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On Ingeae
Systematics of synandrous mimosoids

JULIA FERM

Abstract
Ferm, J. 2020. On Ingeae Systematics of synandrous mimosoids. *Digital Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology* 1969. 50 pp. Uppsala: Acta Universitatis Upsaliensis. ISBN 978-91-513-1013-8.

Background: The Ingeae tribe (Caesalpiniodeae, Fabaceae) has a long history of taxonomic complexity with genera being merged and split, and many species with former placements in several different genera. Moreover, phylogenetic studies have shown that the tribe is non-monophyletic with the genus *Acacia* (of tribe Acacieae) nested within Ingeae. This problem of non-monophyly is also reflected at the generic and specific level of ingoid taxa. Phylogenetic relationships have been difficult to resolve, with unsettled generic delimitations as a result. In this thesis, I investigated the systematics and phylogeny of the Ingeae-*Acacia* complex, with reflections on taxonomy and biogeography. **Methods:** Molecular data of plastid (*matK*, *psbA*, *trnL-trnF*, *ycf1*) and nuclear (ETS, ITS) DNA sequences were analysed using Bayesian inference and Ultrafast Bootstrap in order to investigate phylogenetic relationships of the Ingeae-*Acacia* complex. **Results:** In paper I, *Marmaroxylon* was shown to be included in *Zygia* and *Zygia inundata* in *Inga*. *Marmaroxylon magdalenae*, *M. ocumarense* and *Zygia sabatieri* were not recovered in the *Zygia-Marmaroxylon* clade and therefore left without a placement in any genus. In paper II, *Zapoteca* was shown to be monophyletic but the subgenera comprising more than one species, and four species, were non-monophyletic. In paper III, a new subgeneric classification of *Zapoteca* and an identification key to the subgenera are presented, as well as a phytogeographical review of the genus. *Zapoteca formosa* subsp. *schottii* and *Z. formosa* subsp. *gracilis* were recognized as distinct species. In paper IV, *Afrocalliandra* and *Calliandra* were recovered as the earliest diverging lineage within the Ingeae-*Acacia* complex, and the other taxa possessing the same pod-type as *Calliandra*, i.e. *Sanjappa*, *Thailentadopsis*, *Viguieranthus* and *Zapoteca*, were shown to be more closely related to each other and other ingoid genera than to *Calliandra*. **Discussion and conclusions:** Phylogenetic relationships of the Ingeae-*Acacia* complex are possible to resolve with a broad sampling and a combination of several nuclear and plastid informative DNA sequences. Taxonomic revisions are, however, needed for several ingoid genera, as well as for the entire Ingeae tribe since it currently is non-monophyletic with respect to *Acacia*. Shared morphological characters are not always indicative of common ancestry and older morphology-based classifications do not always reflect the evolutionary history of the group. One example is the "*Calliandra*-pod" fruit type. While it has often been argued to indicate close relationships, I show that this seemingly specific type of pod occurs in several unrelated genera.

Keywords: Fabaceae, Ingeae, Systematics, Phylogenetics, Taxonomy, Morphology

Julia Ferm, Department of Organismal Biology, Systematic Biology, Norbyv. 18 D, Uppsala University, SE-75236 Uppsala, Sweden.

Ruusu on ruusu,
Ja oli aina ruusu.
Mutta teoria menee nyt
Että omena on ruusu,
Ja päärynä on, ja niin on
Luumu, luulisin.
Rakas tietää vain
Mikä todistaa seuraavaksi ruusun.
Olet tietysti ruusu -
Mutta ollaan kaiki aina ruusuja.
– Robert Frost

List of Papers

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

I Ferm J., Korall P., Lewis G. P. & Ståhl B. (2019) Phylogeny of the Neotropical legume genera *Zygia* and *Marmaroxylon* and close relatives. *Taxon*. 68(4): 661-672.

II Ferm J. (2019) A preliminary phylogeny of *Zapoteca* (Fabaceae: Caesalpinioideae: Mimosoid clade). *Plant Systematics and Evolution*. 305(5): 341-352.

III Ferm J. & Ståhl B. A revised classification of the Neotropical genus *Zapoteca* (Caesalpinioideae; Fabaceae), with one new subgenus and two new species combinations. [Manuscript submitted for publication.]

IV Ferm J., Ståhl B., Wikstöm N. & Rydin C. Phylogenetic relationships of the mimosoid Ingeae–*Acacia* complex (Fabaceae), based on plastid and nuclear data. [Manuscript.]

Contents

Abbreviations

DNA	Deoxyribonucleic acid
PCR	Polymerase Chain Reaction
s.l.	sensu lato (in the broad sense)
s.s.	sensu stricto (in the narrow sense)
sp.	Species (singular)
spp.	Species (plural)
subsp.	Subspecies
subg.	Subgenera
ser.	Series
sect.	Section
LPWG	Legume Phylogeny Working Group
POWO	Plants of the World Online

Introduction

Systematics

Systematics is the study of evolutionary relationships of taxa at all levels, of groups of organisms and lineages over time. These relationships can be visualized through phylogenetic trees, which illustrates common ancestry and diversification in a straight forward way that is easy to interpret. Systematics includes also taxonomy, i.e. the formal classification and naming of taxa. Nowadays phylogenetic analysis is an important foundation for taxonomic work and evolutionary studies. With new techniques for the production of enormous amounts of DNA data, the possibilities for addressing and answering evolutionary questions has increased well beyond expectation in a short period of time. By using modern phylogenetic analysis as a basis we can construct classifications that actually reflect the evolutionary relationships amongst taxa. With a robust phylogeny as a basis, questions on for example diversification dynamics, biogeography and morphological evolution can be addressed. The occurrence of the same morphological characters in different clades can be due to convergent evolution in distantly related taxa, or represent an ancestral state that has been lost in some lineages. Although morphological characters might not always provide an easily understandable indication of kinship it can often still be useful for understanding evolution and for the purpose of classification. In particular in combination with molecular data and when material for DNA extraction is not available, as with fossils, morphology is useful. Morphology is also important for species identification and the communication of species, for example in identification keys.

In this thesis, I present my systematic research, including discussions of character evolution and phytogeography, on a group of tropical legumes pertaining to the Ingeae tribe (Caesalpinioideae; Fabaceae).

The Ingeae–*Acacia* complex

Why study Ingeae?

The Ingeae tribe represents a group of tropical legumes of trees and shrubs including approximately 750 species in about 36 genera. The tribe is positioned within the mimosoid clade, a monophyletic group previously defined as subfamily Mimosoideae but now placed in subfamily Caesalpinioideae

(LPWG 2017). The mimosoid clade consists of four tribes, Acacieae, Ingeae, Mimoseae and Mimozygantheae (Lewis et al. 2005).

The taxonomy of Ingeae has long been under investigation but its classification (Lewis & Rico Arce 2005) is still in flux with many genera being merged or divided (e.g. Souza et al. 2013, 2016; Iganci et al. 2016). The taxonomic instability at the generic level means that most species of the tribe have been placed in different genera. For example, *Hydrochorea corymbosa* (Rich.) Barneby & J.W.Grimes has since it was described for the first time in 1792 (as a species of *Mimosa* L.) been placed in seven different genera, and the well-known raintree, *Samanea saman* (Jacq.) Merr., has occurred in no less than nine genera (POWO 2020). Moreover, as shown in paper I, species with uncertain placements, e.g. *Marmaroxylon magdalenae* Killip ex L.Rico and *Zygia sabatieri* Barneby & J.W.Grimes, continue to be highlighted through new research.

Several recent phylogenetic studies based on molecular data have shown that relationships within Ingeae are difficult to resolve (e.g. Souza et al. 2013; Shinwari et al. 2014; Iganci et al. 2016), exposing poorly defined generic boundaries and showing that many genera and species are non-monophyletic following the current classification. Even the Ingeae tribe itself has been shown to be non-monophyletic in relation to the genus *Acacia* Mill., of the tribe Acacieae, in several studies (Miller & Bayer 2001; Miller et al. 2003; Brown et al. 2008; Bouchenak-Khelladi et al 2010; LPWG, 2017). In fact, all mimosoid tribes have been shown to be non-monophyletic and nested with each other (Luckow et al. 2003; Miller & Seigler 2012; Kyalangalilwa et al. 2013). Despite this being shown in several studies, little taxonomic action has been taken to adjust the non-monophyly of Ingeae. Miller et al. (2014) presented an alternative, unofficial classification based on the rank-free system of the *PhyloCode* (Cantino & de Queiroz 2020). However, their purpose was to resolve the problem with a non-monophyletic Acacieae, i.e. *Acacia* s.l., and preserve the name *Acacia* for all species previously included in that genus, but now distributed in five different genera, i.e., *Acacia*, *Vachellia* Wight & Arn., *Senegalia* Raf., *Mariosousa* Seigler & Ebinger and *Acaciella* Britton & Rose. Therefore, they proposed the name *Acacia* for the clade including all species of Acacieae, which consequently also include Ingeae and three genera of Mimoseae, since they are all nested with each other (see also Kyalangalilwa et al. 2013). This action may seem unnecessarily complicated and confusing since the well-established name *Acacia*, associated with attributes of species of *Acacia* s.l., does not reflect the diversity seen in Ingeae, nor the large and morphologically heterogenous complex that this clade comprises. And it does not resolve any taxonomic issues of Ingeae per se.

Distribution and morphology of ingoid genera

The members of the Ingeae tribe are found throughout the tropical areas of the world. Most of the larger genera (e.g. *Inga* Mill., *Abarema* Pittier and *Calliandra* Benth.) are restricted to the New World and the highest species diversity is thus found in the Neotropics, but the tribe is also well-represented in Africa, South East Asia and Australia (Lewis et al. 2005). Members of the tribe grow in areas with seasonally dry climates as well as in rainforests, chiefly in the lowlands but some also in montane habitats (Tropicos.org 2020).

Members of the Ingeae tribe generally have bipinnate leaves with one to several pairs of pinnae, each with one to several leaflets/pinna. The genus *Inga* is the exception. It consists of approximately 300 species with pinnate leaves. However, a few additional species with pinnate leaves are present in other genera, viz. *Cojoba rufescens* (Benth.) Britton & Rose (Mohlenbrock 1963), *Sanjappa cynometroides* (Bedd.) E.R. Souza & Krishnaraj (Souza et al. 2015) and *Calliandra hymenaeodes* (Pers.) Benth. (Bentham 1875). As all species of Fabaceae, the members of Ingeae have a fruit with the seeds arranged in two rows in a one-chambered legume, known as a pod (Lewis et al. 2005). Furthermore, ingoid species are recognized by their mimosoid flowers, i.e. actinomorphic flowers with 10 to numerous, showy stamens extending long beyond the corolla. The members of the Ingeae tribe are referred to as the synandrous mimosoids; they generally have the stamen filaments united at the base forming a well-developed tube surrounding the pistil, a feature that distinguishes them from other mimosoids (Bentham 1865).

Taxonomic history of the Ingeae tribe

The Ingeae tribe was described by Bentham (1865) to include nine genera, a number which he later (Bentham 1875) raised to 15 genera "or subgenera", without making any clear distinction between the two ranks. The Ingeae tribe included species formerly placed in tribe Acacieae, described by Dumortier (1829). Bentham (1865) distinguished the taxa of these two tribes on the absence or presence of synandrous flowers, species of Acacieae generally having free stamen filaments. However, some species of the Acacieae tribe do in fact have fused stamen filaments, but without clearly forming a tube. Thus, when Acacieae show fused filaments, these are irregularly united (Bentham 1875). Additionally, some ingoid species, e.g. of *Havardia* Small and *Lysiloma* Benth., have androecia with very short filament tubes, with the filaments fused to the corolla and the disk, thereby forming a stamonozone (Barneby & Grimes 1996). A stamonozone also occurs in other ingoid taxa, e.g. *Viguieranthus* Villiers*,* but then the tube is not as short as in *Havardia* and *Lysiloma*. Tube morphology thus varies and might depend to some extent on degree of fusion and what flower parts are forming the tube.

Older classifications of the tribe were based entirely on morphological characters; species with pinnate leaves were placed in *Inga*, species with a

flattened pod dehiscent from the apex to the base with recurving valves were placed in *Calliandra*, and species that were difficult to place in any genus were often placed in *Pithecellobium* Mart. (Barneby & Grimes 1996), thus serving as a "dust-bin" taxon. Britton & Rose (1928) defined *Pithecellobium* as having stipular spines and arillate seeds, a delimitation that resulted in many species being transferred to *Albizia* Durazz. instead. This treatment made *Albizia* heterogenous and difficult to define based on morphology (Barneby & Grimes 1996). *Albizia* is one of the largest genera of Ingeae, with 127 accepted species and with a pantropical distribution, but the genus seems to comprise an assemblage of unrelated species (POWO 2020).

Over the years the number of ingoid genera has increased. Nielsen (1981) recognized 21 genera and Polhill (1994) recognized 25. In the latest formal classification of Ingeae, based on phylogenetic studies of molecular data and with consideration of morphology (Lewis & Rico Arce 2005), divides the tribe into 36 genera placed in seven informal alliances. More recent phylogenetic studies of Ingeae have, however, shown that this classification does not always reflect monophyletic groups and generic delimitations are repeatedly being revised in the light of new knowledge (e.g. Souza et al. 2013, 2016; Iganci et al. 2016). A few genera of the Ingeae tribe have been studied in more detail. Souza et al. (2013) showed that *Calliandra* was monophyletic after the inclusion of *Guinetia* L.Rico & M.Sousa (Rico Arce et al. 1999). In the same paper, *Afrocalliandra* E.R.Souza & L.P.Queiroz was established, to accommodate two African species previously referred to *Calliandra* (Thulin et al. 1981), which made *Calliandra* geographically restricted to the Neotropics. In a different study (Iganci et al. 2016), the Neotropical *Abarema* was shown to be non-monophyletic. The type species, *Abarema cohliacarpos* (Gomes) Barneby & J.W.Grimes, was resolved in a position that excluded it from the other species of *Abarema*, and the type of the genus is evidently more closely related to other ingoid taxa. Moreover, the remaining species of *Abarema* were nested in a clade together with species of *Hydrochorea* Barneby & J.W.Grimes, *Balizia* Barneby & J.W.Grimes and *Albizia*, further complicating the classification of these genera. Phylogenetic relationships in *Albizia* have also been difficult to resolve (LPWG 2017) and the genus is clearly non-monophyletic as it is currently circumscribed (Luckow et al. 2003; Shinwari et al. 2014).

Considering this complex taxonomic history and difficulties in resolving phylogenetic relationships, I found the Ingeae–*Acacia* complex to be an interesting and challenging group to study systematically. I decided to focus on a few ingoid genera (*Zygia* P.Browne, *Marmaroxylon* Killip and *Zapoteca* H.M.Hern.), which had not previously been tested thoroughly using molecular data or modern phylogenetic analyses (papers I-III). I also wanted to investigate generic relationships of the Ingeae–*Acacia* complex in its entirety but with special emphasis on a few supposedly closely related genera (*Calliandra*, *Afrocalliandra*, *Faidherbia* A.Chev., *Sanjappa* E.R.Souza & Krishnaraj,

Thailentadopsis Kosterm., *Viguieranthus* and *Zapoteca*) by adding a new gene region that has not been used so much in the past, at least not on this particular plant group (paper IV).

Selected ingoid genera

Zygia and Marmaroxylon

The genera *Zygia* and *Marmaroxylon* are small to medium sized, cauli- and/or ramiflourous trees with white to pink flowers. The cauliflory distinguishes them from other ingoid genera, although a few species of *Inga* also show cauliflory (Pennington 1997). According to Rico Arce (1991), *Zygia* and *Marmaroxylon* are distinguished on differences in leaf morphology. Species of *Zygia* have leaves with one pair of pinnae, often with few leaflets only, while species of *Marmaroxylon* have more than one pair of pinnae, often with numerous pairs of leaflets (Fig. 1). Both genera are strictly Neotropical and found in moist or wet lowland or lower montane forest (Barneby & Grimes 1997).

Fig. 1. A. *Marmaroxylon basijugum*; B. *Zygia latifolia*; C. *Zygia heteroneura*
Photos: Bertil Ståhl

Zapoteca

The genus *Zapoteca* comprises small trees or scandent shrubs with terminal, globose inflorescences and leaves with several pairs of pinnae with numerous leaflets, although a few species have one pair of pinnae with one or a few pair(s) of leaflets/pinna only (Fig. 2). The pods of *Zapoteca* are flat with thickened margins and dehiscent from the apex to the base with recurving valves. *Zapoteca* occurs in tropical dry forest and disturbed habitats in seasonally dry areas, but also in lowland rainforest and montane wet forest, from southern USA (Texas, Arizona) to northern Argentina, and the Caribbean (Hernández 1989, Tropicos 2020). One species, *Z. portoricensis* (Jacq.) H.M.Hern., has been introduced to western Africa (Ghana, Togo, Benin, Nigeria, Cameroon) (Hutchinson & Dalziel 1958) and Asia (Bangladesh, Indonesia: Java) (POWO 2020).
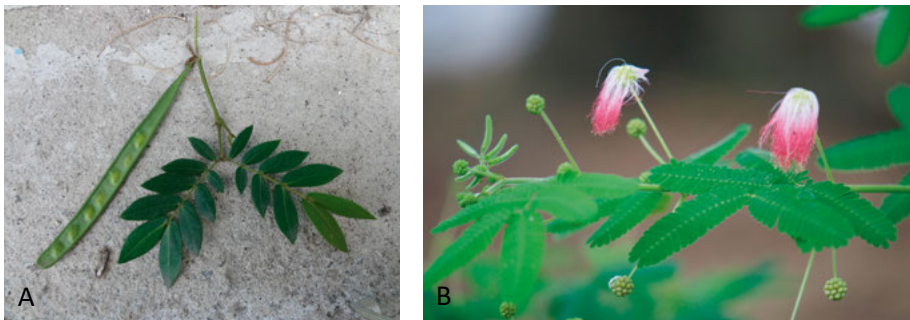

Fig. 2. A. *Zapoteca aculeata*; B. *Zapoteca andina*
Photos: Bertil Ståhl

Calliandra, Afrocalliandra, Faidherbia, Sanjappa, Thailentadopsis and Viguieranthus

The genera *Calliandra, Afrocalliandra, Faidherbia, Sanjappa, Thailentadopsis* and *Viguieranthus* consist of shrubs and small trees. *Calliandra* is the largest of these, consisting of some 135 species restricted to the Neotropics. *Afrocalliandra* (2 spp.) is African and *Faidherbia* (1 sp.) is found in Africa, Saudi Arabia, Jordan and Syria. *Viguieranthus* (18 spp.) is confined to Madagascar and the Comores, and *Sanjappa* (1 sp.) and *Thailentadopsis* (3 spp.) are Asian. *Calliandra, Afrocalliandra*, *Sanjappa*, *Thailentadopsis* and *Zapoteca* all have the same type of pod, in this thesis referred to as "*Calliandra*-pod". The "*Calliandra*-pod" is flattened with thickened margins and dehiscent from the apex to the base with the valves recurving. The possession of the "*Calliandra*-pod" could be an indication of a common evolutionary history of these genera. In addition, they also share a taxonomic history, with most of these taxa having previously been included in *Calliandra* (s.l.) due to the similarity in pod morphology (Bentham 1840, 1844, 1875; Harms 1921; Thulin et al. 1981). Since *Calliandra* and *Zapoteca* are both Neotropical and none of

the other genera with a similar pod type are found in the Neotropics, it seemed likely they should be sisters. To test this hypothesis, I included all genera with the "*Calliandra*-pod" in the same Bayesian inference analysis, and *Zapoteca* and *Viguieranthus* were resolved as sisters with strong support. However, these results have never been presented since I considered a larger sample of ingoid taxa necessary in order to draw any conclusions about generic relationships of these genera, and also their relationship to other ingoid taxa. Some phylogenetic studies based on molecular data have suggested also *Faidherbia* to be closely related to these genera (e.g. Bouchenak-Khelladi et al. 2010; Souza et al. 2016). Thus, I found also this genus interesting when investigating phylogenetic relationships of the genera with a "*Calliandra*-pod", even though *Faidherbia* possesses a different type of pod.

Fieldwork

One important skill of a systematist and a botanist is the ability to detect and identify plants in the field, which helps us survey the world's diversity, and also, find what we are looking for. Moreover, by knowing which species exist, and where they are distributed, the conservation status can be evaluated, endangered species be identified and the extinction of species be prevented. Collecting specimens in the field provides high quality leaves suitable for DNA extraction, specimens to use for morphological studies and the opportunity to study species in their natural habitat. Moreover, by depositing the specimens we collect in herbaria the material becomes available for other researchers all around the world and is a way of preserving the biodiversity we see today for later generations. A perfect way of complementing samples collected during fieldwork is to use leaf material from previous fieldwork, stored in national herbaria. A herbarium can contain large collections from large areas making it an important source for obtaining material and study specimens from areas not visited. For this thesis I have carried out fieldwork in Ecuador, Jamaica, Puerto Rico and Costa Rica. With the help of Tropicos.org and label data from older collections I was able to map and visit localities of particular interest.

Ecuador

Although a quite small country in South America, Ecuador has many different types of environments with the rainforests of Amazonia, the cloudforests of the Andes and dry forests near the coast. Many mimosoid genera are present in Ecuador and of these I was able to find and collect *Zygia latifolia* (L) Fawc. & Rendle, *Z. Heteroneura* Barneby & J.W.Grimes, *Z. longifolia* (Humb. Bonpl. Ex Willd.) Britton & Rose, *Z. basijuga* (Ducke) Barneby & J.W.Grimes (=*Marmaroxylon basijugum* [Ducke] L.Rico), *Pseudosamanea guachapele* (Kunth.) Dugand, *Abarema macradenia* (Pittier) Barneby & J.W.Grimes, *Abarema ganymedea* Barneby & J.W.Grimes, *Vachellia farnesiana* (L.) Wight & Arn. and *Samanea saman*, as well as specimens of *Inga*, *Zygia*, *Calliandra*, *Abarema* and *Acacia*, not yet determined to species.

Jamaica

Being located in the Caribbean, Jamaica has a tropical climate, but with lower temperatures in the mountains. The genus *Zygia* was originally described from a Jamaican plant, nowadays treated as *Z. latifolia*. No recent collections of this

species from Jamaica were available and therefore it was interesting to collect, especially since *Z. latifolia* was not recovered as monophyletic in paper I.

Puerto Rico

Puerto Rico is a small island with the Caribbean Sea to the south and the Atlantic to the north. Puerto Rico suffered much damage from the hurricane Maria in 2017 and many areas were therefore hard to reach, especially in the mountains. Still, with the help of local botanists, I managed to collect *Zapoteca portoricensis* subsp. *portoricensis*, *Inga laurina* (Sw.) Willd., *I. vera* Willd., *Enterolobium cyclocarpum* (Jacq.) Griseb. and *Pithecellobium dulce* (Roxb.) Benth. Moreover, the herbarium that belongs to the Botanical Garden/University of Puerto Rico (UPRRP) has quite a big collection of species of *Inga* brought to the island in the past with the purpose of forestation. These are of great value when sampling material for DNA extraction.

Costa Rica

In Costa Rica, diversity of ingoid species is large. The nature is diverse with hot and dry areas in the north, close to the border to Nicaragua, mountains in the south, and the southern peninsula covered with rainforest. I visited all of these areas. I was able to study species of *Zygia*, *Cojoba* Britton & Rose and *Inga* in the wild and collections were sent to the Museo National de Costa Rica for storage in the herbarium (CR). Unfortunately, I have not yet managed to obtain the permit for using the samples for DNA extractions, and the material is thus not used in the studies included in this thesis.

Storys from the field

I spent three weeks in Jamaica in November 2018, searching for *Zygia latifolia*. It was growing in Castleton Botanical Garden, but I could not collect it from there. On my last day of fieldwork I went by motorcycle with my guide Roger Thompson, an experienced forest ranger from Blue Mountains, far into the country side of Portland parish, following the river Rio Grande. *Zygia latifolia* has a habit of growing next to rivers. After a day of no luck we stopped in a tiny village called Moore Town. Outside of the village combined shop and bar, two older men were sitting and drinking Irish beer. They were curious of my mission and I told them what I was looking for. One of them said "*Oh I know which tree it is, do you want me to show you? I will go get my machete.*" (Fig. 3: A). We crossed the road and walked down to the river, and there it was! I went home with my backpack filled with branches of *Z. latifolia*, cut down by a Jamaican man and his machete. The locals refer to *Z. latifolia* as "horse wood" and they use the wood for carpentry since it has hard wood with a reddish color.

I went to Ecuador the second time in July 2017. The goal was to collect flowers of *Zygia basijuga* (=*Marmaroxylon basijugum*) in Yasuni National

Park. A new "person" had joined the staff at Yasuni research station this time. A tayra that was given to the station as a gift from the local people in a village nearby. Its name was Ocata, which is also the word for tayra in Sabela, the laungage spoken by the Huaorani people. Ocata followed me around wherever I went. Every evening we went for a walk on the road to the station and sat by the river hoping to see an Amazon river dolphin. Even though I had the cutest field assistant my search for flowers was quite unsuccessful, I only found one tree, and not even with flowers, only buds. Deep into the forest, after walking for hours I came across this one tree of *Z. basijuga* with a few flower buds on the stem (Fig. 3: B). This tree is quite common in this area and the people at the station told me they had flowered already in May. Anyways, I was lucky to find this one tree about to blossom. I went back a couple of days later, hoping the buds would have opened. But only one single bud was showing its stamens and that was all I found in terms of flowers on this trip. Instead, I collected many specimens with fruit (Fig. 3: D, E) and old, withered flowers, and made a new friend (Fig. 3: C).

Fig. 3. A. Roger Thompson and the machete-man in Moore Town, Jamaica; B. Flower buds of *Zygia basijuga* (=*Marmaroxylon basijugum*) in Yasuni, Ecuador; C. Ocata collecting plants in Yasuni. D. Seeds of *Z. basijuga*; E. Pod of *Z. basijuga*.
Photos: Julia Ferm

Objectives

The objectives of this thesis were to investigate phylogenetic relationships of the Ingeae tribe (and by extension the Ingeae–*Acacia* complex) and to evaluate the most recent classifications, with special emphasis on some selected ingoid genera. Furthermore, my intention was to make taxonomic changes when needed for the classifications to reflect monophyletic groups and evolutionary relationships.

In paper I phylogenetic relationships of the genera *Zygia* and *Marmaroxylon* are investigated. Paper II and III focus on the genus *Zapoteca* and phylogenetic relationships within this genus. In paper IV phylogenetic relationships on a generic level of the Ingeae–*Acacia* complex are investigated, with special emphasis on the genera *Calliandra*, *Afrocalliandra*, *Faidherbia*, *Sanjappa*, *Thailentadopsis*, *Viguieranthus* and *Zapoteca*.

Materials & Methods

Taxon sampling

I have sampled extensively from the selected genera and also from the Ingeae tribe as a whole. Specimens from Acacieae have been included in all phylogenetic analyses, except for in paper III, which focus on *Zapoteca* and relationships therein.

In paper I, *Zygia* and *Marmaroxylon* were represented by 29 and 7 species respectively, out of a total of approximately 60 species (Rico Arce 1991; Barneby & Grimes 1997). All alliances in Ingeae according to Lewis & Rico Arce (2005) were sampled and represented by two genera each. All included genera were represented by two species each (except for the monotypic ones), and two species of *Acacia* were included. Many species were represented by more than one collection, often representing different subspecific taxa. Moreover, four species of *Senegalia* were included to represent more distantly related species. All trees were rooted on *Vachellia farnesiana* based on results in Kyalangalilwa et al. (2013) and LPWG (2017).

In paper II, the strongly supported clade including *Zapoteca* in paper I was analysed, with additional taxa of *Zapoteca* representing 20 out of 22 recognized species. Also, two species of *Viguieranthus* were included in order to investigate relationships of *Zapoteca*, *Calliandra* and *Viguieranthus*. The trees were rooted on *Vachellia farnesiana* (Kyalangalilwa et al. 2013; LPWG 2017).

In paper III, the datasets included the same specimens of *Zapoteca* as used in paper II, but were complemented with specimens of *Z. andina* H.M.Hern. and *Z. microcephala* (Britton & Killip) H.M.Hern., two species that were not included in paper II. In addition, 30 newly amplified DNA sequences of the other specimens of *Zapoteca* were included. The trees were rooted on *Cojoba arborea* (L.) Britton & Rose, another ingoid species not included in *Zapoteca* (Souza et al. 2013; LPWG 2017).

In paper IV, the sampling reflects the strongly supported clade in LPWG (2017) including all ingoid taxa, together with *Acacia*. The subclades of the Ingeae–*Acacia* clade that were strongly supported in LPWG (2017) are represented by one or a few individuals only. *Zapoteca* and *Viguieranthus* are represented by large samples, 57 and 24 specimens, respectively.

Leaf material for DNA extractions were obtained from extensive fieldwork and herbaria (AAU, CICY, FTG, GB, K, P, S, TAN, UPRRP and UPS). Additional DNA samples were obtained from RBG Kew DNA bank. Already published sequences were downloaded from GenBank. Voucher information and GenBank accession numbers are listed in appendices in respective paper (papers I-IV).

Laboratory work

DNA extraction and whole genome sequencing

Total DNA was extracted following a modified Carlsson-Yoon protocol (Yoon et a. 1991) and if the samples of total DNA did not yield product in PCR the samples were purified using the Illustra GFX PCR DNA and Gel Band Purification Kit (GE Healthcare, Little Chalfont, U.K.) following the protocol of the manufacturer.

In order to examine plastid DNA regions the chloroplast was assembled for *Zapoteca media* (M.Martens & Galeotti) H.M.Hern., *Zapoteca portoricensis* subsp. *portoricensis* and *Viguieranthus perrieri* (R.Vig.) Villiers. Total DNA was sent to the Science for Life Laboratory (SciLifeLab, Uppsala, Sweden) and sequenced using the Illumina MiSeq platform (Illumina, San Diego, California, USA). Library preparation using the Illumina SMARTer Thruplex DNAseq library preparation kit from Rubicon (Rubicon Genomics, Ann Arbor, Michigan, USA) were performed at the SciLifeLab. The chloroplasts were assembled using Geneious Prime® 2020.0.4 (https://www. geneious.com, Kearse & al., 2012). For details see paper IV.

Several plastid DNA regions of *Zapoteca portoricensis* subsp. *portoricensis*, *Zapoteca media* and *Viguieranthus perrieri* were examined and compared to other ingoid species downloaded from GenBank, viz. *Pithecellobium flexicaule* (Benth.) J.M.Coult., *Inga leiocalycina* Benth., *Samanea saman* and *Faidherbia albida* (Delile) A.Chev. *Ycf1* showed the highest variation of all examined plastid DNA regions, and we therefore chose to include sequences of *ycf1* in paper IV. According to Dong et al. (2012, 2015), *ycf1* exhibit high variation in angiosperms and show high species resolution when used. It is more variable than *matK* in Orchidaceae and has also been shown to resolve phylogenetic relationships within the family that in the past only have been resolved when using multiple plastid DNA sequences (Neubig et al. 2009). It has also proven useful when combined with other plastid and nuclear DNA regions (Neubig et al. 2013). The *ycf1* gene has also been used in phylogenetic analyses of the legume genera *Astralagus* Curran, with high resolution as a result (Dastpak et al. 2018), and *Tephrosia* Pers. (Kabongoa et al. 2017).

PCR and sequencing

DNA sequences were amplified using standard PCR protocols, more details can be found in papers I, II and IV. PCR products were sent to Macrogen Europe in Amsterdam, the Netherlands, for amplification using Sanger sequencing, after being purified using ExoProStar 1-Step (GE Healthcare) following the manufacturer´s instructions. Primers were designed in AliView v.1.26 (Larsson 2014). More details about the newly designed primers can be found in paper I and paper IV.

Phylogenetic analyses

In order to resolve phylogenetic relationships that previously have been challenging I used combinations of the nuclear ribosomal external transcribed spacer (ETS) and internal transcribed spacer (ITS), and plastid *psbA-trnH* intergenic spacer, *matK*, *trnL-trnF* (including the *trnL* intron and the *trnL-trnF* spacer) and *ycf1* DNA sequences. Details about which DNA regions that were used in each study can be found in respective paper (papers I-IV).

Multiple alignments of each of the DNA regions were performed using MUSCLE (Edgar 2004), and also adjusted by eye, in AliView v.1.26 (Larsson 2014). The best-fitting nucleotide AICc model for each separate DNA region dataset was determined based on the corrected Akaike information criterion (AICc) as implemented in MrAic.pl 1.4.6 (Nylander 2004).

Datasets of each DNA region were analysed separately (papers I-IV) and as combined nuclear and plastid datasets (paper IV), respectively. Statistically supported incongruences between results based on plastid vs. nuclear data were typically not found (but see e.g. results on *Faidherbia* in paper IV), and a combined dataset of both the nuclear and plastid DNA regions was also analysed. Datasets were concatenated using Abioscripts (Larsson 2010). Combined datasets were partitioned according to the single region datasets and the specific nucleotide models applied to each partition. Both separate and combined datasets were analysed using Bayesian inference (papers I-IV) and Ultrafast bootstrap (UFBoot) (paper IV [Minh et al 2013; Hoang et al 2018]). For more details about the phylogenetic analyses, see respective paper (papers I-IV). Final consensus trees were designed using Inkscape v.0.92 (https://inkscape.org).

Summary of papers

Phylogeny of the Neotropical legume genera *Zygia* and *Marmaroxylon* and close relatives. (Paper I)

In paper I, the monophyly of *Zygia* s.l. (i.e. sensu Barneby & Grimes 1997), the monophyly of the sections within *Zygia* (Barneby & Grimes 1997) and the positions of *Z. inundata* (Ducke) H.C.Lima ex Barneby & J.W.Grimes, *Z. ocumarensis* (Pittier) Barneby & J.W.Grimes (=*M. ocumarense* [Pittier] L.Rico) and *Z. sabatieri* Barneby & J.W.Grimes are investigated. Moreover, the monophyly and status of *Marmaroxylon* sensu Rico Arce (1991) as a distinct genus is evaluated and the monophyly of species of both *Zygia* and *Marmaroxylon* is tested. Furthermore, the phylogenetic relationship of *Zygia* and *Marmaroxylon* to other ingoid taxa is examined

The genus *Zygia* was described by Browne (1756) to accommodate the species now known as *Z. latifolia*. This species was, however, later included in *Pithecellobium* by Bentham (1875). Britton & Rose (1928) again recognized *Zygia* as a distinct genus but many workers continued to treat it within *Pithecellobium* (e.g. Macbride 1943; Standley & Steyermark 1946; Woodson & Schery 1950). The latest classification of *Zygia* was presented in the monograph by Barneby & Grimes (1997), where they described many new species and divided the genus into nine sections. The genus *Marmaroxylon* was described by Killip (in Record 1940) to accommodate the single species *Pithecellobium racemosum* Ducke. Later, Rico Arce (1991) included eight additional species in *Marmaroxylon*, previously treated in *Abarema*, *Klugiodendron* Britton & Killip, *Macrosamanea* Britton & Rose and *Pithecellobium*. *Marmaroxylon* was included in *Zygia* by Barneby & Grimes (1997), but has regardless continued to be recognized in more recent literature (e.g. Lewis & Rico Arce 2005; Ståhl & al. 2015).

The results in paper I (paper I, Fig. 2) show that neither *Zygia* sensu Barneby & Grimes (1997) nor *Marmaroxylon* sensu Rico Arce (1991) are monophyletic. Although a clade comprising most of the species of both *Zygia* and *Marmaroxylon* is strongly supported, but within this clade the species and subspecies of *Zygia* and *Marmaroxylon* are nested among each other. The obvious taxonomic action is therefore to include *Marmaroxylon* in *Zygia*, since the name *Zygia* has priority. Including *Marmaroxylon* in *Zygia* renders *Zygia* as monophyletic, defined morphologically as having cauli- and/or ramiflory (with one exception). The sections of *Zygia* sensu Barneby & Grimes (1997)

are shown to be non-monophyletic. Two of the monotypic sections, *Zygia* sect. *Pseudocojoba* including *Z. sabatieri*, and *Zygia* sect. *Ingopsis* including *Z. inundata*, are shown to be more closely related to *Inga* than to the other species of *Zygia*. *Zygia inundata* is transferred to *Inga* but the placement of *Z. sabatieri* is not addressed. A larger sample of *Inga* is needed to further investigate the position of *Z. sabatieri* and provide the scientific basis for a decision regarding whether it should be included in *Inga* or if a new genus should be described to accommodate it. *Marmaroxylon magdalenae* is shown to be more closely related to *Abarema* and *Hydrochorea*. This position needs further investigation including more specimens of *Abarema* and *Hydrochorea*, especially since the status of *Abarema* is unclear (Iganci et al. 2016). *Marmaroxylon ocumarense* is shown to be the sister to *Macrosamanea pubiramea* (Steud.) Barneby & J.W.Grimes, and this clade is the sister to the major *Zygia–Marmaroxylon* clade. *Macrosamanea* is a genus comprising 11 species, thus further studies including more species of the genus are needed in order to investigate if *Mar. ocumarense* should be included in *Macrosamanea*. Also, including *Macrosamanea* in *Zygia* is not an obvious option since the species of *Macrosamanea* do not show cauli- or ramiflory. Furthermore, the *Inga* alliance (Lewis & Rico Arce 2005) is shown to be non-monophyletic.

The results of paper I show that leaf morphology cannot be used to classify species of *Marmaroxylon* and *Zygia* in two separate genera. Within the *Zygia–Marmaroxylon* clade the occurrence of leaves with one pair of pinnae or leaves with more than one pair of pinnae do not define monophyletic groups. However, nodes are in general not strongly supported, thus future analyses might show a different result. Another example when leaf morphology is used for classification is the genus *Inga*. Even though species of *Inga* all possess pinnate leaves this leaf type is also seen in other ingoid genera. Thus, although defining the species of *Inga*, the possession of pinnate leaves is not unique for this genus and species cannot be included in *Inga* based solely on this character. Characters can evolve several times within a group and is not always shared by all members of a clade. Characters can also be lost over time, as is probably the case for *Z. pithecolobioides* (Kuntze) Barneby & J.W.Grimes, which is the only species within *Zygia* not having cauli- and/or ramiflory.

Within the major *Zygia–Marmaroxylon* clade some species are shown to be monophyletic, viz. *M. racemosum* (Ducke) Killip (=*Z. racemosa* [Ducke] Barneby & J.W.Grimes), *Z. biflora* L.Rico, *Z. bisingula* L.Rico, *Z. confusa* L.Rico, *Z. conzatti* (Standl.) Britton & Rose, *Z. morongi* Barneby & J.W.Grimes, *Z. tetragona* Barneby & J.W.Grimes and *Z. trunciflora* (Ducke) L.Rico. However, most nodes within this clade have poor support and a few species are shown to be non-monophyletic, viz. *M. claviflorum* (Spruce ex Benth.) L.Rico (=*Zygia claviflora* [Benth.] Barneby & J.W.Grimes), *Z. brenesii* (Standl.) L.Rico, *Z. inaequalis* Pittier and *Z. unifoliolata* (Benth.) Pittier, based on two specimens of each species. Moreover, *Z. latifolia* (the type

species of *Zygia*) represented by five specimens, is not recovered as monophyletic. However, the results of paper I does not confirm that *Z. latifolia* is non-monophyletic. All specimens of *Z. latifolia* are found within the same clade, which is not strongly supported, and neither the relationships between taxa in this clade are strongly supported, except for the strongly supported sister relationship of *Z. latifolia* var. *latifolia* and one of the specimens representing *Z. latifolia* var. *communis* Barneby & J.W.Grimes. Thus, the monophyly and definition of *Z. latifolia* and its subspecies needs further investigation.

Marmaroxylon basijugum (=*Z. basijuga*) and *Z. lathetica* Barneby & J.W.Grimes are recovered in a strongly supported clade, but relationships within this clade are not fully resolved. *Zygia lathetica* and *M. basijugum* are difficult to differentiate on morphological characters, and therefore herbarium material can easily be misidentified. It is a possibility that these two species should be regarded as conspecific but more material of both species is needed to further investigate this matter. The occurrence of non-monophyletic species within the *Zygia–Marmaroxylon* clade could be due to cryptic species and that specimens have been incorrectly identified, thus specimens stored under the same name may sometimes represent different species. The poorly supported relationships, and unresolved parts of the *Zygia–Marmaroxylon* clade could perhaps partly be explained by the DNA regions used, possibly not being variable enough to resolve phylogenetic relationships of these taxa.

A preliminary phylogeny of *Zapoteca* (Fabaceae: Caesalpinioideae: Mimosoid clade). (Paper II)

In paper II, the monophyly of *Zapoteca*, and of the subgenera of the genus, as well as phylogenetic relationships within the genus are investigated.

The genus *Zapoteca* was established by Hernández (1986) to accommodate the species of *Calliandra* referred to *Calliandra* ser. *Laetevirentes*, and later also included two species of *Calliandra* ser. *Macrophyllae* (Hernández 1989). Hernández (1989) also described a few new species and placed the taxa of *Zapoteca* in four subgenera, viz. *Zapoteca* subg. *Nervosa*, *Zapoteca* subg. *Aculeata*, *Zapoteca* subg. *Amazonica* and *Zapoteca* subg. *Zapoteca*, based on morphological characters such as variation in leaf formula and leaflet venation. Additional taxa have later been described or transferred to *Zapoteca*, and one additional subgenus, *Zapoteca* subg. *Ravenia* H.M.Hern., established (Hernández 2015, 1990; Hernández & Hanan-Alipi 1998; Hernández & Campos 1994; Levin and Moran 1989).

The results in paper II (paper II, Fig. 2) show that *Zapoteca* is monophyletic but that none of the subgenera (Hernández 1989, 1990) containing more than one species are monophyletic. In addition, *Zapoteca* is shown to be sister to

Calliandra, and they together are in turn the sister to *Viguieranthus*. These results were, however, poorly supported and contradicted by results in subsequent work (see paper IV). Within *Zapoteca*, *Zapoteca* subg. *Nervosa*, with the only species *Z. nervosa*, is the sister to the remaining taxa of *Zapoteca*. *Zapoteca* subg. *Aculeata* is recovered as the sister to *Zapoteca* subg. *Amazonica* and *Zapoteca* subg. *Zapoteca*. *Zapoteca ravenii* H.M.Hern. and *Z. tehuana* H.M.Hern., placed in *Zapoteca* subg. *Ravenia* (Hernández 1990), are found nested with the taxa of *Zapoteca* subg. *Zapoteca*, as is *Z. quichoi* H.M.Hern. & Hanan-Alipi of *Zapoteca* subg. *Amazonica*. Moreover, *Z. filipes* (Benth.) H.M.Hern. and *Z. scutellifera* (Benth.) H.M.Hern. form a clade excluded from the other species of *Zapoteca* subg. *Zapoteca*, the subgenus they were originally placed in. Thus, a new subgeneric classification is needed in order for the subgenera to reflect monophyletic groups. However, two species, *Z. andina* and *Z. microcephala*, were not included in this analysis and therefore taxonomic changes were considered premature.

Zapoteca formosa (Kunth) H.M.Hern., represented by seven subspecies (out of eight subspecies in total) was shown to be non-monophyletic. Although *Z. formosa* subsp. *soccorensis* (I.M.Johnst.) G.A.Levin and *Z. formosa* subsp. *rosei* (Wiggins) H.M.Hern. were strongly supported as sisters, which might be an indication that these two specimens in fact represent the same taxon. *Zapoteca formosa* subsp. *rosei* has a distribution on the west coast of Mexico while *Z. formosa* subsp. *socorrensis* is endemic to the Socorro and Clarión islands, located off the west coast of Mexico. Hernández (1989) treated these two species as synonyms, but Levin & Moran (1989) considered them to be two distinct subspecies. To further investigate the relationship of these two taxa more samples from each subspecies are needed. *Zapoteca portoricensis* was also shown to be non-monophyletic with *Zapoteca portoricensis* subsp. *portoricensis* recovered in a strongly supported clade and *Zapoteca portoricensis* subsp. *pubicarpa* H.M.Hern. found in a position excluded from this clade. The two subspecies of *Z. caracasana* (Jacq.) H.M.Hern. on the other hand, are strongly supported as monophyletic and the status of this species as defined by Hernández (1989) is confirmed.

The results of paper II show that the classification of *Zapoteca* do not always reflect evolution in this group and that a new subgeneric classification is needed.

A revised classification of the Neotropical genus *Zapoteca* (Caesalpinioideae; Fabaceae), with one new subgenus and two new species combinations. (Paper III)

Phylogenetic relationships and diversification within *Zapoteca* are further examined in paper III, with the addition of the two species not included in paper

II, *Z. andina* and *Z. microcephala*, placed in *Zapoteca* subg. *Zapoteca* and *Zapoteca* subg. *Amazonica*, respectively (Hernández 1989). Taxonomic changes necessary for the subgenera to reflect monophyletic groups are made and the distribution and diversification of *Zapoteca* is briefly described and discussed.

The results in paper III (paper III, Fig. 2) show that *Z. andina* is the sister to remaining species of *Zapoteca* subg. *Zapoteca* and is therefore still included in *Zapoteca* subg. *Zapoteca*. *Zapoteca microcephala* is resolved as the sister to *Z. amazonica* and thus should be referred to *Zapoteca* subg. *Amazonica*, as it was originally placed. The third species of *Zapoteca* subg. *Amazonica*, *Z. quichoi*, is found with the species of *Zapoteca* subg. *Zapoteca* and therefore is transferred to this subgenus. The species of *Zapoteca* subg. *Ravenia*, *Z. tehuana* and *Z. ravenii*, are also found with species of *Zapoteca* subg. *Zapoteca*, and included there. *Zapoteca filipes* and *Z. scutellifera* are found in a clade as sister to *Zapoteca* subg. *Aculeata*, *Zapoteca* subg. *Amazonica* and *Zapoteca* subg. *Zapoteca*, and a new subgenus, *Zapoteca* subg. *Subamazonica*, is described to accommodate these two species. Two subspecies of *Z. formosa*, *Z. formosa* subsp. *schottii* (S.Watson) H.M.Hern. and *Z. formosa* subsp. *gracilis* (Griseb.) H.M.Hern., are shown to be monophyletic based on three specimens each (also shown in paper II), but not resolved with the other subspecies of *Z. formosa*. These two subspecies are raised to species level, i.e. *Zapoteca schottii* (Torrey ex S.Watson) Ferm and *Zapoteca gracilis* (Griseb.) Ferm.

Zapoteca subg. *Nervosa* (monospecific) is the first diverging lineage of *Zapoteca*. This subgenus is distinguished from other subgenera of *Zapoteca* in lacking lens-shaped thickenings in the polyads. Moreover, *Zapoteca* subg. *Nervosa* has extra floral nectaries and leaves with one pair of pinnae with 3-4 pairs of leaflets/pinna. *Zapoteca* subg. *Nervosa* is endemic to Hispaniola. The next diverging lineage consists of *Zapoteca* subg. *Subamazonica* (2 spp.). This subgenus also has extra floral nectaries, as seen in *Zapoteca* subg. *Nervosa*, and has lens-shaped thickenings on one side of the polyads. *Zapoteca* subg. *Subamazonica* is distributed in Brazil and Bolivia. The next diverging lineage is *Zapoteca* subg. *Aculeata* (monospecific), which represents the only tree in *Zapoteca*, the other species are shrubs. *Zapoteca* subg. *Aculeata* is distinguished from the other subgenera in having spiny stipules. Moreover, *Zapoteca* subg. *Aculeata* have lens-shaped thickenings on two sides of the polyads and is distributed in Andean Ecuador. Lens-shaped thickenings on two sides of the polyads are also seen in *Zapoteca* subg. *Amazonica* (2 spp.), which is the next diverging lineage within *Zapoteca*. Moreover, *Zapoteca* subg. *Amazonica* has leaves with one pair of pinnae and one pair of large leaflets only. *Zapoteca* subg. *Amazonica* is distributed in Amazonian Ecuador, Brazil and Peru, and in the Magdalena Valley in Colombia. The last diverging lineage within *Zapoteca*, i.e. *Zapoteca* subg. *Zapoteca*, includes most species of *Zapoteca* (19 spp.) and has a distribution from southern Arizona (US) to northern Venezuela, including the Caribbean.

The diversity of species of *Zapoteca* is the highest in South America and Mesoamerica, with many of the taxa within *Zapoteca* subg. *Zapoteca* endemic to Mexico (paper III, Fig. 3). Some species have a wider distribution occurring throughout the Neotropics, viz. *Z. caracasana*, *Z. formosa*, *Z. portoricensis* and *Z. tetragona* (Willd.) H.M.Hern., but if these species have originated in Mexico and then colonized other areas in the Neotropics, or spread to Mexico and Central America from other parts of the Neotropics remains to be clarified.

Phylogenetic relationships of the mimosoid Ingeae–*Acacia* complex (Fabaceae), based on plastid and nuclear data. (Paper IV)

In paper IV, we went deeper into the evolutionary history of the Ingeae–*Acacia* complex. Generic relationships of the Ingeae–*Acacia* complex (LPWG 2017) were investigated, with special emphasis on the, supposedly, closely related genera *Calliandra*, *Afrocalliandra*, *Faidherbia*, *Sanjappa*, *Thailentadopsis*, *Viguieranthus* and *Zapoteca*. Phylogenetic studies based on DNA sequence data have indicated that these genera are closely related, although mostly with poor support and with poor taxon sampling (e.g. Luckow et al. 2003; Miller et al. 2003; Brown et al. 2008; Bouchenak-Khelladi 2010; Iganci et al. 2016; Souza et al. 2016).

Interestingly, the genera possessing similar pods, the "*Calliandra*-pod" (*Calliandra*, *Afrocalliandra*, *Sanjappa*, *Thailentadopsis*, *Viguieranthus* and *Zapoteca*), are found in different parts of the world, *Zapoteca* and *Calliandra* are strictly Neotropical (Hernándes 1989; Souza et al. 2013) (except for the recent introduction of *Z. portoricensis* to Africa and Asia [Hutchinson & Dalziel 1958; POWO 2020]), *Afrocalliandra* is distributed in Africa (Souza et al. 2013), *Sanjappa* is endemic to India (Souza et al. 2016), *Thailentadopsis* found in Asia (Vietnam, Sri Lanka and Thailand) (Lewis & Schrire 2003) and *Viguieranthus* is endemic to Madagascar, with *V. subauriculatus* Villiers also found in the Comoro islands (Villiers 2002). Taking into consideration not only the similarity in pod morphology but also these differences in distributions, it seemed intriguing to investigate the systematics and phylogenetic relationships of these genera, and their relationships to other ingoid genera. Especially their relationship to *Faidherbia*, with a distribution in Africa, Saudi Arabia, Jordan and Syria, was interesting as *Faidherbia* does not possess the "*Calliandra*-pod", but has been shown to be closely related in previous studies (Bouchenak-Khelladi 2010; Souza et al. 2016).

Calliandra, *Afrocalliandra*, *Faidherbia*, *Sanjappa*, *Thailentadopsis*, *Viguieranthus* and *Zapoteca*, had never been included in the same study before, except for in LPWG (2017) where generic relationships of these genera were

not resolved. Thus, phylogenetic relationships of these genera were not extensively investigated and it was necessary to include as many representatives as possible in order to examine evolutionary relationships between them. A large sample of ingoid genera (32 out of 36), with *Viguieranthus* and *Zapoteca* represented by large samples, and 34 specimens of *Acacia* were included in order to further investigate relationships within this complex. Moreover, the plastid gene *ycf1* was included in the analyses in order to resolve phylogenetic relationships that previously have been difficult to resolve (e.g. LPWG 2017). The results showed more resolution and stronger support values within the Ingeae–*Acacia* complex when including *ycf1* than when analysing only ETS, ITS, *matK* and *trnL-trnF*.

The results in paper IV recovered *Calliandra* and *Afrocalliandra* as the earliest diverging lineage of the Ingeae–*Acacia* complex (Clade 1 of the Ingeae–*Acacia* complex; Paper IV, Fig. 1), which is supported also by morphological characters and is in line with Hernández (1989), who stated that *Calliandra* was an "evolutionary divergent" lineage of the Ingeae tribe with many unique characters. *Calliandra* has 8-grained calymmate polyads and homo- or heteromorphic inflorescences (Souza et al. 2013). Generally species of the Ingeae–*Acacia* complex have 16-grained acalymmate polyads and homomorphic inflorescences, and *Afrocalliandra*, *Faidherbia*, *Sanjappa*, *Thailentadopsis*, *Viguieranthus* and *Zapoteca* all have homomorphic inflorescences (Hernandez 1989, 1990, 2015; Hernández & Hanan-Alipi 1998; Hernández & Campos 1994; Levin and Moran 1989; Villiers 2002; Barnes & Fagg 2003; Lewis & Schrire 2003; Souza et al. 2013, 2016). The leaf formula in *Calliandra* is varying between species and they can have one to many pairs of pinnae per leaf (Barneby 1998). *Afrocalliandra* on the other hand has leaves with one pair of pinnae per leaf only, possess extra floral nectaries and can have stipular spines and thorns; extra floral nectaries, spines and thorns are not present in *Calliandra* (Souza et al. 2016). Moreover, *Afrocalliandra* possesses 7-grained acalymmate polyads, a unique character within the Ingeae–*Acacia* complex (Souza et al. 2013).

Zapoteca and *Viguieranthus* are sisters according to the results in paper IV. Both genera have leafy stipules (Hernández 1989, 1990, 2015; Levin and Moran 1989; Hernández & Campos 1994; Hernández & Hanan-Alipi 1998; Villers 2002), although the stipules of *Viguieranthus* are coriaceous and therefore can be "somewhat spiny" according to Villiers (2002). Moreover, both genera have 16-grained acalymmate polyads. *Zapoteca* and *Viguieranthus* can be distinguished from each other on other morphological characters. *Viguieranthus* has leaves with one pair of pinnae and an extra floral nectary on the apex of the petiole (Villiers 2002) while the species of *Zapoteca* have leaves with more than one pair of pinnae (except for the species of *Zapoteca* subg. *Amazonica* and *Z. quichoi* having one pair of pinnae) and mostly lack extra floral nectaries, (with the exception of three species, *Z. nervosa*, *Z. filipes* and *Z. scutellifera*) (Hernández 1989). *Viguieranthus* has the stamens fused not only

to each other but also to the corolla and the disc (when present) forming a stamonozone. Stamonozone is not present in *Zapoteca*. In addition, *Viguieranthus* is endemic to Madagascar and the Comores (Villiers 2002) while *Zapoteca* is distributed in the Neotropics (Hernández 1986).

Zapoteca and *Viguieranthus* are in turn the sister to a clade comprising the Old World genera *Faidherbia*, *Sanjappa* and *Thailentadopsis*. *Sanjapppa* and *Thailentadopsis* are sisters and together the sister to *Faidherbia*, although there are indications of cytonuclear discordance regarding the position of *Faidherbia* (Paper IV, results section). *Sanjappa* and *Thailentadopsis* have 16-grained acalymmate polyads (Lewis & Schirie 2003; Souza et al. 2016) while *Faidherbia* has 16-32-grained polyads (Kenrick & Knox 1982; Barnes & Fagg 2003). All three taxa have extra floral nectaries and spine-like stipules (Barnes & Fagg 2003; Lewis & Schirie 2003; Souza et al. 2016). Moreover, *Faidherbia* does not have the "*Calliandra*-pod" but instead a pod that is coiled, twisted or falcate, and indehiscent. Indehiscent pods are not common within ingoid genera but seen in the genus *Inga* (Pennington 1997).

The possession of the "*Calliandra*-pod" consequently does not coincide with the phylogenetic relationships of *Calliandra*, *Afrocalliandra*, *Sanjappa*, *Thailentadopsis*, *Viguieranhus* and *Zapoteca*. Instead, this pod type must have evolved independently several times within the Ingeae–*Acacia* complex. Alternatively, it may represent the ancestral state, with other pod types having evolved in *Faidherbia* and in the sister clade to the clade comprising *Faidherbia*, *Sanjappa*, *Thailentadopsis*, *Viguieranthus* and *Zapoteca* (i.e. the clade comprising the remaining taxa of the Ingeae–*Acacia* complex). Hence, as also shown in papers I-III, morphological characters used for classification in the past do not always characterize monophyletic groups.

Finally, the results in paper IV show that the clade comprising *Faidherbia*, *Sanjappa*, *Thailentadopsis*, *Viguieranthus* and *Zapoteca* (Clade 2 of the Ingeae–*Acacia* complex; Paper IV, Fig. 1) is the sister to a clade comprising the remaining taxa of the Ingeae–*Acacia* complex. Within this clade (Clade 3 of the Ingeae–*Acacia* complex; Paper IV, Fig. 1), *Cojoba* and *Lysiloma* are sisters and this subclade is in turn the sister to remaining taxa. Phylogenetic relationships among remaining taxa of this clade are mostly unresolved or not statistically supported, although some genera are shown to be monophyletic, for example, *Inga* and *Chloroleucon* Britton & Rose ex Record. The species of *Acacia* are not supported as monophyletic, but are clearly placed within this clade which is in line with indications in previous studies (Miller & Bayer 2001; Miller et al. 2003; Brown et al. 2008; Bouchenak-Khelladi et al. 2010; LPWG 2013, 2017).

Concluding remarks

The results of my thesis show that morphological characters used in the past for classification do not always reflect closely related groups. The patterns we see in nature, and the morphological characters we interpret as kinship are not always a reflection of a common evolutionary ancestry. Rather, nature is complex, with characters at least seemingly similar sometimes evolving and disappearing repeatedly. And it can be difficult to use only morphology for classification. Furthermore, the results of my thesis show that the classification of tribe Ingeae is far from settled, especially since the tribe itself is non-monophyletic with *Acacia* nested among the ingoid taxa. Thus, phylogenetic relationships within the Ingeae–*Acacia* complex need further studies. However, since phylogenetic relationships of the Ingeae–*Acacia* complex, as well as within genera, have been difficult to resolve also based on molecular data, new studies based on yet more data should be conducted. By using more variable DNA sequences or preferably whole genomes, still unresolved evolutionary questions can be further addressed in the future. Moreover, more extensive sampling of taxa is needed, in particular of large genera such as *Inga*, in order to further resolve the evolutionary history of the taxa in the Ingeae–*Acacia* complex.

Svensk sammanfattning

Systematik

Systematik är studier av evolutionärt släktskap av taxa på alla nivåer, av grupper av organismer och relationer över tid. Ett sätt att visualisera evolutionärt släktskap är med hjälp av fylogenetiska träd som kan baseras på t ex morfologiska karaktärer eller DNA-sekvensdata. Fylogenetiska träd visar gemensamt ursprung och diversifiering på ett sätt som kan tolkas av både forskare och lekmän. Systematik inkluderar taxonomi, vilket innebär klassifikation och namngivning av taxa. Klassifikationer ska reflektera monofyletiska grupper, så att alla representanter som är placerade i samma grupp (t ex ett släkte) har gemensamt ursprung. Moderna fylogenier baserade på DNA kan användas för att undersöka evolutionärt släktskap och är användbara för att utvärdera tidigare klassifikationer, både äldre klassifikationer som ofta är baserade på morfologi och nyare klassifikationer baserade på tidigare fylogenetiska (DNA) studier. Genom att kombinera systematik och biogeografi kan vi också utvärdera evolutionära grupper, deras utbredning och varför de finns där de finns.

För att kunna bygga robusta fylogenier baserade på DNA, och studera morfologi, krävs tillgång till bra material av den organismgrupp som studeras. Ett viktigt sätt för en växtsystematiker att få bra material är att samla det själv, i fält. För denna avhandling har jag gjort fältarbete i Ecuador, Jamaica, Puerto Rico och Costa Rica. Men tidigare insamlat material som förvaras i olika herbarier i Europa, USA, Västindien och Sydamerika har också använts för att kunna få tillgång till ett tillräckligt stort forskningsmaterial.

Den mimosoida tribusen Ingeae

Tribusen Ingeae är en av fyra tribusar i den mimosoida kladen inom angiospermfamiljen Fabaceae, som vi dagligt tal kallar för ärtväxter. Mimosoider känns igen på sina ofta små blommor med långa, starkt färgade ståndare som ofta är samlade i täta blomställningar. Tribusen Ingeae skiljer sig från övriga mimosoider genom att de har blommor med förenade ståndarsträngar, som bildar en tub som omger pistillen. Medlemmarna i tribusen Ingeae har oftast dubbelt sammansatta blad, men det finns ett undantag i släktet *Inga* (ca. 300 arter), som istället har enkelt sammansatta blad. Dessutom finns det åt-

minstone tre ytterligare ingoida arter från andra släkten som har enkelt sammansatta blad: *Cojoba rufescens*, *Sanjappa cynometroides* och *Calliandra hymenaoides*.

Ingeae beskrevs av den brittiske botanisten George Bentham. Han placerade alla arter med ståndartub i den tidigare beskrivna tribusen Acacieae i Ingeae och delade sedan upp tribusen i 15 släkten. Sedan dess har antalet släkten i Ingeae blivit fler och den senaste formella klassifikationen av Ingeae (från 2005) innehåller 36 släkten. Ökningen av släkten beror bland annat på att vissa släkten delats upp i flera släkten och dels på nya upptäcker. En del släkten har dock inkluderats i andra som ett resultat av nya studier och omvärderingar av släktgränser. Äldre klassifikationer är baserade på morfologiska karaktärer och med nya fylogenetiska metoder baserade på DNA kan ibland dessa gränser omvärderas. Genom dessa studier har det visat sig att äldre klassifikationer inte alltid representerar monofyletiska grupper. Till och med Ingeae som helhet har visats vara parafyletisk med släktet *Acacia*, för närvarande placerat i tribusen Acacieae, nästlad inom Ingeae. Denna situation har dock ännu inte lett till några större förändringar av klassificeringen och namnsättningen av detta Ingeae–*Acacia* komplex. I grunden är detta dock sunt eftersom fortsatta studier skulle kunna revidera vår syn på släktskapsförhållandena inom gruppen ännu mer, vilket kan göra att nya klassifikationer och namn snabbt blir omoderna.

För mina studier valde jag att fokusera på några specifika släkten inom Ingeae–*Acacia* komplexet men även undersöka komplexet som helhet. DNA-sekvenser från olika regioner av genomet (ETS, ITS, *trnL-trnF*, *psbA*, *matK* och *ycf1*) analyserades med hjälp av statistiska metoder för att undersöka evolutionära släktskap inom Ingeae–*Acacia* komplexet.

Zygia och *Marmaroxylon*

Marmaroxylon och *Zygia* är två släkten som länge har ansetts vara närbesläktade, men åsikterna har gått isär om huruvida *Marmaroxylon* skulle erkännas som ett eget släkte eller inkluderas i *Zygia*. *Marmaroxylon* beskrevs 1940, men blev senare inkluderat i *Zygia*. Många forskare har trots detta fortsatt att behandla *Marmaroxylon* som ett eget släkte. Både *Zygia* och *Marmaroxylon* är små, stamblommande träd med vita till mörkt rosa blommor. Lite förenklat kan man säga att släktena skiljts åt med en enda karaktär: *Zygia* har blad med bara ett par pinnae (sidogrenar) och *Marmaroxylon* har blad med fler än ett par pinnae.

I artikel I testades monofylin hos *Zygia* och *Marmaroxylon*, separat och tillsammans, vidare testades monofylin hos flera arter inom båda släktena genom att inkludera flera individer av samma art. *Zygia* och *Marmaroxylon*'s position i förhållande till andra ingoida släkten och grupperingar undersöktes också. De DNA-regioner som analyserades var ETS, ITS, *trnL-trnF* och *psbA*.

Resultaten i artikel I visade att varken *Zygia* eller *Marmaroxylon* är monofyletiska. Dessutom visade sig två arter, *Z. inundata* och *Z. sabatieri*, vara närmare släkt med *Inga*. *Zygia inundata* flyttades därför till Inga, ett beslut som också stöds av att arten har enkelt sammansatta blad som övriga arter i Inga. *Zygia sabatieri* visade sig vara syster till *Z. inundata* och *Inga*, men inga taxonomiska åtgärder togs eftersom det inte är bekräftat att *Z. sabatieri* verkligen tillhör *Inga*, eller om ett nytt släkte behöver beskrivas för att inrymma arten. Dessutom visade resultaten att en av arterna i *Marmaroxylon*, *M. magdalenea*, är närmare släkt med *Abarema* och *Hydrochorea*, men vidare studier behövs för att fastställa artens exakta position och i vilket släkte den bör placeras. *Marmaroxylon ocumarense* visade sig vara syster till *Macrosamanea*, men det skulle behöva inkluderas ett större urval arter av *Macrosamanea* för att vidare undersöka *Mar. ocumarense*'s relation till detta släkte.

Zapoteca och närbesläktade (?) taxa

Zapoteca är ett neotropiskt släkte med små, nattblommande träd eller buskar. De har axillära, sfäriska blomställningar med ståndare som är vita, röda, eller tvåfärgade (vita mot basen och rosa till röda i toppen). *Zapoteca* har frukter (baljor) med förtjockade kanter som spricker upp från toppen och nedåt med valv som böjer sig bakåt. Den här typen av baljor finns också hos släktena *Calliandra*, *Afrocalliandra*, *Sanjappa*, *Thailentadopsis* och *Viguieranthus*. *Zapoteca* beskrevs så sent som 1986. Arterna var sedan tidigare kända som en särskild grupp inom *Calliandra* (*Calliandra* ser. *Laetevirentes*) men placerades i *Zapoteca* eftersom de har polyader som består av 16 pollenkorn med separat exin medan övriga arter i *Calliandra* har polyader som består av 8 pollenkorn med ett gemensamt exin. Ytterligare två arter som var placerade i *Calliandra* men har polyader med 16 pollenkorn har senare även de inkluderats i *Zapoteca*. Tidigare forskning placerade arterna i *Zapoteca* i 4 undersläkten: *Nervosa*, *Aculeata*, *Amazonica* och *Zapoteca*. Under senare år har fler arter beskrivits eller flyttats till *Zapoteca* och ytterligare ett undersläkte, *Ravenia*, har beskrivits. Släktskapsrelationerna inom *Zapoteca* hade inte analyserats med DNA tidigare även om en del fylogenetiska studier baserade på DNA har inkluderat arter från släktet. Detta innebär att monofylin av släktet, och av undersläktena, inte undersöks genomgående tidigare. Dessutom var monofylin hos enskilda, mångformiga arter intressant att undersöka, t ex hos *Z. formosa*, som var indelad i inte mindre än åtta underarter.

I artikel II undersöktes om *Zapoteca* var monofyletiskt och fylogenetiska relationer inom släktet. De DNA-regioner som analyserades var ETS, ITS och *trnL-trnF*. Resultaten i artikel II visade att *Zapoteca* är monofyletisk och att släktet bildar fem monofyletiska klader. Dessa klader överensstämmer dock inte helt med den tidigare undersläktesklassifikationen. Inget av undersläktena som innehöll fler än en art var monofyletiska, och dessutom var många arter

och underarter inte heller monofyletiska. *Zapoteca formosa* hade t ex endast två av sju inkluderade underarter, *Z. formosa* subsp. *rosei* och *Z. formosa* subsp. *socorrensis*, monofyletiska tillsammans.

I artikel III undersöktes monofylin hos undersläktena i *Zapoteca* vidare och ytterligare två arter som inte var med i analyserna i artikel II inkluderades, *Z. andina* och *Z. microcephala*. De DNA-regioner som analyserades var ETS, ITS och *trnL-trnF*. I artikel III presenterades en ny undersläktesklassifikation av *Zapoteca*, med ett nybeskrivet undersläkte, undersläkte *Subamazonica* som inkluderar arterna *Z. filipes* och *Z. scutellifera*. Undersläkte *Ravenia* inkluderades i undersläkte *Zapoteca*. *Zapoteca formosa* subsp. *schottii* och *Z. formosa* subsp. *gracilis* erkändes som egna arter, *Z. schottii* respektive *Z. gracilis*. I artikel III publicerades förutom den nya klassifikationen också en bestämningsnyckel till undersläktena och en diskussion om släktets utbredning.

I artikel IV undersöktes släkesrelationer inom Ingeae–*Acacia* kladen, med speciellt fokus på *Calliandra*, *Afrocalliandra*, *Faidherbia*, *Sanjappa*, *Thailentadopsis*, *Viguieranthus* och *Zapoteca*. Eftersom dessa släkten, förutom *Faidherbia*, har likande baljor skulle man förmoda att de representerar en monofyletisk grupp och att de är närmare besläktade med varandra än med andra släkten inom Ingeae–*Acacia* komplexet. Dessutom har fylogenetiska studier indikerat olika systersläktskap mellan dessa släkten. I tidigare fylogenetiska studier baserade på DNA har *Zapoteca* visats vara syster till *Calliandra*. *Sanjappa*, *Thailentadopsis* och *Faidherbia* har visats vara syster till *Viguieranthus*, och *Zapoteca* syster till *Faidherbia*. Tidigare studier har dock bara inkluderat ett fåtal arter av varje släkte och de relationer som visats har dessutom ofta haft svagt stöd vilket gjorde det särskilt intressant att undersöka relationer mellan dessa släkten. De DNA-regioner som analyserades var ETS, ITS, *trnL-trnF*, *matK* och *ycf1*. ETS, ITS, *trnL-trnF* och *matK*, har ofta använts tidigare i fylogenetiska studier av Fabaceae, i artikel IV inkluderades även sekvenser av plastidgenen *ycf1*. Hela kloroplastgenomet sekvenserades av *Zapoteca media*, *Zapoteca portoricensis* subsp. *portoricensis* och *Viguieranthus perrieri* för att undersöka om det fanns någon gen med hög variation och bra områden för att placera primers, som sedan kunde Sanger-sekvenseras. *Ycf1* visade hög variation på släktesnivå, och även variation på artnivå, och har visats vara användbar i tidigare studier. *Ycf1* sekvenserades för så många släkten som möjligt, och flest sekvenser togs fram från arter av *Zapoteca* och *Viguieranthus*. Resultaten i artikel IV visade att *Calliandra* och *Afrocalliandra* representerar den första divergerande gruppen inom Ingeae–*Acacia* komplexet. De är syster till alla andra Ingeae och *Acacia*. *Faidherbia*, *Sanjappa* och *Thailentadopsis* bildar tillsammans en klad som är syster till *Viguieranthus* och *Zapoteca*. *Viguieranthus* och *Zapoteca* är i sin tur systrar. Kladen med *Faidherbia*, *Sanjappa*, *Thailentadopsis*, *Viguieranthus* och *Zapoteca* är syster till resten av Ingeae och *Acacia*. De släkten som har samma typ av balja bildar således inte en monofyletisk grupp. Av detta kan vi dra slutsatsen att den typen av balja måste ha uppstått flera gånger inom Ingeae–*Acacia* komplexet. Alternativt att

den här typen av balja representerar det ursprungliga tillståndet och att andra baljtyper har uppstått hos övriga släkten som har andra typer av baljor. Inte heller bildar *Calliandra*, *Afrocalliandra*, *Faidherbia*, *Sanjappa*, *Thailentadopsis*, *Viguieranthus* och *Zapoteca* monofyletiska grupper baserat på deras utbredning, vilket betyder att en spridning över atlanten måste ha skett flera gånger.

Slutsats

Tidigare klassifikationer baserade på morfologiska karaktärer representerar inte alltid monofyletiska grupper och klassifikationen av ingoida taxa är fortfarande bara i sin början. Trots att framsteg gjorts med dessa studier krävs många analyser för att utreda släktskap inom tribusen. Dessutom behöver definitionen av tribusen Ingeae förändras eftersom *Acacia* är närmare släkt med taxa inom Ingeae än med de övriga släktena i tribusen Acacieae.

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