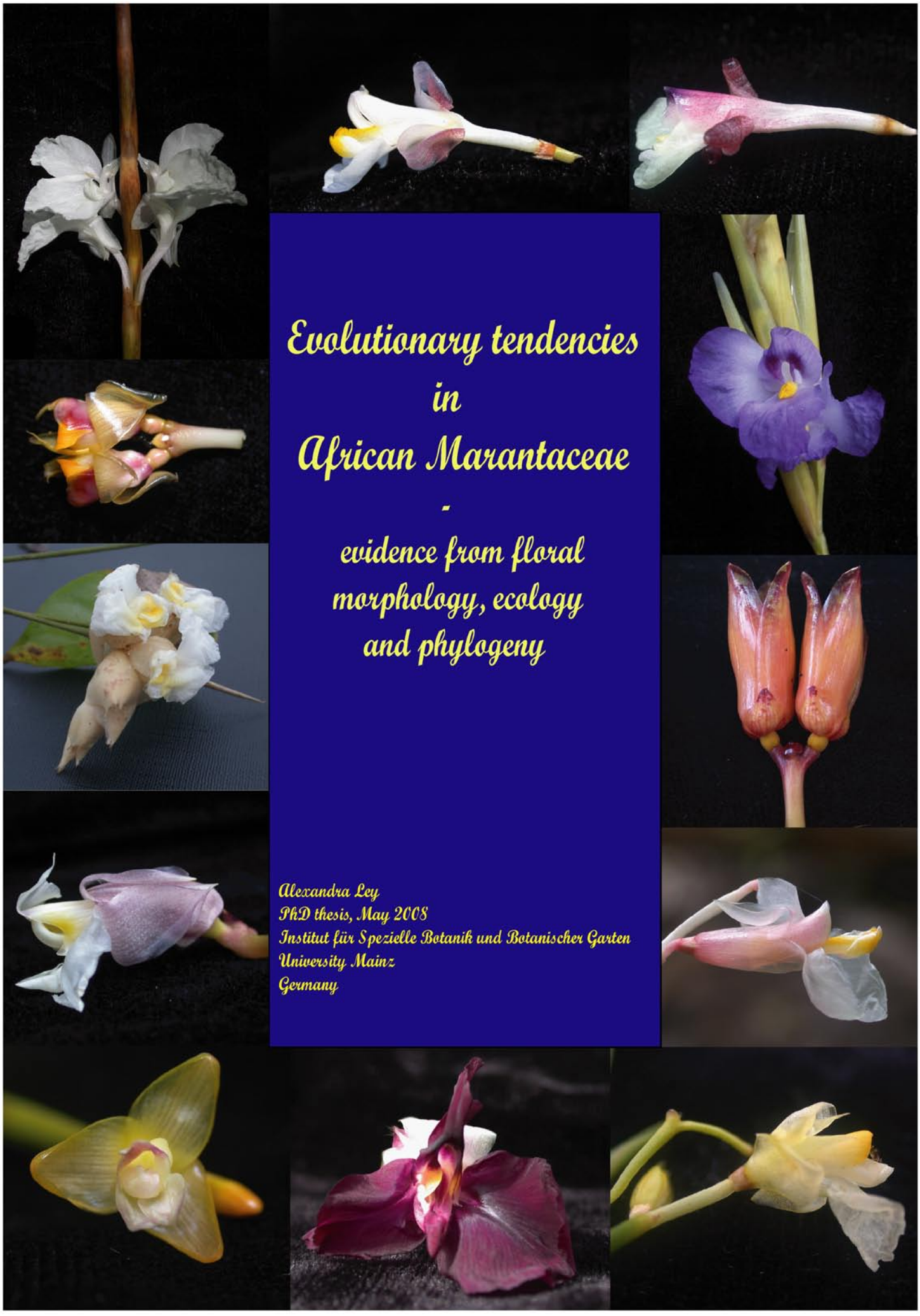

Evolutionary tendencies in African Marantaceae - evidence from floral morphology, ecology and phylogeny

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- evidence from floral morphology,

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Meinen Eltern gewidmet

View on the river Ivindo from the biological station “Ipassa”,
13 km east of Makokou, Gabon (2006)

We travel together, passengers on a little space ship, dependent
Upon its vulnerable reserves of air and soil – all committed
For our safety to its security and peace, and preserved
From annihilation only by the care, the work, and,
I will say, the love, we give our fragile craft.

Adlai Stevenson

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CONTENTS

Summary of the thesis

This thesis presents for the first time a survey on the floral biology and phylogeny of the African Marantaceae (~40 species). The Marantaceae (550 species) are a family of worldwide distributed perennial herbs and lianas in the understorey of tropical lowland rainforest. At the start of this project the African species were worldwide the least known. A comparison of the two major African clades should elucidate exemplarily evolutionary patterns in the family. These two clades are especially suitable due to their phylogenetic position: the *Sarocphrynium* clade is sister to all other Marantaceae and the *Marantochloa* clade stands in a derived position in the family phylogeny.

Analyses were conducted during three field trips of three to four months each to the African diversity centre in Gabon. Flower morphological investigations in 30 species reveal four flower types based on flower size and pigmentation, spatial arrangement of the floral tube and presence/absence of nectar guides and conspicuous outer staminodes. Each type is associated with a specific pollinator guild as shown by pollinator observations. The *Hypselodelphys hirsuta*-type is predominantly pollinated by medium-sized bees (*Amegilla vivida*, *Thrinchostoma bicometes),* the *Haumania danckelmanniana*–type by large bees (*Xylocopa nigrita, X. varipes*), the *Marantochloa congensis*-type by small bees (*Thrinchostoma* spp., *Allodapula ornaticeps)* and the *Thaumatococcus daniellii*-type by sunbirds. Pollination experiments confirm that 18 species are self-compatible. Among them, only *Halopegia azurea* and *Marantochloa leucantha* are autogamous and are thus independent of a pollen vector. At least 10 morphologically similar species share pollinators by flowering sparsely over a long period. In contrast, the similar *Afrocalathea rhizantha* and *Marantochloa* sp.2 avoid competition for pollinators by short consecutive mass flowering events. Independent of phenological patterns, fruit-set is generally low (~10 %) whereas the vegetative vigour is high in most species.

The flowers of the Marantaceae present an example of complex synorganization facilitating an explosive pollination mechanism. To understand the evolutionary significance of this unique process of pollen transfer for the Marantaceae, 66 species covering all major phylogenetic clades of the Marantaceae are analysed under a functional morphological view. The results show that all species correspond in a `tunnel´-shaped fleshy staminode with inner stiff swellings which

narrow the floral tube exactly towards the tip of a lateral trigger appendage which is part of the hooded staminode. The forced deflection of this trigger appendage affects an explosive style movement which guarantees the transfer of pollen. The latter is secondarily presented on the back of a characteristic style head at the distal end of the style. However, despite high selection pressures on this functional unit there is also a lot of morphological variation realising the same functional demands. Thereby variations in the length of the fleshy staminode relative to the complex of style and hooded staminode affect a differential pollen deposition on the pollinator which might be a source for mechanical isolation. Furthermore, subtle morphological changes in the stylar head and the hood of the hooded staminode have led several times independently to a shift from allogamy to autogamy.

A positive influence on the divergence of the Marantaceae is ascribed to their unique explosive pollination mechanism which has been proposed to be a key-innovation. To test this hypothesis a phylogeny of an almost complete sample set of the two major African clades (*Sarcophrynium*- and *Marantochloa* clade) with data from nrDNA (ITS, 5S) and cpDNA (*trnL-F*) is established. It is used as a basis to parsimoniously reconstruct morphological and ecological traits and geographic distribution pattern. The resulting relationships including the nesting of the genus *Ataenidia* within *Marantochloa* are congruent with the existing family phylogeny and are supported by morphological characters. Therefore, a new circumscription of *Marantochloa* is proposed. Incongruencies between the datasets of the two gene regions from different genomes are attributed to hybridization events which contributed to speciation. Furthermore, a few examples of morphological changes in the explosive pollination mechanism leading to ecological or mechanical isolation could be found. However, strong selection pressures have shaped the maintenance of a functional and precise pollen transfer mechanism with a hidden pollen load throughout the whole family. Its flexibility to produce different flower tube lengths and size classes as adaptation to different pollinators may have induced the splits between and within genera. Closely related sympatric taxa, though, often demonstrate highly similar floral morphologies and share the same pollinators. Pleistocene climatic fluctuations are hypothesized to have fostered the genetic divergence in refugia. Dispersal or vicariance events onto different continents at the rise of the Marantaceae affected the primary splits at the backbone of the tree.

Therefore the designation of the unique explosive pollination mechanism as a key innovation in the Marantaceae depends on the definition of a key-innovation.

Zusammenfassung

Diese Doktorarbeit präsentiert zum ersten Mal einen Überblick über die Blütenbiologie und Phylogenie der afrikanischen Marantaceae (~40 Arten). Die Marantaceae (550 Arten) sind eine Familie weltweit verbreiteter Stauden und Lianen im Unterwuchs tropischer Tieflandregenwälder. Zu Beginn des Projektes waren die afrikanischen Arten weltweit am wenigsten erforscht. Ein Vergleich zwischen den zwei größten afrikanischen phylogenetischen Ästen soll beispielhaft evolutionäre Muster in der Familie beleuchten. Diese Äste eignen sich besonders, da sie zwei unterschiediche Positionen in der Phylogenie der Familie einnehmen: der *Sarcophrynium* Ast ist Schwestergruppe zu allen anderen Marantaceae, während der *Marantochloa* Ast in einer abgeleiteter Position steht.

Die Analysen wurden während dreier Feldaufenthalte von jeweils drei bis vier Monaten Dauer im afrikanischen Diversitätszentrum Gabun durchgeführt. Blütenmorphologische Untersuchungen an 30 Arten ergaben vier Blütentypen basierend auf Blütengröße und –farbe, räumlicher Anordnung der Blütenröhre und der An-/Abwesenheit von Nektarführungshilfen und auffälligen äußeren Staminodien. Bestäuberbeobachtungen haben gezeigt, dass jeder Type mit einer spezifischen Bestäubergilde verbunden ist. Der *Hypselodelphys hirsuta*-Typ wird vornehmlich von mittelgroßen Bienen bestäubt (*Amegilla vivida*, *Thrinchostoma bicometes),* der *Haumania danckelmanniana*–Typ von großen Bienen (*Xylocopa nigrita, X. varipes*), der *Marantochloa congensis*-Typ von kleinen Bienen (*Thrinchostoma* spp., *Allodapula ornaticeps)* und der *Thaumatococcus daniellii*-Typ von Nektarvögeln. Bestäubungsexperimente belegen, dass 18 Arten selbstkompatibel, aber nur zwei, *Halopegia azurea* und *Marantochloa leucantha*, autogam sind, also keine Bestäubungsvermittler benötigen. Mindestens 10 morphologisch sehr ähnliche Arten teilen sich dieselben Bestäuber, indem sie über einen langen Zeitraum jeweils wenige Blüten pro Tag hervorbringen. Im Gegensatz dazu vermeiden *Afrocalathea rhizantha* und *Marantochloa* sp.2 die Konkurrenz um dieselben Bestäuber, indem sie nacheinander blühen und dabei jede über einen kurzen Zeitraum jeweils viele Blüten gleichzeitig hervorbringt. Unabhängig von den unterschiedlichen saisonalen Blühmustern ist der Fruchtansatz i. d. R. gering (10 %), wohingegen die vegetative Vermehrung in den meisten Arten sehr stark ist.

Die Blüten der Marantaceae weisen eine komplexe Synorganization auf, welche einen explosiven Bestäubungsmechanismus ermöglicht. Um die evolutionäre Bedeutung dieses einzigartigen Prozesses für die Marantaceae zu verstehen, wurden 66 Arten, alle wichtigen Äste der Marantaceae abdeckend, unter einem morphologisch-funktionalen Gesichtspunkt untersucht. Die Ergebnisse zeigen, dass alle Arten in einem `tunnel´-artig geformten Schwielenblatt mit einer inneren versteiften Schwiele übereinstimmen, die die Blütenröhre exakt auf die Spitze des seitlichen Triggeranhanges des Kapuzenblattes hin verengt. Die so erzwungene Auslenkung dieses Triggeranhanges löst eine explosionsartige Bewegung des Griffels aus, welche die Pollenübertragung garantiert. Der Pollen wird dazu bereits im Knospenstadium auf der Rückseite des charakteristischen Griffelkopfes präsentiert. Obwohl ein hoher Selektionsdruck auf dieser funktionalen Einheit lastet, weisen die Blüten eine große morphologische Variationsbreite auf. Variationen in der relativen Länge der einzelnen Staminodien zueinander bedingen einen unterschiedliche n Pollenablageort auf dem Bestäuber, was möglicherweise eine Quelle für mechanische Isolation darstellt. Außerdem führen kleinste morphologische Veränderungen im Bereich des Griffelkopfes und der Kapuze des Kapuzenblattes mehrmals unabhängig zu einem Wechsel im Reproduktionssystem von Allogamie zu Autogamie.

Dem Bestäubungsmechanismus wird eine hohe Bedeutung bei der Artaufspaltung der Marantaceae zugeschrieben und er wurde sogar als Schlüsselinnovation diskutiert. Um diese Hypothese zu testen, wird die Phylogenie einer fast kompletten Artensammlung der beiden größten afrikanischen Äste (*Sarcophrynium*- and *Marantochloa*) mit Daten von nrDNA (ITS, 5S) und cpDNA (*trnL-F*) erstellt. Diese Marker wurden als Basis für die Merkmalsrekonstruktion nach dem Parsimonyprinzip genutzt. Die resultierenden Verwandtschaftsbeziehungen, inklusive der Stellung der Gattung *Ataenidia* innerhalb der Gattung *Marantochloa*, stimmen mit der existierenden Familienphylogenie überein. Da dies auch von morphologischen Merkmalen unterstützt wird, wird eine neue Umschreibung der Gattung *Marantochloa* vorgeschlagen. Inkongruenzen in den Topologien der phylogenetischen Bäume der verschiedenen Genregionen werden Hybridisierungsereignissen zugeschrieben, die zur Artbildung beitrugen. Einige Beispiele belegen, dass möglicherweise auch morphologische Änderungen der Blüte im explosiven Bestäubungsmechanismus zur Artbildung in Verbindung mit

ökologischer oder mechanischer Isolation beigetragen haben. Allerdings hat ein starker Selektionsdruck die Erhaltung des präzise funktionierenden Pollenübertragungsmechanismus mit versteckter Pollenladung in der gesamten Familie erzwungen. Erst die Potenz verschieden lange Blüten-Röhren und –Größenklassen als Anpassung an verschiedene Bestäuber zu entwickeln, induzierte möglicherweise die Aufspaltung zwischen und innerhalb von Gattungen. Darüber hinaus weisen nah verwandte Arten oft eine sehr ähnliche Blütenmorphologie auf und teilen sich dieselben Bestäuber. Es wird angenommen, dass die genetische Divergenz dieser heute sympatrisch vorkommenden Arten durch die geographische Isolation in Refugien während pleistozäner Klimaschwankungen vorangetrieben wurde. Langstreckenausbreitungs- oder Vikarianz- Ereignisse auf verschiedene Kontinente in der frühen Entwicklung der Marantaceae beeinflussten die Artaufspaltung an der Basis des phylogenetischen Familienstammbaumes. So ist abschließend die Beschreibung des explosiven Bestäubungsmechanismus als Schlüsselinnovation in den Marantaceae abhängig von der Definition einer Schlüsselinnovation.

1 General introduction

Extraordinary floral morphologies and complex plant-pollinator interactions with a variety of different pollinators have been discovered in the (sub-)tropical Zingiberales (sensu Dahlgren et al., 1985) (Table 1.1; Kress and Specht, 2005). The order forms a strongly supported monophylum within the monocotyledons based on morphological and molecular data (Dahlgren et al., 1985; Chase et al., 2000; Stevenson et al., 2000; Janssen and Bremer, 2004; Givnish et al., 2006). It includes eight families which can be divided into two informal groups: the basal paraphyletic `banana families´ (Musaceae, Strelitziaceae, Heliconiaceae, Lowiaceae) with a still unresolved topology and the monophyletic and well resolved derived `ginger´ families (Zingiberaceae, Costaceae, Cannaceae and Marantaceae) (Fig. 1.1; Kress, 1990, 1995; Kress et al. 2001; Prince and Kress, 2004).

Figure 1.1: The phylogeny of the Zingiberales (taken from Kress 1990).

The separation into `banana´ and `ginger´ families is based on the different expression of the organs of the androecial whorl (Kress, 1990; Rudall and Bateman, 2004). In the `banana´ families there are generally five fertile anthers with the sixth anther missing (except in Heliconiaceae), whereas in the `ginger´ families most anthers have undergone reductions to petaloid staminodes. In the Zingiberaceae and Costaceae only one fertile anther remains, whereas the Marantaceae and Cannaceae exhibit only half a fertile anther (Fig. 1.2).

The most species rich families of the Zingiberales are three of the four families from the `ginger´ group: the Zingiberaceae (over 1200 spp., Kress et al., 2002), Marantaceae (550 spp., Andersson, 1998) and Costaceae (115 spp., Specht, 2001) (Table 1.1). These three families exhibit each a unique floral feature which is closely connected to the transformation of fertile stamens to petal-like staminodia: the Costaceae possess a prominent “labellum” based on various patterns of fusion of the petaloid structures (Specht, 2001), some Zingiberaceae developed a lever

Table 1.1: Taxonomic, geographic and ecological data of the families of the Zingiberales. Number of taxa and distribution after Stevens, 2001 onwards; * after Specht, 2001; ° after Kress et al., 2002; pollinators summarized in Kress and Specht, 2005; flower anthesis and breeding system from summary in Endress, 1994; autogam., autogamous species present; gen, genera; sc, self-compatible species present; sp, species; ?, no data available.

family	Gen	Sp	distribution	pollinators	flower anthesis	breeding system
Musaceae	3	42	palaeotropical (Asia, Africa)	bees, bats, tree shrews?	1♂-3♀days	sc; autogam.
Strelitziaceae	3	7	(sub-)tropical South America, South Africa, Madagascar	birds, lemurs, bats	1 week	?
Lowiaceae	1	2	palaeotropical (Asia)	tree shrews?, beetles	?	?
Heliconiaceae	1	80	neotropical	birds, bats	1 day	sc; autogam.
Costaceae	4*	115*	pantropical	birds, bees, flies	1 day	some species partly sc
Zingiberaceae	53°	>1200°	pantropical	birds, bees, bats, hawkmoths?	1 day	sc
Cannaceae	1	10	neotropical	birds, bees, bats	1 day	sc
Marantaceae	31	550	pantropical	birds, bees	1 day	sc; autogam. (~8%)

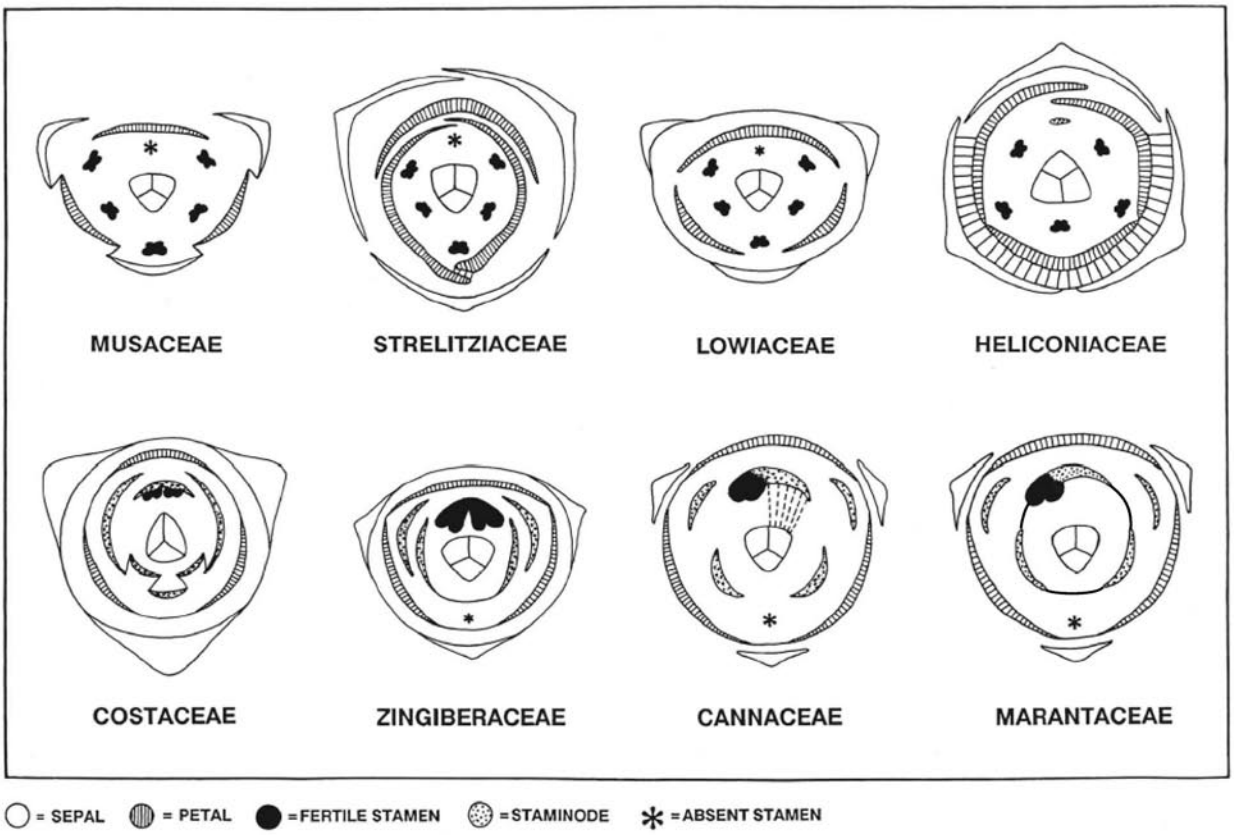


Figure 1.2: Floral diagrams representing the eight families of the Zingiberales with perianth whorls, fertile stamens, staminodia and carpels (taken from Kress, 1990, Marantaceae slightly altered).

Table 1.2: Numbers of genera and species per continent. * after Andersson (1998), ° own observations, " after Borchsenius (pers. com.). Genera in bold are distributed over more than one continent.

America*		**Africa°**		**Asia"**	
Calathea	300	*Afrocalathea*	1	*Cominsia*	3
Ctenanthe	10	*Ataenidia*	1	*Donax*	1
Hylaeanthe	6	***Halopegia***	1	***Halopegia***	1
Ischnosiphon	35	*Haumania*	3	*Monophrynium*	2
Koernickanthe	1	*Hypselodelphys*	7	*Phacelophrynium*	10
Maranta	25	*Marantochloa*	15	*Phrynium*	19
Monophyllanthe	2	*Megaphrynium*	5	*Schumannianthus*	3
Monotagma	37	*Sarcophrynium*	4	*Stachyphrynium*	10
Myrosma	1	*Thaumatococcus*	2		
Pleiostachya	2	*Trachyphrynium*	1		
Sanblasia	1	***Thalia***	1		
Saranthe	5-10				
Stromanthe	15-20				
Thalia	6				
	446-456		41		49

mechanism (in *Globba, Roscoea*) and flexistyly (in *Alpinia*) (Troll, 1929; Sun et al., 2007) and the Marantaceae are renowned for their explosive stylar movement with secondary pollen presentation (Gris, 1859; Claßen-Bockhoff, 1991). The latter is a very complex mechanism based on the close synorganization of the style and two morphologically highly specialized staminodes exhibiting one of the fastest movements in the plant kingdom (~0.03 sec.; Claßen-Bockhoff, 1991). This mechanism is postulated to be a key-innovation in the Marantaceae influencing its species richness (Kennedy, 2000).

The Marantaceae (Petersen, 1889) are perennial herbs or lianas which are readily identified by the pulvinus (see Tomlinson, 1961). 83 % of the species occur in America, 9 % Asia and 8 % in Africa (Table 1.2; Fig. 1.3; Dhetchuvi, 1996; Andersson, 1998; Kennedy, 2000; Suksathan, 2005). Genera are generally endemic to the respective continent except *Halopegia* and *Thalia* occurring in either Africa and Asia or Africa and America, respectively (Table 1.2). They often dominate the understorey of the tropical lowland rainforests ("Marantaceae forest" see Letouzey, 1968) and exhibit a wide range of economic uses from ornamental plants mainly through species from Asia and America, comestible goods (*Maranta arundinacea*/arrow root; Piperno et al., 2000) and nutrition sweetener (thaumatin

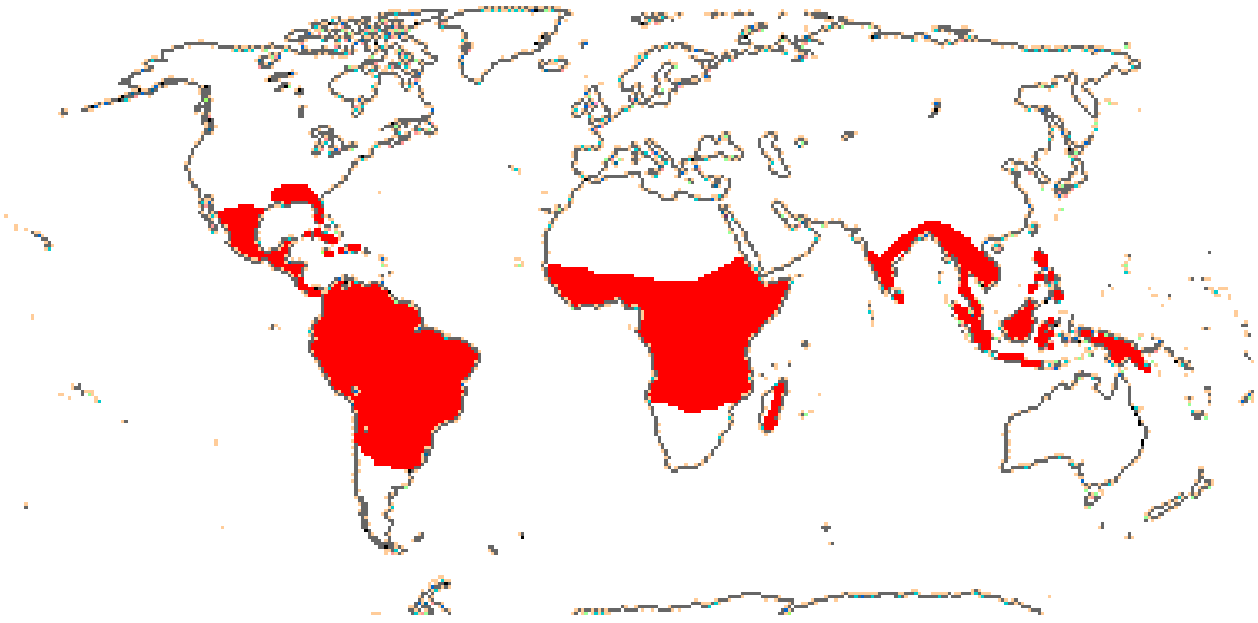


Figure 1.3: The geographic distribution of Marantaceae (taken from Stevens, 2001 onwards).

in *Thaumatococcus daniellii*, Most et al., 1978; Bartoszewski et al., 2003) to the employment of the large leaves of certain African species to wrap up various dishes such as fish or mash made of manioc flour (own observations, Cameroun and Gabon). Many species of the African Marantaceae also play an important role for apes and gorillas which preferentially use their large leaves for nest construction and eat their fruits and pith (Rogers et al., 1990; Tutin and Fernandez, 1993).

The phylogenetic structure of the Marantaceae on genus level is illuminated in Andersson and Chase (2001) and Prince and Kress (2006*a*, *b*). The analyses are based on different and continuously more genetic markers and are congruent in the recognition of major clades identifying several non-monphyletic genera. Thereby major clades are generally confined to a single continent. However, the resolution along the backbone of the tree remains further unresolved and renders the reconstruction of the geographic history of the family difficult (Prince and Kress 2006*b*). The current most likely hypothesis assumes several dispersal events from Africa to both the New World and to Asia. An analysis of the phylogenetic structure of the Asian species identifies several probably non-monophyletic genera and recurrent dispersal events between distant islands in the Indo-Malayan-region (Suksathan, 2005).

Ecological investigations on the American (for pollinators see Fig. 1.4; Kennedy, 1977, 1978, 2000; Le Corff, 1992; Locatelli et al., 2004) and Asian species (see Bawa, 1983; Kato, 1996; Clausager and Borchsenius, 2003) reveal a high diversity in phenological pattern, floral morphologies (e.g. long and short tubed flowers; closed flowers) and pollinators (e.g. different bee species and birds). A review of the breeding system suggests 8 % of the species worldwide to be autogamous with independent origins (Fig. 1.4, Kennedy, 2000).

Detailed morphological investigations on some American species can be found in e.g. Eichler (1884) and Claßen-Bockhoff and Heller (2008*a*) and about some American and African species in Kunze (1984) with details on seed morphology to be found in Costerus (1918) and Humphrey (1896).

At the beginning of this project there was almost nothing known about the ecology of the African species. Only geographic distribution ranges and habitat descriptions were available (see Dhetchuvi, 1996) and a PhD thesis on the vigour in vegetative reproduction of *Megaphrynium macrostachyum* (Brncic, 2003).

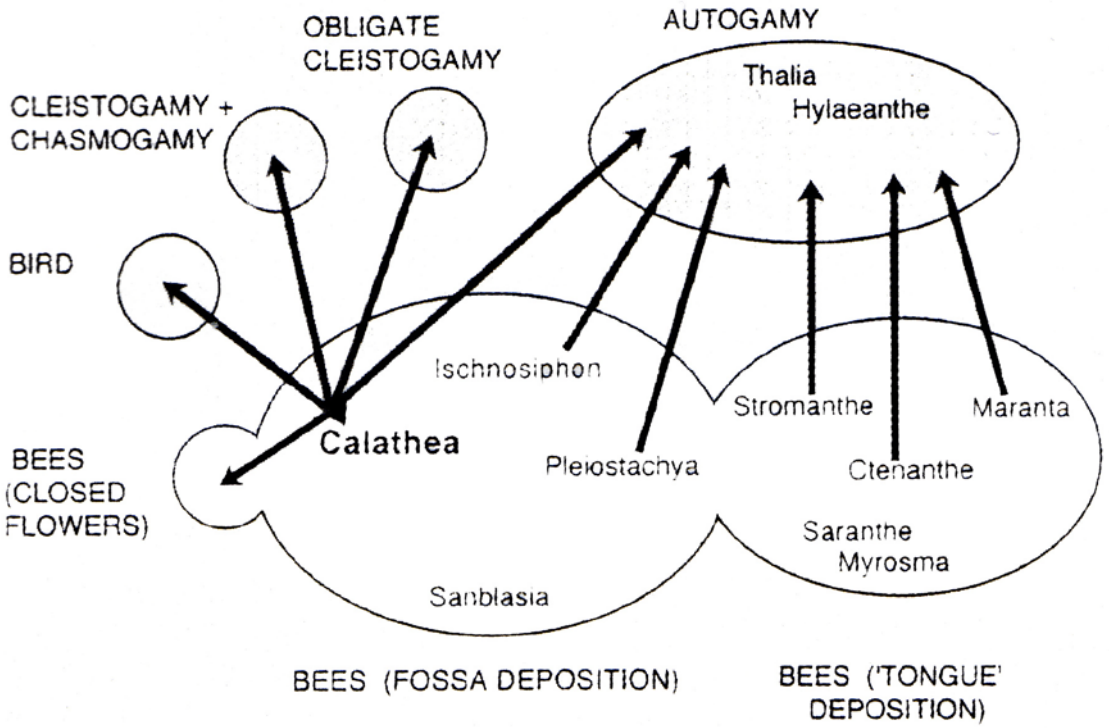


Figure 1.4: Pollination and breeding system in American Marantaceae (taken from Kennedy, 2000).

However, the African species present a very interesting part of the Marantaceae as they are distributed in mainly two clades which are phylogenetically independent from each other (see Prince and Kress, 2006*a*). One of those clades, the *Sarcophrynium* clade, is sister to all other Marantaceae whereas the other, the *Marantochloa* clade, stands in a more derived position in the pylogenetic tree. The aim of this study is a comparison of the reconstructed evolutionary processes within each of these clades including morphological and ecological parameters which shall shed more light onto the evolution of the family and lead to a better understanding of the factors that promoted the far larger diversification in the Marantaceae than in its sister family Cannaceae.

Thus in the present thesis comprehensive field studies in Gabon elucidate for the first time the diversity in plant pollinator interactions in Africa and provide information on breeding systems and fruit set. Detailed flower morphological investigations establish a basis for the understanding of the floral synorganization and extract possibilities for mechanical isolation via differential pollen deposition. Finally, a species level phylogeny forms the basis to set ecological and morphological characters into an evolutionary context.

2 Field Investigations in African Marantaceae: plant architecture, plant-animal interactions, breeding systems and fruit-set

2.1 ABSTRACT

The Marantaceae (550 spp.) is the most derived family in the order Zingiberales and exhibits a complex explosive pollination mechanism. To understand the evolutionary significance of this unique process of pollen transfer, comparative morphological and ecological studies were conducted in Gabon. The chapter presents the first survey on the biology of African Marantaceae.

During a total stay of 11 months, 30 species of Marantaceae were investigated at different sites in Gabon. The study includes analyses of architectural and floral diversity of the plants, observations on flower phenology and the pollinator spectrum, ecological measurements (e.g. flower size, nectar sugar concentration, pollen ovule ratio) as well as pollination experiments.

Analyses reveal four flower types based on flower size and pigmentation, spatial arrangement of the floral tube and presence/absence of nectar guides and conspicuous outer staminodes. Each type is associated with a specific pollinator guild. The *Hypselodelphys hirsuta*-type is predominantly pollinated by medium-sized bees (*Amegilla vivida*, *Thrinchostoma bicometes),* the *Haumania danckelmanniana*–type by large bees (*Xylocopa nigrita, X. varipes*), the *Marantochloa congensis*-type by small bees (*Thrinchostoma* spp., *Allodapula ornaticeps)* and the *Thaumatococcus daniellii*-type by sunbirds. Pollination experiments confirm that 18 species are self-fertile but depend on pollinators for pollen transfer. *Halopegia azurea* and *Marantochloa leucantha* are autogamous. At least ten morphologically similar species share pollinators by flowering sparsely over a long period. In contrast *Afrocalathea rhizantha* and *Marantochloa* sp.2 avoid competition for pollinators by short consecutive mass flowering events. Fruit-set is generally low (~10 %) whereas the vegetative vigour is high in most species.

The longevity of Marantaceae individuals and the omnipresence of their pollinators allowed the specialisation to a given pollinator guild. Intermediate ecological values however make occasional pollinator overlap possible indicating

possible pathways of pollinator shifts. Similar radiation tendencies observed on other continents hint to similar selective pressures and evolutionary constraints.

2.2 INTRODUCTION

In tropical ecosystems the main interest is usually directed to the diversity of trees and the life in their canopies. Only little is known about the plants living in the understorey of tropical rainforests. This also applies to the Marantaceae, a pantropically distributed family of perennial herbs and lianas from the order Zingiberales (Kress, 1995).

The Marantaceae are characterized by a unique pollination mechanism including proterandry, secondary pollen presentation and an irreversible style movement (Claßen-Bockhoff, 1991; Yeo, 1993; Kennedy, 2000; Locatelli et al., 2004). Flowers are asymmetrically and attract their pollinators with conspicuous staminodes and nectar. Still in the bud, the pollen is deposited onto the back of the `head´ of the style (Kennedy, 1978; Claßen-Bockhoff and Heller, 2008*a*). The style is then held under tension by the hooded staminode (Pischtschan and Claßen-Bockhoff, 2008). When the pollinator touches the trigger-like appendage of the hooded staminode, the style springs forward, scrapes off the pollen from the pollinator and places its own pollen on its mouth parts or into the proboscidial fossae. Each flower is open for a single day, having just one chance of being pollinated and dispersing its own pollen since the explosive pollination mechanism cannot be reset (Kunze, 1984; Claßen-Bockhoff, 1991; Kennedy, 2000).

In view of the high species number in Marantaceae (about 550 species, 31 genera; Andersson, 1998) compared to the low number in their sister group, the Cannaceae (10 species, 1 genus; Kubitzki, 1998), it is likely that the peculiar pollen transfer mechanism might have enhanced speciation in the family (Kennedy, 2000). However, too little is known about the pollination biology and sexual reproduction in the Marantaceae to reconstruct the evolutionary significance of the explosive style movement (see Kato, 1996; Momose et al., 1998; Kennedy, 2000; Clausager and Borchsenius, 2003; Locatelli et al., 2004; Claßen-Bockhoff and Heller, 2008*b*). There are approximately 40 African species which fall into six separate clades, the basal *Sarcophrynium* clade (~15 spp.), the more derived *Ataenidia* clade (~16 spp.) and four small clades with only one to three species each (*Afrocalathea, Halopegia,*

Haumania, Thalia) (Dhetchuvi, 1996; Prince and Kress, 2006*a*). As Africa is assumed to be the continent of origin of the family (Prince and Kress, 2006*b*) a comprehensive research project was started on the African species to gain a deeper insight into the pollination ecology and breeding system of the Marantaceae.

The species are dominant in the understorey of lowland rainforests (`Marantaceae forest´; Letouzey, 1968; De Foresta, 1990) where they form large probably purely clonal stands (Dhetchuvi, 1996; Brncic, 2003). The geographic range extends from Senegal (West Africa) to Kenya (East Africa) and Madagascar. The centre of diversity is in Gabon with about 35 species (~85 %) that have highly overlapping distributional ranges (Dhetchuvi, 1996).

Bees (Euglossinae, *Bombus, Melipona*) and hummingbirds (Kennedy, 2000; Locatelli et al., 2004; Leite et al., 2007; Claßen-Bockhoff and Heller, 2008*b*) are reported to be pollinators in the New World, solitary bees (*Amegilla, Xylocopa*, *Halictidae*) are described as pollinators in Asian Marantaceae (Claßen-Bockhoff, 1991; Kato, 1996; Momose et al., 1998; Kennedy, 2000; Clausager and Borchsenius, 2003). Furthermore, moth pollination is assumed in *Cominsia* spp. which are distributed from East Indonesia (Sulawesi) to Irian Jaya and Papua New Guinea (Kennedy, 2000). Nothing is known about the pollination biology of the African species.

Marantaceae from America and Asia have repeatedly been reported to be self-compatible (East, 1940; Kennedy, 1978; Kress and Beach, 1994; Locatelli et al., 2004; Claßen-Bockhoff and Heller, 2008*a*), but concrete data are rarely available. Kennedy (2000) however, estimates the percentage of autogamous species in the family to be about 8%. Nothing is known about the breeding systems in the African species.

The present chapter based on data collected during comprehensive field studies in Gabon represents the first survey on the biology of African Marantaceae. It provides information about floral diversity, pollinator guilds, phenological patterns, mechanisms to avoid geitonogamy, fruit-set and the rate of sexual versus vegetative reproduction. Apart from increasing the knowledge on Marantaceae, it contributes to a more general understanding of the biology of understorey plants in tropical rainforests.

2.3 MATERIAL AND METHODS

2.3.1 RESEARCH SITE

Field investigations were conducted in Gabon, first from October 2004 to January 2005 during an explorative voyage to different sites (Dibouka/Lastoursville, Libreville, Lope, Makokou, Mayumba, Mikongo, Sindara/Waka, Tchimbele/Monts de Cristal, Fig. 2.1), then from October 2005 to January 2006 at the biological station Ipassa (0°31´N, 12°48´E) near Makokou and finally from October to December 2006 in Tchimbele (0°36.8´N, 10°24.0´E) in the Monts de Cristal mountain range.

Ipassa is situated at the border of the river Ivindo on a plateau at about 500 m above sea level. The mean annual temperature is 24° C, the annual rainfall 1700 mm (Saint-Vil, 1977; Makanga, 1997). The local forest type of Makokou is a transition between the evergreen lowland rainforest in the west and the semi-deciduous forest in the east (Caballé, 1978) with Caesalpinoideae as predominant tree species. A tree inventory has been compiled by Azizet Issembe (2002).

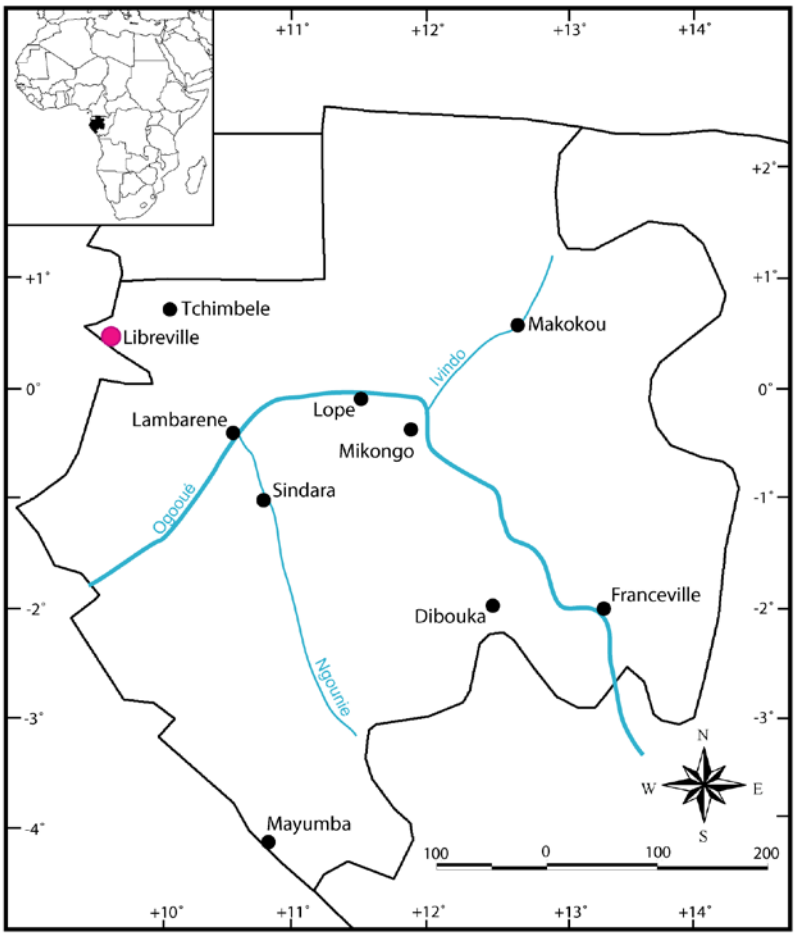


Fig. 2.1: Research localities in Gabon.

Tchimbele is located at 450 m in the Monts de Cristal mountain range reaching from Equatorial Guinea to Gabon (Sunderland et al., 2004). The mean annual temperature is 26° C, the mean annual rainfall between 2000 and 3500 mm (De Saint-Aubin, 1963; Reitsma, 1988). Monts de Cristal is covered by evergreen rainforest, characterized by an abundance of *Aucoumea klaineana* Pierre (Bruseraceae), *Desbordesia glaucescens* Tiegh. (Irvingiaceae), *Dacryodes buettneri* (Engl.) H.J.Lam (Bruseraceae), *Erismadelphus exsul* Mildbr. (Vochysiaceae) and in particular by different species of *Bikinia* Wieringa (syn. *Monopetalanthus,* Leguminosae) (Christy et al., 2003). The mountain range is assumed to be the most species rich area in Gabon (Wilks, 1990).

There are marked seasons in both areas, two rainy seasons (September to December and March to May) and two dry seasons (December to February and June to September) (Leroux, 1975; Saint-Vil, 1977; Davis et al., 1994; Vande wegh, 2004).

2.3.2 PLANT MATERIAL

In total, 30 species were investigated of which 28 were encountered in Gabon (Table 2.1). Fifteen species of Marantaceae were studied at Makokou (Ma), 17 species in the Monts de Cristal area (MC). Some species occurred in both locations. In total five new species have been identified (*Hypselodelphys* sp.1, *Marantochloa* sp.1, *M*. sp.2, *M*. sp.3, *Thaumatococcus* sp.1; unpubl. data). Additional data of further species was obtained from individuals at Dibouka, Lope, Sibang and from cultivated greenhouse plants at Mainz University, Germany.

Marantaceae are perennial herbs and lianas with persisting rhizomes (Table 2.1). Therefore it is highly difficult to identify genetically different individuals in the field. From the plagiotropic rhizomes groups of shoot systems and long stalked leaves arise in distinct units which is called “individual units” here and to which is refered in the present chapter.

The African Marantaceae are predominantly sparsely flowering plants with sometimes long distances between individuals and/or populations. Thus, it is often difficult to find sufficient synchronously open flowers for pollination experiments especially when aiming at statistically significant samples sizes. For some species such studies demand long walks through the forest which were only possible in the company of a local guide in particular in regard to potential encounters with dangerous animals.

Table 2.1: List of species included in the present chapter. Gabon: Di, Dibouka; Lo, Lope; Ma, Makokou; MC, Monts de Cristal; Mi, Mikongo; Si, Sibang; Germany: MZ, Mainz greenhouse.

species	abbreviation	site	growth habit	voucher
Afrocalathea rhizantha K. Schum.	*Afro rhiz*	Ma, MC	perennial herb	Ley 7, 58, 164, 184, 214, 251, 263 (LBV, WAG)
Ataenidia conferta (Benth. in Benth. Hook f.) Milne-Redh.	*Atae conf*	Ma	perennial herb	Ley 159 (LBV, WAG)
Haumania danckelmanniana (J.Br. & K. Schum.) Milne-Redh.	*Haum danc*	Ma, MC	liana	Ley 2, 4, 6, 60, 62, 162 (LBV, WAG)
Haumania liebrechtsiana (De Wild.& Th. Dur.) J. Leonard	*Haum lieb*	MC	liana	Ley 50, 51, 52, 53 (LBV, WAG)
Hypselodelphys hirsuta (Loes.) Koechlin	*Hyps hirs*	Ma, MC	liana	Ley 156, 167, 174, 269 (LBV, WAG)
Hypselodelphys poggeana (K. Schum.) Milne-Redh.	*Hyps pogg*	Ma	liana	Ley 168, 169 (LBV, WAG)
Hypselodelphys scandens Louis & Mullenders	*Hyps scan*	Ma	liana	Ley 160 (LBV, WAG)
Hypselodelphys violacea (Ridley) Milne-Redh.	*Hyps viol*	Si	liana	Ley 28 (LBV, WAG)
Hypselodelphys sp.1	*Hyps* sp.1	Lo	liana	Ley 141, 125 (LBV, WAG)
Marantochloa congensis (K. Schum.) J. Leonard Mullenders	*Mara cong*	Lo, Ma, MC	perennial herb	Ley 3, 18, 157, 163, 166, 240, 243 (LBV, WAG)
Marantochloa cordifolia (K. Schum.) Koechlin	*Mara cord*	Ma, MC	perennial herb	Ley 170, 173 (LBV, WAG)
Marantochloa filipes (Benth. In Hook.) Hutch.	*Mara fili*	MC, Si	perennial herb	Ley 30, 262 (LBV, WAG)
Marantochloa incertifolia Dhetchuvi	*Mara ince*	Ma, MC	perennial herb	Ley 179, 182, 236, 248 (LBV, WAG)
Marantochloa leucantha (K. Schum.) Milne-Redh.	*Mara leuc*	Di, MZ	perennial herb	Ley 66 (LBV, WAG)
Marantochloa mannii (Benth.) Milne-Redh.	*Mara mann*	Mi	perennial herb	living collection university of Mainz
Marantochloa monophylla (K. Schum.) D`Orey	*Mara mono*	Ma, MC	perennial herb	Ley 183, 191, 197, 198, 203, 209, 217, 238, 249, 270 (LBV, WAG)
Marantochloa purpurea (Ridley) Milne-Redh.	*Mara purp*	Ma, Lo	perennial herb	Ley 102, 140, 180 (LBV, WAG)
Marantochloa sp.1	*Mara* sp.1	MC	perennial herb	Ley 268 (LBV, WAG)
Marantochloa sp.2	*Mara* sp.2	MC	perennial herb	Ley 190, 194, 195, 204, 205, 207, 212, 235, 267 (LBV, WAG)
Marantochloa sp.3	*Mara* sp.3	MC	perennial herb	Ley 256 (LBV, WAG)
Megaphrynium gabonense Koechlin	*Mega gabo*	Ma	perennial herb	Ley 1, 9, 10, 11, 14, 23 (LBV, WAG)
Megaphrynium macrostachyum (Benth.) Milne-Redh.	*Mega macr*	MC, Si	perennial herb	Ley 186, 260 255 (LBV, WAG)
Megaphrynium trichogynum Koechlin	*Mega tric*	Ma, MC, Di	perennial herb	Ley 5, 22, 187, 221, 264, 271 (LBV, WAG)
Sarcophrynium brachystachyum (Benth.) K. Schum.	*Sarc brac*	MC	perennial herb	Ley 189, 192, 193, 199, 211, 219, 220, 233 (LBV, WAG)
Sarcophrynium prionogonium (K. Schum.) K. Schum.	*Sarc prio*	MC	perennial herb	Ley 55, 200, 208, 222, 223, 226, 227, 241, 244, 247, 265 (LBV, WAG)
Sarcophrynium schweinfurthianum (Kuntze) Milne-Redh.	*Sarc schw*	Ma	perennial herb	Ley 224, 225, 232, 245, 246 (LBV, WAG)
Thalia geniculata L.	*Thal geni*	MZ	perennial herb	living collection University of Mainz
Thaumatococcus daniellii (Benn.) Benth.	*Thau dani*	Di	perennial herb	Ley 69, 96 (LBV, WAG)
Thaumatococcus sp.1	*Thau* sp.1	MC	perennial herb	Ley 56, 201, 202, 218 (LBV, WAG)
Trachyphrynium braunianum (K. Schum.) Baker	*Trac brau*	Ma, Lo	liana	Ley 103, 171, 172 (LBV, WAG)

Species identification is based on available keys (Koechlin, 1964; 1965; Dhetchuvi, 1996), type description and comparison with type specimen in various herbaria (BR, K, LBV, P, WAG). Vouchers are deposited at the National Herbarium in Libreville (LBV), Gabon, and at the Herbarium Vadense in Wageningen (WAG), The Netherlands (Table 2.1). Inflorescences and flowers were fixed in 70% ethanol for further microscopic investigations. Photos of growth forms, inflorescences, flowers and flower details were taken on fresh material in the field with a Nikon Coolpix 995.

2.3.3 PHENOLOGICAL SEASONALITY

General seasonal phenological pattern for almost all Central African Marantaceae species can be found in Detchuvi (1996). This information formed the basis for the timing of the field trips. The patterns were confirmed and refined between September and January for Gabon as the field trips generally exceeded the invididual flowering time of each species. It is indicated in the results wherever this was not the case.

2.3.4 FLOWERING SEQUENCE

To determine the longevity of the inflorescence and flower anthesis, up to ten inflorescences of different individuals per species were observed daily between 0545 h (just before sunrise) and 1700 h (about 1.5 hours before sunset) for two to eight weeks recording the number of open flowers, the timing of their opening and their position on the inflorescence. Additionally, the number of flowers per inflorescence was counted on one to 27 postfloral inflorescences per species. If the total flowering time of an inflorescence could not be observed, the longevity of an inflorescence was extrapolated: the average number of flowers per inflorescence counted on the postfloral inflorescences devided by the average number of open flowers per week recorded during the weeks of observation.

2.3.5 MORPHOMETRIC MEASUREMENTS (FIG. 2.2)

The length of the fleshy staminode (a), the distance between flower entrance and nectar (b) and the width of the flower entrance (c) are of special importance for the matching in size of flower and pollinator. These length measurements were taken for each species on up to ten fresh flowers of different individuals with a millimetre grid paper. To determine the distances from the flower entrance to the tip of the trigger the fleshy staminode was removed with a razor blade. This allowed additionally a

view into the interior of the flower without influencing the rest of the flower in order to determine the nectar level.

2.3.6 NECTAR

Nectar concentration and volume was generally measured in the morning hours between 0600 h and 1000 h on about ten untriggered bagged flowers of different individuals per species. The volume of the nectar per flower was determined by extracting subsequently all the nectar present with SIGMA microcapillary tubes (1 µl, 2 µl) and adding up the extracted volumina. Nectar concentration was determined with an Eclipse refractometer (0 – 50 %) especially designed for small quantities.

2.3.7 POLLEN

In order to estimate the time of pollen deposition buds were harvested at different times of the day from all species available. The start of pollen deposition is defined here as the moment when the theca opens at its tip. At this time first pollen grains are pressed out of the theca onto the pollen plate at the back of the stylar head.
The number of pollen grains per anther was counted on about ten buds per species a day before opening, i.e. just before pollen deposition on the pollen plate. Pollen grains were diluted in water and counted under a binocular using a 3 mm-grid. The

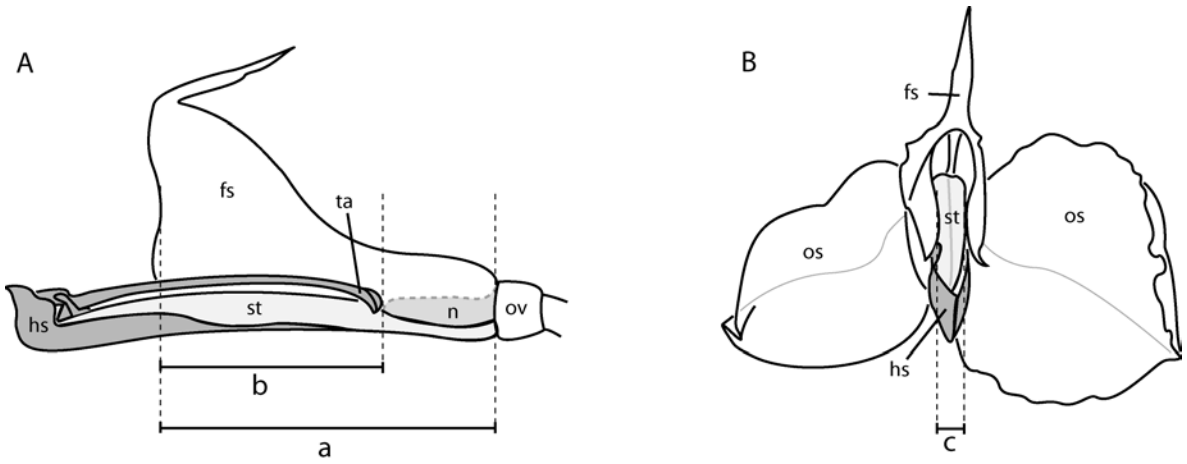


Figure 2.2: Flower morphometric data exemplified on *Hypselodelphys hirsuta*. A, lateral view. B, frontal view. a, length of fleshy staminode; b, distance between flower entrance and nectar; c, width of flower entrance. hs, hooded staminode (dark grey); fs, fleshy staminode; n, nectar (intermediate grey); os, outer staminode; ov, ovary; st, style (light grey); ta, trigger appendage; fertile theca with appendage removed.

P/O-ratio was calculated as the number of pollen grains per theca divided by the three ovules per flower. To compare the values from the African species with other Marantaceae species from America and Asia where no data is yet available I also counted the pollen grains in a few selected species from the greenhouse in Mainz (*Calathea bachemiana, C. rufibarba, C. veitchiana, C.* sp*., Maranta leuconeura, M. noctiflora, Myrosma sp., Pleiostachya pruinosa, Stromanthe sanguinea, Donax canniformis*). Pollen diameter was roughly estimated under the binocular based on a 1 mm grid in the background.

2.3.8 POLLINATORS AND FLOWER VISITORS

To determine the pollinators of each species direct observations were conducted on untriggered flowers. Only animals that are able to trigger the flower were considered as potential pollinators. The observations were conducted preferentially at different times of the day and at different sites (Makokou, Mikongo, Monts de Cristal and Sibang/Libreville) for a minimum of eight hours to a maximum of 42 hours per species (an overall total of 469 hours of observation). For each visit the time of the day, the visitor species, its time spent in the observed plant population, the duration and mode of flower-handling and the unreleased or released stage of the style were recorded. From these data the average visitation rate, i.e. the number of visits per visitor species per plant population per hour was calculated. Furthermore, the flowering stages of the flowers visited were recorded, i.e. whether they were buds or fresh or wilted open flowers.

As far as possible, the interactions between pollinators and flowers were documented on video tape with a digital video camera (Sony DCR-TRV30E). The videos are deposited at the Institut für Spezielle Botanik und Botanischer Garten, Johannes-Gutenberg-Universität Mainz, Germany. They are the basis for the estimated average flower handling time per insect and Marantaceae species [see supplementary information - CD].

To measure the fitting of insects and flowers it was tried to obtain a specimen sample of as many insect pollinators as possible. The insects were identified by C. Eardley (Pretoria, South Africa). Specimens of *Lipotriches*, *Megachile* and *Thrinchostoma* could not yet be identified to species level as these genera first need revision. For each sample body length, head width and proboscis length were determined. To account for the maximal reach of the insect to suck the nectar the

proboscis length was measured as the length of the glossa/galea in long tongued bees (e.g. *Amegilla*). In short tongued bees (e.g. *Thrinchostoma*) the lengths of prementum and mentum were added. Only specimens with a complete dataset were used for statistical analyses.

In *Afrocalathea rhizantha* pollination efficiency tests were conducted. Individual flowers were marked after observed style release by birds and their fruit-set was recorded hereafter.

Data of flower and pollinator characteristics were analysed statistically using SPSS Version 15.0. To determine whether datasets were significantly different from each others a non-parametric test (Kolmogorov-Smirnov) was applied as not all datasets to compare were normally distributed. Furtheron correlation between datasets were tested with a two-sided correlation analysis after Pearson.

2.3.9 POLLINATION EXPERIMENTS

To study the breeding system of the African Marantaceae four different experiments were conducted. On random samples of inflorescences (n = 2 to 52) from different populations the fruit-sets of a) open control inflorescences, b) bagged and untreated inflorescences, c) bagged and self-pollinated flowers and d) bagged and cross-pollinated flowers were counted. Inflorescences were bagged in nylon-mesh-bags with an interior cage made of wire in order to provide an almost unaltered microclimate for the inflorescences (see Fig. 2.3A, B). Hand-pollination was conducted by artificially releasing the style of an open flower, scraping off the pollen from the pollen plate with a needle and then transferring it into the stigmatic cavity of the same or a genetically different flower.

2.3.10 FRUIT DEVELOPMENT, SEED SET AND INSECT FEEDING

To estimate the duration of fruit development pollinated flowers were followed for two to five weeks to final fruit size. Observations indicate that in some species full-grown fruits are not yet mature. Length and pigmentation of fruits and seeds were recorded. Seed set was recorded in 19 species of one to 279 randomly collected fruits from different individuals and populations. In addition, observations of insects feeding on flowers, ovaries and fruits were noted.

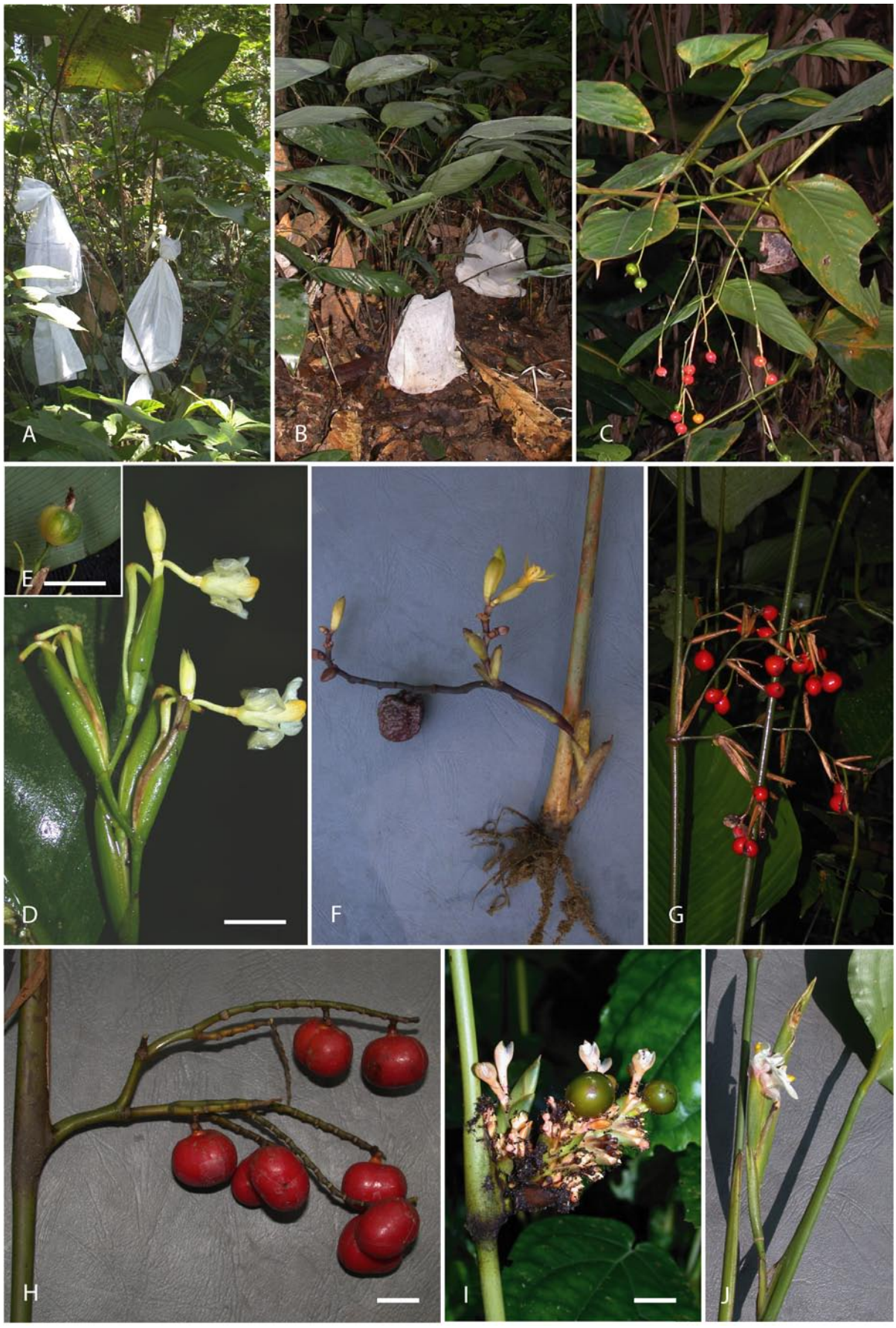


Figure 2.3: Bagging experiments (A – B) and inflorescences (C – I). (A) *Megaphrynium gabonense*. (B) *Afrocalathea rhizantha*. (C) *Marantochloa leucantha*. Note the long ➔

2.4 RESULTS

2.4.1 ARCHITECTURE, INFLORESCENCES AND PHENOLOGY

Architecture

Of the 30 species observed, 22 grow as perennial herbs and eight as lianas (Table 1). Individuals grow in dense stands of well defined populations of variable sizes or are scattered throughout the forest so that circumscription of a population becomes difficult. However, `individual units´ can always be readily distinguished. They produce one to ten inflorescence(s) in the herbaceous species and up to 100 inflorescences in the lianescent species.

The growth form of the plant influences the height, accessibility and attractiveness of the inflorescences. Here I distinguish between hidden and well exposed inflorescences being arranged in different distances from the forest floor.

- Inflorescences are arranged near the forest floor (maximal height of 15 cm) in *Afrocalathea rhizantha* (Fig. 2.4A-C), *Marantochloa* sp.2 (Fig. 2.4D-F) and *Thaumatococcus* spp. (Fig. 2.3F) and reach up to a height of less than 60 cm in *Halopegia azurea* and *Megaphrynium trichogynum*. They are hidden under a one meter high and dense canopy of lanceolate leaf blades. In the species of *Thaumatococcus* spp. the leaf petioles are up to 3 m long and the leaf blades are large and oval (30 to 50cm long).
- The inflorescences of *Megaphrynium gabonense, M. macrostachyum* (Fig. 2.3H), *Sarcophrynium* (Fig. 2.3I), and *Ataenidia* are arranged at a height of 0.6 to 1.50 m. The vegetative growth form of these species resembles that of the *Thaumatococcus* species with short non-branching shoots and long leaf petioles of about 1.50 m in *Sarcophrynium* and up to 4 m in *Megaphrynium* carrying large (30 to 50cm long) and mostly oval leaf blades.
- The inflorescences of *M. incertifolia* (Fig. 2.3D), *M. sulphurea* and *M. monophylla* are presented at a maximum height of 1 to 1.2 m. They are located among or

→inflorescence internodes. (D) *Marantochloa incertifolia* (Makokou). Note the consecutive flowering within a flower pair. (E) *Marantochloa monophylla*. Fruit. (F) *Thaumatococcus* sp.1. Inflorescences are close to the ground. (G) *Sarcophrynium schweinfurthianum* (Makokou). Note the large red berry-like fruits. (H) *Megaphrynium macrostachyum*. Note the large red berry-like fruits. (I) *Sarcophrynium brachystachyum*. Note the condensed inflorescence. (J) *Marantochloa cordifolia*. Note the condensed inflorescence. Bars: 1 cm.

above the numerous leaf blades which are much smaller (5 to 20 cm long) and lanceolate than in the before mentioned species and originate from short petioles on multi-branching aerial shoots (except *M. monophylla* with only one leaf per aerial shoot).

- A similar growth form is found in *Marantochloa purpurea, M.* sp.1, *M. leucantha* (Fig. 2.3C), *M. filipes* and *M. congensis.* However, these species are taller and their inflorescences are hanging on slender axes at a height of 2 m. *M. cordifolia* (Fig. 2.3J) is comparable but the inflorescences are condensed and stand upright.
- In the climbing species of *Hypselodelphys, Trachyphrynium* and *Haumania* (Fig. 2.5I, J), the flowers are generally arranged in well exposed inflorescences at a height of 1 to 10 (-20) m. Especially in *Hypselodelphys* spp. and *Trachyphrynium braunianum* there is much space in front of the flower entrance facilitating access for the pollinators. Leaves are rather small (predominantly between 10 and 30 cm long).

Inflorescences (Table 2.2, p.51)

The inflorescences of the African Marantaceae are arranged terminally (Fig. 2.6A) and except in *Afrocalathea rhizantha* (Fig. 2.4B, C) and *Haumania* spp. (Fig. 2.5I) enriched by lateral partial inflorescences (lpi). Internodes (it) within the partial inflorescences can be either relatively long (e.g. *Marantochloa incertifolia, M. leucantha, M. purpurea;* Fig. 2.3C, D) often resulting in long and slender inflorescences or very short leading to highly condensed inflorescences (e.g. *Ataenidia conferta*, *Sarcophrynium brachystachyum* Fig. 2.3I) (Table 2.2). The proximal internodes between and within partial inflorescences are generally longer than the distal ones. Each partial inflorescence is a thyrse terminating in a flower-pair (T) (Fig. 2.6). It bears 2 ± 0.75 to 15.35 ± 8.13 bracts subtending one or up to eight flower pairs (paraclade) arranged in a drepanium. In *Marantochloa congensis* paraclades are highly variable (Fig. 2.6B–H). The internodes among and within the partial inflorescences are always arranged in a zigzag-shaped pattern. The size of the angles between consecutive internodes varies between species. Bracts are generally missing at branches of higher order except in *Ataenidia conferta*. Each lateral flower pair has usually one prophyll which is only missing in the genus *Thaumatococcus*.

Dependent on the number of partial inflorescences, bracts and flower pairs per bract the total number of flowers per inflorescence varies from on average between 6.73 ± 6.52 in *Marantochloa filipes* to 147.29 ± 106.09 in *Sarcophrynium schweinfurthianum*. However, the effective number of fertile flowers is much lower because of the abortion of buds (e.g. in *Hypselodelphys* spp., *Haumania danckelmanniana* and *Sarcophrynium schweinfurthianum*) and by damage through feeding insects (e.g. in *Hypselodelphys* spp., *Megaphrynium* spp.). The latter is especially high in *Halopegia azurea* in which usually all first flower pairs of all bracts are colonized by caterpillars so that only the second or third flower pairs come to flower. Only one flower pair per bract sets one to two fruits.

Phenology

Seasonal phenology (Table 2.3, p. 52)

Inflorescences of one species either come into bloom rather synchronously which leads to a short flowering period for the species concerned (e.g. one to two months in *Afrocalathea rhizantha* and *Marantochloa* sp.2) or they come into bloom sequentially leading to a flowering season of several months (e.g. *Hypselodelphys hirsuta, Megaphrynium macrostachyum, Sarcophrynium brachystachyum*).

During the observation months between September and February some species flower only during the rainy season from September to December and others only during the short dry season from January to February.

Flowering sequence

Flowering sequence within the inflorescence goes by branch order, i.e. the terminal unit starts flowering and then the remaining partial inflorescences follow successively. Within the partial inflorescences the flowering sequence is strictly acropetal along the main axis. However, in *Marantochloa congensis, M. incertifolia M. cordifolia* and *M.* sp.3 it overlaps with the flowering sequence of the lateral flower pairs resulting in a mixed flowering pattern.

The terminal flower pair is either the first flowering in the partial inflorescence (*Marantochloa congensis, M. incertifolia M. cordifolia, M*. sp.2, *M*. sp.3) or it flowers only shortly before the most distal lateral flower pairs (*Afrocalathea rhizantha, Ataenidia conferta, Haumania* spp., *Marantochloa leucantha, M. mannii,*

Figure 2.4: Growth form and flower type in co-occurring *Afrocalathea rhizantha* (A – C) and *Marantochloa* sp.2 (D – F). Bars: 1 cm.

Figure 2.5: Examples of pollination and fruit predation. (A – C) *Halopegia azurea*, (A) open flower in the morning; (B – C) closed flower with up-folded outer staminode in the afternoon. (D) *Thrinchostoma bicometes*. Note the frontal elongation of the head. (E) *Thrinchostoma bicometes* sucking nectar on *Halopegia azurea*. (F) *Megaphrynium gabonense*. Flower. ➔

M. monophylla, M. purpurea, M. sp.1*, Sarcophrynium* spp., *Trachyphrynium braunianum* and *Thaumatococcus* sp.1). In *Halopegia azurea* the tip of the partial inflorescence remains inhibited in the bud stage. In *Hypselodelphys* spp. and *Megaphrynium* spp. these tips generally fall off.

Inflorescence longevity (Table 2.2, p. 51)

The duration of flowering (phenology pattern) of an entire inflorescence depends on the number of flowers per inflorescence and the timing of flowering. Dependent on species there are two to 14 flowers open per day, i.e. 4 to 30 % of the total flower number per inflorescence. The two flowers of a pair develop predominantly simultaneously and only rarely successively. Six different patterns are found within the Marantaceae (Table 2.2: ph, phenological pattern):

- Species that have few flowers (< 20) per inflorescence (A) may
  - have numerous open flowers on consecutive days resulting in a short total flowering time of one to two weeks per inflorescence (Aa),
  - flower less frequently for one month (Ab) or
  - flower sparsely for two months (Ac).
- Species that have an intermediate number of flowers (20 to 100) per inflorescence (B) flower
  - daily for about two weeks only (Ba) or
  - more sparsely for one month (Bb).
- Species that have many flowers (> 100) per inflorescence (C) flower regularly for a long period of several months.

←(G) *Megaphrynium macrostachyum*. Flower. (H) *Xylocopa varipes* from ventral side with pollenload around the proboscis. (I) *Xylocopa negrita* on *Haumania danckelmanniana*. (J) *Haumania danckelmanniana.* Note the closed flower entrance with yellow nectar guides and conspicuous outer staminodes. (K) small red flea beetle (Alticini/Chrysomelidae) on flower of *Marantochloa congensis*. (L) *Hypselodelphys hirsuta.* Fruit with worm infection. (M) black beetle (Dryophtoridae) feeding on the ovary of *Hypselodelphys scandens* flower. Bars: 1 cm.

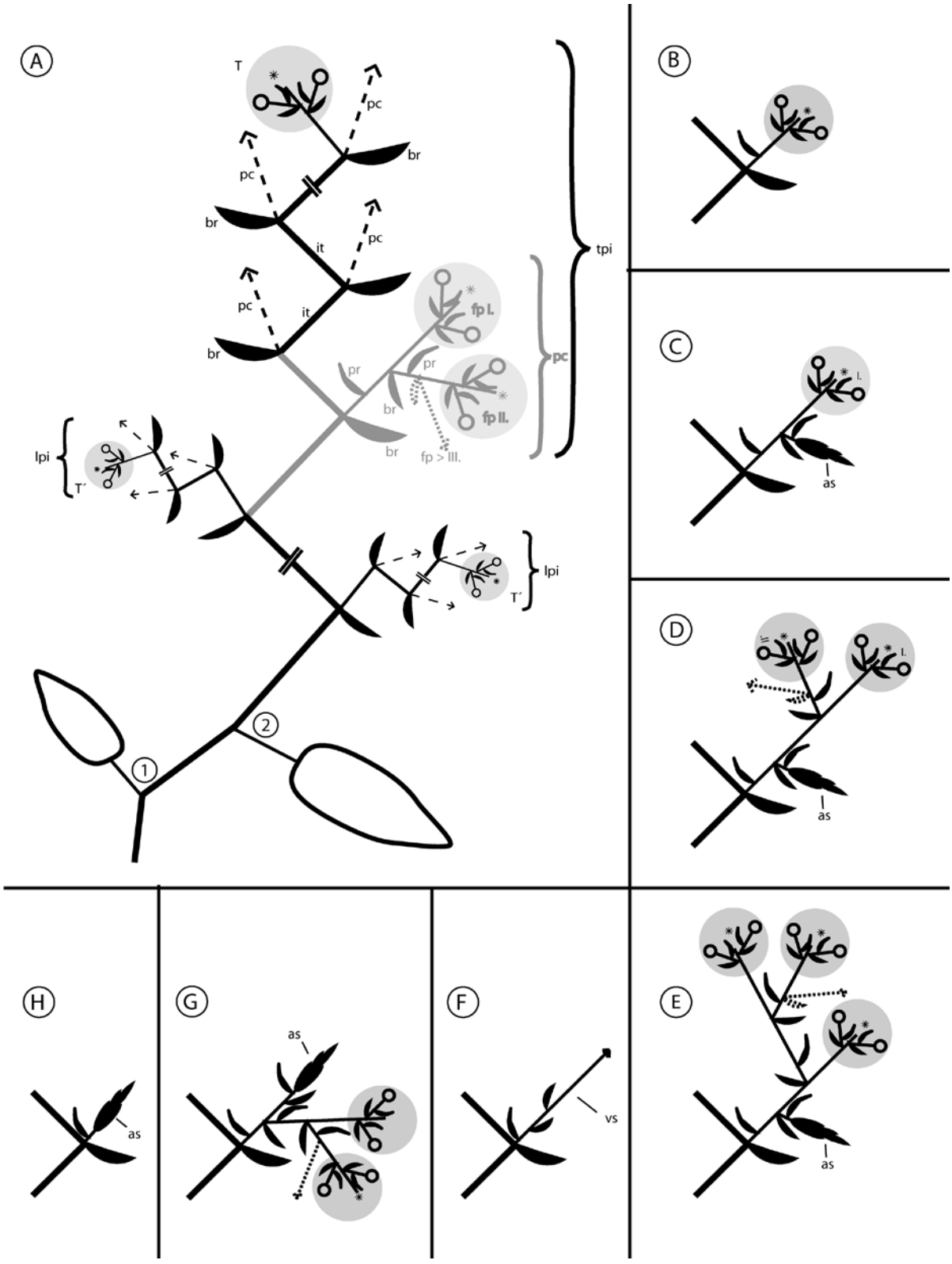


Figure 2.6: Basic inflorescence structure in African Marantaceae. (A) Schematical side view of an inflorescence composed of a terminal (tpi) and lateral partial inflorescences (lpi). Note that the axes of flower pairs are generally reduced on the plant. br, bract; fp, flower pair in paraclade (numbered by order - I., II.); it, internode; pc, paraclade; pr, prophyll (numbered by hierarchical order); pi, partial inflorescence; T, terminal flower pair of partial inflorescence; tpi, terminal and lpi, lateral partial inflorescence; 1, 2 encircled: positions of adventive shoots; dotted arrow, indicates the position of further flower pairs;➔

Daily flower phenology (Table 2.3, p. 52)

The individual flowers are open for one day only. Flowering starts more or less synchronously within the population of a given species but differs among species (Table 2.3). Usually, flowers open early in the morning (0600 to 0800 h). Some taxa (e.g. *Marantochloa cordifolia*) start to flower later in the day with a sequential flower opening from 0900 h to noon. The flowers usually wilt between 1600 and 1800 h. Exceptions are *Sarcophrynium brachystachyum* which starts wilting at around 1100 h by closing its petals in front of the flower entrance irrespective of whether it is pollinated or not, and *Afrocalathea rhizantha* that continues to flower until the next morning at about 0800 h. In most of the species flowers are shed in the evening, but in the dense inflorescences of *Ataenidia conferta, Marantochloa cordifolia* (Fig. 2.3J), *M. mannii* and *Afrocalathea rhizantha* (Fig. 2.4B) where the flowers have long tubes and the axes of a flower pair are shorter than the bracts they remain within the inflorescences. They are easily distinguished from young flowers by the colour and tissue turgescence. In *Marantochloa congensis, M. incertifolia* (Fig. 2.3D), *M. filipes, M. monophylla* and *M. sulphurea* flower abscission is independent of triggering the style. Flowers that have been triggered are regularly shed one to three hours afterwards, while flowers that have not been triggered are usually not shed before 1500 h.

In a few species (e.g *Haumania* spp., *Hypselodelphys* spp.) the lower side of the style turns brown after triggering. Only in *Haumania* spp. the brownish part of the style is directed towards the flower entrance and hence visible to the insects.

→*, no further growth at apical meristem; different thickness of axis indicate different orders; grey, flower pair. (B - H) *Marantochloa congensis.* Variable design of paraclades. (B) single terminal fp. (C) single terminal fp with lateral adventive shoot. (D) terminal fps arranged in a drepanium and lateral adventive shoot. (E) single terminal fp with laterally fp arranged in a drepanium and adventive shoot. (F) bract subtends vegetative shoot only. (G) adventive shoot with lateral fps arranged in a drepanium. (H) bract subtends vegetative shoot.

2.4.2 FLORAL DIVERSITY AND ATTRACTANTS

2.4.2.1 Floral diversity (Table 2.4, p.53)

The African Marantaceae display a high floral diversity. Nevertheless, certain characteristics in floral size and pigmentation, distance to the nectar, floral tube orientation and presence or absence of nectar guides and conspicuous outer staminodes allow the establishment of four distinct flower types:

- *Hypselodelphys hirsuta*–type (Fig. 2.7A, E): Eleven species (Table 2.3) belong to this type. They have generally large bluish (Fig. 2.5A), rose or violet-white (Figs 2.5F, 2.9B-H) flowers with horizontally arranged tubes and conspicuous outer staminodes. Only in *Megaphrynium gabonense* (Fig. 2.5F) and *M. macrostachyum* (Fig. 2.5G) the outer staminodes are highly reduced. They are small and lanceolate. The flowers of *M. macrostachyum* can be either violet white or yellow (see Fig. 2.5G). Conspicuous yellow nectar guides are formed by the trigger appendage or the petaloid appendage of the fertile theca, the yellow hooded staminode or yellow spots on the fleshy staminode. No scent is discernable. The average length of the fleshy staminode in this type is 15.55 ± 3.63 mm, the average distance to the nectar 9.32 ± 2.35 mm (n = 48) (Fig. 2.2, Table 2.4).
- *Haumania danckelmanniana*–type (Fig. 2.7B, F): The three species of this type have white or dark violet flowers with large outer staminodes (Fig. 2.5J). *Haumania* species have conspicuously yellow nectar guides originating from the petaloid appendage of the fertile theca and the fleshy and hooded staminodes. The trigger appendage completely obstructs the flower entrance and is made of a firm tissue (Figs 2.5H, 2.7F). The flowers exhibit a strong sweet scent. The average length of the fleshy staminode is 9.83 ± 0.92 mm, the average distance to the nectar is 2.17 ± 0.41 mm (n = 6) (Fig. 2.2, Table 2.4).
- *Marantochloa congensis*–type (Fig. 2.7C): The group comprises eight species that have small (less than 10 mm in length) white flowers (Fig. 2.9D, E, H, I, L) and *Marantochloa filipes* with rose flowers (Fig. 2.9L). Except the size, floral morphology is equal to the *Hypselodelphys hirsuta*-type with horizontally orientated floral tubes, relatively large outer staminodes and a yellow trigger as nectar guide. No scent is discernable. The average length of the fleshy staminode

in this type is 6.83 ± 1.69 mm, the average distance to the nectar 4.30 ± 1.05 mm (n = 23) (Fig. 2.2, Table 2.4).

- *Thaumatococcus daniellii*-type (Fig. 2.7D): The nine species belonging to this type have generally large yellow (Figs 2.3F, 2.9A), yellow to red (Fig. 2.9C) or white flowers (Figs 2.4C, F, 2.9B) with long thin floral tubes. The latter are usually longer than 10 mm except in *Marantochloa mannii, Megaphrynium trichogynum* and *Marantochloa* sp.2 which have a tube length of 4 to 6 mm. Flowers are vertically arranged and have no nectar guides (except *Marantochloa cordifolia, Marantochloa* sp.2) and no discernable scent. *Ataenidia conferta* and *Marantochloa mannii* have white flowers surrounded by conspicuous red bracts. The outer staminodes are usually large except in *Megaphrynium trichogynum* and *Thaumatococcus* spp. where they are highly reduced providing the flower with a superficial actinomorphic symmetry. The tissue of these flowers is exceptionally hard and rubber-like. *Megaphrynium trichogynum* has hanging flowers with straight petals that are not bent outwards or even reflexed as in all other species. The average length of the fleshy staminode is 18.11 ± 4.49 mm, the average distance to the nectar 7.55 ± 3.63 mm (n = 40) (Fig. 2.2, Table 2.4).

The average lengths of the fleshy staminode and the distance to the nectar (Fig. 2.2: a, b) differ significantly among the types except between the *Hypselodelphys hirsuta* and the *Thaumatococcus daniellii*-type (Fig. 2.8; Table 2.5, 2.6).

2.4.2.2 Nectar reward (Table 2.7, p.56)

A few hours before anthesis nectar production is initiated. In the morning before visitation nectar is found up to the proximal end of the trigger appendage (see Fig. 2.2). Nectar volume is significantly correlated with floral tube size (Spearman-Rho correlation coefficient = 0.724, n = 76, P < 0,001) and ranges from less than 0.50 µl to 10 µl per flower.

Nectar sugar concentration ranges between 25 and 40 %. The values for nectar concentration are significantly different between all types except between the *Hypselodelphys hirsuta*- and the *Marantochloa congensis*-type (Fig. 2.8; Table 2.6). The highest concentration is found in the *Haumania danckelmanniana*-type (37.41 ± 2.49 %), followed by the *Hypselodelphys hirsuta*-type (33.34 ± 4.11 %), the *Marantochloa congensis*-type (31.25 ± 2.14 %) and the *Thaumatococcus daniellii*-type (25.69 ± 3.01 %).

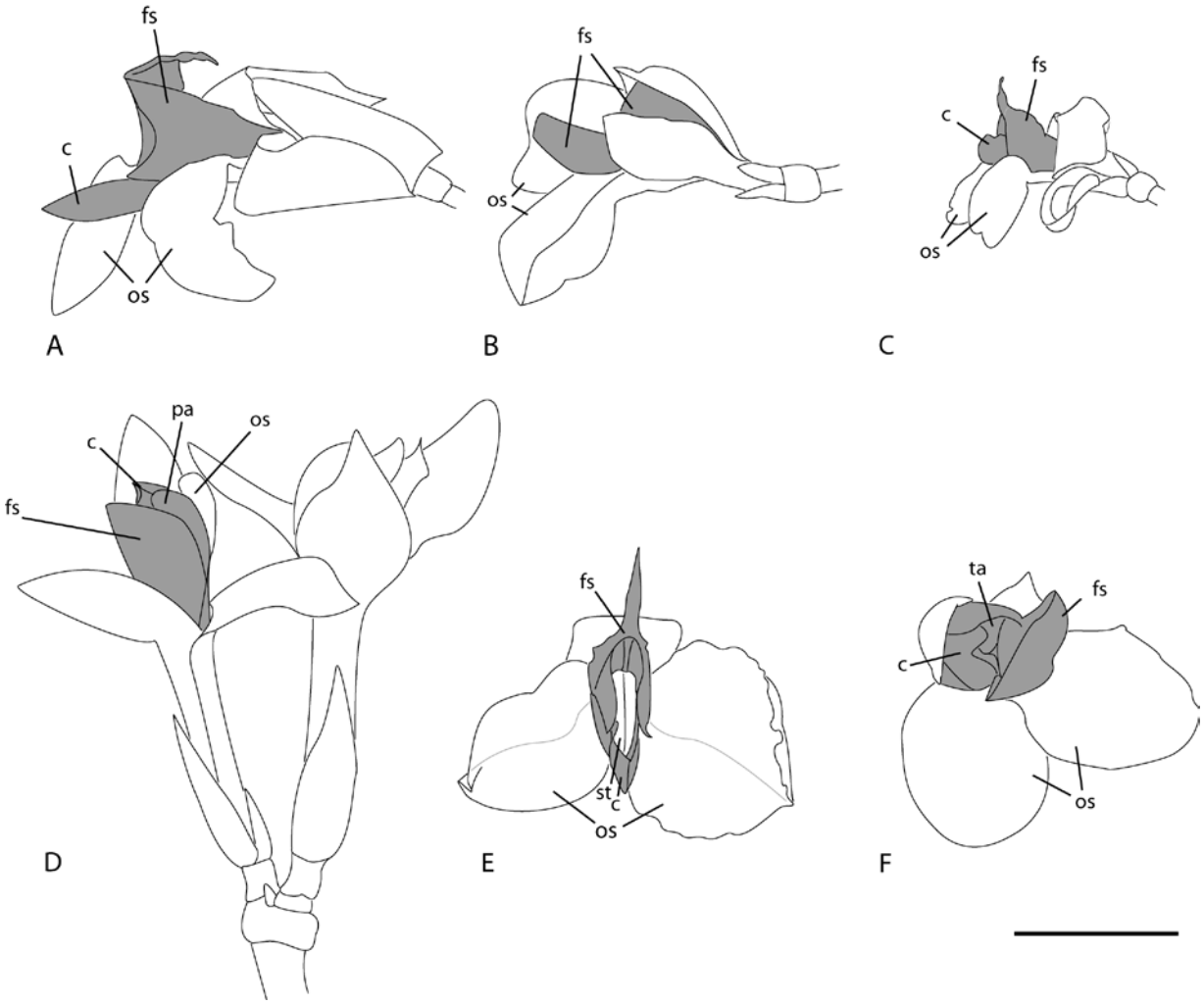


Figure 2.7: Floral types represented by *Hypselodelphys hirsuta* (A, E), *Haumania danckelmanniana* (B, F), *Marantochloa congensis* (C) and *Thaumatococcus daniellii* (D). A–D, side view; E, F, frontal view. c, functional unit composed of the style enveloped by the hooded staminode and the petaloid appendage of the fertile theca; fs, fleshy staminode; os, outer staminode; pa, petaloid appendage of fertile theca; st, style; ta, trigger appendage of the hooded staminode; grey, organs of inner androecial whorl. Bar: 1 cm.

2.4.2.3 Pollen load (Table 2.7, p. 56)

The thecae open about 12 to 24 hours before anthesis (Table 2.3) thereby transfer pollen to the pollen plates of the styles. The pollen/ovule-ratio usually ranges between 34 : 1 and 138 : 1 per flower. Solely, the three *Sarcophrynium* species are a remarkable exception. They have only about 2.5 pollen grains per ovule. These pollen grains are the largest found in the African Marantaceae with a diameter of about 0.2 mm compared to about 0.1 mm in all other investigated species. The number of pollen grains per theca differs significantly between the floral types

(Fig. 2.8; Tab. 2.6). The highest values of pollen grains per theca are found in the *Haumania danckelmanniana*-type (393.18 ± 46.59) followed by the *Thaumatococcus daniellii*-type (360.51 ± 161.44), the *Hypselodelphys hirsuta*-type (225.78 ± 109.22) and the *Marantochloa congensis*-type (187.88 ± 79.39).

The p/o-ratio of the selected American and Asian species ranges on average between 78.0 and 410.75 (Table 2.8).

2.4.3 PLANT ANIMAL INTERACTION

Bees and birds were observed to trigger and thus to pollinate the African Marantaceae (Table 2.4). Plant species that were observed at different localities and in different years (*Haumania danckelmanniana, Hypselodelphys hirsuta, Marantochloa filipes, Megaphrynium macrostachyum*) always show the same pollinators or pollinator guild. Butterflies and further unidentified insects also visited the flowers but were never found to trigger a flower.

Within the bees, three groups can be distinguished according to the morphometric data of their mouthparts, body lengths and head width (Tab. 2.9). The data of mouth parts and head width are significantly different between the groups at a level of $p < 0.05$ (Kolmogorov Smirnov test) and correlated with the distance from the floral entrance to the nectar (Spearman-Rho correlation coefficient = 0.822, N = 19, $P < 0.001$). Small bees (*Thrinchostoma, Allodapula*) are characterized by a narrow head and body (head: 2.3 ± 0.2 mm; n = 9) and short mouthparts (3.80 to 6.35 mm), medium-sized bees (*Amegilla, Thrinchostoma*) by slightly longer mouthparts (10.00 to 13.90 mm) and by heads and bodies that are at least twice as broad as in the small bees (5.0 ± 0 mm; n = 6). Large and heavy bees (*Xylocopa*) have comparable head width (6.00 ± 0 mm; n = 2) and mouthparts lengths (10 mm; n = 2) whereas *Megachile* have extremely short mouthparts (0.3 ± 0 mm; n = 2). The fourth group of pollinators, the sunbirds, has beaks representing the longest mouthpart in the group of pollinators identified (~ 20 mm). They only visited the large flowers of the *Hypselodelphys hirsuta*- and *Thaumatococcus daniellii*-type.

All pollinator groups are active from sunrise to sunset. No constant activity pattern with higher or lower frequencies at special hours of the day can be defined. Instead, visitation is found to be highly variable within and between different days and localities (see Table 2.4).

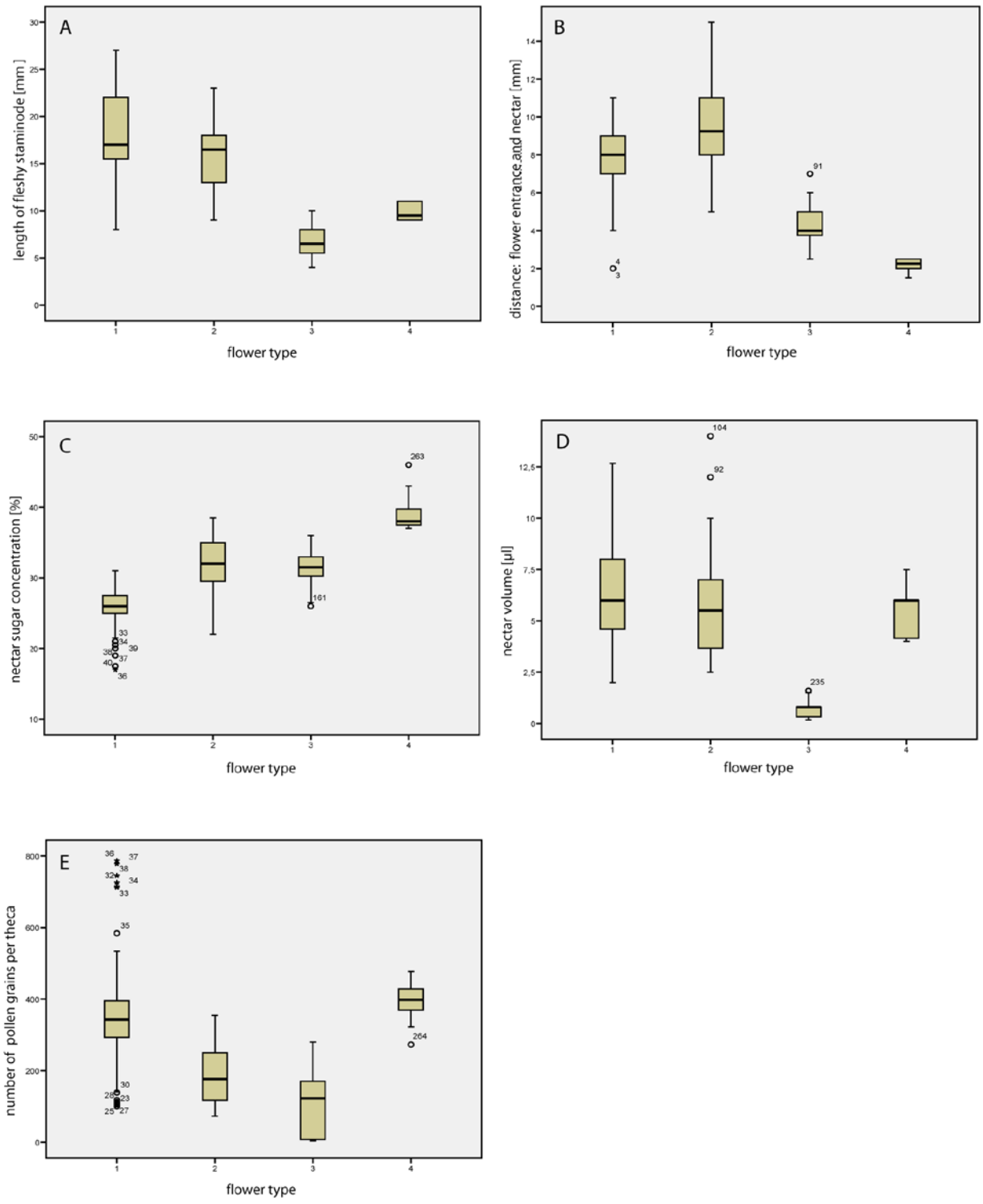


Figure 2.8: Flower morphological and ecological data summarized by flower type (1, *Thaumatococcus daniellii*-type. 2, *Hypselodelphys hirsuta*-type. 3, *Marantochloa congensis*-type. 4, *Haumania danckelmanniana*-type). (A) length of fleshy staminode. (B) distance between flower entrance and nectar. (C) nectar concentration. (D) nectar volume. (E) pollen grains per theca.

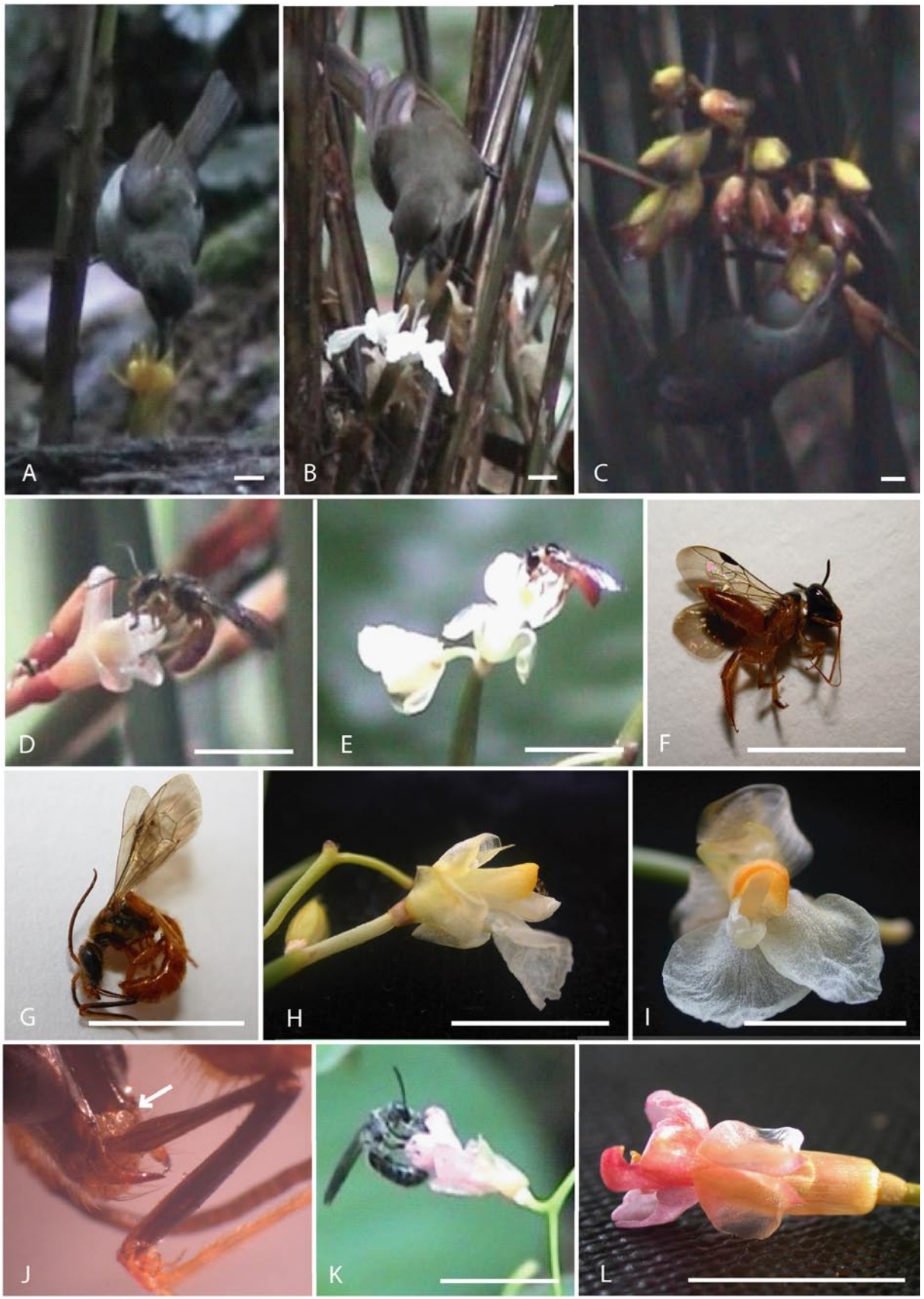


Figure 2.9: Pollination by birds and small-sized bees. (A–C) sunbird pollination in: (A) *Thaumatococcus* sp.1. (B) *Afrocalathea rhizantha.* (C) *Megaphrynium trichogynum*. Note hanging flowers and non reflexed petals. (D) *Thrinchostoma* sp.4 nectar feeding on ➔

2.4.3.1 Bees

Bees pollinate flowers of the *Hypselodelphys hirsuta*-, *Marantochloa congensis*– and *Haumania danckelmanniana*-type that provide a landing platform with their large and conspicuous outer staminodes (Fig. 2.7). Flowers that are twisted and present their staminodes in an unusual position are less frequently visited. While perching on the staminodes the bees are always forced into the same position so that they can get pollen precisely deposited into the proboscidial fossae (Figs 2.9J, 2.11). However, in *Hypselodelphys* flowers pollen is occasionally found on the fleshy staminode indicating that not all pollen grains are removed by the *Amegilla* bee. In *Megaphrynium gabonense* and *M. macrostachyum* outer staminodes are lacking. *Amegilla* bees either settle on the back-folded petals or hover in front of the flowers when sucking nectar. The large carpenter bees (*Xylocopa* spp.) have to use the second flower of a pair as a landing and perching site. They first suck the nectar from the one flower and then turn around to feed from the other.

Medium-sized bees

- *Amegilla vivida* (Smith, 1879): The bee (Fig. 2.10A) was exclusively observed on flowers of the *Hypselodelphys hirsuta*-type (except *Halopegia azurea*). This bee species is a very fast flying insect, highly aware of any disturbance from its surrounding. Occasionally even small insects drive the bees away. In general, *Amegilla* bees visit all open flowers of an individual plant thereby flying the shortest distances. To find further open flowers, they also visit not flowering inflorescences that had open flowers a few hours or even a day before. The bees extend their proboscis (glossa ~ 4 - 5 mm long) still in flight and hover in front of the flower before landing on the outer staminodes (Figs 2.10B–D, 2.11). During the landing process the proboscis is inserted into the flower tube and then the head is pushed forward until the fleshy staminode

← *Sarcophrynium prionogonium*. (E) *Allodapula ornaticeps* nectar feeding on *Marantochloa monophylla*. (F) *Allodapula ornaticeps*. (G) *Thrinchostoma* sp.1. Note long three-parted proboscis. (H–I) lateral and frontal view of flower of *Marantochloa congensis*. (J) pollen grains (arrow) hidden in the proboscidial fossae of *Thrinchostoma sp*.1. (K) *Thrinchostoma* sp.3 nectar feeding on *Marantochloa filipes*. (L) flower of *Marantochloa filipes*. Bars: 1 cm.

circumvents further penetration (Fig. 2.11). When the bee's proboscis touches the trigger appendage and releases the explosive movement of the style the bee sometimes startles for a moment, retracts its proboscis momentarily but keeps on foraging by further extending the galea to reach the nectar.

Handling time per flower is rather short with an average of 3.50 ± 3.90 seconds (n = 46; Table 2.10). Individual flowers are visited repeatedly during the day by different *Amegilla vivida* individuals. The style is sometimes only triggered

after up to eight visits, but, almost all flowers are released by noon. Nevertheless, insects continue to visit the flowers irrespectively until dusk.

Sometimes the bees carry conspicuous yellow pollen loads on their hind legs which they must have collected on other species, e.g. on *Decellandra barteri* (Melastomataceae) and *Bertieria* sp. (Rubiaceae).

- *Thrinchostoma bicometes* (Enderlien, 1903): The bee (Fig. 2.5D, E) visits *Halopegia azurea* at slow running creeks and swamps. This bee is also a fast flier with a long but thinner body than *Amegilla vivida* (Table 2.9). It constantly moves back and forth between individual plants at a height of 20 cm above the water level. Before landing it flies around in the given *Halopegia* population. Then it abruptly lands on the spacious lower outer staminode of a selected flower, inserts its proboscis into the floral tube and sucks the nectar. It stays on a flower for a few seconds (n = 4, 12.25 ± 6.65 sec; Table 2.10). Before leaving it has to lean backwards to fully extract the three-part proboscis that has to be folded up into the proboscidial fossae underneath the long `snout´ (Fig. 2.5D). The style is released immediately during the first visit. Triggering is accompanied by a short tentative upwards movement of the lower outer staminode. After triggering this outer staminode starts to slowly fold up. After about one hour the flower entrance is totally closed and no further insect visit is possible (Fig. 2.5A - C).

Figure 2.10: Flowers pollinated by *Amegilla vivida.* (A) side view of the bee. (B – D) The bee on nectar search in front of a *Hypselodelphys poggeana* flower. Note the extended proboscis in (C) and the large pollen load on the hind limbs in (B - D). Note the high similarity in flower size, shape and colour in *Hypselodelphys poggeana* (B), *H. hirsuta* (E)*, H. violacea* (F)*, H. scandens* (G) and *Trachyphrynium braunianum* (H). Bars: 1 cm.

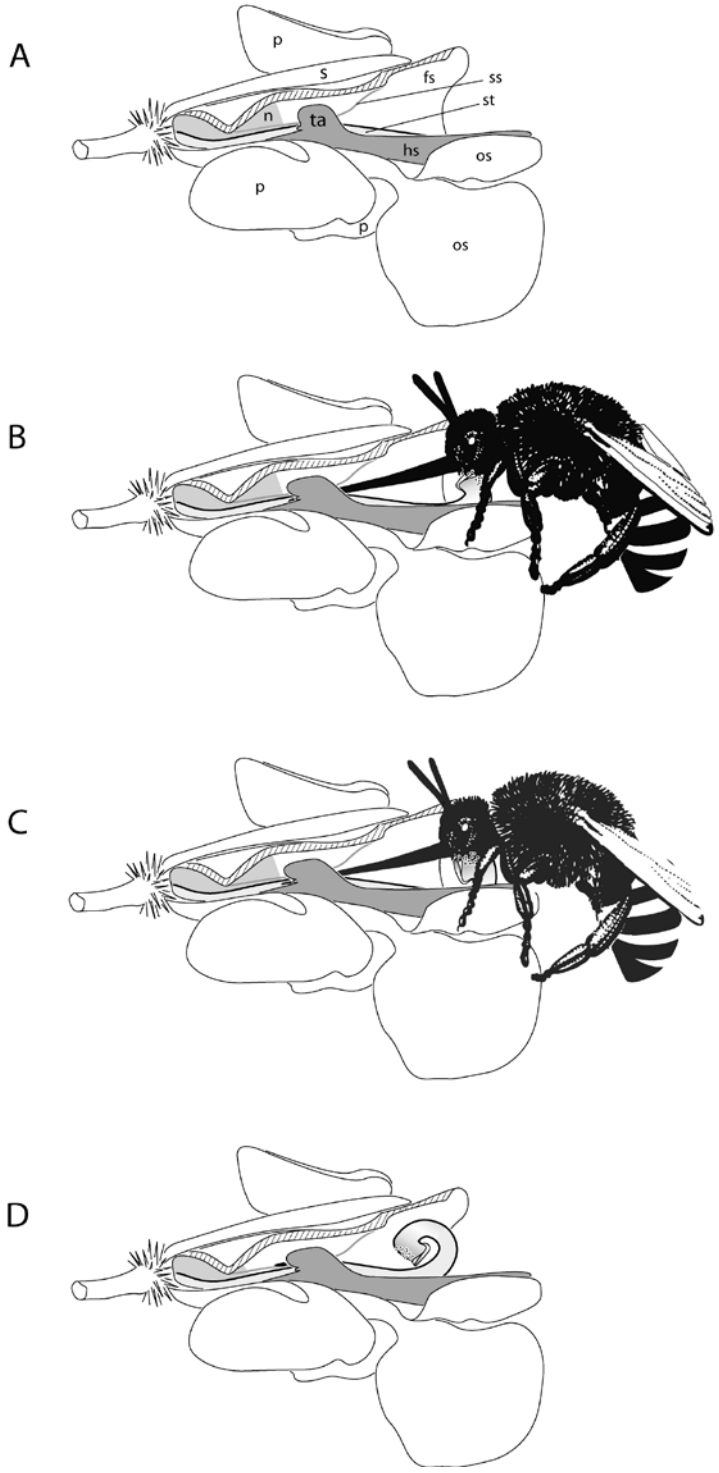


Figure 2.11: Bee-pollination exemplified by *Marantochloa purpurea* and *Amegilla vivida*. (A) Flower before insect visit (hatched = cut open to allow insight into floral tube): style (st) straight, held under tension by the hooded staminode (hs) bearing the trigger appendage (ta). Stiff swelling (ss) of the fleshy staminode (fs) blocking access to the nectar (n, light grey); os, outer staminode; p, petal; s, sepal. (B) Style release after the trigger appendage is deflected by the pollinator; pollen transfer from the proboscidial fossae of the insect into the stigmatic cavity (pollen reception). (C) Pollen from the pollen plate at the back of the stylar head is placed into the proboscidial fossae of the insect (pollen deposition). (D) After visitation the style is completely and irreversibly rolled up inside the fleshy staminode.

Large bees

- *Xylocopa nigrita* (Fabricius, 1775) (Fig. 2.5I) and *Xylocopa varipes* Smith, 1854 (Fig. 2.5H): The bee visits *Haumania danckelmanniana* and *Megaphrynium gabonense. Xylocopa* bees are large (Table 2.9) and heavy and often the entire inflorescence moves under their weight when they land and pollinate the flowers. Handling time for a single flower takes about five seconds (n = 45, 4.06 ± 2.09 sec, range: 2 to 10 sec; Table 2.10). In *Haumania danckelmanniana* the bees hold onto the external staminodes while pushing their proboscis into the flower. They visit up to 10 flowers per minute and stay up to 10 minutes in a single *Haumania danckelmanniana* plant or in a large population of *Megaphrynium gabonense* flying from one inflorescence to the next. Thereby, *Xylocopa nigrita* is faster and more attentive than *X. varipes*. A heavy pollen load accumulates around the whole proboscis of the *Xylocopa* bees that was never observed to be cleaned during visiting subsequent flowers (Fig. 2.5H). An unidentified *Xylocopa* species has also once been documented visiting *Ataenidia conferta* flying from one flower to the next probably pollinating them.

- *Megachile* spp.: These bees visit the same species as the *Xylocopa* bees. The slightly smaller *Megachile* sp.1 was observed on *Megaphrynium gabonense*, the larger *Megachile* sp.2 on *Haumania danckelmanniana* (Table 2.4). The bees are of an intermediate body size between *Amegilla* and *Xylocopa* and have extremely short mouth parts (Table 2.9). The frequency of visitation was highly variable in Makokou and the bees were totally absent in Monts de Cristal. The individuals fly from one flower to the next and stay for several minutes in one *Haumania danckelmanniana* individual. Their handling per flower takes on average eight seconds (n = 11, 8 ± 2.68 sec; Table 2.10). Triggering of the flowers could not be observed.

Small bees

Several *Thrinchostoma* species (Halictidae; Fig. 2.9D, G, K) and *Allodapula ornaticeps* (Apidae; Fig. 2.9E, F) visit the small flowers of the *Marantochloa congensis*-type. The bee species have a long proboscis compared to their body length (Table 2.9). Consequently, they have to lean back to retract and fold up their proboscis after nectar sucking. Before leaving the flower they brush their proboscis

without however removing all pollen grains from their proboscidial fossae (Fig. 2.9J). Handling time of the small insects is on average 11.41 ± 11.39 seconds (n = 94; Table 2.10). *Thrinchostoma* spp. have occasionally been observed carrying pollen loads on their hind limbs originating from other food plants.

While individual *Sarcophrynium brachystachyum* and *S. prionogonium* flowers are visited repeatedly during the day, flowers of *Marantochloa incertifolia, M. monophylla, M. congensis* (Fig. 2.9H, I) and *M. filipes* (Fig. 2.9L) are visited only once. They are all triggered on the first visit.

2.4.3.2 Sunbirds

Sunbirds (Fig. 2.9A-C) (probably the Olive Sunbird *Cyanomitra olivaceus,* Nectariniidae) are the exclusive visitors of the *Thaumatococcus daniellii*–type flowers (Fig. 2.12). Only on *Marantochloa cordifolia* an *Amegilla* sp. was once observed. The

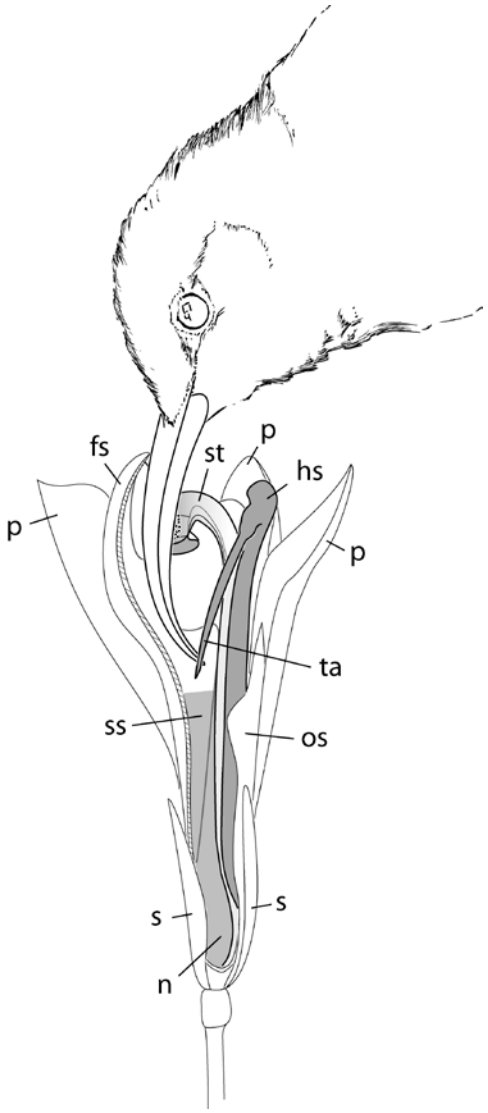


Figure 2.12: Pollination of the vertically-arranged bird-pollinated *Thaumatococcus daniellii.* Flower is cut open to allow view inside the floral tube (hatched). The Olive Sunbird (*Cyanomitra olivaceus* cf.) intrudes its beak into the flower tube thereby deflecting the trigger appendage which leads to the rolling-in movement of the style and the subsequent pollen deposition onto the beak. The nectar is sucked by elongating the tongue. fs, fleshy staminode; hs, hooded staminode (dark grey); n, nectar (medium grey); os, outer staminodes; p, petal; s, sepal, ss, stiff swelling; st, style (light grey); ta, trigger appendage; dots, pollen grains.

birds are faster than the insect pollinators with a handling time per flower of less than a second to a maximum of two seconds (Table 2.10). Within one minute they enter a given population, choose a few flowers, hold on to a nearby petiole or hover in front of the flower, intrude their beak into the tubes, suck the nectar, change to the next flower and finally leave the population rather quickly. The birds are able to reach the nectar from any side of the flowers and therefore the pollen is not deposited precisely in one spot on the beak but all around it [see also supplementary information - CD].

In *Ataenidia conferta* leftover of pollen can sometimes be found on the fleshy staminodes. Occasionally, the birds clean their beak after having visited all flowers of an individual unit. Pollination efficiency tests on *Afrocalathea rhizantha* yield a definite fruit-set of 64.70 % after visitation by birds (n = 17).

Visitation rate is highest at rich blooming shoot systems where the birds visit all open flowers consecutively. However, the birds are also capable of regularly finding the single, small and inconspicuous white flowers of *Marantochloa* sp.3 hidden between the large leaves and they visit and release *Afrocalathea rhizantha* flowers early in the morning before they are entirely open.

Megaphrynium trichogynum is the only species with hanging flowers and floral tubes elongated by the petals (Fig. 2.9C). As their inflorescences are arranged near the ground the birds perch on the petioles of the densely arranged leaves, pull the flower towards them and stick the beak deep into the flower tube. As already observed in *Hypselodelphys* spp. visited by *Amegilla vivida* styles are not always triggered.

The sunbirds also visit and subsequently trigger the flowers of *Megaphrynium gabonense* and of *Hypselodelphys* species which are predominantly pollinated by *Amegilla* bees. As the inflorescence axes in these species are strong they provide a perching site for the birds or hold the flowers in place when the birds hover in front of them while introducing their beak and sucking nectar. The birds occasionally visit and probably pollinate flower of *Haumania danckelmanniana* and have once been seen on *Sarcophrynium schweinfurthianum* while perching on nearby shoots. They also visit flowers of other plant species at the same locality (e.g. *Costus* spp./ Costaceae, *Afromomum* spp./ Zingiberaceae).

2.4.3.3 Pollinator visitation rate

The visitation rate by pollinators differs between flower types. It is higher in those types that are predominantly bee pollinated (*Hypselodelphys hirsuta*-type: 161 hours of observation, 1,66 visits per hour; *Marantochloa congensis*-type: 153 hours of observation, 1,38 visits per hour; *Haumania danckelmanniana*-type: 31,5 hours of observation, 4,25 visits per hour) than in the exclusively bird pollinated *Thaumatococcus daniellii*-type (108 hours of observation, 0.68 visits per hour).

2.4.3.4 Nectar robbers

Various species of butterflies often stay for several minutes to even half an hour on a flower with their proboscis extended into the flower tube but they have never been observed to trigger any flower. Small flies and midges also visit the flowers but are likewise unable to release the style.

Piercing caused by *Lipotriches* sp. (Halictidae) is extremely severe in *Marantochloa* sp.1. At 0800 h already 95% of the open flowers have little holes at the base of the floral tube. Nevertheless all flowers are frequently visited by *Amegilla vivida* throughout the day. Evidence of nectar robbing is also found in *Haumania danckelmanniana, Hypselodelphys hirsuta* and *Marantochloa cordifolia.*

In *Megaphrynium trichogynum* the heads of wasps are found clamped between style and fleshy staminode. The wasps are obviously decapitated by the fast and strong movement of the style.

2.4.3.5 Ants

Different ant species suck the nectar of all Marantaceae. They were observed roaming inside the flowers but without triggering the style. Additionally they are found on the extrafloral nectaries of the bracteoles just below the flowers in species of the genera *Hypselodelphys, Megaphrynium, Sarcophrynium, Thaumatococcus* and *Trachyphrynium*. Some ants build nests on inflorescences of *Sarcophrynium brachystachyum* leaving only the flowers sticking out. Ants tend to react to disturbance by moving towards and on intruders, although they apparently have no efficient means to avert them.

2.4.3.6 Beetles

A small red flea beetle (Alticini/Chrysomelidae) feeds on the outer staminodes of *Marantochloa congensis, M. incertifolia, M. monophylla* and *M.* sp.1. The flowers remain untriggered but lose attractiveness. No bees are found on flowers visited by beetles. A second beetle (Dryophtoridae) was observed to feed on the ovary of open *Hypselodelphys* flowers. This causes the flowers to drop down.

2.4.4 BREEDING SYSTEMS AND FRUIT-SET

2.4.4.1 Breeding system

Self-pollination experiments prove the self-compatibility of all investigated species (Table 2.11). *Marantochloa leucantha* and *Halopegia azurea* are autogamous as verified by the bagging experiments.

2.4.4.2 Fruit-set (Table 2.11, p.59)

Natural fruit-set in the African Marantaceae ranges between 2 and 35 %. Cross-pollination experiments generally result in a higher fruit-set than under natural conditions. The low fruit-set is in part influenced by fruit predators especially by feeding worms and insects (Fig. 2.5K-M). Fruit-set in *Afrocalathea rhizantha* appears to be positively correlated with the rate of visitation and triggering. In Makokou at two random occasions 46.35 % (n = 151) and 40 % (n = 55) of all flowers were triggered until the evening. The overall fruit-set of 10.75 % in this region was much lower than in Monts de Cristal where on three observation days (n = 10, n = 8 and n = 11 flowers) 100 % of flowers were triggered and the overall fruit-set in the respective population was 44.43 %. The example illustrates that there is a large discrepancy between triggering and successful fruit-set. This was also documented in *Ataenidia conferta* at Makokou. The percentage of triggered flowers on three different days was 74.13 % (n = 58 / 18 inflorescences), 62.9 % (n = 62 / 29 inflorescences) and 84.95 % (n = 113 / 26 inflorescences). However, fruit-set did not exceed 11 %. In a pollinator efficiency test on *Afrocalathea rhizantha* sunbird visitation yielded a fruit-set of only 64.70 % (n=17), while hand pollination resulted in 93.33 % (n=30).

Fruit-set seems to be further correlated with fruit size. Species of the genera *Haumania, Hypselodelphys* and *Thaumatococcus* (fruit size about 4 cm) show a clear lower fruit-set than species with small fruits (e.g. *Afrocalathea rhizantha,*

Marantochloa filipes, M. purpurea, M. sp.2, *Trachyphrynium braunianum*, Table 2.11). Self-pollination experiments indicate that large fruits tend to be aborted in a premature stage. In *Hypselodelphys* spp. and *Thaumatococcus* sp.1 fruits were aborted at a diameter of 10 mm, in *Megaphrynium* spp. at a diameter of 5 mm.

Finally, natural fruit-set is correlated with the breeding system. The highest percentage of fruit-set is found in the two autogamous species *Marantochloa leucantha* and *Halopegia azurea* with 31.16 % and 35.17 %, respectively.

No fruit-set was recorded in *Marantochloa cordifolia* and *M.* sp.1 though the flowers were rarely (*M. cordifolia)* and frequently visited (*M.* sp.1*)* by *Amegilla* bees. Pollen grains in *M.* sp.1 appeared less turgescent than in all the other species. Only one fruit per population was found in *Marantochloa* sp.3 although flowers were regularly triggered by sunbirds. In *Marantochloa congensis* only one or two fruits per population were found.

2.4.4.3 Fruits and seeds

The fruits of the African Marantaceae (Figs 2.2, 2.13) are either nuts in *Afrocalathea, Halopegia*, *Hypselodelphys*, *Marantochloa,* capsules in *Trachyphrynium braunianum* and *Marantochloa filipes* or berry-like nuts in *Sarcophrynium*, *Megaphrynium* and *Thaumatococcus*. The fruit of *Afrocalathea rhizantha* is here described for the first time. It is 10 to 20 mm long, lanceolate and green with a smooth surface producing one to three white seeds (Fig. 2.13C, D). The fruits persist on the plant and are even found on wilted inflorescences on the ground.

Fruit surface is usually smooth with a few hairs except in *Hypselodelphys* and *Haumania* where the surface shows very short more or less prominent spines (Fig. 2.13G, H). Fruit colour varies between the species (Table 2.12) and changes during maturation from green to orange in *Trachyphrynium braunianum*, from yellow to yellow/rose/red in *Marantochloa filipes* and from brown to red in *Thaumatococcus* sp.1 (Fig. 2.13O, P).

Seed size ranges between 5 and 35mm in length. Seed colour varies among species and fruit types (Table 2.12). They are adhered to or embedded into a variety of different effigurations whose origin is still unknown. These effigurations are white and small restricted around the funiculus in all *Afrocalathea, Halopegia, Marantochloa, Hypselodelphys* and *Trachyphrynium* species. Only in *Marantochloa filipes* it is conspicuously red coloured contrasting with the black seed (Fig. 2.13F). In *Ataenidia*

conferta it forms a long pointed appendage (Fig. 2.13A). In *Sarcophrynium* and *Thaumatococcus* the seeds are embedded in a glibbery substance (Fig. 2.13M) and in *Megaphrynium* long fruity strands wrap around the seeds (Fig. 2.13J). In *Trachyphrynium braunianum* the effiguration is large conspicuously white and hard contrasting with the black seed and the orange carpel at maturation (Fig. 2.13K, L). The number of seeds per fruit ranges from one to three with almost equal percentages (Table 2.12). An exception is *Halopegia azurea* that regularly produces just one seed per fruit. The time to fruit maturation takes one to two or even three months and is correlated to fruit size, i.e. the larger the fruit the longer it takes to reach fruit maturity. However, the completion of fruit growth does not necessarily indicate fruit maturation. In *Thaumatococcus* sp.1 young fruits are brown containing white seeds with a soft sarcotesta. At maturity weeks after having reached their final size they turn red now containing black seeds with a hard sarcotesta (Fig. 2.13P). An equal development has been observed in *Marantochloa filipes* (Fig. 2.13F).

In all species the fruits can sometimes be found on the ground just beneath individual plants. Seedlings have been found in *Ataenidia conferta, Halopegia azurea, Marantochloa* sp.2 and *Sarcophrynium schweinfurthianum*.

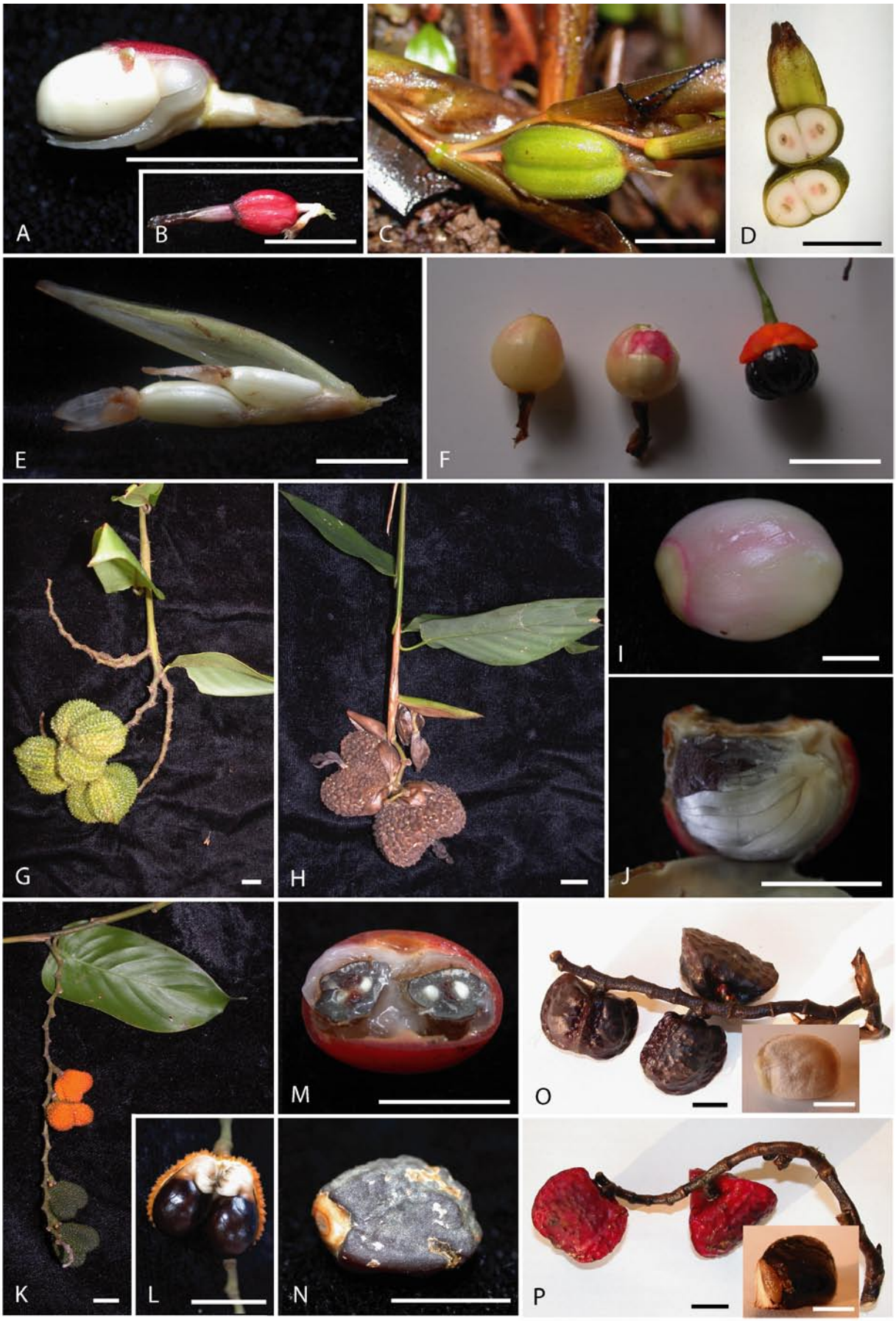


Figure 2.13: Fruits and seeds: (A - B) *Ataenidia conferta*. Note long white seed appendage. (C – D) *Afrocalathea rhizantha*. (E) *Halopegia azurea*. Fruits have always only one seed. ➔

2.4.4.4 Vegetative reproduction

All African Marantaceae are able to reproduce vegetatively via rhizomes. In addition all species from the genera *Ataenidia* and *Marantochloa* produce adventive shoots located in the vegetative leaf axils except *M. leucantha* and *M. filipes*. The production of these shoots is most vigorous in *Marantochloa cordifolia*. Further adventive shoots are produced at the base of the inflorescence in *Marantochloa congensis, M. incertifolia*, *M. monophylla* and *M. sulphurea* or within the inflorescence in *M. congensis* (Fig. 2.6C–H).

→ (F) fruits of *Marantochloa filipes:* young fruit closed and opened and mature fruit. Note colour contrast of black seed and red effiguration in mature fruit. (G) *Hypselodelphys hirsuta.* Note large size of fruits and highly structured fruit surface. (H–I) fruit and seed of *Haumania danckelmanniana*. (J) *Megaphrynium macrostachyum.* Note fruity strands around seeds. (K–L) *Trachyphrynium braunianum*. Note colour change from young (green) to mature (red) fruits and white effiguration in mature fruit. (M–N) *Sarcophrynium schweinfurthianum*. Cut fruit and seed. Note dry red pericarp and glibbery substance around the dark seeds. (O–P) young (fruit brown / seed white) and mature (fruit red and seed black) infructescence in *Thaumatococcus* sp.1. Bars: 1 cm.

Table 2.2: Inflorescence architecture and phenology of African Marantaceae. br, bract: (a) < 20 mm; (b) 20-30 mm; (c) 30-40 mm; (d) > 40 mm; fp, flower pair; inf, inflorescences; it, internode: (a) < 5 mm; (b) 5-10 mm; (c) 10-20 mm, (d) >20 mm; ph, phenological pattern (see 2.4.1); pi, partial inflorescence.

	inflorescence architecture									phenology						
	length classes										open flowers per day		open flowers per week			
	it	br	n (inf)	pi / inf	n (pi)	br / pi	fp/ br	n (inf)	flower / inf	n (inf)	average	max (% of total)	average	max. (% of total)	flowering in weeks	ph
***Hyps hirs*-type**																
Halo azur	c	d	34	2.17 ±1.02	75	11.88 ±2.97	3	24	32.25 ±12.27	5	0.61 ±0.91	4 (12.40%)	5.00 ±2.20	10 (31.00%)	~6.00	Bb
Hyps hirs	a	b	20	2.25 ±1.37	45	9.37 ±5.67	1	16	35.87 ±23.65	6	0.82 ±0.93	4 (11.15%)	5.70 ±3.28	12 (33.45%)	6.29	C
Hyps pogg	b	b	14	2.64 ±2.56	23	14.17 ±5.49	1	11	44.72 ±22.47	2	1.35 ±1.30	5 (11.18%)	9.60 ±4.06	8 (17.88%)	4.65	C
Hyps scan	c	c	16	2.62 ±1.70	44	4.97 ±3.05	1	15	22.13 ±12.59	10	0.72 ±0.82	3 (13.55%)	4.82 ±2.14	15 (67.78%)	4.59	Bb
Hyps viol	c	b	3	4.66 ±2.30	5	12.60 ±4.15	1	1	22.00 ±0							
Mara sp.1	d	c	12	1.16 ±0.38	14	4.35 ±0.63	3	10	13.20 ±5.00	7	0.46 ±0.76	4 (30.30%)	2.79 ±1.55	7 (53.03%)	4.00	Ab
Mara purp	d	c	15	4.20 ±1.08	62	3.59 ±0.83	2	24	31.83 ±10.84	6	0.59 ±0.86	4 (12.56%)	4.20 ±2.04	10 (31.41%)	7.57	Bb
Mega gabo	b	a	4	6.75 ±0.95	26	5.38 ±2.87	1	4	67.00 ±18.00	4	2.41 ±2.26	6 (8.95%)	17.00 ±9.66	30 (44.77%)	3.94	Ba
Mega macr	b	b	8	5.37 ±1.68	39	15.35 ±8.13	1	6	145.33 ±30.89	2	2.52 ±1.53	6 (4.12%)	16.07 ±5.47	24 (16.51%)	~12.00	C
Trach brau	b	b	20	1.50 ±0.82	28	12.46 ±5.94	1	20	34.10 ±18.57	3	1.60 ±0.49	2 (5.86%)	6.00 ±1.09	8 (23.46%)	5.68	C
***Haum danc*- type**																
Haum danc	b	b	8	1.00 ±0	8	8.50 ±1.41	2	6	14.16 ±10.49	6	1.02 ±1.60	5 (35.31%)	7.66 ±3.24	15 (105.93%)	1.85	Aa
Haum lieb	a	b	16	2.00 ±0	16	6.13 ±0.81	2	16	12.25 ±1.61							Aa
***Mara cong*-type**																
Mara cong	c	b	12	1.66 ±1.07	20	2.40 ±0.75	3	9	12.00 ±3.46	6	0.31 ±1.01	2 (16.66%)	1.12 ±1.28	6 (50.00%)	10.66	Ac
Mara fili	d	b	20	1.15 ±0.36	22	2.18 ±0.50	2	11	6.73 ±6.52	7	0.39 ±0.71	2 (29.71%)	1.90 ±1.28	4 (59.43%)	2.47	Ab
Mara ince (Ma)	c	a	17	1.88 ±1.05	30	2.00 ±0.78	2	15	9.86 ±4.80	3	0.17 ±0.38	2 (20.28%)	1.18 ±0.87	4 (40.56%)	8.36	Ab
Mara ince (MC)	c	b	9	1.66 ±0.70	15	2.00 ±0.75		5	11.60 ±2.19			2 (17.24%)				Ab
Mara leuc	c	c	9	3.00 ±0.86	25	4.00 ±1.15	3	3	50.66 ±11.71	3	1.37 ±1.62	8 (15.79%)	9.73 ±4.16	4.16 (8.21%)	5.00	Bb
Mara mono	c	a	21	1.80 ±0.92	35	2.51 ±0.85	3	10	13.00 ±6.56	4	0.15 ±0.35	2 (15.38%)	1.13 ±1.25	4 (30.76%)	11.55	Ab
Sarc brac	a	a	10	2.6 0±0.84	27	6.00 ±1.61	5	5	156.80 ±37.03	3	1.60 ±1.42	7 (4.46%)	12.13 ±3.85	21 (13.39%)	12.92	C
Sarc prio	c-d	b-c	3	3.33 ±2.30	20	4.35 ±0.81	8	2 - 3	181.50 ±33.23	3	3.26 ±3.36	14 (7.71%)	21.33 ±0	42 (23.14%)	~8.00	C
Sarc schw	c	c	19	4.00 ±1.37	69	7.08 ±1.95	8	14	147.29 ±106.09	6	1.32 ±1.38	10 (6.78%)	6.03 ±6.74	29 (19.68%)	15.80	C
***Thau dani* - type**																
Afro rhiz	c	c	10	1.00 ±0	10	5.70 ±1.15	2	24	14.58 ±3.74	8	0.98 ±1.27	4 (27.43%)	7.18 ±3.20	12 (82.30%)	2.03	Aa
Atae conf	a	c	17	5.94 ±2.24	97	4.77 ±1.53	4	3	116.66 ±28.58	1	2.21 ±2.05	7 (6.00%)	15.25 ±7.41	27 (23.14%)	7.65	C
Mara cord	c	c	26	1.53 ±0.94	39	4.48 ±1.29	2	13	18.84 ±3.86	5	0.36 ±0.70	4 (21.23%)	2.55 ±1.42	9 (47.77%)	7.39	Ab
Mara sp.2	c	c	30	3.13 ±1.50	90	2.38 ±0.93	3	7	10 .00 ±6.75	6	0.65 ±0.87	3 (30.00%)	3.42 ±0	6 (60.00%)	1.42	Aa
Mara mann	a	b-c	7	2.71 ±1.38	15	5.26 ±1.75	3	6	35.33 ±29.66	6	0.59 ±0.75	3 (8.49%)	4.56 ±3.44	13 (36.79%)	5.80	Bb
Mara sp.3	a	b	18	1.50 ±0.78	27	3.88 ±1.08	4	25	18.32 ±11.41	9	0.51 ±0.62	2 (10.91%)	3.72 ±1.51	6 (32.75%)	4.15	Ab
Mega tric	b	a	9	7.66 ±3.60	61	5.08 ±2.28	1	7	80.28 ±43.82	4	2.93 ±2.49	9 (11.21%)	21.00 ±11.99	44 (54.80%)	3.82	Bb
Thau dani	b	b					1	1	26.00 ±0							Ba
Thau sp.1	b	b	36	1.52 ±1.10	54	9.07 ±3.40	1	27	19.62 ±11.51	6	1.39 ±1.44	8 (40.77%)	4.33 ±1.36	32 (163.09%)	6.00	Ba

Table 2.3: Seasonal and daily phenological pattern per species compiled at Makokou and Monts de Cristal. p, time of pollen deposit; t [hrs], number of hours between onset of pollen deposition in the bud and anthesis; ?, start/end of daily flowering out of observation time; black, flowering time; light grey, estimated phenological pattern where phenological seasonality of a given species exceeded the time of direct observations; dark grey, sequential opening/closing of individual flowers in a given species; grey in time scale, hours of darkness; hatched, time span during which flowers fall-off consecutively after being visited; +, flower wilted and fallen off; (+), flowers remain wilted in the inflorescence.

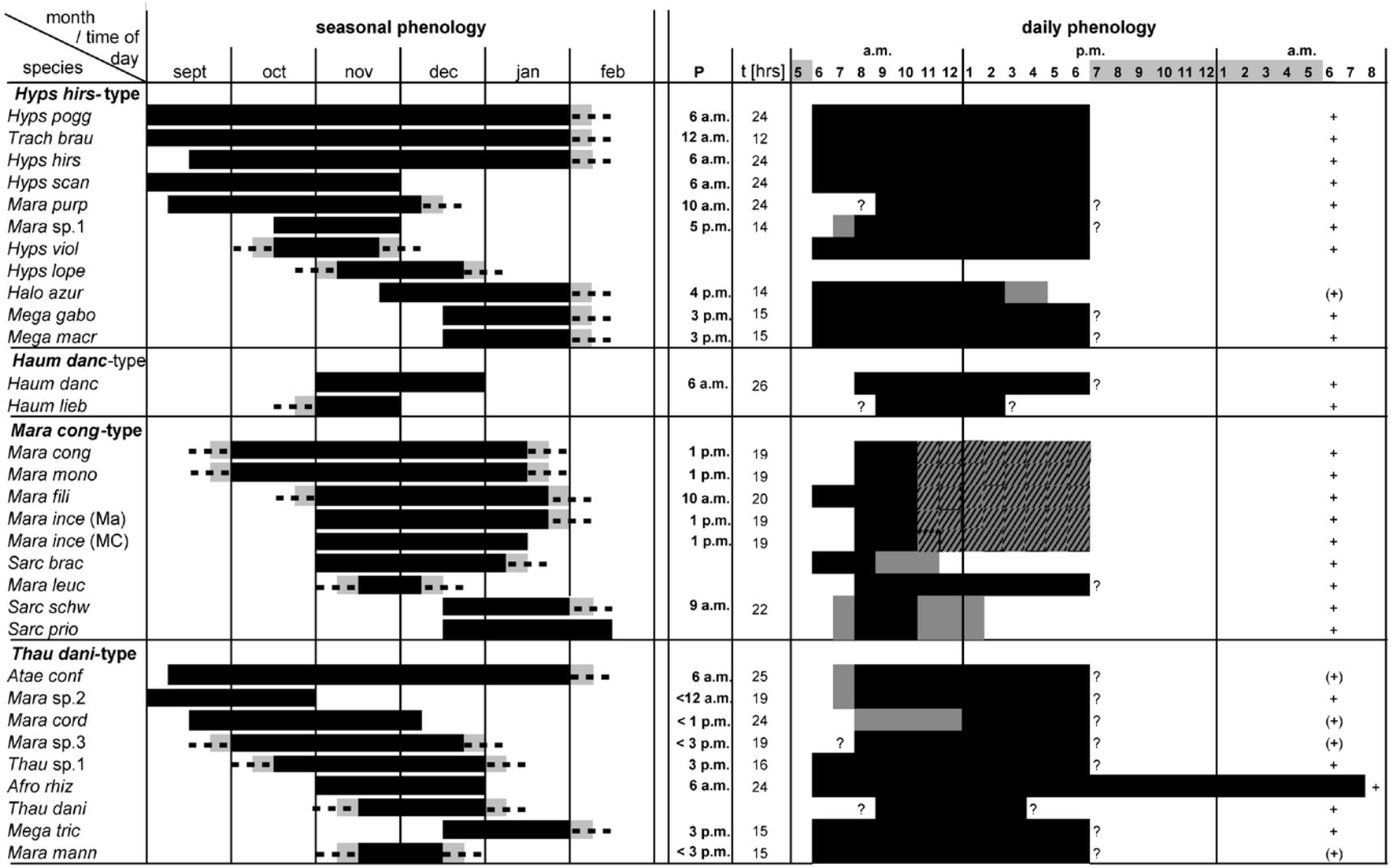


Table 2.4: Flower morphometric data and pollinator observations. Flower measurements: a, length of fleshy staminode; b, distance between flower entrance and nectar; c, width of flower entrance; deviations minute (see Fig. 2.2). bl, blue; br, bract; inf, inflorescence; ip, inflorescence position above ground (1: 0 - 0.60 m; 2: 0.60 – 1.50 m; 3: 1.50 – 2 m ; 4: up to over 10 m); p, purple; r, red; t, hours of observation; v, violet; w, white; y, yellow; grey, dominant pollinator; #, single observation; ?, assumed pollinator.

	inf		flower					Pollination [visits per hour]						
								Apidae	Anthophoridae					
	ip	flower colour	n	a [mm]	b [mm]	c [mm]	t	*Amegilla vivida*	*Xylocopa nigrita*	*Xylocopa varipes*	*Megachile* sp.1*, *M.* sp.2**	*small red insect*	sunbird	butterfly
***Hyps hirs*-type**														
Halo azur	1	bl	15	10.06 ± 1.53	9.33 ± 1.03	2.00	26.00					0.67 ± 0.39	0.05 ± 0.13	0.41 ± 0.45
Hyps hirs	4	v	8	18.75 ± 1.28	9.75 ± 1.14	2.00	26.00	0.49 ± 0.63					0.28 ± 0.58	0.79 ± 1.17
Hyps pogg	4	v	9	16.50 ± 1.06	9.06 ± 2.10	2.00	13.00	0.82 ± 1.27						0.91 ± 1.31
Hyps scan	4	v	8	17.50 ± 1.19	11.75 ± 1.04	2.00	14.00	2.78 ± 1.68						1.874 ± 1.35
Hyps viol	4	v	3	19.00 ± 1.00	7.67 ± 1.52	2.00		#						
Mara sp.1	3	w	4	15.25 ± 0.5	9.00 ± 0.00	3.00	27.25	1.45 ± 1.43						
Mara purp	3	p	7	11.78 ± 0.39	7.42 ± 1.13	2.00	9.75	3.66 ± 2.98						1.45 ± 1.05
Mega gabo	2	r, y	3	10.00 ± 0	7.00 ± 0.00	1.00	18.00	0.12 ± 0.13		1.89 ± 2.17	0.03 ± 0.05*		0.32 ± 0.50	0.69 ± 0.56
Mega macr	2	r, y	5	15.20 ± 0.44	7.50 ± 0.70	1.00	19.00	0.33 ± 0.30						0.77 ± 0.16
Trach brau	4	v	3	21.00 ± 1	11 .00 ± 1.00	2.00	8.00	2.14 ± 1.11						0.36 ± 0.51
***Haum danc*-type**														
Haum danc	4	w	3	10.3 ± 0.12	2.00 ± 0.00	2.00	31.50		0.30 ± 0.46	0.66 ± 0.80	3.56 ± 4.15**		0.06 ± 0.15	0.58 ± 0.86
Haum lieb	4	w	2	10.00 ± 0	2.00 ± 0.00	2.00				?				
Thal geni	4	v	1	8.00 ± 0.00	3.00 ± 0.00	2.00								
***Mara cong*-type**														
Mara cong	3	w	7	7.35 ± 0.47	5.10 ± 0.25	1.00	10.75					0.52 ± 0.45		
Mara fili	2	r	10	9.55 ± 0.5	3.30 ± 0.65	1.50	21.00					0.99 ± 0.77		
Mara ince (Ma)	2	w	1	7.00 ± 0		1.00	15.00					0.33 ± 0.07		
Mara ince (MC)	2	w	3	7.00 ± 0	5.00 ± 0.00	1.00						?		
Mara leuc	3	w	5	4.88 ± 0.45	3.60 ± 0.65	1.00						?		
Mara mono	2	w	3	5.66 ± 0.57	3.50 ± 0.86	1.00	14.50					1.10 ± 0.05		
Sarc brac	2	rose	2	11.00 ± 0	5.00 ± 0.00	1.00	12.25					1.74 ± 1.22		
Sarc prio	2	rose	4	9.50 ± 0.57	5.88 ± 0.62	1.00	24.75					3.00 ± 2.46		
Sarc schw	2	beige	2	9.50 ± 0.7	5.50 ± 0.00	1.00	12.25					?	#	

Table 2.4: (cont.).

	inf	flower					Pollination [visits per hour]						
							Apidae		Anthophoridae				
	ip	flower colour	n	a [mm]	b [mm]	c [mm]	hrs of obs	*Amegilla vivida*	*Xylocopa nigrita*	*Xylocopa varipes*	*Megachile* sp.1*, *M.* sp.2**	*small red insect*	sunbird	butterfly
***Thau dani*-type**														
Afro rhiz (MA)	1	w	5	24.40 ± 2.07	4.25 ± 1.70		9.50						0.08 ± 0.17	0.0.22 ± 0.26
Afro rhiz (MC)	1	w					22.25						0.66 ± 0.45	
Atae conf	2	w, r br	8	18.19 ± 0.65	7.69 ± 1.34	1.00	42.25			#			0.98 ± 0.82	0.29 ± 0.59
Mara cord	3	w, y	10	18.75 ± 2.32	8.33 ± 1.37	2.00	7.75	0.36 ± 0.50					0.23 ± 0.32	0.52 ± 0.38
Mara sp.2	1	w	5	17.70 ± 1.09	11.70 ± 0.97	2.50	19.50						?	
Mara sp.3	3	w	4	17.87 ± 1.43	8.26 ± 0.48	2.00	15.00						0.20 ± 0.17	1.11 ± 0.74
Mega tric	1	r, y	10	14.30 ± 0.94	8.81 ± 0.75	2.00	20.50						0.95 ± 1.12	
Thau dani	1	w											?	
Thau sp.1	1	y	5	25.00 ± 1	8.60 ± 0.54	2.50	20.00						0.56 ± 0.40	
						total	469							

Table 2.5: Test for normal distribution of morphological and ecological data of four flower types (Kolmogorov Smirnov test with significance correction after Lilliefors).

flower type	data set	statistics	df	significance
Hypselodelphys hirsuta	length of fleshy staminode	0.155	48	0.006
	distance: flower entrance and nectar	0.116	48	0.111
	nectar concentration	0.089	90	0.078
	nectar volume	0.153	42	0.015
	pollen grains per theca	0.133	88	0.001
Marantochloa congensis	length of fleshy staminode	0.165	23	0.105
	distance: flower entrance and nectar	0.309	23	0.000
	nectar concentration	0.137	52	0.017
	nectar volume	0.212	31	0.001
	pollen grains per theca	0.217	87	0.000
Haumania danckelmanniana	length of fleshy staminode	0.302	6	0.094
	distance: flower entrance and nectar	0.293	6	0.117
	nectar concentration	0.270	20	0.000
	nectar volume	0.245	7	0.200
	pollen grains per theca	0.105	20	0.200
Thaumatococcus daniellii	length of fleshy staminode	0.123	40	0.132
	distance: flower entrance and nectar	0.182	40	0.002
	nectar concentration	0.180	70	0.000
	nectar volume	0.180	27	0.025
	pollen grains per theca	0.188	65	0.000

Table 2.6: Pairwise comparison for distinction between flower type (ft) datasets by using the non-parametric Kolmogorov Smirnov test. (A) grey, length of fleshy staminode; white, distance between flower entrance and nectar. (B) grey, nectar concentration; white; nectar volume. (C) pollen grains per theca. first value, Kolmogorov-Smirnov-Z; second value, p-value (2-sided). 1, *Hypselodelphys hirsuta*-type; 2, *Marantochloa congensis*-type; 3, *Haumania danckelmanniana*-type; 4, *Thaumatococcus daniellii*-type. *, significantly different at a level of $p < 0.01$.

A

ft	1	2	3	4
1		3.197; 0.000*	2.309; 0.000*	1.518; 0.020
2	3.690; 0.000*		2.087; 0.000*	2.795; 0.000*
3	1.976; 0.002*	1.707; 0.006*		2.170; 0.000*
4	1.207; 0.109	3.630; 0.000*	2.170; 0.000*	

B

ft	1	2	3	4
1		4.223; 0.000*	0.642; 0.805	0.982; 0.285
2	1.553: 0.160		2.390; 0.000*	3.789; 0.000*
3	3.820; 0.000*	3801; 0.000*		0.873; 0.431
4	4.492; 0.000*	4.232; 0.000*	3.944; 0.000*	

C

ft	1	2	3	4
1				
2	2.585; 0.000*			
3	3.560; 0.000*	3.968; 0.000*		
4	3.870; 0.000*	4.997; 0.000*	1.805; 0.003*	

Table 2.7: Nectar sugar concentration, nectar volume and P/O-ratio. av, average, n, number of flowers; stdv, standard deviation.

	nectar				pollen	
	sugar concentration [%]		volume [µl]		P/O-ratio	
	n	av ± stdv	n	av ± stdv	n	av ± stdv
***Hyps hirs*-type**						
Halo azur	15	28.13 ± 0.74	5	4.33 ± 0.94	10	34.50 ± 7.64
Hyps hirs	12	34.17 ± 1.52	6	5.61 ± 1.66	10	103.10 ± 16.29
Hyps pogg	10	33.70 ± 1.49	4	9.50 ± 1.91	10	59.63 ± 7.03
Hyps scan	13	35.73 ± 1.17	4	8.50 ± 3.78	10	94.93 ± 11.53
Hyps viol						
Mara sp.1	11	29.81 ± 1	8	6.53 ± 1.87	9	45.57 ± 4.53
Mara purp	11	31.27 ± 2.03	10*	2.68* ± 0.30	10	78.96 ± 13.25
Mega gabo	10	37.10 ± 1.44	3	6.26 ± 0.46	11	43.03 ± 8.89
Mega macr	10	34.95 ± 1.79	1	5 ± 0	8	34.30 ± 3.48
Trach brau	20	30.50 ± 2.92	1	4 ± 0	8	72.12 ± 7.32
***Haum danc*- type**						
Haum danc	24	36.04 ± 4.67	5	5.90 ± 1.24	10	138.36 ± 14.03
Haum lieb	10	40.70 ± 2.71	2	4.15 ± 0.21	10	123.33 ± 15.4
Thal geni					2	133.167 ± 4.01
***Mara cong*-type**						
Mara cong	6	28.58 ± 0.93	5	0.37 ± 0.12	9	52.55 ± 12.01
Mara fili	10	32.15 ± 0.63	10	0.80 ± 0	10	56.30 ± 8.67
Mara ince (Ma)				<1	11	39.87 ± 6.9
Mara ince (MC)	1	32.00	1	0.40 ± 0	9	47.73 ± 18.99
Mara leuc	10	32.95 ± 0.65	5	0.40 ± 0.1	9	77.60 ± 7.38
Mara mono	8	30.68 ± 1.34	3	0.30 ± 0	13	48.94 ± 23.3
Sarc brac	10	32.95 ± 0.87	6	0.55 ± 0.12	10	2.63 ± 0.53
Sarc prio	7	33.92 ± 1.37	8	1.17 ± 0.41	10	2.50 ± 0.42
Sarc schw				<1	10	2.20 ± 0.44
***Thau dani*-type**						
Afro rhiz	10	25.35 ± 2.68	9	6.74 ± 2.81	10	118.10 ± 12.88
Atae conf	27	26.94 ± 1.3	10	5.78 ± 1.67	10	139.73 ± 18.94
Mara cord	12	30.46 ± 1.19	3	5.06 ± 2.65	10	45.50 ± 12.04
Mara sp.2	10	27.09 ± 0.33	10	5.85 ± 1.1	9	84.48 ± 8.79
Mara mann	11	27.27 ± 0.65		~8.00	3	100.60 ± 4.53
Mara sp.3	14	30.25 ± 1.71		~8.00	10	217.00 ± 43.47
Mega tric	12	27.70 ± 1.28	4	11 ± 1.15	11	105.57 ± 14.02
Thau dani						
Thau sp.1	12	27.04 ± 0.63	4	11 ± 1.15	10	108.06 ± 9.9

Table 2.8: P/O-ratio of selected Marantaceae from America and Asia. Am, America; As, Asia; cont, continent; n, number of flowers sampled; stdv, standard deviation.

	cont	autogamous	n	P/O-ratio
Calathea bachemiana	Am	-	2	256.50 ± 0.70
Calathea rufibarba	Am	-	4	121.00 ± 16.55
Calathea sp.	Am	-	2	410.50 ± 6.36
Calathea veitchiana	Am	-	3	290.66 ± 4.04
Maranta leuconeura	Am	-	5	98.00 ± 20.08
Maranta noctiflora	Am	+	6	68.83 ± 6.96
Myrosma sp.	Am	-	2	78.00 ± 0.00
Pleiostachya pruinosa	Am	+	4	149.75 ± 19.61
Stromanthe sanguinea	Am	-	5	153.20 ± 21.52
Donax canniformis	As	-	4	265.25 ± 26.65

Table 2.9: Morphometric data of pollinators and nectarrobbers. n, number of individuals measured; MC, Monts de Cristal; Si, Sibang; *, body length after Eardley (1983).

		average size of pollinator [mm]		average length of proboscis [mm]		
insects	**n**	**body length**	**head width**	**prementum + mentum**	**glossa / galea**	**total**
Halictidae						
Thrinchostoma sp. 1 on *Marantochloa congensis*	2	14.0 ± 0.0	2.5 ± 0.0	2.5 ± 0.007	2.9 (n = 1)	6.35
on *Sarcophrynium brachystachyum*	2	11.5 ± 0.7	2.1 ± 0.10	2.5 ± 0.0	1.5 (n = 1)	4.0
Thrinchostoma sp. 2 on *Marantochloa filipes* (Si)	2	9.0 ± 0.0	2.1 ± 0.07	2.3 ± 0.0	?	> 2.3
Thrinchostoma sp. 3 on *Marantochloa filipes* (MC)	1	10.0	2.0	1.9	1.9	3.8
Thrinchostoma sp. 4 on *Sarcophrynium prionogonium*	1	16.0	2.5	2.5	1.5	4.0
Thrinchostoma bicometes (Enderlien, 1903)	1	20.0	3.0	5.2	8.7	13.9
Lipotriches sp.	1	12.0 ± 0.0	3.0 ± 0.0	1.9	0.1	1.9
Apidae						
Amegilla vivida (Smith, 1879)	5	14.6 ± 1.9	5.0 ± 0.0		~5 / 5.86 ± 0.43	~10
Allodapula ornaticeps Michener	1	7.0	2.0		3.90	3.9
Anthophoridae						
Xylocopa varipes Smith, 1854	2	20.0 ± 0.0	6.0 ± 0.0		~5 / 5.0 ± 0	~10
Xylocopa nigrita (Fabricius, 1775) * Eardley 1983		35.0				
Megachilidae						
Megachile sp.1	1	15.0	5.0		0.3	0.3
Megachile sp.2	1	22.0	5.0		0.3	0.3
Sunbird (probably olive sunbird *Cyanomitra olivaceus*)		130 to150				~20

Table 2.10: Handling time of pollinators per flower [sec] based on videos of flower visits [supplementary information - CD]. n, number of individuals observed; Si, Sibang; MC, Monts de Cristal.

Pollinator species	Marantaceae species	n	handling time [sec]
Allodapula ornaticeps	*Marantochloa monophylla*	2	45.00 ± 35.35
Amegilla vivida	*Hypselodelphys hirsuta*	5	8.00 ± 7.38
Amegilla vivida	*Hypselodelphys poggeana*	5	2.20 ± 0.83
Amegilla vivida	*Hypselodelphys scandens*	11	2.09 ± 1.70
Amegilla vivida	*Marantochloa* sp.1	18	3.28 ± 3.46
Amegilla vivida	*Marantochloa purpurea*	3	1.00 ± 0
Amegilla vivida	*Trachyphrynium braunianum*	4	5.75 ± 4.50
Megachile (Pseudomegachile) sp. 2	*Haumania danckelmanniana*	11	8.00 ± 2.68
Xylocopa nigrita	*Haumania danckelmanniana*	28	4.32 ± 1.61
Xylocopa varipes	*Haumania danckelmanniana*	17	5.23 ± 2.65
small red insect	*Halopegia azurea*	4	12.25 ± 6.65
small red insect	*Marantochloa congensis*	5	11.40 ± 4.87
small red insect	*Sarcophrynium brachystachyum*	19	12.63 ± 12.23
small red insect	*Marantochloa filipes* (Si)	3	7.00 ± 2.64
small red insect	*Marantochloa filipes* (MC)	6	24.00 ± 2.64
small red insect	*Sarcophrynium prionogonium*	60	7.85 ± 3.75
sunbird	*Afrocalathea rhizantha*	62	~ 1
sunbird	*Ataenidia conferta*	9	~ 1
sunbird	*Marantochloa* sp.3	4	~ 1
sunbird	*Megaphrynium trichogynum*	16	~ 1
sunbird	*Thaumatococcus* sp.1	33	~1

Table 2.11: Fruitset in pollination experiments. inf, number of inflorescences; fl, total number of flowers; Ma, Makokou.

	control				bagged				self-pollinated			cross-pollinated		
	n (inf)	n (fl)	n (fruits)	**fruitset [%]**	n (inf)	n (fl)	n (fruits)	**fruitset [%]**	n (fl)	n (fruits)	**fruitset [%]**	n (fl)	n (fruits)	**fruitset [%]**
***Hyps hirs*-type**														
Halo azur	15	290	102	**35.17**	5	267	121	**45.3**	10	2	**20.00**			
Hyps hirs	22	438	39	**8.90**	5	222	0	**0**	22	6	**27.27**	45.00	24	**53.33**
Hyps pogg	4	122	3	**2.46**	7	98	0	**0**	16	2	**12.50**	4.00	2	**50.00**
Hyps scan	7	164	8	**4.88**					28	2	**7.14**	5.00	5	**100.00**
Hyps viol	2	62	4	**6.45**										
Mara purp	28	926	275	**29.70**	4	66	0	**0**	19	5	**26.32**			
Mara sp.1	10	128	0	**0**	5	31	0	**0**	31	0	**0**	10.00	0	**0**
Mega gabo					4	174	0	**0**	16	11	**68.75**	4.00	0	**0**
Mega macr					2	78	0	**0**	45	11	**24.44**			
Trac brau	12	266	36	**13.53**	2	40	0	**0**	11	6	**54.55**			
***Haum danc*-type**														
Hau dan	52	725	86	**11.86**	7	147	0	**0**	12	0	**0**	48.00	5	**10.42**
Haum lieb	16	196												
***Mara cong*-type**														
Mara cong	7	50	0	**0**	no fruitset in the greenhouse									
Mara fili	13	63	11	**17.46**	4	34	0	**0**	42	10	**23.81**			
Mara ince (Ma)	18	165	5	**3.03**					11	2	**18.18**			
Mara leuc					6*	215*	67*	**31.16***						
Mara mono	13	124	16	**12.90**	4	43	0	**0**	17	3	**17.64**			
Mara sulp	7	31	2	**6.45**										
Sarc brac	3	250	25	**10.00**	5	171	0	**0**	39	2	**5.13**	4.00	2	**50.00**
Sarc prio	1	158	21	**13.29**	4	36	0	**0**						
Sarc schw	23	2221	235	**10.58**	4	119	0	**0**	36	12	**33.33**	10.00	1	**10.00**

Table 2.11: (cont.).

	fruitset														
	control				bagged				self-pollinated				cross-pollinated		
	n (inf)	n (fl)	n (fruits)	**fruitset [%]**	n (inf)	n (fl)	n (fruits)	**fruitset [%]**	n (fl)	n (fruits)	**fruitset [%]**		n (fl)	n (fruits)	**fruitset [%]**
***Thau dani*-type**															
Afro rhiz (Ma)	51	744	80	**10.75**	12	173	0	**0**	30	28	**93.33**		13.00	10	**76.92**
Atae conf	17	661	73	**11.04**	2	226	0	**0**	8	5	**62.50**		27.00	8	**29.63**
Mara cord	24	152	0	**0**	5	0	0	**0**	12	0	**0**		11.00	0	**0**
Mara sp.2	42	466	156	**33.47**	5	36	0	0	27	18	**66.66**		7.00	6	**85.71**
Mara sp.3	21	373	1	**0.27**	3	17	0	**0**	23	0	**0**				
Mega tric					7	282	0	**0**	29	6	**20.69**		19.00	4	**21.05**
Thau dani															
Thau sp.1	33	582	45	**7.73**	8	248	0	**0**	50	13	**26.00**		23.00	4	**17.39**
Total	**153**	**3983**	**401**	**10.07**		**2723**	**188**	**6.90**	**157**	**29**	**18.47**		**62.00**	**8**	**12.90**

Table 2.12: Fruit and seed characteristics in African Marantaceae and inferred dispersal agent (° data from green house cultivars at the University of Mainz). Fruit type: ca, capsule; be, berry-like. Colour: bl, black; br, brown; gr, green; or, orange; ro, rose; w, white; y, yellow. fruit dev., fruit development. dispersal agents: a, apes; bi, bird; m, monkey; pi, pig; wa, water; * data after Williamson et al. 1990, White and Abernethy 1997.

	fruit				seed					
						number of seeds per fruit [percent]				dispersal agent
	type	colour	length [mm]	fruit dev. [week]	colour	n	1	2	3	
***Hyps hirs*-type**										
Halo azur	ca	w	12		w	22	100.00	0.00	0.00	bi, wa
Hyps hirs	ca	gr	30	4	w	30	26.67	23.33	50.00	?
Hyps sp.1	ca	gr	30		w	2	50.00	50.00		?
Hyps pogg	ca	gr	40	4	w					?
Hyps scan	ca	gr	40		w					?
Hyps viol	ca	gr	30		w	5	0.00	20.00	80.00	?
Mara purp	ca	red	7	2	w	220	16.82	45.00	38.18	bi, wa
Mega gabo	be	gr/red	15		grey					a, m*
Mega macr	be	gr/red			grey					a, m*
Trac brau	ca	gr/or	15	4	bl + w aril	20	15.00	40.00	45.00	bi
***Haum danc*-type**										
Haum danc	ca	br	30	4	w	89	10.11	37.08	52.81	?
Haum lieb	ca	br	30		w					?
***Mara cong*-type**										
Mara cong	ca	y	6		w					bi, wa
Mara fili	ca	y, red	7	~8	bl + or aril	30	3.33	26.67	70.00	bi, wa
Mara inc (Ma)	ca	y			w	1	0.00	100.00	0.00	bi, wa
Mara leuc°	ca	gr/red	8		w	125	12.00	42.40	45.60	bi, wa
Mara mono	ca	y	6		w	18	33.33	27.77	38.88	bi, wa
Mara sulp	ca	y	7		w	2	50.00	0.00	50.00	bi, wa
Sarc brac	be	red	15		grey	55	36.36	21.82	41.82	a, m*
Sarc prio	be	red	17		grey	19	15.79	10.53	73.68	a, m*
Sarc schw	be	red	15	3	grey	277	20.94	50.54	28.52	a, m*
***Thau dani*-type**										
Afro rhiz	ca	gr	20	3	w	59	76.271	6.7797	16.949	water
Atae conf	ca	red	7	2	w + w aril	279	26.52	36.20	37.28	bi, wa
Mara cord	ca									bi, wa
Mara sp.2	ca	red	7	4	w	144	23.611	29.167	47.222	bi, wa
Mara sp.3	ca	red			w					bi, wa
Mega tric	be	gr/red	15		grey					a, m*
Thau dani	be	red	35		bl					a, m*
Thau sp.1	be	br/red	35	8-12?	bl	54	33.33	20.37	46.30	a, m*, pi

2.5 DISCUSSION

2.5.1 FLOWER TYPES AND POLLINATION SYNDROMES

Inflorescence and flower morphology is highly diverse within the African Marantaceae. However, by combining specific characters it is possible to distinguish four different floral types. All members of one type produce nectar of a distinct range in volume and sugar concentration and are associated with the same pollinator or pollinator group (except *Megaphrynium gabonense*). They thus illustrate the well-known close relationship between a set of specific floral characteristics such as flower size, shape, colour and exposition, nectar values, and pollinator guilds (Heinrich, 1975; Schemske, 1981; Gottsberger, 1989; Sakai et al., 1999; Specht et al., 2001; Kay and Schemske, 2003). This allows the description of two pollination syndromes with four subsyndromes, respectively, in the African Marantaceae.

2.5.1.1 Bee-pollination-syndrome

Based on data from America and Asia (Claßen-Bockhoff, 1991; Kato, 1996; Momose et al., 1998; Kennedy, 2000; Clausager and Borchsenius, 2003; Locatelli et al., 2004; Claßen-Bockhoff and Heller, 2008*b*), the most important pollinators of the Marantaceae are bees. This is also true for the majority of the African species that are adapted to medium-sized (*Amegilla, Thrinchostoma),* large-sized *(Xylocopa*) or small-sized bees (Halictidae/*Thrinchostoma*, Apidae/*Allodapula*).

Medium-sized bees and *Hypselodelphys hirsuta*-flower type

All species of the *Hypselodelphys hirsuta*-type are predominantly visited by *Amegilla vivida* producing an intermediate nectar volume and sugar concentration. In *Marantochloa purpurea* and *M.* sp.1 very large and heavy carpenter bees are probably excluded from the flowers as the hanging inflorescences are too slender for these bees to land on. No exclusion factors are yet known for the remaining species. The restricted occurrence of *Halopegia azurea* in shallow slow running creeks and its bluish flowers presented just above the water level might play a role in the unique and strict relation to *Thrinchostoma bicometes*.

Our reconstruction of the style movement effectuating pollen deposition on *Amegilla vivida* visiting *Marantochloa purpurea* (Fig. 2.11) allows the assumption of a complete pollen transfer (collection and deposition) during the first upward-directed

stage of the movement of the stylar head (Fig. 2.11B-C). This contradicts the illustration given by Locatelli et al. (2004) for *Saranthe klotzschiana* (Koer.) Eichl. in which the authors are of the opinion that the pollen deposition onto the insect takes place during the downwards movement, resulting in it being placed on top of the insect´s proboscis. However, they do not explain how pollen deposited on the top of the proboscis is removed by a style coming from below (see also chapter 3).

Carpenter bees and *Haumania danckelmanniana*-flower type*:*

The species of *Haumania* and *Thalia* are predominantly visited by *Xylocopa* bees (for *Thalia geniculata* see Davis, 1987; Claßen-Bockhoff, 1991; Yeo, 1993). Occurring in open habitats they closely match the preferences of *Xylocopa* bees which usually visit flowers in clearings and at forest edges (Appanah, 1990). As the individuals are rich blooming and produce high nectar sugar concentration they provide the bees with much food in a short time (Roubik et al., 1995). Thereby, they account for their extremely high metabolic costs caused by a high wing load and flight speed (Louw and Nicolson, 1983; Gerling et al., 1989).

Haumania spp. might exclude other bees due to its closed flowers. Probably considerable strength is needed to push the covering leaves of the fleshy staminode aside and to deflect the trigger appendage. The short distance to the nectar makes the flowers also attractive to the short-tongued *Megachile* sp.2 but it remains unclear whether this bee is a pollinator or a nectar thief.

Small bees and *Marantochloa congensis*-flower type*:*

The species of the *Marantochloa congensis*-type are exclusively visited by small bee species (*Thrinchostoma* spp*., Allodapula ornaticeps)*. The extremely small amount of nectar of an intermediate concentration might be unprofitable for larger bees and birds (Willmer and Stone, 2004). The same species of *Thrinchostoma* has been found on *Marantochloa congensis* and *Sarcophrynium brachystachyum* (Table 2.9) and two different species of *Thrinchostoma* have been found on *Marantochloa filipes* indicating a broader mutual relation on the level of a flower type and pollinator guild. The average handling time per flower of the *Thrinchostoma* bees takes a few seconds but is on average twice as long as of the large bees. This might be caused by a reduced intake rate due to their smaller size and slender proboscis (Harder, 1986; Borrell and Krenn, 2006).

2.5.1.2 Bird-pollination-syndrome

All almost exclusively bird-pollinated species belong to the *Thaumatococcus daniellii*–type. The flowers are usually characterized by a high number of open flowers per inflorescence, decreasing energy consuming movements of the birds (Westerkamp, 1990). Thus massively blooming populations yield the highest visitation rates (compare to Gentry, 1974; Stephenson, 1979). The vertical bracts of *Ataenidia conferta* additionally capture rainwater possibly rendering the inflorescences an important water supply for birds.

Bees are probably excluded by the vertical arrangement of the floral tube that might not fit the forward operation of their proboscis (Nilsson et al., 1985) (Fig. 2.10B-D). In *Megaphrynium trichogynum*, small insects were found decapitated in a few flowers illustrating that these insects are not able to handle the vigorous style movement of these large flowers. The inflorescences near the ground in closed forests probably do not closely match the preferences of *Xylocopa* bees for open areas (Louw and Nicolson, 1983; Gerling et al., 1989).

Megaphrynium trichogynum, Thaumatococcus sp.1 and occasionally *Afrocalathea rhizantha* (see Letouzey 14305 BR, YA) share the typical colours associated with bird pollination, yellow and red, with the three *Calathea* species of the New World described to be bird pollinated (*C. timothei, C. lutea, C. platystachya*; Kennedy 2000, Claßen-Bockhoff and Heller, 2008*b*). The white flowers of *Ataenidia conferta* are subtended by red bracts. White, as a further well-known bird colour (see Vogel, 1954), plays an important role in African bird-pollinated species (see *Afrocalathea rhizantha, Ataenidia conferta, Marantochloa cordifolia, M.* sp.2, *M*. sp.3).

Though bird pollination has not yet been observed in *Marantochloa* sp.2 it is highly likely because growth form and flower morphology resemble those of the bird pollinated *Afrocalathea rhizantha.* Both species occur sympatrically in Monts de Cristal. However, in contrast to the uniform white flowers of *Afrocalathea rhizantha* the flowers of *Marantochloa* sp.2 have nectar guides indicating that *M.* sp.2 might also be pollinated by bees (Manning and Goldblatt, 2005). A similar case is given by the bird-pollinated *Marantochloa cordifolia* and *M.* sp.3. Again both species share a similar growth form, inflorescence architecture and flower morphology but only *M. cordifolia* exhibits conspicuous nectar guides and is visited additionally by bees.

Specific advantages of bird pollination over bee pollination in African Marantaceae could not be found as there is no separation of species in specific habitats or altitudinal zones (see Kay and Schemske, 2003). Although visitation rate is lower in bird pollinated species fruit-set in bee and bird pollinated species of the same breeding system and fruits size is comparable. The occasionally simultaneous visit by birds to flowers predominantly pollinated by medium to large sized bee might indicate that pollinator specialization is not absolute and suggest a potential mechanism for pollinator shifts (Kay and Schemske, 2003).

2.5.1.3 Specialization to pollinator guilds

Only very few species of the high number of insects in the tropical rainforest pollinate the African Marantaceae. The latter thus show a degree of specialization. The observations are from two to three distant sites in two different years revealing the same results so that I am confident that the project sheds a comprehensive light on the floral biology of African Marantaceae. As the distribution ranges of all identified pollinators (*Amegilla vivida, Thrinchostoma bicometes* and olive sunbird) span from Central to West Africa (Eardley, 1983) it is well possible that the documented associations between plant and pollinator hold across their entire distribution range. Major accounts of new pollinator species are only expected for the *Marantochloa congensis*-type species, though I believe this to stay within the guild of small-sized bees.

The observed pollinators (*Amegilla, Halictidae*, *Xylocopa*, sunbirds) are known as reliable long distance pollinators (Gess and Gess, 1996; Momose et al., 1998) which are constantly present over several months or even all year round. This is a prerequisite for specialization that can only be established in plant species that are associated with rather constant pollinators so that the plant can optimise its pollen transfer by adapting its floral traits to pollinator body characteristics. Individuals in Marantaceae are large and have many reproductive seasons so that both partners can rely on the presence of the counterpart (Waser et al., 1996; Manning and Goldblatt, 2005). As approximately the same pollinator guilds are known in Asian Costaceae, Marantaceae and Zingiberaceae (Momose et al., 1998; Sakai et al., 1999; Specht et al., 2001; Kay and Schemske, 2003) and in Neotropical Marantaceae (hummingbird versus Euglossine bee, Kennedy, 2000) these

associations indicate some universality in equal evolutionary selection pressures and architectural effects.

Nevertheless the specialization is unidirectional. As the pollen is hidden in Marantaceae on the back of the stylar head covered by the hood of the hooded staminode and later in the proboscidial fossae of the insect the flowers are only attractive for nectar. However, the bees need additional food sources such as pollen which contribute additional essential nutrients (Simpson and Neff, 1983; Westrich, 1996; Michener, 2000). Therefore each insect pollinator visits several different plant species (see also Gerling et al., 1989; Gess and Gess, 1996; Eardley, in prep.). In contrast the investigated African Marantaceae species are specialized on one dominant pollinator (*Hypselodelphys hirsuta*-type) or pollinator guild (*Marantochloa congensis*-type). Evolutionary selection pressures might favour a close match in size between flower and pollinator allowing optimal pollen deposition for the plant and nectar foraging for the insect. The same has been observed in American Marantaceae (Kennedy, 1978) and Costaceae (Kay and Schemske, 2003).

2.5.2 BREEDING SYSTEM

All investigated species of the African Marantaceae are proven to be self-compatible. With a P/O-ratio of two to 150 they may be characterized as facultatively autogamous (after Cruden, 1977). However, only two species are indeed proven to be autogamous while the remaining species depend on pollinators. The low P/O-ratio in African Marantaceae in comparison to other angiosperms might thus be a hint towards an efficient pollination mechanism which allows the reduced production of costly pollen grains. The P/O-ratio is similarly low in selected American and Asian species (Table 2.8). The extremely low P/O-ratio in *Sarcophrynium* with only two to three pollen grains per ovule is very surprising as such a low ratio has only been observed in cleistogamous species (Cruden, 1977). However, *Sarcophrynium* species are neither cleistogamous nor autogamous but depend on pollinators and have the same fruit-set as the other Marantaceae species.

2.5.2.1 Geitonogamy versus xenogamy

The non-autogamous species do not set seeds when bagged and their styles wilt unreleased if not visited. Rather, due to the trap-lining behaviour of the pollinators (Heinrich and Raven, 1972; Crawford, 1984, Murawski, 1987; Franceschinelli and

Bawa, 2000) they might be geitonogamous to a high extent. Geitonogamy genetically resembles autogamy, but might be more expensive as the plant invests costs for pollinator attraction without profiting from out-crossing (de Jong et al., 1993). Being aware of the adverse consequences of inbreeding such as the loss of diversity and reduced fitness of progeny (Holsinger et al., 1984; Schoen et al., 1996; Takebayashi and Delph, 2000; Good-Avila et al., 2003) the question arises whether there are specific mechanisms in the African Marantaceae to increase out-crossing.

One well-known mechanism to reduce geitonogamy is the presentation of only a few synchronously open flowers per inflorescence (Rathcke and Real, 1993; Newstrom et al., 1994). In Marantaceae, the inflorescences indeed flower sparsely but as the individual plants usually have many inflorescences and occur in large clonal stands, geitonogamy is probably not severely reduced by this mechanism.

Instead, the delayed trigger release found in a few species might be of some importance. Flowers of the genera *Hypselodelphys*, *Megaphrynium* and *Thaumatococcus* are not always tripped at the first visit of a pollinator but rather randomly during one of several visits in the morning hours. A similar behaviour was also noted in *Calathea ovandensis* (Schemske and Horvitz, 1984) and in *Calathea lutea* (Claßen-Bockhoff and Heller, 2008*b*). The delayed style release raises the chance that foreign pollen is transferred to the stigma. As pollen exchange does not take place at every flower visited by the insect the probability increases that two consecutively released flowers on a bee´s foraging trip are from different individuals. This will then result in xenogamy in the respective species.

A partial incompatibility with own pollen in combination with a premature abortion of self-pollinated fruits might be a further mode to promote out-crossing (Kay, 2006; Sun et al., 2007). Hints to such a mechanism are tentatively given by the hand pollination experiments in African Marantaceae illustrating that it was difficult to induce self-pollinated fruits in certain species. Possibly foreign pollen is preferred, but under adverse conditions, i.e. absence of pollinators at new locations (Kennedy, 2000) or variation in pollinator availability (Davis, 1987), self pollination may compensate for the absence of cross pollen (see Schoen et al., 1996; Barrett and Harder, 1996*;* Barrett et al., 1996; Franceschinelli and Bawa, 2000; Takebayashi and Morrell, 2001; Anderson et al., 2003; Rathcke, 2003). This temporary solution is not uncommon in the tropical understorey (Kress and Beach, 1994), where the density of

individuals per species is often low reducing the chance of cross pollination. The latter then depends on the flight radius of the pollinators.

Foraging ranges in other tropical solitary bees from America extend to about 20 km (Janzen, 1971) and are correlated with body length (Gathmann and Tscharntke, 2002). From Asia the pollinators observed in Africa (*Amegilla, Xylocopa,* Halictidae*,* sunbirds) are known as reliable long-distance pollinators (Momose et al., 1998). Males of *Amegilla dawsoni* apparently form 75 m wide territories (Alcock, 1996) and thus may contribute to out-crossing to some extend. Unfortunately no data is yet available on the foraging radius of any of the encountered bee species in central tropical Africa that would allow conclusions on possible gene flow.

2.5.2.2 Autogamy

Autogamy might be of an advantage in sites of low, variable or absent pollinator communities as a mean of self-assurance (see Schoen et al., 1996; Barrett and Harder, 1996*;* Barrett et al., 1996; Franceschinelli and Bawa, 2000; Takebayashi and Morrell 2001; Anderson et al., 2003; Rathcke, 2003). It provides plants with the ability to colonize disturbed habitats where plant density is not yet high enough to attract pollinators (Kennedy, 2000). However, in Marantaceae local population establishment is also supported by vigorous vegetative reproduction. To estimate the significance of autogamy it would be of prime importance to determine the degree of autogamy (Kay, 2006; Sun et al., 2007) i.e. the number of selfed versus outcrossed fruits in comparison to non-autogamous plants.

2.5.3 PHENOLOGY AND POLLINATOR SHARING

The African Marantaceae present two different phenology patterns: a consecutive flowering of inflorescences over a long flowering period and a synchronous blooming for a short time. Both patterns provide a continuously rich food resource to the pollinators and attract a stable and constantly present pollinator community (Gottsberger, 1989).

A long flowering period can be a mechanism to prevent reproductive failure that might occur due to a fluctuation in pollinator availability in space and time (Bawa, 1983; Rhatcke and Lacey, 1985) or a high rate of predation (Primack, 1987). Indeed

observed pollinator frequency in African Marantaceae was highly variable and unpredictable and beetles were repeatedly found feeding on the ovaries and flowers, in *Hypselodelphys* spp., *Marantochloa* sp.1 and *M. monophylla*. These effects might be levelled out by a longer flowering period. Additionally predation might be shared between the species and therefore be less destructive for the individual species. Furthermore, the long flowering period will also lengthen the time for fruit dispersal where similar restriction factors (e.g. predation and available dispersal agents) might be influential.

Within the *Hypselodelphys hirsuta* and the *Marantochloa congensis*-type sparse-flowering over a long period is coupled with pollinator sharing (Pojar, 1974; Frankie et al., 1976; Stiles, 1977; Waser, 1978). The species involved are highly similar in flower morphology and pigmentation within each type, co-exist in the same habitats and flower simultaneously. Their synchronous flowering increases the effective flower density and nectar supply for the pollinator (Schemske, 1981). As *Amegilla vivida* and the members of the small bee guild are omni-present and are known to be polylectic (Gess and Gess, 1996) the pollination service is still adequate for the Marantaceae species involved. This is supported by a nearly 100 % triggering of all flowers by midday.

Pollinator sharing might enable hybridization but no hybrids have yet been described within the African Marantaceae. In *Sarcophrynium* spp. the differential daily phenology might prevent interspecific pollination (Table 2.3). However, in general the reproductive isolation mechanisms are unknown. A more detailed analysis concentrating on a few sister species is needed (see Kay, 2006).

The advantage of a highly synchronous flowering is the far greater attractiveness to pollinators (Wolf and Hainsworth, 1990; Mitchell, 1994), which probably leads to a more frequent pollen transfer between the individuals of the same species. Assuming that competition for pollinators might become an issue between massively blooming species this is circumvented by a consecutive flowering in the respective species. Consecutive mass flowering is currently only known from the bird pollinated *Afrocalathea rhizantha* and *Marantochloa* sp.2 in the Monts de Cristal region. As the far more widespread and evolutionary probably older species *Afrocalathea rhizantha* (see Dhetchuvi, 1996; Prince and Kress, 2006*a*) shows the same phenological pattern at different sites, it is possible that it shaped the pattern of *M*. sp.2 in Monts

de Cristal. The latter mimics the morphological adaptations of *Afrocalathea rhizantha* towards bird pollination but escapes its competition by flowering two months earlier.

2.5.4 FRUITSET AND VEGETATIVE VIGOUR

In view of the self-compatibility, the precise pollination mechanism, the low P/O-ratio and the specialized plant-pollinator relationship an overwhelming fruit-set should be expected in the Marantaceae. But the opposite is the case. Natural fruit-set is, with 3 to 35 % (average fruit-set 10 %, Tab. 2.11), extremely low compared to the average fruit-set of 72.5 % in hermaphroditic plants (Sutherland, 1986). Similar results have been found in *Calathea ovandensis* (Schemske and Horvitz, 1988). Considering that in 70 % of the African Marantaceae only one or two of the three seeds per ovary develop the actual number of seeds is even lower.

There are several reasons for the low fruit-set conceivable.

- Pollinator limitation may play a role at localities where visitors were only rarely recorded and the percentage of triggered flowers just before wilting was low (e.g. *Afrocalathea rhizantha*).
- The efficiency of the pollination mechanism might be overestimated (see also Schemske and Horvitz, 1984). In the bird pollinated species *Thaumatococcus* sp.1 and *Ataenidia conferta* almost 100 % of all open flowers were usually triggered at the end of the day and were thus expected to set fruit. However, only around 10 % fruit-set was found, whereas hand-pollination resulted generally in a much higher fruit-set (up to 93 %, Tab. 2.11). The same discrepancy was found in *Afrocalathea rhizantha*. These findings in addition to observed pollen leftovers on fleshy staminodes after visitation indicate an imperfect pollen transfer. Especially in bird pollinated flowers pollen might additionally get lost by the deposition all around the beak not coming into contact with the stigmatic cavity. Indeed the two above mentioned autogamous species show the highest fruit-set.
- Fruitset is further reduced through predation by insects feeding on buds, ovaries and maturing fruits. In almost all African species the flowers emerge from the bracts during anthesis thus leaving the flowers without protection. The only exception is *Ataenidia conferta* with condensed inflorescences which indeed showed less damage by insects. Ants feeding on the extrafloral nectaries of the

bracteoles have not been observed defending the plants against any of the documented predators (see Buckley, 1982; Koptur, 1992; Heil and Bueno, 2007).

- Fruit abortion was observed after self-pollination, especially in species with large fruits (e.g. *Hypselodelphys scandens*) where resource limitation and selective abortion of fruits might favour high quality fruits (Sutherland, 1986; Horvitz and Schemske, 1988). Indeed, natural fruitset is much lower in the large fruiting *Hypselodelphys* spp. (2.5 to 9 %) than in *Marantochloa purpurea* (~30 %) within the same pollination syndrome but with much smaller fruits.

The observed low fruit-set in the African Marantaceae appears to be in part compensated by the vigorous asexual reproduction via rhizomes and adventive shoots (Brncic, 2003). The species with the lowest fruit-set *Marantochloa cordifolia* and *Marantochloa congensis* show the highest vegetative reproduction. In contrast the two autogamous species with the highest fruit-set demonstrate except rhizomes no additional features for vegetative reproduction. At least in *Halopegia azurea*, whose seedlings have repeatedly been found below adult plants autogamously produced fruits might be an alternative for local population maintenance.

2.5.5 DISPERSAL

No investigations have so far been conducted on the dispersal of African Marantaceae. As almost all species of African Marantaceae show an extended distribution area (Dhetchuvi, 1996) either efficient long distance dispersal agents or a long history of short distance dispersal events or a continuous slow expansion of the distribution area via vegetative reproduction have to be expected. To approach the dispersal biology of the species, indirect conclusions on the dispersal agent may be drawn from the morphology of the fruits and seeds (further investigations on fruit and seed morphology see Eichler, 1884; Humphrey, 1896; Grotjen, 1983). An important feature for the zoochory of the seed is certainly its arillus-like structure (see Eichler, 1884).

2.5.5.1 Water

- The fruits in the genus *Marantochloa* are small and may float. Indeed, the little streams and omnipresent flash floods after tropical rainfalls are easily able to

move the small and light fruits. The same might be true for the fruits of *Afrocalathea rhizantha* and *Ataenidia conferta.* In the latter the fruits fall probably out of the wilting inflorescence when the bracts turn from an upward position into a downward position. In addition, bird dispersal of the small red fruits might occasionally play a role for long distance dispersal.

- The fruits in *Halopegia azurea* are probably water dispersed as the species only occurs along small creeks and swamps. However, they require prior removal from the inflorescence where they are firmly enclosed. This could either be done by birds which have been observed to extract fruits from their protected location between leaf sheaths or by trampling bush pigs and elephants or autonomously after the short-lived shoots were decomposed.

2.5.5.2 Mammals

- The large and sweet fruits of *Thaumatococcus daniellii* are found near the ground. They are conspicuously red when ripe and are probably eaten by pigs or other large frugivorous mammals. The fruits are well-known for their high sugar content and serve as sweetener and taste modifier in tropical countries (Most et al., 1978; Bartoszewski et al., 2003). The black seeds are very hard and might pass the gut without damage.
- The fruits of *Megaphrynium* spp. and *Sarcophrynium* spp. form an important part of the diet of apes and monkeys. Entire seeds are found in their faeces after the animals have eaten the sweet effigurations (Williamson et al., 1990; Tutin and Fernandez, 1993; White and Abernethy, 1997) and are probably still viable due to their hard testa.
- The large and heavy but rather inconspicuous brown and green fruits of *Haumania* spp. and *Hypselodelphys* spp., respectively, might be dispersed mechanically by gravity (see also Tutin, 1998). The spiny structures on the fruit surface are not long enough to provide a mean for adhesion. These seeds were repeatedly found below the respective mother plants but no seedlings have been seen so far.

2.5.5.3 Birds

- *Marantochloa filipes* and *Trachyphrynium braunianum* are the only two species within the African Marantaceae with capsules. They present black seeds with an extremely conspicuous orange or white efiguarions that contrasts to the conspicuous orange colour of the inner fruit surface. This colour pattern is well known in bird dispersed fruits (Müller-Schneider, 1977).

2.6 CONCLUSIONS

The presented data give a comprehensive insight into the ecology of African Marantaceae. Through the development of different flower morphologies the Marantaceae have adapted to a variety of highly different pollinators. Shifts between pollinators might have played a crucial role in speciation e.g. in the genus *Marantochloa*. The role of the explosive pollination mechanism is not yet clear as the observations indicate a perhaps less efficient pollen transfer than expected in view of its complexity. Though fruit-set is generally low, Marantaceae in Africa are widespread and often dominate the understorey probably due to their high vegetative vigour. Here the data hint at a close interrelation of different modes of sexual versus asexual reproduction.

3 Diversity in floral synorganization affects pollendeposition and breeding system in Marantaceae

3.1 ABSTRACT

The flowers of the Marantaceae (~550 species) present an example of complex synorganisation facilitating an explosive pollination mechanism. In the present chapter the floral construction of 66 species covering the five major phylogenetic clades of the family Marantaceae are analysed under a functional morphological view. The results show that all species correspond in a `tunnel´-shaped fleshy staminode with an inner stiff swelling which narrows the floral tube exactly towards the tip of a lateral trigger appendage which is part of the hooded staminode. The deflection of this trigger appendage affects an explosive style movement which guarantees the transfer of pollen. The latter is secondarily presented on the back of a characteristic style head at the distal end of the style. However, despite high selection pressures on this functional unit there is also a lot of morphological variation realising the same functional demands. Thereby variations in the length of the fleshy staminode relative to the complex of style and hooded staminode affect a differential pollen deposition on the pollinator which might be a source for mechanical isolation. Furthermore, subtle morphological changes in the stylar head and the hood of the hooded staminode led several times independently to a shift from allogamy to autogamy.

3.2 INTRODUCTION

The zoophilous flowers of the angiosperms are highly diverse and coevolved with their pollinators. Thereby both have shaped the other´s diversity through reciprocal adaptations (Hess, 1983; Leppik, 1969; Lunau, 2004). The attraction of a flower is achieved through its synorganisation. This term was first introduced by Remane (1956) who referred to the interaction of individual parts of the organism to form a functional unit. Synorganisation is usually found in flowers. They form a single attractive unit and often exhibit a high physical matching with the respective pollinator. This is obtained either through the synoranization of the individual floral

organs from the same and/or adjacent whorls (e.g. brad petal circle in Malvaceae, lip flower in Lamiaceae) or through the synorganization of multiple flowers (e.g. umbrella inflorescences in Apiaceae or “blossoms” in Asteraceae). Thereby the seemingly indefinite morphological possibilities of a flower are guided by historical, architectural and ecological frameworks (Endress, 1994). Some flowers obtain even higher functionally synorganized entities in which several formerly independent organs increasingly specify, thereby obtaining new functions and achieving a higher order of functionality through close interaction (e.g. fusion of the anthers for secondary pollen presentation in Asteraceae, gynostegium in Asclepidaceae, gynostemium in Orchidaceae; see Endress, 1994).

A further example of extraordinary synorganizational complexity is placed by the Marantaceae (550 spp.; Anderson, 1998; Claßen-Bockhoff and Heller, 2008*a*). Their historical background is set by the order Zingiberales in which they are one of the most derived families (Kress, 1995; Kress and Specht, 2006*a*). Among the families of the order Zingiberales a continuous reduction of fertile anthers can be recognized (Kress, 1990). The basal Musaceae, Strelitziaceae, Heliconiaceae and Lowiaceae have still two and three fertile anthers in the outer and inner androecial whorl, respectively. The flowers of the Marantaceae, however, have in the outer androecial whorl only two staminodes and in the inner androecial whorl just one half fertile anther, the other primordia also develop into staminodes. The latter underwent major transformations (Gris, 1859; Eichler, 1884; Costerus, 1918; Loesener, 1930; Kunze, 1984) forming an explosive pollination mechanism unique in the Zingiberales (Costerus, 1918; Claßen-Bockhoff, 1991; Kennedy, 2000).

The functionality of this explosive pollination mechanism is due to an intimate relation between the style and two staminodes of the inner androecial whorl, the hooded and the fleshy staminode. Hereby the elaborate head of the trimerous style is enveloped by the hooded staminode. Through a differential growth of both organs during bud development the style is set under tension by the shorter hooded staminode (Pischtschan and Claßen-Bockhoff, 2008). As the theca is placed in the interlace between stylar head and hood of the hooded staminode, its pollen is squeezed out onto the pollen plate at the back of the stylar head to be secondarily presented (Claßen-Bockhoff, 1991; Yeo, 1993).

The established tension of the style is only released through the deflection of a lateral protruding appendage of the hooded staminode (Kunze, 1984; Claßen-

Bockhoff, 1991; Pischtschan and Claßen-Bockhoff, 2008). At the base of this trigger appendage a small fold, the `basal plate´, can almost universally be found (Pischtschan et al., in prep.). The deflection of the trigger appendage results in an immediate curling-in of the style. During this motion cross-pollen is scraped off from the arriving pollinator by the stigmatic cavity and self-pollen from the pollen plate is subsequently glued onto the insect or bird (for illustration see chapter 2). A bulge of sticky glandular material at the upper rim of the pollen plate serves to stick the pollen grains onto the pollinator (Claßen-Bockhoff, 1991; Yeo, 1993). The movement is irreversible and one of the fastest movements in the plant kingdom (~0.03 sec. *Thalia geniculata* in Claßen-Bockhoff, 1991).

This unique pollination mechanism has been postulated to be a key-innovation for the speciation of Marantaceae (Kennedy, 2000) (550 spp. in Andersson, 1998) as this family is by far more species rich than its sister family Cannaceae (10 spp. in Kubitzki, 1998). A phylogenetic analysis of the Marantaceae distinguishes five major clades (Prince and Kress, 2006*a*, Fig. 3.1): The *Sarcophrynium* clade is sister to all other Marantaceae. The *Calathea* clade (*Calathea* I and II) and the *Donax* clade are subsequently sister to a clade formed by the *Stachyphrynium*- and the *Maranta* clade.

However, the explosive pollination mechanism in the Marantaceae appears rather constringent with only a single chance per flower to be pollinated and a rather small stigmatic cavity and pollen plate and a small pollen quantity (chapter 2) for a successful pollen transfer. This implies a very precise floral synorganization to guarantee the excitation of the mechanism and an effective pollen transfer. Kunze (1984) hypothesized that swellings on the adaxial side of the fleshy staminode might lead the pollinator's mouthparts exactly to the trigger appendage to guarantee an excitation of the pollination mechanism. The cave formed by the stiff swellings of the fleshy staminode might serve as secondary nectar cave.

However, the Marantaceae are pollinated by a variety of different pollinators mainly bees of different sizes (small-, medium- to large-sized) and occasionally also birds (chapter 2; see also Kennedy, 2000; Locatelli et al., 2004). Furthermore, a survey on the morphology of the trigger appendages yielded ten distinct types (Fig. 3.1; Ley et al., 2007; Pischtschan et al., in prep.). These range from long lanceolate horizontally arranged trigger appendages (sword type) emerging distally on the hooded staminode to short forms (e.g. cushion type).

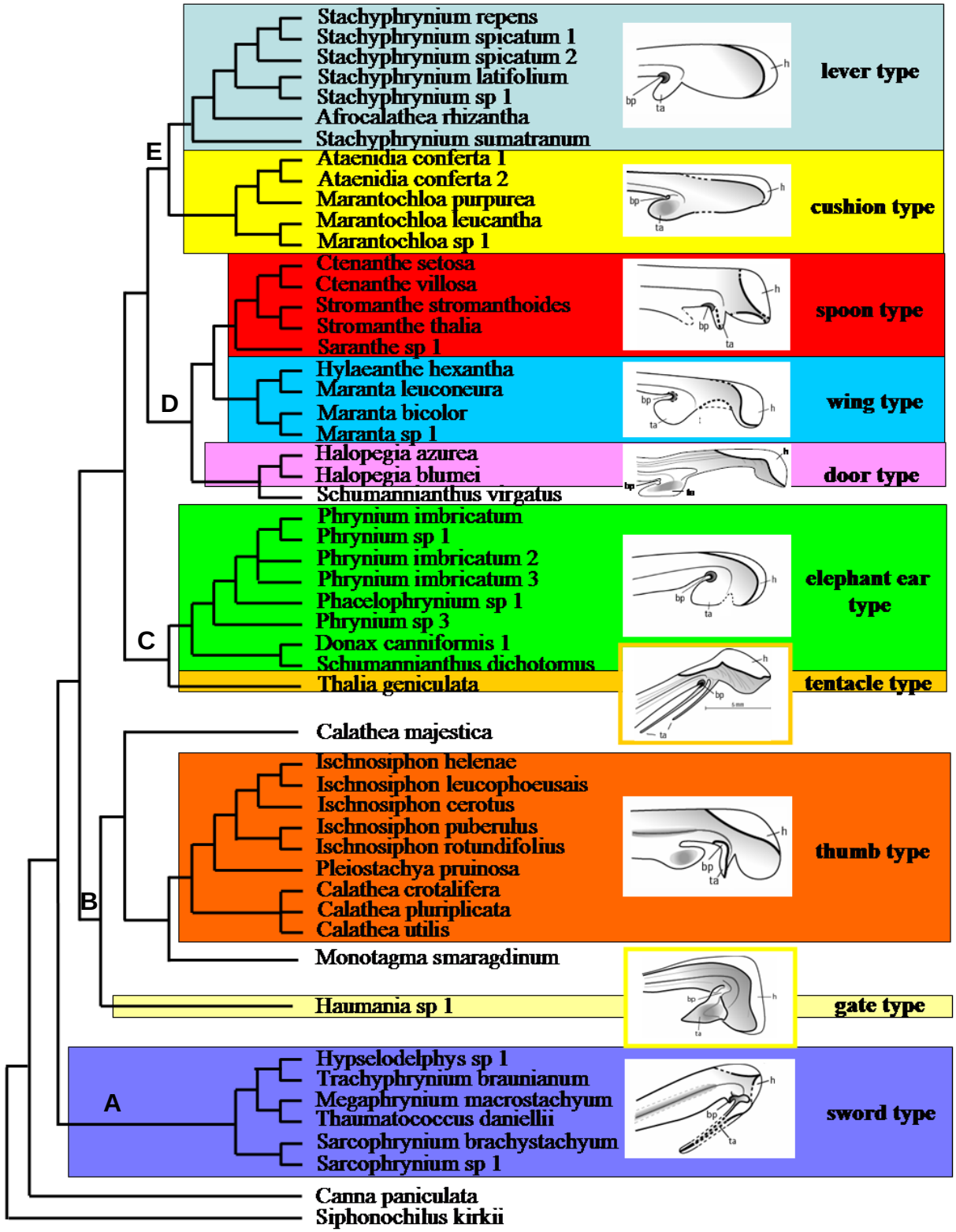


Figure 3.1: Ten different trigger types of the hooded staminodes in the Marantaceae flowers mapped onto the phylogenetic tree by Prince and Kress (2006*a*) (after Ley et al., 2007). bp, basal plate; h, hood of hooded staminode; ta, trigger appendage. A, *Sarcophrynium* clade; B, *Calathea* clade; C, *Donax* clade; D, *Maranta* clade; E, *Stachyphrynium* clade.

The short forms can be more or less broad and flat lobes which emerge either far proximal in the floral tube (cushion and door type) at an intermediate position (lever and wing type) or at the distal end of the hooded staminode (elephant type). Spoon and thumb type are short upright standing appendages ending is a pointed tip located at the distal part of the hooded staminode. Outstanding are the two appendages of the tentacle type and the stout, in the flower entrance vertically positioned door type. Both, pollinator body size and trigger type, have implications for the pollination process.

In this chapter it will be investigate in detail how these flowers are synorganized and if there are differences between clades. A family wide survey (based on phylogenetic clades after Prince and Kress, 2006*a*) over the morphological variability of the involved staminodes and their interaction in the functional system shall address the question whether the same precision is reached with each of those pollinators and trigger types and how do the morphologies of the individual organs possibly correlate with each other to maintain precision. A special attention is given to floral proportions and the probable site of pollen deposition on the pollinator.

Differences in floral synorganization might also be important for the configuration of the breeding system. Despite being self-compatible most of the Marantaceae are allogamous due to a strict spatial separation of the stigmatic cavity and the pollen plate (chapter 2). However, at least 44 species are listed to be autogamous and setting seed in the absence of pollinators (Kennedy, 2000; further data see chapter 2). For *Marantochloa leucantha,* Kennedy (2000) described a pathway how pollen might reach the stigmatic cavity during bud development. In the here presented study a comparison between the four unrelated autogamous species *Halopegia azurea, Maranta noctiflora, Marantochloa leucantha* and *Pleiostachya pruinosa* (Andersson, 1986; Kennedy, 2000; chapter 2; compare Prince and Kress, 2006*a*) shall elucidate the diversity of possible pathways of autogamous pollen transfer dependent on the individual phylogenetic background.

3.3 MATERIAL AND METHODS

The present study is based on the analysis of 66 species of Marantaceae from all over the world (Table 3.1). They were investigated based on material collected from specimen in Gabon (chapter 2) and La Gamba/Costa Rica, cultivars of the Botanical

Garden Mainz and alcohol material (70 % ethanol) from the botanical gardens in Aarhus/Denmark and Meise/Belgium. Explicit digital documentation of fresh material and material preserved in 70 % ethanol was undertaken with a Nikon Coolpix 995. The flowers were studied in detail under the dissecting microscope and all relevant structures were measured, drawn and compared between species.

To gain a better understanding of the origin of the fleshy staminode´s structures a survey on its ontogeny was conducted in 25 species (see Table 3.1 adding *Calathea ornata*). Different developmental stages are documented by photographs and drawings from specimens under the binocular.

Four autogamous Marantaceae species (*Halopegia azurea*, *Maranta noctiflora, Marantochloa leucantha, Pleiostachya pruinosa*) available in the living collection of the Botanical Garden at Mainz University (Germany) were chosen to study the process of pollen transfer in detail. At four different developmental stages the presence/absence of pollen grains in the stigmatic cavity were verified:

1) in mature buds after pollen deposition from the theca onto the stigmatic cavity,
2) in flowers at the onset of anthesis:
    a) before the excitation of the style,
    b) after excitation of the style with prior removal of the fleshy staminode to prevent collision of the stylar head with the swelling of the fleshy staminode;
3) after self-triggering of the style in untreated wilted flowers.

Fruit set was documented on five bagged inflorescences of *Halopegia azurea* in Gabon (see chapter 2) and specimen of *Maranta leuconeura, M. noctiflora* and *Pleiostachya pruinosa* in the greenhouse at Mainz University, Germany.

Abbreviations:

al, adaxial lobe;
bp, basal plate;
dss, distal stiff swelling;
gl, gland;
hs, hooded staminode;
fl, frontal lobe;
fs, fleshy staminode;
ls, lateral swelling of the hs
ov, ovary;
pa, petaloid appendage of fertile thecae;
pp, pollen plate;
pss, proximal stiff swelling;
sc, stigmatic cavity;
sh, stylar head;
sl, surrounding lobe;
ss, stiff swelling;
st, style (grey);
ta, trigger appendage.
x, indicates the passage to the nectar.

3.4 RESULTS

3.4.1 GENERAL PRINCIPLES OF FLORAL CONSTRUCTION IN MARANTACEAE

All investigated flowers correspond in the basic morphology and synorganisation of the three organs of the inner androecial whorl: style, hooded and fleshy staminode.

The central part of the flower is formed by the trimerous style (Fig. 3.2) with distally an asymmetric `head´ which stands in a 90° angle to the rest of the style and ends in the stigmatic cavity (sc). The latter is formed by three generally well distinguished stigmatic lobes (I. – III., Fig 3.2). The style bears a vertical standing, slightly abaxially inclined pollen plate at its back. Here a well defined packet of pollen grains is secondarily presented for transfer onto the pollinator. The bulge of glandular secretion at the upper part of the pollen plate and the high rim of the pollen plate in relation to the localisation of pollen deposition generally prevent self-pollen to reach the stigmatic cavity.

The explosive pollination mechanism is based on the envelopment of the style and especially the stylar head by the hooded staminode. Ontogenetic observations reveal that at a rather progressed state of bud development the originally flat leaf of the hooded staminode (hs) forms a `hood´ around the head of the style (st, Fig. 3.3). By a more proliferating growth of the lamina in comparison to the periphery of the hooded staminode the margin folds up whereas the lamina forms a pouch. The base of the stylar head grows into this pouch forming the first firm contact between style and hooded staminode (arrow, Fig. 3.3). Often the base of the stylar head is enlarged (see Figs 3.2; 3.4A, B, D), marks the most distal point (e.g. Fig. 3.4A) and/or forms a distinct ridge (see Figs 3.11, 3.14). This first contact marks the onset of a more rapid growth of the style in comparison to the hooded staminode resulting in a continuously tighter envelopment of the hood of the hooded staminode around the stylar head and the built-up of pressure in the style. This localized pressure point is maintained in the open flower so that e.g. in *Thalia dealbata* all parts of the hood except for the tissue around the base of the stylar head could be removed without releasing the style. In *Donax canniformis* the hood is rather open with upright standing margins so that the restricted contact point is clearly visible from above in an open flower (Fig. 3.5A, B). However, the hooded staminode does not only reach around the base of the stylar head but also covers the pollen plate and often even the stigmatic cavity (frontal lobe) protecting the pollen grains from the exterior view.

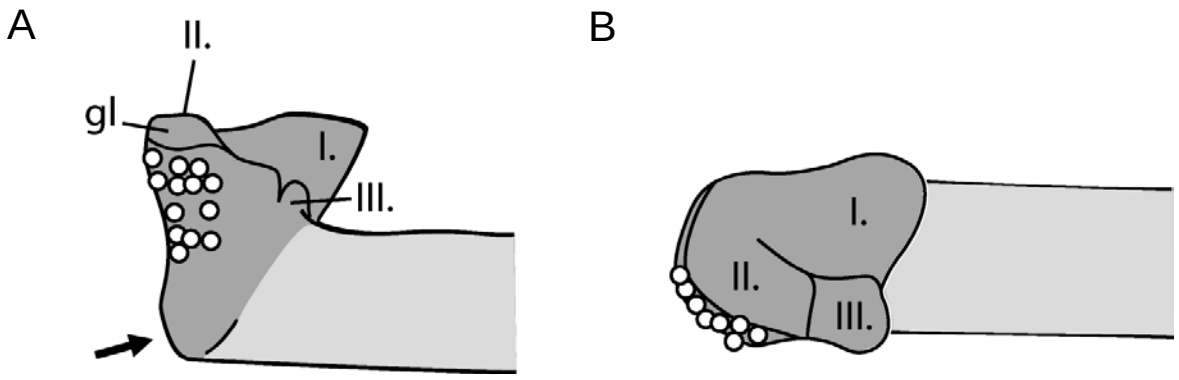


Figure 3.2: Model of a style in the Marantaceae. (A) lateral view. (B) top view. light grey, style; dark grey, stylar head; white dots, pollen grains on pollen plate. black arrow indicates pronounced base of the stylar head. stigmatic lobes are numberd I. to III. and form the stigmatic cavity.

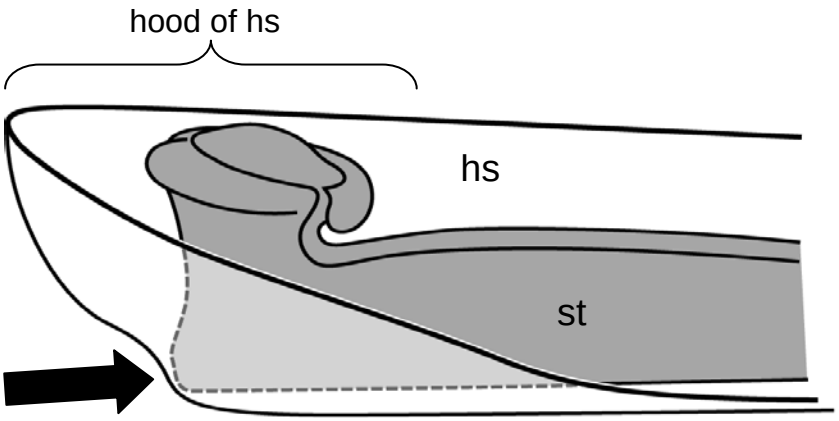


Figure 3.3: Late bud stage of *Marantochloa leucantha* illustrating the restricted point of pressure (arrow) between hooded staminode (hs, white) and style (st, grey) at the base of the stylar head.

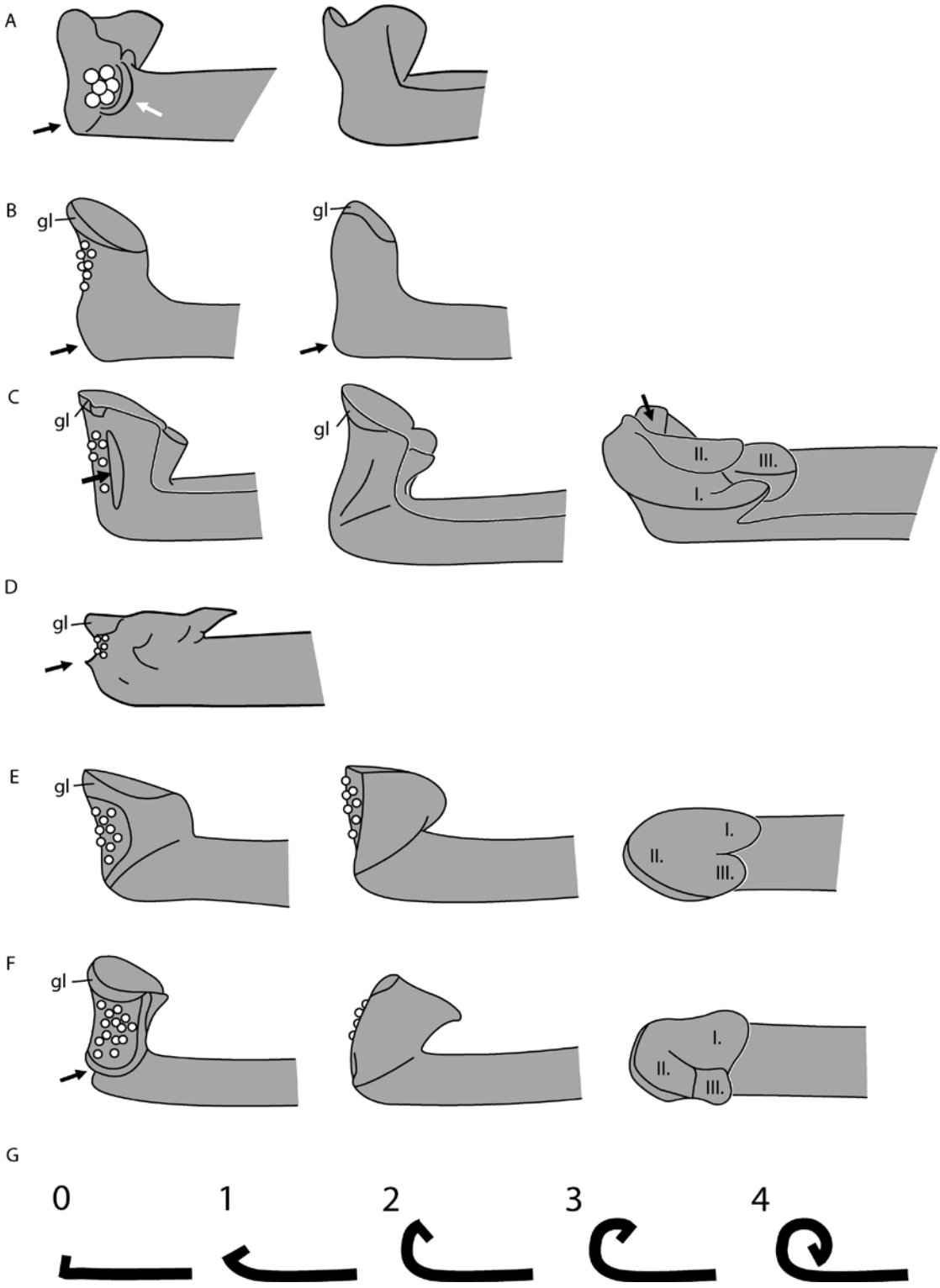


Figure 3.4: Diverse morphologies of stylar heads in six unrelated species and four species specific types of stylar bending after excitation of the explosive pollination mechanism. (A) *Sarcophrynium prionogonium*. Note the lateral appendage (white arrow) and the enlarged base (black arrow). (B) *Ischnosiphon helenae*. Note the elongated stylar head and the pronounced base of the stylar head (arrow). (C) *Hylaeanthe hoffmannii*. Note the lateral pronounciation (arrow). (D) *Stachyphrynium latifolium*. Note the enlarged, pointed base of the stylar head (arrow). (E) *Marantochloa cordifolia.* Note the short stylar head. (F) *Marantochloa filipes*. Note the stepped pollen plate (flash). (G) four schematic types of stylar bending (1 to 4; 0, starting position). white dots, pollen grains; I. - III., stigmatic lobes of trimerous style.

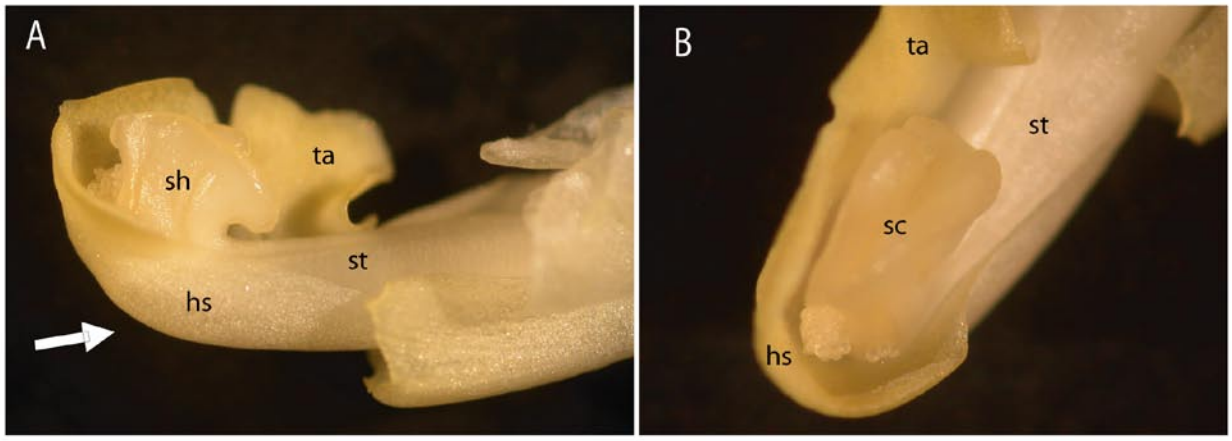


Figure 3.5: The restricted point of pressure in an open flower of *Donax canniformis* (indicated by an arrow). Note the upright standing rim of the hooded staminode (hs). (A) from a lateral point of view, (B) view from above.

The release of the explosive movement of the style is affected by the deflection of the `trigger appendage´ (ta, Fig. 3.5) at the margin of the hooded staminode. The distance between the tip of the trigger appendage where the excitation takes place and the pollen plate which transfers the pollen determines together with the length of the polinator´s mouthparts the localization of pollen deposition onto the pollinator (see Table 3.1). After excitation the style remains bended. The degree of bending is species specific (Fig. 3.4).

The `fleshy staminode´ is located opposite to the complex of style and hooded staminode (Fig. 3.8). It is recognized by its rather stiff nature forming a `tunnel´ along the style and giving a tubular shape to the flower. Only the mouthparts of the pollinator can usually enter the narrow floral tube.

Additionally, this `tunnel´ is narrowed by a swelling (dss, pss, ss Fig. 3.6). This swelling is usually pronounced and can be either bipartite as e.g. in the genus *Megaphrynium* (dss, pss Fig. 3.6A-C) or long and elongated as in some species of the genus *Marantochloa* (ss, Fig. 3.6D-F). In the bipartite case one pronounced part of the stiff swelling is generally located directly at the flower entrance (distal stiff swelling, dss), whereas the other pronounciation is found further down in the floral tube (proximally stiff swelling, pss).

The final shape of the stiff swelling can already be recognized in the bud at the time of its first appearance (see Fig. 3.7). The stiff swelling is a secondary, superficial structure usually located lateral to the midrib. It only develops after the lamina and

the midrib are already present (Fig. 3.7). Thereby it has generally no influence on the vascular bundle and it is only innervated when it is very large (see Fig. 3.6E).

The swelling is always opposite to the trigger appendage and both structures highly correlate in their respective shape (see Figs 3.9 to 3.14) so that the proximal nectar storage compartment can only be reached by passing by the trigger appendage and deflecting the latter.

In the proximal part of the flower all organs of the inner androecial whorl and the style are congenitally fused forming the floral tube. This part elongates only a few hours before anthesis. The style is very thin and the stiff swelling of the fleshy staminode rather faint or even absent increasing the possible storage space for the nectar. In this part the explosive mechanism cannot be excited.

The attraction of a flower is reached by either large surrounding lobes of the fleshy staminode (Fig. 3.8), large outer staminodes (Fig. 3.8) and/or straight broad petals (only in *Megaphrynium trichogynum,* see chapter 2, Fig. 2.8C). The surrounding lobes of the felshy staminode are the soft and petaloid parts of the fleshy staminode which extend beyond the mere flower entrance.

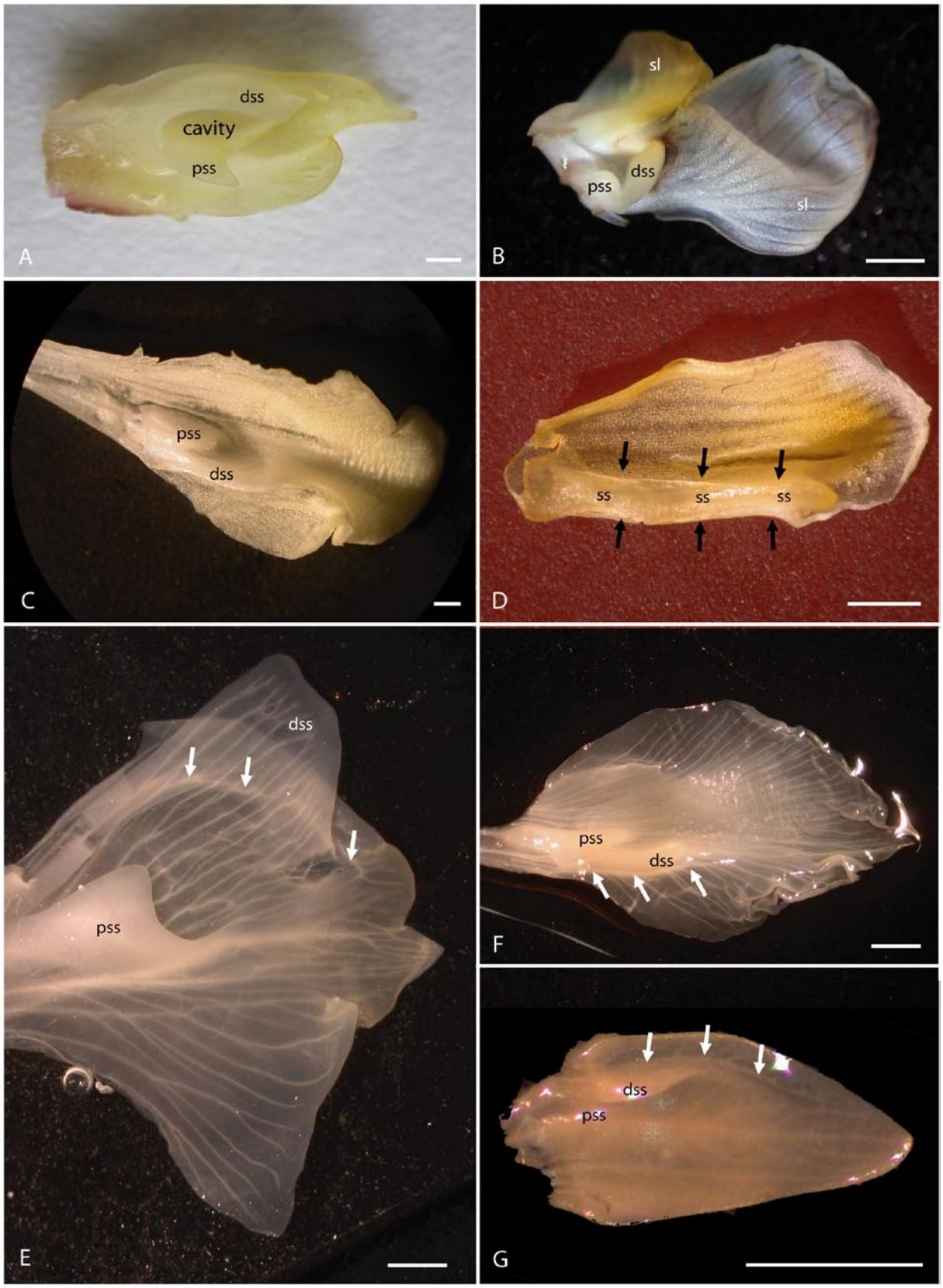


Figure 3.6: Diversity in the morphology of the fleshy staminodes (fs). Note especially the morphology of the stiff swelling (ss). (A) *Megaphrynium macrostachyum*. Note the pronounced proximal part of the stiff swelling (pss) which forms a cavity. (B) *Haumania danckelmanniana*. Note the two parts of the ss and the two large surrounding lobes (sl). (C) *Donax canniformis*. (D) *Marantochloa leucantha*. Note the continuous long stiff swelling which is delimited by black arrows. (E) *Thaumatococcus* sp.1. Note the innervations of the large distal stiff swelling (dss). (F) *Donax canniformis*. (G) *Hypselodelphys hirsuta.* Note in E, F and G the deviation of the lateral vascular bundle (white arrows). Bars: 1mm.

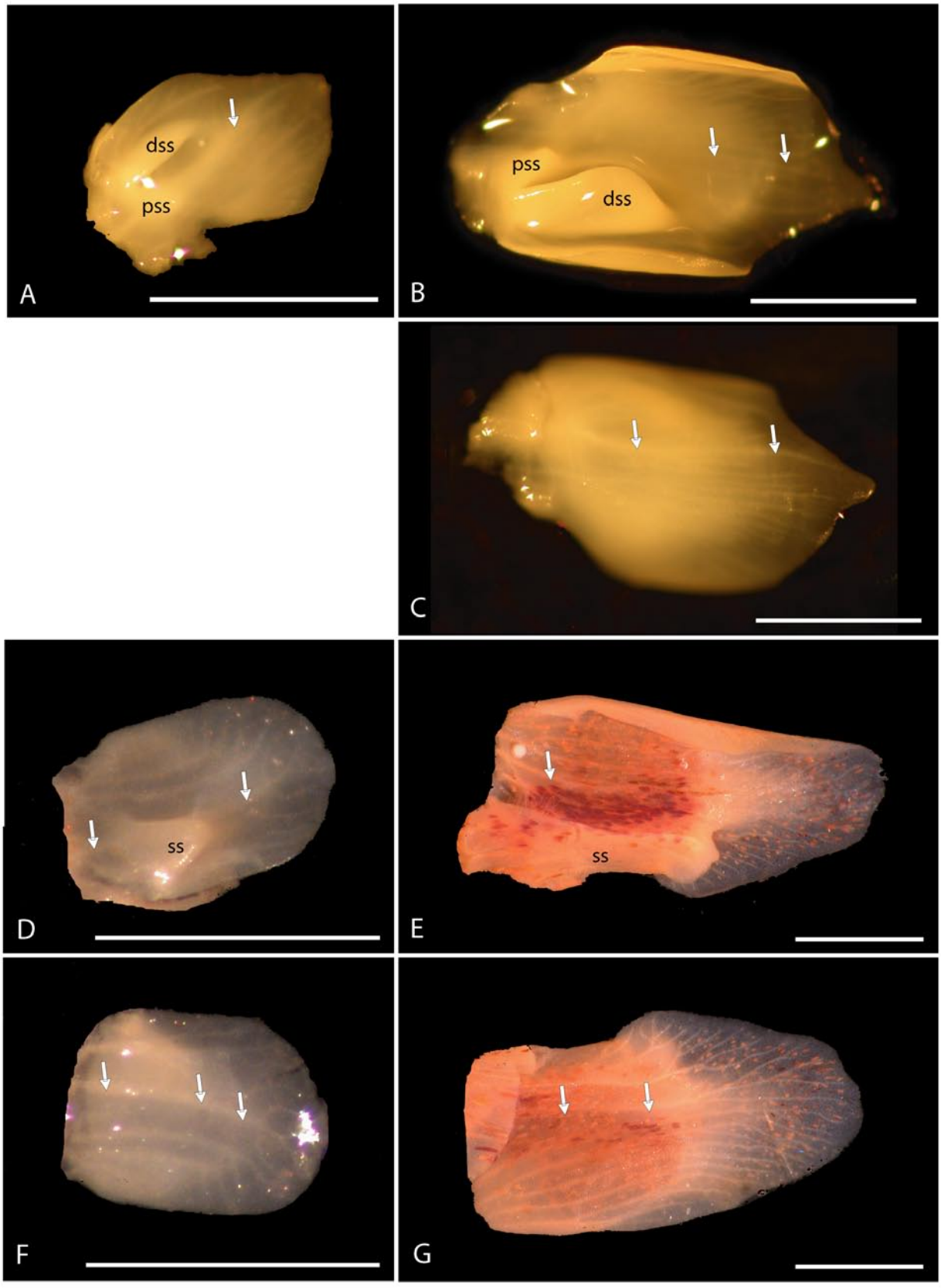


Figure 3.7: Formation of the stiff swelling (ss) during the ontogeny of the fleshy staminode. Note the position of the stiff swelling lateral to the midrib (course of the midribe indicated by white arrows). (A-C) *Megaphrynium trichogynum.* Note the two distinct parts of the stiff swelling (dss, distal stiff swelling; pss, proximal stiff swelling). (D-G) *Marantochloa leucantha*. Note the single long stiff swelling. (A, D, F) bud 2 mm long. (B, C, E, G) bud 5 mm long. (C, F, G) Note the straight course of the vascular bundles independent of the stiff swelling on the abaxial side of the leaf. Bars: 1 mm

Figure 3.8: Attractive elements in the flowers of Marantaceae. (A) *Haumania danckelmanniana*. The yellow coloration of parts of the surrounding lobes (sl), the petaloid appendage of the half fertile anther and the hooded staminode in the flower centre indicate the flower entrance. (B) *Maranta leuconeura*. Note the synorganized colouration of the surrounding lobes of the fleshy staminode and outer staminodes (os). (C) *Halopegia azurea*. Note the contrasting yellow and blue/violet coloration of the petaloid appendage of the half fertile anther and the staminodes, respectively. (D) *Hypselodelphys hirsuta*. Note the yellow nectar guides on the fleshy staminode (arrow). (E) *Donax canniformis*. Note the symmetric surrounding lobe and the large outer staminodes.

Table 3.1: Morphological and synorganizational features of Marantaceae ordered by phylogenetic clades (Prince and Kress, 2006*a*) and trigger type (Pischtschan et al., in prep.). **onto. invest.**, ontogenetic investigations conducted; **curling-in of style**: 1, very little, 2, little, 3 far, 4 very far (for illustration see Fig. 3.4); **frontal lobe**: 1, total cover of stigmatic cavity; 2, half cover; 3, only distal rim covered; 0, no cover; **adaxial lobe**: 1, total cover of adaxial side of stylar head; 2, half cover; 0, no cover; **proximal/distal stiff swelling (pss/dss)**: 1, pronounced: a) pointed, b) long; 2, inconspicuous: a) swollen long; x, continuous long stiff swelling; **trigger position**: A to E, see Fig. 3.17; **surrounding lobes (sl) of fleshy staminode (fs)**: 1, conspicuously symmetrical: a) with tip, 2, conspicuously asymmetrical: p) on opposite side of ss, q) on side of ss; 3, inconspicuous, totally reduced: a) with tip; **hs**, hooded staminode; **n**, number of flowers measured / of outer staminodes; **distance x**, distance between trigger tip and distal end of hs; **distance y**, distance between trigger tip and floral entrance; **os**, outer staminodes; **red**., reduced. **sl**, surrounding lobes; **ten.**, tentacle; *, surrounding lobe of fleshy staminode reach in front of floral entrance; °, note comment in the results; grey, flowers with pollen disposition probably into the proboscidial fossae underneath the insect´s head; all other species, pollen deposition onto insect´s mouthparts.

clade	trigger type	species	floral characteristics									floral measurements [mm]						
			onto. Invest.	curling-in of style	frontal lobe	adaxial lobe	dss	pss	pubescence of pss	trigger position	sl of fs	n	fleshy staminode	hooded staminode	hs – fs	distance x	distance y	n of os
Sarcophrynium	sword	*Hypselodelphys hirsuta* (Loes.) Koechlin	+	4	1	1	1	1	-	C	3a	8	18.8 ± 1.3	22.4 ± 1.3	3.6 ± 1.3	13.5 ± 1.7	9.8 ± 1.1	2
		Hypselodelphys poggeana (K. Schum.) Milne-Redh.	+	4	1	1	1	1	-	C	3a	9	16.5 ± 1.1	20.3 ± 1.2	3.9 ± 0.8	12.9 ± 2.2	9.1 ± 2.1	2
		Hypselodelphys scandens Louis et Mullenders	+	4	1	1	1	1	-	C	3a	8	17.5 ± 1.2	21.3 ± 0.5	3.8 ± 1.3	15.5 ± 1.2	11.8 ± 1.0	2
		Hypselodelphys violacea (Ridley) Milne-Redh.		4	1	1	1	1	-	C	3a	3	19.0 ± 1.00	24.0 ± 1.0	5 ± 1.7	12.7 ± 3.1	7.7 ± 1.5	2
		Megaphrynium gabonense Koechlin	+	4	2	0	1	1a	+	C	3a	4	10.0 ± 0.0	9.5 ± 0.6	-0.3 ± 0.6	6.5 ± 0.6	7.0 ± 0.0	2 red.
		Megaphrynium macrostachyum (Bentham) Milne-Redhead		4	2	1	1	1a	+	C	3a	5	12.4 ± 0.89	12.6 ± 0.6	0.2 ± 1.3	4.9 ± 0.9	7.5 ± 0.7	2 red.
		Megaphrynium trichogynum Koechlin	+	4	2	0	1	1a	+	C	2a,p	8	14.1 ± 1.0	15.6 ± 0.5	1.4 ± 10.1*	10.4 ± 0.6	8.8 ± 0.8	2 red.
		Sarcophrynium brachystachyum (Bentham) K.Schumann	+	2	3	1	1	1a	+	C	3a	2	10.0 ± 0.0	10.0 ± 0.0	0.0 ± 0.0°	5.0 ± 0.0	5.0 ± 0.0	2
		Sarcophrynium prionogonium (K. Schum.) K. Schum.		2	3	1	1	1a	+	C	3a	4	8.8 ± 1.0	7.75 ± 0.5	-1.0 ± 0.8°	4.1 ± 0.3	5.9 ± 0.6	2
		Sarcophrynium schweinfurthianum (Kuntze) Milne-Redh.		2	3	1	1	1a	+	C	3a	1	7	7	0°	5.5	5.5 ± 0.0	2
		Thaumatococcus daniellii (Bennet) Bentham		4	2	1	1	1a	-	C	3a	1	25	25.5	0.5	10	9.5	1 red.
		Thaumatococcus sp.1	+	4	2	1	1	1a	-	C	3a	5	25 ± 1.0	25.2 ± 0.8	1.6 ± 0.9	8.8 ± 0.8	8.6 ± 0.5	1 red.
		Trachyphrynium brauneanum (K. Schumann) Baker		4	1	1	1	1	-	C	3a	3	21 ± 1.0	23.3 ± 2.1	2.3 ± 2.1	13.3 ± 1.5	11 .0 ± 1.0	2
Calathea	gate	*Haumannia danckelmanniana* (J. Braun et K. Schumann) Milne-Redhead		3	0	0	1	1	-	D	2q	1	12	10	-2	3	4.0 ± 0.0	2
		Haumannia liebrechtsiana (de Wild. & Th. Dur.) J. Leonard	+	3	0	0	1	1	-	D	2q	7	n/a	13.9 ± 0.9	~-2	3	4.0 ± 0.0	2

clade	trigger type	species	floral characteristics									floral measurements [mm]						n of os
			onto. Invest.	curling-in of style	frontal lobe	adaxial lobe	dss	pss	pubescence of pss	trigger position	sl of fs	n	fleshy staminode	hooded staminode	hs – fs	distance x	distance y	
Calathea	thumb	*Calathea crotalifera* S.Watson		3	1	1	2	2	+	B	3a	1	n/a	n/a	1	4	3	1
		Calathea cylindrica (Roscoe) K.Schum.		2	1	1	2	2	+	A	3	1	34	35	1	3	2	1
		Calathea microcephala (Poeppig & Endlicher) Koernicke		3	1	2	x 2		+	D	1	1	10	12	2	1	-1	1
		Calathea lutea G.Mey.		2	1	2	1a	2a	+	D	3	1	16	13	3	4	1	1
		Calathea picturata (Linden) Koch et Linden		n/a	2	2	1	2	+	D	3a	1	17	20	3	2	-1	1
		Calathea platystachya Standl. & L.O.Williams		3	2	2	1a	2a	+	D	1	1	33	32	1	2.5	1.5	1
		Calathea bachemiana E.Morren	+	2	3	2	1	2a	+	D	1	1	36	34	2	1	1	1
		Ischnosiphon heleniae Koernicke		3	2	2	2	2	-	D	1	1	25.5	27	1.5	2	0.5	1
		Pleiostachya pruinosa (Regel) K. Schumann	+	3	1	2	1	2	+	D	3	1	42	39	3	4	1	1
Donax	elephant	*Donax canniformis* (G. Forster) K. Schumann	+	3	0	2	1	1a	+	C	1	1	18	17	-1	3.5	4.5	2
		Phacelophrynium interruptum Warb. ex K.Schum.	+	2	0	1-2	1	1a	+	C	1	1	5	4.5	0.5	2	1.5	1
		Phacelophrynium maximum Blume (K. Schum.)		3	0	0	1	1a	+	B	1	1	21	21	0	3	3	1
		Phryium hainense T.L. Wu & S.J. Chen		2	0	1	1	1a	+	B	2p	1	10	10	0	3.5	3.5	2
		Phrynium imbricatum Roxb.		2	0	1	1	1a	+	C	2p	1	22	21	1	4	3	2
		Phryium obscurum Teijsm. & Binn.	+	3	0	1	1	1a	+	B	1	1	28	25	0 to -2	4	4 to 7	2
		Phryium pubinerve Blume		2	0	2	1	1a	+	B	2p	1	14	14	0	3	3	2
		Schumannianthus dichotomous (Roxburgh) Gagnepain	+	3	0	2	1	1a	+	C	1	1	30	30	0	5	5	2
	ten.	*Thalia dealbata* Fraser		4	0	0	1	2a	-	B	3	1	7	7	0	3	3	1
		Thalia geniculata Linné	+	4	0	0	1	2a	-	B	3	1	9	9	0	3	3	1
Maranta	door	*Halopegia azurea* (K. Schumann) K. Schumann		3	1	2	1	1	-	C	1	6	12.2 ± 1.6	13.3 ± 0.8	1.2 ± 1.2	10.5 ± 0.6	9.3 ± 1.0	2
		Halopegia blumei (Koern.) Schum.		3	1	2	1	1	-	C	1	1	9	9	0	4	4	2
	spoon	*Ctenanthe lubbersiana* (E. Morren) Eichler ex Petersen	+	2	3	1	1	1	-	B	3a	1	7	7	0	2	2	2
		Ctenanthe oppenheimiana (E. Morren) K. Schumann		n/a	n/a	2	1	1a	+	B	2p		17	16	-1	2.5	3.5	?
		Myrosma setosum Bentham	+	2	3	0	1	1	-	B	1	1	11	11	0	4	4	2
		Stromanthe porteana Gris.		2	n/a	1	1	1	-	A	2p	1	7	8	1	1	0	2
		Stromanthe sanguinea Sond.		2	3	2	1	1a	+	A	1	1	6.5	7	0.5	1.5	1	2
		Stromanthe tonckat (Aublet) Eichler		3	3	1	1	1	-	A	1	1	6	6	0	2	2	2

clade	trigger typen	species	floral characteristics									floral measurements [mm]						n of os
			onto. Invest.	curling-in of style	frontal lobe	adaxial lobe	dss	pss	pubescence of pss	trigger position	sl of fs	n	fleshy staminode	hooded staminode	hs – fs	distance x	distance y	
Maranta	wing	*Hylaeanthe hoffmannii* (K. Schumann) Jonker et Jonker	+	2	1	2	2	2a	+	C	3	1	16	17	1	9	8	2
		Maranta arundinacea L.		3	3	1	1	1	+	B	2p	1	22	23	1	4.6	4	2
		Maranta depressa E. Morr.		4	3	1	1	2	+	B	3a	1	8.5	9.5	1	2	1	2
		Maranta leuconeura E. Morr.	+	n/a	2	1	1	2	-	B	3a	1	7.5	8.5	1	2.5	1.5	2
		Maranta noctiflora Koernicke		4	3	1	1	1a	+	B	2p	1	17	18	1	4	3	2
Stachyphrynium	cushion	*Ataenidia conferta* (Bentham) Milne-Readhead	+	4	0	1	2	2a	-	C	3	8	16.5 ± 0.5	19.3 ± 0.8	2.6 ± 0.7	9.9 ± 3.8	7.7 ± 1.3	2
		Marantochloa congensis (K.Schumann) J. Léonard et Mullenders		2	3	1	x 2b		+	E	2p	7	6.2 ± 0.6	7.4 ± 0.6	1.1 ± 0.8	6.1 ± 1.1	5.1 ± 0.3	2
		Marantochloa cordifolia (K. Schum.) Koechlin	+	2	1	2	2	1b	-	C	3	8	20.3 ± 9.0	25.4 ± 0.9	4.7 ± 1.4	13.0 ± 0.6	8.3 ± 1.4	2
		Marantochloa cuspidata (Roscoe) Milne.-Redh.		4	2	1	2	1b	-	C	3	1	12	17	5	12	8	2
		Marantochloa filipes (Benth. In Hook.) Hutch.		1	2	1	1	2a	+	C	2p	10	10.5 ± 0.6	10.5 ± 0.8	1.1 ± 0.6	4.2 ± 0.4	3.3 ± 0.7	2
		Marantochloa incertifolia Dhetchuvi (Makokou)		2	3	1	x 2b		+	E	2p	1	6	6	0	5	5	2
		Marantochloa incertifolia Dhetchuvi (Monts de Cristal)		2	3	1	x 2b		+	E	2p	3	7.0 ± 1.7	6.7 ± 0.6	-0.3 ± 1.2	4.0 ± 0.0	2.5	2
		Marantochloa leucantha (K. Schumann) Milne-Redhead	+	2	3	2	x 2		+	E	3	6	4.8 ± 0.5	6.3 ± 0.4	1.3 ± 0.5	4.3 ± 0.4	3.6 ± 0.7	2
		Marantochloa mannii (Bentham) Milne-Redhead		4	2	2	2	2a	+	C	3	1	15	18	3	10	7	2
		Marantochloa monophylla (K. Schum.) D´Orey		2	3	1	x 2b		+	E	2p	3	5.7 ± 0.6	6.0 ± 0.0	0.3 ± 0.6	3.8 ± 0.3	3.5 ± 0.9	2
		Marantochloa purpurea (Ridley) Milne-Redhead	+	4	1	1	2	1b	-	C	3	7	11.5 ± 1.7	15.1 ± 0.8	3.8 ± 1.1	10,5 ± 1.4	7.4 ± 1.1	2
		Marantochloa sp.1		4	1	1	2	1b	-	C	3	4	14.3 ± 0.5	19.0 ± 1.2	4.7 ± 1.0	12.8 ± 1.0	9.0 ± 0.0	2
		Marantochloa sp.2		3	2	1	2	1	-	C	3	5	16.3 ± 0.7	19.4 ± 1.34	3.1 ± 1.0	13.4 ± 0.6	11.7 ± 1.0	2
		Marantochloa sp.3		2	0	1	2	1	-	C	3	4	17.9 ± 1.4	18.3 ± 1.0	1.5 ± 0.6	9.0 ± 0.0	8.3 ± 0.5	2
	lever	*Afrocalathea rhizantha* K. Schumann	+	3	2	2	1	2	-	C	3a	5	24.4 ± 2.1	28.3 ± 2.7	4.0 ± 1.4	10.3 ± 1.5	4.3 ± 1.7	2
		Stachyphrynium jagornianum (K. Koch) K. Schum.	+	n/a	2	0	1	2	+	C	3a	1	16	15	0	3	3	2
		Stachyphrynium latifolium (Blume) K.Schum.		2	2	1	1	1a	+	C	3	1	36	36	0	3.5	3.5	2
		Stachyphrynium placentarium (Lour.) Clausager & Borchsenius		2	2	0	1	1a	-	C	3a	1	25	27	2	5	3	2
		Stachyphrynium spicatum (Roxb.) K. Schum.		2	2	1	1	1a	+	C	3	1	29.5	29	0.5	4	3.5	2

3.4.2 SPECIFIC TRAITS IN THE *SARCOPHRYNIUM* CLADE

In the *Sarcophrynium* clade (Fig. 3.1) the trigger appendage (ta) is located in an extremely distal position on the hooded staminode and forms a long lengthwise folded appendage pointing in proximal direction (Fig. 3.9). It is located laterally to the style and is most sensitive at its tip. A slight deflection results in the release of the curling-in movement of the style.

In all species of this clade there is a long lateral swelling (ls, Fig. 3.9 IC, IIC) in the hooded staminode parallel to the elongated trigger appendage. It causes that the style is slightly shifted to the adaxial side in the unreleased flower. Additionally, depending on stiffness of the floral tissue, it affects a backwards bending of the hooded staminode after excitation in all species of the genera *Hypselodelphys* and *Trachyphrynium.*

The stiff swelling of the fleshy staminode is in all species bipartite but highly different in its pronounciation between the genera.

3.4.2.1 Hypselodelphys and *Trachyphrynium* (Fig. 3.9 II)

All species of the genera *Hypselodelphys* and *Trachyphrynium* form a morphologically homogenous group. Their flowers are the largest in the clade (Table 3.1) presenting a high and wide flower entrance often flanked by two yellow spots on the lateral walls of the `tunnel´ of the fleshy staminode. Additionally, two white circular rounded outer staminodes contribute to the appearance of a large flower and substantially increase their attraction. The rose/violet petals are reflexed backwards and the surrounding lobes of the fleshy staminode are reduced except an elongated pointed tip which is bent backwards. Thus none of those latter two structures significantly contribute to the flower´s attraction.

The trigger appendage in these two genera is the longest in the clade (Table 3.1) resulting in a large distance between the flower entrance and the tip of the trigger appendage and the there behind stored nectar, respectively (chapter 2 Fig. 2.1). The tip of the trigger appendage is sometimes curved in abaxial direction (Fig. 3.9 IIC) so that it stands vertically. Thereby it blocks the passage to the nectar and forces its deflection by any nectar searching animal.

The trigger tip is located opposite to the proximal stiff swelling of the fleshy staminode, however, the latter is not very prominent in these two genera. The

narrowing of the floral tube is still reached by the overall form of the fleshy staminode which is not equally wide over its whole length but becomes considerably narrower at the height of the trigger tip (see chapter 2 Fig. 2.1A).

The fleshy staminode is several millimetres shorter than the complex of style and hooded staminode (Table 3.1, Fig. 3.9 IIC) so that the style movement takes partly place outside the flower tube and pollen is deposited into the proboscidial fossae underneath the head of the insect. Thereby the large distance between the tip of the trigger appendage and nectar reward and the flower entrance forces the insects to maximally introduce their proboscis into the flower. This results in an exact positioning of their head above the stylar head which carries the pollen packet.

After excitation the final position of the style is directed slightly in adaxial direction so that it leaves a passage for the insect's proboscis facilitating recurrent visits throughout the day.

3.4.2.2 Megaphrynium and *Thaumatococcus* (Fig. 3.9 I)

In these genera the proximal stiff swelling (pss) of the fleshy staminode is extremely pronounced leaving only a tiny passage to the nectar (red cross in Fig. 3.9). It additionally forms a longitudinal separation of the floral tube so that after rolling-in the style is separated from the passage to the nectar. As the fleshy staminode is as long as or even longer than the complex of style and hooded staminode the curling-in movement of the style takes place inside the floral tube which consequently leads to a pollen deposition on the introduced mouthparts of the pollinator and not underneath its head as in *Hypselodelphys* and *Trachyphrynium* (see chapter 3.4.2.1). Thereby, *Thaumatococcus* differs from *Megaphrynium* in a much longer floral tube (Table 3.1). The distance between flower entrance and the tip of the trigger appendage however is identical in those two genera so that pollen is probably deposited onto the identical locality of the pollinator´s mouthparts. Only in *Megaphrynium gabonense* and *M. macrostachyum* this distance is about 2 mm shorter due to an overall smaller flower size compared to *M. trichogynum* and *Thaumatococcus* spp (see Table 3.1).

The outer staminodes of all these species are highly reduced and thereby inconspicuous. They are narrow and lanceolate and lie alongside the floral tube and do not extend beyond the length of the petals. Instead, *Megaphrynium trichogynum* attracts pollinators through the outstretched broad yellow and red petals which give

the flower the appearance of a long and broad tube. All other species have reflexed petals. *M. gabonense* and *M. macrostachyum* are additionally rather small and thereby less conspicuous. The flowers of *Thaumatococcus* are very large which might compensate for the less attractive reflexed petals. The predominant colours of these flowers are yellow and red.

Megaphryium trichogynum stands out against all other species of this group in that its entrance of the floral tube is obscured by the surrounding lobes of the fleshy staminode. In all other species the entrance is freely accessible and the surrounding lobes of the fleshy staminode are reduced to a reflexed elongated tip.

As in the genera *Hypselodelphys* and *Megaphrynium,* all species possess a lateral swelling in the hooded staminode. However, as these flowers exhibit an extremely strong floral tissue the hooded staminode is prevented from bending backwards after excitation.

3.4.2.3 Sarcophrynium

The species of the genus *Sarcophrynium* form again a very different but highly uniform group within the clade. They differ from all before mentioned species in a smaller overall flower size. As the surrounding lobes of the fleshy staminode are reduced except for a short tip their attraction is mainly based on the two conspicuous outer staminodes and the petals which are not entirely flexed backwards (see chapter 2, Fig. 2.8D).

The trigger appendages of these species are the shortest (Table 3.1) and broadest in the clade. Therefore the distance between the tip of the trigger appendage and the flower entrance is reduced (Table 3.1). Still pollinators with a proboscis of about this length are forced to maximally introduce their proboscis into the flower. An additional guiding structure is provided by a `roof´ formed by the tip of the fleshy staminode which forces the insect's body right in front of the flower entrance close to the stylar head. Although the complex of style and hooded staminode protrudes only little beyond the fleshy staminode the pollen is probably deposited into the proboscidial fossae due to the narrow head of the observed visiting insects which can enter the narrow tunnel of the fleshy staminode only a little.

Inside the floral tube the fleshy staminode exhibits a prominent proximal stiff swelling. It creates a small `cave´ in which the stylar head disappears after excitation.

Thus in the triggered stage the stylar head is entirely separated from the `tunnel´ through which the insects reach the nectar allowing recurrent visits.

The stylar head of the *Sarcophrynium* species bears a unique feature in the Marantaceae in that its pollen plate is located on a lateral appendage and has a pronounced lateral outgrowth (Fig. 3.4A, white arrow). This exceptional asymmetric position is an important feature in the process of pollen deposition onto the insect.

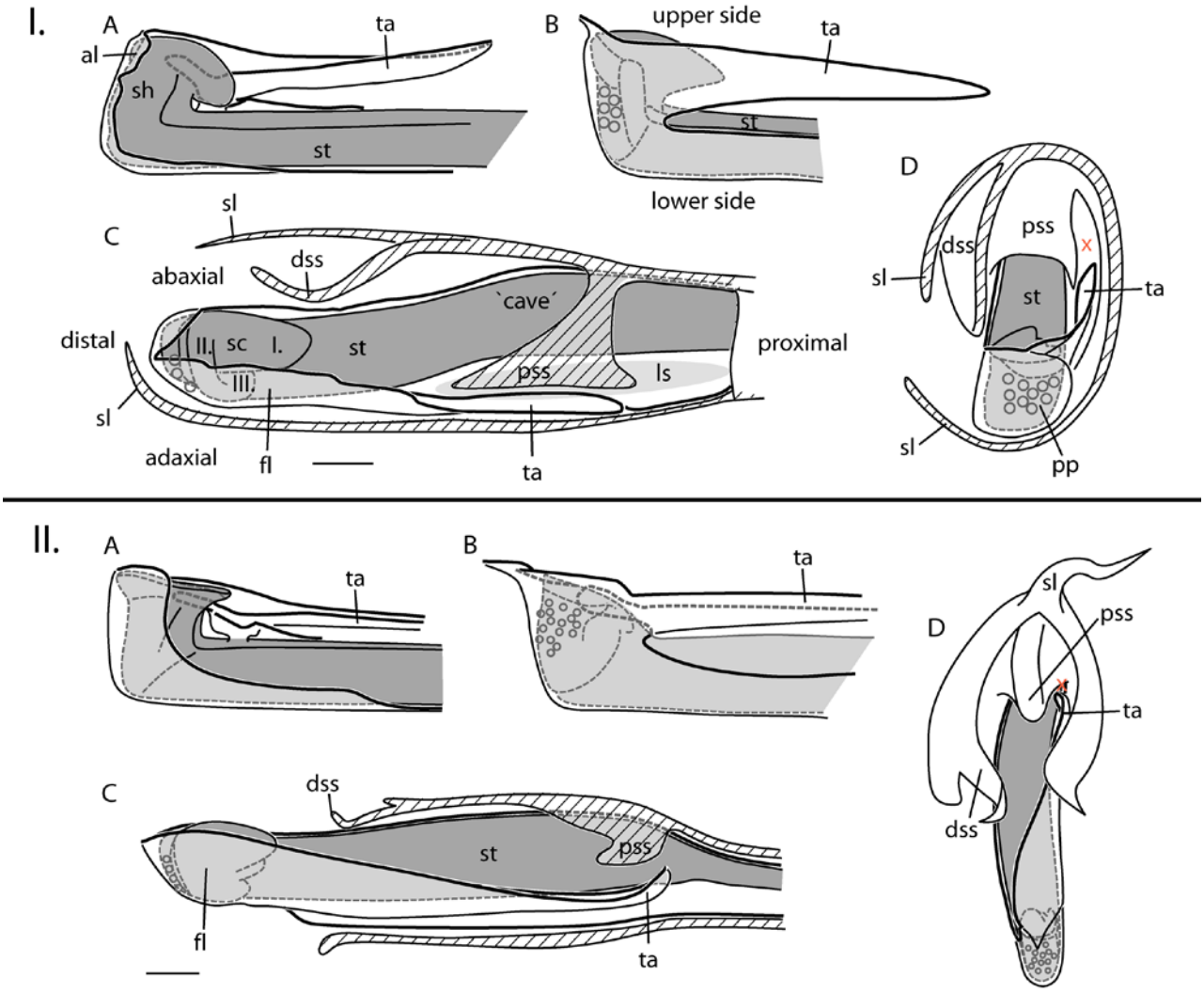


Fig. 3.9: Floral synorganization in the *Sarcophrynium* clade. A: abaxial view on style head; B: adaxial view on style head; C: supervision of distal part of longitudinal section; cutting edges of fleshy staminode are hatched D: frontal view of flower entrance. (I) *Megaphrynium trichogynum*. A, Note the long, lanceolate trigger appendage and the reduction of the adaxial lobe. The style head stands in a 90° angle at the end of the style. C, Note the three stigmatic lobes and the `cave´ formed by the proximal stiff swelling. C, D, Note the small passage to the nectar (cross). (II) *Hypselodelphys hirsuta*. C, D, Note the extended complex of style and hooded staminode which is longer than the fleshy staminode. D, Note the reflexed tip of the trigger appendage. Bars: 1 mm.

3.4.3 SPECIFIC TRAITS IN THE *CALATHEA* CLADE

In the *Calathea* clade (Fig. 3.1) the trigger is again located very distally on the hooded staminode (Fig. 3.10). However, there are two different types: a large vertically standing trigger appendage in all *Haumania* species (gate type; Fig. 3.10 I) and a small pointed one in the remaining species (Fig. 3.10 II,III).

A prominent lateral swelling of the hooded staminode pushes the style to the adaxial side providing a passage to the nectar before and after excitation of the style and resulting in all species in a backwards bending of the hooded staminode after excitation.

3.4.3.1 Haumania (Fig. 3.10 I)

The trigger appendage is short and broad, stands perpendicular to the floral tube and is located next to the stylar head (Fig. 3.10 IA-C) so that the distance from the flower entrance to the excitation point is only about 5 mm (Table 3.1).

The flower entrance in front of the trigger appendage is totally blocked (Fig. 3.10 ID) as the `tunnel´-shape fleshy staminode tightly envelopes the complex of style and hooded staminode and the abaxial surrounding lobe of the fleshy staminode folds inwards in front of the flower entrance such as in *Megaphrynium trichogynum*. The flower entrance is therefore only indicated by a colour contrast: the yellow colour of the hooded staminode, the appendage of the fertile theca and the abaxial surrounding lobe of the fleshy staminode against the white colour of the remaining fleshy staminode and the outer staminodes. These colour patterns present at the same time the major attraction of the flower (Fig. 3.8A).

The complex of style and hooded staminode is shorter than the fleshy staminode allowing only for a pollen deposition onto the insect's proboscis as the rolling-in movement of the style takes place inside the `tunnel´ of the fleshy staminode. Thereby the pollen plate is flanked by vertical rims (pronounciations of stylar head) on both sides matching the broad proboscises of the pollinating bee.

After excitation the curled-in style, whose head rests in the `cave´ formed by the proximal stiff swelling, slightly pushes the fleshy and hooded staminodes apart allowing a view into the flower. Here the increasingly brownish colour of the now upstanding back of the style is a reliable indication of prior insect visits.

The style and the organs of the inner androecial whorl are of a similar thick tissue as in the genus *Megaphrynium* which renders the flower stout for the pollination process by heavy and strong bees.

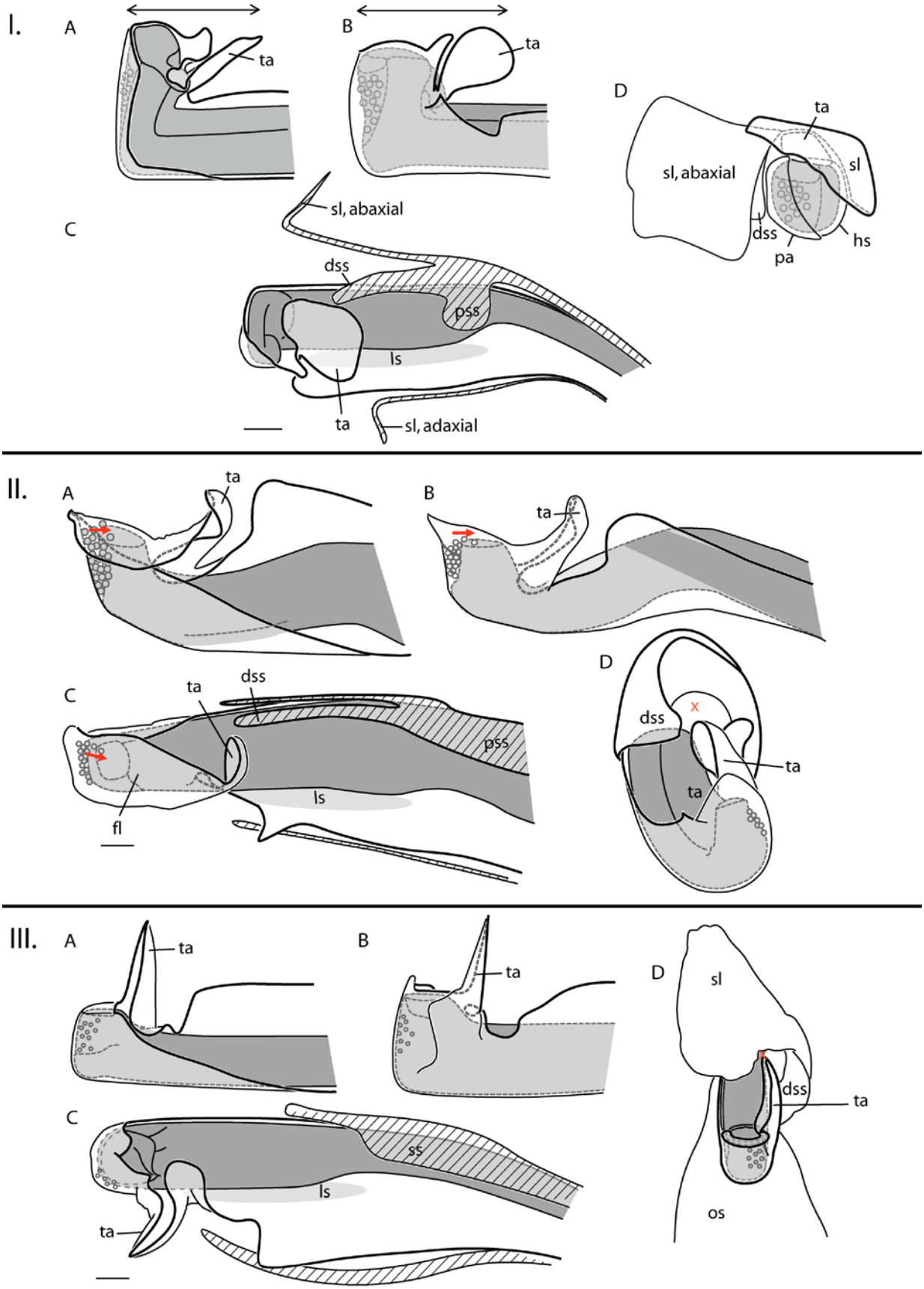
3.4.3.2 Calathea, Pleiostachya and *Ischnosiphon* (Fig. 3.10 II, III)

In these species the complex of style and hooded staminode exceeds the length of the fleshy staminode and the trigger appendage is very distally on the hooded staminode so that it is located outside the floral tube. Here two different positions of the trigger can be distinguished:

In *Calathea lutea, C. warscewiczii* (trigger appendage: 3 mm long!) and *Pleiostachya pruinosa* (Fig. 3.10 II) the tip of the trigger appendage is directed more in proximal direction with a broad rounded tip. It thereby blocks the flower entrance and offers a broad surface against which the pollinator's proboscis has to press. The distance between trigger tip and style head with the pollen plate is about 1 to 2 mm only. Thus pollen will be deposited either onto the pollinator's mouthparts or underneath its head depending on the relative length of the mouthparts to this distance.

In the other investigated species of the *Calathea* clade (e.g. *Calathea picturata* and *Ischnosiphon helenae)* the trigger appendage stands up straight with a pointed tip (Fig. 3.10 III). This positioning results in the location of the trigger appendage in front of the distal stiff swelling. Thus, this trigger does not provide any broad parts to press against; neither does it exactly block the passage into the flower. However, in these long tubed flowers the distance to the nectar is far so that the insect is forced to maximally insert its proboscis into the floral tube to reach the nectar. It thereby places its head exactly in front of the flower entrance where it will obligatorily deflect the trigger appendage with the head. Pollen is then deposited underneath the pollinator's head.

Inside the floral tube the stiff swelling of the fleshy staminode is sometimes rather faint compared to the before mentioned species from the *Sarcophrynium* clade and the genus *Haumania*. Still it is possible to distinguish its bipartite form with a distal and a proximal swelling (Fig. 3.10 II, III). The distal stiff swelling at the flower entrance is small and pointed. The proximal stiff swelling is elongated and partly covers the style narrowing the floral tube towards the abaxial side. Only in *Calathe microcephala* the transition between the two swellings is continuous.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Attraction is mainly obtained through the single outer staminode which is large and conspicuous. The additional surrounding lobes of the fleshy staminodes are variable in this group. They are more or less absent in *Pleiostachya pruinosa* (Fig. 3.10 III: D) and *C. lutea*, conspicuous and symmetrical in *C. platystachya, C. microcephala* and *C. bachemiana* and rather asymmetrical with an elongated tip in *C. picturata* (Fig. 3.10 II: D).

Pleiostachya pruinosa is autogamous and therefore differs from the other species. The folding of the hooded staminode around the stylar head is not tight around the pollen plate but prolongs a little bit behind the stylar head leaving a triangular space behind the pollen plate (Fig. 3.10 III). Additionally the frontal lobe does not lay tight over the rim of the stigmatic cavity. This allows the pollen grains to be squeezed upwards after pollen deposition over the rim of the stigmatic cavity. The pollen grains first adhere to the underneath of the frontal lobe. They can never be found in the stigmatic cavity at this stage. After excitation, when the style curls inward the stigmatic cavity scrapes up those pollen grains. Additionally the stigmatic head roles in so far that it hits on the proximal part of the style hereby deforming the distal rim of the stigmatic cavity where the pollen grains are placed. Flowers in this species are always self-triggered by noon. In 100 % of randomly selected flowers (n = 10) pollen grains were found in the stigmatic cavity resulting in self-pollination in the absence of pollinators. However, fruit-set reaches only 28.29 % (n = 516). A maximum of one fruit per bract develops in the last flowering flower pair of the respective bract.

Fig. 3.10: Floral synorganization in the *Calathea* clade. A: abaxial view on style head; B: adaxial view on style head; C: supervision of distal part of longitudinal section; cutting edges of fleshy staminode are hatched D: frontal view of flower entrance. (I) *Haumania danckelmanniana*. A, B, Note the short distance between the style head and the tip of the trigger appendage (arrow). C, Note the lateral shift of the style due to the lateral swelling of the hooded staminode. D, Note the closed floral entrance. (II) *Pleiostachya pruinosa*. Note the rounded trigger tip and its more horizontal arrangement in comparison to *Calathea picturata*. Note the space behind the pollen plate where pollen grains can squeeze upwards and consequently above the stigmatic cavity (red arrow). (III) *Calathea picturata*. A, B, Note the thin, pointed, upright standing trigger appendage. C, Note the lateral deflection of the style due to the lateral swelling of the hooded staminode. Bars: 1 mm.

3.4.4 SPECIFIC TRAITS IN THE *DONAX* CLADE

There are again two different trigger types in this clade (*Donax* clade, see Fig. 3.1). Whereas the trigger appendage in *Thalia* is assumed to be bipartite (`tentacle type´) and found more proximal in the floral tube (Fig. 3.11 I), all other species have a large flat trigger (`elephant ear type´) in a rather distal position on the hooded staminode (Fig. 3.11 II).

None of the species of the *Donax* clade has a lateral swelling in the hooded staminode, neither have any species of the following *Maranta* and *Stachyphrynium* clade (see below),. In contrast to the species, where such a swelling affects the backwards bending of the hooded staminode after excitation of the style (see chapter 3.4.2.1), the hooded staminode here remains straight when the style curls-in. It only looses its tension.

3.4.4.1 Thalia (Fig. 3.11 I)

The stiff swelling of this species is continuous. A pronounced distal part located right at the flower entrance merges into a proximal small lanceolate swelling which narrows the floral tube and reaches to the flower bottom (Fig. 3.11 IC). The two thin tentacle-like appendages stand in between the two swellings. The movement of the style in the genus *Thalia* is unique in the Marantaceae in that it curls in spirally. The final position of the stylar head is beyond the proximal stiff swelling. The head rests in a vertical position to the style with the stigmatic cavity facing downwards and the pollen plate facing adaxially. The long stigmatic appendage reaches the flower bottom. As the fleshy staminode is as long as the complex of style and hooded staminode (Fig. 3.11 IC) the curling-in movement of the style takes place inside the floral tube so that pollen can only be deposited onto the proboscis of the insect.

The stylar head of the two *Thalia* species is unique in the Marantaceae Fig. 3.11 IA-B). It is the largest and bears a large conspicuous appendage which stands up almost straight thereby partly closing the flower entrance (Fig. 3.11 ID). The pollen plate is arranged perfectly perpendicular to the style at the distal end of the stylar head and is on both sides flanked by a high thin rim. The pollen plate is large and vertically arranged. In *Thalia dealbata,* beneath the white glandular excretions at its upper rim, it is completely covered with pollen grains which are thereby strictly separated from the stigmatic cavity. The base of the stylar head is

deposed from the upper part of the stylar head and closely enveloped by the hood of the hooded staminode maintaining the style under pressure. In contrast, the upper part of the stylar head, including the pollen plate and the stigmatic cavity, is only loosely covered by the large hood.

Attraction is obtained through the single conspicuous violet outer staminode as the surrounding lobes of the fleshy staminode are highly reduced (Fig. 3.11 ID). It is further increased by the synchronous flowering of the two flowers of a flower pair mimicking together a zygomorphic bee blossom.

A different length in the stylar head could be detected in the two species of the genus (shorter in *T. geniculata* than in *T. dealbata*). This results in a different pollen deposition on the pollen plate allowing pollen grains in *T. geniculata* to enter the stigmatic cavity over the lowered distal rim of the stigmatic cavity.

3.4.4.2 Donax (Fig. 3.11 II), *Schumannianthus and Phrynium*

Within the *Donax* clade the species of the genera *Donax, Schumannianthus* and *Phrynium* form morphologically a highly homogenous group. In all examined species the fleshy staminode develops a distinct bipartite stiff swelling (Fig. 3.11 IIC). The distal part narrows the flower entrance at the height of the stylar head, the proximal one is located opposite or slightly more proximal than the trigger appendage allowing a passage to the nectar only by deflecting the trigger appendage.

The hood of the hooded staminode has an upright standing margin and therefore does not cover the stigmatic cavity (Fig. 3.11 IIA-B, Fig. 3.5). Nor is it close to the pollen plate. The sole firm contact exists at the base of the stylar head providing the tension of the style (see arrow in Fig. 3.5). The trigger appendage with its basal plate is located slightly more proximal in comparison to all before mentioned species (Fig. 3.11 IC). This leads to an increase in the distance between the flower entrance to the trigger appendage. The movement of the style takes place inside the floral tube depositing the pollen onto the pollinator’s mouthparts.

Attraction is obtained by the two conspicuous outer staminodes (Fig. 3.8E). The surrounding lobes of the fleshy staminode are present but inconspicuous. They appear almost symmetrically around the entrance in *Donax canniformis* (Fig. 3.8E), *Schumannianthus dichotomous* and *Phrynium pubinerve* and asymmetrically in the remaining species (Table 3.1).

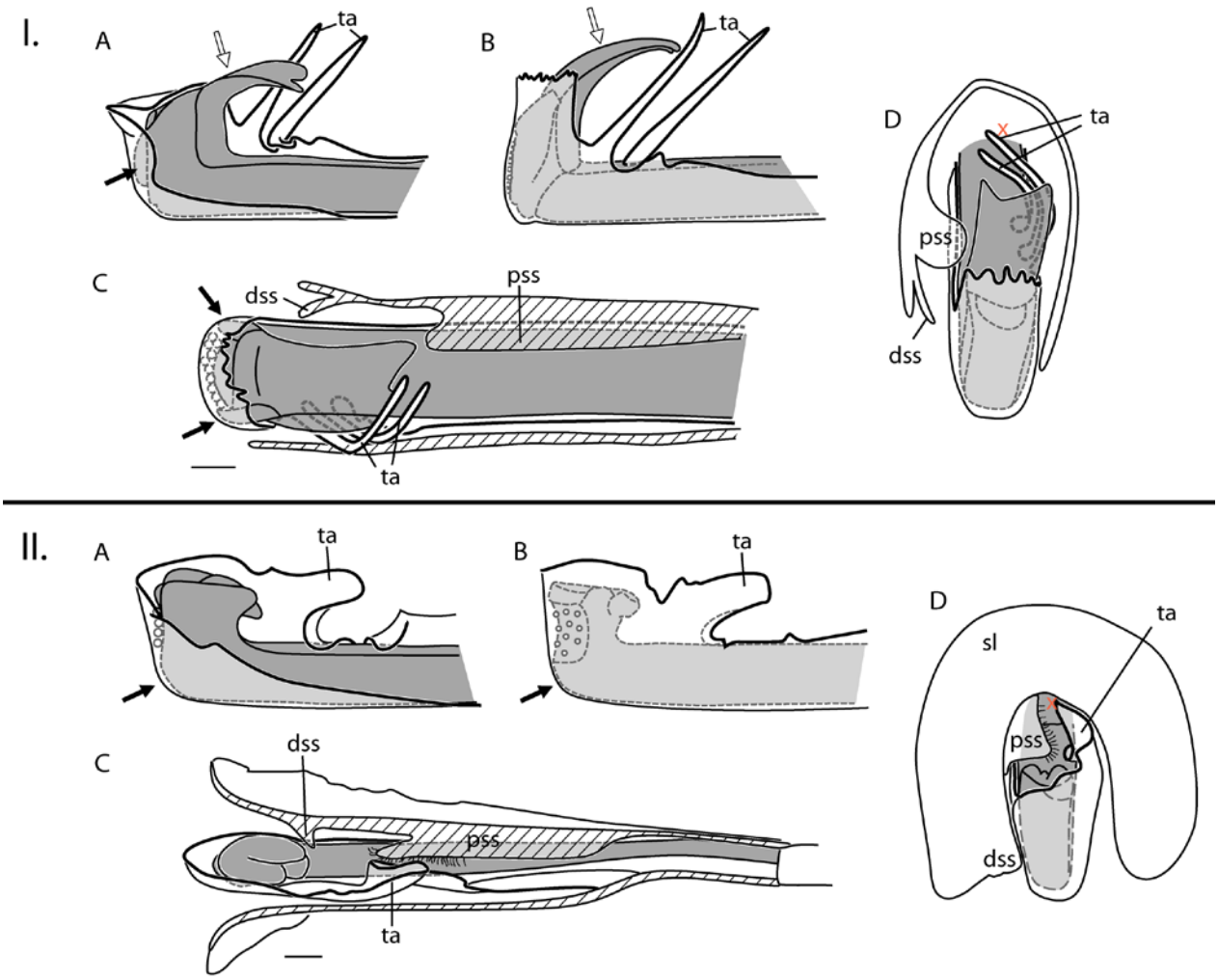


Fig. 3.11: Floral synorganization in the *Donax* clade. A: abaxial view on style head; B: adaxial view on style head; C: supervision of distal part of longitudinal section; cutting edges of fleshy staminode are hatched D: frontal view of flower entrance. (I) *Thalia dealbata*. Note the large stigmatic lobe (white arrow), the large distal rims (black arrows) around the pollen plate and the two tentacle-like appendages of the hooded staminode. (II) *Donax canniformis*. Note the prominent base of the stylar head (arrow). Bars: 1 mm.

3.4.5 SPECIFIC TRAITS IN THE *MARANTA* CLADE

The species of this clade (*Maranta* clade Fig. 3.1) are characterized by three different trigger types which all correspond in their significantly more proximal location in the floral tube than in any of the before mentioned species (Fig. 3.12). The most proximal trigger types with the largest distances between flower entrance and trigger appendage are found in *Hylaeanthe* and *Halopegia* (Fig. 3.12 V).

3.4.5.1 Maranta (Fig. 3.12)

The fleshy staminode has usually a pronounced bipartite stiff swelling. The trigger appendage stands opposite in between the two so that a passage past the trigger appendage without deflection is prevented (Fig. 3.12 C). However, the proximal stiff swelling is functionally replaced by an accumulation of hairs in *Maranta depressa* and *M. leuconeura* (Fig. 3.12 II). Here the effect of narrowing of the floral tube towards the trigger appendage is achieved by the overall form of the fleshy staminode. In *M. arundinacea* and *M. noctiflora* the whole floral tube is additionally slightly twisted so that there is a large space along side the style proximal to the trigger appendage (Fig. 3.12 I, III C).

In all species the fleshy staminode is generally 1 mm shorter than the complex of style and hooded staminode on its adaxial side while its abaxial side is equally long. This renders it difficult to decide where consequently the pollen will be deposited on the pollinator, underneath the head or onto the proboscis.

Floral attraction is obtained through the two conspicuous outer staminodes and the surrounding lobes of the fleshy staminodes. The latter are large on the abaxial side in *M. arundinacea* and *M. noctiflora* and form an enlarged tip with colour patterns in *M. leuconeura* (Fig. 3.8B) and *M. depressa*.

In *M. noctiflora* the formation of the hood of the hooded staminode is unique in the family in that it forms a little `tunnel´ across the rim of the stigmatic cavity (Fig. 3.12 III: A). Here single pollen grains can be squeezed through in the bud after pollen deposition. This allows self-pollination. Pollen grains can be found in the distal part of the stigmatic cavity and/or adhering to the underneath of the frontal lobe entering the stigmatic cavity when the style is self-released from its tension. Thereby the stigmatic cavity takes up the pollen grains during the stylar movement. In 100 % of all flowers examined shortly before anthesis (n = 12) and after self-triggering (n = 15) pollen could be found in the distal part of the stigmatic cavity. Fruit-set in the greenhouse reached 30.54 % (n = 275).

3.4.5.2 Hylaeanthe hoffmannii

In *Hylaeanthe hoffmannii* the trigger appendage is located even more proximally than in the genus *Maranta* and differs from all other species in that a basal plate is not readily discernible. Instead there is a long faint swelling parallel to the upper side of

the style. The stiff swelling of the fleshy staminode is rather inconspicuous but a general stiffening of the tissue guarantees a `tunnel´ like shaping across the style as in all other Marantaceae species. This limits the access to the nectar and forces the pollinators to pass by the trigger appendage.

The stylar head is enlarged by a slight outgrowth of the pollen plate (Fig. 3.4C). This effects the final position of the pollen plate to be rather at the back of the stylar head. The fleshy staminode is only 1 mm shorter than the complex of style and hooded staminode which renders a deduction about the localization of the pollen grains on the pollinator difficult.

Floral attraction is obtained by the two white conspicuous outer staminodes and the not entirely reflexed white petals contrasting with the yellow centre constituted by the yellow petaloid appendage of the fertile theca. The surrounding lobes of the fleshy staminodes are highly reduced.

3.4.5.3 Ctenanthe, Myrosma and *Stromanthe* (Fig. 3.12 IV)

In all three genera the two parts of the bipartite swelling of the fleshy staminode are well developed and leave only a very narrow passage to the nectar. The trigger appendage stands opposite to the distal swelling in the genera *Ctenanthe* and *Stromanthe* and slightly more proximal between distal and proximal swelling in *Myrosma* enforcing in each case its deflection by the visiting pollinators.

The fleshy staminode and the complex of style and hooded staminode are equal in length ((Fig. 3.12 IV.C; except *Stromanthe porteana*, see Table 3.1). Additionally, the distance between flower entrance and trigger appendage is only 1 to 2 mm (except 4 mm in *Myrosma setosum*) resulting probably in a pollen deposition in the case of a long proboscis at its tip and in the case of a short proboscis on its upper part.

All species additionally present two conspicuous outer staminodes. The surrounding lobes of the fleshy staminode appear conspicuous and symmetrical in *Myrosma* and *Stromanthe* attributing to their attraction. However they are asymmetrical and merely inconspicuous in the two *Ctenanthe* species (Fig. 3.12 IV).

3.4.5.4 Halopegia (Fig. 3.12 V)

In the two *Halopegia* species the trigger appendage is again located far proximal in the floral tube (Fig. 3.12 V.C) increasing the distance between flower entrance and trigger appendage as in *Hylaeanthe hoffmannii*. The distance is largest in *Halopegia azurea* as it exhibits the larger overall flower size (Table 3.1). The proximal part of the fleshy staminode´s bipartite stiff swelling is located opposite to the trigger appendage preventing access to the nectar without deflecting the latter. The distal and the proximal parts of the stiff swelling together form a `cave´ in which the stylar head rests when the style is curled in (Fig. 3.13A).

The stylar head is very distinct from the other species of the *Maranta* clade. It does not rise very high above the upper side of the style (Fig. 3.12 V: A) and the rim of the stigmatic cavity lowers proximally to the upper surface of the style. Thereby the pollen plate becomes triangular and its surface is rounded and slightly bent proximally. In both investigated species the hooded staminode totally covers the stylar head. The fleshy staminode is of equal length to the complex of style and hooded staminode in *Halopegia blumei* but a bit shorter in *H. azurea*. This results in a stylar movement within the `tunnel´ of the fleshy staminode and a pollen deposition onto the insect's proboscis provided that the insect's head cannot enter the `tunnel´.

The attraction of the flower is ensured by the two conspicuous outer staminodes (Fig. 3.8C). Additionally the fleshy staminode has conspicuous symmetrical surrounding lobes around the flower entrance which highly contrast with the yellow flower centre.

Halopegia azurea presents a further case in which the flowers self-trigger in the afternoon in 100 % (n = 20) of the flowers. The style of this species curls in very far so that the stigmatic cavity faces towards the flower entrance (Fig. 3.13A, Tab. 3.1). By curling-in the stylar head beats against the stiff swellings of the fleshy staminode which form a narrow cavity in which the stylar head fits exactly. The crushing into the stiff swelling of the fleshy staminode pushes the pollen grains from the pollen plate towards the proximally lowered rim of the stigmatic cavity. The first pollen grains then slide into the stigmatic cavity allowing for self-pollination (Fig. 3.13A). Fruit-set reached in this autogamous species in the absence of pollinators 45.3 % (n = 267).

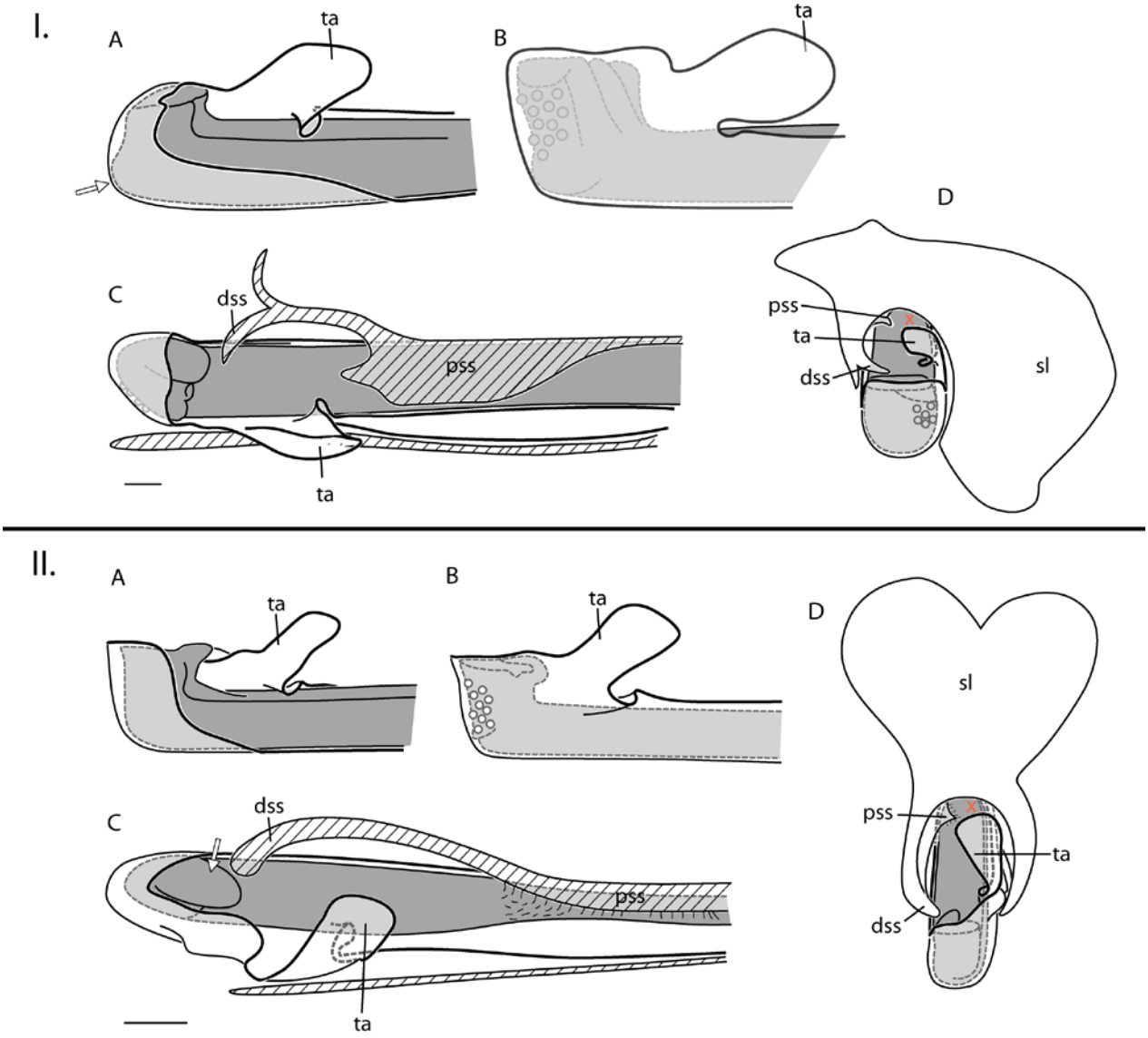
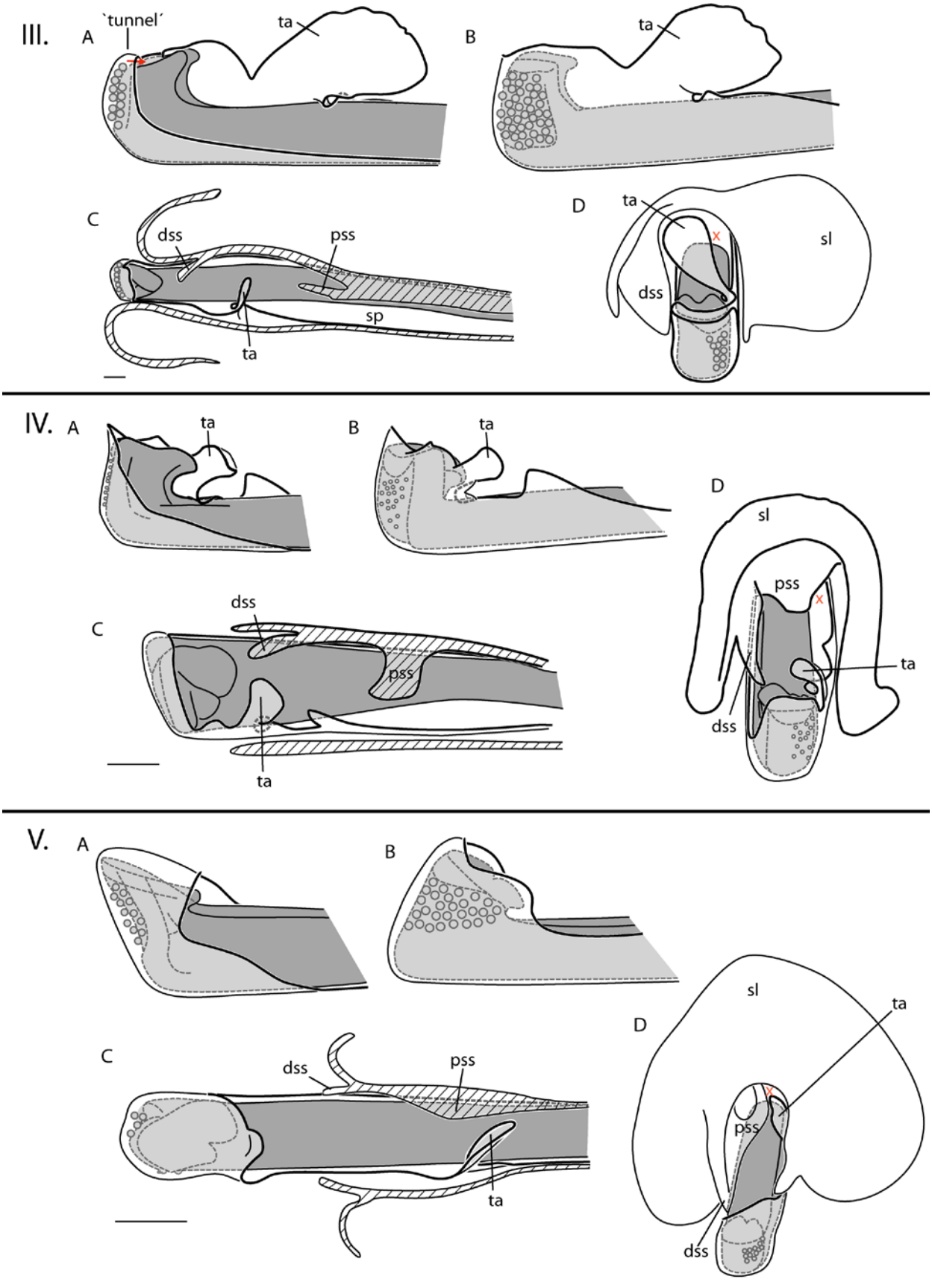


Fig. 3.12: Floral synorganization in the *Maranta* clade. A: abaxial view on style head; B: adaxial view on style head; C: supervision of distal part of longitudinal section; cutting edges of fleshy staminode are hatched D: frontal view of flower entrance. (I) *Maranta arundinacea*. (II) *Maranta leuconeura*. C, Note the pronounced stigmatic lobe (arrow). D, Note the conspicuous surrounding lobes of the fleshy staminode. (III) *Maranta noctiflora*. A, Note the tunnel that forms across the rim of the stigmatic cavity through which pollen grains can squeeze into the stigmatic cavity (red arrow). C, Note the lateral space (sp) in the hooded staminode due to a torsion in the floral tube. (IV) *Stromanthe tonckat*. C, Note the prominent proximal stiff swelling of the fleshy staminode. (V) *Halopegia azurea*. B, Note the triangular shape of the pollen plate. C, D, Note the total cover of the stigmatic cavity by the frontal lobe and the rather proximally positioned trigger appendage. Bars: 1 mm.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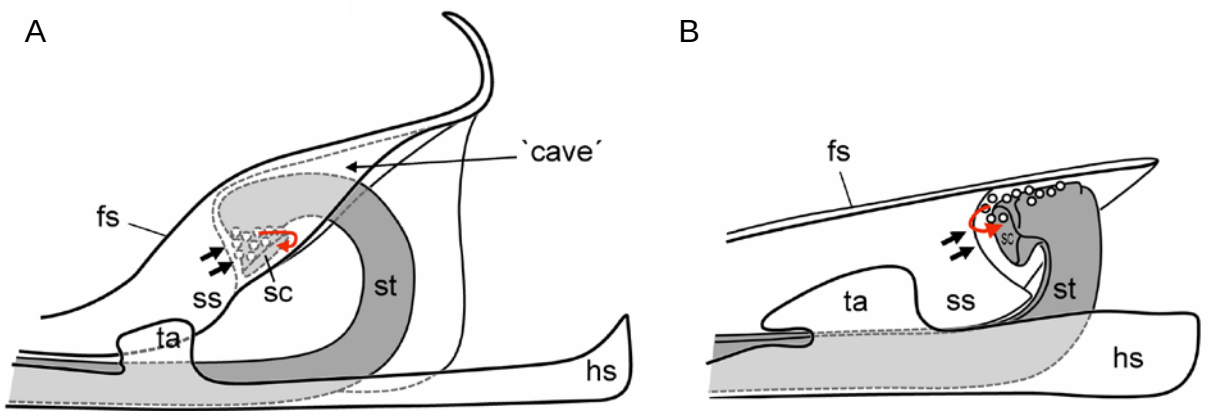

Figure 3.13: Pollen transfer in autogamous species. The stylar head hits the stiff swelling (ss) of the fleshy staminode (fs) and the pollen grains are pushed over the lowered proximal rim (arrow) of the stigmatic cavity in *Halopegia azurea* (A) and over the distal rim (arrow) of the stigmatic cavity in *Marantochloa leucantha* (B).

3.4.6 SPECIFIC TRAITS IN THE *STACHYPHRYNIUM* CLADE

This is the second clade (*Stachyphrynium* clade, Fig. 3.1) with proximally positioned trigger types (Fig. 3.13), especially in the genera *Marantochloa* and *Ataenidia.* There are two different types of stiff swellings in the fleshy staminode. Whereas most species exhibit a bipartite swelling, a few species of the genus *Marantochloa* possess a single long stiff swelling.

3.4.6.1 Afrocalathea (Fig. 3.13 I)

The trigger appendage stands opposite to the proximal stiff swelling of the fleshy staminode blocking the passage to the nectar and forcing its deflection by any nectar foraging animal (Fig. 3.13 I C, D). However, the flower entrance is rather open (compare with *Calathea picturata,* Fig. 3.10 II) as the abaxial side of the fleshy staminode is very short and hardly reaches the position of the trigger appendage. The oposite adaxial `wall´ of the fleshy staminode is longer but still the complex of style and hooded staminode exceeds it for about 4 mm (Table 3.1).

Due to this open flower entrance pollen deposition is not exact onto the top of the birds´ beak tip. It can be deposited in an area between 5 and 10 mm from the tip of the beak. Attraction is reached by the two large outer staminodes and the broad open fleshy staminode presenting a bright white upright standing open funnel.

3.4.6.2 Stachyphrynium

The narrowing of the floral tube towards the trigger appendage is ensured either by a pronounced and hairy stiff swelling of the fleshy staminode (e.g. *Stachyphryium spicatum, S. placentarium* and *S. latifolium*) or by the pure presence of hairs in place of a stiff swelling (e.g. *S. jagornianum*). The surrounding lobes of the fleshy staminode are highly reduced in all species so that the two outer staminodes contribute most to the attraction of the flowers.

Except *S. placentarium* all species have a pronounced elongation at the base of the pollen plate which marks the pressure point with the hooded staminode (Fig. 3.4D *S. latifolium*). The fleshy staminode is about as long as the complex of style and hooded staminode in three species and only exceeds the latter by 2 mm in *S. placentarium,* possibly resulting in a pollen deposition into the proboscidial fossae underneath the insect's head. In the other species the pollen is assumed to be deposited onto the proboscis.

3.4.6.3 Marantochloa (Fig. 3.14 II-IV) and *Ataenidia*

In the genus *Marantochloa* there is a lot of variation in floral size from small flowers of less than 10 mm in the length of the fleshy staminode to about 20 mm (Table 3.1). Thus, it is the length of the flower which determines which insect can reach the nectar.

There are two types of stiff swellings in the fleshy staminode. In most of the species (*Ataenidia conferta, Marantochloa cuspidata, M. mannii, M. purpurea, M. cordifolia*, *M*. sp.1, *M*. sp.2 and *M*. sp.3, Fig. 3.14 IV) the stiff swelling is bipartite whereby the distal stiff swelling is rather faint except in *Ataenidia conferta*. In the remaining species there is a continuous, elongated lateral stiff swelling of equal width starting at the flower entrance and reaching into the floral tube until the height of the trigger appendage (Fig. 3.14 II, III).

In the flowers with a single long swelling the stylar head bounces against it after excitation (Fig. 3.13B). In the remaining species the style can curl in entirely inside the `tunnel´ of the protective fleshy staminode. However, in *M. cordifolia* the style is so long that it generally bounces against the `roof´ of the fleshy staminode and in *M. cuspidata* it curls in in front of the floral entrance, outside the `tunnel´ of the fleshy staminode.

In most of the species the floral morphology allows a pollen deposition into the proboscidial fossae of the insect. There are a few species (e.g. *M. monophylla, M. sulphurea, M. incertifolia*) where pollen is deposited onto the proboscis. Only in *M. filipes* the curling-in movement of the style is rather faint to absent still posing an open question to where pollen might be deposited (Fig. 3.4 G1).

Irrespective of the type of swelling in these species the floral tube is narrowed opposite of the trigger appendage to about half the width of the style. Stiff swelling and trigger appendage together completely block the passage to the nectar and divide the floral tube into two compartments, a distal one and a proximal one with nectar reward (Fig. 3.14 II-IV).

The surrounding lobes of the fleshy staminode are highly reduced in all species. Only *M. incertifolia* and *M. monophylla* have a small extended rounded lobe on the abaxial side (Fig. 3.15). The main attractions of these flowers are the two large outer staminodes (see chapter 2, Fig. 2.8I). Additionally, the petaloid appendage of the fertile theca and the hooded staminode in the floral centre are often coloured yellow contrasting with the white colour of the surrounding organs.

M. leucantha merits a more detailed consideration (Fig. 3.14 III). Here the hooded staminode does not lay as tight on the rim of the stigmatic cavity (Fig. 3.14 IIIA, B) as in e.g. *M. congensis* (Fig. 3.14 IIA, B) or *M. purpurea* (Fig. 3.14 IVA, B). In addition the bulge of secretion from the gland is not as prominent as in the other *Marantochloa* species and the pollen plate is rather rounded and slightly bent in proximal direction. This allows the pollen grains to be easily pushed to the upper rim of the stigmatic cavity through the pressure that prevails between style and hooded staminode (Fig. 3.14 III). Pollen grains then generally cling to the underneath of the frontal lobe of the hooded staminode. In none of the investigated flowers (n = 20) pollen grains were found in the stigmatic cavity before excitation of the style. However, when the style is released from its tension and the stigmatic cavity moves upwards it first bumps into the covering frontal lobe of the hooded staminode and subsequently into the single stiff swelling of the fleshy staminode. This then presses the pollen grains that stand over the rim of the pollen plate into the stigmatic cavity (Fig. 3.13B) resulting in self-pollination. 100 % (n = 40) of the untreated flowers were self-triggered in the evening. Repeatedly pollen grains wer found in the most distal part of the stigmatic cavity after excitation before and after crushing into the swellings of the fleshy staminode. Fruit set reached 31.16 % (n = 215) in the greenhouse.

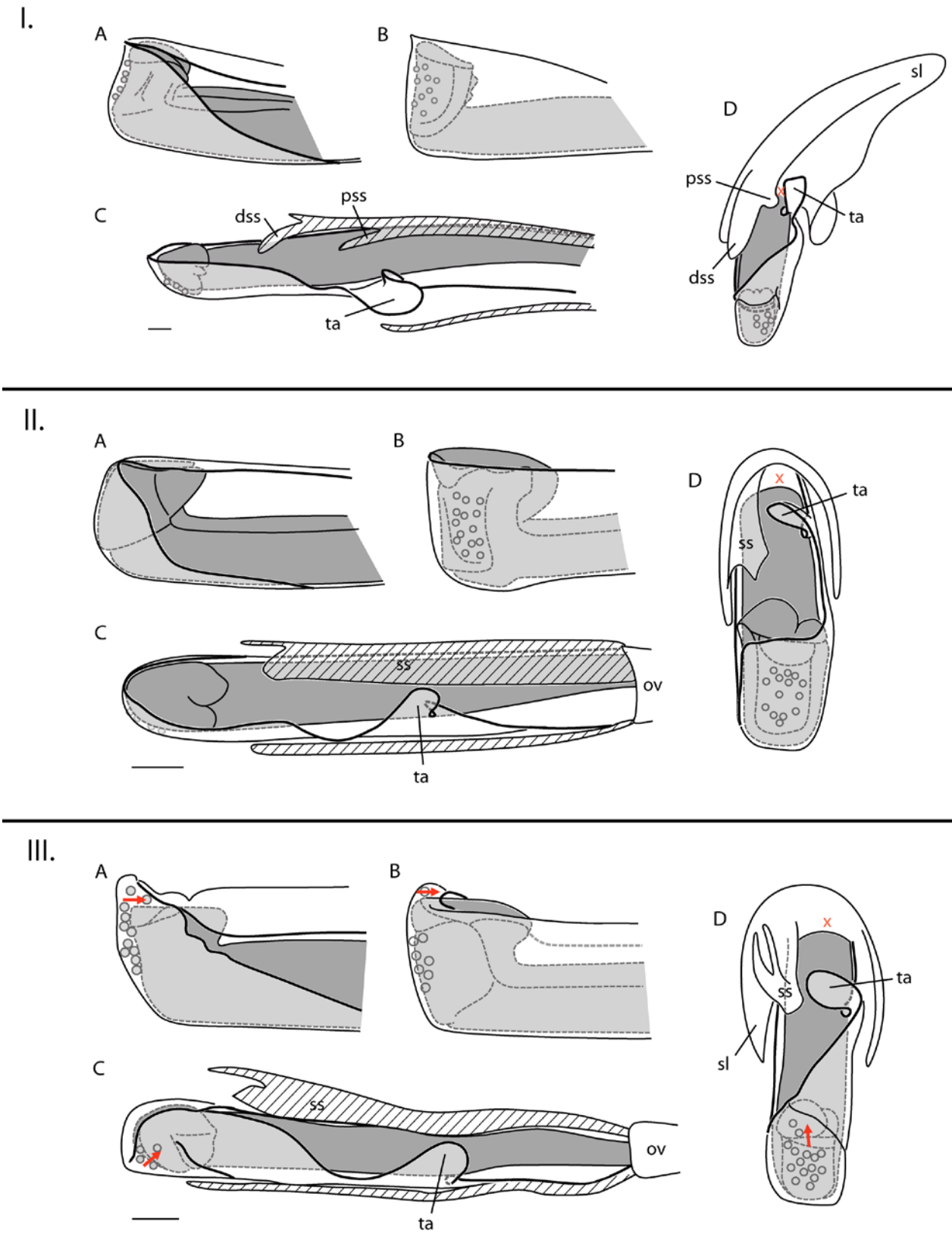
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Fig. 3.14

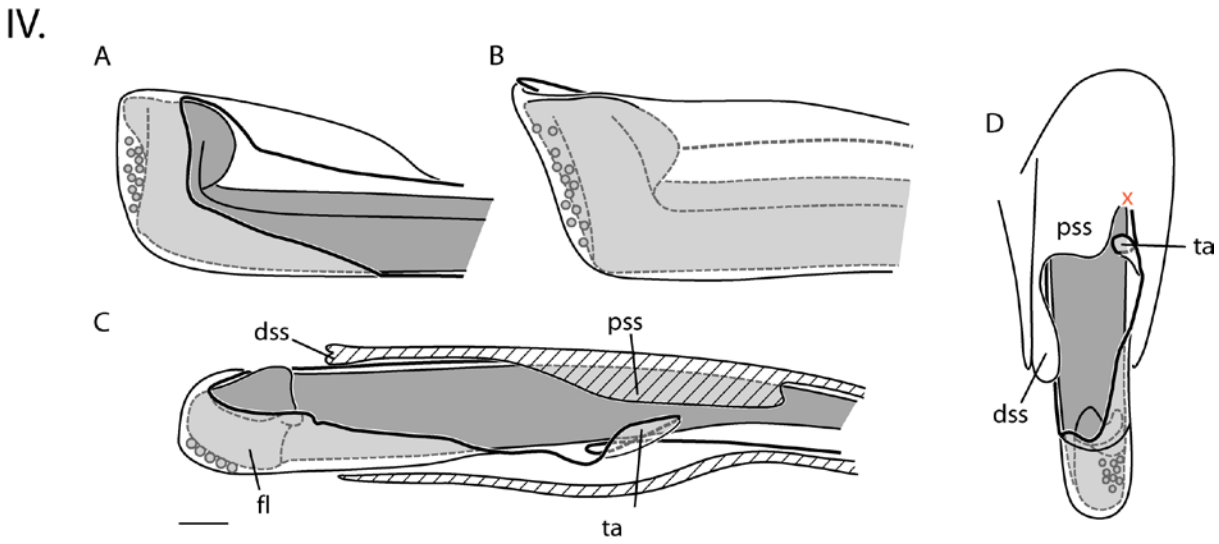


Fig. 3.14: (cont.) Floral synorganization in the *Stachyphrynium* clade. A: abaxial view on style head; B: adaxial view on style head; C: supervision of distal part of longitudinal section; cutting edges of fleshy staminode are hatched D: frontal view of flower entrance. (I) *Afrocalathea rhizantha*. D, Note the asymmetric fleshy staminode which is longer on the abaxial side than on the adaxial side and thereby affects a wide flower entrance. (II) *Marantochloa congensis*. C, Note the single long stiff swelling of the fleshy staminode and the proximally positioned trigger appendage. (III) *Marantochloa leucantha*. A, Note the free space above the rim of the stigmatic where pollen grains can pass through (red arrow). C, Note the proximally positioned trigger appendage. (IV) *Marantochloa purpurea*. C, Note the very proximally positioned trigger appendage and the reduced proximall swelling in the proximal part of the flower where the nectar is stored. Bars: 1 mm.

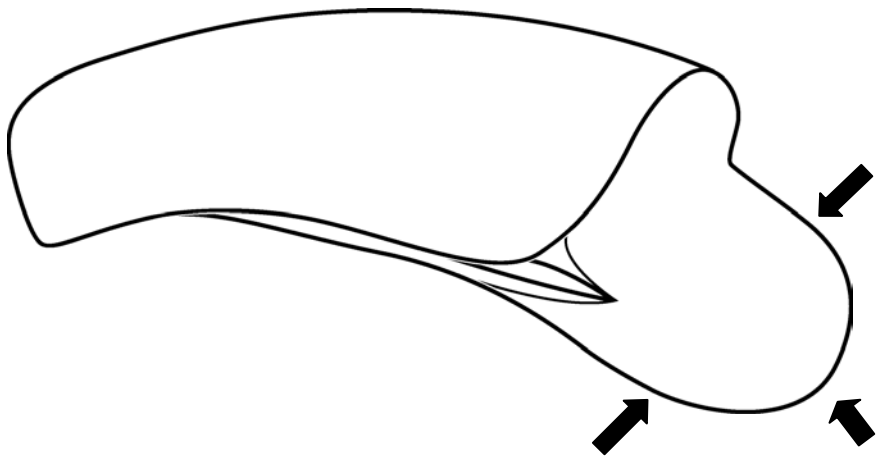


Fig. 3.15: Species specific morphological characteristic of *Marantochloa incertifolia.* Note the abaxial elongation of the leaf (delimited by black arrows).

3.5 DISCUSSION

3.5.1 MORPHOLOGICAL DIVERSITY AND SELECTION PRESSURE

The angiosperm flower evolved as a device to allow sexual processes (Endress, 1994). Thereby it underlies selective pressures which drive the optimization of its function and foster i.e. their attraction to pollen vectors (pollinators) and the successful transfer of pollen onto and from the pollinator. These functions can be achieved on diverse though not countless ways. This proves the flower to be a highly plastic structural system on the one hand, able to acquire an overwhelming diversity, which on the other hand is nevertheless phylogenetically restrained.

In the Marantaceae the attraction of pollinators is obtained by broad colourful petals, conspicuous surrounding lobes of the fleshy staminode, colour contrasts between the floral centre and its periphery and/or conspicuous outer staminodes (one or two see Table 3.1). Thereby, the outer staminodes present the most attractive device present as large conspicuous lobes in most Marantaceae species (see also Heller and Claßen-Bockhoff, 2008*a*). The species are frequently bee-pollinated so that the outer staminodes also serve as landing platform (chapter 2; see also Kunze, 1984; Endress, 1994). In the bird pollinated *Megaphrynium trichogynum* and *Thaumatococcus* species, however, outer staminodes are reduced in size and/or number, probably due to a loss in function (see Walker-Larsen and Harder, 2000). Here attraction is obtained by the petals and the function of the outer staminodes as landing platform is obsolete and their presence probably more perturbing than advantageous in the pollination process. The reduced outer staminodes in the two closely related but bee pollinated species *Megaphrynium gabonense* and *M. macrostachyum* might be an example of phylogenetic constraints. Here, *Amegilla* bees hover in front of the flower and *Xylocopa* bees use always one flower of the flower pair for landing while they suck nectar in the second one and then turn around (chapter 2). However, in *Afrocalathea rhizantha,* despite being exclusively bird pollinated (see chapter 2), the outer staminodes are still very large and thus contribute essentially to the attraction of the flower as the rest of it is rather slender.

Important for the successful pollen transfer between flowers is their close adaptation to the body size of the respective pollinators (Endress, 1994; Sakai et al., 1999; Lunau, 2004). Floral size in the investigated Marantaceae ranges from 4.5 mm to 39 mm (length hooded staminode Table 3.1) and has been proven to closely

match pollinator body size in the African Marantaceae (chapter 2). Also differences in floral tube length are commonly known as adaptations to different pollinators excluding pollinator species with shorter proboscis (see also *Impatiens*/Balsaminaceae and *Pelargonium*/Geraniaceae in Vogel, 1954; *Disa*/Orchidaceae in Johnson and Steiner, 1995; *Petunia*/Solanaceae in Ando et al., 2001; *Tritoniopsis*/Iridaceae in Goldblatt and Manning, 2005; Nilsson, 1988). In the Marantaceae this is especially prevalent in the long tubed species from the *Calathea* clade (see also MacBride, 1931; Woodson and Schery, 1945; Jonker-Verhoef and Jonker, 1957; Kennedy, 1997*a,b*; Heller and Claßen-Bockhoff, 2008*b*). There is even variation in tube length within a single species which mirrors the adaptation to several different pollinators across the wide distribution range of the species (*Calathea crotalifera,* Kennedy, 2000).

The pollen transfer in the Marantaceae onto the insect is ultimately accomplished by the stylar head (Claßen-Bockhoff, 1991). Apart from a constant position of the pollen plate at the back of the stylar head its exact shaping seems to be of minor importance as it correlates rather with phylogenetic clades/genera than with pollinators. However, the independently occurring long stylar head with ridges alongside the pollen plate in the genera *Thalia* and *Haumania* might be recognized as a special adaptation to the broad proboscis of the predominant pollinators, *Xylocopa* bees (chapter 2; Claßen-Bockhoff, 1991).

Most important in the transfer of pollen is a minimum degree of stylar bending. The stylar head has to separate completely from the hood of the hooded staminode to freely pass along the pollinator's body in order to deposit its pollen load (for illustration see chapter 2). The further bending of the style though is variable (see Table 3.1). Only in *Marantochloa filipes* the degree of stylar bending is extremely reduced to almost absent (Fig. 3.4 G1). Here the process of pollen transfer onto the pollinator is still unknown.

In most flowers there is a trade-off between pollen transfer and pollen loss due to pollen collecting bees (Schremmer, 1972; Gerling et al., 1989; Castellanos et al., 2003). Pollen loss is prevented in the Marantaceae by hiding the pollen on the pollen plate which is covered by the hood of the hooded staminode (see also Westerkamp, 1997; Westerkamp and Claßen-Bockhoff, 2007). The degree of coverage though beyond the pollen plate – i.e. across the stigmatic cavity is highly homoplasious

across the species of the family and therefore the possible function of a protection of the stigmatic cavity against dirt is not mandatory in the family.

Marantaceae are nectar-flowers with nectar being stored in the floral tube. Lateral hairs in the floral tube might contribute to capillary upward transport of nectar in the corolla tube (e.g. Müller, 1931). However, hairs are neither universally present in the Marantaceae nor is there a correlation between presence/absence of hairs and e.g. corolla tube length or pollinators.

3.5.2 THE OBLIGATE EXCITATION OF THE EXPLOSIVE POLLINATION MECHANISM (FIG. 3.16)

All investigated Marantaceae species follow the same Bauplan (chapter 3.3.1). Important for the transfer of pollen is the curling-in motion of the style (Claßen-Bockhoff, 1991; Kennedy, 2000). This movement is facilitated through a release of tension stored in the style which is based on its tight enclosure by the hooded staminode (Pischtschan and Claßen-Bockhoff, 2008).

Important for the set-up of tension is the here described and universally found locally restricted contact point between style and hooded staminode at the base of the stylar head (Fig. 3.3). The minuteness of the contact point might explain the ease with which style and hooded staminode part after excitation (see Claßen-Bockhoff and Heller, 2008*a*). The movement itself is probably facilitated by a rapid shift of the style's internal water body through cell-wall perforations rendering the parenchyma extremely permeable (Pischtschan, 2007).

Oposite of the complex of style and hooded staminode stands the fleshy staminode which generally exhibits the form of a long and narrow `tunnel´. Inside the `tunnel´ it possesses a stiff swelling which is usually bipartite. In all investigated taxa this swelling continuously narrows down the `tunnel´ from the flower entrance exactly towards the tip of the trigger appendage (except *Calathea*). Stiff swelling and trigger appendage completely close the passage to the nectar and the pollinator's mouthparts are guided (see also Kunze, 1984) to affect the deflection of the trigger appendage. This consequently leads to the excitation of the explosive pollination mechanism and the transfer of pollen. The obligate triggering of the flower is especially important in an environment with a low and/or unpredictable pollinator frequency (chapter 2; see also Bawa, 1983; Rhatcke and Lacey, 1985).

Equal precision across the diversity of different trigger types is achieved by diverse morphologies of the fleshy staminode. However, there is no direct matching of distinct types of fleshy staminodes with specific types of trigger appendages. In contrast, the stiff swelling of the fleshy staminodes appears slightly more variable than the trigger appendage of the hooded staminodes. There are for instance two types of fleshy staminodes in the *Sarcophrynium* clade characterised by the sword like trigger appendage (see *Megaphrynium/Thaumatococcus/Sarcophrynium* and *Hypselodelphys,* Fig. 3.9) and in the genus *Marantochloa* characterized by the cushion like trigger appendage (see *Ataenidia conferta* and *Marantochloa leucantha,* Fig. 3.14 II-IV). In contrast, highly similar morphological types can be found in two unrelated taxa (e.g. *Afrocalathea rhizantha*/lever type Fig. 3.14 I and *Calathea picturata/*thumb type Fig. 3.10 III). Furthermore, the morphological expression of the stiff swelling ranges from a well developed to a highly reduced stiff swelling within the genus *Maranta* which is characterized by the wing type trigger appendage (chapter 3.4.5.1).

This high diversity of the fleshy staminode and its homoplasious occurrence in the Marantaceae might be due to the amorph shape of the stiff swelling and the broader range of functional phenotypes in contrast to the trigger types. Due to the presence of a bipartite swelling in the fleshy staminode the same effect of an obligate excitation of the pollination mechanism can be obtained by a combination of the trigger appendage with the distal (Fig. 3.16B) or the proximial (Fig. 3.16D) part of the stiff swelling, a combination of both (Fig. 3.16C) or even a single long lateral swelling (Fig. 3.16E). Swellings attributed to guiding the insect's proboscis within the flower have also been described in other families (e.g. Bruniaceae, Quint and Claßen-Bockhoff, 2006) and internal amorph rearrangements within the flower contributing to a precise pollen transfer are best known from examples of the Orchidaceae (Dressler, 1981).

Only in a few *Calathea* species where the trigger appendage stands upright in front of the fleshy staminode no opposing positioning of stiff swelling and trigger appendage has been developed (Fig. 3.16A). Here it is the floral tube length which forces pollinators to deflect the trigger appendage with their head by trying to reach as far as possible into the floral tube to gain the nectar (see Kennedy, 2000).

Schemske and Horvitz (1984) showed, however, that not all visitors in *Calathea ovandensis* are effective pollinators (see also Locatelli et al., 2004). The

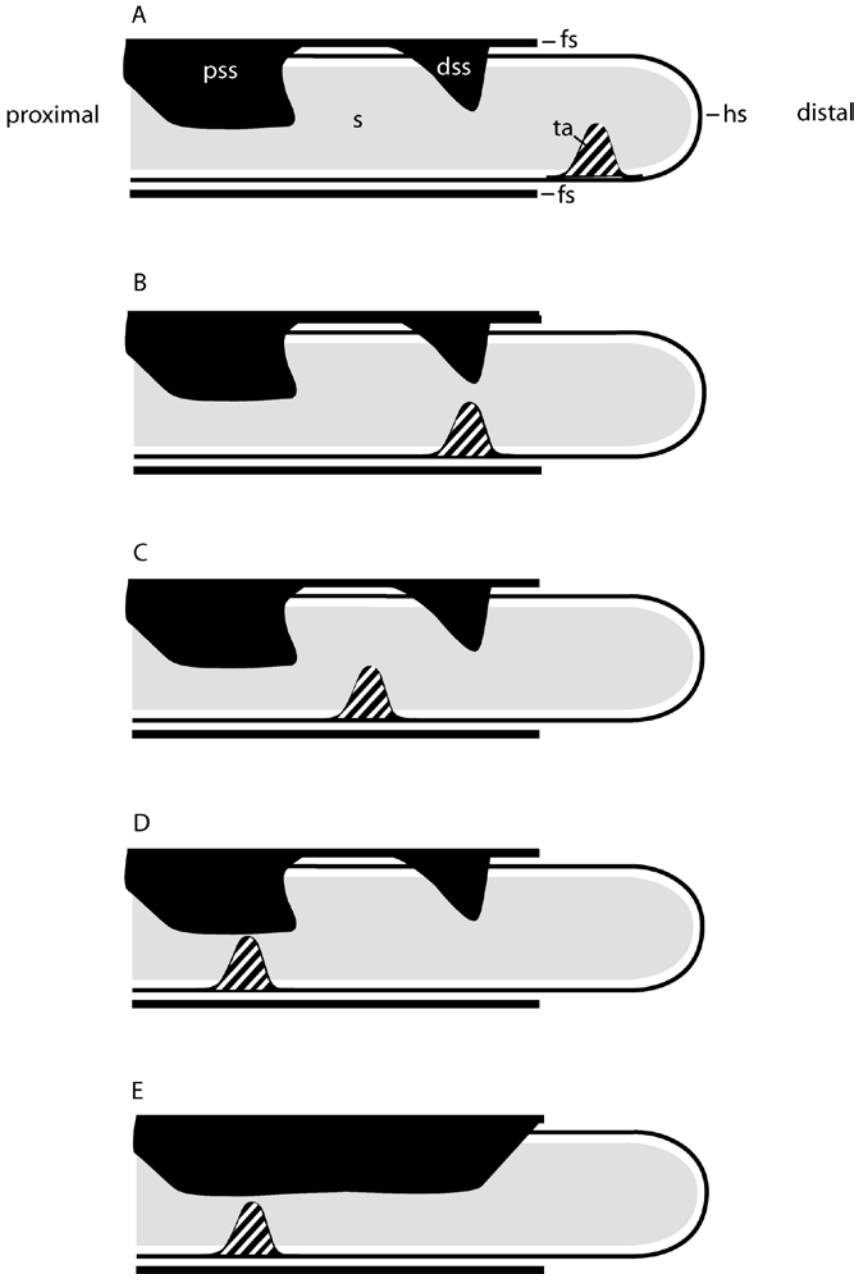


Figure 3.16: Five models of floral synorganization. Top view of longitudinal flower sections. Except in (A) the passage to the nectar is always blocked by the synorganisation of the trigger appendage (ta, hatched) of the hooded staminode (hs, black line) and the two parts of the stiff swelling of the fleshy staminode (fs, black; proximal, pss and distal, dss). grey, style. (A) ta distal to the fs. (B) ta opposite the distal ss together blocking the passage to the nectar. (C) ta in between the distal and the proximal ss. (D) ta opposite the proximal ss. (E) ta opposite a sinlge long ss.

authors discussed those differences in the context of selection for specialization. It is here assumed that the morphological basis for this postulated spezialisation might be found in the fitting between flower and pollinator which is primarily expressed in the differential proboscis length and thickness of the insect in relation to the length and

width of the floral tube (see also e.g. *Impatiens* and *Pelargonium* in Vogel, 1954). A close evolutionary relation of those measurements is for example supported by variations in tube length within the species *Calathea crotalifera* which match the proboscis length of several different pollinators across its wide distribution range (Kennedy, 2000).

Based on these functional interpretations the hypothesis is here rejected that the `cave´ of the fleshy staminode formed by its two swellings (Figs 3.9 I, 3.13A) is a secondary nectar cave (Kunze, 1984). The distal stiff swelling often partly covers this `cave´ which makes access to the latter more difficult than reaching beside it. More importantly, reaching the `cave´ would not effect a triggering of the explosive pollination mechanism and observations generally revealed a nectar stand proximally to the proximal swelling.

Instead, the proximal stiff swelling might serve to retain the nectar in the floral tube as it almost entirely closes the proximal part of the flower (except for the passageway at the position of the trigger appendage) creating a separate compartment (see equal functions e.g. in *Salvia* in Wester and Claßen-Bockhoff, 2007).

3.5.3 PRECISION OF POLLEN DEPOSITION

Apart from an obligate excitation of the explosive pollination mechanism a high precision of the pollen transfer is fundamental. The pollen plate and the pollen load are particularly small, the explosive pollination mechanism irreversible allowing for a single pollination chance per flower only and the pollen deposition and reception is effected by the same organ, the style (chapter 2; see also Claßen-Bockhoff, 1991). An effective pollen transfer thus requires an always identical pollen placement onto the insect.

A lateral deviation of the pollen deposition is restricted by the long and narrow `tunnel´ shaping of the fleshy staminode. The pollinator’s mouthparts and likewise its body are forced into a straight position in front of the flower (see illustrations in chapter 2). This is further supported by the conspicuous outer staminodes which serve as landing platform for the bees influencing their position relative to the flower (chapter 2; secondary zygomorphy in Kunze, 2005). A longitudinal deviation of the pollen deposition is controlled by a constant intraspecific distance between flower

entrance and tip of the trigger appendage and a close matching of this distance with the pollinator's mouthpart (see chapter 2).

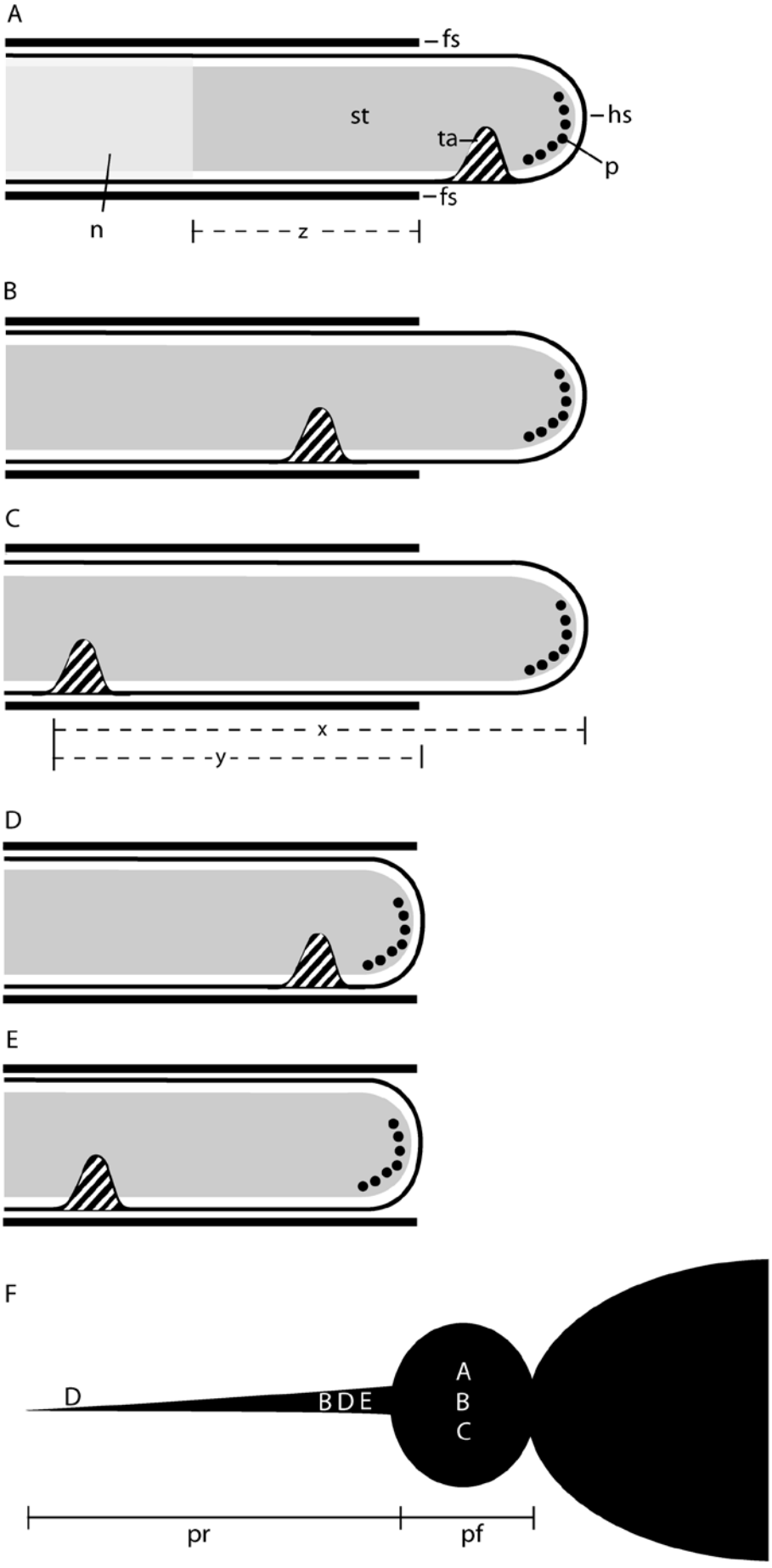
An additional guiding structure in some of these species might be provided by a slightly longer tip of the fleshy staminode forming a "roof" above the flower entrance which might contribute to positioning the pollinator's head correctly in front of the floral tube and closely above the stylar head (e.g. *Sarcophrynium*; see supplementary information - CD).

However, analyses in *Calathea insignis* (Kennedy, 1983) have shown that only 50 % of triggered flowers have pollen in their stigma. Further investigations are needed to confirm whether these observations are universally valuable in the family. A low pollen transfer might be one possible explanation for the low fruit-set in the Marantaceae (~10%, chapter 2; see also Locatelli et al., 2004; Heller and Claßen-Bocklhoff, 2008*b*). While the source of imprecision in bee pollinated species is still unknown, bird pollinated flowers are visited from all directions so that pollen deposition and uptake can possibly occur on all sides and thereby fail if by chance deposition and uptake occurs on two different sites of the beak (e.g. *Afrocalathea rhizantha, Thaumatococcus* sp.1; see chapter 2).

3.5.4 MECHANICAL ISOLATION THROUGH DIFFERENTIAL POLLEN DEPOSITION? (FIG. 3.17)

Kennedy (2000) observed in selected American taxa that, depending on species, pollen might be deposited at different positions on the insect - either on the proboscis or into the proboscidial fossae underneath the head. The morphological comparison across the whole family elucidates that these differences are based on a differential synorganization of style, hooded and fleshy staminode. Five different types of synorganization are illustrated in Fig. 3.17 based on the relative length of the fleshy staminode in comparison to the complex of style and hooded staminode, the position of the trigger appendage inside or in front of the floral tube and the distance between trigger appendage and stylar head.

Pollen is deposited onto the pollinator´s mouthparts if the fleshy staminode and the complex of style and hooded staminode are equally long. In that case the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rolling-in movement of the style occurs inside the floral tube where generally only the mouthparts can enter (e.g. species of the spoon, elephant ear and lever type; Fig. 3.17D-F). *Thrinchostoma bicometes,* however, has an extremely narrow elongated front part of the head (see chapter 2 Fig. 2.5D) so that here pollen from *Halopegia azurea* might possibly be deposited into the proboscidial fossae.

Generally though, pollen deposition underneath the head or other body parts of the pollinators is only possible if the complex of style and hooded staminode exceeds the length of the fleshy staminode. Here the insect´s head can be placed directly above the stylar head (Fig. 3.17A-C) and thereby become the locality of pollen deposition (e.g. *Hypselodelphys* spp*., Marantochloa purpurea*). If the mouthparts are longer than the distance between trigger appendage and stylar head pollen will be deposited again onto the mouthparts. All these variations are independent of the trigger type (see e.g. sword type, lever type; Table 3.1).

Furthermore, the positioning of the flower on the plant and thereby its relative position towards the pollinator especially with reference to the style movement can play a role in the locality of pollen deposition. The style movement might thereby come either strictly from underneath (e.g. *Marantochloa, Hypselodelphys,* chapter 2), from the side (e.g. *Ctenanthe* see Kennedy, 1978; Kennedy, 2000) or from above (see drawings in Clausager and Borchsenius, 2003).

However, the importance of mechanical isolation for the interruption of gene flow in the absence of any other barriers (e.g. infertility between species, geographic isolation) has still to be tested experimentally between sister species (see chapter 4). It can not yet be excluded that pollen mixture occurs due to the proximity of the pollen placements on proboscis or proboscidial fossae and the retraction of the proboscis into the proboscidial fossae.

Figure 3.17: Floral synorganization (A-E) and respective pollen deposition on the insect pollinator (F). top view of longitudinal flower section. (A) trigger appendage (ta) in front of the fleshy staminode (fs, bold black line); complex (c) of style (st, dark grey) and hooded staminode (hs, thin black line) longer than fs; nectar level exemplified; distance to the nectar (z, light grey) dependent on flower tube length. (B) ta inside fs; c longer than fs. (C) ta in proximal part of fs; c longer than fs. (D) ta in distal part of fs; c as long as the fs. (E) ta in proximal part of fs; c as long as fs. The locality of pollen deposition in each model is depicted in (F). Pollen is deposited either on the tip or on the proximal part of the proboscis (pr) or into the proboscidial fossae (pf) beneath the insect´s head. x, distance between ta and flower entrance; y, distance between ta and style head. black dots indicate pollen grains.

3.5.5 MORPHOLOGICAL INFLUENCES ON BREEDING SYSTEM - FROM ALLOGAMY TO AUTOGAMY

The comparison of the four investigated autogamous species with their closely related non-selfing species stresses the minuteness of morphological alterations that exert the switch in the breeding systems. Only minor changes in the morphology of the pollen plate and the envelope of the hood of the hooded staminode around the stylar head facilitate the breakdown of strict separation of pollen packet and stigmatic cavity. An important additional indispensable trait found in all four autogamous species is the self-triggering of the style. Solely this trait guarantees the deposition of the pollen grains in the stigmatic cavity. Prior to this movement they often just adhere to the underneath of the frontal lobe. The mechanism which allows triggering in the absence of pollinators is still unknown. The universal self-compatibility in Marantaceae (chapter 2; see also Kenney, 2000; Locatelli et al., 2004) is regarded as an important prerequisite for the success in switches to autogamy. Autogamy which is generally coupled with a considerably higher fruit set in the Marantaceae (see chapter 2) might be a mechanism for self assurance in an environment of highly variable pollinator availability and a mean for local population maintenance (chapter 2; see also Takebayashi and Morrell, 2001; Barrett, 2002). A correlation of autogamy and reduced vegetative propagation is described in chapter 2. In the American species *Calathea micans* (Le Corff, 1992) and *Pleiostachya pruinosa* (Heller and Claßen-Bockhoff, 2008*b*) even cleistogamy was found dependent on light and nutrient availability.

The different mechanisms of selfing in the four species are equally effective. In each species a pollen transfer in 100 % of all investigated flowers was documented. Thus astonishing is the low fruit set in all four species. This might indicate a reduced acceptance of self pollen as postulated in the hypothesis of bet hedging and resource limitation (Sutherland, 1986; Horvitz and Schemske, 1988). The determination of the degree of autogamously produced fruits would be an important step to deduce the ecological significance of the switch in breeding system (Kress, 1983; Barrett, 2002).

The fruit-set in *Pleiostachya pruinosa* and *Halopegia azurea* might additionally be influenced by architectural constraints. In both species fruits develop closely enveloped by the bracts. In *Halopegia azurea* where the peduncles of the two flowers of a flower pair have a differential length two fruits develop one above the other. In

contrast in *Pleiostachya pruinosa* with equal peduncle lengths within a flower pair only one fruit per bract can be found. Similarly, a distinct pattern of fruit set was described for *Calathea insignis* (Kennedy, 1983). In many other species the common axis of a flower pair is longer than the bract and therefore fruits develop free hanging without special restrictions. In those species two fruits per flower pair and several flower pairs fruiting per bract can be counted.

3.6 CONCLUSION

The “adaptive value” of an organ addresses its traits that have transformed in order to best address the external factors it has to deal with (Sun et al., 2007). The greatest challenge of zoophilous flowers is the effective transmission of pollen. In the Marantaceae this is reached through an explosive mechanism. The close floral synorganization of style, hooded and fleshy staminode allowed the evolution of an inevitable stylar movement which is rapid (~ 0.03 sec in *Thalia* in Claßen-Bockhoff, 1991) and thus difficult to avoid by the pollinator but not too forceful to deter it from any further visits. A hiding of the pollen packet from the pollinator in the flower and later on the insect allows for an economic production of the latter. An obligate and precise pollen transfer is guaranteed by the control over the positioning of the pollinator’s body by the provision of a landing platform, the development of a long and narrow floral tube and the internal correlation of the stiff swelling and the trigger appendage. The ecological functionality of the explosive pollination mechanism in the Marantaceae is underlined by its evolutionary maintenance in such a high number of species.

4 Evolution in African Marantaceae - evidence from phylogenetic, ecological and phenotypic studies

4.1 ABSTRACT

The Marantaceae (~550 spp.) are one of the most species rich families within the order Zingiberales inciting the search for evolutionary factors of their speciation. A positive influence on their divergence is ascribed to their unique explosive pollination mechanism which has been proposed to be a key-innovation. To test this hypothesis a phylogeny of an almost complete sampling of the two major African clades (*Sarcophrynium* and *Marantochloa* clade) is based on data from nuclear (ITS, 5S) and chloroplast (*trnL-F*) DNA. It is used to parsimoniously reconstruct morphological and ecological traits and geographic distribution pattern. The resulting relationships are congruent with the existing family phylogeny. As in previous studies the genus *Ataenidia* is nested within *Marantochloa* which is also supported by morphological characters so that a new circumscription of *Marantochloa* is proposed. However, there are a few incongruencies between the two gene regions from the different genomes. Here hybridisation events might have contributed to speciation. Only a few examples of morphological changes in the explosive pollination mechanism leading to ecological or mechanical isolation could be found. Instead strong selection pressures have shaped the maintenance of a functional and precise pollen transfer mechanism with a hidden pollen load throughout the whole family. Its flexibility to produce different flower tube lengths and size classes as adaptation to different pollinators induced the splits between genera and subclades. Pleistocene climatic fluctuations are hypothesised to have influenced the genetic divergence in refugia of closely related sympatric taxa which demonstrate today highly similar floral morphologies and share the same pollinators. Dispersal or vicariance events onto different continents at the rise of the Marantaceae affected the primary splits at the backbone of the tree. Therefore the designation of the unique explosive pollination mechanism as a key innovation in the Marantaceae depends on the definition of a key-innovation.

4.2 INTRODUCTION

“Traits evolve and themselves influence the rate of evolution…” (Dodd et al., 1999). From this reciprocal relationship arises the idea that certain “key innovations” in the evolution of life have unlocked new adaptive zones in which species have proliferated at an increased rate (Maynard Smith and Szathmary, 1995). An example of an increased diversification rate correlated with the appearance of a new trait is placed by the Marantaceae (~550 spp.) (Andersson, 1998; Kennedy, 2000). The Marantaceae are one of the most derived families of the Zingiberales (Kress, 1995) and are significantly more species rich than their sister family Cannaceae (10 spp.; Kubitzki, 1998) which is correlated with the acquisition of a unique explosive pollination mechanism (chapter 2). Kennedy (2000) first postulated this explosive pollination mechanism to be a key innovation in the family which should have contributed markedly to their species richness.

Following Heard and Hauser (1995) three levels can be distinguished where key-innovations might act: key innovations might allow the escape from competition by exploring a new niche, increase the individual plant fitness or contribute directly to reproductive and ecological speciation. To test the first two levels, one has to compare the niche occupation of the species and the fitness of the individuals of the Marantaceae with an explosive pollination mechanism against the most closely related species of the Cannaceae without such a mechanism. The third level refers solely to the speciation processes within the Marantaceae. These can only be evaluated in a phylogenetic context by correlating the divergence of traits with the molecular inferred splits between taxa (see Sanderson and Donoghue, 1994; Dodd et al., 1999; Lunau, 2004; Perret et al., 2007).

The most recent molecular phylogeny of the Marantaceae is on genus level comprising 71 taxa from 27 of the 31 recognized genera (Prince and Kress, 2006*a*) and extracts five major clades: The first branching clade is the *Sarcophrynium* clade followed by the *Calathea* and the *Donax* clade, respectively. The latter is sister to a clade containing the *Stachyphrynium* and *Maranta* clade. In this project additionally a phylogeny on species level was compiled for two of these clades. Their distribution is restricted to Africa and nrDNA and cpDNA were used to account for the possibility of differential signals produced by the independent evolution of the different genomes (Doyle et al., 2003; Tsitrone et al., 2003; Gomez-Zurita and Vogler, 2003). The two

African clades occupy two evolutionary distant positions in the family phylogeny each containing about 20 species: the *Sarcophrynium* clade is sister to all other Marantaceae and the *Marantochloa* clade (including all species of the genera *Ataenidia* and *Marantochloa*) is part of the *Stachyphrynium* clade. The species are widely distributed from Senegal to Ethiopia in the north and Angola and Madagascar in the south with the diversity centre in Gabon (Perrier de la Bâthie, 1946; Koechlin, 1964; Dhetchuvi, 1996). They are perennial herbs or lianas and often dominate the understorey of the tropical lowland rainforest (Letouzey, 1968).

The aim of this chapter is to evaluate the importance of the explosive pollination mechanism for the speciation within the Marantaceae - thus its direct contribution to mechanical and ecological isolation. Therefore the evolutionary pattern of distribution areas and different vegetative and floral traits (see chapter 2 and 3) were reconstructed on the basis of the available and the here newly established phylogenetic hypotheses. Referring the character states to the phylogenetic tree will lead to a hypothesis about the crucial factor at each node which forced the divergence into two lineages. A summary of this data across the family will then allow estimating the relative importance of a certain trait for the diversification of the family into major clades, subclades and species in space and time (Perret et al., 2007).

4.3 MATERIALS AND METHODS

4.3.1 TAXON SAMPLING

43 taxa were included in the analysis (Table 4.1), i.e. 85 % of the species of the two clades (Dhetchuvi, 1996). No sequences could be obtained from *Hypselodelphys zenkeriana, Megaphrynium distans* and *Sarcophrynium villosum* (*Sarcophrynium* clade) and *Marantochloa comorensis, M. sulphurea* and *M. ramosissima* (*Marantochloa* clade). However, five new species were found and included (unpubl. data). As outgroup species from related clades (see Prince and Kress, 2006*a*) were chosen: *Calathea rufibarba* and *Canna indica* for the *Sarcophrynium* clade and *Afrocalathea rhizantha* and *Phacelophrynium interruptum* for the *Marantochloa* clade. Species identification was based on available keys (Koechlin, 1964, 1965; Dhetchuvi, 1996), type descriptions and comparisons with type specimens in various herbaria

(BR, K, LBV, P, WAG). Origin of material, voucher information and sequence accession numbers are given in Table 4.1.

4.3.2 DNA EXTRACTION, AMPLIFICATION AND SEQUENCING

Total genomic DNA was extracted from leaf tissue using the NucleoSpin® Plant DNA extraction kit (Macherey-Nagel, Düren, Germany) following the manufacturer's instructions. Amplifications of the target loci, internal transcribed spacer (ITS; including ITS1, 5.8S and ITS2), *trnL-trnF* intergenic spacer and 5S nrDNA (including 5S nrDNA gene and spacer region) were conducted in a Biometra® T3 or PTC 100™ MJ Research thermocycler via standard PCR in 25µl volume containing 2.5µl 10X PCR buffer (without $MgCl_2$), 0.25µl 20mM dNTPs, 1.25µl 50mM $MgCl_2$, 1.25µl 0.01mM each forward and reverse primers, 0.15µl *Taq* DNA polymerase (BioTherm DNA polymerase 5u/µl from GeneCraft, Germany), 18µl H_2O and 1µl genomic DNA extract. 2µl genomic DNA were occasionally used for herbarium specimen. PCR cycles were as follows for ITS and 5S: one cycle 1 min at 94°C, 27 cycles of 0.2 min at 55°/52°C, 4 min at 60°C, 0.1 min at 96°C with a final extension period of 0.1 min at 51.4°C and 4 min at 60°C. For *trnL-F*: one cycle of 4 min at 94°C, 35 cycles of 45 s at 94°C, 45 s at 52°C, 2.5 min at 72°C with a final extension period of 10 min at 72°C.

Amplification of ITS was performed using the primer 18S (5´-CCT TMT CAT YTA GAG GAA GGA G-3´) and 28S (5´-CCG CCT ATT KAT ATG CTT AAA-3´) (Schlötterer, 1998). The 5S was amplified with the primers designed by Cox & al. (1992) *5S* forward (5'-TGG GAA GTC CTY GTG TTG CA-3') and 5S reverse (5'-KTM GYG CTG GTA TGA TCG CA-3'). For *trnL-F* ucp-f (5´-ATT TGA ACT GGT GAC ACG AG- 3´) and ucp-c (5´-CGA AAT CGG TAG ACG CTA CG-3´) (Taberlet et al., 1991) were applied. The DNA fragments were checked on 0.8% agarose gels and purified prior to sequencing using the QIAquick® PCR purification kit (QIAGEN, Hilden, Germany) according to the manufacture`s instructions. Purified PCR products were checked on 0.8 % agarose gels. Purified PCR products were cycle-sequenced with the ABI Prism Dye Terminator Cycle Sequencing Ready Reaction Kit (BD 3.0 in 10 µL reactions) by Perkin Elmer using the PCR primers listed above and following the manufacturer's protocol. Products were purified and analysed by Genterprise (Mainz, Germany). Forward and reverse sequences were manually edited and merged into consensus sequences using BioEdit version 5.0.6. (Hall, 1997-2001).

Sequences were preliminarily aligned in MacClade 4.0 (Maddison and Maddison, 2000) and Mesquite version 1.11 (Maddison and Maddison, 2006) and then manually adjusted and exported in Nexus format for the import in PAUP 4* (Swofford, 2003). Indel coding followed the instructions for “simple indel coding” by Simmons and Ochoterena (2000).

4.3.3 PHYLOGENETIC ANALYSIS AND BRANCH SUPPORT

The *Sarcophrynium* and *Marantochloa* clades (after Prince and Kress, 2006*a*) were analysed separately analysing the datasets of the different gene regions individually and combined.

Unweighted Maximum Parsimony (MP) analyses were performed using PAUP*4.0b10 (Swofford, 2003) applying the heuristic search algorithm with 1000 heuristic search replicates of random sequence addition and tree-bisection-reconnection branch swapping (TBR). Statistical support for branches was estimated via bootstrap with 1000 replicates (100 addition sequence replicates). Due to few variable characters in the bootstrap analyses of the *trnL-F* dataset, the analysis was unable to run to completion. Therefore no more than 1000 trees were saved per replicate.

Maximum Likelihood (ML) analyses were performed by using PAUP*, applying the best-fitting molecular evolution model and parameters determined by Modeltest 3.7 (Posada and Crandall, 1998) according to the Akaike Information Criterion (AIC) (Akaike, 1974). Heuristic searches with 10 replicates of random sequence addition and TBR were applied. Statistical support for branches was estimated via bootstrap with 100 replicates (10 addition sequence replicates). In the bootstrap analyses of the *trnL-F* dataset no more than 1000 trees were saved. Bootstrap values referred to in the text are either weak (70 to 80), moderate (81 to 90) or high (90 to 100).

Bayesian analyses were conducted in MrBAYES 3.1.2 (Huelsenbeck et al., 2001) using three replicates of 10 million generations of Markov Chain Monte Carlo searches and a sample frequency of 1000. Model parameters were set as described for ML analysis. Burn-in was determined by visual inspection of the log likelihood values. Saturation was reached after 2000 generations.

To assess the level of congruence between the 5S, ITS (nr-DNA) and *trnL-F* (cp-DNA) data sets, each dataset was analyzed independently to see if a similar topology was achieved. An incongruence length difference test (ILD) (Farris et al.

1995) implemented in PAUP* (100 replicates of heuristic searches, 10 addition sequence replicates, MAXTREE = 1000000) on combined data matrixes resulted in p = 0.01 for the *Marantochloa* clade, p = 0.13 for the *Sarcophrynium* clade and p = 0.01 for the *Hypselodelphys* clade.

4.3.4 CHARACTER RECONSTRUCTION

Nine characters were mapped onto the single ML trees of the combined datasets for the *Marantochloa* and the *Sarcophrynium* clade using Mesquite version 1.11 (Maddison and Maddison, 2006). Character state reconstruction assumed parsimony of unordered states (Fitch, 1971).

Character states are based on morphological and ecological data (chapter 2 & 3; Dhetchuvi, 1996). The analysis comprises growth form (herb/liana), number of leaves per shoot, leaf orientation on the shoot (homotrop/antitrop; Tomlinson, 1961), average length of inflorescence internodes, number of flower pairs per bract (1/>2), average length of fleshy staminode, flower tube morphology, presence/absence of conspicuous outer staminodes, pollinators (large bees, small bees, birds), breeding system, fruit type (nut/capsule/berry-like), fruit colour as well as geographic distribution areas (West Africa, Central Africa). Geographic distribution areas were further submitted to a DIVA analysis (Ronquist, 1997).

Thereby only life from, flower pairs per bract, outer staminodes and flower colour are variable and are therefore mapped in the *Sarcophrynium* clade. Leaves per shoot, leaf morphology, floral tube morphology and breeding system are only mapped for the *Marantochloa* clade. Flower size, pollinators and geographic distribution are applicable to both clades.

To obtain a higher resolution within the genus *Hypselodelphys* morphology of the leaf base, pubescence (presence/absence) of inflorescence internodes and length of the fruit spines on its surface were additionally considered and mapped.

4.4 RESULTS

4.4.1 *SARCOPHRYNIUM* CLADE

ITS phylogeny (Fig. 4.1): The ITS dataset comprised 21 taxa including two outgroup taxa. The alignment was 778 bp long including 21 indels. This matrix showed

uncorrected pairwise distances of 0.393 % - 20.216 % for the ingroup and 13.941 % - 24.003 % between ingroup and outgroup species. A single repetition of 76bp in *Megaphrynium gabonense* (bp 331 to 398 in the alignment) was excluded from the analysis. Three MP trees of 489 steps were generated (for tree statistics see Table 4.2). Indel coding slightly increased tree scores and branch supports. The TIM+G model was selected as the best model (substitution rates: A<>C 1.0000, A<>G 4.367, A<>T 1.6291, C<>G 1.6291, C<>T 7.5680, G<>T 1.0000 and base frequencies: A=0.1964, C=0.3079, G=0.3105, T=0.1852). Maximum likelihood analysis generated a single best tree.

The topology of the MP, ML and Bayesian trees is identical. The whole *Sarcophrynium* clade is moderately supported when indels are included. The four genera *Hypselodelphys* / *Trachyphrynium*, *Megaphrynium, Sarcophrynium* and *Thaumatococcus* are highly supported as monophylla in all analyses. Moderately to highly (including indels) supported is the sister relationship between *Megaphrynium* and *Thaumatococcus*. The relationship of the three clades *Megaphrynium/Thaumatococcus*, *Hypselodelphys* and *Sarcophrynium* is not resolved.

Within the genus *Sarcophrynium*, *S. brachystachyum* is sister to the other three species – the two accessions of *S. prionogonium* form a monophylum and are sister to *S. schweinfurthianum*. Within the genus *Megaphrynium*, *M. trichogynum* is sister to a clade comprising *M.* sp. 1 and *Megaphrynium macrostachyum*. Together they form a sister clade to *M. gabonense* which has an exceptionally long branch. Within the genus *Hypselodelphys* no resolution was obtained apart from a few sister relationships (*H. violaea/H. scandens; H. poggeana/H. hirsuta, H. triangularis/H.* sp.). These sister pairs, together with *H. velutinum,* stay in a polytomy with *Trachyphrynium braunianum*.

trnL-F phylogeny (Fig. 4.2): The *trnL-F* dataset comprised 19 taxa including two outgroup taxa. The final alignment was 1036bp long including 15 indels. This matrix showed uncorrected pairwise distances of 0.0 % - 4.421 % for the ingroup and 3.202 % - 5.418 % between ingroup and outgroup species. 4617 MP trees of 134 steps were generated (for tree statistics see Table 4.2). Indel coding slightly increased tree scores and branch supports. Tree statistics are better for the *trnL-F* dataset than for the ITS dataset. The K81uf+G model was selected as the best model

(substitution rates were: A<>C 1.0000, A<>G 1.1327, A<>T 0.3078, C<>G 0.3078, C<>T 1.1327, G<>T 1.0000 and base frequencies were A=0.3441, C=0.1684, G=0.1620, T=0.3255). Maximum likelihood analysis generated three best trees.

The topologies of the MP, ML and Bayesian trees are identical with the exception of the position of *Megaphrynium trichogynum.* It appears as sister to all other *Megaphrynium* species on a weakly supported branch in the MP analysis including indels but forms a polytomy with the *Megaphrynium* and *Thaumatococcus* clades in all other analyses. The position of *Megaphrynium trichogynum* is the only hard incongruence to the ITS dataset.

Otherwise, congruence in the topology of the *trnL-F* and ITS dataset is achieved in the support of the monophyly of the individual genera *Hypselodelphys/Trachyphrynium, Megaphrynium, Thaumatococcus* and *Sarcophrynium*. The sister relationship of *Megaphrynium* and *Thaumatococcus* is highly supported. In the MP analysis of the *trnLF* dataset the sister relationship between *Hypselodelphys/Trachyphrynium* and *Megaphrynium/Thaumatococcus* is weakly supported. The monophyly of the whole *Sarcophrynium* clade against the outgroup taxa though has no support. Instead *Sarcophrynium* and *Calathea rufibarba* stay in a polytomy with the clade of the remaining species. The relationships established within the genus *Sarcophrynium* are identical with the ones in the ITS dataset. There is no resolution within the genus *Hypselodelphys*.

combined analysis (Fig. 4.3): The combined analysis comprised 20 taxa including two outgroup taxa. The two taxa missing in the *trnL-F* dataset were coded as missing data in the combined dataset. The final alignment was 1813bp long when 36 indels were included. The partition homogeneity test across the two data partitions ITS and *trnL-F* yielded a p = 0.13. Six MP trees of 629 steps were generated (for tree statistics see Table 4.2). The combination of the two dataset ITS and *trnL-F* increased tree statistics against the ITS dataset but not against the *trnL-F* dataset. Indel coding slightly increased tree statistics and branch support. The GTR+G model was selected as the best model (substitution rates were: A<>C 0.7314, A<>G 2.4047, A<>T 0.6586, C<>G 1.3963, C<>T 3.4640, G<>T 1.0000 and base frequencies: A=0.2813, C=0.2320, G=0.2247, T=0.2620). Maximum likelihood analysis generated a single best tree. Tree topology is identical in the three analyses.

The monophyly of the individual genera is highly supported. However no resolution can be obtained for the sister relationships between the genera. Topology within genera is identical with the phylogenetic signal of the ITS dataset. The slightly lower bootstrap value on the sister relationship of *Megaphrynium trichogynum* to the clade consisting of *M.* sp. 1 and *M. macrostachyum* mirrors the existing incongruence between the ITS and the *trnL-F* dataset with respect to the position of *M. trichogynum*.

4.4.2 THE GENUS *HYPSELODELPHYS*

5S phylogeny (Fig. 4.4): The 5S dataset comprised nine taxa including eight species from the genus *Hypselodelphys* as ingroup taxa and *Sarcophrynium schweinfurthianum* as outgroup taxon. Alignment was straight forward in the ingroup but a bit difficult towards the outgroup. No other 5S nrDNA sequences could be obtained than the once reported here. Obtained sequences gave a clean and unambiguous signal. The final alignment was 420bp long. There were no indels to be coded. One MP tree of 239 steps was generated (for tree statistics see Table 4.2). The TVM+G model was selected as the best model (substitution rates: A<>C 1.0621, A<>G 2.4414, A<>T 0.8603, C<>G 1.9445, C<>T 2.4414, G<>T 1.0000 and base frequencies: A=0.2375, C=0.2481, G=0.2907, T=0.2237). Maximum likelihood analysis generated a single best tree.

The resulting tree topologies from the different analyses are identical with the exception of a higher resolution in the MP analysis concerning the *Hypselodelphys violacea* clade (see below). There are consistently higher support values in the MP and Bayesian analyses than in the ML analysis. All *Hypselodelphys* species form a moderately supported monophylum. *Trachyphrynium braunianum* and the outgroup stand in a polytomy with the latter. Within the genus *Hypselodelphys* the species split into two highly supported clades with three (*H. hirsuta* clade) and four (*H. violacea* clade) species, respectively. In the *H. hirsuta* clade, *H. hirsuta* is sister to *H. poggeana* which is congruent to the ITS dataset and both species together are sister to *H. velutinum*. In the *H. violacea* clade *H. violacea* is sister to *H.* sp.1. The positions of *H. triangularis* and *H. scandens* as further sister species, respectively, are only resolved in the MP analysis (MP bootstrap = 75). The 5S topology of the *H. violacea* clade is incongruent with the ITS topology.

combined phylogeny (Fig. 4.5): The combined analysis comprised nine taxa including one outgroup taxon. The alignment was 2197bp long. The partition homogeneity test across the three data partitions ITS, *trnL-F* and 5S (p = 0.01) indicates some incongruence in the data. One MP tree of 470 steps was generated (for tree statistics see Table 4.2). The TVMef+G model was selected as the best model (substitution rates: A<>C 0.8349, A<>G 2.5368, A<>T 0.6404, C<>G 1.4590, C<>T 2.5368, G<>T 1.0000 and base frequencies were equal). Maximum likelihood generated a single best tree. Tree topology is identical in all three analyses.

The combined dataset exhibits the same basal bifurcation of the *Hypselodelphys* taxa and the same topology in the *H. hirsuta* clade as found in the 5S dataset. Topology within the *H. violacea* clade though matches the species pairs of the ITS dataset (*H. violacea/H. scandens, H.* sp. 1/*H. triangularis*).

Table 4.1: List of taxa sampled for the phylogenetic analysis of the African Marantaceae.

taxon	origin	voucher	GenBank accession numbers ITS	*trnL-F*	5S
***Marantochloa* clade**					
Ataenidia conferta (Benth. in Benth. Hook f.) Milne-Redh.	cultivar bot. gard. Mainz, Germany		EU605892	EU647803	
Marantochloa congensis (K. Schum.) J. Leonard Mullenders	Lope, Gabon	Ley 107 (LBV, WAG)	EU605903	EU647811	
Marantochloa cordifolia	Dibouka, Gabon	Ley 63 (LBV, WAG)	EU605894	EU647804	
Marantochloa cuspidata(Rosc.) Milne-Redh.	San Pedro, Ivory Coast	Jongkind 4739 (WAG)	EU605906	EU647814	
Marantochloa filipes (Benth. In Hook.) Hutch.	Lope, Gabon	Ley 149 (LBV, WAG)	EU605900	EU647808	
Marantochloa incertifolia 2 Dhetchuvi	Monts de Cristal, Gabon	Ley 213 (LBV, WAG)	EU605905	EU647813	
Marantochloa incertifolia 3 Dhetchuvi	Makokou, Gabon	Ley 179 (LBV, WAG)	EU605910	EU647812	
Marantochloa incertifolia 1 Dhetchuvi	Foret des Abeilles, Gabon	Dhetchuvi 1596 (WAG)	EU605904		
Marantochloa leucantha (K. Schum.) Milne-Redh.	cultivar bot. gard. Mainz, Germany		EU605901	EU647809	
Marantochloa mannii (Benth.) Milne-Redh.	cultivar bot. gard. Mainz, Germany		EU605897	EU647806	
Marantochloa microphylla (Koechlin) Dhetchuvi	Ngounie, Gabon	Wieringa 3098 (WAG)	EU605899		
Marantochloa mildbraedii Loes. ex. Koechlin	Estuaire, Gabon	Simons 279 (WAG)	EU605893		
Marantochloa monophylla (K. Schum.) D`Orey	Monts de Cristal, Gabon	Ley 217 (LBV, WAG)		EU647810	
Marantochloa monophylla (K. Schum.) D`Orey	Sindara/Waka, Gabon	Ley 45 (LBV, WAG)	EU605902		
Marantochloa purpurea 1 (Ridley) Milne-Redh.	Lope, Gabon	Ley 140 (LBV, WAG)	EU605895		
Marantochloa purpurea 2 (Ridley) Milne-Redh.	cultivar bot. gard. Mainz, Germany		EU605896	EU647805	
Marantochloa sp.1 nov.	Monts de Cristal, Gabon	Ley 250 (LBV, WAG)	EU605909	EU647807	
Marantochloa sp.2 nov.	Monts de Cristal, Gabon	Ley 194, 195 (LBV, WAG)	EU605898	EU647817	
Marantochloa sp.3 nov.	Monts de Cristal, Gabon	Ley 230 (LBV, WAG)	EU605891	EU647802	
Marantochloa sp.5	Dibouka, Gabon	Ley 74 (LBV, WAG)	EU605890	EU647801	
Marantochloa sp.6	Dibouka, Gabon	Ley 92 (LBV, WAG)	EU605889	EU647800	
Sarcophrynium clade					
Hypselodelphys hirsuta (Loes.) Koechlin	Makokou, Gabon	Ley 156 (LBV, WAG)	EU605913	EU647820	EU647793
Hypselodelphys sp.1 nov.	Mikongo, Gabon	Ley 125 (LBV, WAG)	EU605918	EU647825	EU647798
Hypselodelphys poggeana (K. Schum.) Milne-Redh.	Makokou, Gabon	Ley 168 (LBV, WAG)	EU605912	EU647819	EU647792
Hypselodelphys scandens Louis & Mullenders	Makokou, Gabon	Ley 160 (LBV, WAG)	EU605917	EU647824	EU647797
Hypselodelphys triangularis Jongkind	Sassandra, Ivory Coast	Jongkind 4671 (WAG)	EU605915	EU647822	EU647795

Table 4.1: (cont.).

taxon	origin	voucher	GenBank accession numbers ITS	*trnL-F*	5S
Sarcophrynium clade					
Hypselodelphys velutina Jongkind	Man, Ivory Coast	Jongkind 4839 (WAG)	EU605911	EU647818	EU647791
Hypselodelphys violacea (Ridley) Milne-Redh.	Sibang/Libreville, Gabon	Ley 28 (LBV, WAG)	EU605914	EU647821	EU647794
Megaphrynium gabonense Koechlin	Makokou, Gabon	Ley 155 (LBV, WAG)	EU605924	EU647830	
Megaphrynium macrostachyum (Benth.) Milne-Redh.	Ashanti Region, Ghana	Jongkind 4000 (WAG)	EU605923	EU647829	
Megaphrynium sp.1	Abid+n, Ivory Coast	de Koning 4870 (WAG)	EU605925		
Megaphrynium trichogynum Koechlin	Mikongo, Gabon	Ley 114 (LBV, WAG)	EU605921	EU647828	
Megaphrynium velutinum (Bak.) J. Koechlin	South Province, Cameroon	Tine v. Andel et al 3679 (WAG)	EU605922	EU652953	
Sarcophrynium brachystachyum (Benth.) K. Schum.	Sindara/Waka, Gabon	Ley 32 (LBV, WAG)	EU605926	EU647831	
Sarcophrynium prionogonium 1 (K. Schum.) K. Schum.	Monts de Cristal, Gabon	Ley 55, 222 (LBV, WAG)	EU605927	EU647832	
Sarcophrynium prionogonium 2 (K. Schum.) K. Schum.	Abgboville, Ivory Coast	Wieringa 5389 (WAG)	EU605929		
Sarcophrynium schweinfurthianum (Kuntze) Milne-Redh.	Makokou, Gabon	Ley 224 (LBV, WAG)	EU605928	EU647833	EU647799
Thaumatococcus daniellii (Benn.) Benth.	Dibouka, Gabon	Ley 96 (LBV, WAG)	EU605919	EU647826	
Thaumatococcus sp.1 nov.	Monts de Cristal, Gabon	Ley 56 (LBV, WAG)	EU605920	EU647827	
Trachyphrynium braunianum (K. Schum.) Baker	Makokou, Gabon	Ley 171 (LBV, WAG)	EU605916	EU647823	EU647796
outgroups					
Afrocalathea rhizantha K. Schum.	Makokou, Gabon	Ley 7 (LBV, WAG)	EU605908	EU647816	
Calathea rufibarba Fenzl	cultivar bot. gard. Mainz, Germany		EU605930	EU647834	
Canna indica L.	cultivar bot. gard. Mainz, Germany		AF434893	AM113702	
Phacelophrynium interruptum Warb. ex K. Schum.	cultivar bot. gard. Aarhus, Denmark		EU605907	EU647815	

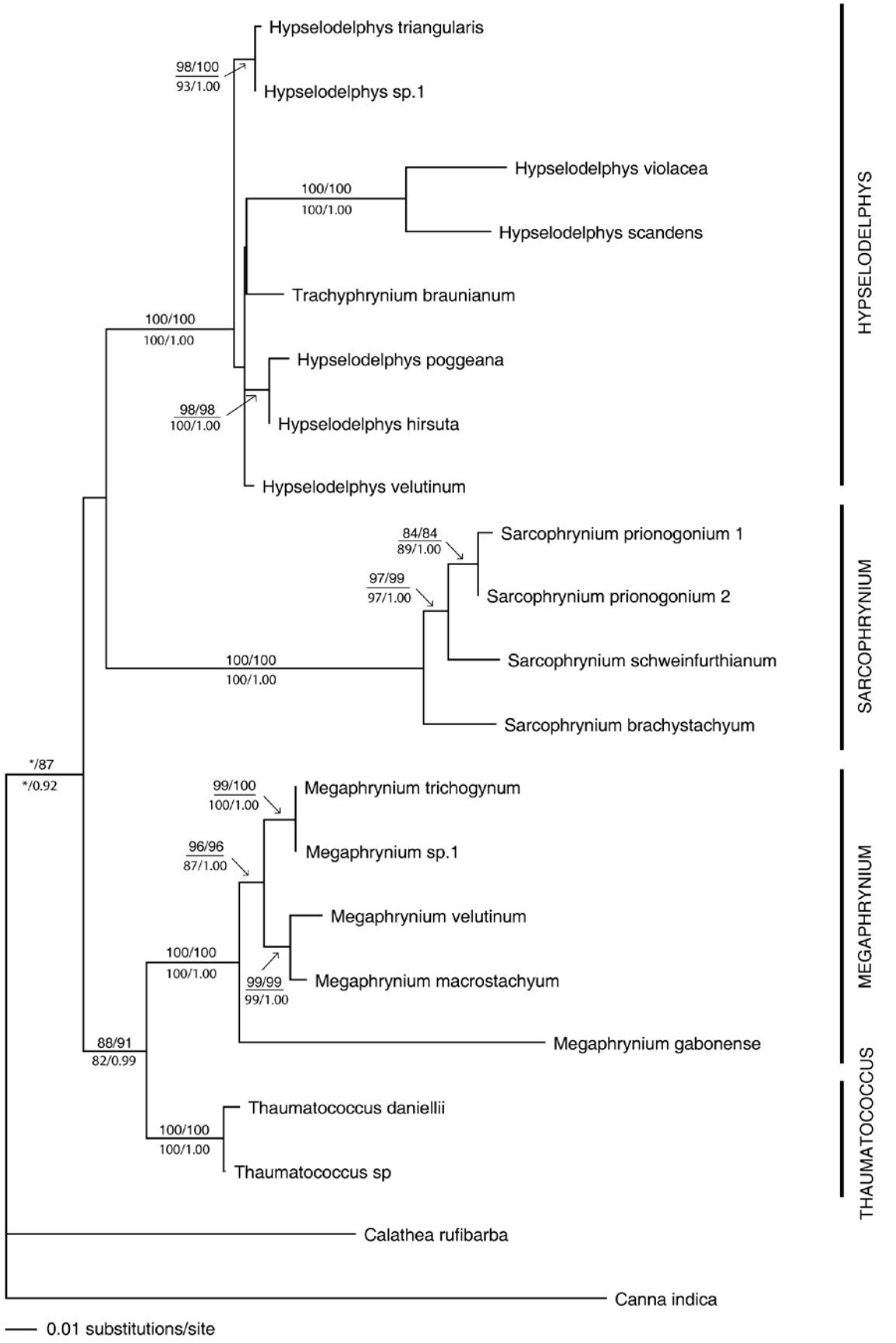

Figure 4.1: Single maximum likelihood (ML) phylogram based on ITS sequence variation of the members of the *Sarcophrynium* clade (sensu Prince and Kress, 2006a). Numbers above branches are MP bootstrap values without / with indels, numbers below branches are ML bootstrap values / Bayesian posterior probability. *, bootstrap value below 75. outgroup-taxa: *Calathea rufibarba* and *Canna indica.*

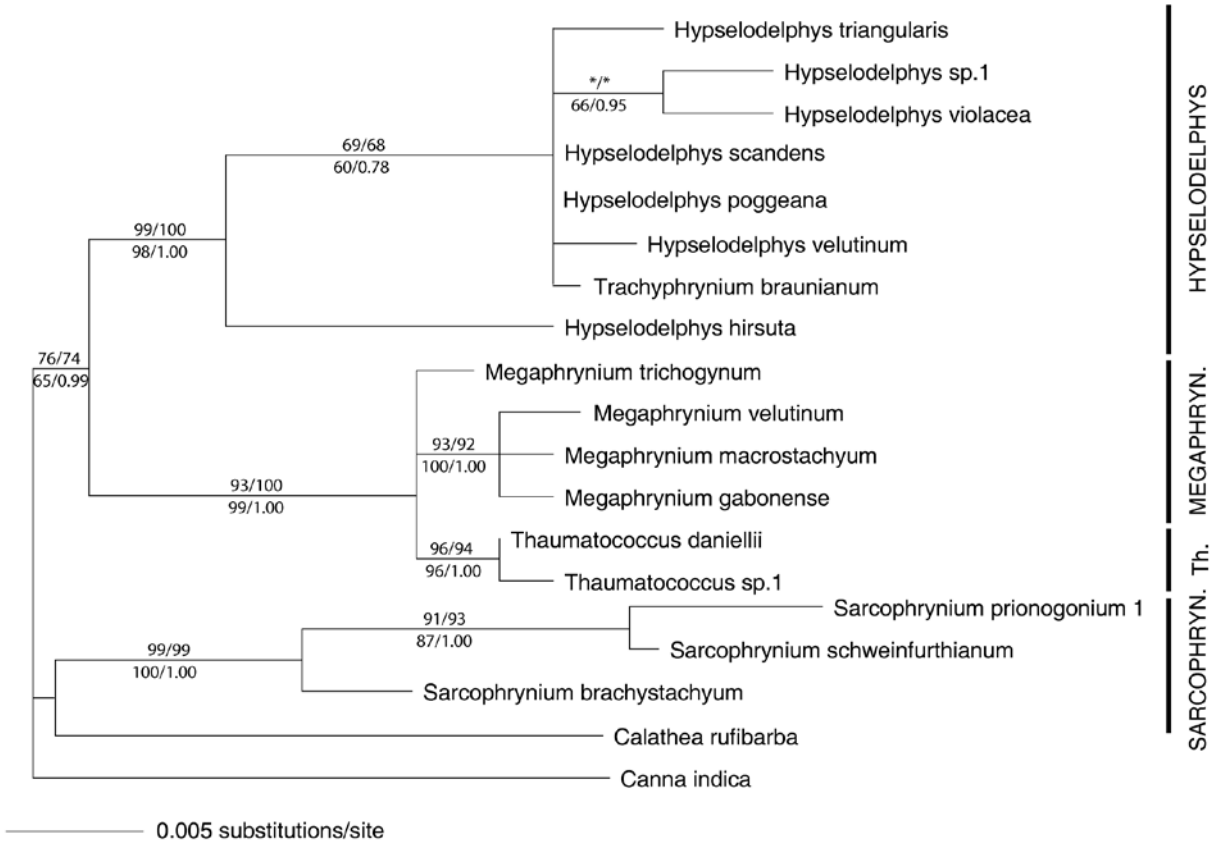

Figure 4.2: One of three maximum likelihood (ML) phylograms based on *trnL-F* sequence variation of the members of the *Sarcophrynium* clade (sensu Prince and Kress 2006a). Numbers above branches are MP bootstrap values without / with indels, numbers below branches are ML bootstrap values / Bayesian posterior probability. Th., *Thaumatococcus*. *, bootstrap value below 75. outgroup-taxa: *Clathea rufibarba* and *Canna indica.*

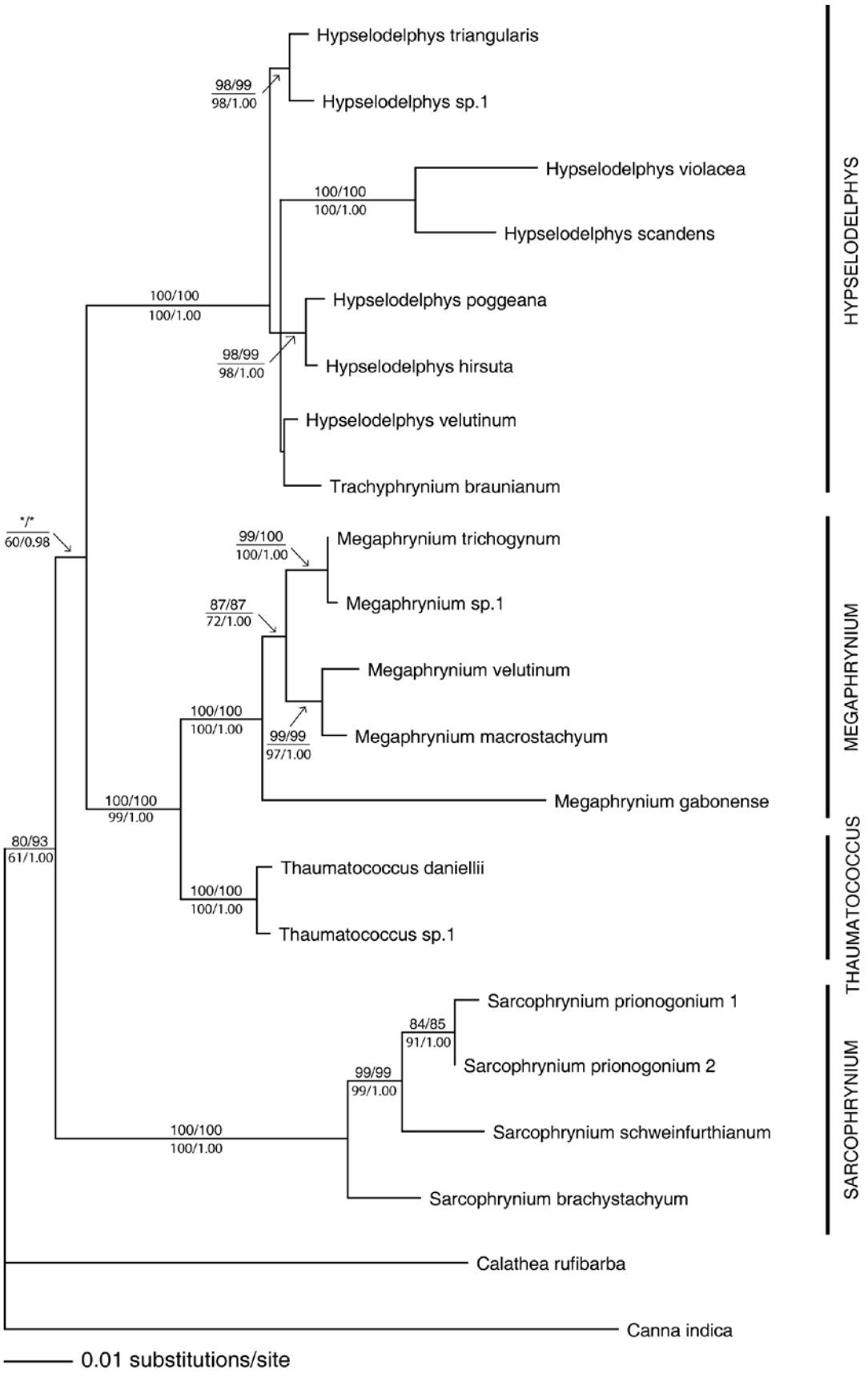

Figure 4.3: Single maximum likelihood (ML) phylogram based on a combined dataset of ITS and *trnL-F* sequence variation for members of the *Sarcophrynium* clade (sensu Prince and Kress, 2006). Numbers above branches are MP bootstrap values without / with indels, numbers below branches are ML bootstrap values / Bayesian posterior probability. *, bootstrap value below 75. outgroup-taxa: *Clathea rufibarba* and *Canna indica.*

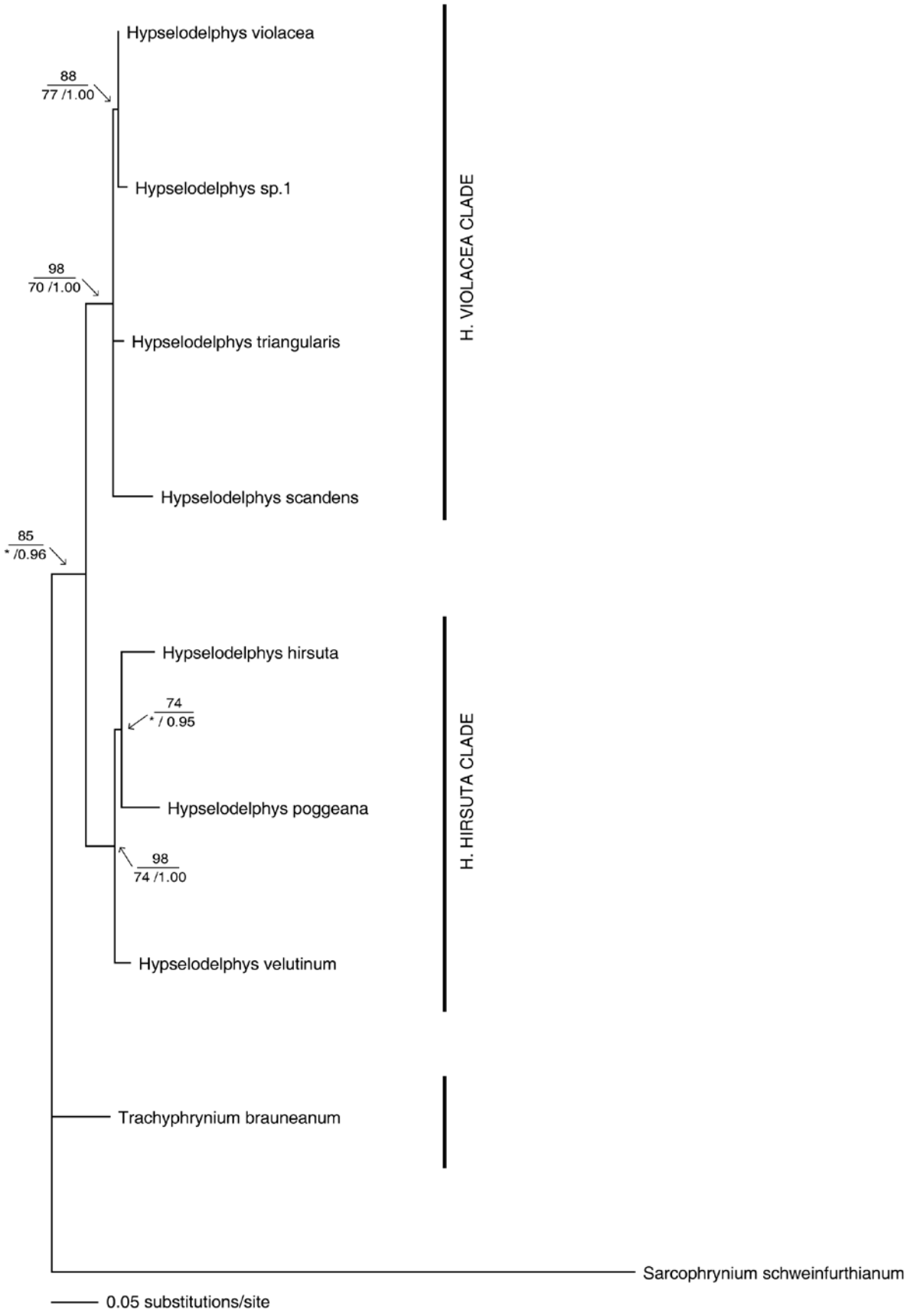

Figure 4.4: Single maximum likelihood (ML) phylogram based on 5S sequence variation for members of the genus *Hypselodelphys*. Numbers above branches are MP bootstrap values without indels, numbers below branches are ML bootstrap values / Bayesian posterior probability. *, bootstrap value below 75. outgroup-taxon: *Sarcophrynium schweinfurthianum.*

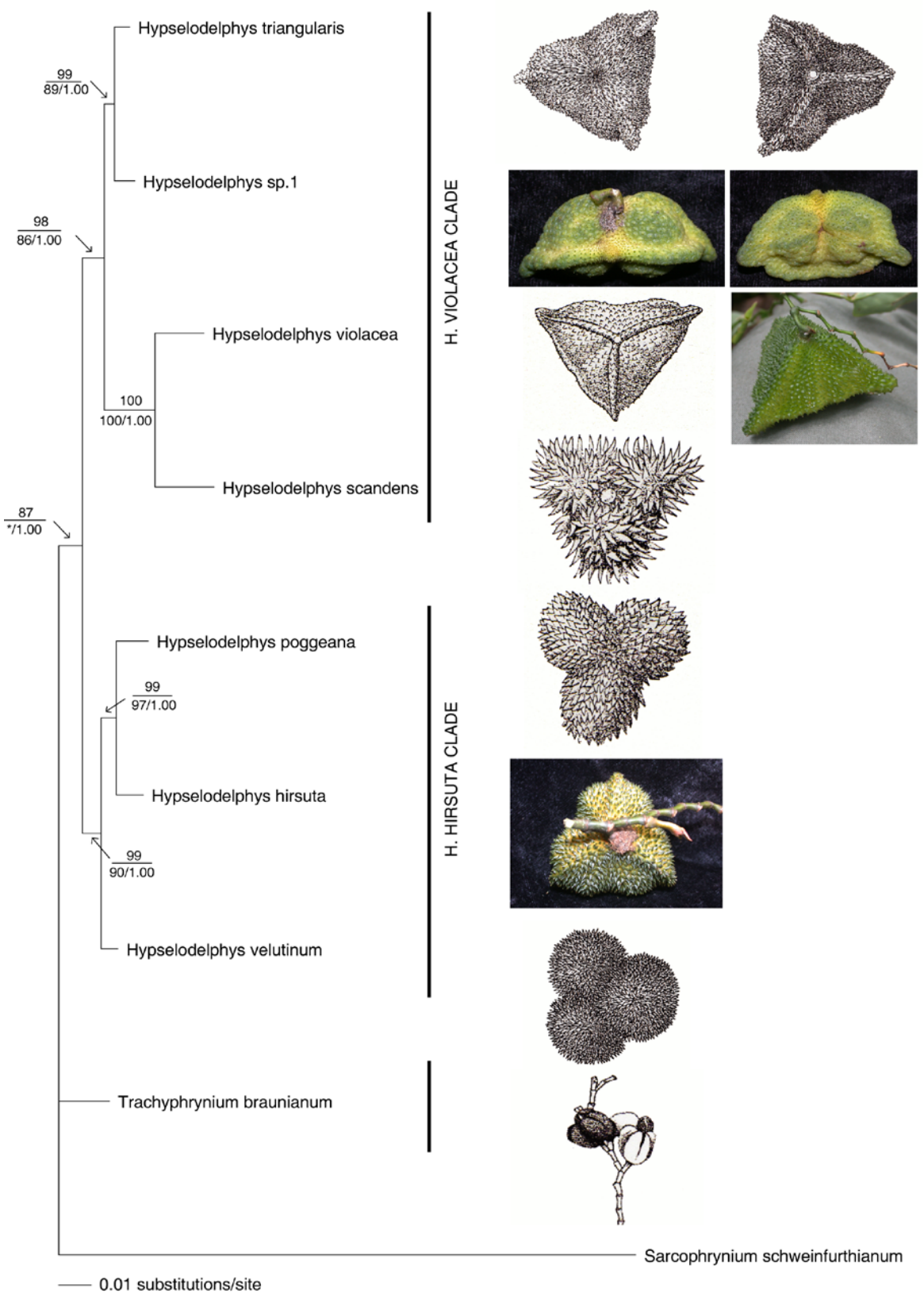

Figure 4.5: Single maximum likelihood (ML) phylogram based on combined dataset of *trnL-F*, ITS and *5S* sequence variation of the members of the genus *Hypselodelphys*. Numbers above branches are MP bootstrap values without indels, numbers below branches are ML bootstrap values / Bayesian posterior probability. Fruit morphology mapped onto the tree (drawings: *H. triangularis, H. velutinum* and *T. braunianum* taken from Jongkind, (in press), *H. violacea, H. poggeana, H. scandens* taken from Koechlin, 1964 and Leonard and Mullenders, 1950). *, bootstrap value below 75. outgroup-taxon: *Sarcophrynium schweinfurthianum*.

4.4.3 *MARANTOCHLOA* CLADE

ITS phylogeny (Fig. 4.6): The ITS dataset comprised 22 taxa including two outgroup species. The aligned ITS-region was 660bp long including 11 indels. This matrix showed uncorrected pairwise distances of 0.0 % - 20.85 % within the ingroup and 13.01 % - 24.03 % between ingroup and outgroup species. Three MP trees of 455 steps were obtained (for tree statistics see Table 4.2). Indel coding slightly increased tree scores and branch support. The GTR+G model was selected as the best model (substitution rates: A<>C 0.6785, A<>G 2.6880, A<>T 1.4457, C<>G 0.5255, C<>T 4.7503, G<>T 1.0000 and base frequencies: A=0.2247, C=0.3020, G=0.2904, T=0.1829). Maximum likelihood analysis generated a single best tree.

The topology of the MP, ML and Bayesian trees was identical with the exception of the position of *Marantochloa cuspidata* being sister to the *M. purpurea* clade in the Bayesian analysis (posterior probability of 0.50). Three clades are highly supported: the *M. congensis*-, *M. purpurea*- and *A. conferta* clade. *Ataenidia conferta* is nested within the *A. conferta* clade with moderate branch support. The *A. conferta*- and *M. purpurea* clades are part of a weakly supported polytomy together with *M. cuspidata, M.* sp. 1 and *M. cordifolia*. This polytomy again is part of a polytomy with the *congensis* clade and *M. leucantha* and *M. filipes* of the *M. leucantha* clade. There is no support for a common ancestry of the latter two species in any of the analyses. The *M. congensis*- and the *M. purpurea* clades are the only clades which are totally resolved (except *M. purpurea*/*M. mannii*) with identical topology and high bootstrap and posterior probability values in all analyses. In the *M. congensis* clade *M. monophylla* is sister to *M. incertifolia* 1 and they together are sister to a clade of *M. incertifolia* 2 and 3. These four species are again sister to a clade of *M. congensis* and *M. microphylla*. The species of the *M. purpurea* clade (*M. purpurea* 1 and 2 form a polytomy with *M. mannii* and are together sister to *M*. sp. 2) show a lot of specific single base mutations also within the *5.8S* region. The two different accessions of *M. purpurea* from Gabon (1) and the greenhouse in Mainz (2) differ in 7bp in the ITS sequence. *M. purpurea* + *M. mannii*, M. sp.2 and *M. cordifolia* have particularly long branches. The *A. conferta* clade consists of a polytomy of equal ITS sequences in *M*. sp.5 and 6 and *M. mildbraedii*. All three species form a polytomy with *Ataenidia conferta* and successively being sister to *M*. sp.3 with high support.

trnL-F phylogeny (Fig. 4.7): The *trnL-F* dataset comprised 18 taxa including two outgroup species. The aligned *trnL-F*-region was 998bp long including 13 indels. No *trnL-F* sequence could be obtained for *Marantochloa incertifolia* 1*, M. microphylla, M. mildbraedii* and *M. purpurea* 1. This matrix showed uncorrected pairwise distances of 0.0 % - 2.48 % for the ingroup and 2.03 % - 4.18 % between ingroup and outgroup species. 100979 MP trees of 100 steps were generated (for tree statistics see Table 4.2). Indel coding slightly increased tree scores and branch support. Tree statistics are better for the *trnL-F* dataset than for the ITS dataset. The K81uf+G model was selected as the best model (substitution rates: A<>C 1.0000, A<>G 1.2024, A<>T 0.2039, C<>G 0.2039, C<>T 1.2024, G<>T 1.0000 and base frequencies: A=0.3461, C=0.1748, G=0.1619, T=0.3172). Maximum likelihood analysis generated 14 best trees. One ML phylogram is shown in Fig. 4.7. The topology of the MP, ML and Bayesian trees are identical.

The *trnL-F* topology is congruent with the ITS topology only within the *M. congensis* clade although its branch support is only weak. In the strict consensus tree (not shown) *Marantochloa congensis* appears in a polytomy with a weakly supported *M. leucantha* and *M. filipes* group and a weakly supported group of the remaining three species of the *M. congensis* clade. This polytomy is highly supported only when indels are included in the MP analysis. The remaining species of the *Marantochloa* clade form a weakly supported monophylum when indels are included. Within this clade all species form a single polytomy which is sister to a moderately to highly supported clade consisting of *M. purpurea* and *M. cuspidata*.

combined phylogeny (Fig. 4.8): The combined dataset comprised 22 taxa. In species where no *trnL-F* data could be obtained base pairs were coded as missing data. The final alignment was 1658bp long when including 24 indels. The homogeneity test between the two data partitions ITS and *trnL-F* yielded a p = 0.01. Nine MP trees of 550 steps were obtained (for tree statistics see Table 4.2). The combination of the two dataset (ITS and *trnL-F*) increased the tree scores and branch support against the ITS dataset but not against the *trnL-F* dataset. The TIM+I+G model was the best model (substitution rates: A<>C 1.0000, A<>G 2.6902, A<>T 0.7803, C<>G 0.7803, C<>T 4.0309, G<>T 1.0000 and base frequencies: A=0.2955, C=0.2273, G=0.2155, T=0.2617). Maximum likelihood analysis generated two best trees. One is shown in Fig. 4.8. Tree topology is identical in all analyses.

The topology of the combined dataset and the ITS dataset is identical except for the resolved position of *M. leucantha* and *M. filipes* in the ITS dataset which are highly supported sister to the *M. congensis* clade when indels are included. There is moderate to high support in the MP and Bayesian analysis for a polytomy of the *A. conferta*-, *M. purpurea* clade, *M*. *cordifolia* and *M*. sp.1 excluding *M. cuspidata*. *M. cuspidata* is weakly to moderately supported sister to this polytomy.

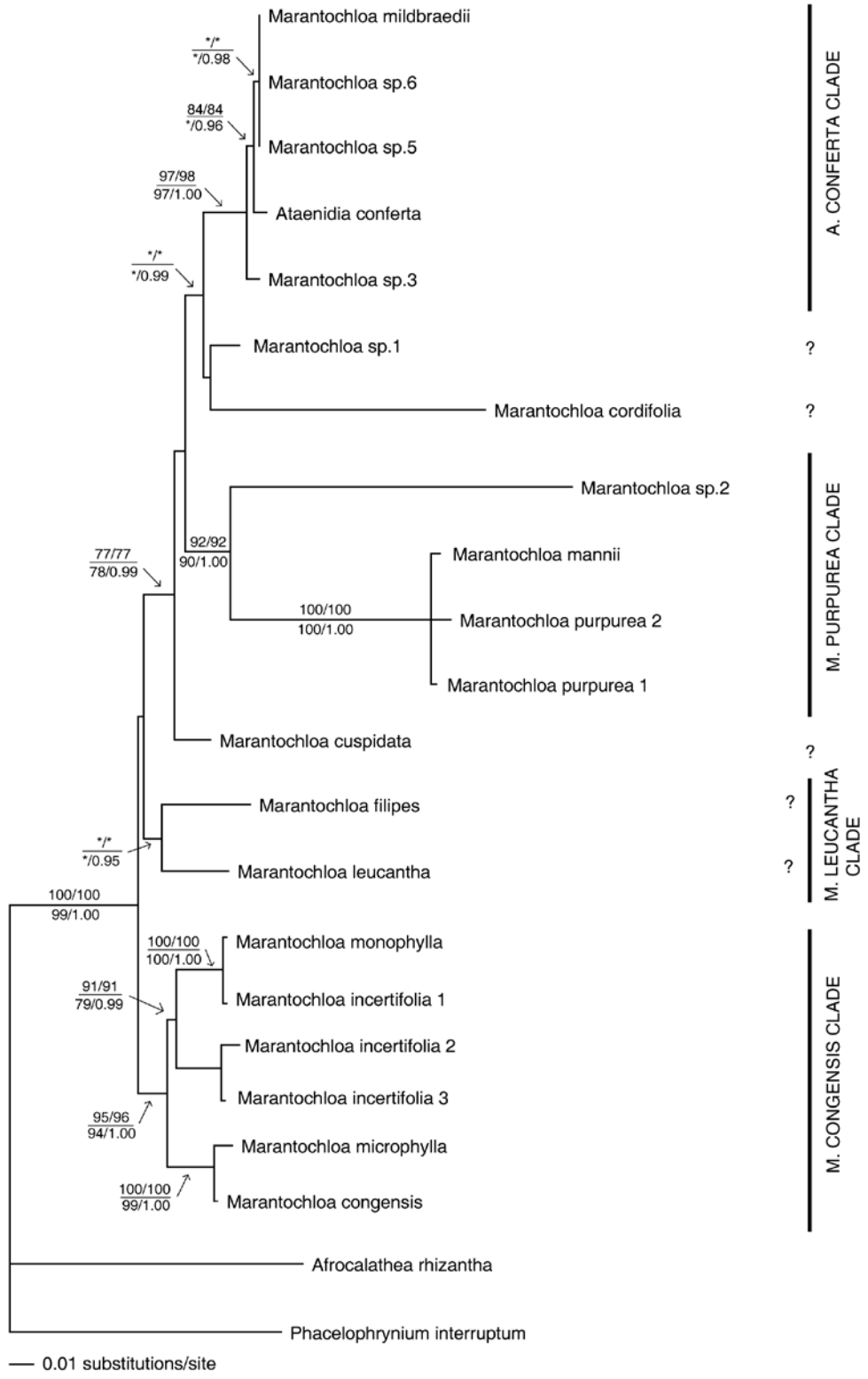

Figure 4.6: Single maximum likelihood (ML) phylogram based on ITS sequence variation of the members of the *Marantochloa* clade. Numbers above branches are MP bootstrap values without / with indels, numbers below branches are ML bootstrap values / Bayesian posterior probability. *, bootstrap value below 75. ?, uncertain clade affiliation. outgroup-taxa: *Afrocalathea rhizantha* and *Phacelophrynium interruptum*.

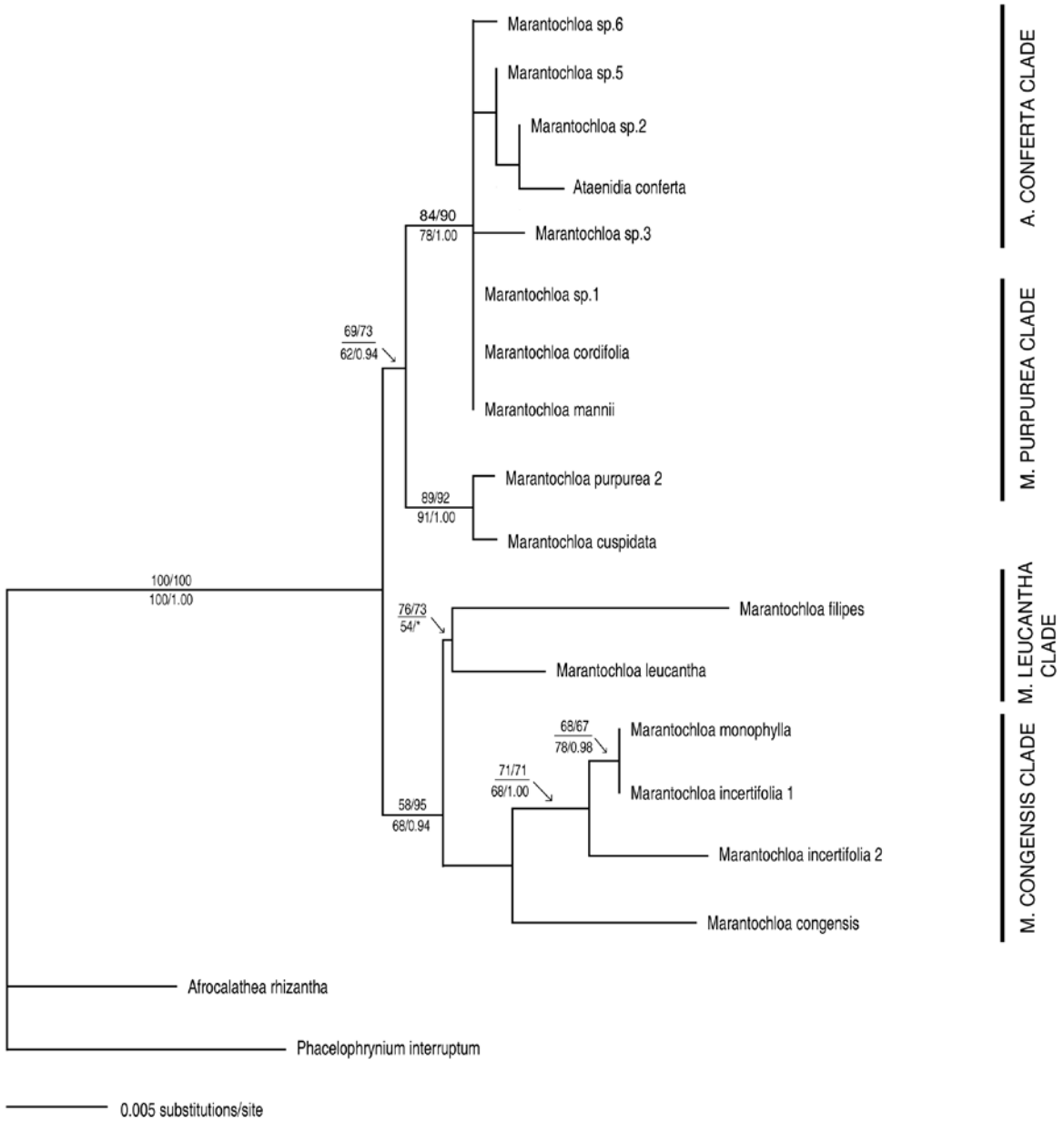

Figure 4.7: One of 14 maximum likelihood (ML) phylograms based on *trnL-F* sequence variation of the members of the *Marantochloa* clade. Names of subclades adjusted from ITS tree (fig. 4.6). Numbers above branches are MP bootstrap values without / with indels, numbers below branches are ML bootstrap values / Bayesian posterior probability. *, bootstrap value below 75. outgroup-taxa: *Afrocalathea rhizantha* and *Phacelophrynium interruptum*.

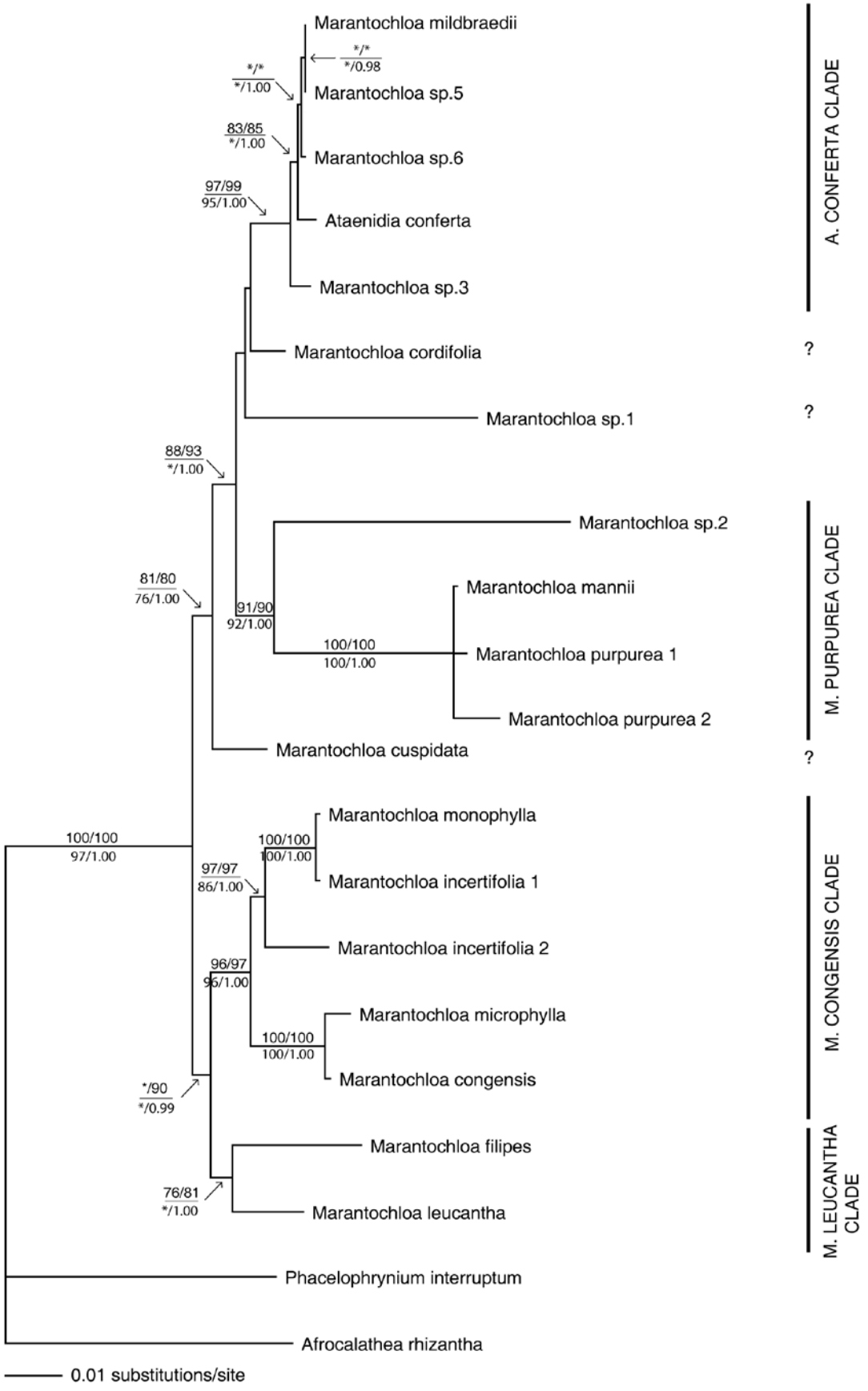

Figure 4.8: Single maximum likelihood (ML) phylogram based on a combined dataset of ITS and *trnL-F* sequence variation of the members of the *Marantochloa* clade. Numbers above branches are MP bootstrap values without / with indels, numbers below branches are ML bootstrap values / Bayesian posterior probability. *, bootstrap value below 75. ?, uncertain clade affiliation. outgroup-taxa: *Afrocalathea rhizantha* and *Phacelophrynium interruptum*.

Table 4.2: Statistics from DNA analyses. CI, consistency index; MP, maximum parsimony; ML, maximum likelihood; RI, retention index; RC, rescaled consistency index.

clade	data partition	taxa	analysis	total characters	constant characters	variable characters uninformative	parsimony informative characters	trees retained	islands	length	CI	RI	RC
Marantochloa	ITS	22	MP	649	355	154	140	3	5	455	0,798	0,778	0,621
			+indels	+11		161	144	3	4	466	0,803	0,78	0,626
			ML					1	2				
	trnLF	18	MP	985	-75	44	31	100979	?	87	0,92	0,891	0,819
			+indels	+13	908	52	38	96894	1	100	0,93	0,92	0,856
			ML					14	2				
	ITS & *trnLF*	21	MP	1634	1265	198	171	9	3	550	0,807	0,779	0,629
			+indels	+24	1265	211	182	9	2	575	0,814	0,789	0,642
			ML					1	1				
Sarcophrynium	ITS	21	MP	757	446	141	170	3	1	489	0,816	0,853	0,696
			+indels	+21	446	143	189	6	2	512	0,82	0,863	0,708
			ML					1	1				
	trnLF	19	MP	1021	907	66	48	4617	1	134	0,91	0,918	0,836
			+indels	+15	907	75	54	513	2	149	0,919	0,93	0,855
			ML					3	2				
	ITS & *trnLF*	21	MP	1777	1350	210	217	6	1	629	0,831	0,86	0,715
			+indels	+36	1350	221	242	6	1	667	0,838	0,872	0,73
			ML					1	1				
Hypselo-delphys	5S	9	MP	420	238	139	43	1	1	239	0,925	0,769	0,711
			ML					1	1				
	5S & ITS & *trnLF*	9	MP	2197	1813	296	88	1	1	470	0,93	0,75	0,697
			ML	2197				1	1				

4.5 DISCUSSION

4.5.1 MOLECULAR EVOLUTION: IMPLICATIONS FOR SPECIATION

Overall, the molecular results from this analysis are congruent with the recent family phylogeny (Prince and Kress, 2006*a*). The principle relationships between genera and major clades are confirmed. Again *Ataenidia conferta* is nested within the genus *Marantochloa* so that a new circumscription of *Marantochloa* is proposed which is also supported by morphological characters (see Appendix 4.7). The here established phylogeny on species level for the two larger African clades is based on an almost complete taxon sampling and is almost entirely resolved with generally moderate to high support values presenting a suitable framework for evolutionary interpretations.

4.5.1.1 Sarcophrynium clade

The topologies based on two markers from two independently evolving genomes (nuclear and chloroplast) are congruent in most parts and thereby confirm the monophyly of all morphologically circumscribed genera within this clade. Only the topology within the genus *Megaphrynium* is contradictory between the markers. The latter might be the result of incomplete lineage sorting or hybridization events (Rieseberg, 1995; Steen et al., 2000) within the genus which resulted in different evolutionary histories of the two genomes.

The species level relationships in the *Hypselodelphys* clade are not fully resolved neither with *trnL-F* nor with ITS sequence analyses. The overall short branch length between the species and the moderate resolution with a highly variable gene region (ITS*,* Soltis and Soltis, 1998) suggest a young evolutionary origin due to Pleistocene climatic oscillations (see chapter 4.4.3.3) and/or recurrent hybridization events which prevented further differentiation in this clade (see also e.g. Andreason and Baldwin, 2003; Mummenhoff et al., 2004).

Resolution is only improved by adding data from the 5S nrDNA, a gene region estimated to be slightly more variable than ITS (Soltis and Soltis, 1998). The here obtained topology of a sister relationship of *Trachyphrynium braunianum* to all *Hypselodelphys* species is supported by different fruit types and obvious differences in leaf base morphology (see Koechlin, 1964) (see Fig. 4.9).

The obtained molecular resolution of the relationships within the genus *Hypselodelphys* however remains spurious on the morphological level. The most obvious character to identify species (Koechlin 1964, 1965) has long been nut morphology (Fig. 4.5). Fruit form varies from clearly rounded to sharply triangular. Fruit surface is muricate. Spikes vary from very short and almost flat in *H*. sp.1 to 1 cm in length in *H. scandens* (Fig. 4.9). Four species exhibit a ridge on the surface (*H. hirsuta, H.* sp.1, *H. triangularis, H. violacea;* Fig. 4.9). Internodes are about 5 mm long in all species except *H. scandens* and *H. violacea* (10 - 20 mm and 12 mm, respectively) and generally glabrous except in *H. hirsuta* and *H. velutinum*. However, none of the characters reveal a phylogenetic signal matching any of the obtained topologies through the molecular analysis.

Unfortunately, still no support is obtained for the resolution of the relationship between major clades within the *Sarcophrynium* clade (Fig. 4.3; see also Prince and Kress, 2006*a, b*) despite an almost complete sampling and the addition of further genetic markers. The sister-relationship of *Hypselodelphys/Trachyphrynium* and *Megaphrynium,* weakly supported in the *trnL-F* dataset, is obscured in the combined ITS/*trnL-F* dataset by the higher number of informative characters in the ITS dataset which (including indels) provide support only for the common ancestry of all three major clades. Reasons might include an accumulation of mutations as supported by the long branches leading to the clades and the high morphological differences between genera (Fishbein et al., 2001).

Even character reconstructions of morphological traits constant for entire genera only result in a one step shorter tree, when a sister relationship between *Hypselodelphys/Trachyphrynium* and *Sarcophrynium* is rejected (Fig. 4.10). However this result is consistent independent of the outgroup.

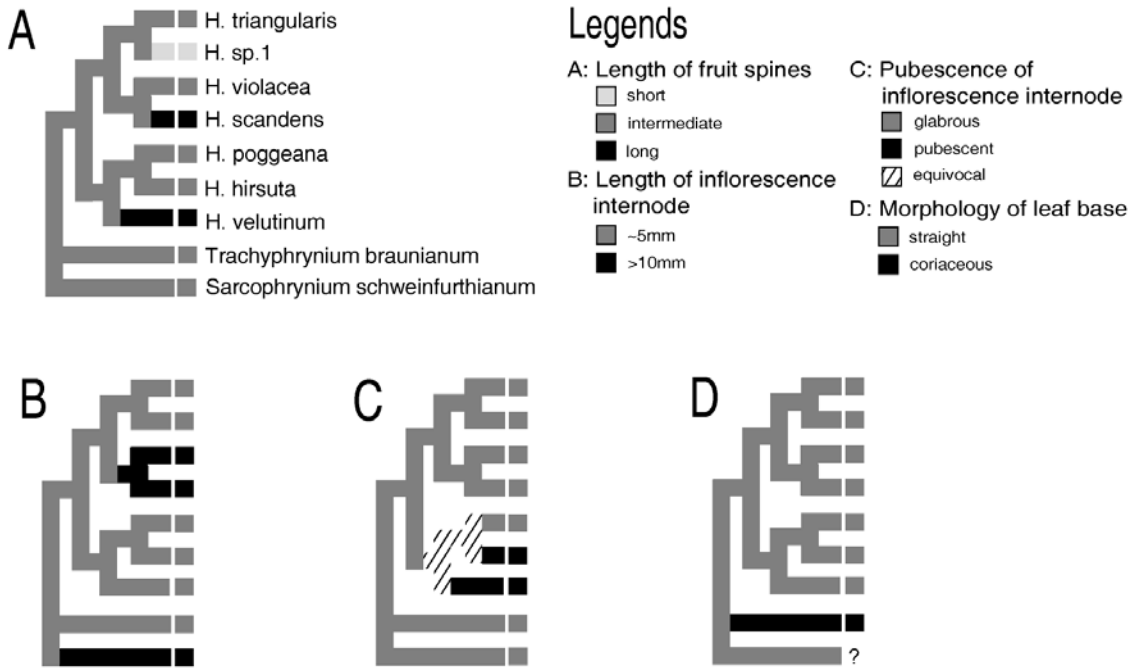

Figure 4.9: Character state reconstruction in species of the genus *Hypselodelphys* assuming parsimony of unordered states. (A) length of fruit spines. (B) average length of inflorescence internodes. (C) pubescence of inflorescence internodes. (D) morphology of the leaf base. ?, indicates missing data.

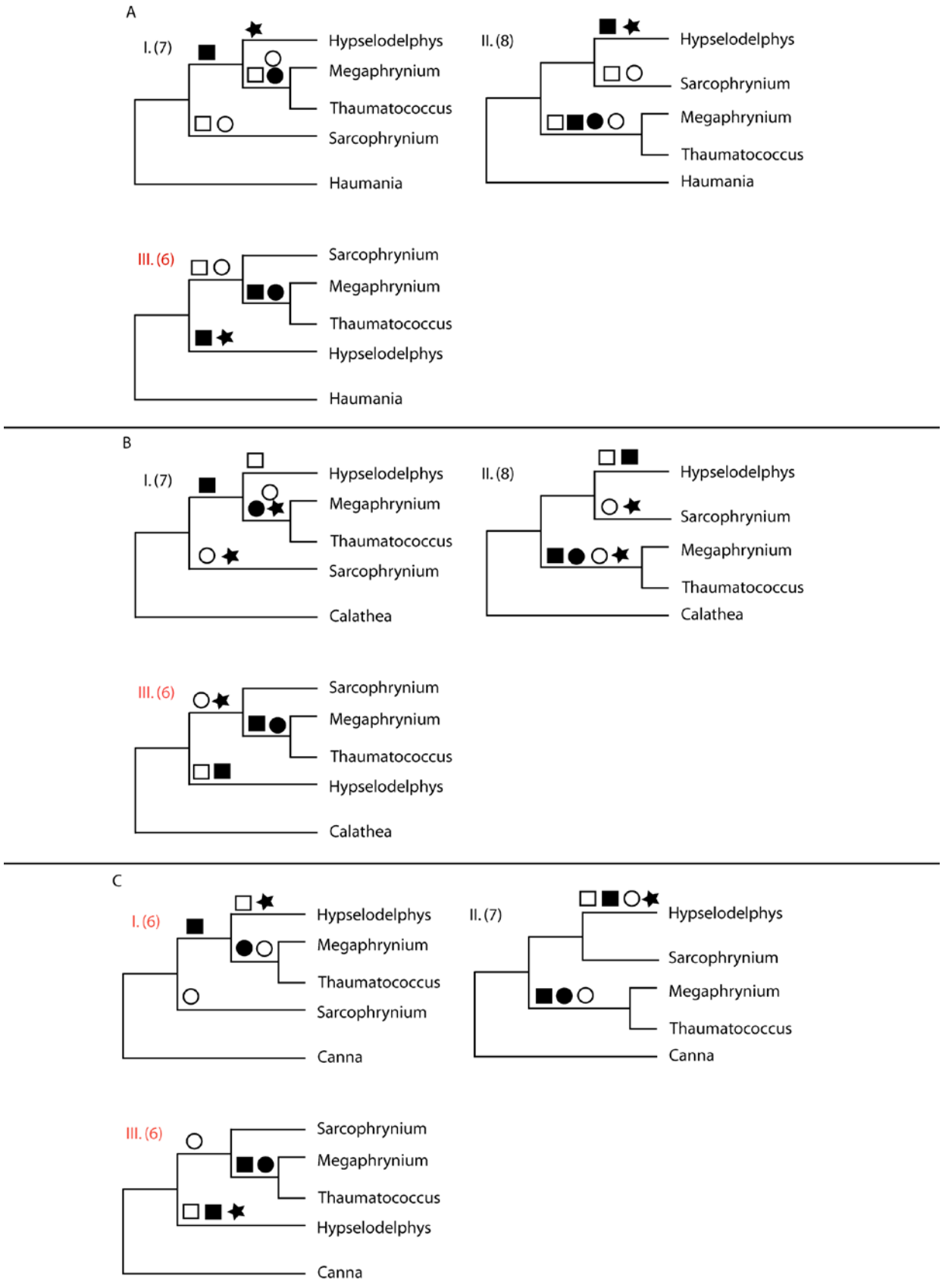

Figure 4.10: Reconstruction of the phylogenetic relationships within the Sarcophrynium clade. Evaluation of the most parsimonious solution in state changes of five morphological characters considering different outgroups. (A) outgroup *Haumania,* (B) outgroup *Calathea,* (C) outgroup *Canna;* numbers in brackets, evolutionary steps. □ life form: liana/perennial herb. ■ flower pairs per bract: 1/~8. ● outer staminodes: conspicuous/reduced. ○ fruit type: nut/berry-like. ★ length of fleshy staminode compared to complex of style and hooded staminode: longer / equal length.

4.5.1.2 Marantochloa clade

In this clade again there is incongruence in the tree topologies between the different markers (ITS vs. *trnL-F* spacer) which could be interpreted as an indication for a hybrid origin of *Marantochloa purpurea* (Rieseberg, 1995) (Fig. 4.11). In this case the phylogeny would indicate *M. cuspidata* to be the mother species because it shares the same chloroplast type with the putative hybrid. The father could be *M. mannii* or *M*. sp.2, being the next relatives according to the ITS dataset. However, as *M. cuspidata* is currently restricted to West-Africa and *M*. sp.2 only known from a locally restricted area at Monts de Cristal in Gabon, Central Africa (see Table 4.1) the latter might be excluded as potential father due to the improbability of pollen transfer between the geographically distant species. A contrasting hypothesis might identify *M*. *mannii* and *M.* sp.2 as hybrids – this assumption is only one step less

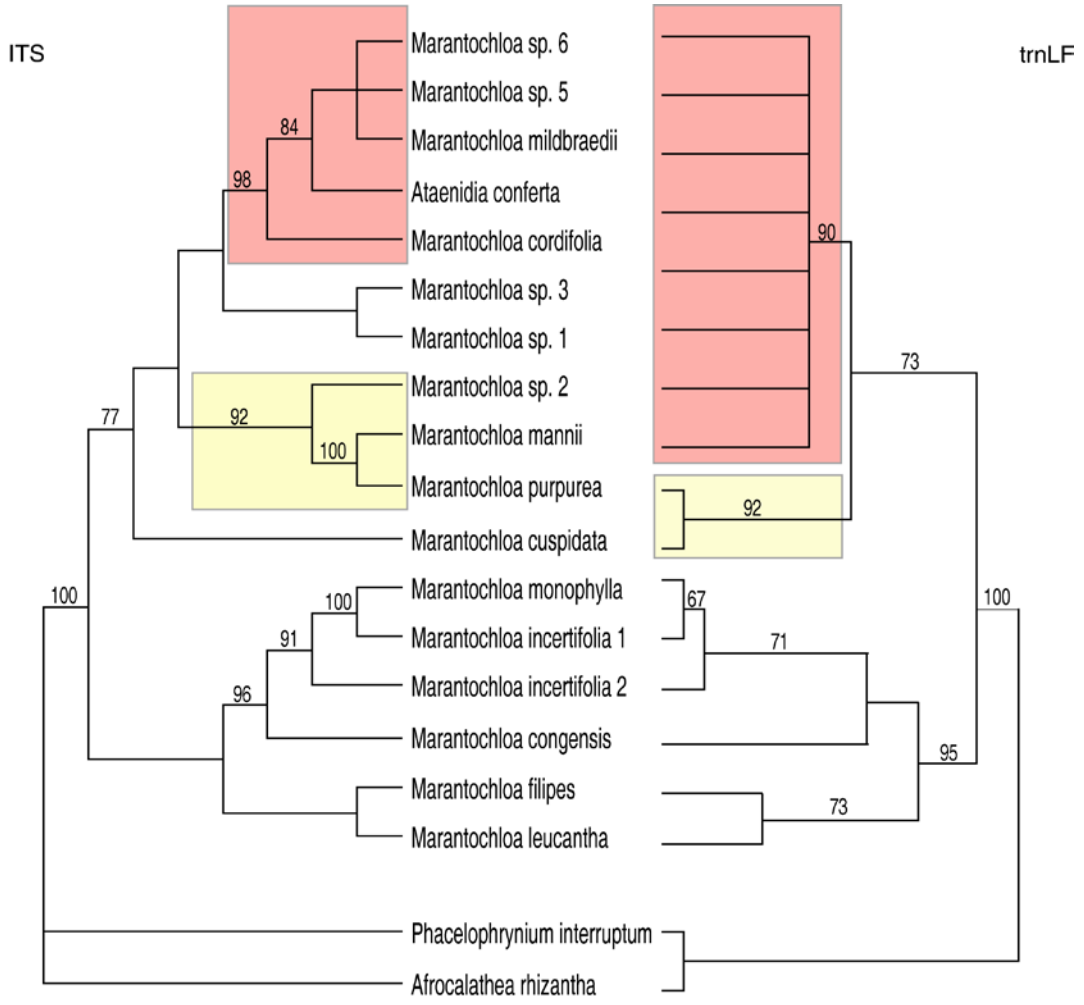

Figure 4.11: Topological incongruence between MP trees based on ITS (left) and *trnL-F* (right) in the *Marantochloa* clade. Bootstrap values above branches. red, well supported clade including *Ataenidia conferta*; yellow, well supported clade including *Marantochloa purpurea*.

parsimonious (Fig. 4.11). In this case *M. purpurea* could be regarded as a possible father and any species of the A. *conferta* clade as mother. Hybridization events in *M*. *mannii* and *M.* sp.2 are supported by an intermediate set of characters (see Schipper, 1928). In both species flower tube type is identical to *M. purpurea* whereas the condensed inflorescence architecture is close to the species from the *A. conferta* clade. Leaf morphology (anti-/homotropy) in *M. mannii* is identical to the species of the *A. conferta* clade (Fig. 4.12). However, this is only a possible but not a mandatory consequence of hybridization (see Rieseberg, 1995) and in the vegetative growth form and the position of the inflorescence *M*. sp.2 is totally different from both postulated parents.

In the ITS phylogeny there are furthermore *M.* sp.3 and *M*. sp.1 unresolved. *M.* sp.3 shows a high similarity in inflorescence architecture (length of fleshy staminode, Fig. 4.12C) and floral morphology (Fig. 4.12D, E) to *M. cordifolia* as well as *M.* sp.1 to *M. purpurea.* There are strong indications of male infertility (pollen deformation in *M*. sp.1) and total infertility (no fruit set in *M.* sp.3) in the respective species (see chapter 2) – probably a consequence of hybridization (Grant, 1964; Heiser et al., 1969; Moyle and Graham, 2005). In these species, population maintenance after a hybridization event might have been ensured by vigorous vegetative reproduction (chapter 2). *M*. sp.1 and 3 are restricted to the Mount de Cristal area. As there are no molecular signs of hybridization (e.g. double peaks in the ITS chronograms) in any of the sequences the hybridization events might have been ancient which allowed enough time to homogenize different ITS copies within the putative hybrid genomes (Carine et al., 2007).

Further hybridization events are postulated within the *A. conferta* clade. The species *M*. sp.5 and *M*. sp.6 represent an intermediate flower (flower colouration; length of fleshy staminode) and inflorescence morphology (bract number, width and colouration; internodium length) between *M. mildbraedii* and *Ataenidia conferta* (Fig. 4.13). The latter two species occupy an overlapping distribution range and habitat preference and probably share the same pollinators (birds, chapter 2). The short branch lengths between the parent species in both data sets (ITS and *trnL-F*) support that the DNA sequences of the species might not yet have differentiated to an extent that would render hybridization unlikely (Wiens et al., 2006). Thus hybridization has probably largely influenced speciation processes in the *Marantochloa* clade. Based on conspicuous morphological similarities in vegetative

habit, inflorescence and flower morphology *M. ramosissima* (Koechlin, 1965) (not included in the molecular analysis) is postulated to be an additional member of the *A. conferta* clade, *M. comorensis* of the *M. leucantha* clade and *M. sulphurea* a sister species to *M. incertifolia*.

4.5.2 CHARACTER EVOLUTION (FIG. 4.12, 4.14)

Nine different vegetative and floral characters were mapped onto the phylogenetic trees. For each clade (*Sarcophrynium* and *Marantochloa* clade) the tree based on the combined dataset (ITS & *trnL-F*) was chosen as it yielded the most resolved and best supported tree. Whereas the traits `leaves per shoot´ (Fig. 4.12A) and `average length of the inflorescence internodes´ (Fig. 4.12B) appear rather homoplasious in both clades, all other characters reflect relationships inferred from the molecular analysis. The traits `average length of the fleshy staminode´ and `pollinators´ show parallel pattern of evolution in the two clades. In both clades the first branching clade comprises species with small flowers pollinated by small bees. The two following clades exhibit larger flowers being pollinated by either large bees or birds. This parallel evolution is interpreted as an adaptation to the same local environment in Africa (Perret et al., 2007). In both clades fruits include nuts and once each capsuls. Berry-like fruits which are eaten by monkeys and gorillas (Williamson et al., 1990; Tutin and Fernandez, 1993; White and Abernethy, 1997) are only found in the *Sarcophrynum* clade. Most species in both clades show geographic distribution ranges restricted to Central Africa. Only a few species extend their ranges to Westafrica and only one species of the *Marantochloa* and four species of the *Sarcophrynium* clade occur exclusively in Westafrica.

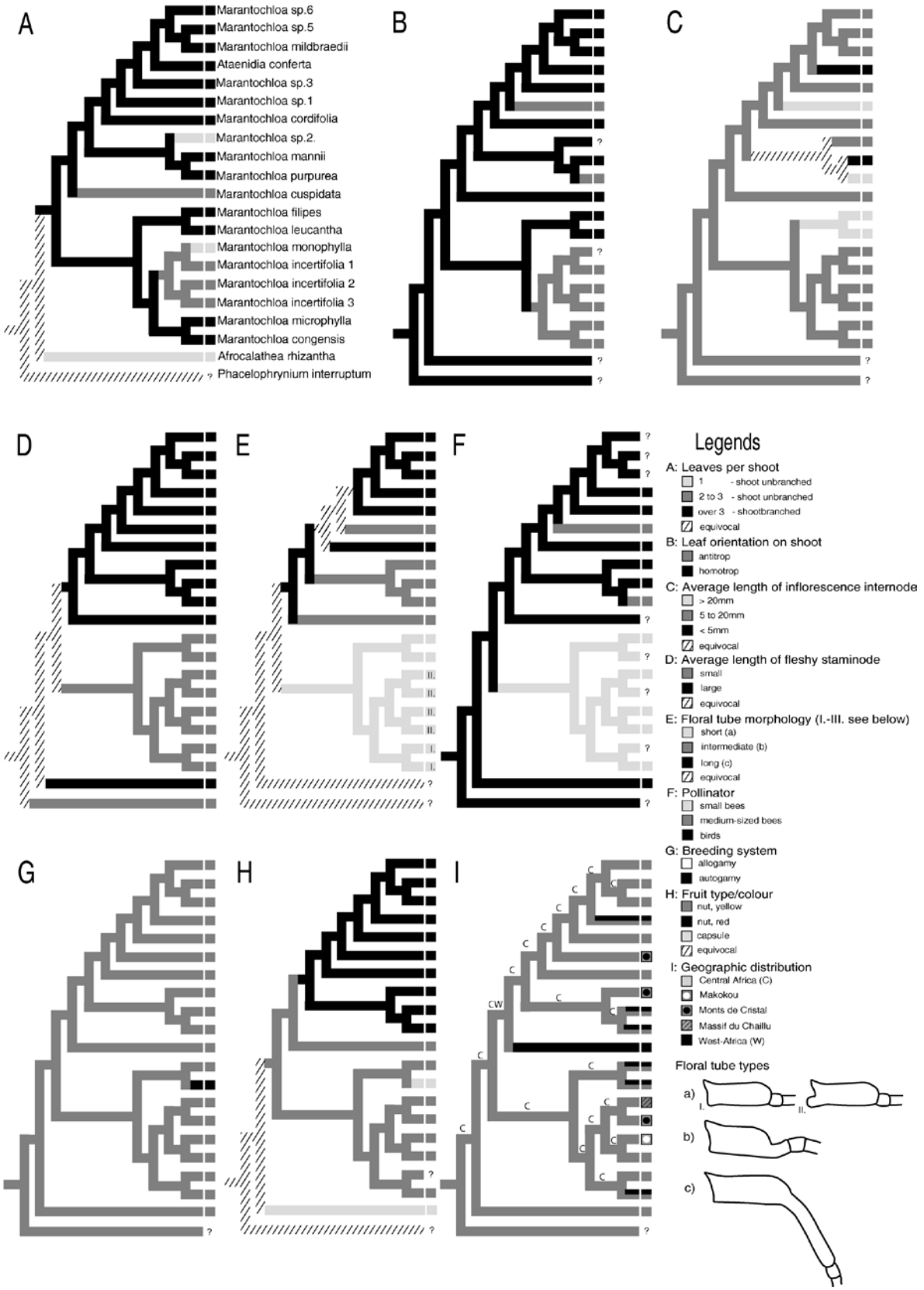

Figure 4.12: Character state reconstruction in species of the *Marantochloa* clade assuming parsimony of unordered states. A, branching pattern of aerial shoot; B, leaf orientation on shoot; C, average length of inflorescence internodes; D, average length of fleshy staminode; E, flower tube morphology; F, pollinators (see chapter 4.4.3.2); G, breeding system; H, fruit colour; I, geographic distribution. ?, no data. (see chapter 1).

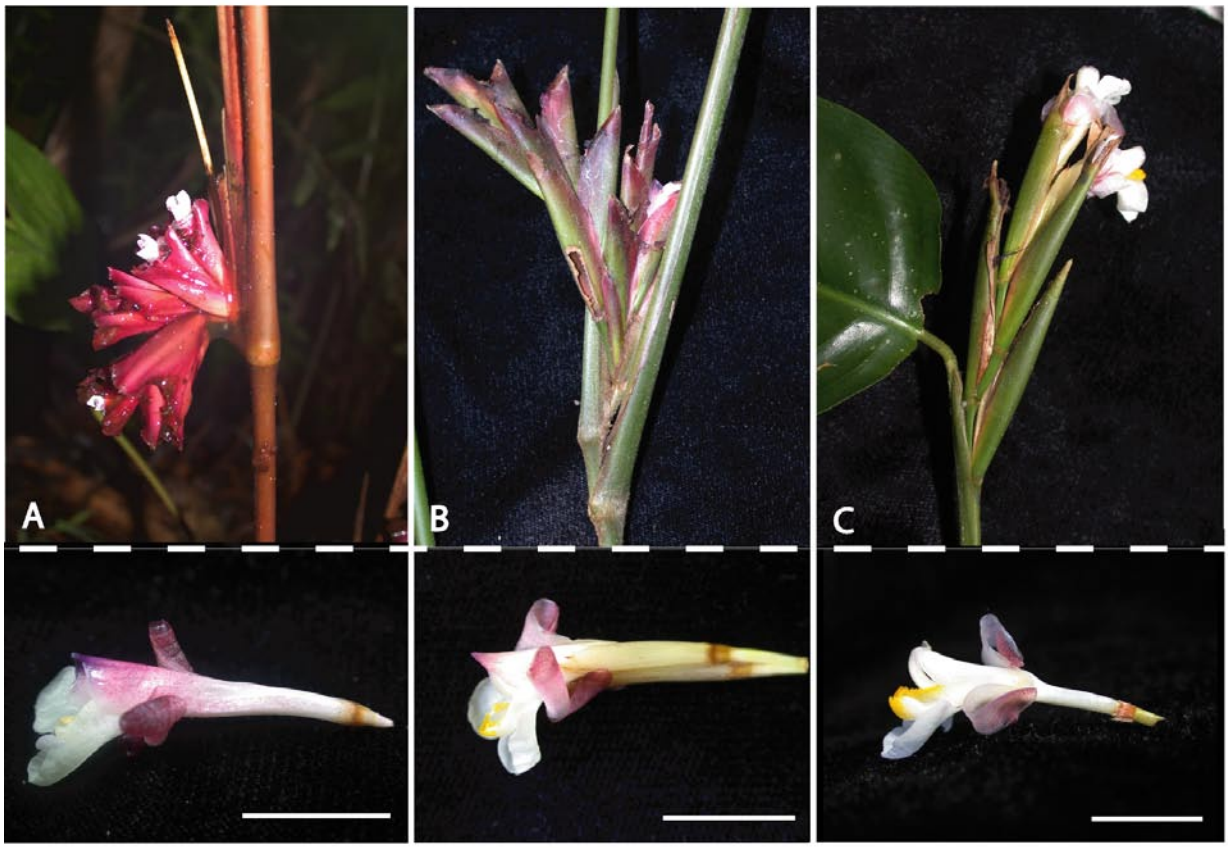

Figure 4.13: Intermediate inflorescence (number and width of bracts) and flower morphology (colouration, form and length of fleshy staminode) between *Ataenidia conferta* (A) and *Marantochloa mildbraedii* (C) illustrated in *M*. sp.5 (B). Bars: 1cm.

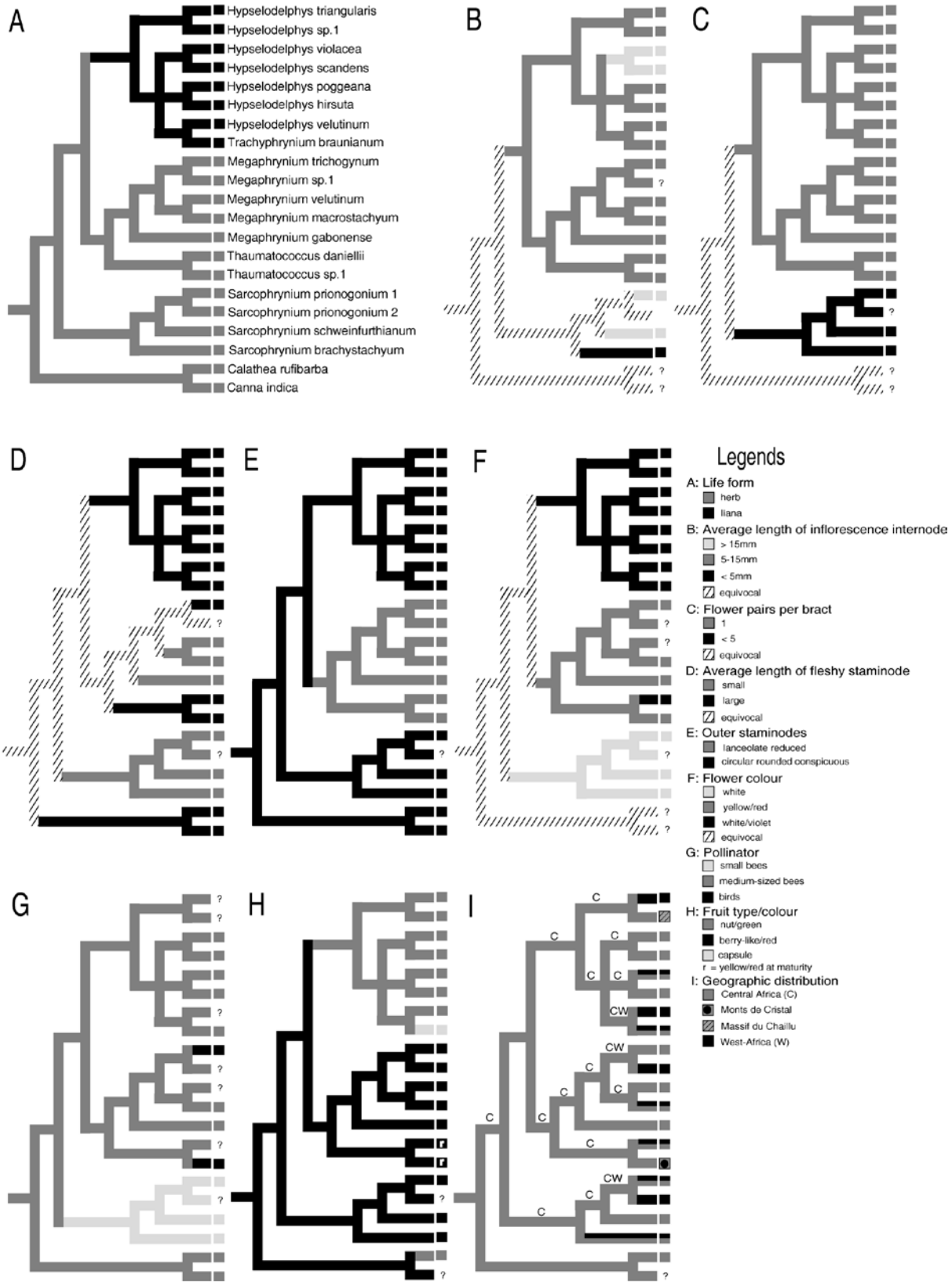

Figure 4.14: Character state reconstruction in species of the *Sarcophrynium* clade assuming parsimony of unordered states. A, life form; B, average length of inflorescence internodes; C, number of flowers per bract; D, average length of fleshy staminode; E, morphology of outer staminodes; F, flower colour; G, pollinators; H, fruit type; I, geographic distribution. ?, no data.

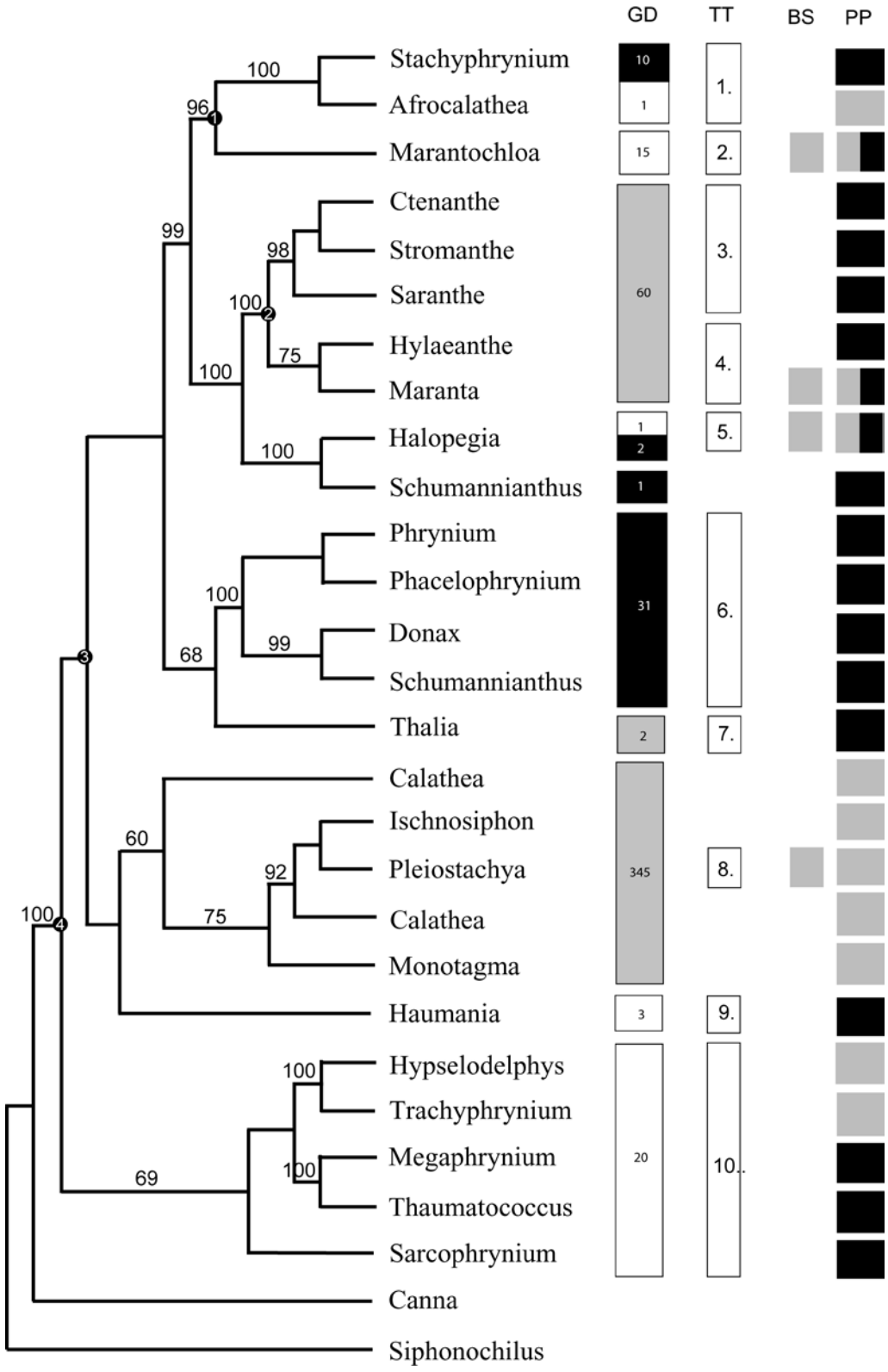

Figure 4.15: Mapping geographic distribution (GD), trigger types (TT), breeding system (BS; grey, autogamous) and pollen placement (PP: grey, proboscidial fossae; black, proboscis) onto the family phylogeny of the Marantaceae (after Prince and Kress, 2006a). bootstrap support above branches; encircled numbers highlight clades on the same continent exhibiting different trigger types (see chapter 4.4.3.1). GD: numbers indicate species richness per continent; colour black, Asia; grey, America; white, Africa (after Andersson, 1998). TT: 1., lever type; 2., cushion type; 3., spoon type; 4., wing type; 5., door type; 6., elephant ear type; 7., tentacle type; 8., thumb type; 9., sword type; 10., gate type (after Pischtschan et al., in prep.).

4.5.3 SPECIATION IN MARANTACEAE

Summarizing all morphological and phylogenetic data at hand allows hypothesizing about the underlying speciation factors throughout the evolutionary history of the Marantaceae. Thereby the importance of the explosive pollination mechanism as key innovation can be evaluated.

4.5.3.1 The backbone of the family phylogeny

The splits into major clades at the backbone of the tree are correlated with the species distribution on different continents (Prince and Kress, 2006*b*; Fig. 4.15). This renders geographic isolation a highly probable speciation factor in the past. A molecular clock approach dates the radiation of the Marantaceae not before 63 ± 5 mya (Kress and Specht, 2006) so that their pantropical distribution can only be explained by long distant dispersal events from Africa to both the New World and Asia (Prince and Kress, 2006*b*). The sudden complete interruption of gene flow through geographic isolation might have led to the substantial flower morphological differences observed today.

The dispersals occurred repeatedly to the same continent (Prince and Kress, 2006*b*), whereby each shift to a new continent is correlated with a new type of trigger appendage (Fig. 4.15 after Pischtschan et al., in prep.) so that distant clades on the same continent possess different trigger types. Within clades, though, trigger types are highly stable and do not show specific adaptations to different pollinators. Obviously, the different trigger types developed primarily incidental and non-adaptive (see also Gittenberger, 1991; Gavrilets, 2003).

Parallel evolution in floral sizes and arrangements which correlate with the same pollinators can be observed between unrelated clades on the same continent. This is probably due to the same selection pressures imposed by the identical local environment (Perret et al., 2007). Thereby the benefits from using the same pollinators probably outweighed the advantage of diverging to reduce competition, especially as all these species are sparsely flowering (chapter 2; see also Schemske, 1981). Pollen mixture seems not to be a problem. Species boundaries are stable although flowers pollinated by the same pollinator often even correspond in the localization of pollen deposition on the insect (chapter 2). Long evolutionary

separation of species from distant clades might have affected their genetical incompatibility.

There are only four examples in the family that include sister clades on the same continent with different trigger types, indicating the action of additional evolutionary factors besides geographic isolation (see Fig. 4.15). For the gate and the sword type in Africa, pollination through different pollinators is proven (see chapter 2), for the American thumb and tentacle type this is highly probable (see Kennedy, 2000; Davis, 1987) and for the American spoon and wing type it still remains to be investigated.

In the case of the African gate and sword type it cannot unambiguously be resolved whether it is solely the trigger type or possibly also the closed structure of the flower which promotes the visitation by different pollinators. Examples from closed flowers in the American *Calathea* species show that they possess the same trigger type as their congenerics with open flowers, but that they are pollinated by different bee species due to different handling requirements (Kennedy, 1978). The same applies for the thumb and tentacle type (see chapter 3) as the representatives of the first exhibit generally open flowers whereas in the latter the flower entrance is rather closed. Also the divergence of the African cushion and lever type seems to be correlated with other factors than trigger type. The species involved are highly variable within types and exhibit differences in flower size, colouration, spatial arrangement of the flower in the inflorescence and the location of the latter on the plant which correlate with different pollinators (see chapter 2). Today both trigger types can be handled by a variety of the same pollinators including birds and different sized bees (chapter 2; see also Kennedy, 2000; Kato, 1996).

It is evident that flowers with the same trigger types can be morphologically very different. In the *Calathea* clade variety between species seems to be mainly due to length differences in the extremely long flower tubes (see Kennedy, 2000). The appearance of long flower tubes in the phylogeny at the rise of the *Calathea* clade is coupled with the migration to the American continent and a switch in diversification rate. Today, the *Calathea* clade includes 340 species which is about three-fold more than its sister clade (including *Donax, Maranta* and *Stachyphrynium* clade: 123 species) (Andersson, 1998) (Fig. 4.12). Neither another American clade with short tubed flowers (e.g. *Maranta* clade) nor an Asian or African clade with long tubed flowers (e.g. *Cominsia*, *Stachyphrynium*, *Thaumatococcus*) has obtained the

same level of diversity. Therefore, the combination of long tubed flowers with the distribution on the topologically rich American continent seems to have triggered speciation. The high topological diversity of the American continent might have facilitated allopatric speciation enhanced by climatic oscillation (see also Kennedy, 2000; Kay et al., 2005; Särkinen et al., 2007) whereas the long corolla tube might have supported sympatric ecological speciation (see also Nilsson, 1988; Hodges and Arnold, 1995; von Hagen and Kadereit, 2003). Whether higher extinction rates in Africa also contributed to this large discrepancy in species number between the continents as discussed in Richards (1973) cannot be solved here. However, it seems to be evident that at the rise of the *Calathea* clade it was not the explosive pollination mechanism that drove speciation and affected a switch in speciation rate at that point in the family phylogeny.

4.5.3.2 Speciation within major clades

Within major clades the adaptations towards specific pollinators and recurrent switches between pollination systems seem to have shaped speciation. Generally, the species of entire subclades are pollinated by different pollinators including small and intermediate sized bees and birds (Fig. 4.12, 4.14; chapter 2). Only in the *Marantochloa purpurea* clade and the genus *Megaphrynium* pollinators vary on species level (Figs 4.12F, 4.14G) giving a plausible speciation factor for these groups. The general importance of pollinator specialization for plant speciation and evolutionary radiation by providing reproductive isolation has already repeatedly been stressed (e.g. Stebbins, 1970; Grant, 1994; Johnson et al., 1998; Specht, 2001; Wilson et al., 2004).

Commonly, pollinators seem to be correlated with floral size and in the *Marantochloa* clade additionally with flower tube shape. However, there are a few exceptions in the *Marantochloa* clade, where species with a long or an intermediate flower tube morphology are pollinated by birds and bees alike (e.g. *M. cordifolia*, *M*. *mannii*, *M*. sp.1). Here inflorescence architecture and the spatial arrangement of the flower seem to be more important in determining the pollinators than floral tube morphology alone (see chapter 2). In conclusion, floral morphology seems to be rather phylogenetically constraint (Endress, 1994) as also already demonstrated for the trigger types. Instead there is more flexibility in other plant parts (e.g. inflorescence) which allow ecologically divergent adaptations.

Regarding the African *Sarcophrynium* clade there are two independent shifts from bee to bird pollination: once in *Megaphrynium trichogynum* and once towards the genus *Thaumatococcus*. The basal genus *Sarcophrynium* and also all possible outgroups are known to be bee pollinated (*Calathea* see Kennedy, 2000; *Haumania* see chapter 2; Cannaceae see Watson and Dallwitz, 1992 onwards) so that bee pollination is assumed to be the ancestral state (symplesiomorphic) in the *Sarcophrynium* clade.

In the *Marantochloa* clade pollinator reconstruction is highly dependent on the coding of the outgroup. Given *Afrocalathea rhizantha* as outgroup, bird pollination comes up to be the ancestral state in this clade (Fig. 4.12). However, most of the species of the *Stachyphrynium* clade closely related to *Afrocalathea rhizantha* are known to be bee pollinated (Kato, 1996). Also the related species with comparable floral morphology to the second outgroup represented by *Phacelophrynium interruptum* are known to be bee pollinated (Kato, 1996). Coding the outgroup as `bee pollinated´ would result in an equivocal ancestral state of bee or bird pollination for the *Marantochloa* clade. If additionally *Marantochloa cuspidata* is coded as bee pollinated, as deduced from its slender hanging flowers which probably exclude birds (see chapter 2), the ancestral state is clearly bee pollinated in the *Marantochloa* clade.

Given this proposed coding (Fig. 4.16), the ancestral state of pollination at the base of the *M. purpurea* and *A. conferta* clade is equivocal between bird and large bee pollination. This is due to the phylogenetic distant position of *Marantochloa purpurea* and *M*. sp.1 which are both bee pollinated whereas all other species of these clades are bird pollinated. However, the position of *M*. sp.1 is not unambiguously resolved and still the hypothesis holds that it might be a hybrid of *M. purpurea* and another species. Excluding *M*. sp.1 from the analysis would result in a single switch to bird pollination towards the two clades *M. purpurea* and *A. conferta* with a single reversal to (large) bee pollination in *M. purpurea*. This seems to be the most parsimonious explanation.

Additionally, mechanical isolation through differential pollen deposition onto the same pollinator might have played a role for speciation (chapter 3; see also Kennedy, 2000). The mapping of different localities in pollen deposition onto the family phylogeny infers repeated switches between different pollen placements dependent on floral synorganisation (Fig. 4.15). However, these switches are only

Fig. 4.16: Alternative character state reconstruction of pollinators in the *Marantochloa* clade. black, small-sized bees; dark grey, large-sized bees; black, birds; hatched, equivocal; ?, no data.

relevant to speciation if they are observed in the absence of any other isolating mechanisms. The currently sole example of an ancient split on the generic level based on differential pollen placement concerns the two genera *Megaphrynium* and *Hypselodelphys.* They are sister to each other (Fig. 4.3) (chapter 3; see also Prince and Kress, 2006*a, b*), occur sympatrically in Central Africa (Dhetchuvi, 1996) and are pollinated by the same bee species (chapter 2). Pollen deposition is onto the proboscis in *Megaphrynium* and into the proboscidial fossae in *Hypselodelphys* (chapter 3).

4.5.3.3 Speciation on species level

Speciation on species level in African Marantaceae could already partly be attributed to hybridization events and adaptation to different pollinators (see above). A few species exhibit isolated distribution ranges in West-Africa pointing to speciation in geographic isolation (Fig. 4.12, 4.14; Jongkind, in press; Hepper, 1968). Whether this isolated occurrence is based on dispersal or vicariance events cannot be answered here as the distribution range of the rainforest has repeatedly been connected and separated in the past by the Dahomey gap in Togo and Benin (see Booth, 1958; Maley, 1996; Dupont et al., 2000; Salzman and Hoelzmann, 2005). However, the origin of the two clades has here been reconstructed to be probably in central Africa due to the strong distributional asymmetry of far more species in central Africa than in West-Africa (*Sarcophrynium* clade: 15:9 species; *Marantochloa* clade: 18:7 species) (Fig. 4.12, 4.14).

Speciation within the genera *Hypselodelphys, Sarcophrynium* and the *M. congensis* clade still pose an enigma. All their species exhibit large overlaps in distribution areas, habitat and phenological pattern (see chapter 2), no indications of speciation through hybridization events, a high similarity in flower morphology and an alliance to the same pollinators. Probably, speciation has been driven by Pleistocene climate changes (Maley, 1996) as already proposed for other African genera as

Aframomum K. Schum. (Harris et al., 2000), *Begonia* L. (Plana et al., 2004) and *Renealmia* L. (Särkinen et al., 2007). During dry periods, African tropical lowland rainforest retracted to mountainous areas (Maley, 1996). This probably severely influenced the distribution pattern of the Marantaceae which are strictly confined to its understorey. Today widely distributed and co-occuring species are hypothesized to got isolated in refugial areas during the Pleistocene. Their isolation led to genetic incompatibility (compare Skrede et al., 2006), thus allopatric speciation, though equal environmental conditions in the refugial areas maintained equal adaptations via the same selection pressures (see also Perret et al., 2007). Pollen incompatibility (de Nettancourt, 1977) and postzygotic isolation (hybrid sterility and inviability) (Orr and Presgraves, 2000) are commonly supposed mechanisms which might also maintain species boundaries in the Marantaceae today. The extant distribution patterns of the three *Haumania* species (see Dhetchuvi, 1996) are still highly conform to different postulated refugial areas which are mainly located in mountainous areas (Fig. 4.17). However all other species of the Marantaceae show distribution areas far more widespread and largely overlapping (see Dhetchuvi, 1996). Here more effective long distance dispersals (e.g. smaller seeds, possible dispersal by birds in the *Marantochloa/Ataenidia* species) might have contributed to their more widespread distribution obscuring past distribution patterns. More detailed investigations on intraspecific genetic diversity pattern and gene flow are needed to exactly identify the mode of speciation and present mechanisms of species maintenance (see Comes and Abbott, 2001).

The mountainous areas of central Africa (e.g. Monts de Cristal and Massif du Chaillu) are not only proposed for ancient speciation events but also hypothesized centres of recent speciation. Repeatedly species at terminal nodes in phylogenetic trees are endemics in these areas (Fig. 4.12, 4.14; see also Fjeldsa and Lovett, 1997). Geographic isolation is further discussed as speciation factor in America and Asia. The deep valleys of the Andes are ideal locations to interrupt gene flow between adjacent populations (Kessler, 1995; Ibisch, 1996). Several analyses have proven the positive correlation of species diversity and topography (Gentry and Dodson, 1987; Barthlott et al., 1999; Ley et al., 2004). The dating of phylogenies of unrelated families suggests a simultaneous event of increased diversification rate with the orogeny of the Andes (e.g. Kennedy, 2000; Kay et al., 2005; Särkinen et al., 2007). In Asia geographic isolation is based on the scattered island landscape

(Borchsenius, pers. com.; see also Cannon and Manos, 2003; Mausfeld and Schmitz, 2003; Outlaw and Voelker, 2007).

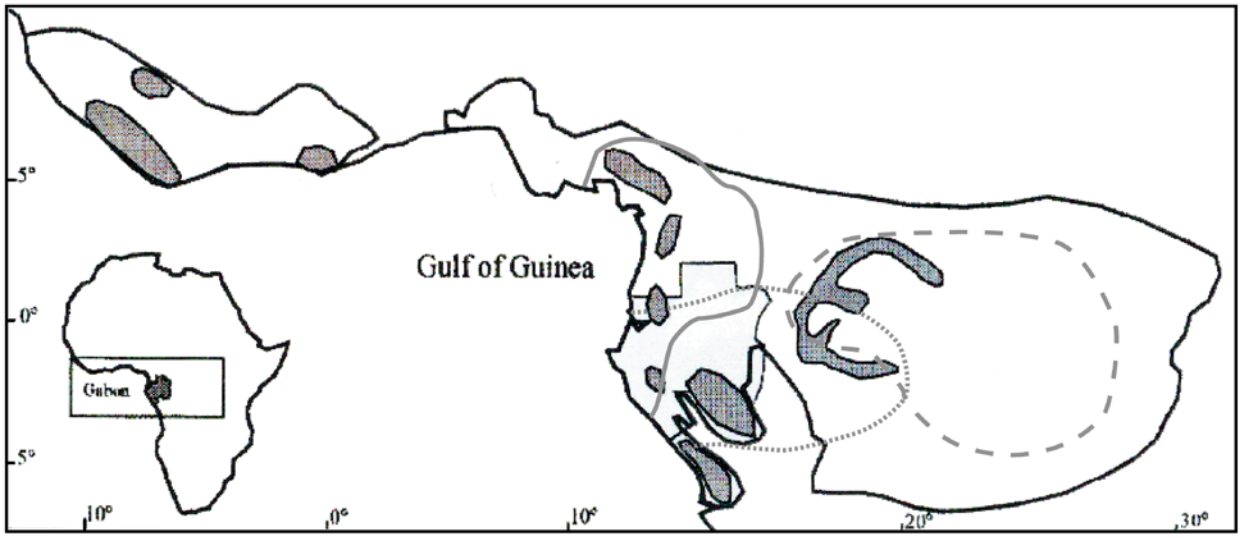

Figure 4.17: The distribution patterns of the species from the genus *Haumania* (after Dhetchuvi, 1996) match the postulated refugial areas for Central Africa (from Leal, 2004; simplified after Maley, 1996). Black line, limit of current rainforest distribution; gey line, distribution area of *Haumania danckelmanniana*; dotted grey line, distribution area of *Haumania liebrechtsiana*, dashed grey line, distribution area of *Haumania leonardiana; dark* grey areas, postulated refugial areas; light grey area, Gabon.

4.6 CONCLUSION

Different processes including hybridization and mechanical, geographical and ecological isolation have presumably driven speciation in Marantaceae. Among them, geographical isolation is the most easily and most often detected factor (see also Ridley, 1996; Barraclough et al., 1998) reoccurring on all levels in the phylogeny of the Marantaceae.

Only a few examples could yet be found across the whole family where the explosive pollination mechanism itself contributed to reproductive and ecological speciation through synorganizational differences between species. More often, ecological speciation is based on adaptations to different pollinators by flower size and tube type and length.

However, the explosive mechanism might have contributed to an overall increase in the individual fitness of the Marantaceae. In its sister family Cannaceae (10 spp.) pollen is secondarily presentated on an open accessible style (Kunze, 1984) probably increasing pollen loss. Thus the advantage of the explosive

pollination mechanism of the Marantaceae may lie in the hidden pollen load, a precise pollen transfer allowing an economic production of pollen grains and the prevention of selfing (chapter 3). Furthermore, the narrow floral structure associated with the explosive pollination mechanism might have allowed closer adaptations to specific pollinators. However, only detailed comparative analysis between the two families of the quantity of pollen transfer and loss, the rate of selfing (including geitonogamy) and the pollinator assemblages will solve this issue.

4.7 APPENDIX

taxonomic consequences

Ataenidia conferta (Benth.) Milne-Redh. is nested within the genus *Marantochloa* Brongn. & Gris., which was already noted by Prince and Kress (2006*a*). The close relationship between the two genera is furthermore strongly supported by morphological characters. The most obvious common characters of both genera, simultaneously separating them from all other Marantaceae genera, are the strongly asymmetric leaves (homo- and antitropy), the absence of bracteoles, the cushion-like trigger appendage of the hooded staminode and the small red or yellow nuts (5-7 mm long) (except capsules in *Marantochloa filipes*).

Marantochloa conferta (Benth.) A. Ley comb. nov. ≡ *Calathea conferta* Benth. in Benth. & Hook. f. Gen. Plant. 3: 653 (1883) ≡ *Ataenidia conferta* (Benth.) Milne-Redh. Kew Bull. 1952: 168 (1952). Type: Cameroun, Mann 2444 (holo-: K, icono-: BR).

5 General Conclusions

For the first time species level phylogenies of two clades of the African Marantaceae are now available. Additionally comprehensive data on floral morphology, pollinators and breeding system has been collected. This allows a more detailed follow-up of their evolutionary pattern (see Barraclough et al., 1998). Close adaptations of flower and pollinator, parallelism in the evolution of floral morphologies (floral size and arrangements) and pollinator shifts between distant clades can be observed (chapter 2). The latter is independent of the morphological diversity of the unique and highly complex explosive pollination mechanism (trigger types) (chapter 3). In the future it would be interesting to compare patterns from African clades with clades from America and Asia to analyse how diversity is obtained in those groups and how this is linked with the respective geological and palaeovegetational history. With a significantly higher level of diversity in America (e.g. *Calathea* clade), which is also found in many other plant and animal groups (see Renner, 2004), a direct comparison between the clades of the different continents might elucidate differential processes of speciation and thereby contribute to answering the long-discussed issue of how this diversity pattern evolved. So far two contrasting hypothesis have been published; the theory of accelerated extinction rates during the Neogene climatic deterioration in Africa (Richards, 1973) and the theory of dynamic recent speciation in America without invoking higher recent African extinctions (Gentry, 1982).

The disparity in species diversity on family level in the Zingiberales might be attributed to their worldwide distribution patterns. Only the three largest families are pantropically distributed (Table 4.1) thereby having access to a higher number of potential niches for speciation. Interestingly the diversity centres of the two most species rich families Zingiberaceae and Marantaceae do not overlap: Zingiberaceae are most species rich in Asia whereas Marantaceae are most species rich in America. A closer worldwide investigation and consecutive comparison of these two families will potentially provide new insight into the evolution of flowering plants in the tropical habitats on different continents.

Family diversity is furthermore correlated with floral symmetry. The three most species rich families exhibit tubular flowers with a pronounced asymmetry in which the petaloid staminodes play a crucial role in attracting pollinators (chapter 2; see

also Kunze, 1984; Kress, 1990; Specht, 2001; Zhang et al., 2003; Rudall and Bateman, 2004). The functional zygomorphic structure might allow closer adaptations to specific pollinators leading to the reciprocal induction of diversification in the respective plant and pollinator community (for examples see Meeuse and Morris, 1984; Dressler, 1981; Endress, 1994; Lunau, 2004).

Zingiberaceae and Marantaceae evolved an even more specific pollen transfer. Aggregated pollen grains are precisely deposited onto the insect via a staminal lever mechanism in Zingiberaceae (Müller, 1831) and an explosive stylar movement in Marantaceae (Claßen-Bockhoff, 1991). The transport of aggregated pollen presents an advantage in environments of infrequent pollinator visits (Harder and Johnson, 2008) and is a prerequisite for the complete success of pollination in Marantaceae where each flower has three ovules but only a single chance of being pollinated. The localized deposition of pollen provides the possibility for mechanical isolation between individuals promoting speciation. A correlation of (functional) zygomorphy and pollen aggregation with species diversity can be found repeatedly in the angiosperms (e.g. *Salvia*, Claßen-Bockhoff et al., 2004; Orchidaceae, Dressler, 1981; see also Harder and Johnson, 2008). The step-wise evolution towards these complex structures can be followed across the order Zinigberales. Basic prerequisites such as the neoteny of the fertile theca, secondary pollen deposition and a close morphological and functional relation of fertile structures are joint possessions within the sister clades of the `ginger´ families (Kunze, 1984).

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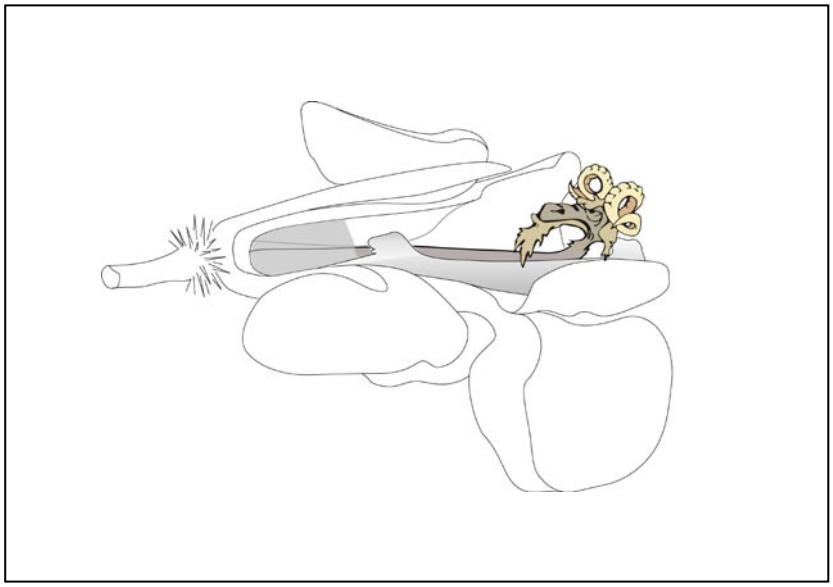

Costerus (1918): „… Reizt man jetzt den Griffel oder drückt man leise den Zahn an die andere Seite der Kapuze, so sieht man den Griffel plötzlich und energisch sich nach vorn beugen, bis er das gegenüberliegende Schwielenblatt berührt. Man bekommt den Eindruck wie von einem Ziegenbock, der seinen gehörnten Kopf kräftig gegen eine Mauer drückt...“