-Saharan Africa, South America, New Zealand and Australia.

Range of Cupressaceae

It is the most widely distributed of all gymnosperm families, occurring in diverse habitats in all continents except Antarctica. Yet, all genera other than *Juniperus* show strongly relictual distributions, with a large number of localised, rare and endangered taxa. Most of the generic diversity is in the southern hemisphere, but the largest genus, *Juniperus*, is chiefly northern-temperate (Silba 1986, Van Royen 1979).

3.6.1. Biology of Selected European Species

3.6.1.1. *Dioryctria abietella*

The larvae live endophagous, boring in cones of *Picea abies* (Annala 1979, Petersen & Gaedike 1980) and possibly other, related host species. Due to misidentification and confusion with other, similar *Dioryctria* species, records of host plants other than *P. abies* are somewhat dubious and are in need of confirmation, especially when mentioned in older literature. According to Petersen & Gaedike (1980), probably reliable host plants and habits include cones of *Picea glauca*, *Abies alba*, *Abies nordmannia*, *Pseudotsuga menziesii*, and *Larix decidua*, as well as galls of *Sacchiphantes viridis* (RATZEBURG, 1843) on *P. abies* and *L. decidua*. All other records of larval feeding habits and hosts need confirmation.

3.6.1.2. *Dioryctria aulloi*

In the original paper a larva can be seen on an almost entirely defoliated terminal twig at the base of the buds of *Abies pinsapo*. Barbey (1930) reports them to feed inside buds and green shoots. Consequently, defoliation may result from drying of the terminal twigs caused by the internal damage inflicted on the plant by the insect.

3.6.1.3. *Dioryctria nivaliensis*

The misconception of Rebel, who concluded that *D. nivaliensis* was closely related to *D. sylvestrella* and the assumption that followed, the larvae of this species were therefore most likely feeding under the bark needs re-investigation. The host plant species *Pinus canariensis* seems likely, as it is the predominant coniferous tree in the Canary Islands.

3.6.1.4. *Dioryctria schuetzeella*

The larvae live in a silken web among needles and young twigs of *Picea abies* and *Picea glauca* (Petersen & Gaedike 1980). Their external feeding habit is rare among *Dioryctria* and seems to be a derived feature.

3.6.1.5. *Dioryctria simplicella*

The endophagous larvae feed in green cones (Fuchs, 1903), annual twigs and buds of *Pinus sylvestris* (Fuchs 1903, Petersen & Gaedicke 1980), as well as in annual twigs and buds of *Picea glauca* (Petersen & Gaedike 1980).

The original host plant certainly is *Pinus sylvestris* as *Picea glauca* has been introduced to Europe only in the early 18th century (Earle 2006). Possibly the chemical composition (monoterpenes) is similar enough to *Pinus sylvestris* to be tolerated by *D. simplicella*.

IV. Discussion

4.1 Discussion of New Assignments to Morphogroups

Treatment of previously ungrouped species was essentially limited to those that belong to the *abietella*-group, as it was the most intensively studied in this thesis. The definition of the new *okui*-group resulted from inconsistencies encountered within the *auranticella*-group.

4.2 Discussion of the New Morphogroup – *okui*-group

Originally intended as outgroup for analysis of European species, two Japanese species were obtained for investigation both as alcohol preserved and dried specimens. Both species have previously been assigned to the *auranticella*-group.

The *auranticella*-group presently comprises species from India (*D. castanea*), China (*D. yiai*), Japan (*D. juniperella*, *D. okui*, *D. pryeri*), and North America (Canada: *D. rossi*; USA: *D. auranticella*, *D. disclusa*).

The morpho-group was originally defined rather ambiguously by the following characters (Mutuura & Munroe 1972): "Forewings without raised scales, maxillary palpus of male squamous or aigrette-like; antenna of male with or without great expansion of specialized scaling at base; shaft simple, ciliated; colour of the forewing often reddish or orange but in several Asiatic species dark grey. Male genitalia with dorsal part of valve distally short and at most slightly falcate, sometimes with a short postapical accessory tooth. Female genitalia with sclerotized part of ductus bursae short, rarely more than five times as long as wide, usually less, and usually shorter than bursa, sclerotization smooth or weakly striated, proximally with strong lateral lobes and weak median lobe, the median area usually striated or wrinkled proximally; distal part of sclerotization simple, without lateral process. North America and Asia. Larvae mostly on pine but *D. okui* on spruce." For the orientation of the female genitalia description obviously proximal and distal were confounded.

The assignment of *D. okui* to the group rest on the rather succinct remark that "genitalia agree with the present group" (Mutuura & Munroe 1972). Yamanaka (1990) places *D. juniperella* into said group based on his observation that "...the configuration of male and female genitalia is closest to that of *D. okui* ...". Both neglected, however, to specify synapomorphic features.

For the North American species Neunzig (2003) added some new traits and specified a number of existing characters, nevertheless ambiguities remained: "... spinelike processes of basal segments of shaft of the male antenna approximately same size, male maxillary palpus either

with relatively short scales or with long, very slender scales; uncus not constricted at base; valve short and wide; or moderately elongate with costa not produced distally or only weakly produced dorsally, and with, or without, lower, distal, weakly developed spur or spinelike element; Vesica usually with large, solitary cornutus and cluster of smaller cornuti or with only a cluster of small cornuti; ductus bursae with sclerotized part shorter than length of corpus bursae, not curved and without sclerotized, posteriorly directed distal lobe;"

Regarding the four species of the *auranticella*-group included here, the comparison of the tree calculated from morphological and ecological data with the molecular and combined trees confirms that there is enough of a morphological resemblance at first glance among these species to have been placed into a closely related group based on morphological means alone, as done by Mutuura and Munroe (1972).

With a modern molecular technique at hand, however, the classification becomes less clear, if not doubtful. Thorough morphological investigation and phylogenetic analyses of sequence and morphological data as well as the results of Du et al. (2005), who investigated *D. auranticella* and *D. yiai*, raise some doubts about the justification of the *auranticella*-group in its current composition. There are strong indications that the *auranticella*-group is likely to be paraphyletic, and so the remaining species assigned to the group have to be reassessed. This will require ample supplies of fresh material for molecular investigation which was, however, out of the scope of this study.

D. okui and *D. juniperella* form a distinct clade in all trees shown, as well as in trial runs conducted during this study. They are clearly set apart from the North American *D. auranticella* and *D. yiai* from China in the combined and molecular trees. When interpreting this result, indications become apparent that justify the proposal of a new species group, the *okui*-group. The *okui*-group, including *D. okui* and *D. juniperella*, is characterized by the morphological features outlined in chapter 3.3.2. Additionally, they differ regarding their larval feeding habit from the vast majority of the genus in feeding externally on foliage (Mutuura 1958, Mutuura & Munroe 1972, Yamanaka 1990). Evolutionary aspects are discussed separately in greater detail, below.

The fact that, in contrast to the *auranticella*-group, all other included species groups are supported by very good bootstrap values, proves that it is possible to rely upon the tree topologies obtained when it comes to assessing the placement and status of the species included. Furthermore, it is very likely that new species that might be added to the analysis in the future can be grouped as well.

4.3 Discussion of Phylogenetic Analyses

A number of tree calculations were performed in order to be able to assess possible influences of matrix information (i.e. morphological/ecological versus molecular and combination of both). Consistent results from different approaches make it more likely one has found the true relations in those cases. Furthermore, the influence of the addition of the European species on the stability of the group supports and tree topology was investigated.

In a first approach, tree calculations were conducted that were based on morphological and ecological characters exclusively, to test whether the existence of the morpho-groups previously defined can be validated. The challenge to find a sufficient number of characters that are reproducible or even translatable into character coding was considerable. This was mainly due to the fact that the variability of potential characters was rather high compared to the great overall likeness in general appearance of the genitalia features.

Although, the data sets were modified, compared to the ones used by Du et al. (2005), the problems encountered by them regarding the resolution of the relationships between the groups were found to remain, as statistical supports in the relevant parts of the trees were poor or moderately at best. This unsatisfactory intergroup resolution in both the trees from morphological/ecological data, and the exclusively molecular trees may be a consequence of the data that seem insufficient to resolve deeper relationships in the tree. It appears that, taking into consideration the difficulties of expanding the morphological data set, more genes need to be investigated that are capable of unveiling "older" speciation events in the tree. At the time the molecular part of this study was conducted, nuclear genes known to be capable to achieve this were out of reach for this study, as the material at hand was for several species too old to yield sufficient DNA for amplification of nuclear genes, as they are less abundant in the number of copies in the cells. The frail DNA material of some rare species also unfortunately made it impossible to reliably sequence a longer fragment of the mitochondrial genome.

It was interesting to observe that the tree obtained from a combined dataset of morphological/ecological and molecular data was shorter (1091 steps) than the tree of Du et al. (2005) (1255 steps), even though the number of species was increased by nearly 70%. This means that an increase of species can actually improve the degree of consistency in the dataset. It is also possible that the differences in the choice and coding of morphological characters might have had an influence. The same is true for the length of the sequenced DNA fragment, since Du et al. (2005) had included COII in their analyses.

The neighbour joining algorithm was chosen as it is a pure distance based method that fully

resolves the tree and includes the branch lengths into the illustration. Therefore, it emphasises the differences in the *simplicella*-species-complex, as the terminal branches do not have the same lengths and therefore contain information about the differences between the terminal taxa of that difficult species-complex. Since intergroup relationships are not quite consistent with the findings from the parsimony tree, one has to be cautious interpreting these.

The main difference between the Bayesian molecular tree and the parsimony analysis was in the arrangement of the species groups. The finding for *D. juniperella* and *D. okui* differs from the other fully resolved trees in this study and can be viewed as a further indication that information on the species group relations are not quite reliable. To date, there is no hypothesis as to the possible sister-group taxa for the genus. *Oncocera faecella* might be just that, as it not only shows some morphological resemblance, but also is featured in the Bayesian molecular tree supported by a 100% value as closest to the base of the genus *Dioryctria*.

4.3.1 The *abietella*-group

The phylogeny within the *abietella*-group, representing the majority of all European species, could not be resolved on the morphological level, alone. This may be explained by the high degree of morphological resemblance in this particular species group, which reaches as far as virtual identity in the members of the *simplicella*-species-complex. On the other hand, there are also species apparently very well characterized and therefore identifiable by several characters. For example the unipectinate antennae in *D. mendacella*, *D. pineae*, and *D. nivaliensis* coincide with quite distinct forewing characteristics. The new species *D. SK1* could not be included into the cladistic analyses as it failed to yield DNA as a result of its age and the fact that the specimens were set and thus most likely relaxed, a practice detrimental to DNA preservation. It was possible, however, to place it into the *abietella*-group based on morphological features. The *abietella*-group is one of the two largest species groups to date, comprising 19 species, followed by *zimmermani*-group with 17 species. Within the *D. abietella*-group there seems to be a species-flock that is morphologically hard to distinguish, the *simplicella*-species-complex.

4.3.1.1 The *simplicella*-Species-Complex

The species of the *simplicella*-species-complex are almost indistinguishable from each other by means of external morphology, but for a slight yet significantly distinctive character in the shape of the flagellomers of the male antenna that became obvious during investigations for this study. The serration of the flagellomers in *D. aulloi* is most pronounced. It was found to be slightly less so in *D. resiniphila*, and flagellomers of *D. simplicella* auct. are lamellate (see plate III.8).

Generally even the genitalia of the various species within the *simplicella*-species-complex are akin to each other to an extent where safe identification on the species level is impossible. Consequently, it seems very unlikely that an alleged sister-species pair (sensu Roesler) within that group, like *D. simplicella* and *D. mutabella*, should display such clear differences as suggested by Roesler (see below).

In order to gain an overview over the *simplicella*-species-complex and the difficulties it presents, it was necessary to comprehend the in part contradicting literature formerly published. Subsequently, it was possible to re-assess the conclusions drawn by several authors in the light of the results obtained in this study.

D. simplicella auct. and *D. mutabella* auct.

The status of two "taxa" of the *simplicella*-species-complex, *D. simplicella* auct. and *D. mutabella* auct., has been a matter of controversial debate for decades (e.g. Heinemann 1865, Rebel 1901, Fuchs 1903, Roesler 1968, Petersen & Gaedike 1980, Hassler & Speidel 1986, Speidel 1996).

In 1865, Heinemann described *D. simplicella* based on a single female from the area of Frankfurt am Main, Germany. Although its status as a member of the genus *Dioryctria* has been questioned, and the type is lost, it is clear from the description that Heinemann was well aware of the diagnostic characters of the genus *Dioryctria*. According to his description *D. simplicella* has reddish brown-grey and glossy forewings without any pattern. This colouration of the forewings is the most outstanding feature of *D. simplicella* and is quite unusual for *Dioryctria* species. This might be the reason why Rebel (1901) regarded *D. simplicella* as synonym of *Salebriopsis albicilla* HERRICH-SCHÄFFER, 1849. However, he was possibly unaware that Heinemann (1865) knew both, *D. simplicella* and *S. albicilla*. Heinemann's description fits well into the range of variation among the dark *Dioryctria* specimens that were investigated here.

Roesler in 1968 revised the status of *D. simplicella* auct. and re-established its status as a *bona species* by identifying dark-winged specimens of a *Dioryctria* from south-western Germany. He claimed to have found significant differences, discussed in detail below, in the genitalia of his *D. simplicella* and all other German *Dioryctria* species, including *D. mutabella* auct. The latter was described from the Rhine valley in south-western Germany by Fuchs in 1903, as a comparatively small, grey-winged "species" with a general wing pattern corresponding well with that of most *Dioryctria* species, but distinctly different from *D. simplicella* sensu Roesler. However, he could not support his conclusions by investigation of the type-specimens, because the types of both, *D. simplicella* and *D. mutabella* are regarded as lost (Heuser et al. 1971, Horn

et al. 1990). Neither he, nor any other author during the ongoing controversy about this problem did designate neotypes¹.

Later, Petersen & Gaedike (1980) had doubts upon Roesler's interpretation of *D. simplicella* and stated that Heinemann's description most probably does not refer to a *Dioryctria* species. Furthermore, they revised the morphology of both, *D. simplicella* and *D. mutabella* sensu Roesler and were, in contrast to Roesler (loc. cit.), unable to find significant morphological differences. Consequently, they synonymised *D. simplicella* sensu Roesler with *D. mutabella*, regardless of the identity of *D. simplicella*.

Hassler & Speidel (1986), partly following Roesler (1968), revived the discussion about the identity of *D. simplicella*. By compiling the state of knowledge, they tended to regard *D. simplicella* and *D. mutabella* as separate species, based on traits assembled in table 3.5.1.

It was not possible to validate the traits described by Roesler (1968) as diagnostic for *D. simplicella* auct. and *D. mutabella* auct. When trying to reproduce his findings by investigating original material, it turned out that his data were obviously based on misinterpretations:

1. When trying to obtain Roesler's original slides, it became obvious that Hassler and Speidel (1986) were right when they suspect that the traits Roesler (1968) names as diagnostic for *D. simplicella* and *D. mutabella*, were not validated by series of genital slides. The original slides from Roesler's paper along with the rest of his genital slide collection and all but one of the *D. simplicella* specimens known to him at the time are deposited at ZSM and no other slides than the ones mentioned by his publication can be found for *D. simplicella*. The fact that he had not prepared series of genitalia slides is understandable for *D. simplicella*, due to its rareness. However, *D. mutabella* series are also missing although he had a number of specimens available. Investigation of series would have been highly desirable, since individual variation can be misleading especially in a genus like *Dioryctria* comprising of highly similar species.
2. Unfortunately, it was not possible to trace the slide for the male *D. mutabella* specimen GU.-Nr. (U.Roesler) 5299 nor the specimen itself, which has been the reference for his diagnosis published in the paper. There is, however, a second slide of a male GU.-Nr. (U.Roesler) 5306, not published, with features contradicting the validity of his diagnostic traits: the valve exhibits characters which resemble those he himself described as diagnostic for *D. simplicella*.

¹ It was refrained from the designation of neotypes in this study as they should be and will be made in taxonomically available publications.

3. The drawing of the genitalia of a male *D. simplicella* specimen published by Roesler (1968), proved inaccurate when compared to the original slide. This is partly due to the fact that the drawings are idealized interpretations only showing the right valve. Additionally, the membranous parts like the sella are prone to yield artefacts when embedded, and the way of illustrating the genitalia chosen by Roesler fails to show possible artefacts of that nature that become more obvious when they show as asymmetries and left and right side can be compared. Also, the way the slide was prepared might implicate an obstruction of details: After maceration the terminalia were placed as far caudal as possible without detaching them from the abdomen. Thus they are partly still covered by the last segment and the phallus is still inside the last segment. As some traits are obscured that way the slide was dissolved in ethanol 90% and the terminalia subsequently prepared according to established standards.
4. Hassler's and Speidel's (1986) mistakes are likely to be a result of lack of material accessible to them and little knowledge regarding the geographic range of the taxon.

Unfortunately, male specimens of *Dioryctria* are much more scarcely represented in collections. All male *D. simplicella* auct. specimens (n=6) accessible were prepared and a series of females (n=25) as well as sufficient numbers of male (n=26) and female (n=25) *D. mutarella* auct. Although statistical analysis of measurements of the few male *D. simplicella* auct. specimens does not appear meaningful, a substantial amount of individual variation was observed (e.g. plate III.9) that prevent a clear separation of *D. simplicella* auct. and *D. mutarella* auct. Furthermore, artefacts can easily occur during embedding, when three-dimensional structures are forced into a plane. Therefore, one has to be cautious when interpreting positioning of structures like e.g. the membranous sella.

Despite the fact that Roesler (1968) described and illustrated differences in male and female genitalia of both taxa, it was impossible to reproduce his findings. The search for any up to now undetected morphological or ecological differences also did not yield any useful characters.

However, from morphological trees (not shown) alone the con-specificity is not evident, as the included specimens will form two separate clades based on the only discernable morphological character "colouration of forewings."

The polytomy in the strict consensus tree of 18 morphological/ecological trees does not allow for any conclusions regarding the intra-group relations of the *simplicella*-species-complex as it includes all species of the *abietella*-group, i.e. morphologically the entire group is unresolved. When examining the 18 trees separately, of the species of the *simplicella*-species-complex, only for *D. aulloi* and *D. resiniphila* there is a slight indication that they are morphologically closer

related, as in $\frac{2}{3}$ rds of the 18 trees they cluster together. The closeness, but yet separate identity of *D. simplicella* auct., *D. aulloi*, and *D. resiniphila* becomes evident in the molecular and combined trees, as the sister-species relations of the three taxa shift.

All this can be deduced from the entirety of the conducted analysis, not, however, from morphological data alone.

Discussion SPCA

As an objective assessment of morphological features SPCA was selected as the method of choice, as any other statistical analysis of the measurements in order to trace possible significant differences between the investigated morphologically highly similar species did not appear expedient for several reasons. First, the number of specimens for *D. simplicella* auct. (6 male) and *D. aulloi* (1 male) was not sufficient. Second, the comparison of any single measurements in this case is not meaningful, as the individual measured values are too similar and display significant overlap, however in the entirety of the collected data there might be information to be detected in a mathematically objective way. The striking likeness in appearance of the male genitals, as well as the sparse number of reproducible measuring points excludes the use of ratios in this case. In addition, the appropriateness of the employment of ratios for analysis, though a widespread practice in taxonomic investigations, have been disputed (Albrecht 1978, Atchley et al. 1976, Atchley 1978, Atchley & Anderson 1978, Corruccini 1977, Dodson 1978, Hills 1978, Mosimanni & James 1979, Pearson 1897), as ratios result in merits which are not independent and furthermore affect the results of PCAs (=principal component analyses) when included instead of individual measurements. (Atchley et al. 1976).

In contrast to other approaches, in SPCA all original measurements of individual specimens are taken into account, rather than values already modified by e.g. being transformed into means and thus the number of potentially informative data consequently already being reduced. In a case like this, with a limited number of input data the application of altered data hampers or even makes impossible the detection of patterns inherent in the data. Therefore, the measuring data obtained from male genitalia slides were subjected to sheared principal component analysis SPCA (Humphries et al. 1981).

SPAC analysis made it possible to detect and illustrate shape differences and variability of male genitalia based on reproducible measurements. The results show that *D. simplicella* auct. and *D. mutarella* auct. cannot be separated even by carefully chosen metric characters. The smaller variance of *D. simplicella* auct. in PC IV (fig. 3.5.1) is likely to be the result of the sparse number of specimens available.

The employment of PCI in one of the graphs is warrantable, despite the fact that in SPCA it contains most of the size information on the overall dataset, as the size effects can be expected to have an inferior effect in this case. First, no growth effect related to the age of the specimens is to be expected, as these insects are holometabolous and do not grow as imagines. Second, the investigated structures are not only very similar in appearance but also size is not easily assessable as a valid trait because of the substantial overlap between species. In addition, the informational value of the illustration including PCI outweighs the possible inaccuracy of using PCI as a reference point.

Molecular Evidence

The conclusions that could be drawn from the SPCA-analyses conducted herein contradicted Roesler (1968), who claimed that *D. simplicella* and *D. mutarella* were indeed different species. To follow up on this new evidence, all complete COI sequences that could be obtained for *D. simplicella* auct. (five specimens) and *D. mutarella* auct. (10 specimens) were assembled in a molecular dataset. A neighbour joining tree was obtained (fig. 3.5.1) in which the specimens form a terminal polytomy without any sorting of morphotypes, as would be expected for two distinct species.

The majority of the investigated specimens share identical COI sequences. All observed mutations in other specimens are inconsistent with the morphotypes. They can thus be regarded either individual, or a special trait of a local population. These possibilities, however, could not be further investigated, as the dark *D. simplicella*-morphotype is very rare both in collections and in the field, and adequate material was missing.

In summary, all molecular data strongly support that *D. simplicella* auct. and *D. mutarella* auct. form indistinguishable clusters in the phylogenetic analyses and are consequently conspecific, with *D. simplicella* auct. merely representing a melanistic form. It was found, in accord with Petersen & Gaedike (1980), that the morphological traits (see table 3.5.1) allegedly separating *D. simplicella* auct. and *D. mutarella* auct. into two species do not withstand close inspection. Therefore, Heinemanns *D. simplicella* is identified with the dark *Dioryctria simplicella* auct. specimens investigated in this paper, and both species are regarded as synonymous. It is somewhat unfortunate that the older and therefore valid species name and the description is referring to a rare melanistic form of the species.

Ultimately, only molecular investigation proved to be the method of choice to definitively end the debate about the identity of both "taxa." The molecular findings support the SPCA results. The fact that a phylogenetic and in this case also a controversially debated taxonomic problem

could be solved is owed to substantial progress in methodology. These modern methods, applied in this field today, were unavailable to the authors that previously worked on the matter. With the insights gained in the course of this theses it is not astonishing, that it was impossible in the past, to definitively solve this issue.

D. aulloi and *D. resiniphila*

D. aulloi and *D. resiniphila* are Mediterranean endemites feeding on indigenous fir species which occur in scattered stands. The former lives in a few pinpoint locations in southern Spain (larval host: twigs and buds of *Abies pinsapo* (Barbey 1930)). The latter inhabits mountainous fir forests in Greece (larval host: cones of *Abies cephalonica* (Seegerer & Pröse 1997)). Despite the different host plants (*A. cephalonica* and *A. pinsapo* phylogenetically belong to different subgeneric sections within the genus *Abies* (*Abies*-group and *Piceaster*-group) (Earle 2007)), the different larval ecology and feeding habit, and the geographical isolation of both taxa, the moths are extremely similar and virtually indistinguishable both externally and by morphology of their genitalia (Barbey 1930, Seegerer & Pröse 1997, and results presented here), but for the morphology of the male antennae.

More or less the same is true for the pine-feeding taxon *D. simplicella* in its grey form, which is widely distributed throughout Europe. Only minute differences in wing pattern have been described to allow the separation of this species from *D. resiniphila* (Seegerer & Pröse 1997). Due to a broad range of variation of wing pattern and genitalia, these three taxa can even be confused with the taxonomically well-defined *D. abietella* (Petersen & Gaedike 1980); every now and then, specimens of *D. abietella* have been caught in southern Germany that show the characteristic wing pattern of a Mediterranean *D. resiniphila* or *D. aulloi* (Seegerer, personal communication).

Biogeography of the simplicella-Species-Complex

Once a sufficient amount of freshly caught or ideally preserved (e.g. frozen) material will be assembled to enable the gain of more and longer sequence, the *simplicella*-species-complex could provide an interesting model for the study of migration patterns in Europe. Studies that focus on population biology and zoogeographical aspects could be conducted in the future.

For example, the two *D. aulloi* specimens from Spain, although from different locations in the Sierra Nevada retain the same obviously plesiomorphic character state A in position 60 of the COI gene. It is remarkable that the Spanish "*D. mutarella* auct." (= *D. simplicella*), unlike all other investigated specimens from outside the Iberian Peninsula, share that trait.

Interestingly, the genetic composition of *P. sylvestris*, which is a host plant for many *Dioryctria* species including *D. simplicella* is unique and distinct from all other European *P. sylvestris* populations in Spain in general and the region of the Sierra Nevada in particular (Sinclair et al. 1999). Molecular as well as morphological evidence and other methods used in tree taxonomy and phylogeny, strongly suggest that Spanish Scots pine populations represent tertiary relics of the species, and that particularly the Andalusian population is so distinct even from the rest of the Spanish stands that it must have been isolated for a considerable amount of time.

The character state "A" found in the grey *D. simplicella* in Spain might well be a geographical specific, resulting from ice age relict population distributions of the hostplant *Pinus sylvestris* or the moths themselves. Unfortunately, it was not possible to retrieve any DNA from the grey *D. simplicella* specimens available for investigation from the south of France and Italy (province of Liguria). It would be desirable to investigate the position 60 of these specimens from that regions, to evaluate if the "A" nucleotide is present in these adjoined populations as well. The Pyrenees and the western Italian Alps are known contact and hybrid zones for populations that expanded from their areas of refuge after the last ice-age (e.g. Schmitt 2007). If these data are available it is clear that more sequence information needs to be added before propositions can be made about the palaeo-biogeography and possible migration routes. However, this one base pair difference might be a hint towards more evidence that waits to be discovered. If more data should verify evolutionary common developments in Spain, they might be a further indicator for a geographic area that has been isolated for a considerable amount of time. Since the grey form of *D. simplicella* seems wide spread throughout Europe and possibly around the northern half of the Mediterranean, while others seem geographically restricted, this species-complex might even hold more potential for inferences regarding evolutionary and biogeographical processes.

In this study it was generally refrained from giving maps illustration the distribution for any of the species treated. Also statements about species being new to a region were not made. The reasons were that faunistical literature is difficult to survey as a result of the uncertainties regarding the authors abilities to correctly identify the species. To be able to present meaningful maps, information about species distribution would have to be drawn up directly from the specimens and published records would need to be validated by inspection of the specimens themselves, which was impossible in the course of this study.

4.3.1.2. *Dioryctria nivaliensis* and *D. SK1 sp.nov.*

The only moderate bootstrap support of the *abietella*-group in the molecular tree is likely to be a result of the basal-most species in that clade, *D. nivaliensis*. This species is endemic to Tenerife

(Canary Islands) and has newly been placed into the *abietella*-group in this thesis. It is evidently a member of the *abietella*-group based on the results of the phylogenetic analysis presented in this study. As an island species it can be suspected that it accumulated autapomorphies during its time of isolation. This might also be the reason why the three species of the *abietella*-group with unipectinate male antenna do not cluster together in the molecular tree.

Once sequence can be obtained from the new species *D. SKI* from La Palma (also Canary Islands) that is externally very similar to *D. nivaliensis*, a new species-complex from this group of islands could occur.

4.3.2. *Dioryctria robiniella*

A species of great interest is *D. robiniella*, which externally strikingly differs from all other *Dioryctria* by the architecture of its labial palpes and its wing markings (plate III.3g). This western Mediterranean species formed a distinct, though statistically poorly supported branch well within the *Dioryctria* ingroup in all trees. The placement of Speidel and Asselbergs (2000) into the genus *Dioryctria* can thus now be confirmed both by morphological and molecular data. Once the sister-species *D. taiella* from Afghanistan can be included into analyses, the evidence might gain even more strength and a good bootstrap support of the *taiella*-group can be expected, as was observed for the *schuetzeella*-group, after *D. schuetzeella* was added to the group that previously included only *D. renicullelloides* (Du et al. 2005). Morphological features of both *D. robiniella* and *D. taiella* were compared, to rewrite the definition of the *taiella*-group. Due to the lack of fresh material and the impossibility of collecting specimens in Afghanistan owing to the political situation in the region, molecular investigation was impossible and the situation is unlikely to improve in the near future.

4.3.3. Genetic Variation

In the course of this study, position 60 of the COI gene turned out to be of particular interest. This site corresponds to the third, completely degenerate position of a glycine, but was found to be highly conservative in all *Dioryctria* specimens investigated here and by Du et al. (2005), for it is usually represented by an adenine. The only exceptions found so far are nearctic *D. renicullelloides* (Du et al. 2005) and part of the population of *D. simplicella* auct.(this study), where the adenine was found to be substituted by a guanine. The possible zoogeographical implications were discussed above, evolutionary considerations follow.

4.4. Evolutionary Considerations

A number of models have been proposed that deal with the possible evolutionary aspects of ecological traits like larval feeding habit.

An early exhaustive integrative attempt to understand the evolutionary mechanisms involved in host plant insect interaction on a wider scope was presented by Ehrlich and Raven in 1964. Reviewing the literature published until then, they proposed an evolution model known as nearly simultaneous co-evolution (Bucheli et al. 2002) or escape and radiation model (Miller & Wenzel 1995).

Since then, alternative co-evolutionary hypotheses have been developed (e.g. Denno et al. 1995, Feeny 1975, Gaston et al. 1992, Janz & Nylin 1998, Jermy 1976). Bucheli et al. (2002) combined results of the latter four papers to create a synthetic model.

In general, caution is required regarding larger scale inferences for example above family level in Lepidoptera, since phylogenetic relationships in the order have not been resolved. Both Microlepidoptera and Macrolepidoptera are considered polyphyletic, with some superfamilies among Microlepidopterans, including the here relevant Pyraloidea, suspected to belong in closer vicinity to Macrolepidopteran taxa (e.g. Powell 1980).

Finding the "best fit" model for the system of *Dioryctria* required investigation of every aspect of host plant interaction separately at first.

The great majority of the genus *Dioryctria* feeds internally predominantly in gymnosperm cones. *Dioryctria* shares this preference for internal larval feeding with the majority of Microlepidopterans (Powell 1980).

Within Lepidoptera internal feeding was detected as a trend towards specialisation, unlike external feeding which is believed to be linked to generalisation. Internally feeding species do not only have the nutrition provided by the host plant but also the shelter along with potential protection from predators. This should link them more intimately with their host plant.

Insects whose larvae feed on woody hosts are allegedly more open to host plant shift, as the plants defence systems and other chemical properties are believed to be less versatile than in herbaceous plants. Apparently woody plants additionally provide the challenge of being of less nutritional value as potential hosts for insect larvae (Bucheli et al. 2002), which would require a higher degree of specialization in order to survive on them.

The predictions derived from the above for the genus *Dioryctria* would be that it is a specialized genus feeding internally on a narrow range of hosts, protected from predation. On the other hand,

their host association with trees would imply that they should be rather flexible in acceptance of their hosts.

In addition leaf feeders on woody plants should be the least faithful to their host and the most likely to switch their host, according the proposals made by Bucheli et al. (2002). Indeed this can be observed for the three species of the *schuetzeella*-group that are known to feed externally on the foliage of terminal shoots. All three species are polyphagous across the range of Pinacean genera, with *D. reniculleloides* as the only one in the group also on *Larix* and *Pinus*, and *D. schuetzeella* not from *Pseudotsuga* and *Tsuga*. This indeed is coherent with the proposal of Bucheli et al. (2002) regarding the effects of external feeding.

A promotion of speciation among species with externally feeding larvae, as one might expect due to the greater potential mobility of larvae, could not be observed. The results clearly show that in the case of *Dioryctria*, by far more diversity and species numbers are observable among the internal feeders than in the external ones, with species in internally feeding species groups like *abietella*- and *zimmermani*-groups by far outnumbering those of externally feeding ones like *schuetzeella*- and *okui*-groups. Therefore, the evolutionary pace and success in *Dioryctria* was obviously enhanced through internal feeding habit and not by ectophagy. So the selective pressure from predators seems to outweigh the benefits of possible flexibility regarding host plant choice in this case.

V. Abstract – Zusammenfassung

5.1. Abstract

In this thesis, the European representatives of the Lepidopteran genus *Dioryctria* were studied. These moths belong to the Microlepidopteran family of the Pyralidae. The main objective was to determine a phylogenetic placement for the European species. In addition, previously unsolved issues regarding taxon identities and species placement were addressed.

In order to understand the relationships of the European species of the genus *Dioryctria*, comprising to date a total 79 species worldwide, morphological and molecular characters were investigated during the first phase of the study. These morphologically hard to distinguish species are better defined in some cases by their geographical distribution, ecology and larval feeding habits than by morphological means. This frequently leads to difficulties, even for experts, when it comes to precise identification of specimens, which can pose problems of an economic extent, as most species of the genus are serious pests on coniferous trees.

Thorough search yielded adequate morphological and ecological characters for subsequent PAUP analyses and re-description of the European species. In the course of this work a new species from La Palma (Canary Islands) was discovered. A key for all known European species was assembled. Difficulties encountered while trying to resolve the interspecies relationships caused by the great degree of morphological likeness of some species were overcome by the application of gene sequence analyses. For that purpose, complete COI sequences were obtained mainly from dried museum specimens. To achieve this with minimal destruction to the specimens and maximal yield of DNA, a new method was developed and published (Knölke et al. 2005) that allows for DNA extraction in combination with established genitalia dissection standards.

For the first time, the data made it possible to develop a phylogenetic framework for the European species and species groups by employing several runs with both PAUP and MRBAYES algorithms. Thus, the relationships of the European species to each other, as well as their placement into the broader context of selected non-European species could be investigated. Among those non-European species were two Japanese representatives of the problematic and most likely paraphyletic *auranticella*-morphogroup. Those species *D. okui* and *D. juniperella* turned out to belong to a separate, hitherto undescribed morpho-group that was newly established as *okui*-group.

Furthermore, some questions that were up to now subject to considerable debate were addressed and could be answered. *D. robiniella* was confirmed to belong to the genus *Dioryctria*. The formerly ungrouped species, *D. nivaliensis*, was placed into the *abietella*-group, and the same was done for *D. peltieri*, *D. postmajorella*, and the newly found species *D. SK1*. The most outstanding taxonomical problem was presented by two members of the *simplicella*-species-complex. This flock of morphologically highly similar species has been a matter of controversy for decades. The relationships within that flock were solved by employing sheared principal component analyses (SPCA) and COI sequence data. It was thus possible to show that *D. simplicella* HEINEMANN, 1865 and *D. mutarella* FUCHS, 1903 are synonymous.

As a base for conclusive evaluation of results, all known species and their species group assignments, as well as a comprehensive assembly of all relevant host plant associations, were compiled for the first time.

Finally, host plant preferences and feeding habits of the European species were re-evaluated in the light of evolutionary aspects, considering the newly obtained recognition of the phylogenetic context.

5.2. Zusammenfassung

Die vorliegende Arbeit ist der Lepidopteren-gattung *Dioryctria* gewidmet. Diese Motten werden den Mikrolepidopteren zugerechnet. Der Hauptfokus der Untersuchungen war die phylogenetische Einordnung der europäischen Vertreter der Gattung und die Aufklärung bisher ungelöster Probleme bezüglich der Identität einiger Taxa, sowie die Überprüfung der Zugehörigkeit von Arten zur Gattung *Dioryctria*.

Die Gattung beinhaltet derzeit weltweit 79 Arten. In der ersten Phase der Arbeit wurden morphologische und molekulare Daten erhoben, um einen Überblick über die europäischen Arten zu erlangen. Diese morphologisch teils sehr ähnlichen Arten sind in manchen Fällen eher aufgrund ihrer geographischen Verbreitung und ihrer Ökologie mit den Ernährungsanpassungen ihrer Larven voneinander zu unterscheiden, als durch morphologische Merkmale. Dieser Umstand führt regelmäßig zu Schwierigkeiten bei der Artbestimmung, die sogar ökonomische Folgen haben können, da einige Arten der Gattung *Dioryctria* zu den ernstzunehmenden Schädlingen an Koniferen zählen und selbst von Experten nicht immer sicher bestimmt werden können.

Intensive Untersuchungen haben morphologische und ökologische Merkmale hervorgebracht, die sowohl für die Neubeschreibung der europäischen Arten also auch in Auszügen für PAUP-Analysen tauglich waren. In Zuge dieser Arbeit wurde eine neue Art von der Kanarische Insel La Palma entdeckt. Diese morphologischen Daten dienten auch als Grundlage für die Zusammenstellung eines Bestimmungsschlüssels der erstmals alle bekannten europäischen *Dioryctria* Arten berücksichtigt. Zur Lösung der Schwierigkeiten bei der Erkennung zwischenartlicher Beziehungen, die in der großen morphologischen Ähnlichkeit einiger Arten begründet sind, wurde genetische Sequenzinformation hinzugezogen. Zu diesem Zweck wurde die vollständige Cytochrom Oxidase I Sequenz von vorwiegend getrocknetem Museumsmaterial verwendet. Um die Beschädigung der untersuchen Individuen bei der Extraktion minimal zu halten und gleichzeitig maximale DNA Mengen zu erhalten, wurde eine neue Methode zu DNA Extraktion etabliert und vorab veröffentlicht (Knölke et al. 2005). Dabei wird die bei Lepidopteren zur Artbestimmung übliche Genitalpräparation mit der Extraktion der DNA kombiniert.

Die Gesamtheit aller Daten hat es erstmals ermöglicht, die europäischen Arten mit Hilfe von PAUP und MRBAYES Algorithmen in einen phylogenetische Zusammenhang zu bringen. In der Folge war es möglich, die Beziehungen der europäischen Arten untereinander und deren Einordnung in das Umfeld der verfügbaren nicht europäischen Arten zu untersuchen. Unter den

außereuropäische Arten gab es zwei japanische Vertreter, *D. okui* und *D. juniperella*, die bisher in die problematische und höchstwahrscheinlich paraphyletische *auranticella*-Gruppe gestellt worden waren. Diese beiden Arten gehören aufgrund der Ergebnisse dieser Studie jedoch in eine separate Morpho-Gruppe, die hier neu etablierte *okui*-Gruppe.

Auch weitere bislang zuweilen kontrovers diskutierte Fragen konnten beantwortet werden. *D. robiniella* konnte als der Gattung zugehörig bestätigt werden. Die Arten *D. nivaliensis*, *D. peltieri*, *D. postmajorella* und die neue Art *D. SK1*, die bislang keiner Gruppe angehörten, wurden der *abietella*-Gruppe zugeordnet. Das wohl herausragendste Problem jedoch, stellte die Artengruppe um *D. simplicella* dar. Der Artstatus zweier Arten dieses morphologisch so gut wie nicht unterscheidbaren "*simplicella*-species-complex" waren Jahrzehnte lang umstritten. Die Beziehungen in dieser Artengruppe konnten durch "sheared principal component analysis"(SPCA) und COI Sequenzanalysen weitgehend geklärt werden. Es war möglich zu zeigen, daß *D. mutarella* FUCHS, 1903 ein Synonym von *D. simplicella* HEINEMANN, 1865 ist.

Als Grundlage für fundierte Beurteilung der Ergebnisse, wurden alle bekannten Arten zusammengestellt und in ihren Artgruppen zusammengefasst, des weitern wurden für alle Arten die verfügbaren Informationen über deren Wirtspflanzen zusammengestellt.

Abschließend wurde die Wirtspflanzennutzung der europäischen Arten im Hinblick auf evolutionäre Komponenten unter Berücksichtigung der hier gewonnenen Erkenntnisse behandelt.

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Appendix 1: Species and Species-Groups Assembled

<i>Dioryctria</i> species-group	<i>Dioryctria</i> ssp.	grouped by	Type locality	Type held at
<i>abietella</i> -group	<i>D. abietella</i> (DENIS & SCHIFFERMÜLLER, 1775)	Mutuura 1971	Austria, Wienergegend	type lost ¹
Mutuura, Munroe & Ross 1969b	<i>D. abietivorella</i> (GROTHER, 1878)	Munroe 1959	USA, Massachusetts, Amherst	BMNH
Mutuura & Munroe 1972	<i>D. assamensis</i> MUTUURA, 1971	Mutuura 1971	India, Assam, Upper Shillong	CNC
	<i>D. aulloi</i> BARBEY, 1930	Mutuura 1971	Spain, Andalusia, Sierra de las Nieves	MNCN
	<i>D. ebeli</i> MUTUURA & MUNROE, 1979	Mutuura & Munroe 1979	USA, Florida, Columbia Co.	CNC
	<i>D. majorella</i> DYAR, 1919	Mutuura & Neunzig 1986	Mexico, Jalapa	USNM
	<i>D. mendacella</i> (STAUDINGER, 1859)	Mutuura 1971	Spain, Chiclana	MNHU
	<i>D. nivaliensis</i> REBEL, 1892	newly assigned	Spain, Canary Is., Tenerife	NHMW
	<i>D. peltieri</i> JOANNIS, 1908	newly assigned	Algeria, Atlas de Blidah	MNHN
	<i>D. peyerimhoffi</i> JOANNIS, 1921	Mutuura 1971	Algeria	MNHN
	<i>D. pineae</i> (STAUDINGER, 1859)	Mutuura 1971	Spain, Chiclana	MNHU
	<i>D. pinicolella</i> AMSEL, 1962	Mutuura 1971	Guatemala	BMNH.
	<i>D. postmajorella</i> NEUNZIG, 1996	newly assigned	Dominican Republic, Independencia, 3km ESE El Aguacate, north slope Sierra de Baoruco (18-18N, 71-42W), 1980m	CMNH
	<i>D. raoi</i> MUTUURA, 1971	Mutuura 1971	North India, Almora, Ranikhet	CNC
	<i>D. resiniphila</i> SEGERER & PRÖSE, 1997	Segerer & Pröse 1997	Greece, Kefalliniá, Mt. Ainos Oros, 1200m	coll. Segerer
	<i>D. simplicella</i> HEINEMANN, 1865	Segerer & Pröse 1997	Germany, Frankfurt am Main	type lost
	= <i>D. mutarella</i> FUCHS, 1903	Mutuura 1971	Germany, Brandenburg	type lost ²
	<i>D. stenopterella</i> AMSEL, 1960	Mutuura 1971	Iran, Belutschistan, Bender Tchahbahar, 0m	SMNK
	<i>D. sysstratiotes</i> DYAR, 1919	Mutuura 1971	Guatemala, Cayuga	USNM
<i>auranticella</i> -group	<i>D. auranticella</i> (GROTHER, 1883)	Mutuura & Munroe 1972	USA, New Mexico	USNM
Mutuura & Munroe 1972	<i>D. castanea</i> BRADLEY, 1969	Mutuura & Munroe 1972	India, Assam, Um Japung	BMNH
	<i>D. disclosa</i> HEINRICH, 1953	Mutuura & Munroe 1972	USA, North Carolina, Tryon	USNM
	<i>D. pryeri</i> RAGONOT, 1893	Mutuura & Munroe 1972	Japan	USNM
	<i>D. rossi</i> MUNROE, 1959	Mutuura & Munroe 1972	Canada, B.C., Nahun	CNC
	<i>D. yiai</i> MUTUURA & MUNROE, 1972	Mutuura & Munroe 1972	China, Taiwan, Hsien, Miaoli, Tahu Forest	CNC
<i>baumhoferi</i> -group	<i>D. baumhoferi</i> HEINRICH, 1956	Mutuura, Munroe & Ross 1969b	USA, Arizona, Prescott	USNM
Mutuura, Munroe & Ross 1969b	<i>D. cibriani</i> MUTUURA & NEUNZIG, 1986	Mutuura & Neunzig 1986	Mexico, Jalisco, Ciudad Guzmán	CNC
Mutuura & Munroe 1972				

¹ destroyed 1848 by fire in Vienna (Horn et al. 1990)

² transferred to Ent. Ver. Nürnberg - there destroyed (Horn et al. 1990)

Appendix 1: Species and Species-Groups Assembled Continued

	<i>D. clarioralis</i> (WALKER, 1863)	Neunzig 2003	USA, North Carolina, Tryon	BMNH
	<i>D. durangoensis</i> MUTUURA & NEUNZIG, 1986	Mutuura & Neunzig 1986	Mexico, Durango, 10 mi W. Salto, 9000 ft.	CNC
	<i>D. gulosella</i> (HULST, 1890)	Neunzig 2003	USA, New Mexico, Hot Springs	AMNH ex. Rutgers
	<i>D. inyoensis</i> NEUNZIG, 2003	Neunzig 2003	USA, California, Inyo Co., White Mts., Westgard Pass	UCB
	<i>D. muricativorella</i> NEUNZIG, 2003	Neunzig 2003	USA, California, Sonoma Co., 4 mi W Plantation	UCB
	<i>D. pentictionella</i> MUTUURA, MUNROE & ROSS, 1969	Mutuura, Munroe & Ross 1969b	Canada, B.C., Pentiction	CNC
	<i>D. sierra</i> NEUNZIG, 2003	Neunzig 2003	USA, California, Inyo Co., Sierra Nevada, Onion Valley, 9200ft.	LACM
	<i>D. subtracta</i> HEINRICH, 1956	Neunzig 2003	USA, New Mexico, Fort Wingate	USNM
	<i>D. vancouverella</i> MUTUURA, MUNROE & ROSS, 1969b	Mutuura, Munroe & Ross 1969b	Canada, British Columbia, Vancouver	CNC
<i>erythropasa</i> -group Neunzig 2003	<i>D. erythropasa</i> (DYAR, 1914)	Neunzig 2003	Arizona, Chiricahua N. P.	USNM
<i>mongolicella</i> -group Wang & Sung 1982	<i>D. mongolicella</i> WANG & SUNG, 1982	Wang & Sung 1982	N.E. China, Heilungkiang prov. Ai-hui Co.	----
<i>okui</i> -group new group	<i>D. juniperella</i> YAMANAKA, 1990	newly assigned	Japan, Hokkaido, Obihiro	coll. H. Yamanaka
	<i>D. okui</i> MUTUURA, 1958	newly assigned	Japan, Hokkaido, Asahigawa	CNC
<i>ponderosae</i> -group Mutuura, Munroe & Ross 1969b Mutuura & Munroe 1972	<i>D. batesella</i> MUTUURA & NEUNZIG, 1986	Mutuura & Neunzig 1986	Guatemala, Chichicastenango	CNC
	<i>D. hogesi</i> NEUNZIG 2003	Neunzig 2003	USA, California, Mono Co., Nr. Lee Vining, 6700ft.	USNM
	<i>D. martini</i> MUTUURA & NEUNZIG, 1986	Mutuura & Neunzig 1986	Mexico, Durango, 10 mi W. Salto, 9000ft.	CNC
	<i>D. okanaganella</i> MUTUURA, MUNROE & ROSS, 1969	Mutuura, Munroe & Ross 1969b	Canada, B.C., Mt. Knox	CNC
	<i>D. ponderosae</i> DYAR, 1914	Mutuura, Munroe & Ross 1969b	USA, Montana, Lamedeer	USNM
<i>pygmaeella</i> -group Neunzig 2003	<i>D. caesirufella</i> BLANCHARD & KNUDSON, 1983	Neunzig 2003	USA, Texas, Kerr County, Kerville State Park	USNM
	<i>D. pygmaeella</i> RAGONOT, 1887	Neunzig 2003	USA, Florida	MNHN Paris
<i>schuetzeella</i> -group Mutuura & Munroe 1972	<i>D. pseudotsugella</i> MUNROE, 1959	Mutuura & Munroe 1973	Canada, B.C., Lillooet, Seton Lake	CNC
	<i>D. reniculleoides</i> MUTUURA & MUNROE, 1973	Mutuura & Munroe 1973	Canada, B.C., Bull River Road	CNC or BMNH
	<i>D. schuetzeella</i> FUCHS, 1899	Mutuura & Munroe 1973	Germany, Rachlau	type lost ²
<i>sylvestrella</i> -group Mutuura & Munroe 1972	<i>D. kunmingella</i> WANG & SUNG, 1985	Wang & Sung 1985	China, Yunnan, Kunming	Institute of Zoology, Academia Sinica
	<i>D. magnifica</i> MUNROE, 1958	Wang & Sung 1985	China, S. Shensi, Tapaishan in Tsinling	ZFMK
	<i>D. rubella</i> HAMPSON, 1901	Wang & Sung 1985	China, Iles Chusan	BMNH

Appendix 1: Species and Species-Groups Assembled Continued

	<i>D. sylvestrella</i> (RATZEBURG, 1840)	Mutuura & Munroe 1972	Germany, Central Bavaria, Regensburg	type lost ³
	<i>D. yuennanella</i> (CARADJA, 1937)	Wang & Sung 1985	China, Yunnan, Yülingshan, 2800-3200m	Musee D'histoire Naturella "Grigore Antipa" Romania
<i>taiella</i> -group	<i>D. robiniella</i> (MILLIÈRE, 1865)	Speidel & Asselbergs 2000	France, Ardèche, Celles-les-Bains	unknown ⁴
Mutuura & Munroe 1974	<i>D. taiella</i> AMSEL, 1970	Mutuura & Munroe 1974	Afghanistan, Salang Pass, 2100m	SMNK
<i>zimmermani</i> -group	<i>D. albovitella</i> (HULST, 1900)	Neunzig 2003	USA, Colorado	AMNH ex. Rutgers
Mutuura, Munroe & Ross 1969b	<i>D. amatella</i> (HULST, 1887)	Neunzig 2003	USA, Florida	AMNH ex. Rutgers
Mutuura & Munroe 1972	<i>D. banksiella</i> MUTUURA, MUNROE & ROSS, 1969	Mutuura, Munroe & Ross 1969a	Canada, Alberta, Grande Prairie	CNC
	<i>D. cambiicola</i> (DYAR, 1914)	Mutuura, Munroe & Ross 1969a	USA, Montana, Flathead Reservation	USNM
	<i>D. contortella</i> MUTUURA, MUNROE & ROSS, 1969	Mutuura, Munroe & Ross 1969a	Canada, B.C., Barrière	CNC
	<i>D. cuitecensis</i> NEUNZIG, 1990	Neunzig 1990	Mexico, Cuiteco, Chih	BMEUC
	<i>D. delectella</i> (HULST, 1895)	Neunzig 2003	USA, Colorado	AMNH
	<i>D. fordii</i> DONAHUE & NEUNZIG, 2002	Neunzig 2003	USA, California, Kern Co., Lake Isabella, Wofford Heights	LACM
	<i>D. merkei</i> MUTUURA & MUNROE, 1979	Mutuura & Munroe 1979	USA, Florida, Baker Co., Olustee	CNC
	<i>D. monticolella</i> MUTUURA, MUNROE & ROSS, 1969	Mutuura, Munroe & Ross 1969a	Canada, B.C., Magna Bay	CNC
	<i>D. mutuurai</i> NEUNZIG, 2003	Neunzig 2003	USA, California, Placer Co., Ward Creek, 2 mi S Tahoe City, 6,250'	LACM
	<i>D. resinosella</i> MUTUURA, 1982	Neunzig 2003	Canada, Ontario, Angus, Lake Simcoe	CNC
	<i>D. taede</i> SCHABER & WOOD, 1971	Neunzig 2003	USA	USNM
	<i>D. taedivorella</i> NEUNZIG & LEIDY 1989	Neunzig 2003	USA, North Carolina, Lenoir County, Kinston	USNM
	<i>D. tumicolella</i> MUTUURA, MUNROE & ROSS 1969	Mutuura, Munroe & Ross 1969a	Canada, B.C., Summerland	CNC
	<i>D. westerlandi</i> DONAHUE & NEUNZIG, 2002	Neunzig 2003	USA, California, Placer Co., 2 mi S of Tahoe City, Ward Creek	LACM
	<i>D. yaetsi</i> MUTUURA & MUNROE, 1979	Mutuura & Munroe 1979	USA, Virginia, Rockbridge Co.	CNC
	<i>D. zimmermani</i> (GROTHER, 1877)	Mutuura, Munroe & Ross 1969a	Canada, Ontario, Toronto	BMNH
incertae sedis	<i>D. actualis</i> (HULST, 1886)		USA, Colorado	
	<i>D. adamsi</i> NEUNZIG & DOW, 1993		Belize, Mountain Pine Ridge, Privacion Line	LCD NCSU USNM
	<i>D. dominguensis</i> NEUNZIG, 1996	possibly <i>zimmermani</i>-group	Dominican Republic, Independencia, 3km ESE El Aguacate, north slope Sa. de Baoruco (18-18N, 71-42W), 1980m	CMNH
	<i>D. horneana</i> (DYAR, 1919)		Cuba, Santiago de las Vegas	USNM
incertae sedis no in the genus	<i>D. symphoniella</i> HAMPSON, 1899		India, Assam, Khasi Hills	BMNH ⁵

³ destroyed during World War II (Horn et al. 1990)

⁴ whereabouts of pyralid collection unknown (Horn et al. 1990)

⁵ Horn et al. 1990

Appendix 1: Species and Species-Groups Assembled Continued

Abbreviations of collections and institutes holding type specimens

AMNH	American Museum of Natural History, NYC, NY, USA
BMEUC	Bohart Museum of Entomology, University of California, Davis, CA, USA
BMNH	British Museum of Natural History, London, UK
CMNH	Carnegie Museum of Natural History, Pittsburgh, PA, USA
CNC	Canadian National Collection, Ottawa, Canada
LACM	Natural History Museum of Los Angeles County, Los Angeles, CA, USA
MNCN	Museo Nacional de Ciencias Naturales, Madrid, Spain
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MNHU	Museum für Naturkunde der Humboldt Universität zu Berlin, Berlin, FRG
NHMW	Naturhistorisches Museum Wien, Vienna, Austria
SMNK	Staatliches Museum für Naturkunde Karlsruhe, FRG
UCB	University of California, Berkley, CA, USA
USNM	Smithsonian National Museum of Natural History, Washington D.C., USA
ZFMK	Zoologisches Forschungsinstitut und Museum Alexander König, Bonn, FRG

Appendix 2: Compilation of Voucher Specimens' Data

Species	GenBank No.	DNA TAX	Collecting data	sex
<i>D. abietella</i>	appendix 3	01570	Germany, 2002, (ZSM)	♀
<i>D. abietella</i>	appendix 3	01571	Germany, 2002, (ZSM)	--
<i>D. abietella</i>	appendix 3	01574	Italy, Brescia, Limone, Voltino de Tremosine, Lf, 650m, 4.vii.2002, leg. Segerer (ZSM)	♀
<i>D. abietella</i>	appendix 3	01575	Italy, Brescia, Limone, Voltino de Tremosine, Lf, 650m, 4.vii.2002, leg. Segerer (ZSM)	♂
<i>D. abietella</i>	AJ 868572	01585	Italy, Brescia, Limone, Voltino de Tremosine, Lf, 650m, 4.vii.2002, leg. Segerer (ZSM)	♂
<i>D. abietella</i>	appendix 3	01595	Italy, Brescia, Limone, Voltino de Tremosine, Lf, 650m, 4.vii.2002, leg. Segerer (ZSM)	♂
<i>D. abietella</i>	appendix 3	01596	Italy, Brescia, Limone, Voltino de Tremosine, Lf, 650m, 4.vii.2002, leg. Segerer (ZSM)	♀
<i>D. abietella</i>	appendix 3	02772	USSR, SW-Altai, Katun valley 10km W Katanda, 1200m, 6.-8.vii.1983, leg. Exp. Mikkola, Hippa & Jalava (ZMUH)	♀
<i>D. abietella</i>	appendix 3	02773	Germany, Regensburg, Kumpfmühl, Lf, 25.viii.2003, leg. Segerer (ZSM)	♂
<i>D. abietella</i>	appendix 3	02799	USSR, Kazakhstan, Zailiskiy Alai, Alma-Atinskiy, Nat-P. 43°5'N*77°15'E, <i>Picea</i> meadow, ad luc., 22.vi.1990, leg. Lkaila & K. Mikkola (ZMUH)	♀
<i>D. abietella</i>	appendix 3	02808	China, Gansu, Min-Shan, ~50km to west from Wu Du, 33°30'N 104°35'E, ~2350m, 27.vii.-14.viii.2000, leg. Plutenko & Siniaev	♀
<i>D. abietivorella</i>	appendix 3	02843	Canada, British Columbia, Fraser Plateau, Clinton, B.C., Lf, 1000m, 27.vi.2004, leg. R. Beck & A. Segerer (ZSM)	♂
<i>D. aulloi</i>	appendix 3	02758	Spain, Andalusien, Sa. Bermeija Reales, Paseo de los pinsapos, Lf, 1155m, 5.viii.2003, leg. Segerer (ZSM)	♀
<i>D. aulloi</i>	appendix 3	02771	Spain, Andalusien, Sa. Bermeija, Reales, Pasea de los pinsapos, Lf, 1155m, 5.viii.2003, leg. Segerer (ZSM)	♂
<i>D. mutatella</i>	appendix 3	01576	Italy, Brescia, Limone, Voltino de Tremosine, Lf, 650m, 4.vii.2002, leg. Segerer (ZSM)	♀
<i>D. mutatella</i>	appendix 3	01577	Italy, Brescia, Limone, Voltino de Tremosine, Lf, 650m, 4.vii.2002, leg. Segerer (ZSM)	♀
<i>D. mutatella</i>	appendix 3	01578	Italy, Brescia, Limone, Voltino de Tremosine, Lf, 650m, 4.vii.2002, leg. Segerer (ZSM)	♂
<i>D. mutatella</i>	appendix 3	01580	Italy, Brescia, Limone, Voltino de Tremosine, Lf, 650m, 4.vii.2002, leg. Segerer (ZSM)	♀
<i>D. mutatella</i>	appendix 3	01588	Corsica, 900m above Evisa, 16.viii.1998, leg. O. Karsholt	♀
<i>D. mutatella</i>	appendix 3	02226	Germany, Württemberg Federseemoor Wildes-Ried, 580m, 26.viii.2000, leg. G. Baisch	♂
<i>D. mutatella</i>	appendix 3	02235	Greece, Pindos Oros Katara-Paß, Lf, 1500-1700m, 29.vi.1997, leg. G.Baisch	♀
<i>D. mutatella</i>	appendix 3	02237	Spain, süd Sierra Nevada Routa de Veleta, LF, 2300m, 14.vii.1991, leg. G.Baisch	♀
<i>D. mutatella</i>	appendix 3	02238	Spain centr. Montes Universales Prov. Cuenca Guadalaviar, 1600m, 06.viii.1991, leg. G.Baisch	♂
<i>D. mutatella</i>	appendix 3	02759	Spain, Andalusien Sierra Nevada, Ruta del Veleta, Lf, 2040m, 7.viii.2003, leg. Segerer (ZSM)	♀
<i>D. mutatella</i>	appendix 3	02806	Germany, Niedersachsen, SFA: Wietzendorf, Lf, 12.viii.2003, leg. Chr. Kayser (ZSM)	♀
<i>D. mutatella</i>	--	02836*	Spain, Prov. Granada, Sierra Nevada ober Mecina-Alfahar, 1900m, Lf, 24.vii.1996, leg. Pöll	♀
<i>D. simplicella</i>	appendix 3	01928	Germany, Brandenburg, Jänschwalde/Ost, 27.vi.2001, leg. A. Stübner	♂
<i>D. simplicella</i>	appendix 3	02780	Germany, Niedersachsen, SFA: Wietzendorf, Lf, 3.ix.2002, leg. Ch. Kayser	♀
<i>D. simplicella</i>	appendix 3	02834	Germany, Occ, Saarland, Limbach, Gackelsberg, Lf, 13.vi.2003, leg. A.Werno	♀
<i>D. simplicella</i>	appendix 3	02835	Germany, Occ, Saarland, Limbach, Gackelsberg, Lf, 13.vi.2003, leg. A.Werno	♂
<i>D. simplicella</i>	appendix 3	02844	Germany, Baden-Württemberg, Wiesental NSG Frankreich, 8°29'59"E * 49°13'50" N, Lf, 112m, 3.viii.2004, leg. Segerer & Knölke (ZSM)	♀
<i>D. resiniphila</i>	AJ 871091	01845	Greece, Phokia, Parnassos Oros, Stavromenos Elatos, Lf, 1300m, 10.viii.2002, leg. Segerer & Knölke (ZSM)	♀
<i>D. resiniphila</i>	appendix 3	01846	Greece, Phokia, Parnassos Oros, Stavromenos Elatos, Lf, 1300m, 10.viii.2002, leg. Segerer & Knölke (ZSM)	♀

Appendix 2: Compilation of Voucher Specimens' Data Continued

<i>D. resiniphila</i>	appendix 3	01847	Greece, Phokia, Parnassos Oros, Stavromenos Elatos, Lf, 1300m, 10.viii.2002, leg. Segerer & Knölke (ZSM)	♂
<i>D. resiniphila</i>	appendix 3	02762	Greece, Peleponnes, 10km östl. Kalavrita Vrachni, Lf, 1400m, 28.viii.2002, leg. G. Baisch	♂
<i>D. mendacella</i>	appendix 3	01556	Greece, Rhodos, 5km S Rhodos, 250m, 04.-08.vii.2000, leg. M.Fibiger	♂
<i>D. mendacella</i>	appendix 3	01592	Cyprus, Platres, N.Limasol, 1150m, 23.-26.VI.1997, leg. M.Fibiger, A.Madsen, D.Nilsson, P.Svedsen	♂
<i>D. mendacella</i>	appendix 3	01594	Cyprus, Moniatis n. Limassol, 850m, 23.-29.vi.1997, leg. M.Fibiger, A.Madsen, D.Nilsson, P. Svendsen	♂
<i>D. mendacella</i>	appendix 3	02760	Spain, Andalusien, Sierra Grazalema, Grazalema, Lf, 957m, 6.viii.2003, leg. Segerer (ZSM)	♂
<i>D. mendacella</i>	appendix 3	02774	Spain, Andalusien, Sierra de la Grazalema, Lf, 957m, 6.viii.2003, leg. Segerer (ZSM)	♂
<i>D. mendacella</i>	appendix 3	02801	Greece, Kreta, Ag. Joannis, b.Koutsou. N. Lassithi, Lf, 390m, leg. W. Ruckdeschel (ZSM)	♂
<i>D. pineae</i>	appendix 3	02225	Italy, Apulien Prov. Lecce Marina di Ugento / Torre S Giovanni Robinsonclub, 29.iv.2000, leg. R. Keller	♂
<i>D. nivaliensis</i>	appendix 3	02807	Spain, Teneriffa, Las Lagunetas, pine forest, 1400m, ix.2002, leg. M. Báez (ZSM)	♂
<i>D. schuetzeella</i>	AJ 868570	02089	Germany, Regensburg, Kallmünz Ginlitzhof, Lf, 18.vi.2002, leg. Segerer (ZSM)	♂
<i>D. schuetzeella</i>	appendix 3	02227	Germany, Schwäbische alb Schmiechen- Halde bei Teuringshofen, 12.vii.2002, leg. G. Baisch	♂
<i>D. reniculelloides</i>	DQ247734	--	Canada, Fort McMurrey, Alberta, 2001, leg. A. Roe	--
<i>D. auranticella</i>	DQ247736	--	USA, Placerville, El Dorado Co., California, 2001, leg. A. Roe	--
<i>D. yiai</i>	DQ247737	--	China, Mt.Xiaowutai, Province Hebei. 2000, Y. Du	--
<i>D. okui</i>	AJ868569	01844	Japan, Hokkaido, Bibai, coll. 28.vi. em. 9.vii.2002, leg. H. Hara (ZSM)	♂
<i>D. juniperella</i>	AJ868571	01848	Japan, Hokkaido, Atsuma, larva coll. 4.vii.2002, host <i>Juniperus chinensis</i> var. <i>sargentii</i> , em. 12.vi.2002, leg. K. Tokikura (ZSM)	♂
<i>D. sylvestrella</i>	appendix 3	01565	Germany, Bavaria centr. Schwandorf Bruck/Opf St. Hubertus Sandgrube, Lf, 26.vii.1998, leg. Segerer (ZSM)	♂
<i>D. sylvestrella</i>	DQ247745	02087	Germany, Landshut/ Bay Postau, Unholzing, Lf, 23.vii.2002, leg. H. Kolbeck (ZSM)	♂
<i>D. sylvestrella</i>	appendix 3	02088	Germany, Landshut/ Bay Postau, Unterköllnbach, Lf, 3.viii.2002, leg. H. Kolbeck (ZSM)	♂
<i>D. sylvestrella</i>	appendix 3	02228	Italy, Ligurien Imperia-Testico, 800m, 08.ix.1990, leg. G. Baisch	♂
<i>D. sylvestrella</i>	appendix 3	02230	Greece, Peleponnes, Olympia, 15.-20.v.1981, leg. G. Baisch	♂
<i>D. sylvestrella</i>	appendix 3	02231	Turkey, Canakkale Kurudaghi Gec, Lf, 350m, 01.vii.1997, leg. G. Baisch	♂
<i>D. sylvestrella</i>	appendix 3	02798	Germany, regensburg, Kumpfmühl, Lf, 20.viii.2003, leg. Segerer	♂
<i>D. rubella</i>	DQ247743	--	China, Mt Baxian Tianjin, 2001, leg. H. Li	--
<i>D. magnifica</i>	DQ247742	--	China, Mt Baiyun, Province Henan, 2002, leg. X. Wang	--
<i>D. robiniella</i>	appendix 3	02995	Marocco, Tahanaoute, Tizi-n-Tagatout, Cedruswald, 1800m, B: 31,26367 L:7,8806, 20.v.2005, leg. A.Werno	♀
<i>D. clariolaris</i>	DQ247732	--	USA, Tishomingo Co., Mississippi, 1994, leg. R.Kergosien	--
<i>D. ponderosae</i>	DQ247733	--	USA, Sierra Diabolo, Texas, 1973, leg D.C. Ferguson	--
<i>D. zimmermani</i>	DQ247730	--	USA, Hinds Co., Mississippi, 1994, leg. M.E.Poshore	--
<i>D. taedivorella</i>	DQ247731	--	USA, Grasonvilly, Maryland, 1986, D.C. Ferguson	--
<i>D. tumicolella</i>	DQ247729	--	USA, CrawfordCo., Kansas, 2002, leg K.O. Bell	--
<i>Aphomia sociella</i>	appendix 3	02998	Germany, Bavaria, Schlagenhofen am Wörthsee, 22.vi.2006, leg. K. Ambil	♂
<i>Ceroprepes. ophthalmicella</i>	DQ247728	--	China, Mt Baiyun, Province Henan, 2002, leg. X. Wang	--
<i>Oncocera. faecella</i>	DQ247727	--	China, Mt Manhan, inner Mongolia, 2002, leg. D. Zhang	--

* = partial sequence

Appendix 3: European Sequences of Molecular Character Matrix

		1	2	3	4	5	6	7	8	9	0	1	2
<i>D. abietella</i>	(DNATAX01570)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. abietella</i>	(DNATAX01571)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. abietella</i>	(DNATAX01574)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. abietella</i>	(DNATAX01575)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. abietella</i>	(DNATAX01595)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. abietella</i>	(DNATAX01596)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. abietella</i>	(DNATAX02772)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. abietella</i>	(DNATAX02773)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. abietella</i>	(DNATAX02799)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. abietella</i>	(DNATAX02808)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. abietivorella</i>	(DNATAX02843)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. aulloi</i>	(DNATAX02758)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. aulloi</i>	(DNATAX02771)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. mendacella</i>	(DNATAX01556)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. mendacella</i>	(DNATAX01592)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. mendacella</i>	(DNATAX01594)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. mendacella</i>	(DNATAX02760)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. mendacella</i>	(DNATAX02774)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. mendacella</i>	(DNATAX02801)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. nivaliensis</i>	(DNATAX02807)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. pineae</i>	(DNATAX02225)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. resiniphila</i>	(DNATAX01846)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. resiniphila</i>	(DNATAX01847)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. resiniphila</i>	(DNATAX02762)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. schuetzeella</i>	(DNATAX02227)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. simplicella</i> auct.	(DNATAX01928)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. simplicella</i> auct.	(DNATAX02780)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. simplicella</i> auct.	(DNATAX02834)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. simplicella</i> auct.	(DNATAX02835)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. simplicella</i> auct.	(DNATAX02844)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. mutabella</i> auct.	(DNATAX01576)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. mutabella</i> auct.	(DNATAX01577)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. mutabella</i> auct.	(DNATAX01578)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. mutabella</i> auct.	(DNATAX01580)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. mutabella</i> auct.	(DNATAX01588)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. mutabella</i> auct.	(DNATAX02226)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. mutabella</i> auct.	(DNATAX02235)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. mutabella</i> auct.	(DNATAX02237)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. mutabella</i> auct.	(DNATAX02238)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. mutabella</i> auct.	(DNATAX02759)	c	g	a	a	a	a	a	t	t	t	t	t
<i>D. mutabella</i> auct.	(DNATAX02806)	c	g	a	a	a	a	a	t	t	t	t	t

Appendix 3: European Sequences of Molecular Character Matrix Continued

			1	2	3	4	5	6	7	8	9	0	1	2	
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	
<i>D. sylvestrella</i>	(DNATAX01565)	cg	g	a	a	a	a	t	g	a	a	a	a	a	a
<i>D. sylvestrella</i>	(DNATAX02088)	cg	g	a	a	a	a	t	g	a	a	a	a	a	a
<i>D. sylvestrella</i>	(DNATAX02228)	cg	g	a	a	a	a	t	g	a	a	a	a	a	a
<i>D. sylvestrella</i>	(DNATAX02230)	cg	g	a	a	a	a	t	g	a	a	a	a	a	a
<i>D. sylvestrella</i>	(DNATAX02231)	cg	g	a	a	a	a	t	g	a	a	a	a	a	a
<i>D. sylvestrella</i>	(DNATAX02798)	cg	a	a	a	a	a	t	g	a	a	a	a	a	a
<i>D. robinella</i>	(DNATAX02995)	cg	a	a	a	a	a	t	g	a	a	a	a	a	a
<i>A. sociella</i>	(DNATAX02998)	cg	a	a	a	a	a	t	g	a	a	a	a	a	a
<i>D. abietella</i>	(DNATAX01570)	c	t	g	g	a	t	c	t	t	a	a	t	t	t
<i>D. abietella</i>	(DNATAX01571)	c	t	g	g	a	t	c	t	t	a	a	t	t	t
<i>D. abietella</i>	(DNATAX01574)	c	t	g	g	a	t	c	t	t	a	a	t	t	t
<i>D. abietella</i>	(DNATAX01575)	c	t	g	g	a	t	c	t	t	a	a	t	t	t
<i>D. abietella</i>	(DNATAX01595)	c	t	g	g	a	t	c	t	t	a	a	t	t	t
<i>D. abietella</i>	(DNATAX01596)	c	t	g	g	a	t	c	t	t	a	a	t	t	t
<i>D. abietella</i>	(DNATAX02772)	c	t	g	g	a	t	c	t	t	a	a	t	t	t
<i>D. abietella</i>	(DNATAX02773)	c	t	g	g	a	t	c	t	t	a	a	t	t	t
<i>D. abietella</i>	(DNATAX02799)	c	t	g	g	a	t	c	t	t	a	a	t	t	t
<i>D. abietella</i>	(DNATAX02808)	c	t	g	g	a	t	c	t	t	a	a	t	t	t
<i>D. abietivorella</i>	(DNATAX02843)	c	t	g	g	a	t	c	t	t	a	a	t	t	t
<i>D. aulloi</i>	(DNATAX02758)	c	t	g	g	a	t	c	t	t	a	a	t	t	t
<i>D. aulloi</i>	(DNATAX02771)	c	t	g	g	a	t	c	t	t	a	a	t	t	t
<i>D. mendacella</i>	(DNATAX01556)	c	t	g	g	a	t	c	t	t	a	a	t	t	t
<i>D. mendacella</i>	(DNATAX01592)	c	t	g	g	a	t	c	t	t	a	a	t	t	t
<i>D. mendacella</i>	(DNATAX01594)	c	t	g	g	a	t	c	t	t	a	a	t	t	t
<i>D. mendacella</i>	(DNATAX02760)	c	t	g	g	a	t	c	t	t	a	a	t	t	t
<i>D. mendacella</i>	(DNATAX02774)	c	t	g	g	a	t	c	t	t	a	a	t	t	t
<i>D. mendacella</i>	(DNATAX02801)	c	t	g	g	a	t	c	t	t	a	a	t	t	t
<i>D. nivaliensis</i>	(DNATAX02807)	c	t	g	g	a	t	c	t	t	a	a	t	t	t
<i>D. pineae</i>	(DNATAX02225)	c	t	g	g	a	t	c	t	t	a	a	t	t	t
<i>D. resiniphila</i>	(DNATAX01846)	c	t	g	g	a	t	c	t	t	a	a	t	t	t
<i>D. resiniphila</i>	(DNATAX01847)	c	t	g	g	a	t	c	t	t	a	a	t	t	t
<i>D. resiniphila</i>	(DNATAX02762)	c	t	g	g	a	t	c	t	t	a	a	t	t	t
<i>D. schuetzeella</i>	(DNATAX02227)	c	t	g	g	a	t	c	t	t	a	a	t	t	t
<i>D. simplicella</i> auct.	(DNATAX01928)	c	t	g	g	a	t	c	t	t	a	a	t	t	t
<i>D. simplicella</i> auct.	(DNATAX02780)	c	t	g	g	a	t	c	t	t	a	a	t	t	t
<i>D. simplicella</i> auct.	(DNATAX02834)	c	t	g	g	a	t	c	t	t	a	a	t	t	t

Appendix 3: European Sequences of Molecular Character Matrix Continued

	1		2		3		4		5		6		7		8		9		0		1		2		3		4	
	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9
<i>D. simplicella</i> auct. (DNATAX02835)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. simplicella</i> auct. (DNATAX02844)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. mutatella</i> auct. (DNATAX01576)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. mutatella</i> auct. (DNATAX01577)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. mutatella</i> auct. (DNATAX01578)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. mutatella</i> auct. (DNATAX01580)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. mutatella</i> auct. (DNATAX01588)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. mutatella</i> auct. (DNATAX02226)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. mutatella</i> auct. (DNATAX02235)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. mutatella</i> auct. (DNATAX02237)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. mutatella</i> auct. (DNATAX02238)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. mutatella</i> auct. (DNATAX02759)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. mutatella</i> auct. (DNATAX02806)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. sylvestrella</i> (DNATAX01565)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. sylvestrella</i> (DNATAX02088)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. sylvestrella</i> (DNATAX02228)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. sylvestrella</i> (DNATAX02230)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. sylvestrella</i> (DNATAX02231)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. sylvestrella</i> (DNATAX02798)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. robiniiella</i> (DNATAX02995)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>A. sociella</i> (DNATAX02998)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. abietella</i> (DNATAX01570)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. abietella</i> (DNATAX01571)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. abietella</i> (DNATAX01574)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. abietella</i> (DNATAX01575)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. abietella</i> (DNATAX01595)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. abietella</i> (DNATAX01596)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. abietella</i> (DNATAX02772)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. abietella</i> (DNATAX02773)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. abietella</i> (DNATAX02799)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. abietella</i> (DNATAX02808)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. abietivorella</i> (DNATAX02843)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. aulloi</i> (DNATAX02758)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. aulloi</i> (DNATAX02771)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. mendacella</i> (DNATAX01556)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c
<i>D. mendacella</i> (DNATAX01592)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c

Appendix 3: European Sequences of Molecular Character Matrix Continued

		2									3									3
		4	5	6	7	8	9	0	1	2	3	4	5	6						4
		1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9
<i>D. mendacella</i>	(DNATAX01594)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. mendacella</i>	(DNATAX02760)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. mendacella</i>	(DNATAX02774)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. mendacella</i>	(DNATAX02801)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. nivaliensis</i>	(DNATAX02807)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. pineae</i>	(DNATAX02225)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. resiniphila</i>	(DNATAX01846)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. resiniphila</i>	(DNATAX01847)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. resiniphila</i>	(DNATAX02762)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. schuetzeella</i>	(DNATAX02227)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. simplicella</i> auct.	(DNATAX01928)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. simplicella</i> auct.	(DNATAX02780)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. simplicella</i> auct.	(DNATAX02834)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. simplicella</i> auct.	(DNATAX02835)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. simplicella</i> auct.	(DNATAX02844)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. mutatella</i> auct.	(DNATAX01576)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. mutatella</i> auct.	(DNATAX01577)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. mutatella</i> auct.	(DNATAX01578)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. mutatella</i> auct.	(DNATAX01580)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. mutatella</i> auct.	(DNATAX01588)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. mutatella</i> auct.	(DNATAX02226)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. mutatella</i> auct.	(DNATAX02235)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. mutatella</i> auct.	(DNATAX02237)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. mutatella</i> auct.	(DNATAX02238)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. mutatella</i> auct.	(DNATAX02759)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. mutatella</i> auct.	(DNATAX02806)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. sylvestrella</i>	(DNATAX01565)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. sylvestrella</i>	(DNATAX02088)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. sylvestrella</i>	(DNATAX02228)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. sylvestrella</i>	(DNATAX02230)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. sylvestrella</i>	(DNATAX02231)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. sylvestrella</i>	(DNATAX02798)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>D. robinella</i>	(DNATAX02995)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
<i>A. sociella</i>	(DNATAX02998)	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc	cc
		3																		4
		6	7	8	9	0	1	2	3	4	5	6	7	8						8
		1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9
<i>D. abietella</i>	(DNATAX01570)	ac	ac	ac	ac	ac	ac	ac	ac	ac	ac	ac	ac	ac	ac	ac	ac	ac	ac	ac
<i>D. abietella</i>	(DNATAX01571)	ac	ac	ac	ac	ac	ac	ac	ac	ac	ac	ac	ac	ac	ac	ac	ac	ac	ac	ac

Appendix 3: European Sequences of Molecular Character Matrix Continued

		3								4								4	
		6	7	8	9	0	1	2	3	4	5	6	7	8					
		1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8
<i>D. sylvestrella</i>	(DNATAX02228)	acaggttgaacagtttatccccccctatcctcaaatatcgcccatagaggtagttcagttgatttagccatTTTTTCCCTCatttagccggtatttccctcaatcttaggagctattaat																	
<i>D. sylvestrella</i>	(DNATAX02230)	acaggttgaacagtttatccccccctatcctcaaatatcgcccatagaggtagttcagttgatttagccatTTTTTCCCTCatttagccggtatttccctcaatcttaggagctattaat																	
<i>D. sylvestrella</i>	(DNATAX02231)	acaggttgaacagtttatccccccctatcctcaaatatcgcccatagaggtagttcagttgatttagccatTTTTTCCCTCatttagccggtatttccctcaatcttaggagctattaat																	
<i>D. sylvestrella</i>	(DNATAX02798)	acaggttgaacagtttatccccccctatcctcaaatatcgcccatagaggtagttcagttgatttagccatTTTTTCCCTCatttagccggtatttccctcaatcttaggggctattaat																	
<i>D. robinielli</i>	(DNATAX02995)	acaggtgaacagttatccccccctatcctcaaatatcgcccatagaggaagatctgttgattttagctTTTTTCCCTCatttagctggaatctctcaatcttaggagcaatattaat																	
<i>A. sociella</i>	(DNATAX02998)	actggatgaaccgtttaaccccccttatctgctaacaatcgcccatagaggaagatctgttagatttagctTTTTTCCCTCatttagctggtatttcatctatttaggagctattaac																	
		4								5								6	
		8	9	0	1	2	3	4	5	6	7	8	9	0					
		1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8
<i>D. abietella</i>	(DNATAX01570)	tttattacaactattattaatataaaaataaatggtttatcttttgatcaaatacctctatttgggtgagctgttaggaattacagctctattattattattatctttacctgtttagct																	
<i>D. abietella</i>	(DNATAX01571)	tttattacaactattattaatataaaaataaatggtttatcttttgatcaaatacctctatttgggtgagctgttaggaattacagctctattattattattatctttacctgtttagct																	
<i>D. abietella</i>	(DNATAX01574)	tttattacaactattattaatataaaaataaatggtttatcttttgatcaaatacctctatttgggtgagctgttaggaattacagctctattattattattatctttacctgtttagct																	
<i>D. abietella</i>	(DNATAX01575)	tttattacaactattattaatataaaaataaatggtttatcttttgatcaaatacctctatttgggtgagctgttaggaattacagctctattattattattatctttacctgtttagct																	
<i>D. abietella</i>	(DNATAX01595)	tttattacaactattattaatataaaaataaatggtttatcttttgatcaaatacctctatttgggtgagctgttaggaattacagctctattattattattatctttacctgtttagct																	
<i>D. abietella</i>	(DNATAX01596)	tttattacgactattattaatataaaaataaatggtttatcttttgatcaaatacctctatttgggtgagctgttaggaattacagctctattattattattatctttacctgtttagct																	
<i>D. abietella</i>	(DNATAX02772)	tttattacaactattattaatataaaaataaatggtttatcttttgatcaaatacctctatttgggtgagctgttaggaattacagctctattattattattatctttacctgtttagct																	
<i>D. abietella</i>	(DNATAX02773)	tttattacaactattattaatataaaaataaatggtttatcttttgatcaaatacctctatttgggtgagctgttaggaattacagctctattattattattatctttacctgtttagct																	
<i>D. abietella</i>	(DNATAX02799)	tttattacaactattattaatataaaaataaatggtttatcttttgatcaaatacctctatttgggtgagctgttaggaattacagctctattattattattatctttacctgtttagct																	
<i>D. abietella</i>	(DNATAX02808)	tttattacaactattattaatataaaaataaatggtttatcttttgatcaaatacctctatttgggtgagctgttaggaattacagctctattattattattatctttacctgtttagct																	
<i>D. abietivorella</i>	(DNATAX02843)	tttattacaactattattaatataaaaataaatgggttatcttttgatcaaataccttatttggatgagctgttaggaattacagctcttttattattattatctttacctgtatttagct																	
<i>D. aulloi</i>	(DNATAX02758)	tttattacaactattattaatataaaaataaatggatttatcttttgatcaaataccttatttggatgagctgttaggaattacagctcttttattattattatctttacctgtttagct																	
<i>D. aulloi</i>	(DNATAX02771)	tttattacaactattattaatataaaaataaatggatttatcttttgatcaaataccttatttggatgagctgttaggaattacagctcttttattattattatctttacctgtttagct																	
<i>D. mendacella</i>	(DNATAX01556)	tttattacaactattattaatataaaaataaatggatttatcttttgatcaaataccttatttggatgagctgttaggaattacagctcttttattattattatctttacctgtttagct																	
<i>D. mendacella</i>	(DNATAX01592)	tttattacaactattattaatataaaaataaatggatttatcttttgatcaaataccttatttggatgagctgttaggaattacagctcttttattattattatctttacctgtttagct																	
<i>D. mendacella</i>	(DNATAX01594)	tttattacaactattattaatataaaaataaatggatttatcttttgatcaaataccttatttggatgagctgttaggaattacagctcttttattattattatctttacctgtttagct																	
<i>D. mendacella</i>	(DNATAX02760)	tttattacaactattattaatataaaaataaatggatttatcttttgatcaaataccttatttggatgagctgttaggaattacagctcttttattattattatctttacctgtttagct																	
<i>D. mendacella</i>	(DNATAX02774)	tttattacaactattattaatataaaaataaatggatttatcttttgatcaaataccttatttggatgagctgttaggaattacagctcttttattattattatctttacctgtttagct																	
<i>D. mendacella</i>	(DNATAX02801)	tttattacaactattattaatataaaaataaatggatttatcttttgatcaaataccttatttggatgagctgttaggaattacagctcttttattattattatctttacctgtttagct																	
<i>D. nivaliensis</i>	(DNATAX02807)	tttattacaactattattaatataaaaataaatggatttatcttttgatcaaataccttatttggatgagctgttaggaattacagctcttttattattattatctttacctgtttagct																	
<i>D. pineae</i>	(DNATAX02225)	tttattacaactattattaatataaaaataaatggatttatcttttgatcaaataccttatttggatgagctgttaggaattacagctcttttattattattatctttacctgtttagct																	
<i>D. resiniphila</i>	(DNATAX01846)	tttattacaactattattaatataaaaataaatggatttatcttttgatcaaataccttatttggatgagctgttaggaattacagctcttttattattattatctttacctgtttagct																	
<i>D. resiniphila</i>	(DNATAX01847)	tttattacaactattattaatataaaaataaatggatttatcttttgatcaaataccttatttggatgagctgttaggaattacagctcttttattattattatctttacctgtttagct																	
<i>D. resiniphila</i>	(DNATAX02762)	tttattacaactattattaatataaaaataaatggatttatcttttgatcaaataccttatttggatgagctgttaggaattacagctcttttattattattatctttacctgtttagct																	
<i>D. schuetzeella</i>	(DNATAX02227)	tttattacaactattattaatataaaaataaatggatttagatttatcttttgatcaaataccttatttggatgagctgttaggaattacagctcttttattattattatctttacctgtttagct																	
<i>D. simplicella</i> auct.	(DNATAX01928)	tttattacaactattattaatataaaaataaatggatttatcttttgatcaaataccttatttggatgagctgttaggaattacagctcttttattattattatctttacctgtttagct																	
<i>D. simplicella</i> auct.	(DNATAX02780)	tttattacaactattattaatataaaaataaatggatttatcttttgatcaaataccttatttggatgagctgttaggaattacagctcttttattattattatctttacctgtttagct																	
<i>D. simplicella</i> auct.	(DNATAX02834)	tttattacaactattattaatataaaaataaatggatttatcttttgatcaaataccttatttggatgagctgttaggaattacagctcttttattattattatctttacctgtttagct																	
<i>D. simplicella</i> auct.	(DNATAX02835)	tttattacaactattattaatataaaaataaatggatttatcttttgatcaaataccttatttggatgagctgttaggaattacagctcttttattattattatctttacctgtttagct																	
<i>D. simplicella</i> auct.	(DNATAX02844)	tttattacaactattattaatataaaaataaatggatttatcttttgatcaaataccttatttggatgagctgttaggaattacagctcttttattattattatctttacctgtttagct																	

Appendix 3: European Sequences of Molecular Character Matrix Continued

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		0	1																2	
		8	9	0	1	2	3	4	5	6	7	8	9			0				
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<i>D. sylvestrella</i>	(DNATAX02230)	gatattagtcttcatgatacttattatggttggtgccatttccattatgttttatctataggggctgtatttgcaatcttagggggatttattcattgatatcctttatttacagggtta																		
<i>D. sylvestrella</i>	(DNATAX02231)	gatattagtcttcatgatacttattatggttggtgccatttccattatgttttatctataggggctgtatttgcaatcttagggggatttattcattgatatcctttatttacagggtta																		
<i>D. sylvestrella</i>	(DNATAX02798)	gatattagtcttcatgatacttattatggttggtgccatttccattatgttttatctataggggctgtatttgcaatcttagggggatttattcattgatatcctttatttacagggtta																		
<i>D. robinella</i>	(DNATAX02995)	gacgtagtcttcatgatacttattatggttggtgctcatttccattatgttctatctataggggctgtatttgcaatttagggggatttattcattgataccctttatttacaggatta																		
<i>A. sociella</i>	(DNATAX02998)	gatgtagtcttcatgatacttattatgtagtagctcatttccactatgttttatctatagggagcagtatttgctattataagaggatttattcattgatatcctttatttactggatta																		
		1																		1
		2	3																3	
		0	1	2	3	4	5	6	7	8	9	0	1			2				
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<i>D. abietella</i>	(DNATAX01570)	tatataaaccccttcttctctaaaaatccaatttttttcaatatttattggagtaaatttaacattcttcccccaacattttctaggttttagcaggcatacctcgacgatatctgattac																		
<i>D. abietella</i>	(DNATAX01571)	tatataaaccccttcttctctaaaaatccaatttttttcaatatttattggagtaaatttaacattcttcccccaacattttctaggttttagcaggcatacctcgacgatatctgattac																		
<i>D. abietella</i>	(DNATAX01574)	tatataaaccccttcttctctaaaaatccaatttttttcaatatttattggagtaaatttaacattcttcccccaacattttctaggttttagcaggcatacctcgacgatatctgattac																		
<i>D. abietella</i>	(DNATAX01575)	tatataaaccccttcttctctaaaaatccaatttttttcaatatttattggagtaaatttaacattcttcccccaacattttctaggttttagcaggcatacctcgacgatatctgattac																		
<i>D. abietella</i>	(DNATAX01595)	tatataaaccccttcttctctaaaaatccaatttttttcaatatttattggagtaaatttaacattcttcccccaacattttctaggttttagcaggcatacctcgacgatatctgattac																		
<i>D. abietella</i>	(DNATAX01596)	tatataaaccccttcttctctaaaaatccaatttttttcaatatttattggagtaaatttaacattcttcccccaacattttctaggttttagcaggcatacctcgacgatatctgattac																		
<i>D. abietella</i>	(DNATAX02772)	tatataaaccccttcttctctaaaaatccaatttttttcaatatttattggagtaaatttaacattcttcccccaacattttctaggttttagcaggcatacctcgacgatatctgattac																		
<i>D. abietella</i>	(DNATAX02799)	tatataaaccccttcttctctaaaaatccaatttttttcaatatttattggagtaaatttaacattcttcccccaacattttctaggttttagcaggcatacctcgacgatatctgattac																		
<i>D. abietella</i>	(DNATAX02808)	tatataaaccccttcttctctaaaaatccaatttttttcaatatttattggagtaaatttaacattcttcccccaacattttctaggttttagcaggcatacctcgacgatatctgattac																		
<i>D. abietivorella</i>	(DNATAX02843)	tatataaaccccttcttctctaaaaatccaatttttttcaatatttattggagtaaatttaacattcttcccccaacattttctaggttttagcaggcatacctcgacgatatctgattac																		
<i>D. aulloi</i>	(DNATAX02758)	tatataaaccttcttctctctaaaaatccaatttttttcaatatttattggagtaaatttaacatttttctcacaattttcttaggttttagcagggtatacctcgacgatactctgattat																		
<i>D. aulloi</i>	(DNATAX02771)	tatataaaccttcttctctctaaaaatccaatttttttcaatatttattggagtaaatttaacatttttctcacaattttcttaggttttagcagggtatacctcgacgatactctgattat																		
<i>D. mendacella</i>	(DNATAX01556)	tatataaaccttcttctctctaaaaatccaatttttttcaatatttattggagtaaacttaacatttttctcacaattttcttaggttttagcagggtatacctcgacgatactctgactat																		
<i>D. mendacella</i>	(DNATAX01592)	tatataaaccttcttctctctaaaaatccaatttttttcaatatttattggggttaaacttaacatttttctcacaattttcttaggttttagcagggtatacctcgacgatactctgactat																		
<i>D. mendacella</i>	(DNATAX01594)	tatataaaccttcttctctctaaaaatccaatttttttcaatatttattggagtaaacttaacatttttctcacaattttcttaggttttagcagggtatacctcgacgatactctgactat																		
<i>D. mendacella</i>	(DNATAX02760)	tatataaaccttcttctctctaaaaatccaatttttttcaatatttattggagtaaacttaacatttttctcacaattttcttaggttttagcagggtatacctcgacgatactctgactat																		
<i>D. mendacella</i>	(DNATAX02774)	tatataaaccttcttctctctaaaaatccaatttttttcaatatttattggagtaaacttaacatttttctcacaattttcttaggttttagcagggtatacctcgacgatactctgactat																		
<i>D. mendacella</i>	(DNATAX02801)	tatataaaccttcttctctctaaaaatccaatttttttcaatatttattggagtaaacttaacatttttctcacaattttcttaggttttagcagggtatacctcgacgatactctgactat																		
<i>D. nivaliensis</i>	(DNATAX02807)	tatataaaccttcttctctctaaaaatccaatttttttcaatatttattggagtaaacttaacatttttctcacaattttcttaggttttagcagggtatacctcgacgatactctgattat																		
<i>D. pineae</i>	(DNATAX02225)	tatataaaccttcttctctctaaaaatccaatttttttcaatatttattggagtaaacttaacatttttctcacaattttcttaggttttagcagggtatacctcgacgatactctgactat																		
<i>D. resiniphila</i>	(DNATAX01846)	tatataaaccttcttctctctaaaaatccaatttttttcaatatttattggagtaaacttaacatttttctcacaattttcttaggttttagcagggtatacctcgacgatactctgattat																		
<i>D. resiniphila</i>	(DNATAX01847)	tatataaaccttcttctctctaaaaatccaatttttttcaatatttattggagtaaacttaacatttttctcacaattttcttaggttttagcagggtatacctcgacgatactctgattat																		
<i>D. resiniphila</i>	(DNATAX02762)	tatataaaccttcttctctctaaaaatccaatttttttcaatatttattggagtaaacttaacatttttctcacaattttcttaggttttagcagggtatacctcgacgatactctgattat																		
<i>D. schuetzeella</i>	(DNATAX02227)	tatataaaccttcttctctctaaaaatccaatttttttcaatatttattggagtaaacttaacatttttctcacaattttcttaggttttagcagggtatacctcgacgatactctgattat																		
<i>D. simplicella</i> auct.	(DNATAX01928)	tatataaaccttcttctctctaaaaatccaatttttttcaatatttattggggttaaacttaacatttttctcacaattttcttaggttttagcagggtatacctcgacgatactctgattat																		
<i>D. simplicella</i> auct.	(DNATAX02780)	tatataaaccttcttctctctaaaaatccaatttttttcaatatttattggggttaaacttaacatttttctcacaattttcttaggttttagcagggtatacctcgacgatactctgattat																		
<i>D. simplicella</i> auct.	(DNATAX02834)	tatataaaccttcttctctctaaaaatccaatttttttcaatatttattggggttaaacttaacatttttctcacaattttcttaggttttagcagggtatacctcgacgatactctgattat																		
<i>D. simplicella</i> auct.	(DNATAX02835)	tatataaaccttcttctctctaaaaatccaatttttttcaatatttattggggttaaacttaacatttttctcacaattttcttaggttttagcagggtatacctcgacgatactctgattat																		
<i>D. simplicella</i> auct.	(DNATAX02844)	tatataaaccttcttctctctaaaaatccaatttttttcaatatttattggggttaaacttaacatttttctcacaattttcttaggttttagcagggtatacctcgacgatactctgattat																		

Appendix 4: Morphological Character Set

The numbers in brackets refer to the character number assigned by Du et al. (2005) for similar characters, to facilitate cross referencing both in this and future studies. Additional characters that were newly included lack these numbers in brackets. Unknown character states are coded (?). For the sake of clarity the codings were chosen uniformly so that character states such as “absent” or “small” were coded (0). Consequently, there can be no character polarisation or phylogenetic information derived from these codings.

Head (plate III.8)

Character 1. (Du:1) Basal scale tuft on male flagellum covering modified flagellomers: (0) absent; (1) scales appressed to the flagellomers ; (2) scales elongated, forming a bud-like structure.

Character 2. Shape of male flagellomeres: (0) cylindrical; (1) lamellate; (2) serrate; (3) unipectinate.

Individual flagellomer shapes result in characteristic appearances of the entirety of the flagellum. The character state "unipectinate" is rare in the genus *Dioryctria*, nevertheless present in 3 of the 10 currently known European *Dioryctria* species, all from the abietella group.

Character 3. (Du2) length of 3rd segment of labial palp: (0) less than 0.5x of 2nd segment; (1) more than 0.5x of 2nd segment.

Character 4. (Du3) Male maxillary palp: (0) narrows distally; (1) broadens distally.

Thorax (plates III.3, 4 & 5)

Character 5. (Du4) Raised scales on forewings: (0) absent; (1) present.

Some non-European species of *Dioryctria* display several areas of raised scales on the forewings.

Character 6. (Du5) Ground colour of forewings: (0) cream; (1) orange to rust; (2) dark copper; (3) grey; (4) grey dusted red; (5) dark grey.

This character of Du et al (2005) was modified as the original coding reflected some autapomorphic character states of individual species and the coding had to be defined more broadly to be meaningful.

Character 7. Dorsal patch anterior of medial line of forewings: (0) absent; (1) macroscopically of rusty-red colouration; (2) macroscopically of greyish to whitish grey colouration.

Variation: can be more or less faded in individuals or display mixed in scales of different coloration e.g. yellow.

Character 8. (Du6) Light streak on cubital vein proximal of discal stigma (0) absent; (1) present
Streak beginning before antemedial line, ending on discal stigma.

Character 9. (Du7) Subbasal line on forewings: (0) absent; (1) present.

Character 10. (Du8) Postmedial line on forewing: (0) weakly dentate, with 2 dentations at most; (1) strongly dentate with at least 4 dentations.

Character 11. Dark line proximad of postmedial line (0) continuous; (1) interrupted at dorsal denture reaching proximad.

Character 12 Angle of postmedial line at costa (0) up to 45°; (1) ~ 60° ; (2) greater nearly 90°.

Appendix 4: Morphological Character Set Continued

This character shows some variability, however, if more specimens are compared, they can be put in the above categories

Character 13. A light spot on hindwing on postmedial line (0) absent; (1) present;

Abdomen

Character 14. Apex of medial plate on S8 (0) slightly concave; (1) with a well developed process; (2) with a strongly elongated process (length more than 40% of total length of basal ridge/ plate); (3) process shouldered by a groove.

Male Terminalia (plate III.6)

Character 15. (Du12) Shape of apical part of uncus: (0) acute; (1) narrowly rounded; (2) broadly rounded with an even, parabolic-like curvature; (3) broad, flattened.

Character 16. Uncus shape: (0) elongated triangular; (1) egg shaped; (2) sub-quadrangular.

Character 17. (Du14/15) Lateral uncus margin: (0) linear or slightly convex; (1) distinctly convex; (2) with a triangular lappet.

The character had to be modified from Du et al. characters 14 and 15 as a consequence of the introduction of the new character 16.

Character 18. (Du30) Shape of sacculus: (0) long and thin; (1) ampulla shaped.

Character 19. (Du20) Shape of costa: (0) broad, length less than 6x width; (1) length 6-8x width; (2) length greater than 8x width.

Character 20. (Du21) Costa length: (0) equal to setiferous region of valve; (1) shorter than setiferous section of valve; (2) longer than setiferous section of valve.

Character 21. (Du22) Terminal ridges of costa: (0) absent; (1) present.

Character 22. (Du24) Preapical spine on costa: (0) absent; (1) present.

The spine is in very small *D. auranticella* but visible under magnification.

Character 23. Position of preapical spine in relation to point of junction of costa and setiferous part of valve: (0) close to apex, emanating significantly distal of point of junction; (1) anterio-dorsally shifted, close to or at point of junction; (2) shifted well proximal of point of junction; (9) if character 19 or 22 was scored 0.

Character 24. (Du26) Shape of preapical spine: (0) blunt; (1) acute; (9) if character 22 was scored 0;

Character 25. (Du27) Shape of costal apex: (0) lacking elongate apex; (1) straight elongate apex; (2) hooked elongate apex.

Character 26. Shape of apical costal hook: (0) broad, (1) slender; (9) costal apex not hooked.

Character 27. (Du28) Costal margins, proximal of apical region: (0) nearly parallel; (1) clearly not parallel.

Character 28. (Du29) Shape of apex tip: (0) broad; (1) narrowed and blunt; (2) narrowed and acute.

Character 29. (Du34) Vinculum length: (0) $< 0.5x$; (1) $0.5x - 0.55x$; (2) $> 0.55x$ total length of genital.

Appendix 4: Morphological Character Set Continued

Character 30. (Du35) Phallus proportion: (0) length less than 4.5x width; (1) length greater than 6x width.

Character 31. (Du36) Cornuti composition: (0) only small spines; (1) cluster of small spines and a large cornutus; (2) cluster of small spines and 2 large cornuti.

Character 32. (Du37) Large cornutus' length: (0) between 5-7x basal width; (1) greater than 7x basal width; (9) if character 31 was scored 0.

Coding of character 37 of Du et al (2005) was changed, because European species display intermediate values.

Character 33. Ratio phallus width : cornutus length: (0) less than 0.8; (1) greater than 0.9; (9) if character 31 was scored 0.

Character 34. Ratio phallus length : cornutus length: (0) less than 5x; (1) more than 7x; (9) if character 31 was scored 0.

Character 35. Assembly of small cornuti in phallus: (0) two scaly assembled clusters; (1) 10-35 spines; (2) 45-55 spines; (3) > 60 spines; (4) ~ 35 spines and a longitudinal band of scaly assembled small spines.

The variability of this character is considerable possibly in part due to spines lost during copula, however, if a number of specimen is investigated the species can be put into the above categories.

Female Terminalia (plate III.7)

Character 36. (Du40) Ductus bursae length of sclerotised part: (0) ≤ 3.8 x width; (1) greater than 5x width.

The length was measured from anterior to posterior part of sclerotisation, the width at posterior end of sclerotisation to ensure a reliable reproducible point of measurement.

Character 37. (Du42) Posterior medio dorsal sclerotised lobe on ductus busae: (0) absent; (1) present.

A membranous lobe, sometimes quite inconspicuous, can be identified when thoroughly investigated in the majority of specimens throughout the genus.

Character 38. (Du43) Longitudinal membranous region of ductus bursae: (0) absent; (1) present.

Character 39. (Du44) Medial field of wrinkles, some transverse, in posterior region of ductus bursae: (0) absent or very faint; (1) present.

Character 40. (Du45) Longitudinal axis of sclerotised part of ductus bursae: (0) essentially straight; (1) curved proximally.

Character 41. (Du46) Longitudinal wrinkles of ductus bursae: (0) nearly absent, ductus primarily smooth; (1) striations laterally not condensed anterior only in centre; (2) striations laterally condensed; (3) striations laterally condensed in anterior half evenly distributed over entire width.

Character 42. (Du47) Ductus bursae width of sclerotised part: (0) more or less equal throughout length; (1) anterior expanded; (2) with a posterior swelling (3) posterior expanded.

Character 43. (Du48) Lateral process of ductus bursae: (0) absent; (1) present on right of bursa; (2) present on left of bursa.

Appendix 4: Morphological Character Set Continued

Character 44. (Du49) Adjacent anterior of ductus bursae: (0) no conspicuous structure; (1) a cluster of spines.

The character definition by Du et al (2005) indicates that the cluster of spines sits on an sclerotisation if present. The European species scored here displaying spines lack a sclerotised plate. As this character cannot be evaluated for all included species, the character definition was modified accordingly.

Character 45. (Du52) Infolded lateral ductus bursae margins: (0) absent; (1) folded ventrally towards medial; (2) forming two lateral grooves.

Ecology (appendix 7)

Character 46. Host plant family: (0) Pinaceae; (1) Cupressaceae; (2) Betulaceae; (?) unknown.

Character 47. Feeding habit: (0) endophagous; (1) ectophagous.

Excluded Characters

Character (Du9) "Discal spots at end of discal cell" was eliminated as character is parsimony uninformative in the matrix here compiled. The presence of a whitish rhenal shaped stigma is an important diagnostic feature characteristic for the genus *Dioryctria*. The coding as "absent" in *D. clarioralis* by Du et al (2005) was found to be doubtful as the two *D. clarioralis* specimens available to us displayed a faint lighter stigma under magnification.

Character (Du10) "Ventral scale tufts of 8th abdominal segment" was taken out as the homology of the structure is questionable, also the distribution of character states is parsimony uninformative.

Character (Du11) "Length of male genitalia" was eliminated as the measurement "measured from...apices of extended valve" as it can be highly variable due to embedding artefacts. In addition the character is parsimony uninformative for the dataset in appendix 5.

Character (Du13) "Uncus length" was recoded into Character 17, as the measurement "uncus width" is variable due to embedding artefacts.

Character (Du18) "Transtilla lobes." Du et al (2005) seem to have mistaken tegumen for transtilla in illustration fig 7. Transtilla is often lost in preparation or weakly sclerotised in *Dioryctria*. The character was eliminated as it is parsimony uninformative.

Character (Du19) "Sacculus shape." Really does not describe the actual shape of the sacculus but the proximad base of sacculus. The shape of the sacculus is described and recoded in character 18. The trait as originally described was eliminated as character is parsimony uninformative.

Character (Du23) "Upper costal margin" was eliminated as it was not reproducible in the available material and the character matrix of Du et al. suggests that it might be an individual variability in one specimen of *D. rubella* and therefore parsimony uninformative as well.

Character (Du25) "Size of preapical spine" was excluded due to high variability.

Character (Du31) "Juxta sclerotisation" was excluded as it was not possible to objectify the findings of Du et al (2005) regarding the grade of sclerotisation of juxta within *Dioryctria*.

Character (Du33) "Vinculum width" was eliminated as measurements of width are unreliable due to embedding artefacts.

Appendix 4: Morphological Character Set Continued

Character (Du51) "Ductus bursa surface" was not included as under great enough magnification there is clearly a sculpted surface in all species. The characteristics are manifold and display intraspecific variation as well as hard to code interspecific differentiations that might even be unique for each species. In addition it was not possible to perform the necessary evaluation for more than one species due to a lack of material. In order to be able to obtain reliable data for subsequent coding, statistically relevant numbers of specimens for each species have to be available.

The following characters were eliminated as they were parsimony uninformative:

Character (Du16) "Gnathos length," **Character** (Du17) "Gnathos shape," **Character** (Du32) "Ventral margin of juxta," **Character** (Du39) "Antrum," **Character** (Du41) "Ductus bursa sclerotisation," and **Character** (Du50) "Signum."

Appendix 5: Morphological Character Matrix

Character Numbers	00000	00001	11111	11112	22222	22223	33333	33334	44444	44
	12345	67890	12345	67890	12345	67890	12345	67890	12345	67
<i>O. faecella</i>	20000	31001	01011	01100	00991	90110	20000	00110	03000	21
<i>D. tumicolella</i>	10001	51010	01032	22111	01112	10221	11002	11001	21011	00
<i>D. zimmermani</i>	10001	21010	01032	22111	01112	10221	11002	11001	21011	00
<i>D. taedivorella</i>	10001	21010	00032	22111	01112	10221	11002	11001	21011	00
<i>D. clarioralis</i>	10001	51110	00030	00020	00991	90211	10002	01000	02012	00
<i>D. reniculelloides</i>	10000	51011	10111	00101	01201	90211	09992	11010	30201	01
<i>D. auranticella</i>	10110	11100	01012	00100	01100	90001	10004	00110	00002	00
<i>D. yiai</i>	20010	11110	01010	00100	01100	91000	10102	00110	00002	00
<i>D. abietivorella</i>	11000	32011	00032	11001	01111	91221	10001	11011	21111	00
<i>D. magnifica</i>	11000	41010	02033	21101	10992	01221	11113	11000	11001	??
<i>D. rubella</i>	10000	41010	02033	21101	10992	01221	11002	11000	11001	00
<i>D. robiniella</i>	21100	00001	10002	00101	00992	11211	10001	01000	02011	1?
<i>D. sylvestrella</i>	11000	31010	02033	21001	10992	01221	10113	11000	11001	00
<i>D. simplicella</i>	11000	32010	01012	11101	01011	91221	10001	10111	21111	00
<i>D. schuetzeella</i>	10000	51011	10111	00101	01201	90211	09992	11010	30201	01
<i>D. resiniphila</i>	12000	32010	01012	11001	01011	91221	10001	10101	21111	00
<i>D. pineae</i>	03000	32010	01022	11001	01011	91121	10001	10110	21111	00
<i>D. nivaliensis</i>	03000	41011	01022	11001	11111	91221	10001	10010	21011	00
<i>D. mendacella</i>	03000	32010	02012	11001	01011	91221	10001	10110	21111	00
<i>D. aulloi</i>	12000	32010	01012	11001	01011	91221	10001	10100	21111	00
<i>D. abietella</i>	11000	31011	00012	11001	01011	91121	10001	10111	21111	00
<i>D. juniperella</i>	21000	51101	01011	00100	01110	90200	10001	01110	00012	11
<i>D. okui</i>	11010	51110	01011	00100	01110	90200	10103	01???	00002	01

? = character state unknown

Appendix 6: Compilation of Specimens' Geographical Data

The data from labels were recorded for each specimen investigated. If possible the data was supplemented by geographical data like province and, if unambiguous, height above sea level. Information given includes, provided their availability, in the following order: Country, province, location, collecting method, height above sea level, date, collector, original collection, and museum collection where the material is currently deposited. Country and province are given in English and native language, if possible, as mostly given on specimens labels. All investigated specimens were labelled with a yellow slip reading: "in Manuskript Europa".

Abbreviations of collections:

MNCN	Museo Nacional de Ciencias Naturales, Spain
MNHU	Museum für Naturkunde der Humboldt Universität zu Berlin, F.R.G.
NHMW	Naturhistorisches Museum Wien, Austria
SMNK	Staatliches Museum für Naturkunde Karlsruhe, F.R.G.
TLMF	Tiroler Landesmuseum Ferdinandeum, Innsbruck, Austria
UASM	E.H. Strickland Entomological Museum, University of Alberta, Edmonton, Canada
ULLT	Universidad de La Laguna, Departamento de Zoología, Teneriffa, Canary Islands
USNM	National Museum of Natural History, Washington D.C., U.S.A.
ZFMK	Zoologisches Forschungsinstitut und Museum Alexander König Bonn, F.R.G.
ZSM	Zoologische Staatssammlung München, F.R.G.
ZMUC	Zoological Museum, University of Copenhagen, Denmark
ZMUH	Zoological Museum, University of Helsinki, Norway

Further abbreviations:

Lf:	caught at light
Tf:	caught during the day
ex ch.:	ex pupa
e.l.:	ex larva

Dioryctria abietella

Austria (Österreich): Burgenland: 3♀ Eisenstadt, 03.vii.1933, 20.vii.1933, 24.vii.1933, leg. Wolfschläger, coll. Klimesch (ZSM); 1♀ Neusiedler See, Hackelsberg, 07.vii.1975, leg. Blum, coll. U. Roesler (ZSM), 1♀ same data but, 7.vii.1972, Kasy (NHMW); 1♂ 2♀ Rechnitz, 450m, Lf, 26.vii., 27.vii., 19.viii.1933, Koschabek (NHMW); **Carinthia (Kärnten):** 2♂ Gailtaler Alpen, 1600m, 17.vii.1923, coll. Kitschelt (NHMW); 1♀ Glocknergebirge, 1400m, 26.vii.1962, leg. Thurner (ZSM); 1♀ Hochstadel, 2000m, 16.vi.1897, leg. Thurner (ZSM); 1♀ Klagenfurt, 14.vii. 1929, Kautz (NHMW); 1♀ Klagenfurt Umgebung, 10.vi.1953, leg. Thurner (ZSM); 1♀ Plöckenpass, 1800m, 19.vi.1930, Kautz (NHMW); 2♂ 2♀ Sachsenburg, 557m, 6.vii.1961, 9.vii.1961, 12.vii.1961, leg. et coll. Baisch; 2♂ 5♀ Sattnitz, 3.vi., 17.vi., 19.vi., 20.vi., 27.vi., 15.viii., 28.viii.1922, leg. Dannehl (ZSM); 1♀ Ulrichsberg, 2000m, 22.vii.1946, leg. Thurner (ZSM); 5♂ 2♀ Zell-Pfarre, 1000m, Lf, 15.7.1935, 21.7.1935, 23.7.1935, 24.7.1935, 25.7.1935, leg. Koschabek (NHMW); **Lower Austria (Niederösterreich):** 3♀ Dürnstein, 24.vi.-05.vii.1932, leg. et coll. Klimesch (ZSM), 1♀ same data but, 21.vi.1930, coll. Reisser (NHMW), 1♀ same data but, Schloßberg, 24.vii.24; 1♀ Fürbachwiesen, östl. Gramatneusiedl, 179m, 27.vii.1978, leg. (NHMW); 1♀ Gießhübl b. Stödling, 416m, Eichberg (ZSM); 3♀ Glaslauerriegel, südl. Gumpoldskirchen, 250m, 26.ix.71, 1.viii.1975, leg. Kasy (NHMW); 1♀ Hundsheimer Berg S, Porta hungarica, 1.vii.1981, Kasy (NHMW); 1♂ Karlstifter Moore, Waldviertel, 5.viii.1960, Kasy (NHMW); 1♀ Oberweiden, Marohfeld, 162m, 28.vi.1952 (NHMW); 1♂ Raabs, Schattental, 01.vii.1925. leg. Ortner, coll. Klimesch (ZSM); 1♀ Rekawinkel, 06.v.1948, e.l., leg. Ortner, coll. Klimesch (ZSM); 1♀ Rohrwald, Michelberg, 409m, 05.viii.1939, leg. Ortner, coll. Klimesch, (ZSM); 2♂ 7♀ St. Egyden, 350m, 27.vii.1952, 8.vii.1959, 8.viii.1959, 20.vii.1963, 8.vii.1979, leg. Thurner (ZSM); **Styria (Steiermark):** 1♀ Gulsen, 600-900m, 27.vi.-3.vii.1953, leg. Freund (ZSM); 1♀ Präbichl, 1206m, 17.vii.1953, leg. Sterzl (ZSM); 3♀ Ramsau b. Schladming, 1050m, Lf, 30.viii.1921, 25.viii.1922, 12.viii.1923(NHMW); 1♀ St. Stefan ob Stainz, 404m,

Appendix 6: Compilation of Specimen Geographical Data Continued

16.viii.38, coll. Janick (NHMW); 1♀ Steiermark, Grofs (ZSM); **Tyrol (Tirol):** 1♀ Gschnitztal, ix.1937, leg. Sterzl (ZSM); 2♀ Innsbruck, 25.viii.1930, 13.viii.1950 (ZSM); 3♂ 5♀ Kauns b. Prutz, Oberinntal, 1000-1400m, 15.-29.vii.1852, leg. Daniel & Wolfsberger, 1♀ same data but 18.-22.vii.1952, leg. Freund, 1♀ same data but 2200m, 24.vii.-3.viii.1951, 2♂ same data but 1200m, 6.-12.vi.1953, 6♂ 15♀ same data but v.1953, 1.-14.ix.1953, leg. Daniel, 1♂ 1♀ same data but 1056m, 11.viii.1955, 11.viii.1956, leg. Sterzl (ZSM); 1♂ 1♀ Landeck „Sonnenhang“ 11.-13.vi.1964, Friedel & Kasy (NHMW); 1♀ Lienz, 673m, 13.viii.1909, coll. Frank (ZSM); 8♂ 4♀ Ötztaler Alpen, Ober Gurgl, 1900-2300m, 26.-29.viii.1951, leg. Pavlitzki (ZSM); 2♂ 3♀ Pitztal/Zaunhof, 1300m, 25.vii.-08.viii.1972, 01.-15.vii.1973, leg. Bettag, coll. U. Roesler (ZSM); 1♂ Vent, 2000m, Lf, 30.vii.1929, Koschabek (NHMW); **Upper Austria (Oberösterreich):** 1♀ Bad Goisern, 500m, 5.viii.1931 (ZSM); 2♀ Hinterstoder, 591m, 15.vi.1929, 05.vii.1929, leg. et coll. Klimesch (ZSM); 1♀ Linz, 266m, vi.09 (NHMW), 3♂ 2♀ same data but Postlingbg, 27.vii.1928, 10.vi.1929, 15.v.1932, leg. et coll. Klimesch, 1♂ 1♀ same data but Lübenauberg, 500m, 2.vii.1929 (ZSM); 1♂ Puchenau b. Linz, 265m, 6.viii.1937, leg. Klimesch (ZSM); 1♀ Rodltal, Gramastetten, 29.v.1948, leg. J. Klimesch (ZSM); 1♀ Gaberg am Attersee, 900m, 31.vii.1919, Kautz (NHMW); **Vorarlberg:** 1♂ Damüls, 1428m, 23.-28.vii.1959, leg. et coll. U. Roesler (ZSM), 1♀ Salib., Hohe Tauern, Sieglitz Tal, 1750m, 14.vii.1959, leg. Auer, coll. Klimesch (ZSM); **Vienna (Wien):** 1♀ Golle in bei Sievering, 1.viii.1953, Kasy (NHMW); 1♀ Neustift. a.W., 22.vii.1952, leg. Sterzl (ZSM); **Bosnia and Herzegovina (Bosna i Hercegovina): Sarajevo Canton (Kanton Sarajevo):** 2♀ Sarajevo, 511m, Lf, 30.vii.1908, leg. Wettl (NHMW); **Republika Srpska:** 2♀ Doboij, 146m, Wettl (NHMW); **Bulgaria (Bǎlgariya): Blagoevgrad Province (Oblast Blagoevgrad):** 7♀ Sandanski District, Pirin Gebirge, Lilyanovo, ca 1000m, 24.vii.-14.viii.1983, 25.&27.vi.1985, 09.viii.-02.ix.1986, 30.vi.-29.vii.1989, leg. et coll. Eichler (ZSM); **Ruse Province (Oblast Russe):** Pyce 1♀ Ost-Bulgarien, Umgebung Obzor, Bjala, 12.viii.1983, leg. Leidenfrost (ZSM); **Croatia (Hrvatska): Dubrovnik-Neretva county (Dubrovačko-neretvanska županija):** 1♂ 16♀ Slano, 07.-17.vii.1976, leg. et coll. U. Roesler (ZSM); **Lika-Senj county (Ličko-senjska županija):** 1♀ Senj, 12.-20.viii.1974, leg. Seidel (ZSM); **Czech Republic (Česká republika): Central Bohemian Region (Středočeský kraj):** 1♀ Kácov, 02.viii.1937, leg. R. Schwarz, coll. U. Roesler, 1♂ 1♀ same data but Kácov/Sázava 12.vii.1967, leg. Schwarz, coll. Eichler (ZSM); 1♂ Řitka, 16.vii.1976, leg. Zouhar (ZSM); **Prague (Praha):** 4♀ Krč, 09.vii.1953, 15.viii.1953, 9.vii.1958, leg. Vorliček, coll. Eichler (ZSM); **South Moravian Region (Jihomoravský kraj):** 1♀ Břeclav, 1949, leg. Vorliček, coll. Eichler (ZSM); 1♀ Klentnice, vii.1948, leg. R. Schwarz, coll. Eichler (ZSM); **South Bohemian Region (Jihočeský kraj):** 1♂ 4♀ Mačkov (Blatná), 440m, 17.vii.1953, 25.vii.1953, 21.viii.1954, 25.viii.1954, 19.vii.1956, 25.vii.1963, leg. V. Zouhar, coll. Eichler (ZSM); **Ústí and Labem Region (Ústecký kraj):** 1♀ Mačkov o BL., 818m, 21.viii.1954, leg. V. Zouhar (ZSM); //1♂ Böhmen (NHMW); **Germany (Deutschland): Baden-Württemberg:** 1♀ Oberld., Dürnachtal, Lf., 12.vii.1936, leg. Reich (ZSM); **Bavaria (Bayern):** 1♀ Bayerisch Eisenstein, Regen, Arber Talstation, 1050m, 27.vi.2002, leg. Kolbeck (ZSM); 3♀ Berchtesgadener Alpen, Hachelwände, E.vii.1949, leg. Pfister, 1♀ same data but Hachel Köpfe, 21.-28.vii.1949, leg. Daniel & Pfister (ZSM); 1♀ Hammelburg, Ruine Trimburg, 260m, 11.vii.1973, leg. Steininger, coll. Eichler (ZSM); 1♂ Hausham, Bayerische Alpen, 765m, 1.vii.1934, leg. Geltinger (ZSM); 1♀ Haunzenberg, Bayerischer Wald, 550m, 24.-26.vii.1947, leg. Daniel (ZSM); 3♀ Hochriß, Bayerische Alpen, vii.1921, A.vii.1926, leg. Heiusdorff (ZSM); 1♀ Hof, Oberfranken, 470-600m, A.vii.1953 (ZSM); 2♀ Landshut, Postau, Unterköllnbach, 3.viii.2002, leg. Kolbeck, 1♀ same data but Unholzing, 23.vii.2002, 1♀ same data but Niederreichbach "Grieß", 19.vi.2002, 1♂ same data but Wenig, Pestendorf, 15.vii.2002n (ZSM); 2♂ 1♀ München NW, Gelände der ZSM, 519m, 01.vii.2002, leg. Reichhof (ZSM); 2♂ 9♀ Oberfränkischer Jura, Umgebung Wallersberg, 350-500m, 22.vi.1952, A.vii.1953, 13.vi.1956, 19.vii.1956, 6.viii.1956, 15.vi.1959, 4.vii.1959, 11.vii.1959, 14.vi.1960, 4.viii.1961, leg. Lukasch, (ZSM); 1♂ 1♀ Regensburg, 26.v.1921, 15.vii.1923, leg. Sälzl, 2♀ same data but Kallmünz, Giglitzhof, 18.vi.2002, leg. Kolbeck, 1♀ same data but, Keilberg, 400m, 30.vii.1991, leg. Segerer (ZSM), 1♂ same data but Kumpfmühl, 25.viii.2003, leg. Segerer (ZSM); 1♀ Roth, Kammerstein, Waikersreuth, 31.vii.2002, leg. Kolbeck (ZSM); 1♀ Schwandorf, Blechhammer, Breitenbrucker Weiher, Lf, 28.vi.1997, leg. Segerer (ZSM); 2♀ Steinebach a. Wörthsee, 15.vii.1949, leg. Daniel, (ZSM); **Mecklenburg-Vorpommern:** 1♀ Rostock, Wieck am Darß, 3m, 20.-30.vii.1975, leg. et coll. Eichler (ZSM); **Lower Saxony (Niedersachsen):** 1♂ Harz, Clausthal, 560m, A.vii., leg. G. Meyer (ZSM); **Rhineland-Palatinate (Rheinland-Pfalz):** 2♀ Altenbamburg, 130m, 02.vi.1960, 03.vii.1966, leg. et coll. U. Roesler (ZSM); 1♀ Bellheim, 113m, 28.viii.1972, leg. et coll. U. Roesler (ZSM); 1♂ 1♀ Bruchhof, 26.viii.1976, leg. et coll. U. Roesler (ZSM); 1♂ Geilweilerhof, 29.vi.1949, leg. de Lattin (ZSM); 2♂ 2♀ Kaiserslautern, 245m, 29.vii.1933, leg. Heuser (ZSM); 2♀ Koblenz, 65m, 22.vii.1933, v.d. Göltz (ZSM); 1♂ Armeiler bei Landau, 26.vii.1949, leg. Jost (ZSM); 3♀ Ludwigswinkel, 240m, 25.vi.1965, 10.vi.1966, leg. et coll. U. Roesler (ZSM); 1♂ Niederkirchen, 07.vii.1972, leg. et coll. U. Roesler (ZSM); 36♂ 48♀ Neustadt, 07.vi.1958, 22.vi.1959, 01.vii.1959, 16.v.1960, 20.vi.1960, 14.vii.1960, 10.vii.1962, 14.vii.1963, 18.vii.1965, 13.vi.1966, 15.vi.1966, 02.vii.1967, 26.vi.1968, 28.vi.1968, 05.vii.1968, 07.vii.1971, 08.vii.1972, 09.vii.1972, 16.vii.1972, 08.vii.1975, 09.vii.1975, leg. et coll. U. Roesler (ZSM); 1♂ 3♀ Oberhausen, 03.vii.1967, 08.ix.1972 leg. et coll. U. Roesler (ZSM); 2♂ Sondernheim, 19.vii.1969, 07.vii.1972, leg. et coll. U. Roesler (ZSM); **Saarland:** 1♂ Karlsbrunn, 22m, 9 25.vii.1931, leg. Nitsche (ZSM); **Saxony (Sachsen):** 2♀ Niederschleina, 26.vii., coll. Osthelder (ZSM); 1♀ Plauen, 412m, v.1967 (ZSM); 1♀ Rosenbach, 237-350m, 23.vii.1930 (ZSM); 1♀ Sächsische Schweiz, Neundorf a. Elbe, 2.-7.viii.1932, leg. Eisenberger (ZSM); 1♂ Vogtland, Mehltheuer, 512m, 01.-10.vii.1973, leg. et coll. Eichler (ZSM); **Saxony-Anhalt (Sachsen-Anhalt):** 1♀ Halle a. Saale, 87m, 22.vi.1914, leg. Bander mann (ZSM); 5♂ 14♀ Lutherstadt Wittenberg, 67m, Dörfurtstraße, 02.vii.1968, 22.vii.1969, 17.vii.1970, 17.vii.1974, 06.viii.1974, 5.xi.1974, 12.vii.1975, 14.vii.1975, 15.viii.1975, 14.viii.1978, 15.vii.1982, 26.viii.1985, 08.vii.1986, leg. et coll. Eichler (ZSM); 1♂ Dübener Heide, Thilenheide, 09.vii.1982, 1♂ same data but Hohenlubast, 09.vii.1983, leg. et coll. Eichler (ZSM); **Thuringia (Thüringen):** 1♀ Bad Blankenburg, 220m, Schieferbruch, 23.vi.1979, leg. et coll. Eichler (ZSM); **Hungary (Magyarország): Southern Transdanubia (Dél-Dunántúl):** 1♀ Cserkut p. Péos, 12.-20.vi.1936, leg. et coll. Klimesch (ZSM);

Appendix 6: Compilation of Specimen Geographical Data Continued

Italy (Italia): Friuli-Venezia Giulia (Friûl-Vignesie Julie): 2♀ Lago Cavazzo, 24.vi.1952, leg. Thurner (ZSM); **Piemont (Piemonte):** 1♀ Pont. Can. Fasano, 03.viii.1966, coll. U. Roesler, (ZSM); **Trentino-Alto Adige/Südtirol:** 1♀ Castel Toblino, 16.viii.1930, leg. Eisenberger (ZSM); 2♀ Gardasee, Nago-Torbole, 65 m, 25.viii.1930, leg. Dannehl (ZSM), 1♀ same data but Mt. Baldo, NO v. Telegrafo, Cavallo di Novezza, 1500m, 29.-30.vi.1986, leg. Schepler (ZMUC); 1♀ Naturns p. Meran, 20.-30.vi.1935, leg. et coll. Klimesch, 1♂ 1♀ same data but 19.vii.1956, leg. Sterzl, 1♂ 1♀ same data but 500m, 20.-30.ix.1954, 550-700m, leg. Freund, 1♂ same data but Schnalstal, Ladurn, 800m, 12.-16.viii.1973, Lf, leg. R. Roesler (ZSM); 1♀ Schnalstal, 2000m, 7.vii.1967, leg. et coll. Baisch; 11♀ Rollepasse, 2000m, 16.-26.vii.1930, leg. Kolb (ZSM); 1♀ Storo, 370-600m, 9.-13.viii.1937, Zerny (NHMW); 1♂ Terlau, 24.vi.1921, leg. Dannehl (ZSM); 1♀ Waidbruck, 471 m, 3.vi.1930 (ZSM); 3♀ Südtirol, 17.v., 1.vi., 28.vi.1921, leg. Dannehl (ZSM); **Lombardy (Lombardia):** 3♂ 3♀ Brescia, Limone, Voltino de Tremosine, 650m, Lf, 2.vii.2002, 4.vii.2002, leg. Segerer (ZSM), 1♀ same data but 680m, 13.-30.viii.1998, leg. Beck (ZSM);

Karachay-Cherkessia (Караचाево-Черкесская республика): 2♀ Caucasus, Teberda, Tourbasa, 1300m, 10.-21.vii.1972, 29.vii.-01.viii.1976; 1♀ same data, but Dshamagat Tal, 2000-2400m, 14.vii.1972; 1♀ same data, but Dombai, 1600 m, 25.viii.1974, leg. B. Müller, leg. et coll. Eichler (ZSM);

Kazakhstan (Казахстан): 1 Zailiskiy Alaiau, Alma-Atinskiy, Nat-P. 43°5'N 77°15'E, Picea/meadow, 22.vi.1990, ad luc., leg. Lkaila & K. Mikkola (ZMUH);

Poland (Polska): 1♀ Schlesien, Heidekretschau, 9.v.1936, leg. E. Linack (ZSM); 1♀ 16.vii.69, leg. Schierke, coll. Eichler (ZSM);

Romania (România): Braşov County (Judeţul Braşov): 1♀ Transilvania, Poiana Brasov, 04.-07.ix.1978, 1200m, leg. V. Zouhar, coll. Eichler (ZSM); **Sibiu County (Judeţul Sibiu):** 1♀ Siebenbürgen, Hohe Rinne, 18.-20.vii.07, Rebel. (NHMW);

Slovakia (Slovensko): Prešov Region (Prešovský kraj): 1♀ Sliepkovce, 29.vii.1965, coll. Eichler (ZSM);

Spain (España): 1♂ S. Grecos, Hoyos D. Cast. 1800m, 3.vii.1934, coll. Reisser (NHMW);

Switzerland (Schweiz): Graubünden: 1♀ Engadin, Turati, viii.1895 (ZSM); 2♀ Pian San Giacomo, 1170m, 15.vii.1964, 30.vii.1964, leg. Sterzl (ZSM); 1♂ St. Moritz, 1800m, vii.1970, leg. Schmidt, coll. U. Roesler (ZSM); **Valais (Wallis):** 2♀ Ausserberg, 900-1000m, 23.vii.1965, leg. Sterzl (ZSM); 1♀ Montana, 28.vii.-15.viii.1935, leg. v.d. Goltz (ZSM); 2♀ Zeneggen, 1374m, 18.vii.1960, leg. Sterzl (ZSM); 4♀ Zermatt, 1,608 m, am Licht, Sommer (18?)97 (NHMW);

D. aulloi

1♂ **Holotype**, Malaga, Ronda, 10.vi.1929, from *A. pinsapo*, (MNCN 11714);

Spain (España): Andalusia (Andalucía): 1♂ 2♀ Sierra Bermeija, Reales Pasaes de los pinsapos, 1155m, Lf, 5.viii.2003, leg. Segerer (ZSM);

D. mendacella

1♂ **Holotype** Chiclana, Origin., ex coll. Staudinger (MNHU); 1♀ Origin., ex coll. Staudinger (MNHU);

Croatia (Hrvatska): Istria county (Istarska županija): 1♀ Pola, 30m, 27.ix.1903 (ZSM); **Dubrovnik-Neretva county (Dubrovačko-neretvanska županija):** 1♂ Umgebung Dubrovnik, 20.viii.-2.ix.1965, leg. Dr. Sielmann (ZFMK); 1♂ Dalmatia mer., Umgebung v. Gravosa, v.1935, leg. Klimesch (ZSM); **Split-Dalmatia county (Splitsko-dalmatinska županija):** 1♂ 1♀ Dalmatia, Hvar, vi.1962, leg. Kusdas (ZSM); **Zadar county (Zadarska županija):** 2♂ Dalmatia, Biograd, 0m, 21.-25.viii.1975, leg. R. Roesler (ZSM); 1♂ Dalmatia (ZSM);

Cyprus (Κύπρος): Limassol (Λεμεσός): 1♀ Platres, N. Limassol, 1150m, 23.-26.vi.1997, leg. Fibiger, Madsen, Nilsson, Svendsen (ZMUC); 1♀ Moniatis n. Limassol, 850m, 23.-29.vi.1997, leg. Fibiger, Madsen, Nilsson, Svendsen (ZMUC);

France: Corsica (Corse): Corse-du-Sud (département): 1♀ 900m above Evisa, 16.viii.1998, leg. Karsholt (ZMUC); Haute-Corse (département): 1♀ Castirla, 12 km N Corte, 400m, 20.vi.1994, leg. Skule & Skou (ZMUC); 1♀ Corte, E.vi.1973, leg. Pfister (ZSM); 1♀ Monte Cinto Gebiet, Ascotal, Haut Asco, 1500m, Tagfang, 23.vii.1998, leg. Keil & Schwarzbauer, coll. Keller; **Provence-Alpes-Côte d'Azur:** Alpes de Haute Provence (département): 1♀ Französische Alpen, Barles, M.ix.1971, BA, leg. M. Pfister (ZSM); Alpes-Maritimes (département): 2♂ Gallia mer., La Turbie d'Nice, 6.-9.v.1962, leg. Klimesch (ZSM); Var (département): 5♀ Esterel, A.ix.1967, M.x.1968, leg. Pfister (ZSM); 1♂ Méounes; 10.5.1978; leg. et coll. Baisch; // 1♀ Französische Alpen, Oranson, A.vi.1967, BA, leg. M. Pfister (ZSM); 1♀ Gallia mer., 1900-1, leg. Staudinger (SMNK);

Greece (Ελλάδα): Central Macedonia (Κεντρική Μακεδονία): 1♀ Olympos E, 8km s Leptokaria, 0m, 8./9.vii.1990, leg. Fibiger (ZMUC); 1♀ Olympos, Fahrweg Leptokaria/Karia, 1100m, 15.vii.1982, Lf, leg. et coll. Baisch; 1♀ Olympos Mon., Hag. Dion, 800m, 25.vi.-6.vii.1957, leg. Klimesch (ZSM); 1♀ Pireas Inoi, 400m, 2.x.1991, leg. Schepler (ZSM); **Crete (Κρήτη):**

1♂ Ag. Joannis, b.Koutsou. N. Lassithi, 390m, LF, 2.v.2003, leg. et coll. Ruckdeschel; 1♂ same data but Nom. Lassithi, 250m, Tf, 1.v.2003; 1♂ 10km o Hierapetra, 18.iv.1971, leg. et coll. Isser (SMNK); 5♂ 1♀ 25,53/35,2°, Ierapetra östl., 0m, 8.iv.1971, Lf, leg. Malicky (SMNK); 1♂ Nom. Lassithi, Koutsounari, 100m, 1.v.2003, Tf, Bl, leg. et coll. Ruckdeschel; 1♀ 24,33/35,11° Spili, 480m, Lf, 25.-26.iv.1971, leg. Malicky & Reisser (SMNK); **East Macedonia and Thrace (Ανατολική Μακεδονία και Θράκη):** 4♀ Thassos, Pefkari, 0m, 14.-17.vii.1990, leg. Fibiger (ZMUC); **Epirus (Ηπειρος):** 2♀ Pindos Oros, Katara-Paß, 1500-1700m, 29.vi.1997, Lf, leg. et coll. Baisch; **Peloponnese (Πελοπόννησος):** Laconia (Λακωνία): 1♀ 5km S Monemvasia, 20.viii.1982; leg. Christensen (ZMUC); Corinthia (Κορινθία): 1♂ Xylokastron, NM v. Korinth, 8.-10.vi.1976, leg. R. Roesler (ZSM); **South Aegean (Βόρειο Αιγαίο):** 1♀ Rhodos, Rhodos Stadt, 3.-14.v.1958, leg. R. & K. Bender (SMNK); 1♀ Rhodos, 5km S Rhodos, 250m, 04.-08.vii.2000, leg. Fibiger (ZMUC); **Thessaly (Θεσσαλία):** 1♀ Skiathis, 6.vii.1991, leg. Somerma & Väisänen (ZMUH); **West Greece (Δυτική Ελλάδα):** Achaia (Αχαΐα): 1♀ Aronia Ori Chelmos, 20km, N f Kalavrita, 29.vi.1990, leg. Schepler (ZSM); Evrytania (Ευρυτανία): 1♀ Not. Pindos-Evrytania, Berg Timfristos, 2000-2300m, Lf, 17.vii.1988, leg. Baisch; Ilia (Ηλεία): 1♀ Olympia; 15.v.1981; leg. et coll. G. Baisch;

Appendix 6: Compilation of Specimen Geographical Data Continued

Italy (Italia): Liguria: 3♂ 5♀ Noli (Savona), 21.-30.vi.1951, 15.-25.ix.1951, 14.-20.ix.1965, leg. Klimesch (ZSM); 1♂ Riverira, Ventimiglia, 15.vii.-3.ix.1970, leg. Riegelbauer (ZSM); **Piedmont (Piemonte):** 1♂ Susa, Mte. Pampalu, 31.viii.1965, leg. Klimesch (ZSM);

Sardinia (Sardegna): Carbonia-Iglesias: 1♀ Umgebung von Musei, Kulturlandschaften, 5.x.1975, leg. Hartig (SMNK); Nuoro: 1♂ Aritzo, Sa Casa, 1000m, 22.vii.1972, leg. Arenberger (SMNK); 1♂ 1♀ Mts. Gennargentu, Belvi, 3km N v. Aritzo, Corylus-Plantage, 750m, 2.ix.1975, 27.ix.1975, leg. Hartig (SMNK), 1♀ same data but 700m, 15.vii.1975, leg. Gozmany (SMNK), 1♂ same data but 800m, leg. et coll. Derra; 2♀ "Su Pranu" bei Aritzo, 1000m, 29.vii.-5.viii. 1981, leg. Hanigk & Kaltenbach (SMNK); Olbia-Tempio: 2♀ Santa Teresa di Gallura 2km N Porto Pozzo, Conca Verde, 16.vi.2002, leg. et coll. Keller; **Tuscany (Toscana):** 1♂ Toscana, v.1962, leg. Zocchi (SMNK); **Sicily (Sicilia):** 1♀ Sicila, Iaul (ZFMK);

Morocco (Maroc): Meknès-Tafilet (برغمل): 1♂ Sahara vic., Ksar es Souk, 25.iv.1974, leg. R. & E. Bender (SMNK); **Gharb-Chrarda-Béni Hssen (الرياح الشرقي):** 1♂ Ouezzanee, 300m, 21.-22.iv.1989 (ZMUC); **Tangier-Tétouan (ناطوط ةجنط):** 1♂ 40km S Larache, 0-20m, 23.-24.iv.1989, (ZMUC); **Tadla-Azilal (الرياح الشمالية):** 1♀ El Ksiba. G. ilex-Wald, 1300m, B: 32,52751 L: 6,02041, Lf, 26.v.2005, leg. et coll. Werno;

Portugal: Lisbon (Lisboa): 1♂ Estremadura, Sintra Mucifal, 22.v.-1.vi.1994, leg. et coll. Grünwald; **Faro:** 1♂ Algarve, Albufeira, coastal pine forest, 27.-29.ii.1991, leg. Mikkola (ZMUH);

Spain (España): Andalusia (Andalucía): Almeria: 1♂ Sierra de Almagro bei Huercal, Overa, 300m, 29.x.1989, leg. et coll. Grünwald; Cadiz: 1♀ Algeciras, 17./18.x.1974, Lf, leg. R. Roesler (ZSM); 1♂ 1♀ Sierra Grazalema, Grazalema, 957m, LF, 6.viii.2003, leg. Segerer (ZSM); Huelva: 1♀ Huelva, Mazagon, 19.-22.v.1994, leg. Schepler (ZSM); 1♂ 1♀ Valverde l. pinos, 300m, 17.-19.vi.1978, leg. R. Roesler (ZSM); Malaga: 3♂ 3♀ Malaga, Neria, 19.v.1971, 20.v.1971, 5.-13.x.1974, Lf, leg. R. Roesler (ZSM); Sevilla: 1♀ Sevilla, Mazagon, 0-100m, 3.x.1975, leg. M. & W. Glaser (SMNK); **Aragon (Aragón):** 1♀ Huesca, Bielsa, 1500m, 7.vii.1991, leg. et coll. Grünwald; **Catalonia (Catalunya/Cataluña/Catalunha):** 1♀ Gerona, Bienes, 27.x.1974, Lf., leg. R. Roesler (ZSM); 1♂ (Gerona), Costa Brava, S' Agaro, 20.v.-1.vi.1978, leg. R. Roesler (ZSM); **Region of Murcia (Región de Murcia):** 2♀ Sra. de Espuña, E.v.1956, 26.v.1956, leg. Eisenberger (ZSM); **Valencian Community (Comunitat Valenciana/Comunidad Valenciana):** Castellon (Castellón Castelló): 6♀ Sierra Espada, Tales, 500m, 18.x.1989. leg. et coll. Baisch;

Tunesia (تونس): Béja Governorate (جانب تيار الو): 2♂ 2♀ Tabarka area, 7.-18.v.1988 (ZMUC); **Jendouba governorate (تونس):** 1♂ 1♀ Ain Draham area, 5.-18.v.1988 (ZMUC); **Sousse Governorate (تونس):** 1♂ Sousse, 1.-10.iv.1983, leg. Mikkola (ZMUH);

Turkey (Türkiye): Ankara: 1♂ 1♀ Tuz Gölü, N-Ufer, 900m, 11.ix.1983 leg. et coll. Derra; **Antalya:** 1♂ 36°45'N * 31°37'E, Gülendac, 24km SW Taskesigi, 200m, Lf, 3.v.1987, leg. Schreier (coll. Derra); **Kayseri:** 1♀ Erciyes Dagi, 2100m, 19.x.1987, leg. Moberg & Hillmann (coll. Derra); **Konya:** 1♀ Tuz Gölü, 20.-30.ix.1968, leg. Pinker (SMNK); // 1♀ Berolige, 2.v.1988, leg. Mittendorf (SMNK);

D. nivaliensis

1♀ **Holotype**, Tenerife 89, leg. Simony (NHMW Prep. Gen. N° MV 16555);

Spain (España): Balearic Islands (Illes Balears/Islands Baleares): Tenerife: 1♀ Baranco Ruiz, leg. Pinker (SMNK); 2♀ Güimar, leg. Pinker (SMNK); 3♀ La Orotava, viii.1966, leg. Pinkler (SMNK); 2♂ Las Lagunetas, pine forest, 1400m, ix.2002, leg. Báez (ZSM); 4♀ Pico de Teide, 2300m, (SMNK), 1♀ same data but Canadas, 2000m, 22.ix.1967, leg. Pinker (NHMW);

D. pineae

Croatia (Hrvatska): Dubrovnik-Neretva county (Dubrovačko-neretvanska županija): 1♂ 1♀ Gravosa, 20.ix.1926, leg. Kautz (NHMW), 1♂ same data but 5.ix.1908, leg. Knitschke (NHMW); **Istria county (Istarska županija):** 1♂ 1♀ Pola, 16.vii.1906, ix.1909 (SMNK); **Split-Dalmatia County (Splitsko-dalmatinska županija):** 1♂ 1♀ Spalato, 1868, coll. Mann (NHMW); // 2♂ 1♀ Dalmatien, Hrug, 1885,e.1., coll. Rebel (NHMW); 1♂ Dalmatia, 26.vii.83 (NHMW); 1♂ 2♀ Dalmatien, e.1., Hortig (NHMW);

France: Provence-Alpes-Côte d'Azur: Alpes-Maritimes (département): 1♀ Mouans-Sartoux, 10.ix.1983, leg. Dujardin (TLMF 1988-40); 1♀ St. Blaise, 05.-06.ix.1981, leg. Dujardin (TLMF); Bouches-du-Rhône (département): 1♂ Environs d'Arles, 15.ix.1934, leg. Henriot (SMNK); Var (département): 1♂ Méounes, 10.ix.1980, leg. Lingenhöle, coll. Baisch; Vaucluse (département): 1♂ 1♀ Sorgues, 16.ix.1954, 14.ix.1957, leg. Henriot (SMNK); **Corsica (Corse):** Corse-du-Sud (département): 1♂ Evisa, 850m, 29.viii.1929, coll. Reisser (NHMW); **Languedoc-Roussillon:** Aude (département): 1♂ Umgebung Narbonne (Autobahnbereich) 21.ix.1991 0-100m, leg. et coll. Baisch; // 1♂ leg. Const., coll. Amsel (SMNK); 1♀ Gallia, (NHMW); 1♀ Gallia mer. (ZSM), 1♂ same data but coll. E. Frank, coll. Osthelder (ZSM), 1♂ 1♀ same data but ex coll. Reutti (SMNK); 1♂ 1♀ same data but viii.1890, 1886 leg. Const.coll. Rebel (NHMW); 1♂ Südfrankreich, leg. Staudinger, coll. J.N. Ertl, (ZSM); 2♀ Franz. Alpen, Oranson, 1971, leg. Pfister (ZSM);

Greece (Ελλάδα): East Macedonia and Thrace (Ανατολική Μακεδονία και Θράκη): 1♂ Evro, Alexandropolis Kirki, 400m, 25.x.1987, leg. Moberg et Hillman (ZMUC); **North Aegeann (Νότιο Αιγαίο):** 1♂ Lesbos, Mitilias vic. 10.-20.x.1987, leg. Roness, coll. Eichler (ZSM); **West Greece (Δυτική Ελλάδα):** Ilia (Ηλεία): 2♂ 3♀ Olympia, 100m, 4.x.1968, 5.x.1968, 12.x.1971, 17.x.1971, 09.x.1977, leg. Lukasch (ZSM);

Cyprus (Κύπρος): Famagusta District (Επαρχία Αμμόχωστου): 1♂ Cap Greco, 55m, ex larva, 18.x.2006, ex *Pinus brutia* Zapfen, leg. Segerer (ZSM);

Jordan (الأردن): Amman: 1♀ Amman, 800m, 18.x.1962, leg. Klapperich (SMNK); 1♀ same data but Jubeiha b. Amman 27.x.1962;

Appendix 6: Compilation of Specimen´ Geographical Data Continued

Italy (Italia): Apulia (Puglia): Lecce: 1♂ Marina di Ugento/Torre Giovanni, Robinsonclub, 29.ix.2000, leg. Keller; **Liguria:** 1♀ Cavi, Umgebung bei Chiavari, 30.ix.1966, leg. Groß (SMNK); 1♂ 1♀ Noil (Savona), 14.-20.ix.1965, leg. et coll. Klimesch (ZSM); **Sardinia (Sardegna):** Olbia-Tempio: 1♂ 1♀ Budoni, Flußmündung, 20m, Schilf- und Dünenregionen, 22.vii.1975, leg. R. & U. Roessler (SMNK); **Sicily (Sicilia):** Messina: 1♀ Mistretta, 1000m, 27.ix.1938, coll. H. Reisser (NHMW); **Tuscany (Toscana):** 1♂ Toscana, 1♀ ix.1962, leg. Zocchi, ex coll. Amsel (SMNK); Grosseto: 1♂ Orbetello, ix.1961 (NHMW);

Libya (ليبى): Bani Walid: 1♀ Museo Libico, Beni Ulid, viii.1907, leg. Kruger (SMNK);

Morocco (Maroc, برغمل): Marrakech-Tensift-El Haouz (زواج شفيسنات شكارم): 1♂ H. Atlas, Oukaimeden, street, 1200m, 26. u. 29.ix., 01.x.1973, leg. Friedel, coll. Eichler, (ZSM); **Tanger-Tétouan (تاوانط ةجنت):** Tanger-Asilah: 1♂ Tanger, 1889 (NHMW);

Spain (España): Andalusia (Andalucía): Sevilla: 1♀ Sevilla, Puerto Real. nördl. Chiclana Ortsrand, 30m, 24.-28.ix.1974, leg. Amsel et R.U. Roessler (SMNK); **Valencia:** Alicante: 2♂ Celpe, 15.-30.1974 (SMNK); // 1♂ La Commeta, 18.-24.ix.76 (SMNK);

D. resiniphila

Greece (Ελλάδα): Central Macedonia (Κεντρική Μακεδονία): 2♂ 3♀ Olympos, Fahrweg Leptokariá/Karia, 24.vii.1981, 500m, 30.vii.1981, 500m, 600m, 900m, 20.vii.1982, 1100m, Lf, leg. et coll. Baisch, 2♂ 12♀ same data but Stavros-Hütte, 950m, 6.vii.1978, 11.vii.1981, 25.vii.1981, 31.vii.1981;

Central Greece (Στερεά Ελλάδα): 1♀ Smolikas, 10 km w. Ag. Paraskevi by Konitsa, 600m, 23.vii.1990. leg. Fibiger (ZMUC); Achaea (Αχαΐα): 12♂ 7♀ 10 km östl. Kalavrita, Vrachni, 1400m, Lf, 28.viii.2002, leg. et coll. Baisch, 1♂ 4♀ same data but 6 km östl. Kalavrita, 800m, 4.ix.2004, 5♀ same data but Paßstraße über Kalavrita, 1200m, 17.ix.2004, 19.ix.2004; Phocis (Φοκίδα): 1♀ Parnassos Oros, Umgebung Delphi, Lf, 17.ix.2002, 500-700m, leg. et coll. Baisch; 1♂ 1♀ same data but Paßstraße Westseite, Lf, 3.viii.1985, 1700m, 24.ix.2004, 1500m, 2♀ same data but Paßstraße Ostseite, 21.ix.2004, 1800m, 2♀ same data but 7 km östl. Aráchova, 7.vii.1986, 1200m, Umgebung Aráchova, 22.x.1995, 800-1100m, 3♀ Parnassos Oros, Stavroménos Elatos, 10.viii.2002, 1300m, leg. Segerer & Knölke (ZSM); **Peloponnese (Πελοπόννησος):** Acardia (Αρκαδία): 15♂ 16♀ Parnon Oros, Paßstraße bei Kosmas, 30.ix.1997, 900-1100m, Lf, 12./13.ix.2004, leg. et coll. Baisch, 1♂ same data but 12.vii.1982, 1200m, leg. Schepler (ZSM); 1♀ Leonidion, Kloster Elona, 500m, Lf, 25.ix.1997 leg. et coll. Baisch; 1♀ Arkadia, Umgebung Vlaherna, 600m, Lf, 5.ix.2004, leg. et coll. Baisch; Laconia (Λακωνία): 1♂ Palaeopangia 12km S Sparti, 350m, 23.vii.1998, leg. Skule & Nilsson (ZMUC); **Epirus (Ηπειρος):** 2♂ 2♀ Pindos Oros, Katara – Paß, 1500-1700m, Lf, 29.vi.1997, leg. et coll. Baisch; // 1♀ Parlon Kosmas, 1200m, 12.vii.1982, leg. Schepler (ZSM);

D. simplicella

Blackish form (*Dioryctria simplicella*):

Germany (Deutschland): Baden-Württemberg: 1♀ Baden, Waghäusel-Wiesental, NSG "Frankreich", 112m, 8°29'59"E 49°13'50"N 15.viii.1986, leg. A. & W. Speidel (ZSM); 1♀ same data but, Lf, 3.viii.2004, leg. Segerer & Knölke (ZSM); 1♀ 18.vi. (ZFMK); 1♂ Karlsruhe-Daxlanden, Saumseen, 11.viii.1978, leg. Traub (SMNK); **Brandenburg:** 1♂ Jänschwalde Ost, 27.vi.2001, leg. et coll. Stübner; **Lower Saxony (Niedersachsen):** 1♀ SFA, Wietzendorf, 66m, 03.ix.2002, leg. Kayser (ZSM); **Northrhine-Westphalia (Nordrhein-Westfalen):** 1♀ Sythen, 40m, 29.vii.1972. leg. Biesenbaum (SMNK); **Rhineland-Palatinate (Rheinland-Pfalz):** 1♂ Altenbamburg, 130m, 01.viii.1961, leg. et coll. U. Roessler, (ZSM); 2♀ Bellheim, 113m, 04.ix.1970, 28.viii.1972, leg. et coll. U. Roessler, (ZSM); 1♂ 14♀ Bruchhof, 09.ix.1969, 24.viii.1973, 22.viii.1976, 26.viii.1976, leg. et coll. U. Roessler, (ZSM); 1♀ Dudenhofen, 102-105m, 28.viii.1968, leg. Bettag, coll. U. Roessler, (ZSM); 1♂ Hassloch b. Neustadt, 14.viii.1977, leg. Blasius (ZSM); 1♀ Kaiserslautern, 245m, 04.vii.1968, leg. Heuser, (ZSM); 1♀ Neustadt, 02.vii.1961, leg. et coll. U. Roessler, (ZSM); 1♀ Schifferstadt, 104m, 05.ix.1970, leg. et coll. U. Roessler, (ZSM); 1♂ 2♀ Speyer, 92-113m, 21.viii.1961, 21.viii.1967, 23.viii.1967, leg. et coll. U. Roessler, (ZSM/SMNK); 1♀ Wahner Heide, 29.vi.1965, leg. U. Roessler (SMNK); **Saarland:** 1♂ 1♀ Limbach, Gackelsberg, 13.vi.2003, leg. et coll. Werno;

Greyish form (*Dioryctria mutarella*):

Austria (Österreich): Carinthia (Kärnten): 1♀ Oberkärnten, Pressegg b Hermagor, 570m, 24.vi.1943, Zerny (NHMW); **Lower Austria (Niederösterreich):** 1♀ Glaslatterriegel, südl. Gumpoldskirche, 17.v.1983, leg. Kasy (NHMW); 1♀ Mödling, 246m, vii.1887, coll. Kalchberg (NHMW); **Styria (Steiermark):** 2♀ St. Stefan ob Stainz, 404m, 16.viii.1938, coll. Janick (NHMW); 1♀ Steyermark, 1918, coll. Mann (NHMW);

Bosnia and Herzegovina (Bosna i Hercegovina): Sarajevo Canton (Kanton Sarajevo): 1♀ Sarajevo, 511m, 16.vi.1908, leg. Wetfl (NHMW);

France: Provence-Alpes-Côte d'Azur: Hautes Alpes (département): 1♀ Südfrankreich, Aspres-sur-Buëch, 3.viii.1980, leg. Bräsius; 2♀ same data but, 900m, 4.-8.viii.1980, leg. Blum (ZSM);

Finland (Suomi): Lapland (Lappi): 4♀ Kuolajarwi, 15.vii.1935, leg. Brandt, coll. Klimesch (ZSM);

Germany (Deutschland): Baden-Württemberg: 1♀ Baden, Waghäusel-Wiesental, NSG "Frankreich", 112m, 8°29'59"E 49°13'50"N 15.viii.1986, leg. A. & W. Speidel (ZSM); 1♂ Krs Balingen, NSG Riedbachtal, 600m, 27.vii.2002, Lf, leg. et coll. Baisch; 1♂ Ulm Umgebung, Ostalb, Hörvelsing, Do. Heide Ofenloch, 1.vi.1982, leg. et coll. Baisch; 1♂ Württemberg Federseemoor Wildes-Ried, 580m, 26.viii.2000, leg. et coll. Baisch; **Bavaria (Bayern):** 1♂ Bavaria inf., Kelheim, Siegenburg, Durnbucher Forst, Lf, 30.vi.1995, leg. Segerer (ZSM); 1♂ 2♀ Oberfränkischer Jura, Umgebung von Wallersberg, 350-550m, Lf, 9.vii.1953, 16.vi.1961, leg. Lukasch (ZSM); 1♀ Salmdorf, 542m, 21.vii.1934, coll. Rebel (NHMW); **Brandenburg:** 1♀ Cottbus Bez., Schw. Pumpe, 1.vi.1981, leg. Fritsch, coll. Eichler (ZSM); **Hamburg:** 1♂ Neugraben, 5.viii.1952, leg. Albers, coll.

Appendix 6: Compilation of Specimen Geographical Data Continued

Klimesch (ZSM); 1 ♀ Finkenwerder, 11.viii.1952, leg. Albers, coll. Klimesch (ZSM); **Mecklenburg-Vorpommern:** 1 ♂ 1 ♀ Rostock Umgebung, Wieck am Darß, 20.-30.vii.1975, leg. et coll. Eichler (ZSM); **Rhineland-Palatinate (Rheinland-Pfalz):** 1 ♂ 1 ♀ Altenbamberg, 130m, 30.viii.1961, leg. et coll. U. Roesler (ZSM); 5 ♀ Bellheim, 113m, 4.ix.1970, 28.viii.1972, leg. et coll. U. Roesler (ZSM); 9 ♂ 30 ♀ Bruchhof, 11.ix.1969, 24.viii.1973, 22.viii.1976, 26.viii.1976, leg. et coll. U. Roesler (ZSM); 1 ♂ Böhl, (Wald), 1.vi.1961, leg. et coll. U. Roesler (ZSM); 1 ♀ Eberburg, 282m, 8.viii.1959, leg. et coll. U. Roesler (ZSM); 6 ♂ 1 ♀ Elmstein, 225m, 29.viii.1972, 4.ix.1972, leg. et coll. U. Roesler (ZSM); 1 ♀ Iggelbach, 375m, 26.viii.1959, leg. et coll. U. Roesler (ZSM); 1 ♀ Lindelbrunn, 440m, 7.vi.1967, leg. et coll. U. Roesler (ZSM); 10 ♂ 41 ♀ Neustadt, 27.vi.1959, 1.vii.1959, 2.vii.1959, 25.vii.1959, 6.ix.1959, 1.vi.1960, 14.vii.1960, 18.viii.1960, 15.ix.1960, 19.vii.1962, 21.vi.1963, 4.vii.1963, 22.vii.1963, 15.viii.1964, 13.vii.1965, 14.vii.1965, 18.vii.1965, 4.vii.1968, 5.vii.1968, 2.vii.1969, 4.vii.1971, 7.vii.1971, 8.vii.1971, 9.vii.1971, 10.vii.1971, 29.vii.1971, 26.vi.1972, 9.vii.1972, 9.viii.1972, 16.vii.1972, 12.vii.1973, 8.vii.1975, 9.vii.1975, leg. et coll. U. Roesler (ZSM); 1 ♀ Oberhausen, 7.ix.1973, leg. et coll. U. Roesler (ZSM); 1 ♀ Silbental, 11.vii.1972, 2.vii.1973, leg. et coll. U. Roesler (ZSM); 5 ♂ 8 ♀ Speyer, 21.viii.1967, 23.viii.1967, 2.ix.1969, 23.viii.1971, leg. et coll. U. Roesler (ZSM); 1 ♂ St. Martin, 225m, 11.vi.1964, leg. et coll. U. Roesler (ZSM); 1 ♀ Steinalb, 2.ix.1967, leg. et coll. U. Roesler (ZSM); 1 ♂ 1 ♀ Totenkopfhäus, 2.viii.1971, leg. et coll. U. Roesler (ZSM); **Saxony-Anhalt (Sachsen-Anhalt):** 1 ♀ Dessau Umgebung, Mosigkauerheide, 1.vi.1978, leg. et coll. Eichler (ZSM); 9 ♂ 15 ♀ Lutherstadt Wittenberg, 2.vii.1986, 29.vi.1986, 30.vi.1986, 3.vii.1986, 7.vii.1986, 8.vii.1986, 30.vi.1987, 7.vii.1987, 9.vii.1987, 10.vii.1987, 19.vii.1987, 21.vii.1987 leg. et coll. Eichler (ZSM); 1 ♀ same data but Braunsdorf, 20.viii.1976; 6 ♂ 18 ♀ same data but Dörfurtstraße, 20.vii.1969, 26.viii.1971, 20.vii.1973, 30.viii.1973, 14.vii.1975, 20.viii.1975, 1.vii.1976, 5.vii.1976, 5.vii.1977, 3.viii.1981, 15.vii.1982, 1.vii.1982, 17.vii.1982, 21.vii.1982, 25.vii.1982, 29.vii.1982, 12.vii.1983, 20.ix.1982, 5.vii.1983, 1.ix.1983, 7.ix.1983, 9.ix.1983, 6 ♂ 7 ♀ same data but Umgebung NSG Thielenheide, Dübenerheide, 9.vii.1982, 15.vii.1983, 2.ix.1983, 12.ix.1985, 13.ix.1985, 2 ♀ Umgebung Ochsenkopf, 9.ix.1983, 1 ♂ same data but Hoher Fläming, Reinsdorf, 2.vii.1982;

Italy (Italia): Liguria: 1 ♀ Alpes Maritimes, Carnina, 1300m, 27.vii.1981, leg. et coll. Derra; **Lombardy (Lombardia):** 1 ♀ Gardaseegebiet, Voltino de Tremosine, 650m, L, 18.vi.2003, leg. Segerer (ZSM);

Turkey (Türkiye): Ankara: 1 ♂ 20km N Kizilcahamam, 1400m, 4.-5.viii.1993, leg. Schepler (ZSM);

Spain (España): Andalucía (Andalucía): 1 ♀ Sierra Nevada, Rota de Veleta, 2300m, Lf, 14.vii.1991, leg. et coll. Baisch; 1 ♀ same data but 2040m, 7.viii.2003, leg. Segerer (ZSM);

D. schuetzeella

Austria (Österreich): Carinthia (Kärnten): 1 ♂ Sattnitz, 19.vi., leg. Dannehl (ZSM); **Lower Austria (Niederösterreich):** 1 ♀ Dürnstein, 24.vi.-5.vii.1932, leg. J.Klimesch (ZSM); **Styria (Steiermark):** 1 ♀ Gulsen, 1.-3.vii.53, 600-900m, leg. Freund (ZSM); 4 ♂ Ramsau b. Schladming, 1050m, Lf, 10.viii.1923, 8.viii.1925, 14.viii.1925 (NHMW); **Upper Austria (Oberösterreich):** 1 ♀ Austria superior, Rodltal bei Gramast, 12.vii.1956, leg. Klimesch, coll. Klimesch (ZSM); 1 ♂ Böhmerwald, Schöneben, 27.vii.1964, leg. J.Klimesch (ZSM);

Denmark (Danmark): Region South Denmark (Region Syddanmark): Langeland: 1 ♂ Østerskov, 25.vi.1953, leg. Svensson (ZSM);

Germany (Deutschland): Baden-Württemberg: 1 ♂ Schwäbische Alb, Schmiechen-halde bei Teuringshofen, 12.vii.2002, leg. Baisch (ZSM); **Bavaria (Bayern):** 3 ♂ 5 ♀ Oberfranken, Hof/Saale, 7.vii.1953, A.vii.1959, leg. Pfister (ZSM); 2 ♂ 4 ♀ Oberfränkischer Jura, Umgebung Wallersberg 350-550m, 1.vii.1953, 15.vii.1958, leg. Lukasch (ZSM); 1 ♀ Oberpfalz, Weiden, M.vii.1977, leg. Pfister (ZSM); 1 ♂ Regensburg, Kallmünz, Giglitzhof, 18.vi.2002, leg. Kolbeck (ZSM); **Rhineland-Palatinate (Rheinland-Pfalz):** 1 ♀ Neustadt, 8.vii.1975, leg. Roesler (ZSM); 1 ♂ Oberhausen/N 7.vii.1973, leg. Roesler (ZSM); **Saxony (Sachsen):** 1 ♂ Rachlau (NHMW), 7 ♂ 3 ♀ same data but e. l., vi.1905, vi.1907, ex *Picea excelsa*, 26.vii.1896 leg. Schütze (ZSM); 2 ♂ Vogtland; Mehltheuer, 512m, 1.-10.vii.1973, leg. Eichler (ZSM); **Saxony-Anhalt (Sachsen-Anhalt):** 1 ♂ Lutherstadt Wittenberg, Dörfurthstraße, 12.vii.1983, leg. Eichler (ZSM); // 1 ♂ 1 ♀ Lausitz, (1914?) (NHMW);

Italy (Italia): Trentino-Alto Adige/Südtirol: 1 ♂ Naturns, A.viii.1964, leg., Pfister (ZSM);

Poland (Polska): Silesian Voivodeship (Województwo śląskie): 1 ♂ Ustroń, Kr Teschen, 25.vii.1941, leg. Gr. v. Tali (ZSM);

D. sylvestrella

Austria: **Burgenland:** 1 ♀ Inzenhof, vii.48, leg. Pinker (NHMW); 1 ♀ Rechnitz, 450m, viii.1939, coll. Pinker. (NHMW); **Carinthia (Kärnten):** 1 ♂ 1 ♀ Sattnitz, 3.vi., 7.vi., 28.vi. 1922, leg. Dannehl (ZSM); **Lower Austria (Niederösterreich):** 1 ♂ Austria inf., 24.vii.1924, Lf, (NHMW); 1 ♂ 1 ♀ Austria inferior, Wien, Oberwiden, 3.viii.1921, coll. Spitz.(NHMW); 1 ♂ Eggenburg, Calvarianberg, Lf, 15.vii.1922, leg. Ortner (ZSM); 2 ♂ Rohrwald, Michelberg, Lf, 7.viii.1937, leg. Ortner (ZSM); 2 ♂ Korneuburg, Bisamberg, 1.viii.1940, 5.viii.1940, ex ch, coll. Janick (NHMW); 2 ♀ Klosterneuburg, Burgberg, Lf, 24.viii.1925, 7.vii.1926, coll. Preisseecker (NHMW); 1 ♀ Glaslauterriegel, südl. Gumpoldskirche, 21.vii.1972, leg. Kasy (NHMW); 1 ♂ Mödling, Richardhof, Lf, 29.viii.1907, (NHMW); 1 ♂ Pfaffenberg, Porta hungarica, 28.viii.1954, Kasy (NHMW), 1 ♂ 1 ♀ same data but, Lf, 1.viii.1927, 19.vi.1936, Preisseecker l. D. Altenburg (NHMW), 1 ♀ same data but Hundsheimer Berg S, 4.viii.1970; **Styria (Steiermark):** 1 ♂ Sausalgebirge, A.vii.1954, leg. Daniel (ZSM); **Upper Austria (Oberösterreich):** 1 ♂ Hinterstoder, 591m, 5.vii.1929, leg. Klimesch (ZSM); 1 ♀ Linz, 28.vi.1910, Knitschke (NHMW); **Vienna (Wien):** 1 ♂ Neustift a.W. 22.vii.1952, leg. Sterzl (ZSM);

Croatia (Hrvatska): Istria county (Istarska županija): 1 ♂ Pola 2.vii.1901 (NHMW); **Dubrovnik-Neretva county (Dubrovačko-neretvanska županija):** 1 ♂ Gravosa, Schwing, ix.1924 (NHMW);

Czech Republic (Česká republika): Central Bohemian Region (Středočeský kraj): 1 ♀ Kácov, 30.vii.1937, leg. Schwarz (ZSM); **Karlovy Vary Region (Karlovarský kraj):** 1 ♀ Keilberg., 9.vii.1932, leg. Retz, coll. Preisseecker (NHMW);

France: Corsica (Corse): Haute-Corse (département): 1 ♂ Monte Cinto Gebiet, Ascotal ca. 1.5km SW Asco, 700m, Lf., 24.vii.1998, leg. Keil & Schwarzbauer (ZSM); 1 ♂ Val Nervia, Piena, M.vii.1961 (ZSM); **Provence-Alpes-Côte d'Azur:** Alpes

Appendix 6: Compilation of Specimen Geographical Data Continued

de Haute Provence (département): 1♂ Barles, M.ix.1971, leg. Pfister (ZSM); Hautes Alpes (département): 1♂ Alpes, Col d'Izoard, 3.viii.1948, (ZSM); // 1♂ SW Frankreich, Les Vivieres, 2m, 23.viii.1978, leg. Oswald (ZSM); // 1♀ Gascogne, e.l. 1883, coll. Rebel (NHMW);

Germany (Deutschland): Baden-Württemberg: 1♀ Württembergisches Oberland, Rißtal-Warthus, e.l. Pinus, 30.vii.1937, leg. G.Reich, coll. Klimesch (ZSM); **Bavaria (Bayern):** 2♀ Bavaria centr. Schwandorf Bruck/Opf St. Hubertus Sandgrube LF 26.vii.1998, leg. Segerer (ZSM); 1♂ Bavaria sept., Weiden/Opf. Schwarzenbach, Lf, 04.viii.1991, leg. Segerer (ZSM); 1♀ same data but Parkstein-Hütten, Lf, 7.vi.2003, 410m; 1♀ Landshut, Postau Unholzing, Lf, 23.vii.2002, leg. Kolbeck (ZSM); 1♀ same data but Unterköllnbach, 3.viii.2002, leg. Kolbeck (ZSM); 1♂ 2♀ Oberbayern, Steinebach, A.ix.1951, leg. Pfister (ZSM); 2♂ 1♀ Oberfränkischer Jura, Umgebung Wallersberg 350-550m, 6.vii.1953, 22.vi.1957, 9.viii.1961, leg. Lukasch (ZSM); 1♂ Regensburg, Kumpfmühl, Lf, 20.viii.2003, leg. Segerer (ZSM); 1♂ Schießplatz Tennenlohe, bei Erlangen Lf, 30.vii.1990, leg. Tannert (ZSM); 4♀ Unterfranken, Münnerstadt, A.viii.1951, leg. Pfister (ZSM); **Rhineland-Palatinate (Rheinland-Pfalz):** 1♂ 1♀ Altenbamburg, 130m, 13.viii.1961, 8.vii.1966, leg. Roesler (ZSM); 7♂ 7♀ Bruchhof, 21.vii.1959, 11.ix.1959, 9.ix.1969, 22.viii.1976, 26.viii.1976, leg. Roesler (ZSM); 1♂ Elmstein, 225m, 31.vii.1962, leg. Roesler (ZSM); 1♂ Hördt, 99m, 11.viii.1969, leg. Roesler (ZSM); 1♂ Königsbach, 150 m, 19.viii.1966, leg. Roesler (ZSM); 5♂ 2♀ Neustadt, 18.vii.1960, 2.vii.1961, 5.vii.1968, 10.viii.1968, 9.viii.1972, leg. Roesler (ZSM); 1♀ Sondernheim, 6.vi.1964, leg. Roesler (ZSM); 1♀ Speyer, 23.viii.1967, leg. Roesler (ZSM); **Saxony-Anhalt (Sachsen-Anhalt):** 1♂ Umgebung Wittenberg, Dübener Heide, Thielenheide, 29.vii.1982, leg. Eichler (ZSM);

Greece (Ελλάδα): West Greece (Δυτική Ελλάδα): Iliia (Ηλεία): 1♂ 1♀ Olympia, 15.-20.v.1981, leg. et coll. Baisch (ZSM);

Italy (Italia): Calabria: 1♂ 1♀ Lago Angitola, 50m, (Vibo Val.), 27.viii.2004, leg. Hausmann (ZSM); **Liguria:** 1♀ Imperia-Testico, 800m, 08.ix.1990, leg. et coll. Baisch (ZSM); 1♀ Isolabona, Val. Nervia, 15.viii.1966, leg. Kuchler (ZSM); 3♂ Noli (Savona), 9.-20.vi.1951, 21.-30.vi.1951, leg. J. Klimesch (ZSM); **Lombardy (Lombardia):** 1♂ Italia sept. Gardaseegebiet, Voltino di Tremosine (650m) LF 18.vi.2003, leg. Segerer (ZSM); 1♂ Norditalien, Mte. Palanzolo, 22.vi.1954, 800m, leg. Freund (ZSM); // 1♂ Italia central, Montagna grande, 1000-1200m, 29.vi.1928, leg. Dannehl (ZSM); // 1♂ Italia, 1900 (ZSM);

Spain (España): Basque Country (País Vasco/Euskadi): 1♀ Bilbao, 10.vi.1881, leg. Seebold (ZSM);

Switzerland (Schweiz): Bern: 1♀ Sigriswil, 800m, vii.1970, leg. Schmidt (ZSM); **Ticino (Tessin):** 1♂ Lugano – Bré, 20.vi.1949, leg. Hörhammer (ZSM);

Turkey (Türkiye): Ankara: 1♂ Tuz Gölü, N-ufer, 900m, 11.ix.1983 leg. et coll. Derra; **Çanakkale Province:** 2♂ 2♀ Canakkale, Kurudaghi Gec, 350m, Lf, 4.vi.1989, 18.viii.1990, 01.vii.1997, leg. et coll. Baisch; **Konya:** 2♂ 1♀ Seytan, Huglu, 28km sw Beysehir, 1300m, 2.ix.1983, leg. et coll. Derra;

Russia (Россия): Altai Republic (Республика Алтай): 1♀ SW-Altai, Katun Valley, 10km W Katanda, 1200m, 6.-8.vii.1983, leg. Exp. Mikkola, Hippa & Jalava (ZMUH);

D. robiniella

Morocco (Maroc, برغمل): Marrakech-Tensift-El Haouz (زواج تنغيسينات شكارم): 1♀ Tahanaoute, Tizi-n-Tagatout, Cedrusforest, B: 31.26367 * L: 7.8806, 1800m, Lf, 20.v.2005, leg. et coll. Werno;

Tunesia (تونس): Béja Governorate (جباب قيوالو): 1♂ Tabarka, 15.v.1985, leg. Wimmer (ZSM).

Additional non-European species:

D. abietivorella

Canada: 2♂ 1♀ British Columbia, Fraser Plateau, Clinton, B.C., 1000m, Lf, 27.vi.2004, leg. R. Beck & A. Segerer (ZSM);

D. auranticella

USA: California: 1♂ Butte Co., Chico, 29.728 –121.837, 7.vi.2001, leg. Grant & Rudolf (UASM);

D. clarioralis

USA: Texas: 2♂ 1♀ Tyler Co., Town Bluff (Dam B), 22.iii.1969, 21.ix.1970, 17.iv.1971, leg. Blanchard (USNM); 1♀ Montgomery Co., Camp Strake, 9.ix.1975 (USNM);

D. juniperella

Japan: Hokkaido: 3♂ 1♀ Atsuma, larva coll. 4.vii.2002 host *Juniperus chinensis* var. *sargentii*, em. 12.vi.2002, 16.vii.2002, 17.vii.2002, leg. H. Torikura, 5♀ same data but Kuroiyama em. 16.vi.2002, 17.vii.2002 (ZSM);

D. magnifica

China: Fujian province: 1♂ holotype 5♂ paratypes, Tapaishan im Tsinling, sued-Shensi, Lf, 26.vi.1935, leg. Höne (ZFMK);

D. okui

Japan: Hokkaido: 3♂, Bibai, coll. 28.vi. em. 9.vii.2002, 14.vii.2002, leg. H. Hara (ZSM);

Appendix 6: Compilation of Specimen Geographical Data Continued

D. reniculelloides

Canada: Alberta: 1♂, Red Lodge Guest Ranch 51.95 – 114.25, 26.vii.2003, leg. Roe (UASM); 1♀ Bearberry, 7 mi E along RR. 7.20 – 51.839, 24.vii.2003, leg. Roe (UASM);

D. rubella

Cambodia: 1♂ S. Cambodia, Sre. Khlong env. Kirirum, 720m, 4.-12.1.2001, leg. L. Chernyshev & V. Kosoy;

Indonesia: Sumatra: 1♀ N., Umg. Holzweg 3, Aek Nauli, Sekundärwald mit *Pinus merkusi*, 1200m, 17.-25.ix.1982, leg. R.U.Roesler (SMNK); 1♀ prov. S. Utor, Sitahoon, 10km O von parapat, verlassenes Sägewerk im Buschwald, 1450m, 11.x.1981, leg. Dr. Diehl (ZSM);

D. taiella

Afghanistan: 1♀ paratype O. Afghanistan, Salang-Paß, N-Seite, (Khinjan), 2100m, 5.-7.vii.1966, leg. Amsel (SMNK);

D. taedivorella

USA: Maryland: 1♂ Natl. Agric., Research center, Beltsville, 23.viii.1980 (USNM);

D. tumicolella:

USA: Kansas: 1♂ Crawford Co, em. 9.ii.2002, Bowens Xmas Trees, Scotch Pine, coll. and reared Bell (USNM), 1♀ same data but em. 9.vi.2002;

D. yiai

China: 1♀ Li-Kiang, Provinz Nord Yuennan, 10.vii.1934, leg. Höne (ZFMK);

D. zimmermanni

USA: Mississippi: 1♂ Warren Co, Vicksberg, 3.xi.1983, coll. Mather (USNM); 1♂ Miss. State University, Okt. Co., 13.ix.1975 (USNM); 1♀ Hancock Co., Bay St. Louis, 17.ix.1992, leg. Kergosien (USNM).

Appendix 7: Host Plant Information – Taxonomic Citations

species	author	common name
<i>Picea</i>	A. DIETRICH 1824	spruce
<i>P. abies</i>	(LINNAEUS) KARSTEN 1881	Norway spruce
<i>P. excelsa</i>	= <i>P. abies</i>	---
<i>P. engelmannii</i>	PARRY EX ENGELMANN 1863	Engelmann spruce
<i>P. glauca</i>	(MOENCH) VOSS 1907	Canada or white spruce
<i>P. mariana</i>	(MILLER) BRITTON STERN & POGGENBURG 1888	black, bog or swamp spruce
<i>P. pungens</i>	ENGELMANN 1879	blue spruce
<i>P. sitchensis</i>	(BONGARD) CARRIÈRE 1855	Sitka spruce
<i>Pinus</i>	LINNAEUS 1754	pine
<i>P. albicaulis</i>	ENGELMANN	whitebark pine
<i>P. arizonica</i>	ENGELMANN 1879	Arizona pine
<i>P. armandii</i>	FRANCHET 1884	---
<i>P. attenuata</i>	LEMMON 1892	knobcone pine
<i>P. banksiana</i>	LAMBERT 1803	eastern jack pine
<i>P. brutia</i>	TENORE 1811-1815	(Turkish pine)
<i>P. caribaea</i>	MORELET 1851	---
<i>P. canariensis</i>	C. SMITH 1828	Canary Island pine
<i>P. cembroides</i>	ZUCCARINI 1832	stoneseed piñon
<i>P. contorta</i>	DOUGLAS EX LOUDON 1838	lodgepole pine
<i>P. coulteri</i>	D. DON 1836	Coulter or pitch pine
<i>P. densiflora</i>	SIEBOLD ET ZUCCARINI 1842	japanese red pine
<i>P. durangensis</i>	MARTÍNEZ 1942	Durango pine
<i>P. echinata</i>	MILLER 1768	shortleaf pine
<i>P. edulis</i>	ENGELMANN 1848	pinyon pine
<i>P. elliottii</i>	ENGELMANN 1880	slash pine
<i>P. halepensis</i>	MILL. 1768	Aleppo pine
<i>P. hartwegii</i>	LINDLEY 1839	Mexican mountain pine.
<i>P. jeffreyi</i>	BALFOUR 1853	Jeffrey pine
<i>P. kesiya</i>	ROYLE EX GORDON 1840	Benguet pine
<i>P. lambertiana</i>	DOUGLAS 1827	sugar pine
<i>P. leiophylla</i>	SCHIEDE EX SCHLECHTENDAL ET CHAMISSO 1831	Chihuahua pine
<i>P. massoniana</i>	LAMBERT 1803	horsetail pine
<i>P. maximinoi</i>	H.E. MOORE 1966	pino canis
<i>P. monophylla</i>	TORREY ET FRÉMONT 1845	singleleaf pinyon pine
<i>P. montezumae</i>	LAMBERT 1832	Montezuma pine
<i>P. monticola</i>	DOUGLAS ET D. DON 1832	western white pine
<i>P. mugo</i>	TURRA 1765	Mugho or dwarf mountain pine
<i>P. muricata</i>	D. DON 1836	bishop pine
<i>P. nigra</i>	J.F. ARNOLD 1785	Austrian or European black pine
<i>P. occidentalis</i>	SWARTZ 1788	---
<i>P. oocarpa</i>	SCHIEDE EX SCHLECHTENDAL 1838	---
<i>P. palustris</i>	MILLER 1768	longleaf (yellow) pine
<i>P. pinaster</i>	AITON 1789	maritime pine
<i>P. pinea</i>	LINNAEUS 1753	Italian stone pine
<i>P. ponderosa</i>	DOUGLAS EX LAWSON ET C. LAWSON 1836	ponderosa pine
<i>P. pungens</i>	LAMBERT 1805	table mountain pine
<i>P. radiata</i>	D. DON 1836	Monterey pine
<i>P. resinosa</i>	AITON 1789	red pine
<i>P. roxburghii</i>	SARGENT 1897	Imodi pine
<i>P. sabiniana</i>	DOUGLAS EX D. DON 1832	grey or foothill pine
<i>P. strobus</i>	LINNAEUS 1753	eastern white pine
<i>P. sylvestris</i>	LINNAEUS 1753	scotch pine
<i>P. taeda</i>	LINNAEUS 1753	loblolly pine

Appendix 7: Host Plant Information – Taxonomic Citations Continued

species	author	common name
<i>P. tabuliformis</i>	CARRIÈRE 1867	Chinese pine
<i>P. tenuifolia</i>	BENTH.	---
<i>P. thunbergii</i>	PARLATORE	Japanese black pine
<i>P. virginiana</i>	MILLER 1768	Virginia pine
<i>P. wallichiana</i>	A.B. JACKS. 1938	Bhutan or Himalayan white pine
<i>P. yunnanensis</i>	FRANCHET 1899	Yunnan pine
Abies	(PLIN. EX TOURN.) MILLER 1754	fir
<i>A. alba</i>	MILLER 1768	European silver fir
<i>A. amabilis</i>	DOUGLAS EX J. FORBES 1839	pacific silver fir
<i>A. balsamea</i>	(LINNAEUS) MILLER 1768	balsam fir
<i>A. cephalonica</i>	LAOD.	Grecian fir
<i>A. concolor</i>	(GORDON ET GLENDINNING) HILDEBRAND 1861	white fir
<i>A. grandis</i>	(DOUGLAS EX D. DON) LINDLEY 1833	grand fir
<i>A. lasiocarpa</i>	(HOOKER) NUTTALL 1849	alpine fir
<i>A. pinsapo</i>	BOISS. 1838	Spanish silver spruce
<i>A. pectinata</i>	= <i>A. nordmanniana</i> (STEVEN) SPACH 1841	Caucasian fir
<i>A. religiosa</i>	(KUNTH) EX SCHLECHTENDAL ET CHAMISSO 1830	sacred fir
Pseudotsuga	CARRIÈRE 1867	Douglas fir
<i>P. menziesii</i>	(MIRBEL) FRANCO 1950	Douglas-fir
Tsuga	(ENDLICHER) CARRIÈRE 1855	hemlock
<i>T. heterophylla</i>	(RAFINESANE) SARGENT 1898	western hemlock
Larix	MILLER 1754	larch
<i>L. laricina</i>	(DUROI) K. KOCH 1873	American larch, tamarack
<i>L. occidentalis</i>	NUTTALL	western larch
Cedrus	TREW 1755	cedar
Cupressus	LINNAEUS 1753	cypress
<i>C. sempervivens</i>	LINNAEUS 1753	Mediterranean cypress
Juniperus	LINNAEUS 1753	juniper, cedar
<i>J. chinensis</i>	LINNAEUS 1767	Chinese juniper
Taxodium	RICHARD 1810	cypress
<i>T. distichum</i>	(LINNAEUS) RICHARD 1810	cypress
Betula	LINNAEUS 1753	birch
<i>B. pendula</i> (?)	ROTH 1788	silver birch
Populus	LINNAEUS 1753	aspen
<i>P. tremula</i>	LINNAEUS 1753	trembling aspen

Information compiled here was taken from literature. Common names were added due to their frequent mentioning in literature addressing *Dioryctria* host plants. Systematic Nomenclature of Gymnosperms J. Earle (2007) from the Gymnosperm Database and Mirov (1967).

URL: <http://www.conifers.org/index.html>

Appendix 7: Host Plant Information - Larval Feeding Habit

	cones	buds	twigs	cambium	phloem	bark	gall	blister_rust_Peridermium	shoots	fusiform rust cancers	flower	trunk	scar tissue	foliage on terminal shoots		cones	buds	twigs	cambium	phloem	bark	gall	blister_rust_Peridermium	shoots	fusiform rust cancers	flower	trunk	scar tissue	foliage on terminal shoots
<i>D. abietella</i>	18_36														<i>D. batesella</i>	23													
<i>D. abietivorella</i>	14_23_27								14					14	<i>D. hogesi</i> #														
<i>D. assamensis</i>									28						<i>D. martini</i> #														
<i>D. aulloi</i>			23						23						<i>D. okanaganella</i>								35						
<i>D. ebeli</i>	30	30								30					<i>D. ponderosae</i>			19_16		16									
<i>D. majorella</i>	16_23_38		23_38												<i>D. caesirutella</i> #														
<i>D. mendacella</i>	6														<i>D. pygmaeella</i>	16													
<i>D. nivaliensis</i> #															<i>D. pseudotsugella</i>	22												22	
<i>D. peltieri</i>	31>														<i>D. reniculellodes</i>	19_22	19_22	19_22					22				22_24		
<i>D. peyerimhoffi</i>										31<					<i>D. schuetzeella</i>		18												13
<i>D. pineae</i>	6														<i>D. kumingella</i>			12											
<i>D. pinicolella</i>	23						23								<i>D. magnifica</i> #														
<i>D. postmajorella</i> #															<i>D. rubella</i>	12							12						
<i>D. raoi</i>									28						<i>D. sylvestrella</i>	36	36										36		
<i>D. resiniphila</i>	8														<i>D. yuennanella</i> #														
<i>D. simplicella</i>	44	1_44	1_44												<i>D. robiniella</i> #														
<i>D. stenopterella</i> #															<i>D. taiella</i> #														
<i>D. sysstratiotes</i> #															<i>D. albotitella</i>	16_23								23					
<i>D. auranticella</i>	16_19_21		16_21*												<i>D. amatella</i>	16								16*					
<i>D. castanea</i>									34						<i>D. banksiella</i>								20						
<i>D. disclosa</i>	16_19_21														<i>D. cambicola</i>	20		20	16		27		20	16					
<i>D. pryeri</i>	21								21						<i>D. contortella</i>			20					20				20		
<i>D. rossi</i>	21_23														<i>D. cuitecensis</i> #														
<i>D. yiai</i>									21						<i>D. delectella</i> #														
<i>D. baumhoferi</i>									16						<i>D. dominguensis</i> #														
<i>D. cibriani</i>	23								23						<i>D. fordii</i>														
<i>D. clarioralis</i>	16														<i>D. merkei</i>	30							30		30				
<i>D. durangoensis</i> #															<i>D. monticolella</i>			20										20	
<i>D. gulosella</i> #															<i>D. mutuurai</i> #														
<i>D. inyoensis</i> #															<i>D. resinosaella</i>	36							36						
<i>D. muricativorella</i> #															<i>D. taede</i>	37							37						
<i>D. pentictionella</i>	27	35													<i>D. taedivorella</i>	15													
<i>D. sierra</i> #															<i>D. tumicolella</i>								20						
<i>D. subtracta</i> #															<i>D. westerlandi</i> #														
<i>D. vancouverella</i>		35													<i>D. yaetsi</i>	30													
<i>D. erythropasa</i>	16_23								23						<i>D. zimmermani</i>			16	16	16			16				40	13	
<i>D. mongolicella</i>			32		32				32						<i>D. actualis</i> #														
<i>D. juniperella</i>															<i>D. adamsi</i> #														
<i>D. okui</i>															<i>D. homeana</i> #														

for references of numbers see appendix 7: Host Plant Associations

= no information on feeding habit available;
 light grey field = internal feeder;
 dark grey field = external feeder.

