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Systematics in *Sileneae* (Caryophyllaceae) – Taxonomy and Phylogenetic patterns

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Abstract

Eggens, F. 2006. Systematics in *Sileneae* (Caryophyllaceae) – Taxonomy and Phylogenetic patterns. Acta Universitatis Upsaliensis. *Digital Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology* 251. 37 pp. Uppsala. ISBN 91-554-6749-0.

The focus for the first part of the thesis is on the systematics of species belonging to *Silene* subgenus *Silene*. Phylogenetic relationships are inferred from DNA sequences from both the plastid (the *rps16* intron) and the nuclear (ITS, intron of the *RPB2* gene) genomes. *Silene* section *Rigidulae* is shown to be non-monophyletic in its previous circumscription, but instead consisting of six separate clades, each correlated to the geographical distribution of the included species. The taxonomic consequences for each clade are discussed. One of the clades is recognized as a new section and described as *Silene* sect. *Arenosae* sect. nov. The morphological descriptions of the species are formalized using a novel implementation of the Prometheus Description Model. Two proposals are included in the thesis, one to reject the name *Silene polyphylla* L., which is a senior synonym to *S. portensis* L. *Silene linearis* Decne. is proposed for conservation against the rarely used *S. linearis* Sweet.

Silene antirrhina, a weedy American annual, is strongly supported as sister to the Hawaiian endemic species of *Silene*, suggesting an American origin for these. Two of the endemics have evolved woodiness after introduction to Hawaii.

In the second part of the thesis we use four nuclear DNA regions, (introns from *RPA2*, *RPB2*, *RPD2a*, *RPD2b*), and the chloroplast *psbE-petG* spacer. A framework is developed to evaluate different phylogenetic explanations for conflicting gene trees, where divergence times are used to discriminate among inter- and intralinear processes. The incongruences observed regarding the relationships among the three major lineages of *Heliosperma* are best explained by homoploid hybridization. The pattern regarding the origin of *Heliosperma* itself is more complicated and is likely to include several reticulate events. Two lineages have probably been involved in the origin of *Heliosperma*, one leading to *Viscaria* and *Atocion* and the other to *Eudianthe* and/or *Petrocoptis*.

Keywords: Sileneae, *Silene*, RNAP, *psbE-petG*, ITS, *rps16*, relative dating, *Rigidulae*, *Heliosperma*, *Arenosae*, phylogeny, homoploid reticulate evolution, *Silene linearis* Decne., *Silene polyphylla* L., Hawaiian *Silene*

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Papers included in this thesis

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

- I Eggens, F., and B. Oxelman. A re-evaluation of *Silene* sect. *Rigidulae* (Caryophyllaceae) based on multiple gene phylogenies. Manuscript.
- II Cafferty, S., B. Oxelman, and F. Eggens. 2001. Proposal to reject the name *Silene polyphylla* L. 1753 (Caryophyllaceae). *Taxon* 50: 923-924.
- III Eggens, F., M. Thollesson, and B. Oxelman. A taxonomic revision of *Silene* sect. *Arenosae* sect. nov. (Caryophyllaceae). Manuscript.
- IV Eggens, F. Proposal to conserve the name *Silene linearis* Decne. against *Silene linearis* Sweet (Caryophyllaceae). Manuscript.
- V Eggens, F., M. Popp, M. Nepokroeff, W. L. Wagner, and B. Oxelman. The Origin and number of introductions of the Hawaiian endemic *Silene* species (Caryophyllaceae). Accepted by *American Journal of Botany*.
- VI Frajman, B., F. Eggens, and B. Oxelman. Hybrid origins and homoploid reticulate evolution within *Heliosperma* (Sileneae, Caryophyllaceae) – a multigene phylogenetic approach. Manuscript.

In all papers, the first author had major responsibility for writing the text, with comments and suggestions given by the co-authors. FE contributed to Paper II with determination of the illustration and selection of the neotype specimen. FE is responsible for all phylogenetic analyses in Paper I, III and V, and for all dating analyses in Paper VI. The studies were planned and conducted in cooperation with the co-authors. Sequences not yet submitted to GenBank are replaced in the tables by placeholders (XX) or accession numbers from the *Sileneae* database at <http://boxtax.ebc.uu.se>; username “Guest”, no password).

Important note. Paper III is a manuscript that contains a description of a new section. This paper will be submitted for publication elsewhere, and in order to make clear that the name of the new section is not validly published in this thesis, the Latin diagnosis as well as reference to type species, both necessary according to the International Code of Botanical Nomenclature, are omitted. Paper III also contains new combinations of names, and the page reference is omitted from the reference of the basionym or replaced synonym in order to make clear that the names are not validly published here.

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Abbreviations

cpDNA

nrDNA

Myr

Mya

MPB

PP

chloroplast DNA

nuclear ribosomal DNA

Million year

Million years ago

Maximum Parsimony Bootstrap

Posterior Probability

Introduction

Taxonomy and systematics within the tribe *Sileneae*

The tribe *Sileneae* DC. ex Ser. (Caryophyllaceae) comprises ca. 700 species and is found mainly in temperate areas in the Northern Hemisphere. It is a predominantly herbaceous group of plants; just a few representatives are small shrubs. The major part of the tribe consists of the species-rich genus *Silene* L., which has a worldwide distribution (although not native in Australia, where it is only found as an introduced weed). The other genera in the tribe have a mainly Eurasian distribution. The most recent generic classification recognizes eight genera in the tribe (Oxelman et al. 2001). This classification is based on molecular phylogenies that have helped to resolve at least parts of the puzzle of inconsistent morphological characters that previous classifications have struggled with. Number of styles, number of capsule teeth, internal structure of the ovary, calyx inflation as well as some seed and petal characters have been heavily used for classification but have been interpreted differently and have often been shown to be variable, even within species. Linnaeus (1753) recognized *Agrostemma* L., *Cucubalus* L., *Lychnis* L. and *Silene*. Most subsequent authors have recognized *Agrostemma*, although mostly with a more narrow circumscription than the one used by Linnaeus. *Cucubalus* has been recognized as monotypic by most authors based on its fruit type, which is a berry rather than a capsule. However, Greuter (1995) put *Cucubalus* in *Silene*, and this has later been supported by molecular phylogenies (e.g. Oxelman and Lidén 1995; Desfeux and Lejeune 1996). Recognized by all authors, *Silene* has usually been the major genus in the tribe, but its recognized size in terms of number of species has varied considerably. Many recent authors (e.g. Greuter 1995) include *Lychnis* in *Silene*. A detailed discussion of intergeneric delimitation of *Sileneae* and the morphological characters used for classification is found e.g. in Chowdhuri (1957), Greuter et al. (1984), Greuter (1995), Oxelman and Lidén (1995), Tzvelev (2001) and Oxelman et al. (2001). As delimited by the latter authors, *Silene* consists of ca. 650 species, the second largest genus *Lychnis* has ca. 30 species whereas *Agrostemma*, *Atocion* Adans., *Eudianthe* (Rchb.) Rchb., *Heliosperma* (Rchb.) Rchb., *Petrocoptis* A. Br. ex. Endl. and *Viscaria* Bernh. are smaller. *Agrostemma* is recognized as sister to the rest of the tribe and *Silene* and *Lychnis*, and *Atocion* and *Viscaria*, form strongly supported sister-groups. Otherwise, the interrelationships among the genera

were unresolved in the phylogeny based on *rps16* intron sequences from the chloroplast genome and nuclear ribosomal internal transcribed spacer (ITS) sequences that was the base for the classification of Oxelman et al. (2001). In order to resolve the relationships in the tribe, Erixon and Oxelman (2006) used a 33,149 character matrix of aligned sequenced from the chloroplast genome. The *Atocion/Viscaria* clade was found in a strongly supported clade with *Heliosperma/Eudianthe*. These four genera form a clade that is sister to a clade with *Silene* and *Lychnis*, whereas *Agrostemma* and *Petrocoptis* are found outside both these clades. The latter result is in strong disagreement with the phylogeny presented by Popp and Oxelman (2004), based on a combined data set with sequences from five nuclear regions (ITS and intron sequences from *RPA2*, *RPB2*, *RPD2a*, and *RPD2b*) and intron sequences from one chloroplast gene, *rps16*. In their tree, *Petrocoptis* is found as sister to *Eudianthe*, with strong support. As the nuclear regions dominate this analysis, these results indicate a strong conflict between nuclear and chloroplast DNA, that could either be due to interlineage processes (hybridization, horizontal gene transfer) or intralineaage processes (incomplete lineage sorting, gene duplication/loss with orthology/paralogy conflation).

Taxonomy and systematics within the genus *Silene*

Oth (1824) presented an early attempt of global infrageneric classification of the genus *Silene*, in which 217 species were included. Boissier (1867) in his *Flora Orientalis* made another important contribution to *Silene* classification. However, this only covered part of the geographical distribution, although the Middle East together with the Mediterranean area is one of the two major centers of diversity for *Silene*, the other is Central Asia. The first more inclusive global revision of *Silene* was made by Rohrbach (1869), who divided *Silene* into two subgenera, the small subgenus *Behen* Rohrb. and the more inclusive subgenus *Silene*. The latter was further divided into two unranked groups, *Conosilene*, a small group above the rank of species, and *Eusilene*, made up of three sections, *Cincinnosilene* Rohrb., *Dichasiosilene* Rohrb., and *Botryosilene* Rohrb., each consisting of a number of series. Almost three decades later, Williams (1896) made a global revision of *Silene* where the infrageneric classification closely followed Rohrbach, but adding about a hundred species described since Rohrbach's revision.

The most recent global infrageneric classification of *Silene* was made by Chowdhuri (1957), who made a revision of the genus at the section level. His 44 sections do in many cases correspond to the series recognized by Rohrbach and Williams, but he discarded ranks above section, considering them unnatural and recognizing only sections and subsections, many of the latter described by himself. The classification of Chowdhuri has been fol-

lowed almost unaltered by most subsequent authors, although slight changes have been made in local Flora projects (e.g. Flora Europaea, Chater et al., 1993; Flora Hellenica, Oxelman and Greuter, 1997; Flora Iranica, Melzheimer, 1988). However, in recent years with the use of molecular phylogenetics, it has become evident that most of the infrageneric groupings are unnatural (e.g. Oxelman and Lidén, 1995; Desfeux and Lejeune, 1996; Oxelman et al., 1997; Oxelman et al 2001; Oxelman et al., unpublished). These studies also indicate that *Silene* seems to be divided into two major groups of approximately equal size. One of these groups includes species from Rohrbach's subgenus *Behen* and from his section *Dichasiosilene*. Also included in this group are species from *Cucubalus*, *Melandrium* Röhl. and *Gastrolychnis* (Fenzl) Rchb. The other major *Silene* group includes at least two major clades, one roughly corresponding to Rohrbach's section *Cincinnosilene* and the other to his section *Botryosilene* (Oxelman and Lidén, 1995). However, both clades include species from section *Dichasiosilene*. The two subgenera *Behen* and *Silene* are also recognized in the multi-gene phylogeny of Popp and Oxelman (2004) and the cpDNA phylogeny of Erixon and Oxelman (2006), although in the latter study the genus *Silene* is not monophyletic, although there is a monophyletic clade with a subgenus *Behen* clade and a subgenus *Silene* clade as sisters to each other. However, there are two clades with *Silene* species that complicate the scenario, one being sister to *Lychnis* and the other to a clade with all other *Silene* and *Lychnis* species included.

Aims

The major part of this thesis concerns the genus *Silene*, in particular parts of subgenus *Silene*, within the “*Botryosilene*” clade.

In **Paper I**, the aim is to test the monophyly of *Silene* section *Rigidulae* (Boiss.) Schischkin, and to provide a framework for future molecular phylogenetic studies of infrageneric relationships in *Silene*. Nomenclatural issues concerning the name of one of the species in this study resulted in **Paper II**, where the aim is to describe the arguments for proposing to reject the name *Silene polyphylla* L.

The framework from Paper I is used in **Paper III** when one of the groups recognized in the first paper is suggested to be a monophyletic group that deserves recognition as a new section. The aim in Paper III is to describe this section and to present a taxonomic revision of the species in the group, including detailed morphological descriptions formalized using a novel implementation of the Prometheus Description Model (Pullan et al. 2005).

Nomenclatural issues concerning the name of one of the species in Paper III resulted in **Paper IV**, where the aim is to describe the arguments for proposing to conserve the name *Silene linearis* Decne. against the name *Silene linearis* Sweet.

In **Paper V**, the aim is to investigate the relationships and origin of the endemic Hawaiian *Silene* and to infer the number of colonization events for them.

In **Paper VI**, the focus is on the relationships within the tribe *Sileneae*, with special emphasis on the genus *Heliosperma*. The major aim of Paper VI is to address the origin of *Heliosperma*, and the interrelationships among the three major lineages within the genus. The relative ages of well supported groups is used to address conflicting gene phylogenies concerning the relationships among the three *Heliosperma* lineages and their implications for the hypothesized hybridization history within the genus, and the relationships to other *Sileneae* taxa.

Material and Methods

Three gene regions are used in **Paper I, III and V**, two from the nuclear genome (ITS and sequences from the second last intron of the low-copy gene *RPB2*) and one from the chloroplast genome (intron sequences from *rps16*). All three have been used in previous studies in *Sileneae* (Oxelman and Lidén, 1995; Oxelman et al, 1997; Popp and Oxelman, 2001; Popp and Oxelman, 2004; Popp et al., 2005). In Paper III, we use the gene phylogenies as an aid for the taxonomic revision.

In **Paper VI**, we use four low copy nuclear DNA sequence regions from the second largest subunit of the RNAP gene family (*RPA2*, *RPB2*, *RPD2a* and *RPD2b*), and the chloroplast *psbE-petG* spacer. We use relative ages to understand the complicated patterns shown to us by conflicting gene phylogenies. Gene copies in aberrant positions were identified if there was mutual conflict, where MPB > 75% and posterior probability (PP) > 0.95. We regard this method as powerful in the sense that the topological location of the conflict is directly identified.

We also estimate the absolute ages of branching points in the phylogenetic trees. A crucial factor when inferring the age of a given monophyletic group is the calibration points, usually in the form of fossils. For many groups of herbaceous plants (e.g. Ranunculaceae, Paun et al. 2005), fossils that can be confidently assigned to ancestral lineages are rare. Caryophyllaceae consists predominantly of herbs, and the scarcity of good fossils for the family is problematic if one wants to reliably date the phylogenetic history. For the calculations of the absolute ages in Paper VI, we use the age of an inflorescence fossil (*Caryophylloflora paleogenica* G. J. Jord. & Macphail) described by Jordan and Macphail (2003), which they determine positioned as sister to or within the “higher Caryophyllaceae” (subfamilies *Alsinoideae* (DC.) Fenzl and *Caryophylloideae*) We estimated the age of the tribe *Sileneae* with the age of this fossil as fixed age for the most recent common ancestor of these two subfamilies in the *matK* tree of Fior et al. (2005). We used the extremes of the age interval 40-55 Myr, which corresponds to the middle to late Eocene age of the fossil (Gradstein et al. 2004), for dating of the *matK*-tree. Depending on calibration point age we get 20 or 27 Myr (Fig. 1) as age for the tribe *Sileneae*, excluding *Agrostemma*.

A new program, PATHd8 (Britton et al. 2006) is used for estimation of the relative and absolute ages. This program is based on the mean path length (MPL) method (Gustafsson and Bremer 1997). For each node the

MPL is calculated as the average of the path lengths (i.e. the sum of the branch length from a node to terminal) to all terminals for the branches above that node. The method smoothes rates between sister groups (Britton et al., unpublished), in contrast to non-parametric rate smoothing and penalized likelihood methods (Sanderson 1997, 2002), which minimizes rate variation between ancestral and descendant lineages. Ericson et al. (2006) recently published a study on bird diversification using the PATHd8 program.

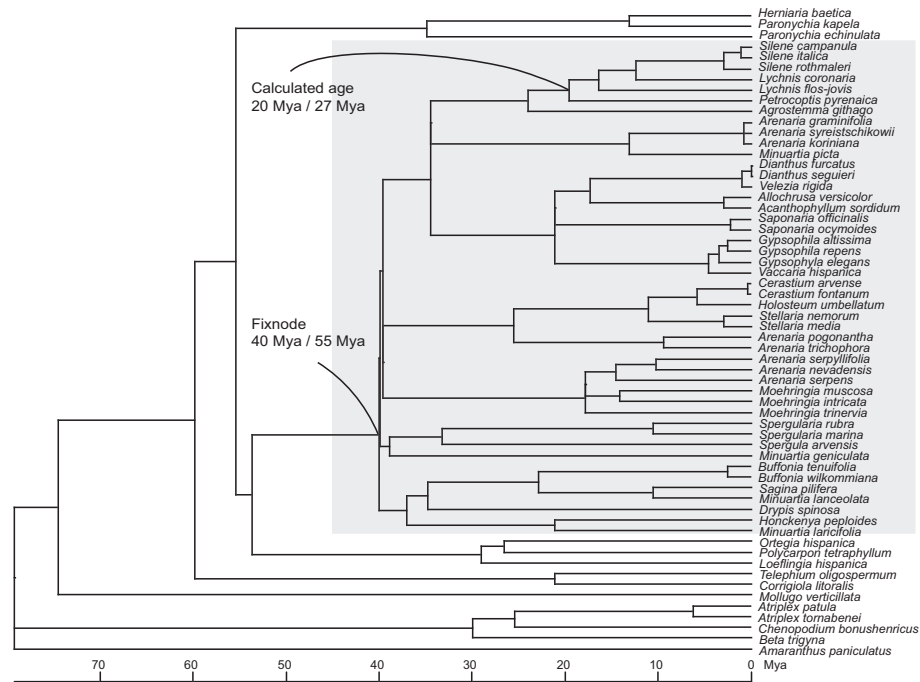


Figure 1. Chronogram of the Caryophyllaceae *matK* sequences (Fior et al. 2005), with the fixage and calculated node marked, and the ages used for calibration (from the age of the inflorescence fossil *Caryophylloflora paleogenica*) and the calculated ages indicated.

Summary of Paper I and II

Paper I is a study of a group of approximately 20 *Silene* species that grow in gravelly habitats in the Mediterranean/Middle East area. The species in this group are annuals that have been characterized by their often oblanceolate to spatulate basal leaves, lax dichasial inflorescences and often nocturnal flowers with bifid petal limbs (Chater et al. 1993; Oxelman and Greuter 1997). These species have been classified under the name *Rigidulae* for a long time. It was first recognized as a group by Boissier (1867) in *Flora Orientalis*, at that time by the rank of series. Almost a century later, *Rigidulae* is one of the 44 sections included by Chowdhuri (1957).

Oxelman et al (1997) in their *rps16* phylogeny noted that one of the species in *Rigidulae*, *S. echinosperma* Boiss. & Heldr., was strongly supported as a sister to *S. cretica* L. These two species has never been placed in the same section. This indicated that the circumscription of the section, although superficially morphologically coherent, needed to be evaluated in a more thorough phylogenetic analysis.

For taxonomic sampling, we used a wide circumscription of the section based on Boissier (1867), Rohrbach (1869), Williams (1896) and Chowdhuri (1957) and later amendments (e.g. Maire, 1963; Zohary, 1966; Coode and Cullen, 1967; Melzheimer, 1988; Oxelman and Greuter, 1997).

Our analyses show that *Rigidulae*, as circumscribed in Paper I, is not monophyletic but instead split into six distinct clades that appear more or less separated (Fig. 2) within the “*Botryosilene*” clade (Oxelman et al., 1997). Each of these six clades can be shown to have a fairly distinct distribution, with one Greek/Aegean (GR/AE), one Northeast Mediterranean (NEM), one SW Anatolian (SWA), and one Middle East (ME) clade and two North African/Western Mediterranean (NA/WM and PORT) clades. Some of these clades are shown to include also, or to be closely associated to species that previously never have been associated with *Rigidulae*.

The six clades recognized in Paper I are used as a backbone for a discussion of possible future classifications. Three possible delimitations for recognition of *Rigidulae* in a strict sense are presented. One is including only the Greek/Aegean group (GR/AE). This group includes the Greek/Aegean Islands endemic species *S. echinosperma*, *S. pinetorum* Boiss. & Heldr. and *S. corinthiaca* Boiss. (= *S. rigidula* Sm.), the latter being the type species of section *Rigidulae*. This group is morphologically coherent and was expected. However, the relationship to *S. cretica* and *S. ungeri* Fenzl suggested by Ox-

elman et al. (2001) is confirmed in this study. These two species, classified in section *Behenantha* sensu Chowdhuri (1957), are geographically agreeing with but morphologically different (e.g. petal morphology) from the GR/AE clade. However, all species in the clade except *S. pinetorum* have mammillate seeds, and all have spatulate basal leaves, but including the *S. cretica/S. ungeri* clade in *Silene* section *Rigidulae* s. str. would make a group less easily diagnosed.

Paper I also identifies the Northeast Mediterranean (NEM) clade as closely related to the GR/AE clade, with two species (*S. echinospermoides* Huber-Mor. and *S. reinwardtii* Roth) that are morphologically similar to the species in the latter clade, but with a slightly more eastern distribution, from the Aegean Islands and eastward to Israel/Palestine. *Silene* sect. *Rigidulae* s. str. could also, in a revised classification, be used for a more inclusive clade with the GR/AE, NEM and *S. cretica/S. ungeri* clades. We believe that our sampling of these three clades are extensive enough so that only few, if any, additional species are likely to belong to them. A more inclusive section has the advantage of including the morphologically similar GR/AE and the NEM groups in the same section, but the disadvantage is that the morphologically deviating *S. cretica/S. ungeri* clade needs to be included.

Silene sect. *Sclerocalycinae* (Boiss.) Schischkin is probably one of the more reliable of the sections of Chowdhuri, consisting of perennials with a mainly northeastern Mediterranean and Middle East distribution. The SW Anatolian clade (SWA) recognized in Paper I consists of a clade with two representatives of *Sclerocalycinae* strongly supported as sister to two annual species from SW Anatolia, *S. cariensis* Boiss. and *S. vittata* Stapf. *S. cariensis* was included in *Rigidulae* by Rohrbach and Williams, although not by Chowdhuri. *S. vittata* has incorrectly been considered as a synonym to “*S. rigidula* Sm.” (for which the correct name is *S. corinthiaca* Boiss. & Heldr.; Oxelman and Greuter, 1997), but is morphologically similar to *S. cariensis* and was included in Paper I as a putative member of *Rigidulae*. A taxonomic implication of the sister-relationship in the SWA clade could be that *S. cariensis* and *S. vittata* are included within *Silene* sect. *Sclerocalycinae*, although this would make the section morphologically more heterogeneous, and thus more difficult to diagnose. *Silene* sect. *Sclerocalycinae* needs to be further investigated.

About half of the species investigated in Paper I (former *Rigidulae* species) have their distribution in the Middle East (from Turkey to Egypt and eastward to Pakistan). The majority of these species are found in a clade referred to as the Middle East clade (ME) in Paper I. This group differs morphologically in, e.g., having lanceolate or oblanceolate rather than spatulate basal leaves, and more or less lanceolate, ciliate calyx teeth with a narrow transparent margin. This group is taxonomically revised and formally described as a new section in Paper III.

The species of the former sect. *Rigidulae* that have their distribution in the western part of the Mediterranean area are found in two clades, two species in the PORT clade and the rest in the North African - West Mediterranean clade (NA/WM). The NA/WM clade is a morphologically incoherent group, including e.g. two Moroccan endemics, *S. cuatrecasasii* Pau & Font Quer and *S. martyi* Emb. & Maire, the latter having an unusual flower morphology with both petals and coronal scale with several lobes. Also in this group is the former *Rigidulae* species *S. reticulata* Desf. (from North Africa), and this species is strongly supported as sister to *S. muscipula* L.. This was an unexpected clade, considering that they have never been placed in the same section. They have, however, one distinct common morphological character in that they have just one large coronal scale. Most *Silene* have two small coronal scales at the base of the petal limbs.

S. inaperta L., a widespread species in the western Mediterranean region, also belongs in the NA/WM clade. This species is partly found in the same area as *S. portensis* L., and the two species have been suspected, based on some morphological similarity and the geographical proximity, to be closely related. Even Linnaeus, although describing both species in *Species plantarum* (Linnaeus, 1753), indicated *S. portensis* as a synonym to *S. inaperta* in the Errata, where *S. portensis* was described. This has nomenclatural consequences for the name *S. portensis*, which are discussed in **Paper II**. The synonymisation means that *S. portensis* is not validly published in the 1753 edition of *Species Plantarum*, but instead in the second edition from 1762. However, the name *S. polyphylla* L. is described in the 1753 edition of *Species Plantarum*, with a plate in Clusius (1601) as the sole original element to be seen today. Studies of the plate suggest that it is an illustration of what almost all authors the last two centuries have considered as *S. portensis*, especially noteworthy are the fasciculate leaves. Although the distribution given by Linnaeus do not fit the distribution of *S. portensis*, we believe that this is a mistake and that the plant on the picture actually is *S. portensis*. *Silene polyphylla* is therefore a senior, but rarely mentioned, synonym to *S. portensis*, a name much in current use. Paper II is therefore a proposal to reject the name *S. polyphylla* L.

Paper I show that *S. portensis* and *S. inaperta* are not supported as being closely related. Instead, the two subspecies of *S. portensis* form a clade (the PORT clade) together with *S. mentagensis* Coss., an allegedly perennial plant endemic to Morocco and placed in section *Rigidulae* by Chowdhuri (1957) but moved to section *Dichasiosilene* subsect. *Auriculatae* Boiss. by Maire (1963). These two species share one unusual morphological character, an almost completely spherical capsule. The common capsule shape in *Silene* is more or less ellipsoid. *S. mentagensis* is nested within *S. portensis*, as sister to the Moroccan endemic subspecies *S. portensis* ssp. *maura* Emb. et Maire. Except for the annual/perennial habit, there are more morphological similarities between *S. mentagensis* and *S. portensis* ssp. *maura*, e.g. in stem, leaf

and calyx pubescence and seed morphology, than between the two subspecies of *S. portensis*. The Moroccan *S. portensis* ssp. *maura* has probably been included in *S. portensis* based on capsule morphology and annual habit. The taxonomic status of these three species are not settled in Paper I, and we conclude that it needs to be further studied.

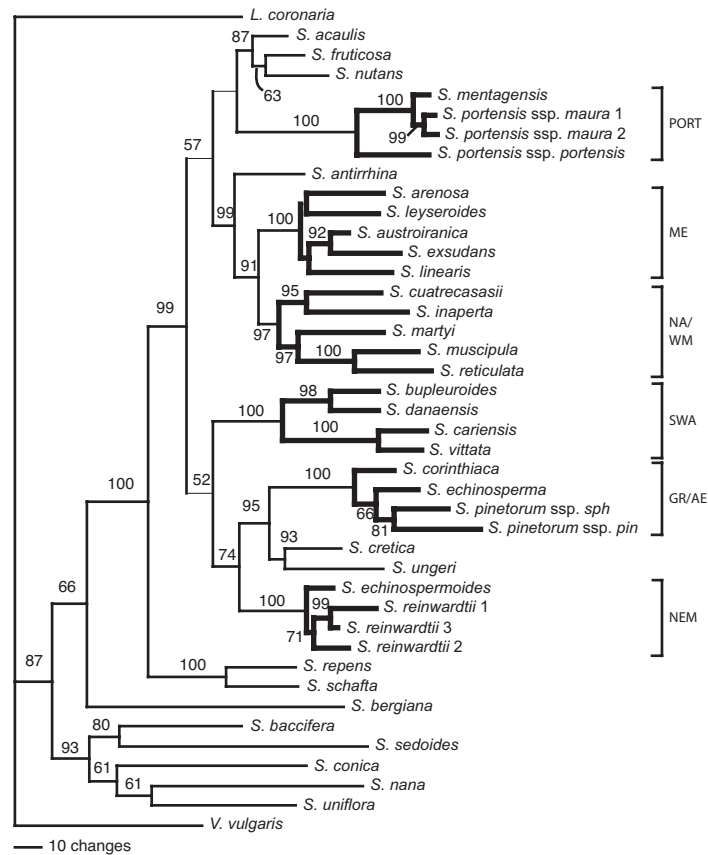


Figure 2. One of the maximum parsimony trees found in the analysis of the combined data (ITS, *rps16*, and *RPB2*). Branches that are collapsed in the strict consensus tree are marked with thin lines. Numbers associated with nodes (above or pointing at branches) indicate MPB frequencies. The clades (NEM, GR/AE, SWA, NA/WM, ME) including former *Rigidulae* species are marked with thick lines. Branch lengths are proportional to number of changes. Numbers next to the taxon names correspond to specimens identifiers in Table 1, Paper I. *S.* = *Silene*; *L.* = *Lychnis*; *V.* = *Viscaria*; *sph* = *sphaciotica*; *pin* = *pinetorum*.

Summary of Paper III and IV

One of the groups recognized and shown to be a monophyletic, well supported group in Paper I (Fig 2) is the group referred to as the Middle East clade. This group has a fairly distinct distribution and has some characters that make it diagnosable. We have therefore decided to describe it as a new section, *Silene* sect. *Arenosae*, and this is done in **Paper III** along with a taxonomic revision of the species in the group.

The revision is based on molecular phylogenies where a number of specimens from the section were included representing different morphological/geographical groups (Fig. 3). These specimens form different clades in the phylogeny, and further morphological studies enabled each clade to be assigned to a taxon. In this way the molecular phylogeny both revealed groups that needed further attention in the morphological studies, and confirmed morphological groups already seen.

The species in *Arenosae* are found in the Middle East area, more specifically from Turkey, Armenia and Azerbaijan and southward to Egypt and the Arabian Peninsula and eastward to Pakistan. The majority of the species have a rather restricted distribution, but two are found over extensive areas. We recognize nine species in the section. The species and their distributions are: *S. linearis* Decne. (Egypt, Arabian Peninsula, Jordan, Israel/Palestine), *S. arenosa* K. Koch (Armenia, Azerbaijan, E Turkey, NW Iran), *S. austroiranica* Rech. f., Aell. & Esfand. (Arabian Peninsula, Kuwait, Iraq and Iran), *S. leyseroides* Boiss. (Iraq, Iran, Kuwait, Afghanistan and Pakistan), *S. chaetodonta* Boiss. (Iran, Turkey, Iraq, Turkmenistan, Afghanistan, Pakistan and Syria), *S. georgievskyi* Lazkov (Syria, N Iraq), *S. striata* Ehrenb. ex Rohrb. (Syria, Lebanon), *S. exsudans* Boiss. & Heldr. (S Mediterranean Turkey) and *S. microsperma* Fenzl (Turkey, Syria, Cyprus, Israel/Palestine and Lebanon). The latter species is the most variable in the section, and is here further divided into four subspecies. We have chosen not to treat these taxa as species for a number of reasons. One is that they are obviously closely related, as seen by strong similarity in the DNA sequences, and by treating them as one species we maintain this information. One taxon, “*modesta*”, has previously been treated as a variant of *S. chaetodonta*, and we wanted to make it clear that this is not the case.

The species in the section are characterized by their calyx teeth that often are lanceolate and tapering into a mucro, often with a ciliate margin, and by their basal leaves that are lanceolate to oblanceolate, rather than spatulate.

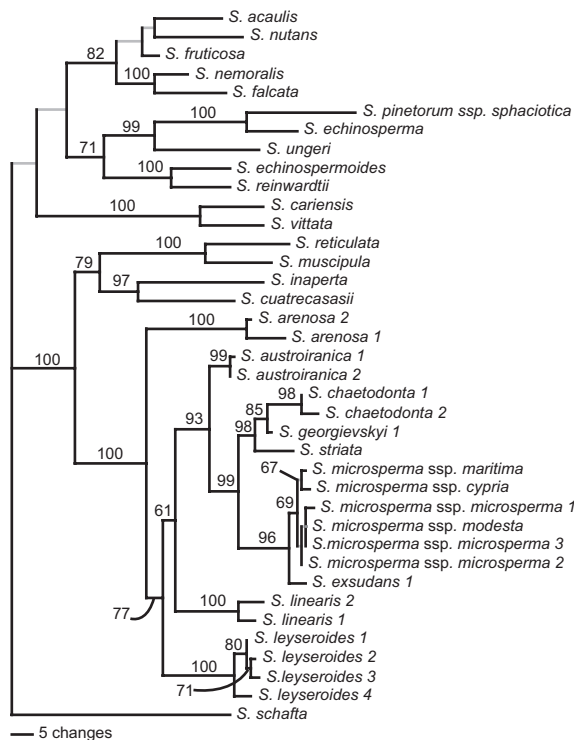


Figure 3. One of the maximum parsimony trees from the combined data (ITS, *rps16*, and *RPB2*). Branches in grey are collapsed in the strict consensus tree. Numbers above (or pointing at) branches indicate MPB numbers. Branch lengths are proportional to number of changes. Numbers next to the taxon names correspond to specimens identifiers in Table 1, Paper III.

The calyx teeth have a transparent margin that makes the teeth appear narrow, with a triangular, green (or sometimes reddish) inner part. This effect is most prominent in *S. linearis* and *S. arenosa*. Both species have slightly rounded teeth but with broad transparent margin and with the green part narrowly triangular. Fig. 4 shows the calyx for four species of *Silene*, three from sect. *Arenosae* (A, B and D) and one representing other *Silene* (C). *S. austroiranica* (B) and *S. georgievskyi* (D) both have typical *Arenosae* calyx morphology whereas *S. linearis* (A) can be recognized as an *Arenosae* species by the long mucro on some of the teeth. Note that the calyx teeth are not monomorphic in *Silene*, a fact that has been neglected in most previous morphological descriptions.

Paper IV is about the name *Silene linearis* Decne., one of the more easily recognized species in the section *Arenosae*, having a distinct mucro and relatively broad transparent margin on the calyx teeth. The name has been used for a long time, both in the global revisions of *Silene* (Rohrbach, 1869; Williams, 1896; Chowdhuri, 1957) and in local Floras e.g. Boissier

(1867), Post (1932), Rechinger (1964), Mouterde (1966), Zohary (1966), Chamberlain (1996) and Boulos (1999).

Silene linearis Sweet is a validly published senior homonym to *S. linearis* Decne. that has been used by very few authors. Marsden-Jones & Turrill (1957) associated it with a part of the *Silene vulgaris*-assemblage, but only in a very informal way. The name is not mentioned in Chater et al. (1993), Aeschimann (1985), Pignatti (1982) or Greuter et al. (1984).

The name *Silene linearis* Decne is a well established name, there is no alternative name for the taxon, and the name *Silene linearis* Sweet has almost never been used. Taking these facts into consideration, I have decided that it would be most desirable to keep the former name. In Paper IV I propose for the conservation of *Silene linearis* Decne. against *Silene linearis* Sweet. The reason for choosing conservation of the former name instead of rejection of the latter is that with this approach, there is still the possibility to use the name *Silene linearis* Sweet as a basionym, in case someone would like to do this.

The species descriptions in Paper III are made in a formalized data format following the Prometheus Description model (Pullan et al. 2005).

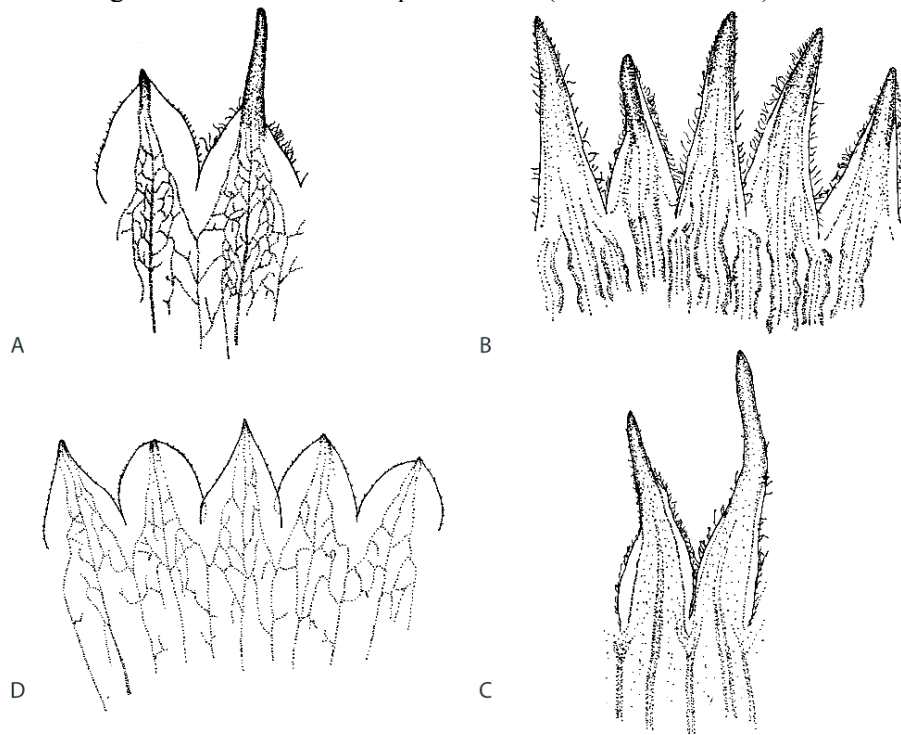


Figure 4. Different types of calyx teeth. A = *Silene linearis* (M. Bierkamp and P. Zinth 177 BSB), B = *Silene austroiranica* (Rechinger 10772 B), C = *Silene corinthiaca* (Bengt Oxelman 1934 GB), D = *Silene georgievskyi* (Rechinger 9828 B). A, B and D are representatives of section *Arenosae*. Illustrations: F. Eggens.

Summary of Paper V

The flora on the Hawaiian Islands is obviously the result of long distance dispersal, since the island group is of volcanic origin and has never had direct connection with any continental landmass. There are, and there have most likely never been any islands to act as steppingstones, since older islands in the same volcanic chain were submerged before the rise of the present islands (the oldest present day island is ca. 5 million years old) (Carson and Clague, 1995). The closest islands are the Polynesian and Micronesian islands in the southwest. There are probably around 1000 species of flowering plants on Hawaii (Wagner et al., 2005a). Fosberg (1948) estimated the number of introductions of seed plants to Hawaii and summarized the contemporary hypotheses on origins for the immigrants, with the Indo-Pacific area and America as the two largest source areas. Strong morphological radiation often makes it difficult to infer the origin of many plant groups from morphological data alone, so molecular phylogenetics is obviously useful and a number of studies have been made using this approach (e.g. Baldwin et al., 1991; Ballard and Sytsma, 2000; Lindquist and Albert, 2002). **Paper V** is a study of the relationships of the endemic Hawaiian *Silene* and what implications those relationships have on their ancestor's hypothetical origin, and the number of colonization events.

There are seven endemic species of *Silene* on Hawaii (Wagner et al. 2005a) that can be divided into two groups based on morphology, one group consisting of subshrubs (*S. alexandri* Hillebr., *S. cryptopetala* Hillebr., *S. degeneri* Sherff, *S. lanceolata* A. Gray and *S. perlmanii* W. L. Wagner, Herbst and Sohmer) and the other of xeromorphic shrubs (*S. struthioloides* A. Gray and *S. hawaiiensis* Sherff). Wagner et al. (2005a) suggest that the native Hawaiian *Silene* are the result of two independent colonizations, leading to these two groups.

No explicit hypothesis on origin for the Hawaiian endemic *Silene* has previously been presented. Fosberg (1948) stated the origin of the Hawaiian *Silene* as "obscure". Chowdhuri (1957), in his revision of the genus, placed the Hawaiian endemic *Silene* (he recognized *S. alexandri*, *S. lanceolata*, *S. struthioloides*) in *Silene* sect. *Paniculatae* Boiss. subsect. *Sclerophyllae* Chowdhuri. He also included two Japanese *Silene* in the same subsection, *S. japonica* Rohrb. and *S. tanakae* Maxim, thereby implying a possible Japanese/Asian origin for the Hawaiian endemics.

The *Silene* species from Hawaii are represented in the phylogenetic analyses in Paper V by *S. alexandri*, *S. lanceolata*, *S. perlmanii*, *S. struthioloides* and *S. hawaiiensis*. They are representatives of both putative colonization events. The Japanese *S. tanakae* is included to test the classification of Chowdhuri, but *S. japonica* is not, since we have not been able to find any material (it is probably only known from the type material, which was likely destroyed during the Second World War bombings of Berlin).

The endemic Hawaiian *Silene* form a monophyletic group (Fig. 5), thereby indicating that *Silene* was introduced to the Hawaiian Islands by a single colonization and the two morphological groups are the result of morphological radiation and adaptation to different habitats. The xeromorphic species (*S. struthioloides* and *S. hawaiiensis*) form a monophyletic group. *Silene perlmanii* and *S. alexandri*, representing the other morphological group, form one strongly supported clade, with *S. lanceolata*, weakly supported as sister to them. The latter taxon is the most widespread, found on several of the islands, while the others are found on just one or two island each.

Silene antirrhina L., widely distributed over the American continents, predominantly in the western parts, is sister taxon to the Hawaiian endemics with strong support (Fig. 5). This close relationship was not expected, since there is no obvious morphological support for this. *Silene antirrhina* is a weedy annual species with inconspicuous flowers. It is not closely related to other native American *Silene*, of which the majority are polyploid and belong in two clades in subgenus *Behen* (Oxelman and Lidén, 1995; Oxelman et al., 1997; Popp and Oxelman, 2004; in press). Instead, the Hawaiian species and *S. antirrhina* together form a sister clade to a group of Mediterranean and Middle East annual species of *Silene*, that previously have been assigned to *Silene* sect. *Rigidulae* (Paper I). From this, it seems reasonable to suggest that the ancestor of the Hawaiian endemic *Silene* was a weedy annual from the American continents, and that woodiness has evolved after the colonization of the Hawaiian Islands. There are a number of examples of this insular woodiness on the Hawaiian Islands, e.g., the silverswords (Baldwin et al., 1991), *Schiedea* Chamisso et Schlechtendal (Wagner et al., 1995, 2005b), the lobelioids (Givnish et al., 1995), the violets (Ballard and Sytsma, 2000), and the mints (Lindqvist and Albert, 2002). Also on other oceanic islands, i.e. Macaronesia, evolution of woodiness has been shown for e.g., *Sonchus* L. (Kim et al., 1996), *Echium* L. (Böhle et al., 1996), and *Convolvulus* L. (Carine et al., 2004).

The Japanese *S. tanakae* is found in a clade together with *S. fortunei* Vis. as well as some other species from East Asia, a clade that is found in a more inclusive clade comprising representatives of a rather large number of *Silene* groups (Fig. 5). It is clear that the classification of Chowdhuri (1957), with *S. tanakae* in the same subsection as the Hawaiian endemic *Silene*, is not congruent with the phylogenetic patterns found here.

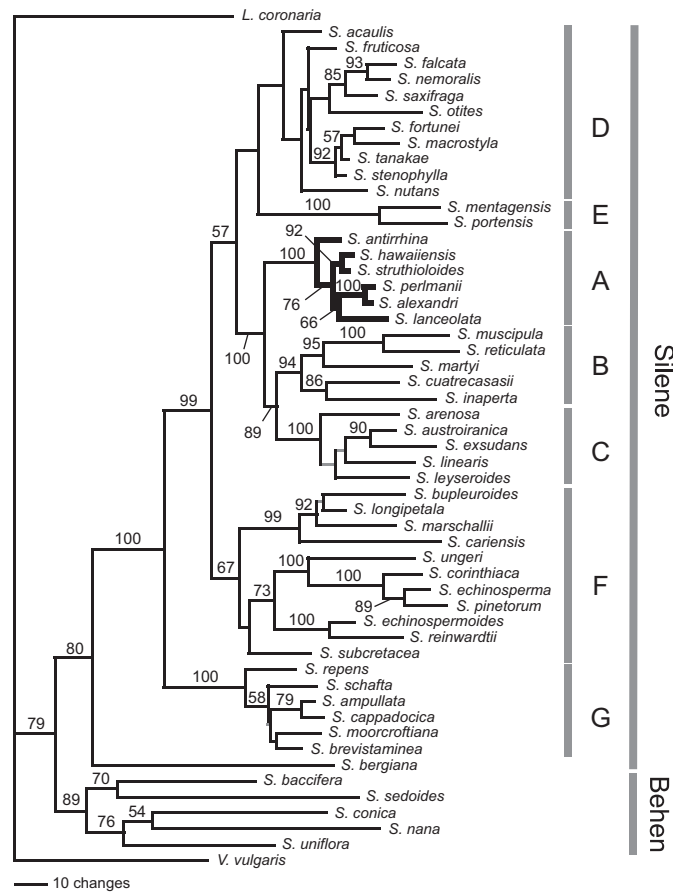


Figure 5. One of the maximum parsimony trees found in the analysis of the combined data (ITS, *rps16*, and *RPB2*). Branches in grey are collapsed in the strict consensus tree. Numbers associated with nodes (above or pointing at branches) indicate MPB frequencies. Branch lengths are proportional to number of changes. The clade with the endemic Hawaiian *Silene* and *S. antirrhina* (clade A) is marked with thick lines.

Summary of Paper VI

The focus in Paper VI turned from within the genus *Silene* to the entire tribe *Sileneae*, with special emphasis on *Heliosperma*, a genus previously often considered to belong in *Silene* but now shown, from nrDNA ITS and cpDNA *rps16* intron sequences, to be clearly outside (Frajman and Oxelman, in press). However, the origin of *Heliosperma* could not be confidently inferred from the ITS and *rps16* data and one of the aims of Paper VI was to infer the phylogenetic origin of the genus. *Heliosperma* includes several diploid ($2n=24$) taxa from the southern and central European mountains (e.g. Jalas and Suominen, 1986) that are found in three major lineages corresponding to the *H. alpestre* (Jacq.) Griseb., the *H. macranthum* Pan i , and the *H. pusillum* (Waldst. & Kit.) Rchb. group. Frajman and Oxelman (in press) discovered strong incongruence between the nuclear and chloroplast data concerning the interrelationships among these three lineages, and suggested that it could possibly be a result of ancient hybridization.

Several processes can affect genes and cause the gene trees to show incongruent phylogenetic patterns (see e.g. Wendel and Doyle, 1998). Such processes can be both interlineage (hybridization, lateral gene transfer between organismal lineages) or intral lineage (incomplete lineage sorting, orthology/paralogy conflation, which may be further complicated by recombination between alleles or genes). Hybridization is perhaps the most commonly used explanation to incongruent topological patterns (e.g. Soltis and Kuzoff, 1995; McKinnon et al., 2001; Okuyama et al., 2005), but arguments based on a formal framework discriminating between different explanations are rarely seen. Nuclear low copy genes have been shown useful for understanding reticulate evolution (for allopolyploids e.g. Cronn et al. 1999; Ferguson and Sang, 2001; Popp and Oxelman, 2001; Doyle et al., 2003; Popp et al., 2005, Huber et al. 2006; and diploids e.g. Cronn and Wendel, 2003; Howarth and Baum, 2005; Poke et al., 2006). A large number of unlinked DNA sequence regions is desirable for a proper understanding of plant phylogenetic relationships, since an increased data size will potentially increase accuracy (resolution and support), and if the phylogenetic history of the studied lineages includes reticulate events, data from a large number of unlinked regions can be used to detect and potentially distinguish these events from intragenomic processes. A homoploid hybrid species tends to have a combination of alleles and/or loci that are specific to either parent

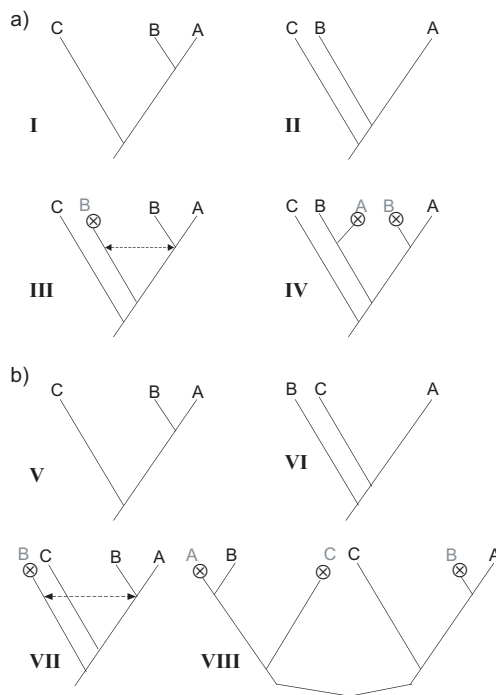


Figure 6. a) Two trees (I and II) with identical topologies but different divergence time between A and B, and hypothetical explanations of their history, III and IV (explaining I and II, respectively), given that the other gene tree reflects the “true” species tree. b) Two trees (V and VI) with different topologies and different divergence time between A and B, and hypothetical explanations of their history, VII and VIII (explaining V and VI, respectively), given that the other gene tree reflects the “true” species tree. A, B and C represent species lineages. Crossed circles represent extinction (or non-sampled gene copies).

(Ferguson and Sang, 2001), and it is likely that hybridization leaves traces in more than one nuclear gene (Cronn et al., 1999). A phylogenetic analysis of several low copy nuclear gene sequences can therefore be a tool to trace the parental lineages involved in the formation of homoploid hybrids.

In Paper VI, we explore the potential of trees where we have the chronological order of the interior nodes of the tree, and how these can be used to determine which processes are most likely as responsible for incongruences seen between gene trees. Specifically, we estimate the relative ages of conflicting groups in different gene phylogenies.

In Fig. 6, hypothetical explanations are presented for different scenarios where one tree represents the “species tree” and where either (Fig. 6a) two trees (I and II) have identical topologies but different divergence time between A and B or (Fig. 6b) two trees (V and VI) have different topologies and different divergence time between A and B.

Chloroplast genes are expected to be free from interlineage recombination and gene duplications are considered to be relatively rare (but see Erixon and

Oxelman, 2006). We have therefore chosen to use the chloroplast tree as representing the "species tree" and the incongruent patterns due to hybridization rather than orthology/paralogy conflict of cryptic cpDNA gene duplications.

Monophyly for *Heliosperma* is supported by three data sets, *psbE-petG*, *RPA2* and *RPD2b* (Fig. 7). The incongruence seen by Frajman and Oxelman (in press) among the three major *Heliosperma* lineages is also seen among the five data sets used in Paper VI. The *H. macranthum* cpDNA sequences are strongly supported as sister to the *H. pusillum* group sequences, whereas *RPA2* and *RPD2b* group *H. macranthum* and *H. alpestre* together as sister to the *H. pusillum* group, which is in agreement with nrDNA ITS (Frajman and Oxelman, in press). A conservative estimate of the coalescence times (using unrealistically large populations sizes and generation times; Maddison and Knowles, 2006). for the bifurcations observed in our gene trees is 2 Myr. The estimated difference in absolute age between *Heliosperma* from the chloroplast DNA data and from the nuclear DNA data is 5-7 Myr. Since this number is much larger than the conservative coalescence time of 2 Myr, incomplete lineage sorting can be rejected as explanation for the incongruences, if we assume that the relative datings of the trees are free from other errors. Instead, the incongruence between the chloroplast DNA and nuclear regions regarding the relationships among the three major lineages of *Heliosperma* are best explained by homoploid hybridization (graph VII in Fig. 6). That is, the relative dates for the divergence times in the respective gene trees are in better agreement with hybridization between the *H. alpestre* and *H. macranthum* lineages, with subsequent extinction of the "original" *H. alpestre* copy, than with ancient duplication of the gene with three subsequent extinctions.

The patterns seen in the *RPD2a* and the *RPB2* trees are a bit more complex. In *RPD2a*, *H. alpestre* groups with *Petrocoptis*, and does not form a monophyletic group with the other *Heliosperma* taxa (Fig. 7). One possible, but very hypothetical, explanation is that *Petrocoptis* as pollen donor was involved in the formation of *H. alpestre*, i.e. its branching from the *H. pusillum*/*H. macranthum* lineage, but such pattern is not seen in any other RNAP tree. Again, the relative dates show better agreement with a hybridization hypothesis rather than a gene duplication/extinction hypothesis.

In the *RPB2* phylogeny, one group of *Heliosperma* sequences share a common origin with the *Viscaria* and *Atocion* sequences (Fig. 7). *H. alpestre* and *H. macranthum* possess a second copy of *RPB2*, which groups confidently with *Eudianthe*, and with *Petrocoptis* as sister to them. If one ignores *Petrocoptis* (whose complex evolutionary history is beyond the scope of this thesis), the complicated relationships seen in the *RPB2* tree can be explained by a tree almost similar to graph VIII in Fig. 6, i.e. the hypothesis of an ancient duplication followed by several losses. The relative dates supports this scenario better than hybridization.

The pattern regarding the origin of *Heliosperma* itself is complicated, perhaps including both gene duplications/extinctions and hybridizations, making a straightforward explanation difficult. The cpDNA tree of Erixon and Oxelman (2006) based on a very large data set, suggests a sister group position of *Heliosperma* to a poorly supported clade including *Eudianthe*, *Viscaria*, and *Atocion*. Different RNAP regions suggest that two different lineages have been involved in the evolutionary history of *Heliosperma*. One lineage is closer to *Viscaria/Atocion* (supported by *RPA2*), and the other closer to *Petrocoptis* and/or *Eudianthe* (supported by *RPD2a*). It is noticeable that all data sets except *RPD2a* either support a sister group relationship of *Heliosperma* to *Viscaria/Atocion* or, at least, do not reject it strongly.

Paper VI shows that a framework with multiple gene trees with the nodes dated relatively to each other can be useful to discriminate among inter- and intralinear processes causing topological conflicts between gene trees, if the absolute time differences are large enough to exclude incomplete lineage sorting of alleles.

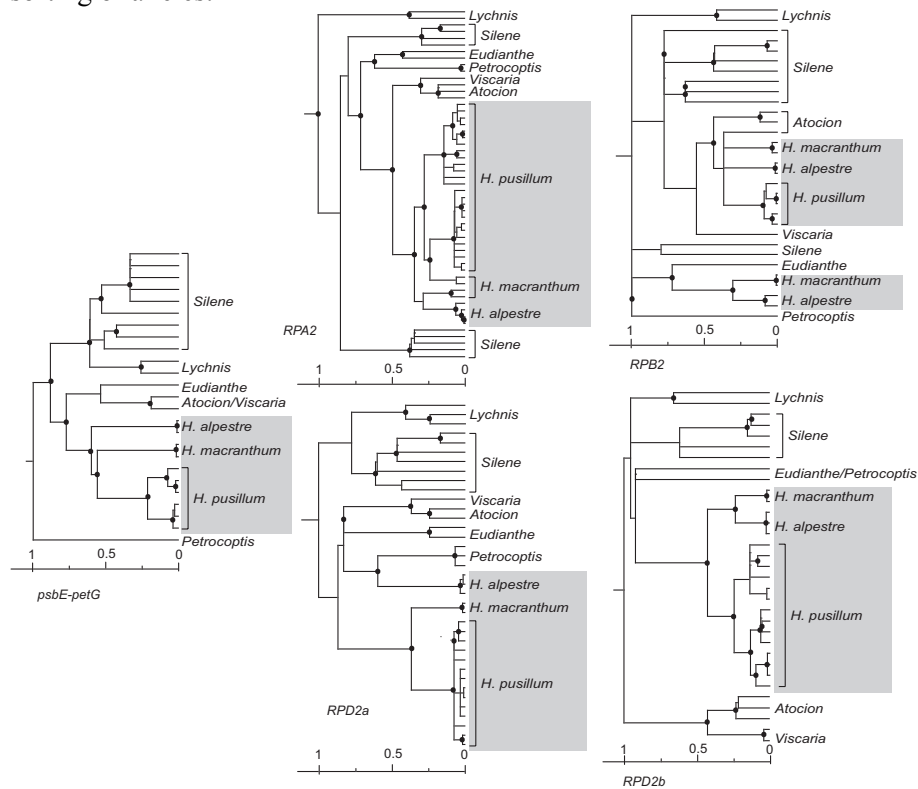


Figure 7. Chronogram for *psbE-petG*, *RPA2*, *RPB2*, *RPD2a* and *RPD2b*. Black dots on a node represent strong support (MPB > 75%/PP > 1) for the clade above that node. *Agrostemma* is not shown in the chronograms.

Sammanfattning (Swedish summary)

Systematik är, som all annan forskning, ett ständigt pågående detektivarbete. Man söker med alla tillgängliga medel finna sanningen, eller en hyfsat godtagbar version av den. Inom växtsystematiken går jakten efter växternas släktskap och deras utvecklings- och förändringshistoria, dvs. deras evolutionära historia. Vi söker finna ett mönster som vi kan använda för att ställa upp hypoteser om släktskapsförhållanden, och hypoteser är också det bästa vi kan åstadkomma. Eftersom vi inte har en tidsmaskin som vi kan använda för att gå tillbaka i tiden och studera vad som händer i direktsändning, måste vi i efterhand försöka rekonstruera vad som har hänt utifrån det vi kan se nu, på samma sätt som en detektiv försöker återskapa ett brottsförlopp utifrån vad som kan ses på brottsplatsen.

Vårt redskap i jakten efter släktskapsförhållanden är likhet. Den traditionella växtsystematiken använder sig av det man kan se på utsidan av en växt, dvs. vilket utseende den har. Man försöker beskriva en växt och dela upp beskrivningarna i olika karaktärer som sedan kan användas för att jämföra olika växter. Om två växter liknar varandra i många avseenden kan man dra slutsatsen att det förmodligen beror på att de har en gemensam anfader som de har ärvt sitt utseende ifrån. Tyvärr är situationen lite mer komplicerad än så, för ibland kan saker vara lika varandra utan att vara släkt och ibland kan saker vara släkt utan att likna varandra. Ofta beror utseendet på vilken miljö växten befinner sig i, på samma sätt som att jag nog vid en hastig blick skulle vara mer lik min granne (som jag inte är släkt med) om vi stod utomhus idag en råkall, dimmig novemberdag än vad jag skulle vara lik min syster om hon i samma stund skulle befinna sig på en solig strand i Thailand.

Dessutom är en ofta växt lika en grupp med växter på några sätt, men lik en annan grupp växter på ett annat sätt. Problemet är att veta vilka karaktärer som man kan sätta tilltro till när man gör sina antaganden om släktskap. Även en ickebotanist kan nog gå med på att det inte är så troligt att ett vitblommande hundkex inte är så nära släkt med en rönn som står bredvid, trots att den också har vita blommor. Blomfärg är alltså oftast inte en så användbar karaktär i släktskapsjämförelser. Däremot har andra karaktärer från själva blomman ofta visat sig vara användbara. En blomma är oftast uppbyggd av honliga delar (pistill), hanliga delar (ståndare) och blomblad av olika typ (kronblad och foderblad). Man kan t.ex. räkna hur många det finns av olika delar, hur de sitter i förhållande till varandra, om de är samman-

vuxna på något sätt, om någon del saknas osv. Med hjälp av karaktärer från blommans utseende, tillsammans med karaktärer för bladform, växtsätt, behåring m.m. kan man således jämföra växter. Ibland kanske man har två växter som är lika varandra på tio olika sätt, men en av dem liknar en annan växt på ett annat sätt. Slutsatsen blir då oftast att de två första växterna är närmare släkt. Situationen blir dock knepigare om man har två växter som är lika varandra på tio olika sätt, men en av dem liknar en annan växt på tio andra sätt. Då får man ge sig ut på jakt efter nya karaktärer att jämföra. Med mikroskopets uppfinnande kunde man börja beskriva och jämföra hur olika celler ser ut. Senare kom man på hur man kan ge sig in i cellerna och räkna antalet kromosomer, vilket kan vara intressant eftersom kromosomantalet ofta kan vara lika inom en viss grupp växter. I kromosomerna finns en organisms arvs massa, där lagras all information om en organism, hur den ska byggas upp och hur den ska fungera. Arvs massan, DNA, finns i form av långa sekvenser av fyra olika byggstenar, där informationen bevaras genom hur dessa byggstenar sitter kombinerade och i vilken ordning de sitter. Närbesläktade organismer kommer naturligtvis att ha liknande sekvenser av kombinationer, eftersom de ser ut och fungerar på samma sätt. Arvs massan förändras dock hela tiden, och grupper som är mer avlägset släkt kommer att ha mer olika DNA-sekvenser. Genom att jämföra sekvenser kan man alltså dra slutsatser om släktskap, och modern systematiks största landvinning är möjligheten att få fram och jämföra dessa sekvenser. Det är nämligen betydligt större mängder information som man kan få fram från sekvenser än från studier av växters utseende, eftersom varje byggsten och dess position utgör en karaktär.

En stor del av systematiken, och den del som kanske de flesta förknippar med systematik, är att organisera växter i olika namngivna grupper, en s.k. klassifikation. Inom modern systematik anser man att dessa grupper ska representera släktskapsgrupperingar, dvs. allt som samlas under ett namn ska vara närmast släkt med varandra och ingen närbesläktad del ska vara utelämnad. Vanligtvis är den minsta släktskapsgruppering man namnger det som man kallar art. Flera arter organiseras i ett släkte och flera släkten i familjer. Ofta använder man sig av ytterligare nivåer i sin organisation, den här avhandlingen berör t.ex. en tribus som kallas *Sileneae*. En tribus är en undergrupp inom en familj, och består av ett eller flera släkten. I tribusen *Sileneae* ingår t.ex. åtta släkten. Det släkte som jag har arbetat mest med heter *Silene*, och det är ett stort släkte som innehåller många arter. Detta släkte har man därför organiserat i ytterligare undergrupper som kallas för sektioner.

I den första artikeln (**Artikel I**) i denna avhandling har vi använt oss av DNA-sekvenser för att testa en grupp från en äldre klassifikation av släktet *Silene*, en sektion som kallas *Rigidulae*. Denna sektion utgörs av växter från Mellanöstern och från Medelhavsregionen. Den äldre klassifikationen är baserad på utseendekaraktärer, men många sådana karaktärer är väldigt variabla inom släktet *Silene*. Det fanns därför skäl att misstänka att sektionen

Rigidulae inte beskrev en naturlig släktgrupp. Det släkträd som vi konstruerade, baserat på jämförelser av sekvenser, visade också mycket riktigt att de arter som hade placerats i sektionen *Rigidulae* inte alls bildade en gren i släkträdet, utan fanns istället i sex olika grenar, utspridda på olika ställen i trädet. Det visade sig att var och en av dessa grupper verkar ha en ganska tydlig och avgränsad utbredning. Vi diskuterar för varje grupp hur de nya rönen skulle kunna avspeglas i en ny klassifikation, men eftersom det behövs ytterligare studier av alla de nyidentifierade grupperna så gör vi ingen ny klassifikation i denna artikel.

En del av detektivarbetet som en systematiker måste utöva är att komma fram till vad äldre tiders systematiker har gjort och menat. Det är inte ovanligt att vad som verkar vara (eller anses vara) en enda art har fått flera olika namn, eller att samma namn använts för olika arter. För att få ett konsekvent användande av namn har man beslutat att alltid använda det äldsta tillgängliga namnet. Denna regel får dock olyckliga konsekvenser ibland, om ett väletablerat namn helt plötsligt visar sig vara ogiltigt, antingen på grund av att det existerar ett äldre namn för samma art, eller för att namnet tidigare använts för något helt annat. Om det andra namnet är sällan använt kan man skriva ett förslag till en kommitté, där man argumenterar för att antingen förkasta ett äldre namn eller bevara ett yngre, beroende på vilket som passar situationen. **Artikel II** i avhandlingen är ett förslag av den första typen, medan **artikel IV** är ett förslag av den andra typen.

Även om jämförelser av DNA-sekvenser nuförtiden är det vanligaste sättet att göra släktskapsanalyser, har fortfarande studier av växternas utseende stor betydelse för beskrivandet av växter. I den tredje artikeln (**Artikel III**) studerar vi närmare en av de grupper som identifierades i artikel I, både med hjälp av utseendekaraktärer och släkträd baserade på sekvenser. Arterna i denna grupp är hemmahörande i mellanöstern. Vi beskriver i denna artikel denna grupp som en ny sektion kallad *Arenosae*. I artikeln presenteras även beskrivningar av arterna i gruppen. Dessa beskrivningar är gjorda enligt en ny modell för digitalisering av växtbeskrivningar.

Med hjälp av olika släktskapsmönster vi ser kan vi inte bara dra slutsatser om just släktskap. Vi kan också göra antaganden om hur växter har spridits över jordklotet. Alla växter på Hawaii måste ha kommit dit genom spridning över långa avstånd, eftersom ögruppen har bildats mitt i Stilla havet och har aldrig varit i direkt kontakt med någon kontinent. Det är vanligt att växtgrupper på isolerade öar får ett speciellt utseende, som gör att det är svårt att identifiera deras närmsta släktingar från andra områden. Speciellt vanligt är det att öväxter utvecklar ett vedartat växtsätt. På de hawaiianska öarna finns det sju arter av inhemska *Silene* (två verkar dock vara utdöda och en finns bara kvar i odling). De har delats in i två grupper baserat på utseende, och det har föreslagits att dessa två grupper är resultatet av två olika introduktioner. I **artikel V** visar vi dock att de bildar en enda gren i släkträdet, vilket tyder på att *Silene* har kommit till Hawaii endast en gång i

historien, och att alla arter som finns där nu har en och samma anfader. En tidigare klassifikation föreslog att de hawaiianska *Silene*-arterna skulle vara nära släkt med två japanska *Silene*-arter, vilket antyder att anfadern skulle ha kommit till Hawaii från norra asien. Vi har dock inkluderat en av dessa japanska arter i vår släktskapsanalys och det visar sig att den inte alls är nära släkt med de inhemska hawaiianska arterna. Istället visar det sig att den närmsta släktingen är ett amerikanskt örtartat ogräs. Det verkar alltså som om att en anfader till den amerikanska arten och de hawaiianska arterna någon gång har spridit sig till Hawaii, där ett vedartat växtsätt har uppstått följt av utvecklingen av de två utseendemässigt olika linjerna.

Släktskapsanalyser baserat på DNA-sekvenser har betytt mycket för förståelsen av relationerna inom många olika grupper, men det är inte alltid säkert att bilden blir klarare av sekvensdataanalyser. Olika regioner av arvsmassan kan ha olika historia och det finns flera olika processer som ligger bakom detta. Ett exempel är när två närstående arter hybridiserar och bildar en avkomma som innehåller arvs massa från båda föräldrararterna. Den släktlinje som bildas av avkomman kommer att innehålla arvs massa där olika delar är närmast släkt med olika arter. Beroende på vilken del av arvs massan man studerar kommer man att få olika historier presenterade för sig. Hybridisering är ett exempel på en process som verkar mellan olika släktlinjer och som resulterar i varierande släkthistoriesmönster. Andra processer verkar istället inom en släktlinje. Ett exempel på det är när en region av arvs massan dupliceras, dvs. bildar två upplagor. Båda upplagorna kommer först att existera inom en släkteslinje, och när denna linje delas upp i två dotterlinjer kommer båda upplagorna följa med i båda linjerna, och detta upprepas när nya "dotterdotter"-linjer bildas. Med tiden kommer dock den ena upplagan försvinna i de olika linjerna, och det är inte alls säkert att två systerlinjer förlorar samma upplaga. Det släktträd som man får av sekvenser från denna region reflekterar därför upplagornas historia snarare än linjernas historia, och linjer som har en och samma upplaga grupperas tillsammans trots att de kanske inte egentligen är närmast släkt med varandra.

I **artikel VI** studerar vi det syd- och centraleuropeiska släktet *Heliosperma* och hur det förhåller sig till andra släkten inom tribusen *Sileneae*. *Heliosperma* är uppdelat i tre större släktlinjer och vi undersöker även hur de förhåller sig till varandra. Till detta använder vi DNA-sekvenser från flera olika regioner, och dessa regioner uppvisar mycket varierande mönster. En del av arvs massan hos växter finns i de s.k. kloroplasterna. Den här delen anses i allmänhet vara mindre utsatt för påverkande processer. Vi har ett träd som är baserat på sekvenser från kloroplasterna, och för att få möjlighet att försöka komma fram till vad som ligger bakom de varierande mönstren vi ser i de andra träden så antar vi att detta träd representerar ett "artträd", dvs. det "rätta" släktesträdets. Genom att räkna ut när olika förgreningar i trädet har skett, dvs. hur de förhåller sig relativt till varandra tidsmässigt, så kan man få en uppfattning om vilken process som mest troligt ligger bakom de

varierande mönstren. För de tre större linjer som finns inom *Heliosperma* så verkar hybridisering vara den mest troliga förklaringen. För *Heliosperma* och övriga släkten inom tribusen är det dock svårare att säga vad som ligger bakom de olika mönster som vi ser, även om hybridisering helt klart har påverkat här också. I ett fall verkar det dock som den mest troliga förklaringen är att en gammal duplicering av en region har skett följt av förlust av olika upplaga i olika linjer.

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