

Ornithophily in the genus *Salvia* L. (Lamiaceae)

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Meinen Eltern gewidmet

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Summary of the thesis

This dissertation presents for the first time a survey of bird pollinated (ornithophilous) *Salvia* species. Within the approximately 1000 species of the worldwide distributed genus roughly 20% (186 spp.) are bird pollinated. Excepting four species in the Old World (South Africa and Madagascar), ornithophilous species are restricted to the New World where they represent about one third of the species. They occur mainly in higher altitudes (1500-3000m) and usually grow as shrubs or perennial herbs (97%). The bilabiate to tubular flowers are often red (at least 49%), averaging 35mm (7-130mm) in length and produce a large to medium volume of nectar with rather low sugar concentration. Pollination by sunbirds and white-eyes is documented in a South African species, and that by hummingbirds in 16 species of the New World (USA, Mexico, Guatemala and Bolivia). Beside pollinator observations, the functionality of the staminal levers, the process of pollen transfer and the fitting between flowers and birds are tested by inserting museum skins and metal rods into fresh flowers. The most surprising result is the finding of two different main pollen transfer mechanisms. In at least 54% of the species an active staminal lever mechanism enables pollen deposition on the birds body. This is illustrated in detail in the South African *S. lanceolata* at which birds were observed to release the lever mechanism and became dusted with pollen. In contrast, the lever mechanism in about 35% of the New World species is reduced in different ways. Pollen transfer by inactive 'levers' is demonstrated in detail in *S. haenkei* in Bolivia, at which four pollinating hummingbird species could be observed. The tubular corolla forced the birds in a specific position, thereby causing pollen transfer from the exerted pollen-sacs to the birds body. With respect to the floral diversity and systematic affiliation of the species, parallel evolution of ornithophily and lever reduction is likely. Considering that bird pollinated species might have derived from bee pollinated species and that the staminal levers have become secondarily inactive, it is concluded that the shift in pollinators induced phenotypic changes even disabling such a sophisticated structure as the staminal lever mechanism.

Zusammenfassung

Die vorliegende Dissertation gibt erstmalig einen Überblick über vogelbestäubte (ornithophile) *Salvia*-Arten. Von den annähernd 1000 Arten der weltweit verbreiteten Gattung sind ungefähr 20% (186 spp.) vogelbestäubt. Bis auf vier Arten in der Alten Welt (Südafrika und Madagaskar) sind ornithophile Arten auf die Neue Welt beschränkt, wo sie ungefähr ein Drittel der Arten ausmachen. Man findet sie vorwiegend in höheren Lagen (1500-3000m) als Sträucher oder Stauden (97%). Die durchschnittlich 35mm (7-130mm) großen Lippen- bis Röhrenblüten sind sehr oft rot (mindestens 49%) und produzieren hohe bis mittlere Nektarmengen von eher niedriger Zuckerkonzentration. An einer südafrikanischen Art konnte Bestäubung durch Nektar- und Brillenvögel, an 16 neuweltlichen Arten (USA, Mexiko, Guatemala und Bolivien) Bestäubung durch Kolibris dokumentiert werden. Neben Bestäuberbeobachtungen wurde die Funktionalität des Staubblatt-Hebelmechanismus, der Prozess des Pollentransfers und die Passung zwischen Blüten und Vögeln untersucht, indem Vogelbälge und Metallsonden in frische Blüten eingeführt wurden. Das wichtigste Ergebnis ist die Dokumentation von zwei verschiedenen Haupt-Pollentransfer-Mechanismen. In mindestens 54% der Arten erfolgt die Pollenablage auf dem Vogelkörper mittels eines Staubblatt-Hebelmechanismus. Dies wurde eingehend an der südafrikanischen *S. lanceolata* demonstriert. Hier wurden Vögel beobachtet, die den Hebelmechanismus auslösten und mit Pollen eingestäubt wurden. Demgegenüber ist der Hebelmechanismus in mindestens 35% der neuweltlichen Arten reduziert, wobei die Inaktivierung der Hebelbewegung auf ganz unterschiedliche Weise erfolgt ist. Pollentransfer ohne Staubblatthebel konnte am Beispiel von *S. haenkei* in Bolivien nachgewiesen werden. An dieser Art wurden vier verschiedene Kolibri-Arten beim Blütenbesuch beobachtet. Die röhrenförmige Blütenkrone brachte die Vögel in eine bestimmte Position, die Pollentransfer von den exponierten Staubbeuteln auf den Vogelkörper ermöglichte. Aufgrund der floralen Diversität und systematischen Stellung der vogelbestäubten Arten ist eine parallele Evolution der Ornithophilie und eine mehrfache Reduktion des Hebelmechanismus wahrscheinlich. Unter der Annahme, dass vogelblütige Arten von bienenblütigen Arten abstammen und der Hebel sekundär inaktiv geworden ist, wird gefolgert, dass der Bestäuberwechsel phänotypische Änderungen induziert, die sogar eine so spezialisierte Einrichtung wie den Hebelmechanismus unwirksam werden lassen.

1 General introduction

One of the most fascinating interactions between plants and animals is the process of pollen transfer by means of the staminal lever mechanism in *Salvia* (reviewed in Claßen-Bockhoff et al. 2003). The two monotheccic stamens are modified to levers. A pollinator searching for nectar has to push back the lower lever arms and thereby presses the pollen-sacs at the end of the upper lever arms onto its head or back. Visiting a second flower of the same species permits pollen transfer to the stigma.

Though this lever mechanism was already described by Sprengel (1793) with the example of *Salvia pratensis* (Fig. 1.1) its evolutionary significance is largely unknown. Only recently was it hypothesised that the staminal lever mechanism may



Figure 1.1. Inflorescence of the melittophilous *Salvia pratensis*. In the upper pair of flowers the staminal levers are released while they are enclosed by the upper lip in the bottom left flower.

function as a key innovation which promotes adaptive radiation (Claßen-Bockhoff et al. 2004b). To test this hypothesis, studies on functional floral morphology and stamen development as well as field investigations and biomechanical experiments have been initiated (Claßen-Bockhoff & Speck 2000, Claßen-Bockhoff et al. 2004a, b).

The present study is part of the project dealing with the reconstruction of floral diversity in *Salvia*. It concentrates on bird pollinated (ornithophilous) sages which are little known as to their number, distribution, floral diversity and pollen transfer mechanisms. To elucidate the functional significance of the lever mechanism it is first needed to get an overview of the bird pollinated species. For that purpose, comprehensive field investigations were conducted in South Africa and different countries of the New World. As two different modes of pollen transfer on bird pollinated sages were already described (Hildebrand 1865, McGregor 1899, Werth 1956, Himmelbaur & Stibal 1932-1934), the diversity of pollination mechanisms has to be detected and illustrated in a second step. Finally, the data are discussed under an evolutionary biological point of view. As bird pollinated sages are supposed to have derived from melittophilous species several times in parallel the functional, phylogenetic and ecological constraints underlying these shifts are reconstructed.

The thesis includes four parts (chapter 2-5). The first two chapters illustrate the two main types of pollen transfer mechanisms in bird pollinated sages. Pollination without a lever mechanism is documented in the Bolivian *S. haenkei* (chapter 2) while the South African *S. lanceolata* represents pollen transfer by means of the lever mechanism (chapter 3). A survey of the pollination syndromes of all New World *Salvia* species with special reference to the ornithophilous species is given in chapter 4. In chapter 5 the diversity of all bird pollinated species is illustrated and discussed in detail.

2 Hummingbird pollination in *Salvia haenkei* (Lamiaceae) lacking the typical lever mechanism

2.1 INTRODUCTION

The genus *Salvia* (Lamiaceae) is well known by its specific dorsal (nototribic) pollen transfer mechanism. The flowers are characterised by only two fertile stamens of which the connectives are modified to act as levers. A pollinator searching for nectar has to push back the (sterile) lower lever arms and thereby presses the pollen-sacs at the end of the upper lever arms onto its head or back. Visiting a second flower of the same species permits pollen transfer to the stigma (reviewed in Claßen-Bockhoff et al. 2003).

Among the more than 900 described *Salvia* species (Alziar 1988-1993), the 'lever mechanism' is modified in various ways. Apart from the dorsal (nototribic) type we find ventral (sternotribic) and lateral (plagiotribic) pollination mechanisms as well as pollen transfer without any active staminal levers (Hildebrand 1865, Claßen-Bockhoff et al. 2004b). The latter is often found among the approximately 200 bird pollinated species: at least 50 of them have inactive or even reduced levers while the remaining ones transfer pollen in the 'typical' *Salvia* manner by means of staminal levers (chapter 5).

The lever-like modification of the stamens represents a highly derived morphological construction including the widening of the connectives, the inhibition of the lower thecae, the functional differentiation of the lower lever arm including new growth centres and the exact positioning of the pollen-sacs for dorsal pollination (Claßen-Bockhoff et al. 2004a). Possible functions are the precise pollen placement on the pollinator's body (Faegri & van der Pijl 1971), pollen portioning due to its easily reversible movement, the increase of the diversity of pollinators by compensating for different body sizes and specific behaviour (Claßen-Bockhoff et al. 2004a, Kuschewitz 2004, chapter 5) as well as the decrease of possible autogamy by herkogamy (Webb & Lloyd 1986). Proceeding from the assumption that bird pollinated species are derived from bee pollinated ones and that inactive levers are derived from active ones the question rises for which phylogenetic and adaptive

reasons so many bird pollinated *Salvia* species might have given up the lever mechanism.

In general, ornithophilous *Salvia* species are less investigated than bee pollinated ones. Early observations of birds visiting *Salvia* flowers date back to Sclater (1856), Salvin (1860), Gould (1861), Müller in Hildebrand (1870), Villada (1873), Mulsant & Verreaux (1874), Waterton (1879) and Scott-Elliot (1890). Only few studies dealt with the morphology of ornithophilous *Salvia* flowers with inactive levers (Hildebrand 1865, Meehan 1871, Trelease 1882, Werth 1956, Himmelbaur & Stibal 1932-1934, Neisess 1983, Baumberger 1987). Field studies do not consider stamen morphology (Pickens 1931, Wagner 1946, Grant & Grant 1968, Stiles 1973, Arizmendi 2001, Lara & Ornelas 2001, Ortiz-Pulido et al. 2002, Van Devender et al. 2004) or the functionality of the lever mechanism (Grant & Grant 1966, Skean & Judd 1988, Grases & Ramírez 1998, Torke 2000).

In the present paper we focus on *S. haenkei* to illustrate pollen transfer in a species lacking the staminal lever mechanism. Some general features of the species have been already described by Bentham (1832-1836), Rusby (1900), Himmelbaur & Stibal (1932-1934), Epling (1939), and Macbride (1960), but field investigations are completely lacking. The interaction between flowers of *S. haenkei* and nectar drinking birds at natural habitats in Bolivia are illustrated. The process of pollen transfer is reconstructed by comparing the morphometric data of the flowers and the birds using museum specimens.

The investigation is part of a comprehensive study on bird pollinated *Salvia* flowers including phenotypic diversity, floral morphology and the process of pollen transfer. As the diversity of stamens and pollen transfer mechanisms is especially high in this group some general insights into the biological significance of the staminal lever mechanism in *Salvia* are expected. The hypothesis is tested that pollen transfer by means of staminal levers is more essential in bee pollinated flowers than in bird pollinated ones and that due to the pollinator shift from bees to birds the specific pollen transfer mechanism has been reduced several times in parallel (chapter 5).

2.2 MATERIAL AND METHODS

Salvia haenkei Benth. occurs in Bolivia and Peru (Epling 1939). It is generally distributed between 2200 and 3600 m where it prefers stream gullies in the dry valleys and open hillsides in areas with more rainfall (J. Wood, pers. comm.). Different populations were all together studied for eleven days (about 75 hours) between February and April 2002 at the following localities in the Bolivian Andes:

(1) Kewiñal, dept. Cochabamba, ca. 10 km east of Arani on the road to Mizque, about 3200 m, dry bushland and subpuna to roadsides and ravines, very frequent. (2) Mecapaca, dept. La Paz, east of the village Mecapaca, about 3000 m, dry bushland, frequent. (3) Huajchilla, dept. La Paz, about 3000 m, dry bushland and matorral, frequent. (4) Liriuni near San Miguel, dept. Cochabamba, about 3100 m, dry bushland, very frequent.

Vouchers of *S. haenkei* are deposited at MJG, LPB and K. Flowers were fixed in 70% ethanol. Seeds were collected in the field and grown in the Botanical Garden of the University of Mainz, Germany. There, the plants flowered in November 2002 and in June/July 2003 and 2004. Colour values follow the CMYK colour space (Küppers 1999). Sugar concentration was measured under greenhouse conditions using a hand held refractometer (Atago, Honcho/Japan: N1). The position of the stigmatic tissue was tested with KMnO₄ stain (10 % solution, for about 30 seconds, Robinsohn 1924) and SEM (ESEM XL 30, Philips).

Field identifications of the birds were verified using Fjeldså & Krabbe (1990), Hilty & Brown (1986) and Schuchmann (1999). The foraging behaviour of the hummingbirds on the flowers of *S. haenkei* was observed with binoculars and documented with photographs and videotapes.

To reconstruct the process of pollen transfer, morphometric data were recorded of both the flowers and the birds (all intact museum specimens of the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany (ZFMK): *Sappho sparganura sparganura* Shaw, *Sappho sparganura sappho* Lesson, *Colibri coruscans* Gould, *Patagona gigas peruviana* Boucard and *Oreotrochilus adela* Orbigny & Lafresnaye). In order to verify the pollen transfer museum specimens of *Patagona gigas* Vieillot, *Sappho sparganura* Shaw and *Colibri coruscans* Gould of the Colección Boliviana de Fauna, La Paz (CBF) were placed in fresh flowers of *S. haenkei*.

2.3 RESULTS

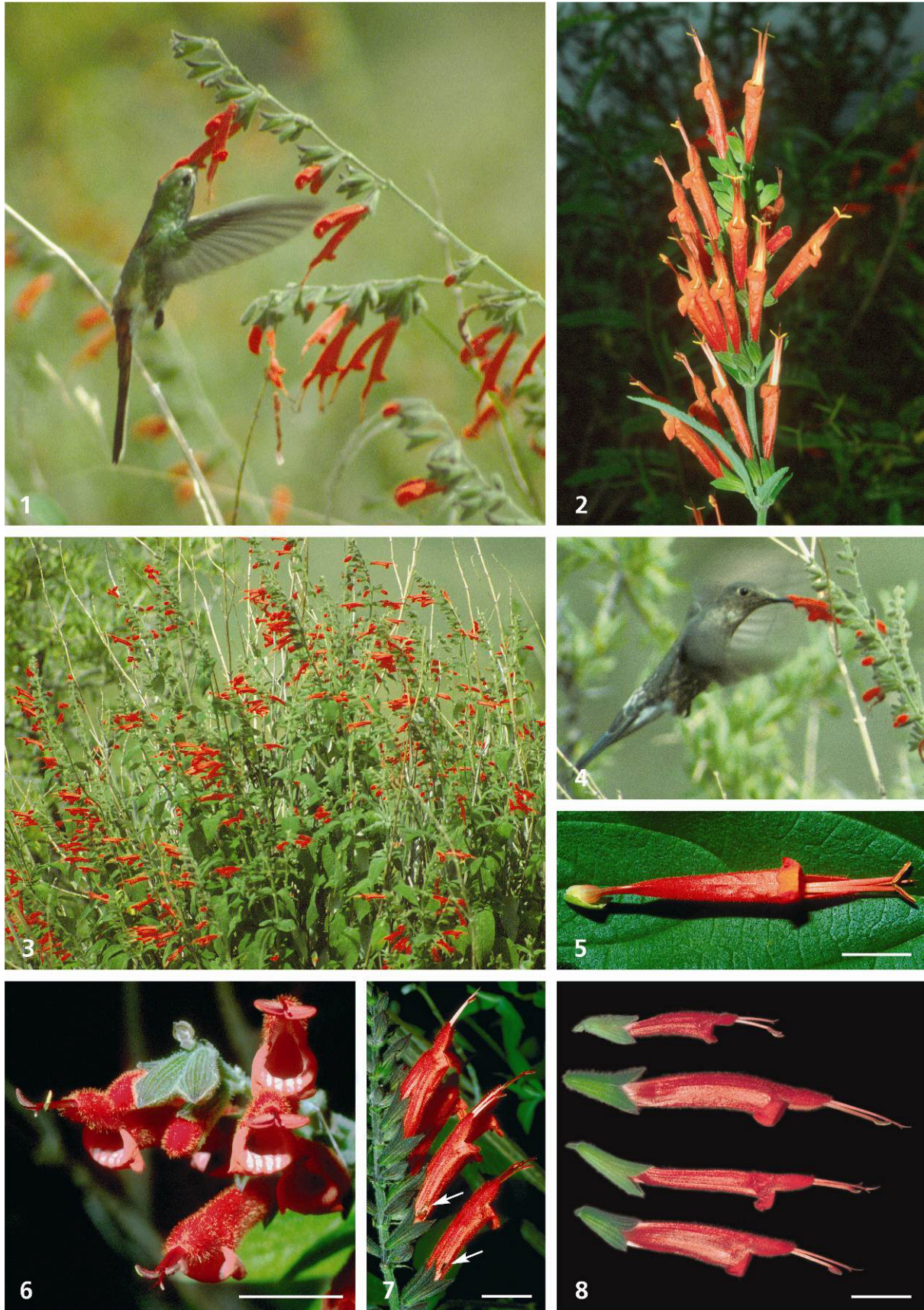
2.3.1 *Salvia haenkei*

S. haenkei is a very attractive shrubby plant of variable size and shape (30 cm to 250 cm in height). It has conspicuous bright red to orange flowers (M99-90 Y99-80 S10, M90 Y70 S00, M60 Y90 S00) which are arranged in large and erect inflorescences (Figs. 2.2, 2.3). Conspicuousness is increased by mass flowering in large populations. At the observed localities, *S. haenkei* was the dominant ornithophilous species competing only with few individuals of *Nicotiana glauca* Graham (Solanaceae), *Salvia orbignaei* Benth. and *S. haenkei* x *S. orbignaei* (all at Kewiñal), *Tecoma arequipensis* (Sprague) Sandwith (Bignoniaceae; Mecapaca and Huajchilla) and *Mutisia acuminata* Ruiz & Pav. (Asteraceae; Liriuni).

Flowering starts at the lowest node and continues acropetally. Each cyme includes three (1-5) flowers which open according to their age and branch order (Figs. 2.1, 2.2), altogether resulting in a mixed flowering pattern with 9-16 simultaneously open flowers (Figs. 2.1, 2.2). The flowers have flexible pedicels and are predominantly placed in a horizontal or slightly upward position with an orientation towards free space (Fig. 2.3). Anthesis of the individual flower lasts for 1.5 to 2 days.

In all populations, flower length is around 4 cm, the floral structures varying in their morphometric data (Tab. 2.1, Fig. 2.8). The long and narrow floral tubes taper towards the base up to a lateral constriction at the base of the flower (Figs. 2.5, 2.9 c). The upper lip is shorter than the stamens and the style. The short lower lip is folded back occasionally showing stripes or spots (Fig. 2.6). The lateral constriction broadens into a nectar chamber (Figs. 2.5, 2.9 nc). The flowers contain nectar of low concentration (26.6 ± 2.2 %, $n=107$) which is produced by the nectary at the ovary (Fig. 2.9 n). The high volume of nectar usually rises slightly over the constriction. It adheres the nectar in combination with the capillary forces of the thin corolla tube and thus prevents it from overflowing (Fig. 2.9 nc, c). There is no noticeable flower scent.

The two stamens are lever-like modified. The lever arms correspond to the connectives of the versatile anthers which are connected to the filaments by ligament-like joints. The upper connective arms are exposed out of the upper lip presenting the thecae (Fig. 2.9, Tab. 2.1 d). They are red and do not contrast to the



Figures 2.1-8. *Salvia haenkei* at its natural habitat in Kewiñal, Bolivia. **1.** Pollen deposited on the head of *Sappho sparganura*. **2.** Inflorescence: indeterminate thyse with sessile cymes. **3.** Bush with red flowers in large inflorescences. **4.** *Patagona gigas* loaded with pollen on the upper side of its head, its forehead and its bill. **5.** Flower from below (without calyx): Note the lateral constriction ►

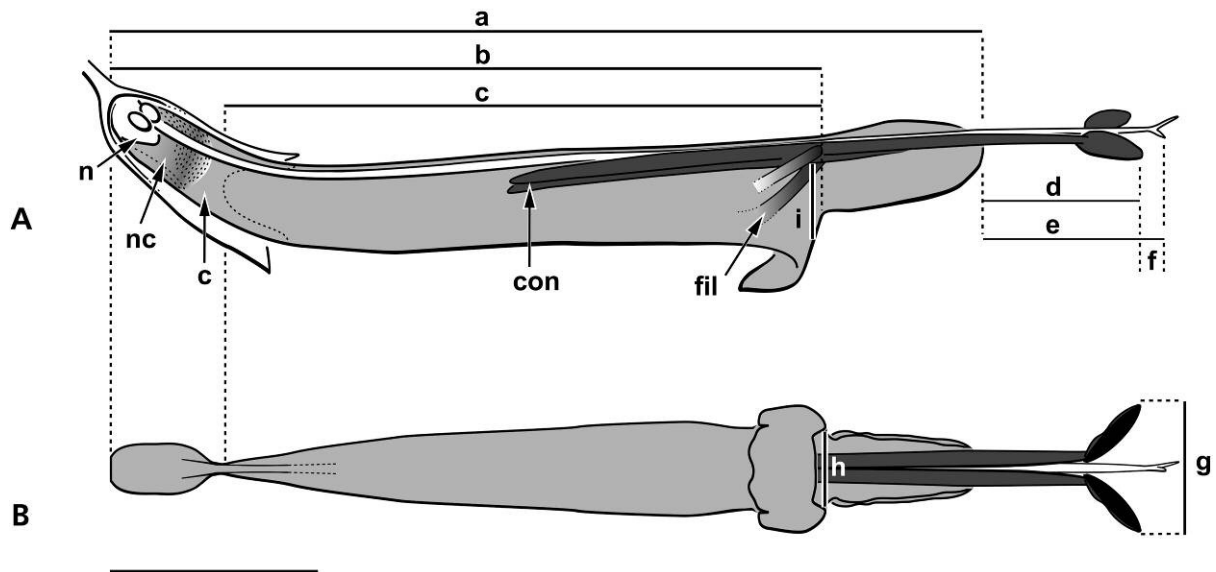


Figure 2.9. Longitudinal section (A) and view from below (B) of a flower of *Salvia haenkei*. Note the lower connective arms closely attached to the upper side of the tubular corolla. con: connective, fil: filament, n: nectary, nc: nectar chamber, c: constriction (from nectar chamber to dashed line); a-i: morphometric data (see Tab. 2.1). Bar = 1 cm.

corolla. The thecae are spread apart (Figs. 2.2, 2.5, 2.6, 2.9 B, Tab. 2.1 g) and release sticky yellow pollen downward. The lower connective arms of the two neighbouring stamens remain sterile. They are weak and flexible and closely attached to each other by hairs. Together they form a plate tightly leaned against the upper tube wall (Fig. 2.9). At the joint area small secondary formations of the filament and connective are present. Though the joint in principle is movable, the lever mechanism remains inactive because there is no space left to release the lever.

The two short stigmatic lobes of the style are likewise red and exposed. They overtop the thecae (Figs. 2.8, 2.9 e,f, Tab. 2.1 f), but have occasionally the same length. Stigmatic tissue was only found at the tip of the lower stigmatic lobe that pollen grains were adhering to. Seed set was very high in the field. Additional greenhouse tests showed that many seeds were viable producing vital flowering plants.

←
 ► and the diagonal arrangement of the thecae. **6.** Front view of the flowers with showy stripes on the lower lip. **7.** Holes made by nectar robbers at the base of the corolla (see arrows). **8.** Variability of flower shape and size. Bars = 1 cm.

2.3.2 Flower visitors

Four different hummingbird species were observed drinking nectar at the flowers of *S. haenkei*: the Red-tailed Comet (*Sappho sparganura*, Fig. 2.1) and the Sparkling Violet-ear (*Colibri coruscans*) visited the flowers very often at Huajchilla, Kewiñal and Liriuni, whereas the Giant Hummingbird (*Patagona gigas*; Kewiñal, Liriuni) was less frequent and the Wedge-tailed Hillstar (*Oreotrochilus adela*; Kewiñal) only once observed at the flowers.

Table 2.1. *Salvia haenkei* - morphometric data of flowers from several plants and populations (a-i see Fig. 2.9).

Morphometric character	n	Size [mm]	
		mean \pm SD	range
Length of entire corolla (a)	19	38.7 \pm 3.5	(18.0 – 45.0)
Length of corolla tube without upper lip (b)	17	31.8 \pm 3.6	(15.0 – 39.1)
Distance: entrance up to distal end of constriction (c)	7	26.8 \pm 5.0	(19.0 – 34.9)
Exsertion of thecae (d)	10	7.7 \pm 1.7	(5.4 – 10.0)
Exsertion of lower stigmatic lobe (e)	9	10.7 \pm 3.0	(6.8 – 15.4)
Distance: lower stigmatic lobe to distal end of theca (f)	8	2.0 \pm 3.0	(-1.3 – 5.4)
Distance between the distal ends of the thecae (g)	7	6.0 \pm 1.0	(4.0 – 8.0)
Diameter of entrance (horizontal) (h)	27	3.7 \pm 0.5	(2.5 – 4.5)
Diameter of entrance (vertical) (i)	27	3.7 \pm 1.0	(2.0 – 5.0)

Foraging behaviour was different among the observed hummingbirds. *Colibri coruscans* and *Sappho sparganura* maintained a territory containing nectar sources. The first species defended *S. haenkei* very aggressively against competitors both of their own species and of other hummingbird species. *Patagona gigas*, however, only visited the flowers in intervals of several hours usually staying in the area for only few, rarely up to 20 minutes. Aggressive behaviour was not noticed.

Sappho sparganura, *Colibri coruscans* and *Patagona gigas* showed a preference for individual plants of *S. haenkei*. They usually visited few of their inflorescences and drank nectar from several flowers (rarely one or all) before flying to another inflorescence. Thereby, they showed no preference for a specific visitation pattern within an inflorescence.

The bird species hovered while drinking nectar except *Sappho sparganura* which occasionally exploited the flowers by perching or by perching and hovering at the same time (hovering-clasping flight).

The bird species showed relatively large pollen patches on the upper side of their heads and bills, respectively. Though no birds were captured, for *Sappho sparganura* and *Colibri coruscans* it was evident from their foraging behaviour and the small number of competing plant species that this pollen originated from *S. haenkei*.

When inserting their bills into the flower tubes the birds often glided along the open pollen-sacs and got pollen smeared on their head or bill. Pollen was thereby deposited on different parts of their body (Tab. 2.2, Fig. 2.10). *Sappho sparganura* and *Colibri coruscans* were loaded with pollen on their heads while the larger *Patagona gigas* carried pollen on the upper side of its head, its forehead and its bill (Fig. 2.4). While perching or hovering-clasping the birds pulled the flowers with their bills to themselves and then inserted their bills to get access to nectar. Especially in these cases, but also occasionally while hovering, the birds additionally entered the flower from below or laterally. Then the thecae touched the birds also laterally, only at a specific spot or not at all. Precise pollen deposition is only possible when the thecae touch the bird so late that there is no gliding along the body any more.

Table 2.2. Morphometric characters of the hummingbird species observed at *Salvia haenkei* flowers (mean \pm SD, range in parentheses; for bill shape see Fig. 2.10).

Hummingbird species	Length of bill [mm] ^{a, b}	Width and height of bill [mm] ^{b, c}		Body mass [g] ^d
<i>Sappho sparganura sparganura</i>	23.9 \pm 3.2 (19.2 – 27.8)	3.5 \pm 0.4 (2.6 – 4.0)	3.0 \pm 0.4 (2.1 – 3.4)	5.2 – 5.9
<i>S. s. sappho</i>	20.9 \pm 1.0 (19.0 – 22.6)	3.3 \pm 0.5 (2.5 – 4.5)	3.6 \pm 0.6 (2.7 – 4.8)	
<i>Colibri coruscans</i>	27.3 \pm 2.0 (21.3 – 30.5)	3.5 \pm 0.6 (2.1 – 4.8)	3.1 \pm 0.7 (2.2 – 4.7)	6.7 – 8.5
<i>Oreotrochilus adela</i>	29.3 \pm 0.9 (28.3 – 30.2)	3.3 \pm 0.4 (2.5 – 3.6)	3.1 \pm 0.5 (2.3 – 3.6)	7.4 – 8.3
<i>Patagona gigas peruviana</i>	42.0 \pm 2.3 (37.6 – 46.2)	5.8 \pm 0.6 (4.7 – 6.7)	4.9 \pm 0.9 (3.9 – 6.7)	18.5 – 20.2 (>23)

^a tip to proximal end of nares

^b museum specimens from ZFMK (*Sappho sparganura sparganura*: n=12, *S. s. sappho*: n=26, *Colibri coruscans*: n=49, *Oreotrochilus adela*: n=5, *Patagona gigas peruviana*: n=20)

^c at proximal end of nares

^d Schuchmann 1999 (data not referring to the subspecies mentioned here)

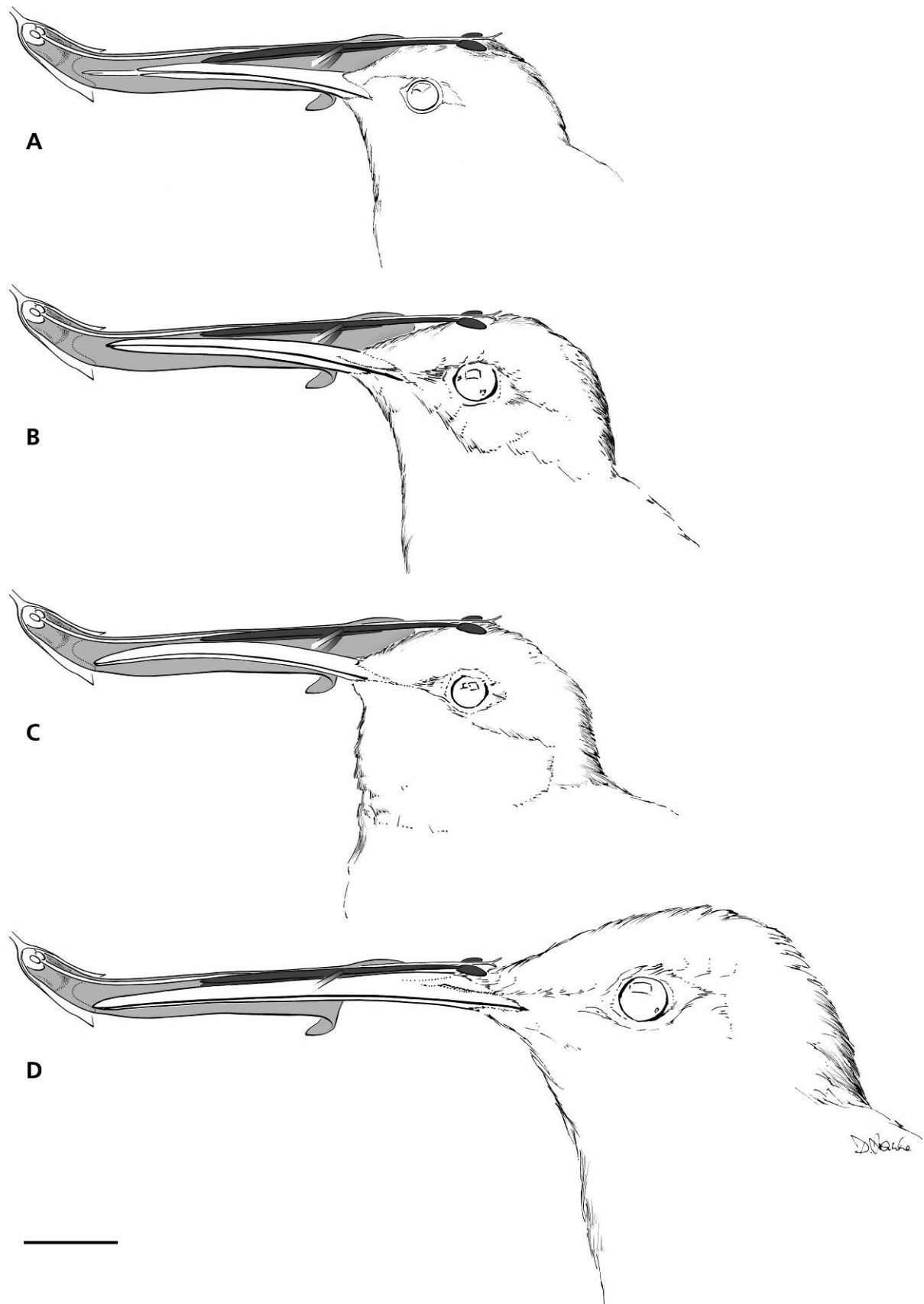


Figure 2.10. Pollen transfer in *Salvia haenkei*: Note the position of the thecae on different body parts in (A) *Sappho sparganura*, (B) *Colibri coruscans*, (C) *Oreotrochilus adela* and (D) *Patagona gigas*. Bar = 1 cm.

In the individual case pollen deposition depended on the relative length of flower tubes and bills, on the amount of nectar, the diameter of the entrance and the exposition of the thecae as well as on the different behaviour of the birds. As all these characters are variable, it is clear that the pollen dusted area on the pollinator increases with the number of successive visits. Field observations were confirmed by comparing the morphometric data of the bills to the diameter and length of the *S. haenkei* flower (Tab. 2.1, 2.2).

Patagona gigas rarely visited *Nicotiana glauca* (Kewiñal) and *Tecoma arequipensis* (Huajchilla). At least *Patagona gigas* and *Sappho sparganura* also visited the hybrids of *S. haenkei* and *S. orbignaei* at Kewiñal.

Besides the regular pollinators, diverse nectar robbers were observed at *S. haenkei*. The flower-piercers *Diglossa sittoides* Orbigny & Lafresnaye and *D. carbonaria* Orbigny & Lafresnaye (Emberizidae) pierced the corolla tube near the base (Fig. 2.7) and even *Sappho sparganura* was observed using these holes. In the Band-tailed Seedeater (*Catamenia analis* Orbigny & Lafresnaye; Emberizidae) the nectar robbing behaviour could be documented for the first time. Several not yet identified bee species of middle to large size (incl. *Xylocopa* sp.) likewise stole nectar through holes near the corolla base. Once a big yellow butterfly (cf. Pieridae) was observed drinking nectar through the flower entrance of *S. haenkei*, but without touching thecae and stigma. Irrespective of birds or insects robbing nectar, damage to the reproductive organs and nectaries of the flowers was never observed.

2.4 DISCUSSION

2.4.1 *Salvia haenkei* as a nectar source for hummingbirds

S. haenkei is a typical ornithophilous plant combining many characters of the corresponding syndrome: red colour of the corolla, long and narrow corolla tube in combination with a long distance between nectar and stigma and thecae, no landing platform, orientation towards free space, no noticeable flower scent and a high volume of low-concentration nectar. The plants grow as richly branched shrubs and bear many large inflorescences, each offering several open flowers simultaneously. Moreover, the individuals occur in large populations. They are thus able to provide the hummingbirds with a high amount of nectar for several months.

The birds differ in their foraging behaviour: *Colibri coruscans* and *Sappho*

sparganura were found to be typical territorial hummingbirds visiting nectar sources in a limited area (see also Hilty & Brown 1986, Ribeira Arismendi 1991, Kraemer et al. 1993, Schuchmann 1999). In contrast, *Patagona gigas*, generally described to be aggressive and territorial (Fjeldså & Krabbe 1990, Schuchmann 1999), was only observed in intervals at the flowers indicating either a traplining behaviour or a large territory (King & Holloway 1990).

From the plant's 'point of view' the chance of pollination is increased with territorial hummingbirds. These are constant pollinators which visit few other plants and therefore transfer more species-specific pollen than trapliners do. However, for the same reason, they contribute less to gene flow among different plant populations. Attracting species with small territories and those with extended ones, *S. haenkei* profits by constant pollinators increasing gene exchange within the limits of the individual population as well as by pollinators promoting cross-pollination over large distances.

As no genetic self-incompatibility is known in *Salvia* (Owens & Uberta-Jiménez 1992; unpubl. data), selfing may be possible in *S. haenkei* by both autogamy and geitonogamy. The first is usually prevented by approach herkogamy (see Webb & Lloyd 1986, Miyajima 2001), the pollen-loaded bird first transferring pollen to the stigma and then touching the thecae. However, in flowers with closely neighboured thecae and stigma autogamy should happen. Geitonogamy is expected to play a significant role in the breeding system of *S. haenkei*. Its rate increases with the number of simultaneously blooming flowers per individual, the duration of flower anthesis, and the time of a pollinator staying with an individual plant.

All observed species hovered while feeding on nectar. Referring to the weight of 9 g, up to which hovering is energetically still efficient (Pyke 1980), the heavier *Patagona gigas* (Tab. 2.2) is usually described to perch and climb when feeding (Fjeldså & Krabbe 1990, Schuchmann 1999), while the lighter *Sappho sparganura* is known mainly to feed hovering (Contino 1975, Fjeldså & Krabbe 1990). In the present study we rather found the opposite: *Patagona gigas* was never observed sitting while feeding on nectar while *Sappho sparganura* exploited the flowers by hovering, perching and hovering-clasping flight. The latter is only described for few other hummingbirds (Kraemer & Schmitt 1991) and some nectar-feeding bats (Paulus 1978, Dobat & Peikert-Holle 1985).

2.4.2 Flower-bird interaction

Both partners in the process of pollen transfer, *Salvia haenkei* and the four hummingbird species, vary considerably in their morphometric proportions (Tab. 2.2; Ortiz-Crespo 1974, Kraemer et al. 1993, K.-L. Schuchmann pers. comm.). In view of an optimal pollen transfer on the flower's side and of a minimisation of energy consumption on the bird's side a higher degree of fit should be expected. However, variation within the limits of guaranteed pollination might be advantageous for both, as it avoids a unilateral dependence between a certain pollinator and plant. This might be true of the present example. Although variable, the distance between nectar and anthers and stigmas in *S. haenkei* generally corresponds to the morphometric data of the bills and tongues in the hummingbirds enabling successful pollination. Neither *S. haenkei* nor the hummingbirds observed are closely dependent on each other. *S. haenkei* is pollinated by different hummingbird species and these are able to get nectar from other plant species.

The relationship between bill length and flower length is often used as an example of coevolution and adaptation (Darwin 1876, Johnsgard 1983). The original supposition was that differences in bill lengths were associated with differences in the abilities to feed at flowers of different sizes. However, experimental studies failed to support this assumption (Temeles 1996). In fact, most hummingbirds visit flowers with floral tubes essentially longer and shorter than their bills (Feinsinger 1976, Snow & Snow 1980, Arizmendi & Ornelas 1990). This was true for *S. haenkei* and its associated hummingbirds which obviously compensate slight variations in flower size and nectar amount with their tongue.

The hummingbirds inserted their bills very deeply in the tubular flowers of *S. haenkei*, which might be favourable for the plant. The more the bill is inserted in a narrow tapering flower tube, the more fixed might be its position in relation to the reproductive organs, whose touching at the corresponding point is necessary for a successful pollination. This corresponds to the observation on *Sappho sparganura* which in general was dusted with pollen when hovering. When perching and hovering-clasping *Sappho* did not always touch the reproductive organs in a normal way. Obviously the sitting position reduces the radius of the birds and prevent them from inserting their bills in an adequate manner.

2.4.3 Pollen transfer without lever mechanism

Whereas the flower of *S. haenkei* is a typical bird pollinated flower it is an atypical *Salvia* flower because its staminal lever mechanism remains inactive. The stamens indeed are modified to act as levers having long upper lever arms and a sterile lower plate. But there is no space left in the flower to move the lever because the sterile plates are closely attached to the upper face of the corolla. Accordingly, additional connective and filament outgrowths around the joint area, which stabilise the lever movement in other *Salvia* species (Correns 1891, Claßen-Bockhoff et al. 2004a), are only weakly developed. Altogether, the flower of *S. haenkei* has a typical, tubular construction with exerted pollen-sacs attracting and rewarding birds. It is however remarkable that the characteristic stamen modification is still present indicating that its function got lost in the course of optimising adaptation to birds as pollinators.

A working lever mechanism might ensure precise pollen placement and thus might be an effective tool for maintaining reproductive isolation among sympatric species (Claßen-Bockhoff et al. 2004b, see also Brantjes 1978, Armbruster et al. 1994, Grant 1994, Ramamoorthy & Elliott 1998). In species like *S. haenkei*, however, pollen placement appears to be only rarely exact and more often imprecise due to a 'smear effect'. Increased by the diagonal orientation of the thecae a larger part of the pollinator's body is dusted with pollen. Thereby, the pollen contact area increases with the number of successive visits. Consequently, mechanical isolation is not likely even among species of differently sized flowers. The 'smear effect' might thus promote hybridisation among co-occurring species as was actually found in *S. haenkei* x *S. orbignaei* (Wester & Claßen-Bockhoff 2002).

At the same time, the 'smear effect' also contributes to a successful pollen transfer in *S. haenkei*. As the receptive tissue of this species is tiny and restricted to the tip of the lower stigmatic lobe the chance of getting pollinated directly increases with the size of the pollen-loaded area on the visiting bird. Furthermore, the 'smear effect' compensates for the variable proportions among the individual *S. haenkei*-flowers (Tab. 2.1) and the different hummingbird species (Tab. 2.2) and their behaviour. Regardless whether the short-billed *Sappho sparganura* or the long-billed *Patagona gigas* visit the flowers and whether the corresponding flower is short or long, all combinations within the given limits result in a successful pollination due to the unprecise pollen transfer.

S. haenkei is not the only ornithophilous *Salvia* species with an inactive staminal lever mechanism, there are at least 50 species similar to *S. haenkei*, or showing more reduced and stiffened staminal levers (chapter 5; see also Hildebrand 1865, Meehan 1871, Himmelbaur & Stibal 1932-1934, Werth 1956). As a part of the ornithophilous *Salvia* species has hidden thecae with an active lever mechanism and a second part with *S. haenkei* has exposed pollen-sacs and inactive levers it is concluded that at least two separate evolutionary pathways may have led to ornithophilous *Salvia* flowers (chapter 5). It is assumed that the highly derived staminal levers secondarily became inactive (see also Himmelbaur & Stibal 1932-1934, Correns 1891). The main argument is the lever apparatus itself which is able to act, but merely hindered by the tubular corolla shape. Werth (1956) argued that stamens and corollas evolved independently in *Salvia*, and that in bird-pollinated plants ornithophilous features might have overlapped with staminal features. Considering that ornithophilous *Salvia* species might have derived from bee-pollinated ancestors (Grant & Grant 1965), we have to elucidate the adaptational constraints changing with the shift from bees to birds as pollinators.

In most of the melittophilous *Salvia* flowers pollen is hidden in the upper lip where it is not visible. This can be interpreted as a protection against pollen collecting bees that collect pollen for their offspring instead transferring it to another flower (Müller 1871, Loew 1886, Correns 1891, Westerkamp 1997). In bee pollinated *Salvia* flowers, the staminal lever mechanism ensures both pollen transfer out of the upper lip and on to the back of the bee where the latter cannot see the pollen and may not reach it with its legs (see also Westerkamp 1996, 1997). Compared to bees, birds are regarded as more reliable pollinators; collecting no pollen, covering larger distances and being more independent from weather, notably in highlands (Cruden 1972, Thomson et al. 2000). As feathers are the optimal medium for pollen transport (Kugler 1970, Faegri & van der Pijl 1971, Johnsgard 1983, Rose 1990, Arizmendi et al. 1996) it is advantageous to ensure pollen deposition on the bird's feathers and not on the smooth bills. Therefore it is necessary to increase the distance between nectar and pollen. This is mainly achieved by either elongating the corolla tube and/or by exposing the pollen-sacs and stigma. The elongation of the corolla tube also excludes bees. If the pollen remains hidden in the upper lip of the bilabiate flower the lever mechanism is still necessary for pollen transfer. This is true for most of the ornithophilous *Salvia* species (chapter 5). In the second case pollen is

presented in an open manner whereby the flowers become independent from the lever mechanism (see also Trelease 1882). This is true for *S. haenkei* and many more species which show various reductions of lever structure and function (chapter 5), a feature which may have directly descended from insect pollinated ancestors or/and from bird pollinated ones with working levers.

2.5 SUMMARY

While in most *Salvia* species pollen is transferred by the 'staminal lever mechanism', in some species the 'levers' are inactive. This is also found in the bird pollinated *S. haenkei* from Bolivia. To understand pollen transfer in a species lacking the lever mechanism field investigations are carried out and the observations are confirmed by means of morphometric measurements of both the flowers and museum skins of the observed hummingbird species. The tubular corolla forces the birds (*Sappho sparganura*, *Colibri coruscans*, *Patagona gigas*, *Oreotrochilus adela*) in a specific position thereby causing pollen transfer from the exerted pollen-sacs to the bird's feathers and bills. The staminal levers are well developed but cannot be moved because the sterile arms are closely attached to the upper face of the corolla leaving no space for any movement. It is assumed that the reduction of the lever mechanism reflects an adaptation to bird pollination.

3 Bird pollination in South African *Salvia* species

3.1 INTRODUCTION

Bird pollination in the mainly melittophilous genus *Salvia* is known since about 150 years when Bridges (in Sclater 1856) described the interaction between hummingbirds and an anonymous *Salvia* species in Panama. After few further observations in the New World (Salvin 1860, Gould 1861, Müller in Hildebrand 1870, Villada 1873, Mulsant & Verreaux 1874, Waterton 1879), Scott-Elliot (1890) described a parallel pattern in the Old World with *S. africana-lutea* (Fig. 3.1 A, Ea) and its pollinator, the Cape White-eye *Zosterops pallidus*. The first impression of an approximately equal distribution of bird pollinated *Salvia* species in the two hemispheres was not confirmed in the following years. While in the New World about 200 of the nearly 600 *Salvia* species are bird pollinated (chapters 4, 5), the South African *S. africana-lutea* remained the only known ornithophilous species among the nearly 370 sages of the Old World (see Claßen-Bockhoff et al. 2003).

In the present paper we follow the question whether further South African *Salvia* species may be adapted to birds. This assumption was supported by the recently described *S. thermanum* (Van Jaarsveld 1999, 2002, 2003) with large red flowers (Fig. 3.1 C, D, Ed) that was observed to be visited by a female *Nectarinia chalybea* in the Botanical Garden Kirstenbosch (Van Jaarsveld, pers. comm). In fact, among the 23 species occurring in South Africa (Codd 1985, Van Jaarsveld 1999) *S. lanceolata* (Fig. 3.1 B) is found to be the third bird pollinated *Salvia* species.

The three ornithophilous species are endemic to South Africa (Fig. 3.2). *S. africana-lutea* is a much-branched shrub of up to 2 m in height (Fig. 3.1 A). It is found from Namaqualand to the Cape Peninsula and eastwards to Port Alfred where it grows in coastal sand dunes and on rocky slopes within arid fynbos vegetation up to 800 m altitude (Codd 1985). *S. lanceolata* occurs from Namaqualand to the Cape Peninsula and eastwards to Montagu. It is a likewise tall and branched shrub (Fig. 3.1 B) and colonises coastal sandveld and arid fynbos up to 300 m altitude (Codd 1985). *S. thermanum* is locally endemic at Goudini Spa near Worcester where it occurs in Proteaceae fynbos (Van Jaarsveld 1999). It is a perennial which renews from stolons and reaches a height of 1 m (Fig. 3.1 C).



Figure 3.1. *Salvia africana-lutea* (A), *S. lanceolata* (B) and *S. thermarum* (C, D) at their natural localities (A-C) and at Kirstenbosch National Botanical Garden (D). (E) Flower longitudinal section and (H) front view (a: *S. africana-lutea*, b: intermediate form between *S. africana-lutea* and *S. lanceolata*, c: *S. lanceolata* and d: *S. thermarum*). (F) *Nectarinia chalybea* at *S. lanceolata* (Kirstenbosch National Botanical Garden). Note the perching behaviour and the thecae touching the bird's head. (G) Illustration of pollination simulation by inserting a skin of *Nectarinia chalybea* into a flower of *S. thermarum*. Bars = 1 cm.

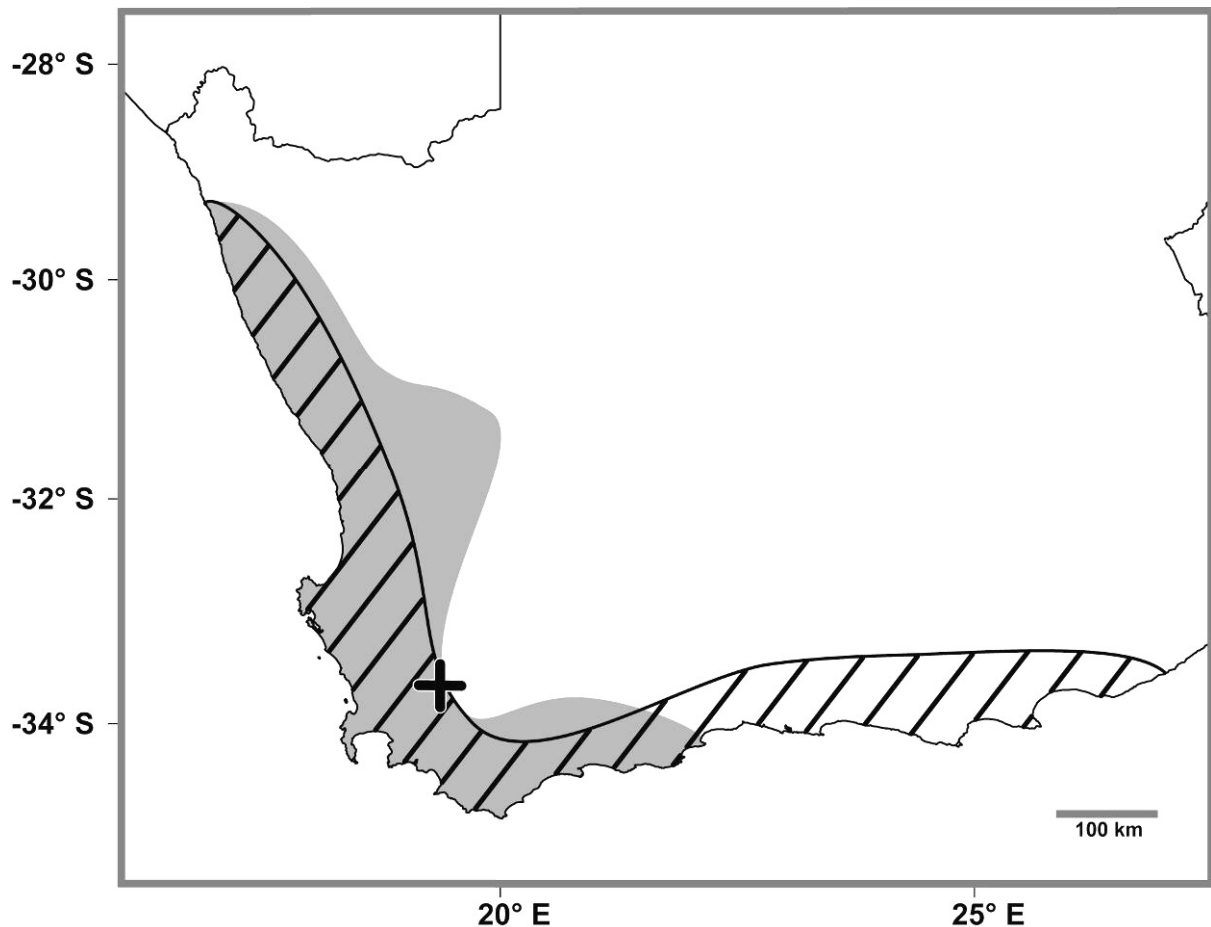


Figure 3.2. Approximate distribution ranges of *Salvia africana-lutea* (hatched), *S. lanceolata* (grey) and location of *S. thermanum* (cross) (modified after Hedge 1974, Codd 1985, Van Jaarsveld 1999).

3.2 MATERIAL AND METHODS

S. africana-lutea L. was studied at Bloubergstrand in an area of succulent fynbos vegetation (S33° 44' 54.3" E18° 26' 35.6"). *S. lanceolata* Lam. was found at Melkbosstrand, about three kilometers north of the *S. africana-lutea* locality. Individuals of intermediate characters co-occurred with *S. africana-lutea*. *S. thermanum* Van Jaarsv. was observed at its sole locality at Goudini Spa near Worcester (above the cottages of Goudini Spa, next to the fence where the Slanghoek trail starts: S33° 39' 49.7", E19° 15' 50.0"). Vouchers are deposited at MJG (*S. africana-lutea*: P. Wester 342, *S. lanceolata*: P. Wester 316, plants intermediate between *S. africana-lutea* and *S. lanceolata*: P. Wester 338, *S. thermanum*: P. Wester 312).

To reconstruct the fitting between flowers and birds, morphometric data were taken from the flowers (Fig. 3.3). Flower material was collected from natural localities, from Kirstenbosch National Botanical Garden (*S. africana-lutea*, *S.*

lanceolata, *S. thermarum*), from the Botanical Garden of the University of Mainz where *S. africana-lutea* was grown from seeds given by the Botanical Society of South Africa, and from the Strybing Arboretum San Francisco, California. Sugar concentration was measured in July/August 2005 from cultivated plants of *S. africana-lutea* and *S. thermarum* at the Botanical Garden of the University of Mainz using a hand held refractometer (Atago, Honcho/Japan: N1: 0-32 % sucrose w/w) and in October/November 2005 from cultivated plants of *S. lanceolata* and *S. africana-lutea* at Kirstenbosch National Botanical Garden using a hand held refractometer (Bellingham & Stanley, Kent/UK: Eclipse 45-81: 0-50 % sucrose w/w). Morphometric data from the birds originate from Maclean (1993).

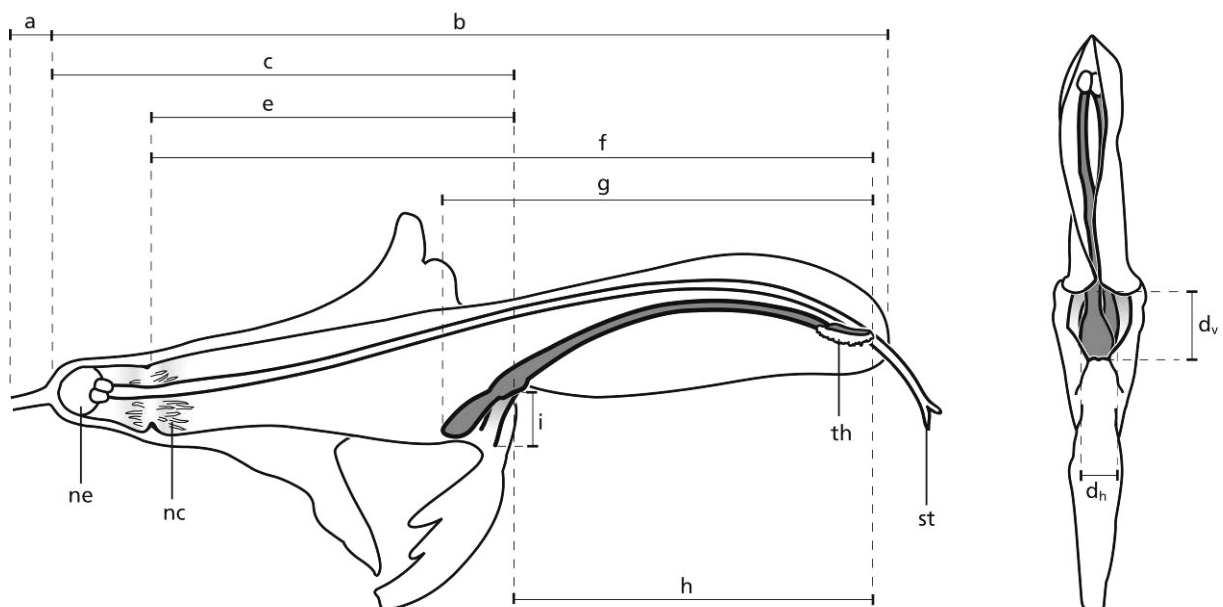


Figure 3.3. Morphometric data taken from *Salvia* flowers (a – i see Tab. 3.1). ne: nectary, nc: nectar cover, th: theca, st: stigma

Studies of bird pollination were conducted in January 2004 and October/November 2005. Flower-bird-interactions were observed at Kirstenbosch National Botanical Garden, all in all, about 25 hours on 9 days. The bird species were identified after Maclean (1993). The foraging behaviour of the birds was documented with photographs and videotapes. Colour values of the flowers follow the CMYK colour space (Küppers 1999).

To reconstruct the process of pollen transfer, pollination simulations were carried out by inserting a thin metal rod into fresh flowers mimicking a bird's bill. To

determine the maximal area of pollen deposition, the rod was inserted as deep as possible into the corolla tube and in close contact to the upper lip thus smearing along the pollen-sacs while releasing the staminal levers. The experiments were extended by using museum specimens (South African Museum, Cape Town) of the five most common nectarivorous birds of the Southwestern Cape (Cape peninsula to Worcester): *Nectarinia chalybea* L.: male, SAM ZO 538/5; *Nectarinia famosa* L.: male, SAM ZO 14929; *Nectarinia violacea* L.: male, SAM ZO 14900; *Zosterops pallidus* Swainson: female, SAM ZO 20134; *Promerops cafer* L.: male, SAM ZO 53991).

3.3 RESULTS

3.3.1 Bird pollination

S. lanceolata was observed to be pollinated by male and female juveniles and adults of the Lesser Double-collared Sunbird *Nectarinia chalybea* (Fig. 3.1 F) and the White-Eye *Zosterops pallidus*. While searching for nectar, the birds perched on the branches of the shrub. Detailed observations were made for *Nectarinia chalybea*: The birds pulled the stalked flowers with their bills upward, downward or sideward to themselves and then inserted their bill to get access to nectar. Thereby, they released the staminal lever and were loaded with pollen. The latter was usually deposited as a relatively small spot on the front head (above the eye to the forehead), but sometimes also at the onset of the bill or, more rarely, on its upper side. Time and site of pollen deposition varied with the relative position of the perching bird to the selected flower. Entering the flower more or less horizontally, the bird touched the stigma first and transferred pollen to it, only later being again loaded with pollen. If the bird inserted its bill from below, it was not always loaded with pollen and did not necessarily come into contact with the stigma. If it visited the flowers from the side, pollen was deposited laterally. Thus, though pollen was precisely transferred during the single flower-bird contact, the pollen loaded area on the pollinator increased with the number of successive visits.

Insects were never observed at the flowers except one hawk moth that neither released the lever nor pollinated the stigmas. Holes at the calyces pointed to nectar robbers.

3.3.2 Floral construction

The flowers of the three *Salvia* species studied are arranged in attractive inflorescences usually presenting several open flowers at the same time (Fig. 3.1 B, D). In *S. africana-lutea* and *S. lanceolata* attraction is increased by the dense growth form of the shrubs and the many simultaneously flowering inflorescences (Fig. 3.1 A, B). *S. thermarum*, in contrast, usually produces only one terminal inflorescence at its dominant shoot being rarely enriched by lateral inflorescences (Fig. 3.1 C, D). Flowers are always oriented towards free space. In *S. lanceolata* and *S. thermarum* they are flexibly stalked and can be pulled up by the perching birds easily.

The flowers are bilabiate with hidden thecae and exposed stigmatic lobes (Fig. 3.1 E). Though they are rather similar at the first glance, they differ in several floral characters.

- (1) The colour of the corolla ranges from yellowish to brownish in *S. africana-lutea* (M50-60 Y90-99 S30-50), to pink-violet-purplish in *S. lanceolata* (M60 C10 S10, M60-80 Y50 S40; younger flowers are also yellowish) and reddish in *S. thermarum* (Fig. 3.1). At the natural locality the latter shows more or less intensive red flowers (M90 Y60 S10) (Fig. 3.1 C), while the plants in cultivation flower paler red to pink or salmon (M50-70 Y40-60 S00) (Fig. 3.1 D). The calyx is usually green to purple-brownish, in *S. thermarum* also reddish. The flowers show no nectar guides at their corolla, but massive filaments and connective plates which sometimes contrast to the corolla by means of whitish, pink or dark brown colours (Fig. 3.1 H).
- (2) The floral proportions differ in the three species as to flower size, diameter of the floral entrance, length and form of the corolla tube, distance between the nectar cover and the flower entrance or the thecae, lengths of the connectives and filaments, relative length of the upper lip to the corolla tube, shape and orientation of the lower lip (Tab. 3.1, Fig. 3.1, 3.3). Variation is also found within the species each having smaller and larger flowers with a flower length difference of about 5 mm in *S. lanceolata* up to 14 mm in *S. africana-lutea* (Tab. 3.1).
- (3) The flowers produce much nectar by their nectary at the flower base. They contain nectar of low-concentration: *S. africana-lutea* (13.6 ± 5.5 %; $n = 42$), *S. lanceolata* (18.6 ± 3.9 %; $n = 28$) and *S. thermarum* (15.6 ± 2.4 %; $n = 39$). In *S. thermarum* nectar is adhered by the capillary forces of the thin and laterally

constricted basal part of the tube, preventing it from overflowing (Fig. 3.1 Ed). The same is true for the dense field of long hairs which is found near the nectary in *S. africana-lutea* (Fig. 3.1 Ea) and in a short distance to the nectary in *S. lanceolata* (Fig. 3.1 Ec). The latter species also has small lateral and basal corolla folds. Despite the various nectar covers, the nectar can rise up to the staminal plates in *S. africana-lutea* and *S. lanceolata* and to about half of the tube length in *S. thermanum*. Flower scent is lacking in all three species.

Table 3.1. Morphometric data of *Salvia africana-lutea*, *S. lanceolata*, *S. thermanum* and an intermediate form between *S. africana-lutea* and *S. lanceolata* (a – i see Fig. 3.3). Average and range in mm.

	<i>S. africana-lutea</i>	Intermediate form	<i>S. lanceolata</i>	<i>S. thermanum</i>
Pedicle length (a)	3.5 ± 0.5 n = 24	4.3 ± 0.6 n = 20	4.8 ± 0.8 n = 26	7.2 ± 1.1 n = 17
Flower length (b)	43.2 ± 3.4 n = 24	41.2 ± 3.4 n = 9	39.2 ± 2.0 n = 10	54.8 ± 2.8 n = 8
Length of corolla tube (c)	14.6 ± 1.1 n = 20	18.9 ± 0.9 n = 8	22.2 ± 1.0 n = 14	32.2 ± 1.9 n = 8
Flower entrance (horizontal x vertical) (d _h x d _v)	2.6 ± 0.4 x 4.0 ± 0.7 n = 19	2.4 ± 0.5 x 3.1 ± 0.3 n = 8	2.0 ± 0.3 x 3.0 ± 0.1 n = 6	4.0 ± 0.5 x 3.7 ± 0.4 n = 11
Distance flower entrance to nectar cover ¹ (e)	12.1 ± 1.0 n = 15	14.2 ± 0.8 n = 6	16.8 ± 0.9 n = 6	24.3 ± 1.8 n = 6
Distance thecae to nectar cover ¹ (f)	34.4 ± 4.0 n = 13	31.0 ± 2.3 n = 6	29.8 ± 4.9 n = 6	42.3 ± 4.7 n = 6
Length of total connective (g)	27.5 ± 3.2 n = 20	22.2 ± 1.7 n = 6	20.4 ± 1.1 n = 6	22.6 ± 1.7 n = 9
Length of upper connective arm (h)	24 ± 2.8 n = 18	18.9 ± 1.3 n = 6	16.6 ± 0.9 n = 6	17.7 ± 1.5 n = 9
Length of filament (i)	6.1 ± 1.1 n = 17	4.5 ± 0.5 n = 7	3.4 ± 0.4 n = 6	5.0 ± 0.3 n = 10

¹ hairy zone in *S. africana-lutea* and *S. lanceolata*, lateral constriction in *S. thermanum*

(4) The three species have the two lever-like modified stamens characteristic for the genus. Each connective is laterally extended and versatily fixed at its filament by a thin ligament-like tissue. The upper connective arm is placed in the upper lip. It always bears a fertile theca and presents white pollen (Fig. 3.1 E). The lower connective arm shows a poorly developed theca, sometimes with pollen. The

lower connective arms of the two stamens are not fused, but their flat ends often overlap and block the entrance of the flower tube completely (Fig. 3.1 H). A pollinator searching for nectar pushes the barrier aside whereby the upper connective arms are pressed against the pollinator and deposit pollen on it. In *S. africana-lutea* and *S. lanceolata*, the upper thecae of the two stamens are postgenitally fused. As a consequence, the two staminal levers act as a unit and show rather identical movements if being released several times in succession. The precision of pollen transfer is furthermore increased by guiding structures round the joint originating from both the filament and the connective. In *S. thermarum*, however, pollen deposition is rather imprecise. The upper thecae are free from each other. Thus, while being released the upper connectives spread from each other and often do not return to their original position. Instead, the lever arms flap around the joint during subsequent releases touching the pollinators on different parts of their body.

At Bloubergstrand individual plants were found with intermediate characters between *S. africana-lutea* and *S. lanceolata* (Fig. 3.1 Eb, Hb). Their flower colour was red-brownish, pink or salmon-yellowish (e.g. M60 Y50 S30), their corolla tubes and nectar covers resembled *S. lanceolata*, while the width of the lower lip was more similar to *S. africana-lutea*. However, the morphometric data of their flowers were not significantly different from those in *S. africana-lutea* and *S. lanceolata* (Tab. 3.1).

3.3.3 Pollination simulation

To determine the area of pollen deposition on the pollinator's body the bill was mimicked by a thin metal rod in a first experiment. The rod was inserted in such a manner that it glided along the pollen-sacs while releasing the staminal levers and got loaded with pollen until its tip reached the nectar cover. The part of the rod covered with pollen indicated the maximal range of pollen deposition on a pollinator's bill or head. Pollen was found to be deposited along a line of 9.0-15.5 mm in *S. africana-lutea* (12.1 ± 1.9 ; n=9), 13.0-16.7 mm in *S. lanceolata* (15.4 ± 1.3 ; n=6) and 18.5-30.5 mm in *S. thermarum* (24.0 ± 4.2 ; n=8). The values differed within the species because of the variable length of the flowers, and among the species because of the increasing distance between the flower entrance and the nectar cover (Tab. 3.1).

In a second experiment, pollination was simulated by inserting museum skins of *Zosterops pallidus*, *Nectarinia chalybea*, *N. violacea*, *N. famosa* and *Promerops cafer* into the flowers. The bills were inserted from different directions and to different depths, thus mimicking the variable behaviour of the birds. Pollen was loaded at the front to the rear head in the short-billed *Zosterops*, at the bill to the front head in the long-billed *Promerops* and *Nectarinia famosa*, and from the bill to the rear head in the two other *Nectarinia* species (Tab. 3.2). Keeping in mind that the length of the bills and the size of the flowers varied, the maximal range of pollen deposition was even larger (Tab. 3.2).

Table 3.2. Area of pollen deposition of *Salvia africana-lutea*, *S. lanceolata* and *S. thermarum* on the skins of different bird species (in brackets: area of pollen deposition considering different bill lengths and flower sizes). bl = bill lengths (after Maclean 1993)

	<i>S. africana-lutea</i>	<i>S. lanceolata</i>	<i>S. thermarum</i>
<i>Zosterops pallidus</i> bl: 9 – 15 mm	middle to rear head	front to middle head	(front to) rear head
<i>Nectarinia chalybea</i> bl: 17 – 24 mm	(bill to) front to middle head	(bill to) front to middle head	(bill to) onset of bill to middle head
<i>Nectarinia violacea</i> bl: 20 – 23 mm	(bill to) front to middle head	bill to front head (to middle head)	(bill to) onset of bill to rear head
<i>Nectarinia famosa</i> bl: 29.5 – 34.5 mm	bill (to front head)	bill (to front head)	bill to front head (to middle head)
<i>Promerops cafer</i> bl: 28 – 34.7 mm	bill to onset of bill (to front head)	bill (to front head)	bill to front head (to middle head)

3.4 DISCUSSION

3.4.1 The ornithophilous syndrome in South African *Salvia* species

Birds are observed to be pollinators of *S. lanceolata*. Together with *S. africana-lutea* (Scott-Elliott 1890, Schmidt 1964, Brieschke 1991) and *S. thermarum* (Van Jaarsveld, pers. comm), three South African sages are now identified to be bird pollinated. The findings do not come unexpected because the three species agree in some typical ornithophilous characters. Flowers are conspicuously coloured, though the bright red colour characteristic for many bird pollinated sages of the New World is matched only by *S. thermarum*. The entrance of the flowers is small (Tab. 3.1), thus excluding bees entering the flower, but granting access for the birds' bills. The distance between nectar cover and pollen is large enough to guarantee pollen deposition on

the bird's head instead of on its smooth bill. The lower lips are reduced or reflexed (Fig. 3.1 E), offering no landing platform for insects but facilitating nectar drinking for birds (Faegri & van der Pijl 1971, Westerkamp 1990). The plants offer enough room to reach the flowers which, on their part, are oriented towards free space. Perching birds are able to reach several flowers from a given position which is facilitated by the long and flexible pedicels in *S. lanceolata* and *S. thermarum* (see Tab. 3.1). Though *Nectarinia chalybea* was observed to hover at some flowers (e.g. *Salvia* spp.: Burchell 1822, Paterson 1958), in this study it only was observed to perch when drinking nectar - as it is common for most of the Old World flower birds (van der Pijl 1937, Westerkamp 1990). A noticeable flower scent and conspicuous nectar guides are missing. A high volume of nectar is offered, which was found to be of low concentration (for *S. africana-lutea* see also Vogel 1954).

Comparing the three species (Fig. 3.1 E), *S. africana-lutea* appears to be least of all adapted to birds. The yellowish-brown flower colour is not very conspicuous and the flower tube is short, probably not absolutely excluding insects. In contrast, the long flower tube in *S. thermarum* only allows birds to exploit nectar which are attracted by the bright red colour.

3.4.2 Flower-bird interactions

Though the single lever movements act rather precisely, pollen deposition in general is imprecise. Reasons are the different flower sizes within a species and even within an individual plant, the different foraging behaviour by the birds predominantly caused by perching and, in *S. thermarum*, the unsufficiently fixed lever arms.

The larger the pollen loaded area on a bird, the higher the chance that pollen is received by the stigmatic lobes of the exposed style. Thus, imprecise pollen deposition may increase the chance of getting pollinated within a given *Salvia* population. However, it likewise increases the chance of receiving unspecific pollen in the case of pollinator sharing by co-occurring species.

As to the distribution ranges of the three *Salvia* species (Fig. 3.2), those of *S. africana-lutea* and *S. lanceolata* broadly overlap in the western Cape, while the locally endemic *S. thermarum* occurs about 10 km (Van Jaarsveld, pers. comm.) away from the next localities of the other two *Salvia* species. However, this distance may be ignored in view of the migration movements of nectarivorous birds (Schmidt

1964, Skead 1967). Referring to the distributions of the three *Salvia* species, common nectarivorous birds are: *Nectarinia chalybea*, *Zosterops pallidus*, and *Promerops cafer*. These three species represent the range of possible pollinator sizes and bill lengths (Fig. 3.4), as all other nectarivorous birds in the area, e.g. *Nectarinia violacea*, *N. famosa*, *N. afra* L., *N. amethystina* Shaw, *N. veroxii* Smith, *N. fusca* Vieillot and *Anthreptes collaris* Vieillot, are intermediate.

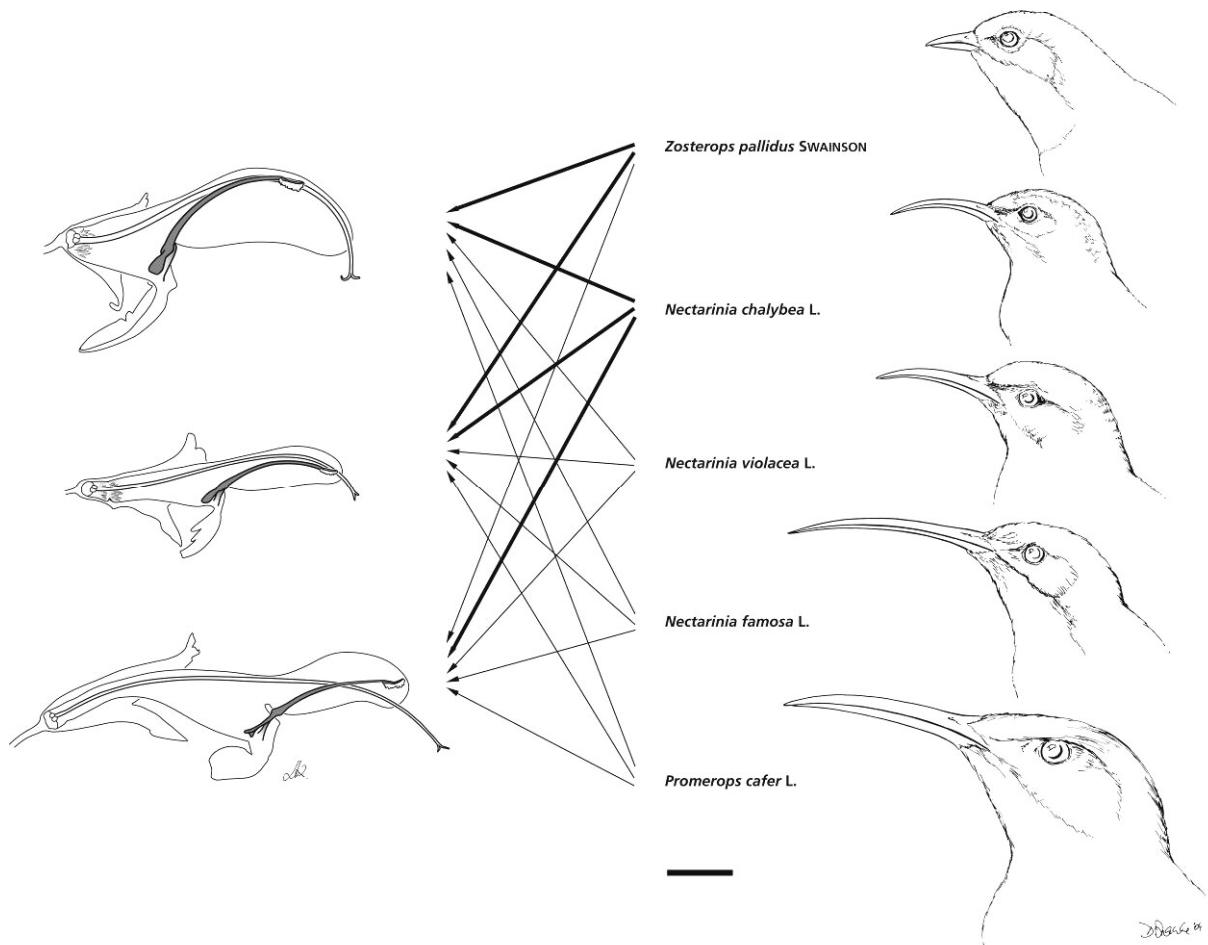


Figure 3.4. Flower-bird interactions in South African *Salvia* species.

Left: longitudinal sections of *Salvia africana-lutea* (above), *S. lanceolata* (middle) and *S. thermarum* (below). Right: selected flower birds of the South Western Cape. Bold arrows: flower visits observed (original data; Van Jaarsveld, pers. comm., Scott-Elliott 1890, Schmidt 1964, Brieschke 1991), thin arrows: pollination possible according to morphometric data and distribution areas. Bar = 1 cm.

Nectarinia chalybea was observed at each of the three *Salvia* species (see also Schmidt 1964, Brieschke 1991). *Zosterops pallidus* was observed pollinating *S. africana-lutea* (Scott-Elliott 1890) and *S. lanceolata*, and *N. afra* visiting the flowers of *S. africana-lutea* in the Eastern Cape (Brieschke 1991). The simulation experiments

indicate that indeed all bird species may be pollinators. However, some birds fit better to some *Salvia* species than others. The short-billed *Zosterops pallidus* for instance might fit best to the short-tubed *S. africana-lutea* and *S. lanceolata*, while the longer-billed *Nectarinia chalybea* and *N. violacea* may be adequate pollinators for each of the three *Salvia* species (Tab. 3.1). The long-billed *Nectarinia famosa* and *Promerops cafer* might be (if at all) less effective pollinators. A large part of the pollen would be deposited on their smooth bills which are regarded as a less effective medium for pollen transfer compared to feathers (Grant & Grant 1968, Kugler 1970, Faegri & van der Pijl 1971, Rose 1990, Arizmendi et al. 1996). As regards *Promerops cafer* the species predominantly prefers Proteaceae (Levaillant 1808, Skead 1967) and probably will not visit sages at all.

The morphometric fitting between flowers and birds support the assumption that pollen of different *Salvia* species may be mixed in case of co-occurrence and pollinator sharing. All birds tested (and probably other species) are able to transfer pollen among each of the three *Salvia* species (Figs. 3.1 F,G, 3.4, Tab. 3.2). Moreover, the sites of pollen deposition of the *Salvia* species overlap on each bird species. The more flowers are exploited the larger the pollen spots on the pollinator and the higher the probability of unspecific pollen transfer. Even if pollen is not mixed on the pollinator, unspecific pollen may be removed by the stigma which acts less precisely than the staminal levers.

In view of the capability of *Salvia* species to hybridise (e.g. Kerner von Marilaun 1891, Hrubý 1935, Epling 1947a, Emboden 1971, Hedge 1982, Wood & Harley 1989, Wester & Claßen-Bockhoff 2002, Claßen-Bockhoff et al. 2004b), the intermediate forms between *S. africana-lutea* and *S. lanceolata* deserve special attention. They may be either phenotypically diverse representatives of one of these species, or hybrids between the two. Both species are indeed described as highly variable, but in spite of their variability they have clear diagnostic characters (Hedge 1974, Codd 1985). However, the intermediate forms co-occurring with *S. africana-lutea*, show many characters in between the two species (Tab. 3.1, Fig. 3.1 Eb, Hb) and are not clearly identifiable. As hybrids are also known from the South African *S. albicaulis* Benth. x *S. granitica* Hochst. and from *S. lanceolata* Lam. x *S. africana-caerulea* L. (Van Jaarsveld 2002), hybrids between *S. africana-lutea* and *S. lanceolata* should be expected.

3.4.3 Phylogenetic considerations

S. africana-lutea and *S. lanceolata* belong to section Hymenospace (Bentham 1848) and were grouped into 'species group G' by Hedge (1974). According to Van Jaarsveld (1999) *S. thermarum* superficially resembles the first two species, but based on morphological characters it is related to the bee pollinated *S. granitica* Hochst. (Hedge's 'species group M'). Sufficient molecular data are still lacking so that we actually cannot elucidate the phylogenetic relationship between the species (see Walker et al. 2004). Proceeding from the assumption that bird flowers derived from bee flowers (Grant & Grant 1965) at least two scenarios are conceivable: the transition from bee to bird pollination happened only once and the three bird pollinated species thus form a monophyletic clade, or the three ornithophilous species have bee pollinated sister groups, so that bird pollination evolved several times in parallel.

Whereas the New World sages often force the birds in a specific position by their long and narrow corolla tubes and might even reduce the lever mechanism and expose the thecae (chapters 2, 5), the South African bird pollinated sages resemble melittophilous species in having bilabiate flowers and pollen-sacs hidden in the upper lip. The latter unquestionably demands a well functioning lever mechanism for successful pollen transfer. As in South Africa, the ornithophilous *Salvia* species are pollinated by perching birds which often enter the flowers without necessarily touching the thecae (Fig. 3.1 G), a mechanism for lowering the pollen-sacs might be advantageous for pollination. Likewise, the progression to exclude bees by long corolla tubes, which is observed from *S. africana-lutea* to *S. lanceolata* and to *S. thermarum* (Tab. 3.1), might ensure pollination. The longer the floral tube, the more precise is the bird's position relative to the pollen-sacs and stigmas.

The finding of more bird pollinated *Salvia* species in South Africa raises the question of any further ornithophilous species in the Old World. Based on morphological characters (Hedge 1974, 1998; photos provided by P. Phillipson) we expect at least one ornithophilous species in Madagascar (*S. sessilifolia* Baker), but no further ones in Africa and Asia except perhaps in China. One reason for the few ornithophilous *Salvia* species in the Old World might be that the distributions of sages and nectarivorous birds only partly overlap (Fig. 3.5). Moreover, there are generally only few *Salvia* species distributed in the areas shared with nectarivorous birds (e.g. Hedge 1974, 1986). The most prominent exceptions, however, are South

Africa with 23 species (Codd 1985, Van Jaarsveld 1999) and China, esp. Yunnan and Sichuan with about 50 species (Hsi-wen & Hedge 1994). Based on morphological characters, there might be some Chinese species being pollinated by birds, but records are completely lacking.



Figure 3.5. Approximate global distribution of *Salvia* (green; hatched: bird pollinated species) and of the most important nectarivorous birds (south of the bold line: Nectariniidae, Zosteropidae, Promeropidae, Dicaeidae, Meliphagidae, Trochilidae; modified after Baikova 1996, Hedge 1986; Moreau & Kikkawa 1985, Salomonsen & Ford 1985, Schuchmann 1999, Cheke & Mann 2001.). The presence of *Salvia* in Australia and the South East Asian islands may be due to anthropogenic activity.

SW-China, Madagascar and the Cape Floristic Region of South Africa belong to the most species rich areas of the world (Jolly et al. 1984, Wu & Wu 1996, Barthlott et al. 1999, Linder 2003). In these areas, geographical and ecological isolations, habitat diversity and geological and climatic changes during the past have promoted adaptive radiations in many lineages. In closing, it is not surprising that the sages are also involved in these radiations – though their evolutionary history is not yet well understood.

3.5 SUMMARY

Approximately one fourth of the more than 900 world-wide distributed *Salvia* species (Lamiaceae) is ornithophilous. With few exceptions they occur in the New World, being predominantly pollinated by hummingbirds. In the Old World only *S. africana-lutea* and the recently described *S. thermarum*, both from the Cape Province of South Africa, were observed to be pollinated by sunbirds and white-eyes. Among the 23 South African *Salvia* species *S. lanceolata* is a further candidate for being bird pollinated. For the first time its pollination by *Nectarinia chalybea* and *Zosterops pallidus* is described and illustrated. The ornithophilous syndrome of the three mentioned *Salvia* species is compared. Their flowers are related to the morphological fitting of the most common nectarivorous birds of the Southwestern Cape (Cape peninsula to Worcester). It is concluded that each of the birds could act as a pollinator and that the three co-occurring *Salvia* species are not mechanically isolated from each other. The degree of specialisation towards bird pollination, possible hybridisation events and evolution of bird pollination in South African *Salvia* species are discussed.

4 Pollination syndromes of New World *Salvia* species with special reference to bird pollination

4.1 INTRODUCTION

Historically, the genus *Salvia* ('sage', approx. 1000 spp.; Lamiaceae) was associated with bee pollinated species like the European *S. pratensis* L. and *S. officinalis* L. at which Sprengel (1793) for the first time observed pollen transfer by means of the spectacular staminal lever mechanism (see Claßen-Bockhoff et al. 2003). Today, this Europe-centred point of view has become inadequate because not only two thirds of all *Salvia* species occur in the New World, but also bird pollinated species which largely lack in the Old World (Alziar, 1988-1993; chapters 2, 3). Morphological investigations (Himmelbaur and Stibal 1932-1934, chapter 5) and phylogenetic data (Walker & Sytsma 2007) indicate that the bird pollinated *Salvia* species may have evolved several times in parallel (Reisfield 1987, chapter 5). The phylogenetic and ecological constraints underlying the shifts from one pollination syndrome to the other are reconstructed, especially from bee to bird flowers (see also Grant & Grant 1965, Reisfield 1987, Baumberger 1987, chapter 5).

Bird flowers in *Salvia* have been known for about 150 years (Sclater 1856), but up to now their number, distribution and floral diversity are largely unknown. To get a general idea, the concept of pollination syndromes ('Stiltypen' = floral styles) is used as a reference framework. According to Vogel (1954) a pollination syndrome is defined as a specific combination of floral traits having evolved in adaptation to a special pollinator guild (see also Faegri & van der Pijl 1971). Although recently being criticised (Ollerton 1996, Waser et al. 1996), it is taken as a helpful tool to roughly assign flowers to syndromes. This assignment is regarded as a hypothesis that has to be verified by field observations.

There are many reports on bees as pollinators (e.g. Hildebrand 1865, Grant & Grant 1964, Kugler 1972, Hedström 1985, Dieringer et al. 1991, Claßen-Bockhoff et al. 2004b), which are certainly the dominant pollinator group in *Salvia*. Only rarely, other insects like butterflies, moths or flies were observed or just assumed to be pollinators (Sprengel 1793, Hildebrand 1865, Müller in Möller 1921, Read 1983, Faegri & van der Pijl 1971, Grases & Ramírez 1998, Potgieter & Edwards 2001,

Fenster et al. 2004, chapters 2, 3). With the exception of four Old World species (chapter 3), bird flowers appear to be restricted to the New World (Delpino 1868-1874, Trelease 1881, Cruden et al. 1983, Reisfield 1987, Ramamoorthy & Elliott 1998, chapter 2). In the latter, hummingbirds are the most important flower visitors (e.g. Salvin 1860, Wagner 1946, Grant and Grant 1968, chapter 2, but see Torke 2000 for *Coereba flaveola* L.).

Assuming a gradual transition between pollination syndromes, for instance between bee and bird pollinated flowers, it is impossible to clearly discriminate between different groups. To determine nevertheless the number of bird pollinated sages in the New World, only four groups are roughly distinguished: one including definite bird flowers, one including unambiguous bee flowers, one including butterfly flowers, and one including all flowers of uncertain affiliation. We then focus on the bird pollinated species and present their floral characteristics illustrating that there is much more than just one 'typical' bird flower in *Salvia*. Finally, the group of the 'intermediates' is discussed with respect to their evolutionary and ecological significance and the value of the pollination syndromes is critically reconsidered.

4.2 MATERIAL AND METHODS

4.2.1 *Salvia* species

In the present study 591 *Salvia* species are included. The data derive from observations at wild and cultivated plants, and are complemented by data from herbarium specimens and the literature.

During field studies in Bolivia (2-4/2002), Mexico and Guatemala (10-12/2003) and the USA (4-6/2004) more than 100 species were observed in their natural habitats, among them 33 ornithophilous species, one psychophilous and 13 intermediate ones.

More than 100 species, among them a total of 65 ornithophilous and intermediate species, were examined in cultivation at the following places:

- Botanical Gardens: Mainz (mainly collected during the own field trips or by A. Schmidt-Lebuhn in Peru and Ecuador, University of Halle, Germany) and Hamburg (both Germany), Berkeley, Rancho Santa Ana, Riverside, The Huntington, Fullerton Arboretum (CA, USA), Chihuahuan Desert Gardens (El Paso, TX, USA),

- nurseries: E. Hügin (Freiburg, Germany), 'Native by native Landscapes' (Johnson City, TX, USA),
- private gardens: F. Berndt (Cochabamba, Bolivia), B. Clebsch (Santa Cruz, CA, USA) and M. Dimmitt (Tucson, AZ, USA).

Fresh flowers were fixed in 70% ethanol for further investigations. Vouchers of the investigated ornithophilous species and all species presented in detail are deposited at MJG, some duplicates of them in B, BIGU, JEPS, K, LPB, MEXU, TEX and UCR (Appendices 1, 2).

Herbarium specimens originated from B, C, COL, COLO, F, FLAS, G, GH, GOET, H, HAO, HUT, K, L, LD, MEXU, MJG, MO, NY, OAX, P, TEX-LL, S, SD, UC-JEPS, UCR, US, W and WU (see Appendices 1, 2).

Species were identified by means of the most recent literature (Appendices 1, 2) and with the aid of J. Wood (OXF), A. Vázquez (IBUG), A. Espejo (UAMIZ), H. Vibrans (CHAPA), M. Véliz (BIGU), C. Froissart (Olivet, France) and A. Sanders (UCR). The determination of herbarium specimens was also checked and only type material and clearly determined specimens were used. As there is no actual revision of *Salvia* subgenus *Calospatha* available, species with an unclear taxonomic status are not included (partly listed as 'nomen dubium' by Epling 1939), as well as still undescribed species (e.g. the two Mexican ornithophilous *S. subbalakshiana* Ramamoorthy and *S. nicolsoniana* in ed. by M. García & E. Martínez; new species found by the author) and probable hybrids originated from cultivation (*S. ianthina* Otto & Dietr.).

4.2.2 Methods

The group of pollinators was inferred from visitor observations and from floral characters pointing to the particular syndrome (Vogel 1954, Faegri & van der Pijl 1971).

Species were identified as **ornithophilous** when bees were either excluded by long corolla tubes or couldn't be loaded with pollen because of the reproductive organs were exerted too far. Ornithophilous flowers often have reduced or reflexed lower lips, unstable or no landing platforms for insects, red colour and a large volume of nectar with a low sugar concentration.

Species were identified as **melittophilous** when they have short corolla tubes

and stable lower lips offering a landing platform. If pollen-sacs are exposed, their exposition is only to such an extent that bees can be touched. Nectar guides and a small volume of nectar with a high sugar concentration also characterise bee pollinated flowers.

Psychophilous flowers have long and relatively narrow corolla tubes with a landing platform formed by the discoidally arranged salverform lips ('Stieltellertyp'). The distance between nectar and the reproductive organs is large. Nectar guides and a more or less sweet scent may be present.

Not all species investigated fit to the three mentioned syndromes because they combine characters of different syndromes, are so variable (e.g. in flower size) that they fit to different syndromes (e.g. ranging from melittophily to ornithophily), or are too little known to be grouped.

Observations of floral visitors including birds, bees, butterflies, hawkmoths and flies were made in the field and in the Botanical Gardens of Berkeley, Rancho Santa Ana, Riverside and Fullerton Arboretum as well as a private garden in Cochabamba (F. Berndt, Bolivia; see also chapters 2, 5).

The birds were determined after Schuchmann (1999) and with the help of J.F. Ornelas and C. González (both from Instituto de Ecología, Xalapa, Mexico), M. Ordano (Universidad Nacional Autónoma de México, México City, Mexico), O. Reyna (Universidad de Guadalajara, Mexico) and G. Stiles (Universidad Nacional de Colombia, Bogotá, Colombia).

To test the fit between flowers and birds, the bill was simulated by inserting either a museum skin or a metal rod into fresh flowers. The skins were borrowed from the ZFMK (Alexander Koenig Research Institute and Museum of Zoology, Bonn, Germany) and the CBF (Colección Boliviana de Fauna, La Paz, Bolivia).

To identify the pollination syndrome floral structures were morphologically investigated and measured morphometrically: The length of the flower was measured from the proximal end of the flower to the distal end of the upper lip, the length of the flower tube from the proximal end of the flower to the flower entrance, the upper lip from its distal end to the flower entrance. As the position of the lower lip is important for excluding bees, it was classified as being 'reflexed' when bent downward more than 90°, 'deflexed' when bent downward about 90° and 'antrorse' when only slightly or not bent downward (<90° to 0°). It was noted when the lower and the upper lips are oriented close to each other (lengthening the tube), or when

the lateral lobes of the lower lip were vertically, rather than horizontally oriented. The lower lip was called 'cup-shaped' when its apical margins were incurved. Flower shape was classified as 'bilabiate' when the lips were dominant compared to the tube, and 'tubular' when the tube was dominant or when the lips functionally lengthen the tube. Flowers with a combination of both shape characters were classified as 'in-between'.

Structures for nectar retention at the base of the flower were classified as definite constrictions (emarginations, folds) of the corolla wall, definite (papillae) or weak outgrowths of the corolla wall (ridges) and hairs. The posterior lever arms, reaching in the proximal part of the flower, may also contribute to nectar retention. The functional flower types refer to the functionality of the staminal lever mechanism (for more details see chapter 5). I: species with working staminal lever mechanism and thecae enclosed by the upper lip. II: species with no lever mechanism showing diversity in the position of thecae and functionality of the joint (H, E, T, S). III: species with working lever mechanism and thecae exposed, varying in the number of fertile thecae and in the functionality of the joint (R, E, L). 'Thecae exertion' means the distance between the distal end of the upper lip to the distal end of the thecae.

The colour of the corolla was determined after the CMYK colour space (Küppers 1999). Colour data from the literature are often not well defined and subjective because of different definitions of different authors. Therefore colour descriptions were classified as follows: red includes all colorations from scarlet, claret, roseate to orange-red, pink includes rose and magenta, purple includes crimson, lavender includes light violet, blue includes royal blue, dark violet includes almost black. If more than one colour is mentioned, the species has colour morphs or is defined in different ways. To get a survey, all *Salvia* species were grouped in one of the following classes: (a) yellow and orange, (b) red, orange and yellow, (c) red, (d) red, purple and pink, (e) purple, pink and lavender (f) blue and dark violet and (g) white. Flowers which were not assignable to these classes because they include combinations with brownish-ochre, red-brown, violet or pale violet, were grouped separately. In the case of colour morphs the most frequent colour was used.

Floral nectar was measured from cultivated plants in the Botanical Garden of the University of Mainz, usually in the morning at the first day of anthesis. Sugar concentration was determined using hand held refractometers (Atago, Honcho/Japan: N1: 0-32 % and N2: 28-62 % sucrose w/w and Bellingham & Stanley,

Kent/UK: Eclipse 45-81: 0-50 % sucrose w/w). The volume of nectar was measured with a 25 µl-microsyringe (ILS, Stützerbach, Germany).

Data on growth forms mainly were based upon the literature (see Appendix 1) and complemented by own observations. As the growth form concept, valid for temperate regions, is partly inadequate for (sub-)tropical plants, the plants were only roughly classified, mentioning more than one growth form if necessary.

4.3 RESULTS

Within the 591 examined New World sages 182 species (30.8 %) are identified as ornithophilous, 343 species (58 %) as melittophilous, only one species (0.2 %) as psychophilous and the remaining ones (11 %) as intermediate or not assignable because of lacking data (see Appendix 3; Tab. 4.1).

4.3.1 Ornithophilous species

In terms of **systematics**, most of the New World ornithophilous sages belong to the widespread subgenus *Calospatha* (177 spp. in 56 sections). Three species belong to the section *Heterospatha* (Arizona to central Mexico), *S. spathacea* (California) to the section *Audibertia* and *S. penstemooides* (Texas) is placed in the section *Euspatha* (see Appendix 3).

The ornithophilous sages show a wide **distribution** in the New World, reaching from California to Chile and Argentina (Fig. 4.1, Appendix 3). Comparing the different countries, Mexico has the largest number of ornithophilous species (56 spp.) and ornithophilous endemics (49 spp.). However, considering the total number of *Salvia* species within the country (about 300 spp., largest species number within a country), the relative number of the ornithophilous species is relatively low (about 19 %) compared to other countries.

Centres of diversity of the bird pollinated species are: (i) the central and southern highlands of Mexico and Guatemala, (ii) the northern part of the South American Andes (Ecuador, Peru, Colombia), where the many species only occur in a part of the corresponding country being largely missing in areas with Amazonian lowland rainforest or deserts, and (iii) South Eastern Brazil where 25 of the 35 Brazilian species occur, being all endemic to Brazil. Relating to the country area El Salvador, Haïti (only endemics), Guatemala, the Dominican Republic and Costa Rica

Table 4.1. Pollination syndromes of New World *Salvia* species.**ornithophilous** (182 spp.)

see Appendix 3

melittophilous (343 spp.)

S. aequidistans Fernald, *S. agnes* Epling, *S. alamosana* Rose, *S. alariformis* L.O.Williams, *S. alba* J.R.I.Wood, *S. albiflora* M.Martens & Galeotti, *S. albocaerulea* Linden, *S. aliciae* E.P.Santos, *S. alvajaca* Oerst., *S. amarissima* Ortega, *S. amissa* Epling, *S. amplifrons* Briq., *S. anastomosans* Ramamoorthy, *S. anguicomma* Epling, *S. angulata* Benth., *S. apiana* Jeps., *S. aratocensis* (J.R.I.Wood & Harley) Fern.Alonso, *S. areolata* Epling, *S. aridicola* Briq., *S. arizonica* A.Gray, *S. arthrocoma* Fernald, *S. assurgens* Kunth, *S. austromelissodora* Epling & Játiva, *S. axillaris* Moç. & Sessé ex Benth., *S. axilliflora* Epling, *S. azurea* Michx. ex Lam., *S. ballotiflora* Benth., *S. betonica* Schult., *S. biserrata* M.Martens & Galeotti, *S. boegei* Ramamoorthy, *S. bogotensis* Benth., *S. borjensis* E.P.Santos, *S. brachyodonta* Briq., *S. brachyphylla* Urb., *S. brandegeei* Munz, *S. breviflora* Moç. & Sessé & ex Benth., *S. brevipes* Benth., *S. caaguazuensis* Briq., *S. cabonii* Urb., *S. calaminthifolia* Vahl, *S. calcicola* Harley, *S. californica* Brandegee, *S. calolophos* Epling, *S. campicola* Briq., *S. candicans* M.Martens & Galeotti, *S. capillosa* Epling, *S. cardenasii* J.R.I.Wood, *S. cardiophylla* Benth., *S. carduea* Benth., *S. caudata* Epling, *S. caymanensis* Millsp. ex Uline, *S. cedrosensis* Greene, *S. cerradicola* E.P.Santos, *S. chalarothyrsa* Fernald, *S. chamaedryoides* Cav., *S. chapalensis* Briq., *S. chicamochae* J.R.I.Wood & Harley, *S. chionophylla* Fernald, *S. clarendonensis* Britton, *S. clinopodioides* Kunth, *S. coahuilensis* Fernald, *S. codazziana* Fern.Alonso, *S. cognata* Urb. & Ekman, *S. collinsii* Donn.Sm., *S. columbariae* Benth., *S. comayaguana* Standl., *S. compsostachys* Epling, *S. congestifolia* Epling, *S. connivens* Epling, *S. consimilis* Epling, *S. consobrina* Epling, *S. cordata* Benth., *S. corrugata* Vahl, *S. costaricensis* Oerst., *S. coulteri* Fernald, *S. crucis* Epling, *S. cruckshanksii* Benth., *S. cryptodonta* Fernald, *S. cuatrecasana* Epling, *S. curta* Epling, *S. curticalyx* Epling, *S. cuspidata* Ruiz & Pav., *S. cyanantha* Epling, *S. cyanicalyx* Epling, *S. cyanotropha* Epling, *S. dasycalyx* Fernald, *S. decumbens* Alain, *S. decurrens* Epling, *S. densiflora* Benth., *S. dorrii* (Kellogg) Abrams, *S. drymocharis* Epling, *S. dryophila* Epling, *S. durantiflora* Epling, *S. durifolia* Epling, *S. duripes* Epling & Mathias, *S. emaciata* Epling, *S. engelmanni* A.Gray, *S. eplingiana* Alziar, *S. eriocalyx* Bertero ex Roem. & Schult., *S. exilis* Epling, *S. expansa* Epling, *S. fallax* Fernald, *S. farinacea* Benth., *S. fernaldii* Standl., *S. festiva* Epling, *S. filifolia* Ramamoorthy, *S. filipes* Benth., *S. firma* Fernald, *S. flaccida* Fernald, *S. flaccidifolia* Fernald, *S. flocculosa* Benth., *S. fluviatilis* Fernald, *S. forreri* Greene, *S. fracta* L.O.Williams, *S. fruticulosa* Benth., *S. fusca* Epling, *S. fuscomanicata* Fern.Alonso, *S. glabra* M.Martens & Galeotti, *S. glechomifolia* Kunth, *S. goldmanii* Fernald, *S. gracilipes* Epling, *S. grisea* Epling & Mathias, *S. griseifolia* Epling, *S. guadalajarensis* Briq., *S. haitiensis* Urb., *S. hamulus* Epling, *S. helianthemifolia* Benth., *S. herbacea* Benth., *S. hermesiana* Fern.Alonso, *S. heterofolia* Epling & Mathias, *S. heterotricha* Fernald, *S. hintonii* Epling, *S. hirsuta* Jacq., *S. hispanica* L., *S. hotteana* Urb. & Ekman, *S. humboldtiana* F.Dietr., *S. igualensis* Fernald, *S. inconspicua* Benth., *S. incumbens* Urb. & Ekman, *S. incurvata* Ruiz & Pav., *S. indigocephala* Ramamoorthy, *S. infusca* Epling, *S. innoxia* Epling & Mathias, *S. inornata* Epling, *S. intonsa* Epling, *S. jacobi* Epling, *S. jaimehintoniana* Ramamoorthy, *S. jamaicensis* Fawc., *S. jaramilloi* Fern.Alonso, *S. keerlii* Benth., *S. lachnostachys* Benth., *S. laevis* Benth., *S. lamiifolia* Jacq., *S. langlassei* Fernald, *S. languidula* Epling, *S. lanicalyx* Epling, *S. lasiocephala* Hook. & Arn., *S. lavanduloides* Kunth, *S. laxispicata* Epling, *S. leninae* Epling, *S. lenta* Fernald, *S. leptostachys* Benth., *S. leucochlamys* Epling, *S. leucophylla* Greene, *S. longifolia* Willd., *S. longispicata* M.Martens & Galeotti, *S. lophanthoides* Fernald, *S. loxensis* Benth., *S. lozani* Fernald, *S. lycioides* A.Gray, *S. lyrata* L., *S. malvifolia* Epling & Játiva, *S. manantlanensis* Ramamoorthy, *S. manaurica* Fern.Alonso, *S. mazatlanensis* Fernald, *S. melissodora* Lag., *S. mellifera* Greene, *S. mexiae* Epling, *S. micrantha* Vahl, *S. minarum* Briq., *S. misella* Kunth, *S. mocinoi* Benth., *S. monantha* Brandegee ex Epling, *S. monclovensis* Fernald, *S. moniliformis* Fernald, *S. montecristina* Urb. & Ekman, *S. mornicola* Urb. & Ekman, *S. mucidiflora* Fernald, *S. munzii* Epling, *S. muscarioides* Fernald, *S. nana* Kunth, *S. nepetoides* Kunth, *S. nervosa* Benth., *S. nitida* Benth., *S. oblongifolia* M.Martens & Galeotti, *S. obtorta* Epling, *S. occidentalis* Sw., *S. occidua* Epling, *S. occultiflora* Epling, *S. ocimifolia* Epling, *S. oligantha* Dusén, *S. ophiocephala* J.R.I.Wood, *S. oreopola* Fernald, *S. ovalifolia* St. Hil. ex Benth., *S. pachypoda* Briq., *S. palifolia* Kunth, *S. pallida* Benth., *S. palmeri* A.Gray, *S. pamplonitana* Fern.Alonso, *S. pannosa* Fernald, *S. paposana* Phil., *S. paraguariensis* Briq., *S. parciflora* Urb., *S. parryi* A.Gray, *S. paupercula* Epling, *S. penduliflora* Epling, *S. pennellii* Epling, *S. perblanda* Epling, *S. peregrina* Epling, *S. perlucida* Epling, *S. perplicata* Epling, *S. personata* Epling, *S. pineticola* Epling, *S. pinguiifolia* (Fernald) Woot. & Standl., *S. pinosiana* Gladkova, *S. platycheila* A.Gray, *S. platyphylla* Briq., *S. plurispicata* Epling, *S. podadena* Briq., *S. polystachya* Ortega, *S. potus* Epling, *S. praeterita* Epling, *S. prasiifolia* Benth., *S. primuliformis* Epling, *S. procurrens* Benth.,

Table 4.1 (cont.).

melittophilous (cont.)
<i>S. propinqua</i> Benth., <i>S. prostrata</i> Hook.f., <i>S. pruinosa</i> Fernald, <i>S. prunelloides</i> Kunth, <i>S. prunifolia</i> Fernald, <i>S. pseudocomosa</i> Epling, <i>S. pseudoincisa</i> Epling, <i>S. pseudomisella</i> Moran & G.A.Levin, <i>S. pseudopallida</i> Epling, <i>S. pseudoprivoides</i> Epling, <i>S. pseudoserotina</i> Epling, <i>S. pteroura</i> Briq., <i>S. purpusii</i> Brandege, <i>S. pusilla</i> Fernald, <i>S. quercetorum</i> Epling, <i>S. ramamoorthyana</i> Espejo, <i>S. ramosa</i> Brandege, <i>S. raymondii</i> J.R.I.Wood, <i>S. reflexa</i> Hornem., <i>S. reitzii</i> Epling, <i>S. remissa</i> Epling, <i>S. remota</i> Benth., <i>S. reptans</i> Jacq., <i>S. rhinosina</i> Griseb., <i>S. rhombifolia</i> Ruiz & Pav., <i>S. rhyacophila</i> Epling, <i>S. roscida</i> Fernald, <i>S. rosmarinoides</i> A.St.-Hil. ex Benth., <i>S. rostellata</i> Epling, <i>S. rubiginosa</i> Benth., <i>S. rubropunctata</i> B.L.Rob. & Fernald, <i>S. rupicola</i> Fernald, <i>S. rypara</i> Briq., <i>S. rzedowskii</i> Ramamoorthy, <i>S. saccifera</i> Urb. & Ekman, <i>S. sacculus</i> Epling, <i>S. sanctae-luciae</i> Seem., <i>S. sapinea</i> Epling, <i>S. sarmentosa</i> Epling, <i>S. scaposa</i> Epling, <i>S. scoparia</i> Epling, <i>S. scytinophylla</i> Briq., <i>S. seemannii</i> Fernald, <i>S. selguapensis</i> A.Molina, <i>S. selleana</i> Urb., <i>S. serotina</i> L., <i>S. serpyllifolia</i> Fernald, <i>S. serranoae</i> J.R.I.Wood, <i>S. setosa</i> Fernald, <i>S. setulosa</i> Fernald, <i>S. shannonii</i> Donn.Sm., <i>S. similis</i> Brandege, <i>S. sinaloensis</i> Fernald, <i>S. sochensis</i> (J.R.I.Wood & Harley) Fern.Alonso, <i>S. sonomensis</i> Greene, <i>S. sophrona</i> Briq., <i>S. sordida</i> Benth., <i>S. sousae</i> Ramamoorthy, <i>S. sparsiflora</i> Epling, <i>S. sphacelifolia</i> Epling, <i>S. sphacelioides</i> Benth., <i>S. stachydifolia</i> Benth., <i>S. styphelus</i> Epling, <i>S. subaequalis</i> Epling, <i>S. subglabra</i> Urb. & Ekman, <i>S. subincisa</i> Benth., <i>S. subobscura</i> Epling, <i>S. subpatens</i> Epling, <i>S. subscandens</i> Epling & Játiva, <i>S. sucrensii</i> J.R.I.Wood, <i>S. synodonta</i> Epling, <i>S. tafallae</i> Benth., <i>S. tarayensis</i> K.M.Peterson, <i>S. tehuacana</i> Fernald, <i>S. tenella</i> Sw., <i>S. tepicensis</i> Fernald, <i>S. teresae</i> Fernald, <i>S. texana</i> (Scheele) Torr., <i>S. thomasiana</i> Urb., <i>S. thymoides</i> Benth., <i>S. thyrsiflora</i> Benth., <i>S. tillifolia</i> Vahl, <i>S. tonalensis</i> Brandege, <i>S. tortuensis</i> Urb., <i>S. trichopes</i> Epling, <i>S. tricuspoidata</i> M.Martens & Galeotti, <i>S. trifilis</i> Epling, <i>S. turneri</i> Ramamoorthy, <i>S. tuxtlenensis</i> Ramamoorthy, <i>S. uliginosa</i> Benth., <i>S. umbraticola</i> Epling, <i>S. unicostata</i> Fernald, <i>S. uribei</i> J.R.I.Wood & Harley, <i>S. urica</i> Epling, <i>S. urolepis</i> Fernald, <i>S. urticifolia</i> L., <i>S. uruapana</i> Fernald, <i>S. Vargasii</i> Epling, <i>S. variana</i> Epling, <i>S. verecunda</i> Epling, <i>S. veronicifolia</i> A.Gray ex S.Watson, <i>S. villosa</i> Fernald, <i>S. viscida</i> A.St.-Hil. ex Benth., <i>S. vitifolia</i> Benth., <i>S. xalapensis</i> Benth., <i>S. xanthophylla</i> Epling & Játiva, <i>S. zacualpanensis</i> Briq., <i>S. zacuapanensis</i> Brandege
psychophilous (1 sp.)
<i>S. whitehousei</i> Alziar
not clearly assignable to a distinct syndrome (ornithophilous, melittophilous, psychophilous)
<ul style="list-style-type: none"> ● ornithophilous, melittophilous or/and 'intermediate' (36 spp.) <i>S. angustiarum</i> Epling, <i>S. arenaria</i> St. Hil. ex Benth., <i>S. aspera</i> M.Martens & Galeotti, <i>S. atrocalyx</i> Epling, <i>S. atropaenulata</i> Epling, <i>S. bullulata</i> Benth., <i>S. camporum</i> Epling, <i>S. carbonoi</i> Fern.Alonso, <i>S. chiapensis</i> Fernald, <i>S. costata</i> Epling, <i>S. dichlamys</i> Epling, <i>S. ecuadorensis</i> Briq., <i>S. eizimatus</i> Ramamoorthy, <i>S. erythrostoma</i> Epling, <i>S. ionocalyx</i> Epling, <i>S. kellermanii</i> Donn.Sm., <i>S. mendax</i> Epling, <i>S. modica</i> Epling, <i>S. muelleri</i> Epling, <i>S. nubigena</i> J.R.I.Wood & Harley, <i>S. nubilorum</i> Epling & Ját., <i>S. obumbrata</i> Epling, <i>S. opertiflora</i> Epling, <i>S. oresbia</i> Fernald, <i>S. pansamalensis</i> Donn.Sm., <i>S. perlonga</i> Fernald, <i>S. pexa</i> Epling, <i>S. praestans</i> Epling, <i>S. pseudorosmarinus</i> Epling, <i>S. punctata</i> Ruiz & Pav., <i>S. purpurea</i> Cav., <i>S. revoluta</i> Ruiz & Pav., <i>S. sharpii</i> Epling & Mathias, <i>S. silvarum</i> Epling, <i>S. umbratilis</i> Fernald, <i>S. viscidifolia</i> Epling ● ornithophilous to ornithophilous, melittophilous or/and 'intermediate' to melittophilous (1 sp.): <i>S. carnea</i> Kunth ● ornithophilous to ornithophilous, melittophilous or 'intermediate' (6 spp.): <i>S. amethystina</i> Sm., <i>S. concolor</i> Lamb. ex Benth., <i>S. mexicana</i> L., <i>S. ochrantha</i> Epling, <i>S. recurva</i> Benth., <i>S. semiatrata</i> Zucc. ● melittophilous or/and 'intermediate' (6 spp.): <i>S. ampelophylla</i> Epling, <i>S. discolor</i> Kunth, <i>S. macellaria</i> Epling, <i>S. macrostachya</i> Kunth, <i>S. retinervia</i> Briq., <i>S. scutellarioides</i> Kunth
<ul style="list-style-type: none"> ● ornithophilous, psychophilous or/and 'intermediate' (4 spp.) <i>S. chionocephala</i> Epling, <i>S. clevelandii</i> (A.Gray) Greene, <i>S. mohavensis</i> Greene, <i>S. pachyphylla</i> Epling ex Munz
<ul style="list-style-type: none"> ● melittophilous, psychophilous, ornithophilous or/and 'intermediate' (2 spp.) <i>S. eremostachya</i> Jeps., <i>S. vaseyi</i> (Porter) Parish
<ul style="list-style-type: none"> ● melittophilous, psychophilous or/and 'intermediate' (2 spp.) <i>S. funerea</i> M.E.Jones, <i>S. greatae</i> Brandege
not assignable (because of lacking data; 8 spp.)
<i>S. alata</i> Epling, <i>S. arborescens</i> Urb. & Ekman, <i>S. brachyloba</i> Urb., <i>S. buchii</i> Urb., <i>S. microdictya</i> Urb. & Ekman, <i>S. psilostachya</i> Epling, <i>S. strobilanthoides</i> C.Wright ex Griseb., <i>S. trichostephana</i> Epling



Figure 4.1. Approximate distribution area of the genus *Salvia* in the New World (grey) and its ornithophilous species (hatched). The first number refers to the total number of ornithophilous species per country, the second to the total number of endemics in that group. Below, the approximate percentage of ornithophilous species per country is indicated. Note that the widespread *S. coccinea* (southern United States of America to southern South America) is not considered as its natural distribution is unclear (maybe Mexico/Central America or Brazil).

have the highest species density of ornithophilous sages.

Bird pollinated *Salvia* species occur in all **habitats** from rainforests to at least mesic habitats in deserts from about 200 up to 4000 m in elevation. They mainly occur in the highlands of the American cordilleras in elevations from about 1500 to 3000 m, and in South East Brazil rather around 1000 to 1500 m.

As to the **growth form**, almost all species (97 %) are perennial herbs, subshrubs or shrubs. Only *S. exserta* and *S. subrotunda* are annuals, while *S. coccinea* varies between being annual and perennial. Three species (*S. dombeyi*, *S. regla*, *S. sessei*) are scandent subshrubs, shrubs or sometimes small trees.

With regard to their flowers, ornithophilous sages are highly diverse (Appendix 3):

- The **total flower length** ranges from 13 cm in *S. dombeyi* (Fig. 4.2A) to 7 mm in *S. confertiflora* (Fig. 4.2D); the length of the **corolla tube** from 9 cm to 5 mm in the aforementioned species (Figs. 4.3, 4.4). Regarding the geographical distribution, the longest flowers occur in the Andes (especially Peru: *S. dombeyi*), in Brazil (where also the shortest species occur), and in Mexico and Honduras.
- The flower **shape** is bilabiate in 32 species (18 %; Fig. 4.2B, L, M, O, Q, R), tubular in 107 species (59 %; Fig. 4.2C-K, N) and in-between in 41 species (23 %) (Fig. 4.2A, P). The shape of the tubular flowers is mostly straight (parallel: e.g. Fig. 4.2 C, I), bellied (Fig. 4.2G) or funnel-shaped (Fig. 4.2E, F, N).
- The **stability of the corolla** ranges from being stiff as e.g. *S. karwinskii*, *S. confertiflora* or *S. madrensis* (Fig. 4.2D, G, K) to weak, e.g. in *S. sagittata* or *S. macrophylla* (Fig. 4.2E).
- The **stability of the lower lip** varies from stable e.g. in *S. confertiflora* (Fig. 4.2D) to weak e.g. in *S. patens* or *S. sagittata*.
- The **length of the lower lip** ranges from 41 mm in *S. patens* to 1 mm in *S. nervata* (Fig. 4.2I) and shows all kinds of **positions**, being mostly antrorse (Fig. 4.2A, L, M), but also deflexed (Fig. 4.2O) to reflexed (Fig. 4.2B, E-G). The lower lips may be additionally cupped so that their front margins are incurved (Fig. 4.2D, H) The lateral lobes may be oriented vertically (Fig. 4.2D, H, K). In flowers with weak, very short, reflexed or deflexed lower lips landing of insects is

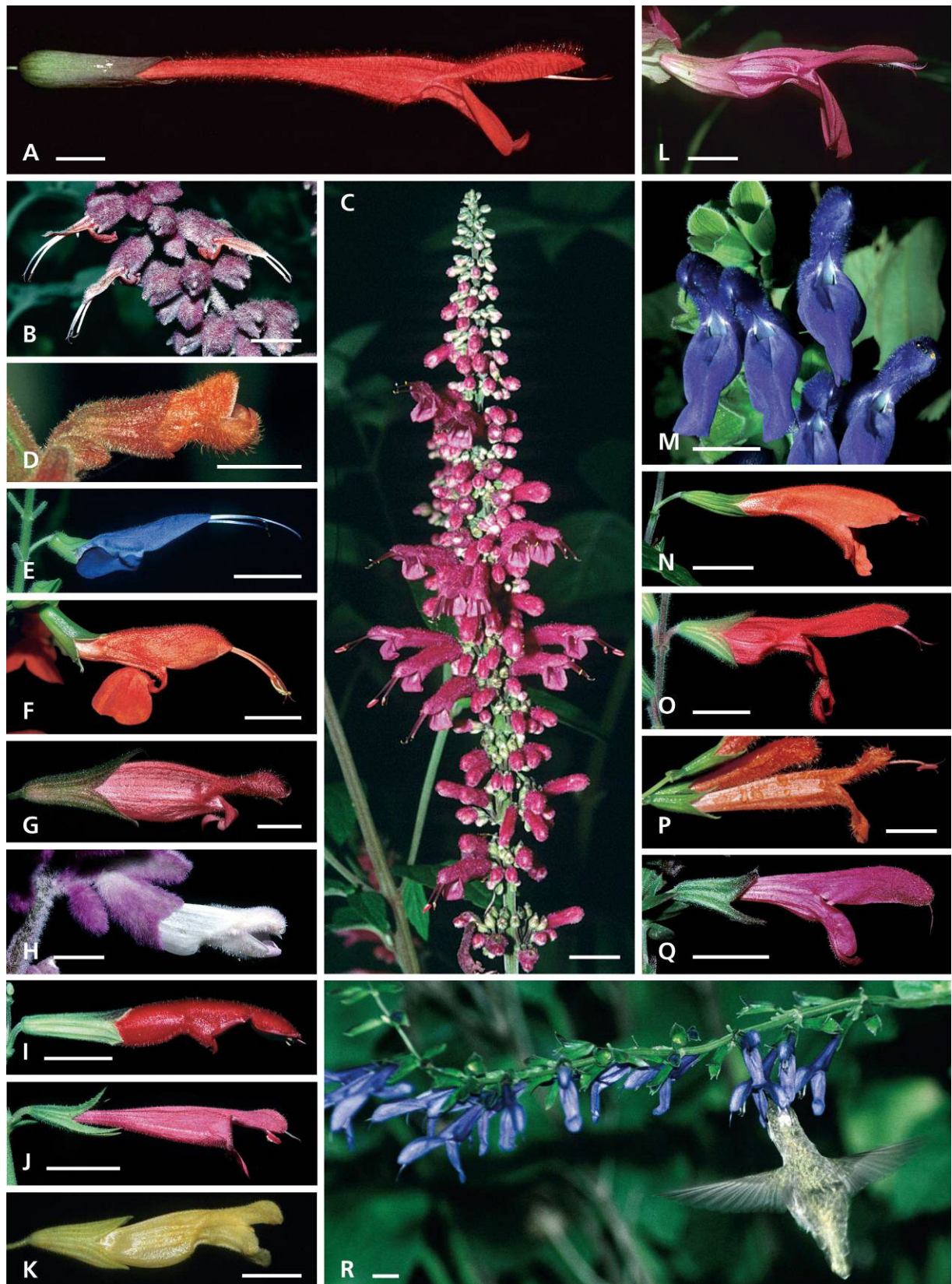


Figure 4.2. Diversity of ornithophilous *Salvia* flowers: A. *S. dombeyi*: largest flower of the genus; B. *S. lasiantha*: part of inflorescence with flowers having greatly exerted thecae and reflexed lower lips; C. *S. iodantha*: inflorescence bearing long-tubed flowers with greatly exerted thecae; D. *S. confertiflora*: flower with cup-shaped lower lip; E and F. flowers with reflexed lower lips and greatly exerted thecae: *S. macrophylla* (E) and *S. pauciserrata* (F); G. *S. karwinskii*: bellied flower with reflexed lower lip; H. *S. leucantha*: flower with antrorse lower lip lengthening the tube; I. *S. nervata*: tubular flower with ▶

impossible or difficult. The same is true for antrorse lower lips that lengthen the functional tubes (Fig. 4.2D, H). Antrorse lip positions bent downward $\gg 0^\circ$ to $<90^\circ$ may offer a potential landing platform, however, bees are excluded by tube length. In species with short flowers the tubular shape and lengthening the tube by antrorse lower lips are more abundant than in long-tubed flowers.

- The flowers are always conspicuous; the **colour** of the corolla is mainly red (49 %), but also orange, yellow, purple, pink, lavender, violet, blue and seldom brownish-ochre or red-brown (Fig. 4.5). A weak colour change occurs in *S. graciliramulosa* and *S. spathacea*. The calyx is mostly green or sometimes weakly coloured in parts. Especially in species with white flowers, the calyx can be more strikingly coloured, e.g. mostly purple in *S. leucantha* (Fig. 4.2H), purple or white/whitish in *S. tomentella* or light violet to whitish in *S. divinorum*. Several other species have coloured calyces and bracts, e.g. red in *S. confertiflora* (Fig. 4.2D) and *S. regla*, yellow in *S. madreensis* (Fig. 4.2K), pink in *S. involucrata*, sometimes purple in *S. gravida* and *S. lasiantha* (Fig. 4.2B), dark red to purple, almost black in *S. spathacea*, violet-black in *S. atrocyanea* or blue-black or whitish-light green in *S. paramicola*. Regarding the geographical distribution, there are no noteworthy characteristics in flower colour, except a high percentage of red in Brazil and blue and dark violet flowers occur mainly in the Andes, Mexico and Central America.
- **Nectar guides** are mostly lacking, but in at least nine species they occur on the lower lip near the entrance and in at least 15 additional species nectar guides are sometimes present. Nectar guides are mostly white and sometimes dark red-blackish; both colours occur in *S. exserta*. The whitish stamens may contrast to the coloured corolla, as for example in *S. atrocyanea* (Fig. 4.2M). In *S. alborosea*, the whole lower lip is white.

←

► very short lower lip); J and K. relatively long-tubed flowers. *S. henryi* (J, usually red) and *S. madreensis* (K); L and M. bilabiate flowers with long tubes and large lips: *S. gravida* (L) and *S. atrocyanea* (M); N. *S. oppositiflora*: funnel shaped flower with slightly exserted thecae; O. *S. oaxacana*: flower with deflexed lower lip; P. *S. rusbyi*: long-tubed flower with exserted thecae (the species also has individuals with thecae enclosed by the upper lip); Q. *S. penstemonoides*: bilabiate flower with tube of medium length and relatively long upper lip; R. *S. guaranitica* visited by a hovering *Calypte costae* with thecae and pollen on the bird's head. Bars = 1 cm in A-C, E, F, I-R; 0.5 cm in D, G, H.

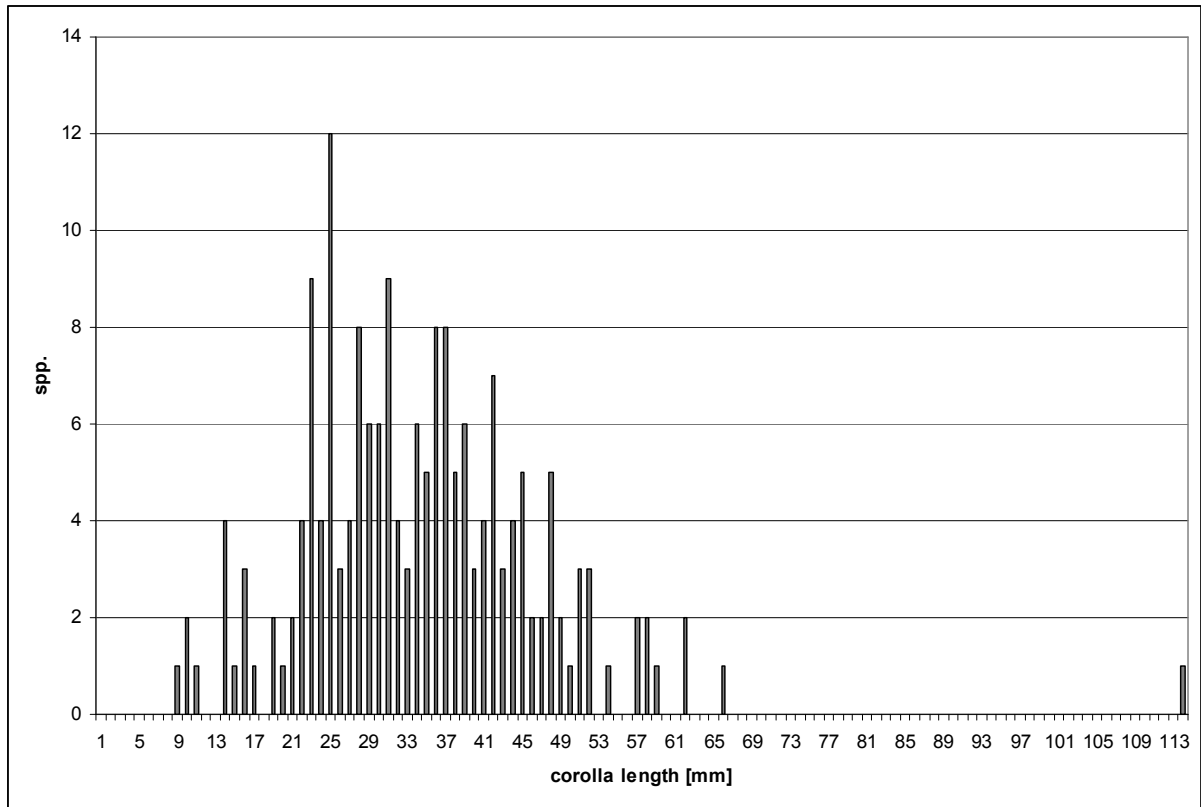


Figure 4.3. Corolla length in ornithophilous *Salvia* species. Lengths were calculated from the average of the minimum and maximum values listed in Appendix 3. n=182.

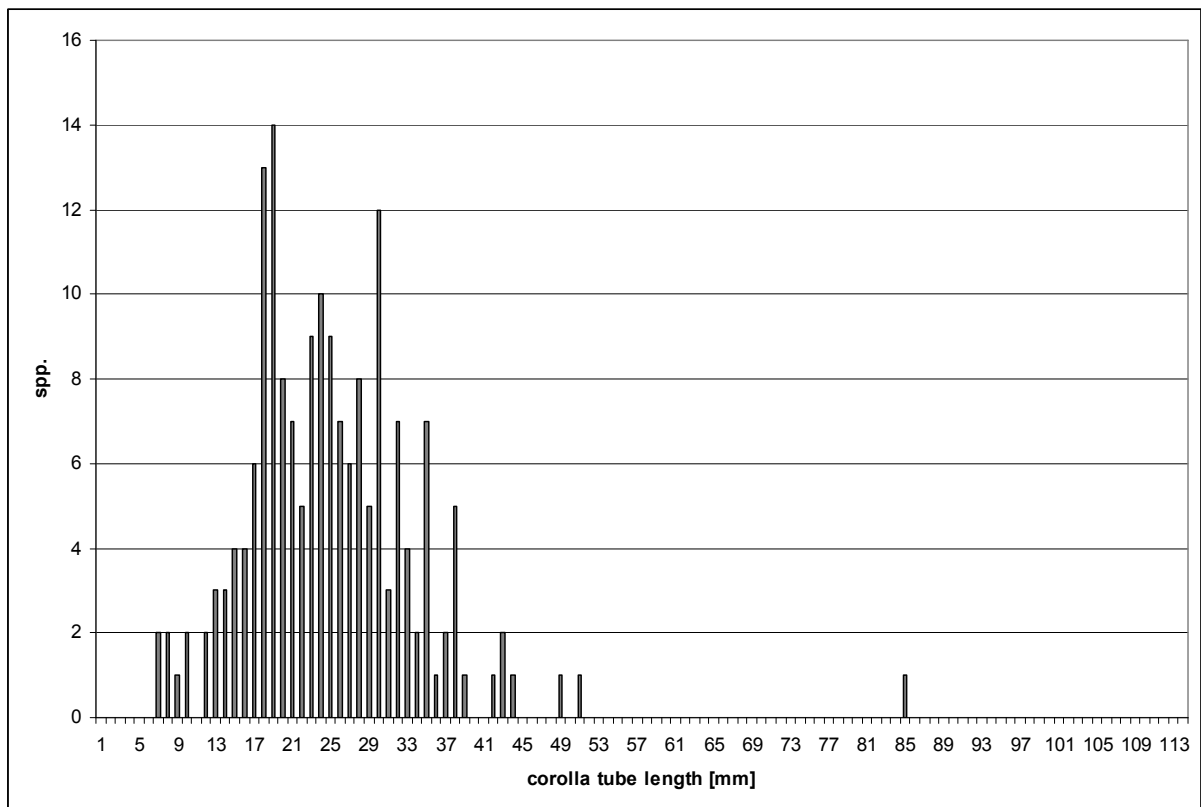


Figure 4.4. Corolla tube length in ornithophilous *Salvia* species. Lengths were calculated from the average of the minimum and maximum values listed in Appendix 3. n=181.

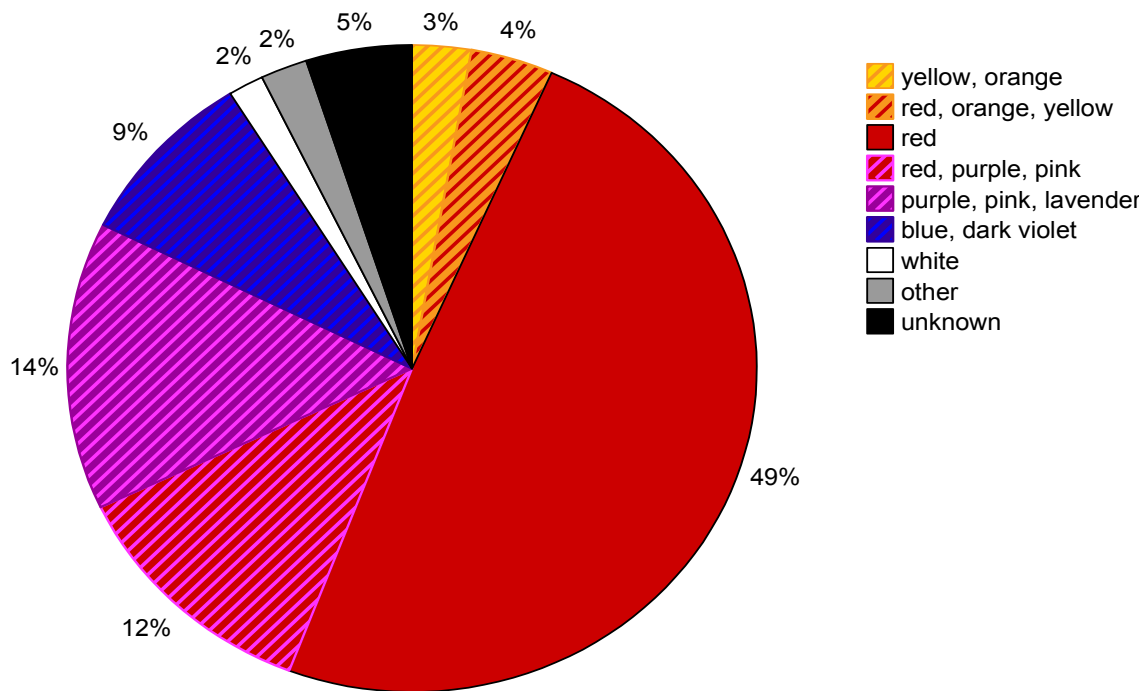


Figure 4.5. Corolla colour of ornithophilous *Salvia* species (see Appendix 3).

- The **nectary length** varies from 1 to 5 mm; some nectaries are very voluminous. In all species examined, a large to medium volume of mostly low- to medium-concentration **nectar** was produced.
- **Nectar retention structures** at the base of the corolla are rather common. In almost all species they appear as slight lateral and horizontal narrowings of the corolla tube (not included in Appendix 3). Beside this, there are strong lateral or abaxial constrictions (including emarginations or folds), lateral ridges, papillae or hairs as well as posterior staminal lever arms.
- In Calospace species, the **connectives** often form **tooth-like structures** near the abaxial side of their joints. They are relatively large in *S. lasiantha*, *S. atrocyanea*, *S. exserta* or *S. guaranitica*, small in *S. dombeyi*, minute in *S. gravida* or even absent as in *S. oppositiflora*. In all flowers they do not occlude the flower entrance, because they are either arranged laterally (*S. atrocyanea*: Fig. 4.2M; *S. exserta*) or greatly distal (*S. lasiantha*: Fig. 4.2B).
- The **thecae position** varies from being enclosed by the upper lip in 99 species (Fig. 4.2A, M) to being exerted up to 43 mm (*S. speciosa*) in 69 species (e.g. Fig. 4.2B, C, E-F). In 10 species the position of the thecae is variable.

- No noticeable flower **scent** was found.
- The **pedicels** are mostly flexible and their length ranges from 34 mm in *S. dombeyi* to being absent in *S. spathacea*.

4.3.2 Melittophilous species

Melittophilous species are the most frequent species within the New World sages (Tab. 4.1, Fig. 4.6A-I). Compared to ornithophilous species, they have a wider distribution and are more abundant for example in Mexico and the USA, in Argentina, Paraguay and Panama (Fig. 4.1). As to the altitude, they grow as high as ornithophilous sages and occur mainly in higher elevations. On the whole, however, they show a wider altitude range. On average, compared to ornithophilous sages, they occur in lower elevation, for instance in Colombia, Ecuador and at least some areas in Mexico (Sierra Manantlán, Valle de México) and Brazil.

At several species pollinating bees were observed visiting the flowers, e.g. at *S. stachydifolia*, *S. rypara* ssp. *platystoma*, *S. cuspidata* ssp. *bangii*, *S. sophrona*, *S. carduacea*, *S. apiana*, *S. mellifera*, *S. leucophylla*, *S. dorrii*, *S. munzii* and *S. columbariae*. Only rarely hummingbirds visited the bee flowers (*S. cf. longispicata*). Bees stealing nectar or/and pollen were observed at e.g. *S. rypara* ssp. *platystoma*, *S. stachydifolia*, *S. apiana* and *S. carduacea*. Nectar stealing butterflies were observed at the flowers of *S. engelmannii*, *S. leucophylla*, *S. columbariae* and *S. carduacea* and a hawkmoth at *S. carduacea*.

Like ornithophilous sages, melittophilous species also vary in many floral characters:

- The **colour of the corolla** is often blue and violet, but also white, pink, purple (Fig. 4.6A-I) or rarely yellowish. As expected, there are often nectar guides at the flower entrance (Fig. 4.6C, G, H).
- A peculiar feature of many bee pollinated Calosphace species is the presence of distinct ventral **teeth or barriers** at the connectives. The latter may be large and contribute to occlude the entrance. In *S. rypara* ssp. *platystoma* (Fig. 4.6D) and *S. pusilla* for instance the lever mechanism is triggered by pushing back these barriers. In species like *S. amplifrons* and *S. cuspidata* ssp. *bangii* the ventral formations are laterally arranged.

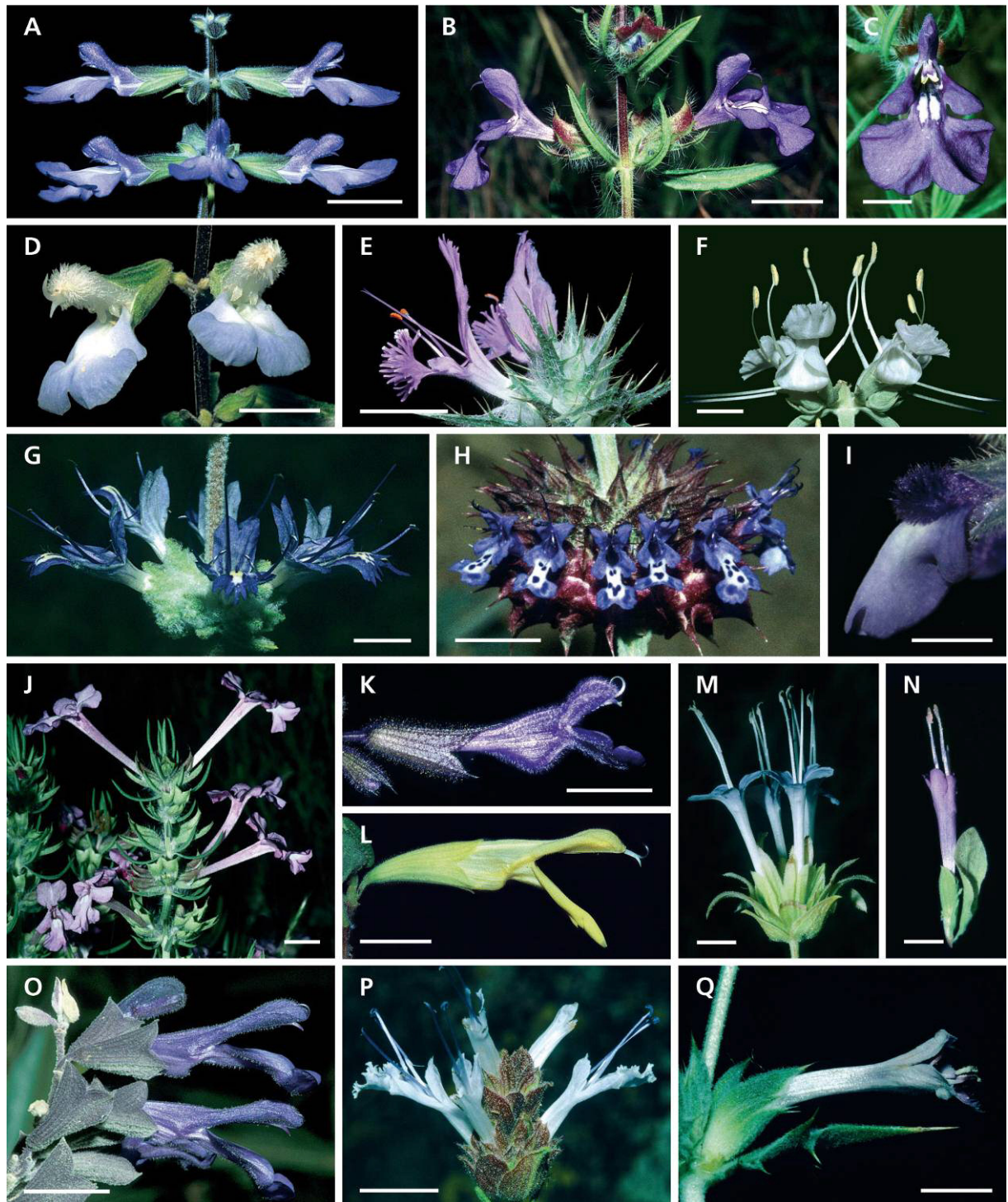


Figure 4.6. Diversity of *Salvia* flowers, being melittophilous (A-I), psychophilous (J) and not clearly assignable to a syndrome (K-Q): A. *S. stachydifolia*: flowers with pollen-sacs enclosed by the upper lip, short corolla tubes and large lower lips as landing platform; B and C. *S. texana*: flowers with large lower lips possessing white nectar guides; D. *S. rypara* ssp. *platystoma*: short-tubed flowers showing large connective outgrowths in the flower entrance; E-H. flowers with exposed thecae and large lower lips: *S. carduea* (E), *S. apiana* (F), *S. californica* (G), *S. columbariae* (H), the latter two with white and patterned nectar guides on the lower lips; I. *S. betonica*: flower entrance more or less hidden by roughly tangent lips; J. *S. whitehousei*: part of inflorescence bearing long-tubed flowers with salverform lips and white nectar guides; K-L. with melittophilous and ornithophilous characters: the variable sized *S. concolor* (K) and *S. aspera* (L); M-N. with ornithophilous and psychophilous characters: *S. mohavensis* with long narrow corolla tubes, salverform lips (M) and exserted thecae, varying ►

- The **pollen-sacs** of most species are enclosed by the upper lip (Fig. 4.6A-D, I). In only few species including all members of the sections Echinosphece (Fig. 4.6E, G) and Audibertia (Fig. 4.6F, H), and individual Calosphece species (e.g. *S. rhombifolia*, *S. tafallae*, *S. palifolia*, *S. paposana*) the pollen-sacs are exposed.
- In most species the **staminal lever mechanism** works (e.g. *S. stachydifolia*, *S. texana*, *S. rypara* ssp. *platystoma*) and only rarely the lever mechanism is lacking as for instance in *S. carduacea* or *S. apiana*.
- In at least *S. betonica* and *S. lavanduloides* of the section Lavanduloideae (Calosphece) the flower **entrance** is more or less **hidden** by roughly tangent lips (Fig. 4.6I), a feature never occurring in ornithophilous sages.
- The flowers of the species investigated are usually **flexibly arranged** (e.g. *S. amplifrons*, *S. uliginosa*, *S. rypara* ssp. *platystoma*), but stable enough to bear the bees weight. If they are more stiffly arranged, they may have shorter (and more stable) pedicels or may be densely arranged in the inflorescence (e.g. *S. betonica*, *S. dorrii*, *S. leucophylla*).
- **Nectaries** in general are smaller as in ornithophilous flowers, producing small amounts of highly concentrated nectar (e.g. *S. stachydifolia*, *S. rypara* ssp. *platystoma*).
- Surprisingly, no noticeable flower **scent** was found in the species examined, except a honeylike or sweetish scent in *S. leucophylla*, *S. apiana*, *S. californica* and *S. carduacea*. In the latter species it cannot ruled out that this scent derive from the leaves.

4.3.3 Psychophilous species

S. whitehousei (Echinosphece) is the only species that is assumed to be psychophilous. Several populations were studied at roadside localities in western Texas. The corolla tube is very long (34.8 +/-4.4 mm, 26-44, n=33) and relatively



► sometimes in width of corolla tube, orientation of lips and corolla colour (N); O. *S. retinervia*: with melittophilous and ornithophilous characters, looking more melittophilous, but is variable in corolla tube length and has a relatively large volume of nectar; P. *S. eremostachya*: with melittophilous, psychophilous and ornithophilous characters; and Q. *S. greatae*: with melittophilous and psychophilous characters. Bars = 1 cm in A, B, E, H, J-L, O, P; 0.5 cm in C, D, F, G, M, N, Q; 0.25 cm in I.

narrow (Fig. 4.6J). The lips together form a more or less radial symmetrical and widespread arranged disc (length of lips 7-13 mm) providing a landing platform. They are found on the end of the long corolla tube resulting in the 'Stielteller'-flower typical of many psychophilous flowers. The light pink to lavender (C10-30 M10-50 S00) flower corresponds to this syndrome. Two white spots below the flower entrance act as nectar guides. The thecae in the flower entrance are whitish and thus likewise conspicuous. There is a light more or less fruity scent of the corolla and the calyx. Nectar was of medium volume, protruding 5-11 mm into the tube.

4.3.4 'Intermediate' or not assignable species

The remaining species do not fit to the three aforementioned categories (Tab. 4.1). Instead, they show character combinations of (a) melittophily and ornithophily, (b) ornithophily and psychophily, (c) melittophily, psychophily and ornithophily and (d) melittophily and psychophily (see Appendix 4).

- **Melittophilous and ornithophilous characters** are found in *S. purpurea* (Calospace). The species is highly variable showing different corolla colours, flower sizes and proportions of tube length to lower lip length, even within one individual. Long-tubed flowers with relatively short lower lips point rather to ornithophily, while flowers with longer lower lips, offering a better landing platform for bees, may be 'intermediate', possibly pollinated by both birds and bees. Hovering and perching hummingbirds were observed visiting the flowers as well as some bees being dusted with pollen or stealing nectar and pollen. Different species of butterflies and hawkmoths stole nectar. The activity of the flower visitors obviously varies, as near Xalapa visiting hummingbirds were less frequent than near Guadalajara, where bees were less abundant.

The yellow flowers of *S. aspera* (Calospace; Appendix 4) vary also in length. Whereas the larger flowers with a relatively large volume of nectar of medium sugar concentration in the flowers measured indicate bird pollination, the smaller ones are rather 'intermediate' or even melittophilous. Their lower lips are relatively narrow, but stable enough for offering a landing platform.

The dark violet corolla of *S. concolor* (Calospace), appears to be melittophilous due to its large lower lip, offering a landing platform. However, the long corolla tube and the medium amount of nectar with relatively low sugar concentration

of the examined flowers indicate bird pollination. Whereas bees, except very long tongued ones, will not reach the nectar of the long-tubed flowers, they might be pollinators in shorter-tubed flowers.

S. mexicana (Calospace) is a quite variable species with two varieties, *S. m. minor* and *S. m. major*. In general the varieties differ greatly in corolla size, in the proportion of the tube length to the lower lip length and in the lower lip position. Additionally, these characters and also corolla colour differs within the varieties. Whereas large flowers of both varieties and those with a relatively short lower lip in comparison to the flower tube are clearly ornithophilous, smaller flowers, especially those with relatively long lower lips look rather 'intermediate' and/or melittophilous. Nectar data of the individuals examined also correspond to ornithophily. At the lighter violet flowers of *S. m. major* unidentified hummingbirds were observed visiting the flowers. Bees were observed stealing nectar.

Ornithophilous individuals evidently lack in the three following species. Their flowers look rather melittophilous with their small to medium sized corolla tube and a large lower lip as landing platform. However, they are not certainly assignable to a syndrome. The blue ***S. scutellarioides*** (Calospace) has white nectar guides on the lower lips and rather short corolla tubes, but a medium volume of nectar with a relatively low sugar concentration as well as exposed thecae which might not be touched by bees. The corolla of ***S. discolor*** (Calospace) is dark violet (almost black), has no nectar guides and contrasts to the large, almost whitish light green calyx. With its large lower lip, its short to medium sized tube and the nectar of high sugar concentration, it exhibits melittophilous characters, but might be very attractive to birds, too, because of its large volume of nectar. The tube length of the dark violet ***S. retinervia*** (Calospace; Appendix 4; Fig. 4.6O) is variable and can be relatively long. The species has a relatively large volume of nectar. In Bolivia, large bees were observed to visit and pollinate the species, whereas other bee species stole nectar.

- **Ornithophilous and psychophilous characters** are shared for example in *S. mohavensis*, Fig. 4.6M) and *S. clevelandii* (both Audibertia). With their relatively long and narrow corolla tubes and exerted thecae bees are excluded as visitors and pollinators. Likewise, the medium volume of nectar with medium to low sugar concentration is not typical for bee pollinated flowers. The blue to blue-violet flowers of ***S. clevelandii*** have a strong sweet scent, not typical for ornithophilous flowers,

but rather for psychophilous ones. They were observed to be pollinated by hovering hummingbirds in Rancho Santa Ana Botanical Garden (California). Different bee species robbed nectar, piercing the flowers at their base. Butterflies visited the flowers.

S. mohavensis, studied at different localities in California, has bracts being partly white or whitish, rarely with pale violet or yellowish areas. The corollas are light blue (Fig. 4.6M). Their lips form a more or less discoidal and widespread arranged disc, making the flowers only little zygomorphic. Together with the corolla tube this lip formation gives the flower the shape of a typical 'Stieltellertyp' flower of psychophilous flowers. In the Fullerton Arboretum (California) hummingbirds were observed visiting the flowers. However, cultivated plants in a private garden in Tucson (M. Dimmitt), originating from an isolated occurrence of the species in Northern Mexico (Pinacate region), have different flowers. The bracts were green and the corolla light pink to violet to lavender. The flowers differed in floral tube width and lip orientation, giving them a tubular shape and thus a more ornithophilous appearance (Fig. 4.6N).

- **Melittophilous, psychophilous and ornithophilous characters** are combined for instance in the (pale) violet-pink to almost white flowers of ***S. eremostachya*** (Audubertia, Fig. 4.6P). Their short to medium sized and relatively narrow corolla tubes and large lower lips, indicate bee pollination. But the thecae are exerted and it is not clear whether bees would touch them. Also the nectar of cultivated plants has a relatively low sugar concentration, thus, fitting better to psychophily or ornithophily.

- **Melittophilous and psychophilous characters** are combined for example in ***S. greatae*** (Echinosphace, Fig. 4.6Q). The species has pinkish-lavender flowers. Being small and tubular, the flowers vary in tube length as well as in the relative proportions of tube and lower lips. When the lower lip is relatively large compared to the tube, bees are more likely pollinators. In contrast, flowers with short lower lips compared to the tube, may be more likely pollinated by butterflies or long-tongued flies. Only once, a hummingbird was observed visiting the flowers (Rancho Santa Ana BG). It cannot be ruled out that it even pollinated the flowers.

4.4 DISCUSSION

4.4.1 Pollination syndromes in the New World *Salvia* species

4.4.1.1 Ornithophily

According to the grouping, about one third of the New World sages is ornithophilous. Referring to all *Salvia* species, about 20 % are bird pollinated, thus a little bit more than are known from angiosperms in general (10-15 % after Feinsinger 1983).

Whereas many of the *Salvia* species already identified as being bird pollinated conform to the grouping (e.g. Delpino 1868-1874, Trelease 1881, 1882, Gams 1927, Zalewska 1928, Himmelbaur & Stibal 1932-1934, Reisfield 1987, Ramamoorthy & Elliott 1998, Torke 2000, Walker & Elisens 2001), there are also disagreements. *S. carduacea* for instance was taken as an ornithophilous species by Zalewska (1928) and *S. cacaliifolia* as a melittophilous one by Cruden (1972, but see Wagner 1946). *S. heerii* is mentioned as an ornithophilous and psychophilous species by Trelease (1882) and *S. lasiantha* is assumed to be myiophilous by Faegri & van der Pijl (1971).

Different groupings result either from a lack of information or from referring the floral characters to different syndrome descriptions. 'Typical' bird pollinated species in the angiosperms are defined to have

- mostly red flower colours (Vogel 1954, Faegri & van der Pijl 1971, Baumberger 1987),
- no clear UV reflectance (Straw 1956, Kugler 1970, Olesen 1985, Baumberger 1987),
- a large distance between nectar and the reproductive organs, and in general long and relatively narrow corolla tubes (Faegri & van der Pijl 1971, Baumberger 1987),
- stiff corollas of mostly tubular shape, with often reflexed, deflexed or short lower lips (Vogel 1954, Faegri & van der Pijl 1971),
- well developed nectar retentions (Porsch 1924, Holm, 1988), that are needed to contain the high amount of watery nectar (Vogel 1954, Baker 1975, Cruden et al. 1983, Pyke & Waser 1981, Baumberger 1987),
- no scent (Vogel 1954, see also Mattern & Vogel 1994) and
- long and flexible pedicels (van der Pijl 1937, Thomson et al. 2000).

As part of the grouping is based on typical ornithophilous features it appears to be a circular reasoning that most of the species identified as bird flowers share the above mentioned typical characters. However, as additionally many species were observed in the field, the process of pollen transfer was reconstructed and the capability to exclude bees was checked, we are of the opinion to present an acceptable compromise for the intention of grouping so many species.

Adding functional observations to the commonly accepted ornithophilous characters the grouping of this work slightly differs from the ornithophilous syndrome published elsewhere. So, for instance, we also identify the small brownish flowers of *S. lasiantha* as being bird pollinated and do not share the opinion of Faegri & van der Pijl (1971) that the flowers in *S. coccinea* are only 'semi-ornithophilous' because of their labiate shape. Correspondingly we disagree with Reisfield (1987) who stated many bilabiate flowers as being 'transition species' between melittophily and ornithophily (e.g. *S. fulgens* and *S. patens*). Another discrepancy concerns corolla stability. Contrary to the common view that ornithophilous flowers are characterised by stiff corollas, we also found weak flowers to be bird pollinated at least in species with short to medium-sized flowers. This fits to the observations that hummingbirds handle the flowers without damaging them (see also Snow & Snow 1980). Stiff corollas are not absolutely needed to protect the flowers against visiting birds and robbing birds or bees, as stated by Proctor et al. (1996): Instead, these animals are also able to pierce strengthened corollas (e.g. *S. grewiifolia* and *S. leucantha*: chapter 5). We conclude that stiff corollas rather stabilise the flowers. Apart from corolla shape and stability the ornithophilous sages also differ in their colouring from the general view. According to Baumberger (1987), 52 % of the ornithophilous angiosperms have multicoloured corollas (including nectar guides), but in sages the corolla only contrasts to the calyx or leaves and nectar guides are relatively rare.

The high diversity of floral characters found within the bird pollinated *Salvia* species clearly illustrates the nature of a pollination syndrome (see Vogel 1954). There are not only typical large and red tubular flowers that only slightly vary in less essential characters, but there is a broad range of colours, shapes, sizes and floral constructions present within the same group. In each species, it depends on the specific combination of varying floral characters whether the resulting flower attracts birds and excludes bees or not. Referring to the latter, bees may be excluded by either a lacking landing platform or by a long and narrow flower tube.

The distribution of ornithophilous New World sages corresponds to that of the hummingbirds. In regions with a high number of ornithophilous species, many of which being endemics (e.g. Colombia/Ecuador, Brazil), the hummingbirds also show the highest species number and diversity (Schuchmann 1999, see also Reisfield 1987). Likewise, the general appearance of bird pollinated plants in higher altitudes (Cruden 1972, Feinsinger 1983, Kay et al. 2005, Pérez et al. 2006), also confirmed for the ornithophilous sages (see also Reisfield 1987), corresponds to high abundance of hummingbirds there (Cruden 1972, Schuchmann 1999, Altshuler et al. 2004). The close interdependence among bird pollinated flowers and hummingbirds becomes also clear by regarding just one character, the tube lengths of ornithophilous sages and ornithophilous angiosperms in general, and the hummingbirds' bill lengths. For example, both the range of bill lengths and tube lengths in general gets broader with lower latitude (Schuchmann 1999, Baumberger 1987).

4.4.1.2 Melittophily

Melittophilous species differ from ornithophilous ones in attracting bees and granting them access to nectar. As in the bird pollinated species, floral variation is high.

Bee pollinated sages differ from the general picture of bee flowers in nearly lacking a definite petal scent (exceptions in sections *Audibertia* and *Echinosphace*). However, they share this character with many Lamiaceae, which instead produce scent in their sepals and vegetative leaves. This scent is assumed to be used for pollination in insect pollinated species while a typical melittophilous scent is largely lacking (Mattern & Vogel 1994).

As to floral constructions, we only point to two peculiar features found in bee pollinated species. First, more or less hidden entrances by roughly tangent lips appear in some species (e.g. in *S. betonica*, *S. lavanduloides*) resembling those e.g. in the *Antirrhineae* (*Plantaginaceae*). The blocking of the entrance protects pollen and forces the bees to handle the flower with physical force (see Westerkamp & Claßen-Bockhoff 2007). Second, there is often one additional staminal barrier in the flowers narrowing the entrance. As Claßen-Bockhoff et al. (2004a) found this barrier may either be the sterile thecae (*S. uliginosa*) or a ventral outgrowth of the sterile connective arm (*S. rypara*, Fig. 4.6D) again illustrating that different morphological structures result in the same functional constructions. The large barrier contributes to

the blocking of the flower entrance and to the release of the lever mechanism as the bees touch this barrier on their search for nectar (see also Reisfield 1987, Claßen-Bockhoff et al. 2004a). As the majority of the species in the New World belong to subgenus *Calosphace*, they have straight posterior lever arms, reaching far behind the flower entrance. By producing ventral protrusions a lever apparatus results that parallels the form of the curved levers, typical for many bee pollinated species of the Old World (see also Himmelbaur & Stibal 1932-1934, Hildebrand 1865, Ogle 1869, Correns 1891). Maybe bee flowers need such a barrier to enable the bees to release the lever mechanism. In contrast, such an auxiliary construction is not needed in bird pollinated flowers as birds are able to touch each kind of abutment with their long bills.

4.4.1.3 Psychophily

The genus *Salvia* encompasses only few species assumed to be psychophilous e.g. *S. scabra* L.f. in South Africa (long-tongued flies assumed by Potgieter & Edwards 2001; unpubl. data) or *S. nanchuanensis* H.t'S.Sun in China (unpubl. data). Up to now no observations of flower pollinator interactions exist in these species and this is also true for *S. whitehousei* (Fig. 4.6J) that we assume to be a further psychophilous species in the New World. The species only known from Texas and Coahuila (Mexico) is little known. The upper lip has not the typical hooded (galeate) shape of most of the sages including the other representatives of the section *Salviastrum* like *S. texana* (Fig. 4.6B,C) and most of the *Calosphace* species and as incorrectly illustrated in the only published description by Whitehouse (1949). Instead, the lips of *S. whitehousei* have a salverform shape and the flower forms a 'Stielteller' flower sensu Vogel (1954), being characteristic for psychophilous flowers. The flower entrance is not blocked by staminal lever arms, thus allowing butterflies, moths or long-tongued flies access to nectar. Bees are largely excluded by the long tube, while birds might not be attracted by the pale flowers.

4.4.1.4 Parallel evolution of pollination syndromes in the genus *Salvia*

As bee and bird flowers are found in both the Old World and in the New World, parallel evolution is obvious considering the different floral morphologies and systematic groups (see also Himmelbaur & Stibal 1932-1934, Reisfield 1987,

chapters 3, 5). Parallel evolution has recently been confirmed by the phylogenetic studies of Walker & Sytsma (2007). Based on molecular data of 82 species the authors found three distinct *Salvia* clades and concluded that *Salvia* might be polyphyletic. Referring our results to their tree, ornithophilous species appear in two of the three clades. A shift from bees to birds is more likely than the inverse direction, because birds are considered to be more effective pollinators than bees (Cruden 1972, Thomson et al. 2000, chapter 5). In clade I, the New World taxa (Heterosphace/*Salviastrum* and *S. penstemonoides*) show two parallel shifts from melittophily to ornithophily and one from melittophily to psychophily, following parsimony (see also Walker et al. 2004). In clade II, shifts from melittophily to ornithophily happened at least twice in subg. Calosphace and at least once in subg. Audibertia (see also Walker et al. 2004). Such shifts from bee pollination to bird pollination likely happened several times in parallel (see also Reisfield 1987, Baumberger 1987, Grant & Grant 1965). Similar shifts have been documented in other genera such as *Costus* (Kay et al. 2005), *Mimulus* (Beardsley et al. 2003), *Penstemon* (Castellanos et al. 2004, Wilson et al. 2006) and *Schizanthus* (Pérez et al. 2006).

4.4.2 Generalisation versus specialisation in *Salvia* and the evolutionary significance of ‘intermediates’

The attempt to group all New World *Salvia* species according to pollination syndromes was successful as the great majority (almost 90 %) of the species could be identified as having either bird or bee flowers. Considering the functional construction of the flowers, essential data are added to previously known characters and arrived at a more appropriate grouping.

Though in our view the usefulness of the concept of pollination syndromes is undisputable, the recent discussion on specialisation versus generalisation cannot remain unconsidered. Two aspects are discussed.

- The first is a methodological one, dealing with the concept of classes and types (see Hempel & Oppenheim 1936, Froebe 1971, Sattler 1996, Claßen-Bockhoff 2005). A class is defined as a group of representatives clearly excluding each other and showing no transitional forms. A type in contrast is defined by a character syndrome that applies to most of its representatives. When Vogel

(1954) introduced the concept of 'Blumenstile' (pollination syndromes) he explicitly pointed out that the syndromes are not classes but types, being characterised by their means and not by their extremes ("Typen sind Mitten, nicht Grenzen": Vogel 1954: 36). Thus, the concept of pollination syndromes not only allows but also requires less typical representatives and even transitional forms, reflecting the dynamic nature of flower-pollinator interactions. The belief, that the diversity of flowers could be strictly classified is delusive and may have contributed to the scepticism against pollinations syndromes.

- The second point of discussion arises from the view that presumably specialised flowers show much more generalisation than expected. For instance, Waser et al. (1996) and Ollerton (1996) stated that many flowers showing specialisation in floral traits were visited by various animals and concluded that they indeed were generalists. Though we confirm their observations we don't follow their conclusion. First, it has clearly to be distinguished between visitors and pollinators, only the latter being relevant for the question of generalisation and specialisation. Second, generalisation means that flowers are visited by a variety of unspecialised visitor groups like short-tongued flies, bees or beetles and show no or only little adaptations to a certain pollinator guild (see also Fenster et al. 2004, Goldblatt & Manning 2006).

In the case of *Salvia* we found clear specialisations to a given pollinator guild and restrictions against another one. This does not exclude illegitimate visitors stealing nectar as it was observed in *S. haenkei*, where butterflies visited the normally bird pollinated flowers (chapter 2). It furthermore does not exclude a secondary pollinator guild, which however only plays a subordinated role compared to the main pollinators (see also Vogel 1954). Hummingbirds occasionally pollinate melittophilous flowers, e.g. *S. longispicata* and *S. lavanduloides* (see also Arizmendi 2001, Schondube et al. 2004), *S. apiana* and cultivated individuals of the Old World *S. officinalis* (Pickens 1929, 1931). Correspondingly, ornithophilous sages are sometimes visited and even pollinated by bees (see chapter 5). However, these secondary pollinator groups are generally not considered in grouping the flowers to a particular syndrome because of their generally low pollination effectiveness (see also Schemske & Horvitz 1984, Stebbins 1970, 1974, Muchhala 2006). Handling the flowers in this liberal manner we again typify and not classify them, referring the ecological data likewise to the most common type and not to an exclusive class.

Specialisation thus means that there is a floral character combination attracting a certain pollinator guild either predominantly or exclusively.

On the other hand, we also found 'intermediate flowers' not clearly belonging to a certain pollination syndrome. We yet disagree with the possible conclusion that the latter might indicate generalisation. On the contrary, the 'intermediate' *Salvia* species are not visited by each kind of insects but by specialised flower visitors. They cannot be grouped because of fragmentary or conflicting descriptions or because they share characters of several syndromes (for instance of bee and bird flowers).

- An example for conflicting/lacking data is given by the highly variable *S. purpurea*. Dependent on the locality and time of observation either hummingbirds, or butterflies or bees are reported to be more abundant (C. González, M. Ordano and A. Luis-Martínez, pers. comm.). The same might be true for *S. clevelandii*, which is reported to be often visited and pollinated by hummingbirds but also by small hawkmoths (Cox 1981, B. O'Brien, pers. comm.). The yellow flowers of *S. aspera* are mentioned to be pollinated by bees (Ramamoorthy & Elliott 1998) but it is possible that this conclusion refers to the yellow colour taken as a typical melittophilous trait. Difficulties also come from taxonomic conflicts. Some taxa are recognised to be identical or species include highly variable subspecies or varieties (*S. arenaria*, *S. amethystina*, *S. carnea*, *S. mexicana*). *S. carnea*, for instance, includes formerly separate species, varying in flower size and colour. The morphs range from ornithophilous ones (*S. carnea* Kunth var. *punicans* (Epling) J.R.I. Wood & Harley) to melittophilous ones ('*S. gracilis* Benth. '), forming a continuum with other 'taxa' like a 'ring of races' (Reisfield 1987). The appearance of different morphs within a species complicates grouping. *S. mohavensis*, for instance, is distributed in South Western USA and Northern Mexico (Neisess 1983, A. Sanders, pers. comm.). The widespread 'normal' light blue 'Stielteller' flowers combine ornithophilous and psychophilous characters and are observed to be visited by hummingbirds and long tongued flies (B. O'Brien and P. Wilson, pers. comm., Fenster et al. 2004), the latter classified as psychoid insects. Individuals in Northern Mexico, isolated by 300 km, have flowers with a rather ornithophilous construction (broader corolla tube, lip orientation, colour), and are reported to be visited by hummingbirds (A. Sanders, pers. comm.). Assuming that there is really no gene flow among these morphs,

speciation is possible and then the morphs have to be taken as separate taxa (species or at least subspecies; compare with Johnson 1997).

- Morphological 'intermediates' sharing characters of two or three pollination syndromes might be interpreted according to different scenarios. If there is a strong unidirectional selection pressure for instance towards birds as more effective pollinators, the intermediates represent momentary transitional stages towards ornithophily (see also Reisfield 1987, for other genera see e.g. Baker 1963, Stebbins 1974, Macior 1986, Sazima et al. 1994, Manning & Goldblatt 2005, Wilson et al. 2006). They might be interpreted as 'despecialised', being attractive for bees (e.g. landing platform, short corolla) and birds (e.g. large volume of nectar) at the same time (e.g. Wilson et al. 2006, Pérez et al. 2006, see also Thomson et al. 2000, Thomson 2003, Hardy 1954). Subsequent 'respecialisation' may occur when bees are excluded by either lower lip reduction or elongation of the corolla tube (Wilson et al. 2006, see also chapter 5).
- The assumed process of respecialisation may however fail to appear, thus stabilising the 'less specialised' intermediate stages. This may happen under weak and/or changing selection pressures allowing persistence of morphological variants in a population (Sahley 1996). Individual populations may (re)adapt for a time to one kind of principal pollinator but the lineages 'descend through an ever changing mosaic of pollinators' (Thomson et al. 2000: 19; see also Wilson & Thomson 1996, Thompson 1994). Otherwise, the 'despecialised' stages might be 'specialised' (or remain 'despecialised') on different syndromes as evolutionary endpoints (Muchhala 2003) being under stabilising selection because it is optimal under an environment with different pollinators (Aigner 2001). Not excluding the one and favouring the other pollinator might be advantageous under unstable environmental conditions (seasonal and geographical variation) in which the presence of a certain pollinator guild is unpredictable.

Given the assumed shift from bee to bird flowers and the ecological constraints, intermediate stages among clearly adapted flowers should be expected. This is especially true for the young and evolutionarily unstable subgenera *Calosphace* and *Audibertia*, which include many endemics and highly variable species (*Calosphace*, Reisfield 1987) and hybrids (especially *Audibertia*; Emboden

1971, Neisess 1983). The limited number of intermediates in *Salvia* indicates a strong selection pressure against the presence of more than one dominant pollinator group, again pointing to specialisation.

4.5 APPENDICES

Appendix 1. List of sources used for the 182 ornithophilous *Salvia* species (see Appendix 3). Sources are listed after the following order: literature, herbarium specimens and plants studied in the field ('wild') and in cultivation ('cult.');

S. acuminata Ruiz & Pav.: Epling 1939; Ruiz & Pavon 1798; *Macbride* 3661 (F); *Weberbauer* 6699 (GH); *S. adenophora* Fernald: Epling 1939; dos Santos 1991; *Nelson* 2093 (syntype/isolectotype, US); *Nelson* 2093 (a) (isotype of *S. cyclophylla*, US); *M. Crone* 7 (MJG, +cult.); *S. alborosea* Epling & Játiva: Epling & Játiva 1966; Sagástegui et al. 2003; López et al. 3724 (holotype, UC-JEPS); *Hart* 1533 (K); *Lezama & Veneros* 15557 (K); *Llatas Quiroz* 2141 (F); *Sagástegui* 15910 (TEX-LL); *S. altimitrata* Epling: Epling 1939; *Goldman* 823 (holotype, US); *S. altissima* Pohl: Epling & Toledo 1943; *Pohl* 1718 (K); *S. apparicii* Brade & Barb.Per.: Brade & Barbosa 1947; *S. arbuscula* Fernald: Epling 1939; *E. Langlassé* 767 (holotype, GH; isotype, K, P, G); *S. arduinervis* Urb. & Ekman: Torke 2000; *Ekman H-3168/b* (isotype, GH, K, NY); *S. articulata* Epling: dos Santos 1991; Epling 1939; Epling & Toledo 1943; *Mosén* 1922 (holotype, S); *S. Vogel* 1965/784 (WU); *Krapovichas & Cristóbal* 35441 (K), *Regnell* 1 312 (K); *W. Hoehne s.n.* (K); *S. atrocaulis* Fernald: Epling 1939; *Pringle* 8887 (holotype, GH; isotype, C, GH, K, P, S, US); *S. atrocyanea* Epling: Epling 1939; Wood in press; Legname 1962; Pontiroli 1993; *P. Wester* 3 (K, LPB, MJG, wild), 5-7 (MJG, wild), 8 (MJG, wild, cult.); *S. ayavacensis* Kunth: Epling 1937, 1939; Kunth 1817; Macbride 1960; *Weberbauer* 6399 (isotype F, GH); *S. bahorucona* Urb. & Ekman: Torke 2000; *S. balaustina* Pohl: Buzato et al. 2000; dos Santos 1991; Epling 1939; *Buzato & Sazima* 26.293 (K); *S. benthamiana* Gardner: dos Santos 1991; Epling 1939; *Gardner* 580 (isotype, G, K, NY, UC-JEPS, US); *S. betulifolia* Epling: Ahlenslager 1984; Epling 1941; *Palmer* 477 (isotype, MO, NY); *Reveal* 3037 (isotype of var. *chasmema*, MO, NY, TEX-LL, US); *S. blepharophylla* Brandegees ex Epling: Epling 1939; *Purpus* 4950 (holotype, UC-JEPS); *Purpus* 5450 (isotype, MO, NY, US); *P. Wester* 450 (MJG, cult.); *S. booleana* B.L.Turner: Turner 1995a; *Lundell* 5470 (TEX-LL); *S. buchananii* Hedge: Hedge 1963; *P. Wester* 545 (MJG, cult.); *S. cacaliifolia* Benth.: Epling 1939; *P. Wester* 416, 558 (MJG, cult.); *S. camarifolia* Benth.: Epling 1939; Fernández Alonso 2002; Wood & Harley 1989; *H.H. Smith* 567 (holotype, NY; isotype, GH, H, K, NY, P, TEX-LL, UC-JEPS); *Smith* 379 (K); *Fernández Alonso et al.* 13352 (holotype of ssp. *ibiricensis*, COL), 13785 (paratype of ssp. *ibiricensis*, COL); *S. chapadensis* E.P.Santos & Harley: dos Santos & Harley 2004; *S. cinnabarina* M.Martens & Galeotti: Epling 1939; Standl. & Williams 1973; *Pringle* 4947 (P, isotype); *P. Wester* 198 283, 290, 302 (MJG, wild), 265 (MEXU, MJG, wild); *S. coccinea* Etl.: Epling 1939; *P. Wester* 12, 237, 299 (LPB, MJG, wild), 556 (MJG, cult.); *S. cocuyana* Fern.Alonso: Fernández Alonso 1995a; *Wood* 5139 (holotype, COL); *S. confertiflora* Pohl: dos Santos 2004; Epling 1939; *P. Wester* 561 (MJG, cult.); *S. cubensis* Britton & P.Wilson: Epling 1939; *J.A. Shafer* 3766 (cotyp, NY); *Howard* 6170 (P); *S. curtiflora* Epling: Epling 1939; *Skutch* 1972 (isotype, NY, US); *Williams et al.* 23188 (TEX-LL); *P. Wester* 294 (MEXU, MJG, wild); *S. curviflora* Benth.: Epling 1939; *Graham* 97 (holotype, K); *S. cyanocephala* Epling: Epling 1939; Fernández Alonso 2003, 2006; Wood & Harley 1989; *Wood* 5409, 5122 (K), *Wood* 5000 (MEXU); *Fernández Alonso, Perez & Filgueira* 14605 (MEXU); *Fernández Alonso & Castillo* 18917 (holotype and isotype of ssp. *macrosigmantha*, COL); *S. cylindriflora* Epling: Epling 1939; *Pearce* 565 (holotype, K); *S. darcy* J.Compton: Compton 1994; *P. Wester* 479, 566 (MJG, cult.); *S. diamantina* E.P.Santos & Harley: dos Santos & Harley 2004; *S. disjuncta* Fernald: dos Santos 1991; Epling 1939; Standl. & Williams 1973; *Ghiesbreght* 76 (syntype, NY); *Ghiesbreght* 753 (MO); *Nelson* 3166 (US); *P. Wester* 254 (MJG, wild), 296, 304 (BIGU, MEXU, MJG, wild); *S. divinorum* Epling & Játiva: Epling & Játiva 1962; Reisfield 1993; *Reisfield* 1242 (K); *P. Wester* 575 (MJG, cult.); *S. dombeyi* Epling: Epling 1939; Macbride 1960; Wood in press; *S. King* 278 (F); *Mandon* 712 (K); *Pearce* 851 (K); *P. Wester* [576-577] (MJG, cult.); *S. dorisiana* Standl.: Standley 1950; *Williams & Molina* 13667 (isotype, US); *P. Wester* 578 (MJG, cult.); *S. dugesiana* Epling: Epling 1939; Dugès 226 (holotype, syntype, GH); *S. elegans* Vahl: Epling 1939; *Galeotti* 685 (isotype of *S. punicea*, P); *P. Wester* 156, 193, 214 (MJG, wild), 165 (MEXU, MJG, wild), 579 (MJG, cult.); *S. ernesti-vargasii* C.Nelson: Nelson 1984; *Nelson* 3678 (isotype, MO); *S. erythrostephana* Epling: Epling 1951; Epling & Mathias 1957; *Tucker* 989 (K); *S. espirito-santensis* Brade & Barb.Per.: Brade & Barbosa 1947; dos Santos 1991; *Brade et al.* 18369 (isotype, K); *S. exserta* Griseb.: Epling 1939, 1941; Wood in press; *Lorentz & Hieronymus* 985 (holotype, UC-JEPS: slide with flower and copy of GOET); *Krapovickas* 19167 (P); *P. Wester* 22, [24], 28 (MJG, wild), 27 (MJG, wild, cult.), 23 (LPB, MJG, wild, cult.); *S. falcata* J.R.I.Wood & Harley: Wood & Harley 1989; *Wood* 4962 (holotype, COL; isotype, K), *Wood* 4944 (K); *S. florida* Benth.: Epling 1939, 1941; *Wasshausen* 949 (K); *Schmidt-Lebuhn* 450 (K, MJG); *S. formosa* L'Hér.: Epling 1939; Mirbel 1810;

Appendix 1 (cont.).

Ruiz & Pavon 1798; *Mathews* 799 (K); *Sandeman* 5/34 (K); *Stork & Horton* 9387 (K); *Woytkowski* 34003 (F); *S. foveolata* Urb. & Ekman: Torke 2000; *Ekman* H7737a, H7799 (K); *Torke* 84 (FLAS); *S. fruticetorum* Benth.: Epling 1939; Epling & Toledo 1943; Schmidt 1858; *Prinz Maximilian zu Neuwied s.n.* (K); *S. fulgens* Cav.: dos Santos 1991; Epling 1939; Ramamoorthy 1984a, 2001; *M. Crone* 15 (MJG); *P. Wester* 159 (MEXU, MJG, wild, cult.), [181] (MJG, wild); *S. funckii* Briq.: Epling 1939; Wood & Harley 1989; *Funck* 280 (holotype, G); *S. gachantivana* Fern.Alonso: Fernández Alonso 1995a; *Fernández Alonso* 8217 (COL); *Wood* 5153 (COL); *S. gesneriiflora* Lindl. & Paxton: dos Santos 1991; Epling 1939; Ramamoorthy 2001; *P. Wester* 164, 194 (MEXU, MJG, wild), 213 (MJG, wild), 591 (MJG, cult.); *S. graciliramulosa* Epling & Játiva: Epling & Játiva 1966; Wood in press; *P. Wester* 14 (LPB, MJG, wild, cult.); *S. grandis* Epling: Epling 1944; Standley & Williams 1973; *Steyermark* 43047 (holotype, UC-JEPS); *S. gravida* Epling: Epling 1940a, 1941; *Hinton* 12355 (isotype, MO, NY, TEX-LL); *P. Wester* 196 (MJG, wild, cult.); *S. greggii* A.Gray: Epling 1939; *P. Wester* 527 cultivar *alba* (MJG, cult.); *S. grewiifolia* S.Moore: Epling & Toledo 1943; Wood in press; *P. Wester* 15 (K, LPB, MJG, wild, cult.); *S. guaranitica* A.St.-Hil. ex Benth.: Epling 1939; Suarez 1965; *P. Wester* 559, 418 (MJG, cult.); *S. haenkei* Benth.: Epling 1939; Wood in press; *P. Wester* 55, 56, 58, 61, 67, 74, 80-82, 88 (MJG, wild, div. cult.), 65 (K, LPB, MJG, wild); *S. hapalophylla* Epling: Epling 1939; *Weberbauer* 7858 (holotype, F; isotype, UC-JEPS); *Wasshausen & Salas* 1188 (K); *S. harleyana* E.P.Santos: dos Santos 2004; *S. hatschbachii* E.P.Santos: dos Santos 1994; *S. heerii* Regel: Epling 1939; Trelease 1882; photo C. Froissart; *S. henryi* A.Gray: Walker & Elisens 2001; *R. Duncan s.n.* (*S. davidsonii*, UCR); *P. Wester* 374 (MJG, cult.); *S. herrerae* Epling: Epling 1939; *Herrera* 3207 (isotype, F; syntypes, UC-JEPS); *S. hidalgensis* Miranda: Miranda 1950; *Rafael H.* 6471 (MEXU); *Miranda* 9451 (MEXU); *Medrano et al.* 10071 (MEXU); *S. hilarii* Benth.: Epling 1939; Epling & Toledo 1943; *W. Hoehne* 4017 (K); *S. hirta* Kunth: Epling 1939; *Hart* 1363 (K); *Lewis et al.* 2625 (K); *Penland* 1200 (UC-JEPS); *Steyermark* 53708 (F); *S. hirtella* Vahl: Epling 1939; *Asplund* 18001 (K); *Harling et al.* 6862 (K); *Schmidt-Lebuhn* 395 (MJG); *Schmidt-Lebuhn* 395 (K, MJG, +cult.); *S. holwayi* S.F.Blake: Epling 1939, 1941; Ramamoorthy 1984a; Standley & Williams 1973; *Holway* 579 (holotype, US); *P. Wester* 287 (MEXU, MJG, wild), 291 (MJG, wild); *S. integrifolia* Ruiz & Pav.: Epling 1939; *Dombey* 273 (isotype, US, P); *López & Sagástegui* 3552 (UC-JEPS); *Lourteig* 3262 (K); *Sandeman* 5317 (K); *S. involucreta* Cav.: Epling 1939; Epling & Mathias 1957; Kunth 1817; Ramamoorthy 1984a; *P. Wester* [580], 581 (MJG, cult.); *S. iodantha* Fernald: Epling 1939; *Pringle* 8039 (isotype, NY, US); *P. Wester* 212 (MJG, wild), 582 (MJG, cult.); *S. iodophylla* Epling: Epling 1939; *Botteri* 793 (holotype, K); *S. itaguassuensis* Brade & Barb.Per.: Brade & Barbosa 1947; *Brade* 18476 (isotype, NY); *S. iuliana* Epling: dos Santos 1991; Epling 1947b; *Steyermark* 56450 (holotype, UC-JEPS); *S. jorgehintoniana* Ramamoorthy: Turner 1995b; *Hinton* 21348 (holotype, TEX-LL; isotype, K); *S. karwinskii* Benth.: Epling 1939; Pool 2001; Ramamoorthy 1984a; Standley & Williams 1973; *P. Wester* 236, 307 (MEXU, MJG, wild), 571 (MJG, cult.); *S. lachnaioclada* Briq.: Torke 2000; *Eggers* 2594 (isotype, B, L); *Ekman* H-5086 (isotype of *S. ottoschulzii* var. *neurocalyx*, NY); *S. lachnostoma* Epling: Epling 1939; *S. lanicaulis* Epling & Játiva: Epling & Játiva 1963; *López & Sagástegui* 2729 (holotype, UC-JEPS); *Sagástegui et al.* 8113 (K); *Sánchez Vega* 7032 (F); *S. lasiantha* Benth.: Epling 1939; *Pittier* 746 (isotype of *S. pittieri*, US); *Rose* 2862 (isotype of *S. populifolia*, US); *P. Wester* 248 (MEXU, MJG, wild), 258 (MJG, wild); *S. lavendula* Alain: Liogier 1988; Torke 2000; *A.H. Liogier* 12911 (holotype, NY; isotype, US); *S. leucantha* Cav.: Epling 1939; Ramamoorthy 2001; Wood & Harley 1989; *P. Wester* [466], 583 (MJG, cult.); *S. leucocephala* Kunth: Epling 1939; *Asplund* 6837 (K), *Asplund* 20501 (TEX-LL); *Camp* E-3122 (K); *Lewis & Klitgaard* 2298 (K); *Schmidt-Lebuhn* 399 (K, MJG, +cult.); *S. libanensis* Rusby: Ahlenslager 1984; Epling 1939; Wood & Harley 1989; *H.H. Smith* 1380 (lectotype, NY; lectotype and isolectotype, GH; isotype, TEX-LL, US); *Viereck s.n.* (K); *S. lineata* Benth.: Epling 1939; *Purpus* 2579 (holotype of *S. hamata*, UC-JEPS), *Purpus* 2579a (isotype of *S. hamata*, NY); *M. Crone* 12 (MJG, +cult.); *S. littae* Vis.: Epling 1939; *P. Wester* 281 (MEXU, MJG, wild); *S. lobbii* Epling: Epling 1939; Fernández Alonso 2006; *Lobb* 293 (holotype, K; isotype, W); *Schmidt-Lebuhn* 475 (K, MJG); *S. longibracteolata* E.P.Santos: dos Santos 1994; *S. longistyla* Benth.: Epling 1939; *P. Wester* 268 (MEXU, MJG, wild), 570 (MJG, cult.); *S. macrocalyx* Gardner: dos Santos 1991; Epling 1939; *S. macrophylla* Benth.: Epling 1939; Wood in press; *Schmidt-Lebuhn* 446 (K, MJG, +cult.); *S. madrensis* Seem.: Epling 1944; *Breedlove* 35690 (MEXU); *S. Barry David* 483 (FLAS); *Taylor & Knees* 382 (K); *Seemann* 2079 (isotype, UC-JEPS); *P. Wester* [584], 601 (MJG, cult.); *S. marci* Epling: Epling 1939; Shreve & Wiggins 1964; Wiggins 1980; *Jones* 27298 (holotype, UC-JEPS); *Carter et al.* 2053 (K); *H.S. Gentry* 4143 (K, MEXU); *R. Moran* 7449 (SD); *S. mattogrossensis* Pilg.: dos Santos 2004; Epling 1939; Epling & Toledo 1943; *S. medusa* Epling & Játiva: Epling & Játiva 1963; Fernández Alonso 2006; *Sagástegui et al.* 2003; *López & Sagástegui* 3535 (holotype, UC-JEPS; isotype, HUT); *Sagástegui et al.* 16328 (HAO); *S. melaleuca* Epling : Epling 1939; Pérez et al. 2006; Wood & Harley 1989; *Killip & Smith* 19735 (holotype of ssp.

Appendix 1 (cont.).

melaleuca, NY; isotype, GH); Wood 3763 (holotype of ssp. *totensis*, COL), Wood 4330, 4332, 4503 (K); *S. melissiflora* Benth.: dos Santos 2004; Epling 1939; Epling & Játiva 1963; Epling & Toledo 1943; Dusén 7784 (isosytype, GH); Hatschbach 30578 (K); Ferreira 28 (K); Kummrow 672 (K); *S. Vogel* 1965/604 (WU); *S. mentiensi* Pohl: Epling 1939; Epling & Játiva 1963; Epling & Mathias 1957; Epling & Toledo 1943; Pohl 1827; *Anonymous s.n.* (WU 38020); *Ball s.n.* (K); *S. microphylla* Kunth: Epling 1939; Standley & Williams 1973; Hansen 7679 (F); *P. Wester* 244 (MEXU, MJG, wild), 155 (MJG, wild), 415, 526 (var. *wislizenii*, MJG, cult.); *S. miniata* Fernald: Epling 1939; 1940a, Standley & Williams 1973; Ghiesbreght 760 (holotype, GH); Schipp S-632 (paratype of *S. lundellii*, GH); *P. Wester* 585 (MJG, cult.); *S. neovidensis* Benth.: Epling 1939; Prinz Maximilian zu Wied s.n. (isotype, GOET); *S. nervata* M.Martens & Galeotti: Epling 1939; Nelson 3635 (holotype and isotype of *S. monochila*, US); *P. Wester* 292 (BIGU, MEXU, MJG, wild); *S. nigrescens* Alain: Liogier 1956; A.H. Liogier 3706 (isotype, NY); *S. oaxacana* Fernald: Epling 1939; *P. Wester* 259 (MEXU, MJG, wild); *S. ombrophila* Dusén: Brade 1943; Epling 1939; Epling & Mathias 1957; Epling & Toledo 1943; Harley 20346, 20346a, 20342 (K); dos Santos 132 (K); *S. oppositiflora* Ruiz & Pav.: Epling 1939; Macbride 1960; Ruiz & Pavón 1798; Pennell 13534 (F); Schmidt-Lebuhn 423, 464 (K, MJG, +cult.); *S. orbignaei* Benth.: Epling 1939, 1947b; Wood in press; *P. Wester* 39-42, 44, 45, 47, 48, 51 (MJG, wild, div. cult.), 50 (K, LPB, MJG, wild); *S. orthostachys* Epling: Epling 1939; Wood & Harley 1989; Fernández Alonso 1995a; Killip & Smith 20746 (holotype, GH); Wood 4510 (K), Wood 4175 (holotype of ssp. *soatensis*, COL); *S. oxyphora* Briq.: Epling 1939; Wood in press; *P. Wester* 16 (LPB, MJG, wild, cult.); *S. palealis* Epling: Epling 1940a; Hinton 14040 (holotype, UC-JEPS; isotype, K, NY, US); *S. paramicola* Fern.Alonso: Fernández Alonso 1995b, 2003; J. Aguirre C. 850 (holotype, COL); *S. paryskii* Skean & Judd: Skean & Judd 1988; Torke 2000; Skean 2096 (isotype, GOET); *S. patens* Cav.: Epling 1939; *P. Wester* 563, [593] (MJG, cult.); *S. pauciserrata* Benth.: Epling 1939; Epling & Mathias 1957; Wood & Harley 1989; Hartweg 1327 (isotype, P); Lehmann 5826 (K); Schmidt-Lebuhn 369 (ssp. *calocalicina*, K, MJG, +cult.); *P. Wester* 555 (ssp. *calocalicina*, MJG, cult.); *S. pavonii* Benth.: Epling 1939, 1941; Lobb 82 (K); McLean s.n. (K); Saunders 689 (K); Stork 10956 (F); *S. peninsularis* Brandegees: Epling 1939; Shreve & Wiggins 1964; Wiggins 1980; Brandegees s.n. (holotype, UC-JEPS); R Moran 18786 (SD); photo J. Rebman (SD); *S. penstemonoides* Kunth & C.D.Bouché: Bentham 1876; Correll & Johnston 1970; Gray 1886; Kunth & Bouché 1848; Walker et al. 2004; Walker & Sytsma 2007; Lindheimer 460 (isotype, NY); *P. Wester* [586] (MJG, cult.); *S. persicifolia* A.St.-Hil.: dos Santos 1991; Epling 1939; *S. phaenostemma* Donn.Sm.: Epling 1939; Nelson 3736 (holotype, US); *S. pichinchensis* Benth.: Fernández Alonso 2006; Mansfeld 1937; Epling 1939; Jameson 797 (isotype of *S. siphonantha*, US, K); Ollgard & Balslev 9815 (K); Schmidt-Lebuhn 381 (K, MJG); *S. plumosa* Ruiz & Pav.: Epling 1939; Ruiz & Pavon 1798; *S. pringlei* B.L.Rob. & Greenm.: Epling 1939; Pringle 4564 (isotype, K, NY, P, TEX-LL, US); Reveal 4029 (TEX-LL; and photos); *S. psilantha* Epling: Epling 1939; Weberbauer 6590 (holotype, UC-JEPS; isotype, F, GH); *S. pubescens* Benth.: Ahlenslager 1984; *P. Wester* 276 (MJG, wild); *S. pulchella* DC.: Epling 1939; Ramamoorthy 2001; Pringle 8674 (isotype of *S. ancistrocarpha*, MO, NY, P, TEX-LL, US); *S. quitensis* Benth.: Epling 1939; Jameson 711 (holotype P; cotype, NY; isotype, K, P); Fleming 36 (K); Harling 6827 (F); *S. raveniana* Ramamoorthy: Ramamoorthy 1984b; Calzada 21603 (MEXU); Manzanero 241 (OAX); Ramamoorthy 4488 (K, MEXU); Reyes 797 (MEXU); Torres et al. 1926 (MEXU); *S. regla* Cav.: Ahlenslager 1984; *P. Wester* 255 (MJG, wild), 356 (MJG, cult.); *S. regnelliana* Briq.: Briquet 1904; Epling 1939; Epling & Toledo 1943; Lindman 1261 (holotype, S); *S. rhodostephana* Epling: Epling 1939, 1941; Killip & Smith 23323 (holotype of *S. hastifolia*, UC-JEPS; isotype, NY, US); Wasshausen & Encarnación 568 (K); *S. rivularis* Gardner ex H.B.Fielding: Brade 1943; dos Santos 1991; Epling 1939; Brade 16371 (K); Martinelli 12029 (K); E. Pereira 247 (K); *S. roemeriana* Scheele: Walker & Elisens 2001; *P. Wester* 347, 350, 371, [348] (MJG, wild), 564 (MJG, cult.); *S. rosei* Fernald: Epling 1939; Fernald 1900; J.N.Rose 2844 (holotype, GH; isotype, US); *S. rubescens* Kunth: Epling 1939; Wood & Harley 1989; Humboldt & Bonpland s.n. (holotype, P); Wood 4161 (holotype of ssp. *dolichothrix*, COL); *P. Wester* 442 (MJG, cult.); *S. rubrifaux* Epling: Epling 1951; Jørgensen & Ulloa 1994; Vargas 6955 (holotype, UC-JEPS; isotype, K); *S. rubriflora* Epling: Epling 1951; Fernández Alonso 2003; Wood & Harley 1989; Haught 5944 (isotype, COL, P, US); Fernández Alonso & G. Perez 12600A (MEXU); Fernández Alonso et al. 12600 A (K); Wood 3979, 4580, 4942 (K); *S. rufula* Kunth: Epling 1939, 1941; Harley 1999; Jørgensen & Ulloa 1994; Wood & Harley 1989; Hartweg 1326 (isotype, LD); Rusbyi 574 (holotype of *S. pseudolantana*, NY); Wood & Harley: Wood 5181 (holotype of ssp. *rufula* var. *nutans*, COL); Cuatrecasas 8184 (topotype of *S. laurifolia*, F); Wood 5347 (ssp. *latens*, K), Wood 4906 (ssp. *paezorum*, K), Wood 5200 (ssp. *paezorum*, K); *S. rusbyi* Britton: Epling 1939; Bang 422 (holotype, NY); Beck 9299, 18308 (K); Gentry et al. 44226 (K); Solomon 9378 (K); Solomon & Nee 12612 (K); Solomon & Stein 11720 (K); Solomon & Uehling 12228 (K); Wasshausen & Salas 1206 (K); Wood 13015 (K); Wood & Mondaca 14545, 14574 (K); Wood & Wasshausen 13755, 13928

Appendix 1 (cont.).

(K); *P. Wester* 31 (LPB, MJG, wild); *S. sagittata* Ruiz & Pav.: Epling 1939; Wood & Harley 1989; *Schmidt-Lebuhn* 331 (K, MJG, +cult.); *P. Wester* 495 (MJG, cult.); *S. salicifolia* Pohl: dos Santos et al. 2005; Epling 1939; Epling & Toledo 1943; *Glaziou* 18279 (P); *Irwin et al.* 29119 (K); *S. scabrata* Britton & P. Wilson: Epling 1939; *J. A. Shafer* 4075 (holotype, NY; slides with flowers in UC-JEPS); *S. scabrida* Pohl: Epling 1939; Epling & Toledo 1943; dos Santos & Harley 2004; *Arbo M.M. et al.* 5248 (K); *Irwin et al.* 25759 (K); *R.L. Mendonsa* 305 (K); *S. scandens* Epling: Epling 1939, 1944; *Weberbauer* 7796 (holotype, US); *S. sciaphila* (J.R.I. Wood & Harley) Fern. Alonso: Fernando Alonso 2003; Wood & Harley 1989; *S. secunda* Benth.: dos Santos 2004; Epling 1939, 1940a; *Vauthier* 408 (isotype of var. *tomentella*, L, G); *Regnell III* 932 (isotype, P); *Forzza et al.* 2841 (K); *S. sellowiana* Benth.: Epling 1939; Epling & Toledo 1943; *G. Gottsberger* 36-9966, 21-9477 (K); *I. Gottsberger & G. Gottsberger* 125-16471 (K); *Hatschbach & Pereira* 11442, 11445 (K); *Hunt* 6396 (K, P); *S. Vogel* 1956/658 (WU); *S. sessei* Benth.: Ahlenslager 1984; *P. Wester* [175] (MJG, wild), 179, 219 (MEXU, MJG, wild); *S. sigchosica* Fern. Alonso: Fernández Alonso 2006; *S. spathacea* Greene: Neisess 1983; *P. Wester* 444 (MJG, wild), [400], 544 (MJG, cult.); *S. speciosa* C. Presl ex Benth.: Epling 1939; *Ferreyra* 14628 (K); *Macbride* 1212 (F); *Sagástegui et al.* 15681 (TEX-LL); *Sagástegui* 9062 (K); *Sanchez Vega* 2253 (CHAPA); *Sandeman* 4638 (K); *S. speirematoides* C. Wright: Epling 1939; *Wright* 3757 (cited as 3657, possible isotype, NY); *Wright s.n.* (isotype, K); *S. splendens* Sellow ex Roem. & Schult.: dos Santos 2004; Epling 1939; Epling & Toledo 1943; *P. Wester* 557 (MJG, cult.); *S. sprucei* Briq.: Epling 1939, *Camp E-3974* (K); *Spruce* 5990 (isotype, P); *S. squalens* Kunth: Epling 1939; Epling & Játiva 1963; Kunth 1817; *Hutchinson & Wright* 5432 (P); *P. Wester* 498, 592 (MJG, cult.); *S. stolonifera* Benth.: Bentham 1839-1857; Epling 1939; Ramamoorthy 1984a; *Hartweg* 70 (isotype, L); *Pringle* 4705 (UC-JEPS); *P. Wester* 247 (MEXU, MJG, wild); *S. striata* Benth.: Epling 1939; Macbride 1960; *Stork & Horton* 10667 (F); *Schmidt-Lebuhn* 575 (K, MJG, +cult.), *s.n.* (MJG, +cult.); *S. subhastata* Epling: Epling 1939, 1940a; *Langlassé* 570 (holotype, K); *S. subrotunda* A. St.-Hil.: Epling 1939; *Saint Hilaire* B1024 (holotype, P); *Balansa* 1156 (holotype of *S. micheliana*, P); *S. Vogel* 1965/551 (WU); *S. subrubens* Epling: Epling 1939; Standley & Williams 1973; *Heyde & Lux* 3120 (holotype, US; isotype, UC-JEPS); *S. summa* A. Nelson: Walker & Elisens 2001; *P. Wester* 373 (MJG, cult.); *S. tenuiflora* Epling: Epling 1939, 1960; *F. Müller* 446 (K); *S. thormannii* Urb.: Torke 2000; *v. Türckheim* 3611 (isotype, K, P, L); *Torke* 105 (FLAS); *S. tolimensis* Kunth: Epling 1939; Wood & Harley 1989; *Purdie s.n.* (K); *Wood* 5086 (K); *S. tomentella* Pohl: Epling 1939; Epling & Toledo 1943; Pohl 1827; *Claussen* 1538 (P); *Hatschbach et al.* 36223 (K); *S. tortuosa* Kunth: Epling 1939; Gilli 1983; Wood & Harley 1989; *Humboldt & Bonpland s.n.* (holotype, P); *E.W.D. & M.M. Holway* 889 (holotype of var. *detonsa*, US); *W. Jameson* 685 (P); *Schmidt-Lebuhn* 350, 351 (K, MJG, +cult.); *Gilli* 284 (*S. corazonica*, W); *S. townsendii* Fernald: Epling 1939; *CHT Townsend* 426 (holotype, GH; isotype, MO, NY); *Tenorio & Romero* 1872 (K); *S. trachyphylla* Epling: Mansfeld 1937; Epling 1939; *Pachano* 202 (holotype, US); *Grubb et al.* 224 (K); *Harling et al. s.n.* (K); *S. tubifera* Cav.: Epling 1939, 1941; Ramamoorthy 1984c; Cavanilles 1791; *P. Wester* 231 (B, BIGU, JEPS, K, MEXU, MJG, TEX, wild); *S. tubiflora* Sm.: Epling 1939; Macbride 1960; Ruiz & Pavón 1798; *Dombey s.n.* (isotypes, P); photo Froissart; *S. tubulosa* Epling: Epling 1939; *Pearce* 261 (holotype, K); *Smith et al.* 1779 (K); *S. tuerckheimii* Urb.: Torke 2000; *v. Türckheim* 2896 (isotype, NY, L); *Ekman H-13625* (holotype of *S. pinetorum*, K; isotype, GH, NY); *Ekman* 13947 (holotype of *S. latibracteata*, S; isotype, K); *S. uncinata* Urb.: Torke 2000; *Ekman H13760* (neoisotype, K); *S. unguella* Epling: Epling 1940a; *Penland* 1173 (holotype, COLO); *S. venulosa* Epling: Epling 1939; Wood & Harley 1989; *Pennell* 10616 (isotype, US); *Wood* 5381, 5384 (K); *S. verapazana* B.L. Turner: Turner 1996; *Contreras* 11224 (TEX-LL); *S. vestita* Benth.: Bentham 1848; Epling 1939; *Lobb s.n.* (holotype, K); *S. wagneriana* Pol.: Epling 1939, 1940b; Nowicke & Epling 1969; Ramamoorthy 1984a; Standley & Williams 1973; Pool 2001; *White & White* 321 (MO); *P. Wester* 285 (BIGU, MEXU, MJG, wild), 443 (MJG, cult.); *S. weberbaueri* Epling: Epling 1939; *S. xanthotricha* Harley ex E.P. Santos: dos Santos 2004; *S. xeropapillosa* Fern. Alonso: Fernández Alonso 1995a, 2003; *Langenheim* 3584 (holotype, COL).

Appendix 2. List of sources used for the non-ornithophilous *Salvia* species presented in detail (see Appendix 4). Sources are listed in the following order: literature, herbarium specimens and plants studied in the field ('wild') and in cultivation ('cult.');

square brackets indicate pickled flowers only.

S. aspera M.Martens & Galeotti: Epling 1939; *Pringle* 6240 (P); *P. Wester* 257 (MEXU, MJG, wild), 261 (MJG, wild), 546 (MJG, cult.); *S. clevelandii* (A.Gray) Greene: Neisess 1983; *P. Wester* 515 (MJG, wild), [406], 487, 560 (MJG, cult.); *S. concolor* Lamb. ex Benth.: Epling 1939; Ramamoorthy 2001; *Beaman* 2068 (MEXU); *P. Wester* 167 (MEXU, MJG, wild, cult.); *S. discolor* Kunth: Epling 1939; *P. Wester* 574 (MJG, cult.); *S. eremostachya* Jeps.: Epling 1938; Neisess 1983; Shreve & Wiggins 1964; *P. Wester* 459 (MJG, wild, cult.), 460 (MJG, wild); *S. greatae* Brandege: Neisess 1983; *P. Wester* 499 (MJG, UCR, wild), 481, 482 (MJG, cult.); *S. mexicana* L.: Epling 1939; var. *minor*: *M. Crone s.n.* (MJG), *P. Wester* 183 (MEXU, MJG, wild), [228] (MJG, wild), 547 (MJG, cult.), var. *major*: *P. Wester*: 200, 203, 263 (MEXU, MJG, wild), 204 (MJG, wild), 548 (MJG, cult.); *S. mohavensis* Greene: Neisess 1983; *Sanders* 369 (UCR); *P. Wester* 469, 491-494, 506, 510, 516-517 (MJG, wild), 507, 508 (MJG, UCR, wild), 599 (MJG, cult.); Pinacate-form: *Sanders & Neisess* 5658 (UCR); *P. Wester* 504 (MJG, UCR, cult.); *S. purpurea* Cav.: Epling 1939; *M. Crone s.n.* (MJG); *P. Wester* 174, 190 (MEXU, MJG, wild), 205, 206, 216, 217, 242, 243, [229, 260, 286] (MJG, wild); *S. retinervia* Briq.: Epling 1939; Wood in press; *P. Wester* 30 (LPB, MJG, wild); *S. scutellarioides* Kunth: Epling 1939; *Schmidt-Lebuhn* 349, 380, 469 (K, MJG, +cult.); *S. whitehousei* Alziar: Whitehouse 1949; *Correll D.S.* 38529 (TEX-LL); *McVaugh* 7930 (P); *P. Wester* 352 (MJG, TEX, wild), 353, 367, 524 (MJG, wild).

Appendix 3. Characteristics of the New World ornithophilous *Salvia* species (n=182).

<i>Salvia</i> spp.	corolla length [mm]	corolla tube length [mm]	upper lip length [mm]	lower lip length [mm]	lower lip position *	flower shape *	nectar retention *	functional flower type *	exposition of thecae [mm]	corolla colour *	corolla colour (CYMK) *	nectar guides on corolla	nectar concentration [%]	nectar volume [μ l] *	nectary length [mm]	pedicel length [mm]	growth form *	country *	systematics	
<i>acuminata</i> Ruiz & Pav.	59-65	47-50	12-15			b/t			0	Re						[13-17]	sh (sometimes sc)	PE	Longiflorae	
<i>adenophora</i> Fernald	22-29	16-23	5-8	5-8	a, cu, v, lc	t	-	I	0	Re	M90 Y80 S00	absent	26.2 +/-2.45 (21.2-30.1) n=26	I	3	4-8	sh	MX	Holwaya	
<i>albrosea</i> Epling & Játiva	24-25	17-18	7-8	4	ah, cu?	t (f)		II H	8-16	Re, Pu?		whole lower lip white				[7-16]	ph	PE, EC	Lopeziana	
<i>altimitrata</i> Epling	23	11	12			b		III L	[4-8]								sh	MX	Mitratiae	
<i>altissima</i> Pohl	29-33	16-18	13-15		[a]	b/t	Cb	I	0	Re						3-4	ph	BR	Hoehneana	
<i>apparicii</i> Brade & Barb.Per.	40-50	35-40	7	4		t(f) or t				Re							ss	BR	Curtiflorae	
<i>arbuscula</i> Fernald	21-23	15-17	6	[3-5]	a	t	P	II H ²	[4-8]	Pu						[2-3]	ss	MX	Iodanthae	
<i>arduinervis</i> Urb. & Ekman	21-28	16-21	5-7	3-5	[a or/andd?]	t		II H	5-8	Pi, Lav				2	2-5	sh	HT	Ekmania		
<i>articulata</i> Epling	41-61	28-45	13-16	12	d, a	b/t		I	0	Pu						4-8	sh	BR	Nobiles	
<i>atrocaulis</i> Fernald	44-47	25-30	19-21	17-20	d, a	b		I	0	Bl-daVi						5-12	ph	MX	Dusenostachys	
<i>atrocyanea</i> Epling	25-48	15-31	10-18	8-17	a, d	b	-	I	0	Bl-daVi	M80-90 C99 S00-10	absent	27.7 +/- 3.1 (21.5-32.7) n=18	I	2-3	3-4	ph	BO, AR	Coeruleae	
<i>ayavacensis</i> Kunth	37-39	27-28	7-10	8-15	a and/or d	t		II H ²	6-7	Bl-daVi						5-13	ph	PE	Cylindriflorae	
<i>bahorucona</i> Urb. & Ekman	19-26	16-21	3-5	2-3	[r, d]	t		II H		Ye, Or, Re					2-3	2-5	sh	HT, DO	Ekmania	
<i>balaustina</i> Pohl	46-55	33-40	13-22		a	b/t		I'	0	Re							6-12	sh	BR	Nobiles
<i>benthamiana</i> Gardner	36-43	23-37	16-18	[13-14]	a	b/t		I	0	Re						4-5	sh	BR	Nobiles	
<i>betulifolia</i> Epling	35-54	23-37	12-19	10-19	a	b/t		I	0	Re						2-5	sh	MX	Erythrosthachys	
<i>blepharophylla</i> Brandegees ex Epling	28-36	18-25	8-11	10-19	mostly d, also r, a	b	Cb	I	0	Re	M99 Y99 S10	absent			3-4	5-10	ph	MX	Brandegeia	
<i>booleana</i> B.L. Turner	30-42	18-27	12-15	10-12	[d]	b		I + III L'	0?	Re							ph	MX	Fulgentes	
<i>buchananii</i> Hedge	39-50	24-30	15-20	15-20	a, d	b	Cb	I	0	Pu	M99 C40 Y10	pale pinkish-white stripes	28.2 +/-3.4 (23-41.8) n=27	10.8 +/-4.7 (4-15.5) n=6; I	2-3	2-4	ph	MX probably	Calospace	
<i>cacaliifolia</i> Benth.	22-28	17-20	4-10	8-10	ah, v, often cu	t (f)	PL	II H	6-10	Bl(rb)	M75 C95 Y00	absent	22.8 +/-3.4 (16.3-30.0) n=45	7.8 +/-2.9 (2-15.5) n=32; m	2-3	4-6	ph	MX, GT, HN	Standleyana	
<i>camarifolia</i> Benth.	15-24	12-19	3-6	3-6	a, cu, v, lc	b/t		I	0	Re						2-5	ss, sh	CO	Tubiflorae	
<i>chapadensis</i> E.P.Santos & Harley	42-46	30-33	12-15	8-10		b/t		I'	0	Re						4-5	ss, sh	BR	Nobiles	
<i>cinnabarina</i> M.Martens & Galeotti	20-33	15-25	5-8	4-6	a	t	PL	II E	4-9	Re	M99 Y70 S10	absent			2	2-4	ph	MX, GT, SV, HN	Incarnatae	
<i>coccinea</i> Eitl.	20-30	13-22	4-8	10-13	d	t	-	II H	3-9	Re	M99 Y99 S00-20	mostly absent, also small white spots	25.7 +/-1.9 (22-27.8) n=19	m	2	2-5	ah, ph	? (probably MX/Central America or BR)	Subrotundae	
<i>cocuyana</i> Fern.Alonso	12-15	11-14	1	2-3	a, v	t	PL?	II H ²	0	Re						4-5	ph	CO	Rubrescentes	
<i>confertiflora</i> Pohl	7-13	5-9	2	2-3	ah, cu, v, lc	t	-	I	0	Re	M90 Y99 S10	absent	43 +/-12.3 (23-62) n=61	m; c. 3.5	2	2-6	ss	BR	Secundae	
<i>cubensis</i> Britton & P.Wilson	18-25	13-19	5-6		[a]	t				Re							sh	CU	Brittonia	
<i>curtiflora</i> Epling	19-31	17-27	2-4	2-4	ah, v	t	PL	II H	1-3	Re, Pu	M99 C30 S20	absent			3	3-4	sh	GT	Curtiflorae	
<i>curviflora</i> Benth.	28-35	18-22	10-13	8	a	b/t	P	I	0	Pu							ph	MX	Purpureae	
<i>cyanocephala</i> Epling	28-45	20-36	4-12	5-15	r, possibly d, [a]	t	PL	II H	1-6	Bl-daVi		absent or white stripes				9-12	ss, sh	CO	Siphonanthae	
<i>cylindriflora</i> Epling	49	43	6	[6]		t			[4]							8-16	sh	PE	Cylindriflorae	
<i>darcyi</i> J.Compton	36-44	24-27	12-17	15-20	d, also weakly r	b	P, Cb	I	0	Re	M90 Y90 S00	absent			3	4-12	ph	MX	Holwaya	
<i>diamantina</i> E.P.Santos & Harley	45	28-30	14-15	7-8		b/t		I'	0	Re						5-8	ph, ss, sh	BR	Nobiles	
<i>disjuncta</i> Fernald	(18)26-46	(14)20-39	(4)6-13	(4)6-13	a, d, sometimes lc	t	RI	I	0	Re	M90-99 Y90-99 S00-10	absent	26 +/-4.1 (20.2-32) n= 12	I	2-4	3-9	ss (sc), sh	MX, GT	Holwaya	

Appendix 3 (cont.).

<i>Salvia</i> spp.	corolla length [mm]	corolla tube length [mm]	upper lip length [mm]	lower lip length [mm]	lower lip position *	flower shape *	nectar retention *	functional flower type *	exposition of thecae [mm]	corolla colour *	corolla colour (CYMK) *	nectar guides on corolla	nectar concentration [%]	nectar volume [μ l] *	nectary length [mm]	pedicel length [mm]	growth form *	country *	systematics
<i>divinorum</i> Epling & Játiva	28-35	19-27	6-10	5-7	a, cu, v, lc	t		I	0	Wh (calyx paVi to whitish)	M00 C00 S00 (calyx whitish with M45-50 C40-45 S00)	absent			3-5	4-9	ph	MX	Dusenostachys
<i>dombeyi</i> Epling	(85)98-130	(60)80-90	22-30	19-24	a	b/t		I	0	Re	M99 Y99 S10	absent	I		3-5	10-34	ss (sc), sh, tr	PE, BO	Longiflorae
<i>dorsiana</i> Standl.	53-64	35-40	19-24	15-23	d, also r	b/t	P, Cb	I	0	Pi	M90 C20-30 S00-10	absent or white/whitish area	I		4	6-14	ph	HN	Holwaya
<i>dugesiana</i> Epling	31-38	23-28	8-9	[8-9]	[a]	b/t		I'	0	Re						8-10	ss	MX	Secundae
<i>elegans</i> Vahl	28-39	18-29	8-13	7-12	a, sometimes d	t	-	II E	0-4	Re	M99 Y80 S20	absent	17.6 +/-4.3 (7.5-24) n=18	m	2-4	2-3	ph, ss	MX	Incarnatae
<i>ernesti-vargasii</i> C.Nelson	24-30	20-24	4-6	3-4	d, bc	t	P?	I'	0	Re						6-10	sh	HN	Calospace
<i>erythrostephana</i> Epling	22-23	17-20	[4-5]	[5-6]	a	t		I'	0	Pi						[5]	ss	GT, SV	Tubiflorae
<i>espirito-santensis</i> Brade & Barb.Per.	55-60	40-45	18-20	15-16	a	b/t		I	0	Re							sh	BR	Nobiles
<i>exserta</i> Griseb.	14-36	10-28	4-9	7-15	r, d	t	H	III E	6-22	Re	M99 Y99 S10	absent or white/blackish stripes	25.4 +/-5.9 (12-45) n=117	I	1-2	2-6	ah	BO, AR	Mineatae
<i>falcata</i> J.R.I.Wood & Harley	26-35	16-33	10-12	5-7	[a]	b/t		I'	0	Re						1-2	ss	CO	Tubiflorae
<i>florida</i> Benth.	30-35	24-30	5-7	[5-8]	d	t	PL	II H	8-11	Pi						6-10	sh (sometimes sc)	PE	Floridae
<i>formosa</i> L'Hér.	38-47	23-28	15-18	13-15	d, a	b	P	I	0	Re						[6-7]	ss	PE	Leonuroideae
<i>foveolata</i> Urb. & Ekman	18-28	14-22	4-6	3-5	[d]	t		II H	7-11	Ye					2-3	1-4	sh	HT, DO	Ekmania
<i>fruticetorum</i> Benth.	38	32	6			t		II H	[1]?	Re or Pu?							sh	BR	Curiflorae
<i>fulgens</i> Cav.	38-61	25-39	13-24	16-23	a, also d, sometimes r	b	P, weak Cb	I	0	Re	M99 Y70 S10	absent	24.4 +/-2.2 (20-27) n=15	12.7 +/-3.1 (9-16.5) n=7; I	3	2-7	ph, ss, sh	MX	Fulgentes
<i>funckii</i> Briq.	25-31	18-21	9-11	13-16		t (f)	PL	II H ²	[13-18]	Bl						4-7	ss (sometimes sc)	CO, VE	Hastatae
<i>gachantivana</i> Fern.Alonso	12-20	11-19	1	1-3	a and/or d, v	t	PL?	II H	0	Re					2	2-6	ph, ss	CO	Rubescentes
<i>gesneriiflora</i> Lindl. & Paxton	50-66	28-44	15-23	15-24	a, d	b	-	I	0	Re	M99 Y80 S10, M95-99 Y99 S00	absent	26.7 +/-1.9 (22.5-31.2) n=44	21.1 +/-10.7 (5.5-42.5) n=17; I	2	5-13	sh	MX	Holwaya
<i>graciliramulosa</i> Epling & Játiva	25-46	18-28	11-18	14-23	a, d	b	P, Cb	I	0	Re	young/adult: M90-99 Y50-90 S30, M99 Y60 S40, M99 Y50 S20 to old: M90-70 Y00 S30	absent or lighter area	31.5 +/-4 (24.6-44) n=25	I	2-3	5-7	ss	BO	Exiles
<i>grandis</i> Epling	22-23	16-17	6	6	[a]	t	P	I	0	Pi, Pu							sh	GT	Steyermarkia
<i>gravidata</i> Epling	44-58	27-36	17-22	20-22	a, also d	b	-	I	0	Re, Pu	M99 C50 S00, M99 C10 S60, M99 C60 Y60	absent or white/light area	23.4 +/-4.4 (11.5-30.5) n=77	27.1 +/-10.2 (16-50) n=13; I	2-4	6-15	ph	MX	Skeptostachys
<i>greggii</i> A.Gray	26-32	18-22	8-11	[13-14]	d, also a, r	b	-	I	0	Re, Pu	M00 C00 S00 (white cultivar)	absent or white			2-3	[5]	ph, ss	MX, US	Flocculosae
<i>grewiifolia</i> S.Moore	18-34	14-20	9-14	9-12	a, v, lc, sometimes cu	t	Cb	I	0	Re	M99 Y99 S00	absent	29.4 +/- 6.6 (19-53.5) n=53	I	3-4	4-7	ss	BR, BO	Hoehneana
<i>guaranitica</i> A.St.-Hil. ex Benth.	30-56	20-37	11-19	10-17	a	b	-	I	0	Bl-daVi	C99 M85-90 S00	absent			3-4	5-8	ph, ss	BR, PY, UY, AR	Coeruleae
<i>haenkei</i> Benth.	18-50	15-40	5-10	5-8	r	t	-	II H	5-10	Re	M90-99 Y80-99 S10, M90 Y70 S00, M60 Y90 S00	absent or sometimes white stripes	27.2 +/-2.2 (14-32) n=144	26.5 +/-12.2 (12-50) n=16; I	2-3	6-11	ss	PE, BO	Cylindriflorae
<i>hapalophylla</i> Epling	32-35	26-28	6-7	[4-5]	[d]	t		II H ²	[5-9]	Re						2-3	ss	PE	Cylindriflorae
<i>harleyana</i> E.P.Santos	8-9	6-8	2	2	[a, v]	t		I'	0	Re							ss	BR	Secundae
<i>hatschbachii</i> E.P.Santos	60-64	43-45	17-19	14-17	[a?]	t		I'	0	Re							ss	BR	Nobiles

Appendix 3 (cont.).

<i>Salvia</i> spp.	corolla length [mm]	corolla tube length [mm]	upper lip length [mm]	lower lip length [mm]	lower lip position *	flower shape *	nectar retention *	functional flower type *	exposition of thecae [mm]	corolla colour *	corolla colour (CYMK) *	nectar guides on corolla	nectar concentration [%]	nectar volume [μ l] *	nectary length [mm]	pedicel length [mm]	growth form *	country *	systematics	
<i>heerii</i> Regel	31-32	25-26	6	c. 6	r	t (f)	PL	II H	[13-20]	Re		white/whitish stripes				[6]	ph	PE	Cylindriflorae	
<i>henryi</i> A.Gray	28-39	22-31	6-8	8-9	d, also a	t	-	III R	0-6	Re, rarely Pi, Pu	M 90 Y20 S00 (cult.)	absent		1	3-4	ph	US, MX	Heterospace		
<i>herrerae</i> Epling	16-22	11-17	3-6	2-5	[a, v]	b/t		I'	0	Re						[4]	sh	PE	Secundae	
<i>hidalgensis</i> Miranda	23-58	18-41	5-18	4-14	[r and/or a]	b/t	H?	I	0	Ye						2-9	ss	MX	Hidalgenses	
<i>hilarii</i> Benth.	40-47	30-34	10-13	[11]		b/t		I	0	Re						6-10	sh	BR	Nobilies	
<i>hirta</i> Kunth	29-32	25	4-6	[4-6]	a	t	PL	II H ²	[7-13]	Re						[5-7]	sh	PE, EC	Cylindriflorae	
<i>hirtella</i> Vahl	24-33	20-29	4-6	6-10	d, also r	t	P	II H	7-17	Re	M90 Y90 S10	absent			2	4-12	ph	EC	Phoeniceae	
<i>holwayi</i> S.F.Blake	24-31	15-24	5-8	5-6	r/bc, also d, [a]	t	P, Cb	I	0	Re, Pi	M99 Y80 S00	absent			4	3-7	ph, ss (sometimes sc)	MX, GT, CR	Holwaya	
<i>integrifolia</i> Ruiz & Pav.	35-46	30-40	5-6	[4-6]		t	PL	II H ²	[4-10]	Or, Re						4-6	sh	PE	Cylindriflorae	
<i>involutrata</i> Cav.	33-43	21-35	7-9	7-10	r+d/bc, sometimes a	t	P, Cb	I	0	Pi	M99 C20 S00	whitish/pink areas	27.8 +/-1.2 (26.2-30.2) n=20	l	2-3	5-9	ph	MX	Holwaya	
<i>iodantha</i> Fernald	20-27	15-20	5-7	4-5	a, d, r	t	P	II H	5-7	Pu	M90 C40 S00	absent		m	2	2-4	ph, ss	MX	Iodanthae	
<i>iodophylla</i> Epling	34-35	27-28	7	[7-8]	[a, r]	t	P	II H ²	4-6	Re						[5-6]	? (ah/ph or sh)	MX	Iodophyllae	
<i>itaguassuensis</i> Brade & Barb.Per.	29	23	4	3		t				Re							ss	BR	Curtiflorae	
<i>luliana</i> Epling	48	30	18	c. 13		b		I'	0							to 15	ph	VE	Nobilies	
<i>jorgehintoniana</i> Ramamoorthy	40-55	32-45	7-10	5-6	r, d, a	t	PL	II H	5-10	Re						[mostly 10-15]	ph	MX	Curtiflorae	
<i>karwinskii</i> Benth.	26-36	18-27	6-10	3-7	r/bc	t	P, weak Cb	I	0	Re, Pi	M90-99 Y40-50 S10	absent			3	8-15	ss (sometimes sc), sh	MX, GT, SV, HN, NI	Holwaya	
<i>lachnaiclada</i> Briq.	17-27	13-22	4-5	3-4	[d]	t		II H	[4-7]	Ye, Or, Re					2	1-4	sh	HT, DO	Ekmania	
<i>lachnostoma</i> Epling	38-43	28-32	10-11	[9]		t		I	0	Re, Pu							sh	PE	Longiflorae	
<i>lancaulis</i> Epling & Játiva	23-25	18-20	5	[5-8]		t (f)		II H ²	[7-11]	Re							5-6	sh	PE	Cylindriflorae
<i>lasiantha</i> Benth.	(12)15-26	(6)8-12	(5)6-16	3-11	r, d, sometimes a	b	Rl	III L	3-8	BrOc, Ye, Or, Re, ReBr, Pi, Pu, Vi	M60-80 Y70-99 S10, M80 Y99 S50, M90 Y70 S60, M99 Y70 S40, M99 Y50 S70, M60 Y30 S60, M90 Y40 S50, M80 Y30 S60	absent			2-3	1-4	sh	MX, GT, CR	Mitratiae	
<i>lavendula</i> Alain	13-17	10-14	3	3-4		t		II H ²	[5]	Lav							4	sh	DO	Calospace
<i>leucantha</i> Cav.	16-20	13-17	3-6	3-5	ah, cu, v, lc	t	-	I	0	Wh (calyx Pu, rarely Wh)	M00 C00 S00 (calyx M90-99 C70-90 Y00-20)	absent			2	2-3	ph, ss	MX	Albolanatae	
<i>leucocephala</i> Kunth	32-44	20-28	12-19	[9-12]	r	b/t	-	I	0	Pu	M99 C70 Y50	absent				[2-4]	sh	EC	Leucocephalae	
<i>libanensis</i> Rusby	53-63	33-43	20-23	17-22	a	b/t		I	0	Re						5-25	sh	CO	Erythrostachys	
<i>lineata</i> Benth.	26-45	20-28	6-12	8-13	a	b	P, Cb	I	0	Re	M90 Y90 S00	absent			(2)	3-4	ph	MX	Fulgentes	
<i>littee</i> Vis.	24-36	15-23	9-14	6-11	r	b	P	I	0	Pi, Pu	M99 C30-50 Y00-20	absent			2	1-3	ph, ss	MX	Purpureae	
<i>lobbii</i> Epling	27-36	21-28	5-6(8)	5-6(8)	d	t (f)	PL	II H	[7-12]	Bl-daVi						5-7	sh	EC, PE?	Siphonanthae	
<i>longibracteolata</i> E.P.Santos	14	11	3	3	ah, cu, v, lc			I'	0	Re							ss	BR	Secundae	
<i>longistyla</i> Benth.	33-45	27-37	6-8	4-9	d, a	t	PL	II H	6-9	Re	M99 Y50-70 S40	absent	25.9 +/-1.6 (20-28) n=22	l	3-4	6-17	ph, ss, sh	MX	Curtiflorae	
<i>macrocalyx</i> Gardner	45-49	30-33	15-16	8-10		b/t		I	0	Re							5-8	sh	BR	Nobilies
<i>macrophylla</i> Benth.	20-26	11-18	6-13	7-11	r	t (f)	PL	II H	10-15	Bl(rb)	C99 M70 S00	absent	24 +/-1.4 (20.5-26) n=15	27.7 +/-1.6 (26.5-29.5) n=3, l	3	4-7	ss	CO, EC, BO, PE	Hastatae	
<i>madrensis</i> Seem.	23-35	18-26	4-9	3-9	a, v, lc	t	-	I	0	Ye	Y80 M10 S10	absent			3-4	9-16	ph	MX	Longipes	
<i>marci</i> Epling	22-38	14-23	10-18	6-16	[d]	b		I	0	Pu						[3-7]	ph, ss, sh	MX	Peninsulares	
<i>mattogrossensis</i> Pilg.	25-35	20-22	5-6	[3-4]	ah, cu, v, lc	t		I'	0	Re							sh	BR	Secundae	

Appendix 3 (cont.).

<i>Salvia</i> spp.	corolla length [mm]	corolla tube length [mm]	upper lip length [mm]	lower lip length [mm]	lower lip position *	flower shape *	nectar retention *	functional flower type *	exposition of thecae [mm]	corolla colour *	corolla colour (CYMK) *	nectar guides on corolla	nectar concentration [%]	nectar volume [μ l] *	nectary length [mm]	pedicel length [mm]	growth form *	country *	systematics	
<i>medusa</i> Epling & Játiva	28-56	21-46	7-12	6-13		t (f)	PL	II H ²	8-10	Bl-daVi, sometimes Pu						15-32(40)	ss	PE	Siphonanthae	
<i>melaleuca</i> Epling	35-45	32-38	6-15	12-20	[d, r?]	b/t	PL	II H	4-7	Re						3-15	ss, sh	CO	Rubescentes	
<i>melissiflora</i> Benth.	14-18	11-16	3-4	[2-3]	[a, also ah]	t			[0-1]?	Re						2-5	ph	BR	Secundae	
<i>mentiens</i> Pohl	28-41	22-34	5-8	5-7	[a]	t			0	Pi, Pu							ph	BR	Curtiflorae	
<i>microphylla</i> Kunth	20-32	14-20	6-12	7-15	d, also a	b	PL	I	0	Re, Pu, Pi	M99 C50 Y00, M90-99 C20-30 Y00-40, M99 C10 Y50	white/light areas or absent			3	2-5	ph, ss, sh	MX, US	Fulgentes	
<i>miniata</i> Fernald	28-42	20-27	8-15	12-14	d, also cu	b	-	I	0	Re	M99 Y90 S10, M99 Y90 C20	absent			2	2-4	sh	MX, GT, BZ	Silicolae	
<i>neovidensis</i> Benth.	29-31	25-26	4-5			t		II H ²	5-7							3-4	ph	BR	Curtiflorae	
<i>nervata</i> M. Martens & Galeotti	30-44	21-29	8-15	1-3	ah, v	t	PL	II H	0-1	Re, Pu	M99 Y30 S60	absent			3	3-5	sh	MX, GT	Curtiflorae	
<i>rigrescens</i> Alain	25-30	[16-19]	[9-10]			t			[1-3]?	Re							3-8	sh	CU	Calospace
<i>oaxacana</i> Fernald	32-42	15-21	7-22	12-15	d, r, rarely a	b	Cb	I	0	Re	M99 Y60-70 S10-20	absent			1	[2-3]	sh	MX	Conzattiana	
<i>ombrophila</i> Dusén	22-28	16-21	5-7	5-9	r, d, [a]	b/t		I	0	Re, Pi?						3-5	sh	BR	Tubiflorae	
<i>oppositiflora</i> Ruiz & Pav.	21-42	16-34	5-11	5-12	a, also ah, v, lc, sometimes cu	t (f)	PL	II H	2-6	Re, Pi	M90 Y90-99 S00	absent	I		2-3	4-8	ph, ss	PE	Biflorae	
<i>orbignaei</i> Benth.	32-51	18-29	10-23	9-21	d	b	P, Cb	I	0	Pi, Pu, rarely Wh	M80-99 C00-30 S00, also M60-80 C00 S00, M5-10 C00 S00	absent or white/light area	30 +/-2.2 (25.2-37.8) n=66	20.3 +/-4.6 (13-28.5) n=13; I	3	4-19	ss	BO	Pavonia	
<i>orthostachys</i> Epling	12-15	11-14	1	2	d, [a, v]	t	PL?	II H	0	Re						2-4	ph, ss	CO	Rubescentes	
<i>oxyphora</i> Briq.	30-48	22-38	5-11	7-12	d, a, also bc	t	P, Cl	I	0	Re, Pi	M90 Y60 S00, M90-99 Y00-30 S00-10	absent, rarely (?) white area	31.8 +/-2 (28.2-38.6) n=30	30.3 +/-9.7 (20-53) n=19; I	2-4	3-4	ph	BO	Tuberosae	
<i>palealis</i> Epling	25-26	17-19	5-6	5-6	[a]	t	P	II H ²	3-6	Re						[2-4]	ph	MX	Pedicellata	
<i>paramicola</i> Fern. Alonso	24-26	18-19	5	[5-6]	[a, cu, lc, d]	t			0	daVi(Black)							ph	CO	Rubescents	
<i>paryskii</i> Skee & Judd	25-31	20-25	5-6	4-5	d	t		II H		Ye, Or						2-3	3-8	sh	HT	Ekmania
<i>patens</i> Cav.	40-63	15-28	23-35	27-41	d	b	Cb	I	0	Bl(rb)	M75 C99 S10	white spots, stripes, also pale	24.9 +/-3.5 (10.4-30.3) n=38	h	2-3	5-9	ph	MX	Blakea	
<i>pauciserrata</i> Benth.	25-59	15-46	7-18	9-15	r, d [a]	t (f)	PL, P	II H	7-12	Re	M99 Y99 S10	absent	24.8 +/-1.2 (22.8-28) n=20	13.8 +/-4.9 (9-20) n=5; I	2-3	3-10	ss, sh	CO, PE, EC, VE, CR	Flexuosae	
<i>pavonii</i> Benth.	16-22	12-18	5-6	4-6	[a]	t		I	0	Ye						3-6	ss	PE	Punctatae	
<i>peninsularis</i> Brandege	21-29	15-23	6-8	6-9	d	b/t		I	0	Pi, Pu, Lav						[5-6]	ph, ss, sh	MX	Peninsulares	
<i>penstemonoides</i> Kunth & C.D. Bouché	27-40	15-27	11-16	9-11	d, a, also cu, v	b	H	I	0	Re, Pu, Pi	M99 C40 S60						ph	US	Eusphace/related to Salviastrum	
<i>persicifolia</i> A. St.-Hil.	45-50	30-35	15	8-9		b/t		I'	0	Re							sh	BR	Nobiles	
<i>phaenostemma</i> Donn. Sm.	23-25	17-18	6-7	c. 6		t			7-8	Bl or daVi						8-10	sh	GT	Sulcatae	
<i>pichinchensis</i> Benth.	31-43	20-26	11-18	[12-18]	[d]	t	PL	II H	[9->15]	Bl, daVi		white area				8-10	ph, sh	EC	Siphonanthae	
<i>plumosa</i> Ruiz & Pav.	47	35	12	15		b/t	P		0							[20-25 in fruit]	ss	PE	Leonoroideae	
<i>pringlei</i> B.L. Rob. & Greenm.	32-44	22-24	15-20	8-10	a, also d	b		I	0	Pu						5	ss	MX	Tubiflorae	
<i>psilantha</i> Epling	34-43	26-33	8-11	[8-9]		t			5-11								4-6	ph	PE	Cylindriflorae
<i>pubescens</i> Benth.	39-68	25-45	14-23	15-23	a	b/t		I	0	Re	M90 Y99 S10	absent		I	3	2-4	sh	MX	Erythrostachys	
<i>pulchella</i> DC.	24-30	16-21	7-9	7-11	a, [d?]	b	P, Cb	I	0	Re		absent				3-6	ph, ss	MX	Fulgentes	
<i>quitensis</i> Benth.	33-39	27-32	6-8	[5-10]		t	PL	II H ²	[8-12]	Re						5-10	sh	EC	Cylindriflorae	
<i>raveniana</i> Ramamoorthy	32-34	19-22	12	[7-10]	[r]	b	P	III L ³	0-3	Re, Pu, Pi						[2-3]	ph	MX	Purpureae	
<i>regia</i> Cav.	27-59	19-41	8-22	8-24	a, d	b/t	-	I	0	Re	M90 Y80 S00	absent, rarely small white spot			3	1-8	sh, sometimes tr	MX, US	Erythrostachys	
<i>regnelliana</i> Briq.	40-44	27-30	13-14	[10-14]	a	t			[3]?	Re, Pu						4-6	ss	BR	Skeptostachys	
<i>rhodostephana</i> Epling	22-34	15-25	7-9	14-18	d	t (f)	PL	II H ²	[7-16]	Pi, Pu, paVi, Bl						3	ph	PE	Hastatae	

Appendix 3 (cont.).

<i>Salvia</i> spp.	corolla length [mm]	corolla tube length [mm]	upper lip length [mm]	lower lip length [mm]	lower lip position *	flower shape *	nectar retention *	functional flower type *	exposition of thecae [mm]	corolla colour *	corolla colour (CYMK) *	nectar guides on corolla	nectar concentration [%]	nectar volume [μ l] *	nectary length [mm]	pedicel length [mm]	growth form *	country *	systematics	
<i>nivularis</i> Gardner ex H.B. Fielding	42-53	30-40	12-13	6-15	a	b/t		I	0	Re						6-8	sh	BR	Nobiles	
<i>roemeriana</i> Scheele	24-47	18-39	6-9	6-15	d, sometimes a, r	t	H	III R	0-7	Re	M90-99 Y60-80 S20	absent	24.5 +/-3.5 (18.8-32.5) n=58	I	2	3-4	ph	US, MX	Heterospace	
<i>rosei</i> Fernald	25-31	18-20	9-11	[8]		b			2-3	Pi, Pu						[3-5]	sh	MX	Pruinosae	
<i>rubescens</i> Kunth	20-39	18-31	2-6	8-10	a, also d	t	PL	II H	0-4	Re	M99 Y90 S10	absent			4	3-12	ss	CO, VE	Rubescentes	
<i>rubrifaux</i> Epling	32-38	24-30	8-11	[8-11]	[a]	b/t			10-13	Re						[4-5]	ph	PE, EC	Cylindriflorae	
<i>rubriflora</i> Epling	25-30	20-22	8-9	8-17	d	t (f)	PL	II H ²	15-18	Re						2-5	ss	CO	Hastatae	
<i>rufula</i> Kunth	16-40	11-25	5-13	4-9	a, [d, r]	b		I	0	Re						1-5	ss	CO, EC	Killipiana	
<i>rusbyi</i> Britton	40-58	29-46	8-14	8-15	d, a	b/t	-	I + III L ⁴	0-11	Re	M90-99 Y99 S00-10	absent				2-3	ss	PE, BO	Cylindriflorae	
<i>sagittata</i> Ruiz & Pav.	23-31	16-21	5-10	12-18	d	t (f)	PL	II H	8-13	Bl(rb)	M80 C99 Y00	white stripes or absent	24.5 +/-2.4 (17.8-31.2) n=28	6.9 +/-4.1 (2.5-13.5) n=5; m	2	2-5	ph	PE, CO, EC	Hastatae	
<i>salicifolia</i> Pohl	47-56	32-36	15-20	10-12	[a]	b/t		I	0	Re						8-10	sh	BR	Nobiles	
<i>scabrata</i> Britton & P. Wilson	32-35	20-22	10-14	8-10	a	t		I	0	Re						5	sh	CU	Muricatae	
<i>scabrida</i> Pohl	35-48	25-30	10-18	5-8	[a]	b/t		I	0	Re						3-4	ph	BR	Nobiles	
<i>scandens</i> Epling	50-63	38-45	12-18	16	a	b/t	P	I	0	daVi						[5]	sh (sometimes sc)	PE	Weberbaueria	
<i>sciaphila</i> (J.R.I. Wood & Harley) Fern. Alonso	35-43				a	b/t	P	I	0	Pu							ph	CO	Carneae	
<i>secunda</i> Benth.	9-13	7-10	2-3	2-3	ah, lc, v, cu	t		I	0	Re						3-4	sh	BR	Secundae	
<i>sellowiana</i> Benth.	42-62	30-45	12-17	11-15	d, a	b/t		I	0	Re						4-6	sh	BR	Nobiles	
<i>sessei</i> Benth.	30-62	20-42	10-22	9-22	a	b/t	-	I	0	Re	M99 Y90 S10	absent		I	2-3	2-7	sh, sometimes tr	MX	Erythrostachys	
<i>sigchosica</i> Fern. Alonso	18-24	11-14	7-10	[c. 10]	[d, r?]	t	[PL?]	II H ²	9-10	daVi		white stripes				3-4	ph or ss	EC	Siphonanthae	
<i>spathacea</i> Greene	28-46	22-37	5-10	6-14	d, r	t	sometimes Cb	II S	7-17	Re, Pu, Pi, rarely Ye	M80 Y40 S30-40 (young), M99 Y30(-00) S50 or M99 C20 S10 to M99 C50 S00 (adult)	absent	20 +/-5.34 (6.8-25.4) n=23	32.6 +/-16.3 (13-51) n=10; I	2-4	0-2	ph	US	Audibertia	
<i>speciosa</i> C. Presl ex Benth.	20-23	15-19	5-8	10-14	a or d	b/t			[22-43]	Pu, daVi						8-15	ss	PE	Macrostachyae	
<i>spirematoides</i> C. Wright	24-27	18-22	5-6	[3-4]		t		II H	4-6	Re						[5]	sh	CU	Brittonia	
<i>splendens</i> Sellow ex Roem. & Schult.	38-49	30-40	8-11	3-6	ah, cu, lc	t	-	II H	0-1	Re	M90-99 Y90-99 S00	absent		I	4	5-6	ph	BR	Secundae	
<i>sprucei</i> Briq.	30	24	6	[9-10]	d	t	PL	II H	[8-10]	Pi		white area or absent				8-10	sh	EC	Cylindriflorae	
<i>squalens</i> Kunth	32-44	22-29	10-17	16-19	d, a	t (f)	PL	II H	2-6	Re, Pi	M99 Y99 S10, M80 Y70 S00	absent or pale whitish area		I	3	6-7	ph	PE, EC	Biflorae	
<i>stolonifera</i> Benth.	(34)39-50	(22)30-35	11-16	9-17	a	b	P, Cb	I	0	Or, Re						2	2-4	ph	MX	Holwaya
<i>striata</i> Benth.	27-45	19-32	6-13	5-11	ah, cu, v, lc	t (f)	PL	II H	0-5	Re, Pi	M30 Y00-20 S00, M50 Y10 S00, M90 Y90 S00	absent	21.2 +/-1.8 (17.6-23.1) n=22	I	2-3	3-9	ss	PE	Biflorae	
<i>subhastata</i> Epling	39-43	27-35	11-13	[11-12]	a	b/t		I	0	Wh, Pi, Ye						10-12	ph to sh	MX	Sphacelioides	
<i>subrotunda</i> A. St.-Hil.	17-29	12-22	4-7	6	d, a	t		II H	3-4	Re		white spots/stripes (always?)				3-6	ah	BR, PY, AR	Subrotundae	
<i>subrubens</i> Epling	33-34	24	9-10	[10]		t			2-3							6-7	? (ph or ss or sh)	GT	Floridae	
<i>summa</i> A. Nelson	26-48	19-39	7-11	13-17	d, rarely a	t	H	III R	0-2	Pi, Pu	M70 C20 S00	absent, or white/pink-purple dots			1-2	6	ph	US, MX	Heterospace	
<i>tenuiflora</i> Epling	32-48	22-38	10	[6]	a	t			4-6	Re						4-5	sh	BR	Curtiflorae	
<i>thormannii</i> Urb.	28-33	22-27	6	6		t		II H	6-11	Or, Re						2	2-6	sh	DO	Ekmania
<i>tolimensis</i> Kunth	22-27	15-16	9-11	[5-7]	[r, d, a]	b	P	I	0	Pu							ss	CO	Purpureae	

Appendix 3 (cont.).

<i>Salvia</i> spp.	corolla length [mm]	corolla tube length [mm]	upper lip length [mm]	lower lip length [mm]	lower lip position *	flower shape *	nectar retention *	functional flower type *	exposition of thecae [mm]	corolla colour *	corolla colour (CYMK) *	nectar guides on corolla	nectar concentration [%]	nectar volume [µl] *	nectary length [mm]	pedicel length [mm]	growth form *	country *	systematics
<i>tomentella</i> Pohl	22-23	17-18	5	3-6	ah, cu, v, lc	t		I	0	Wh (calyx Pu, whitish-grey?)						[3]	ph	BR	Albolanatae
<i>tortuosa</i> Kunth	(18)28-45	(12)15-26	(6)10-16	(4)8-11	d, r	b	-	I	0	Pu						3-5	sh	CO, EC	Tubiflorae
<i>townsendii</i> Fernald	27-34	21-26	6-8	[5]	[a]	t	P	II H ²	5-9	Pu						2-4	ph	MX	Iodanthae
<i>trachyphylla</i> Epling	32-33	25	7-8	10	a	t		II H ²	[10-11]	Re, Pi						4-6	sh	EC	Cylindriflorae
<i>tubifera</i> Cav.	26-31	22-25	5-7	2-6	r	t	PL	II T	0	Re	M99 Y60 S30	absent			2	1-2	ph, ss	MX, possibly GT	Curtiflorae
<i>tubiflora</i> Sm.	40-44	30-35	10-11	[6-8]	ah, cu, v, lc	t (f)	PL	II H	[0-7]	Re						5-7	ph, ss	PE, CL	Biflorae
<i>tubulosa</i> Epling	40-47	30-35	10-12	[9-12]		b/t		I'	0	Re							sh	PE	Longiflorae
<i>tuercckheimii</i> Urb.	27-34	24-30	5-7	3-7	[r and/or d]	t		II H ²	6-10	Or, Re					3	2-9	sh	DO	Ekmania
<i>uncinata</i> Urb.	20-29	16-26	4-6	3-5	[r or d]	t		II H	[7]	Ye, Or, Re					2-3	2-10	sh	DO	Ekmania
<i>unguella</i> Epling	10	9	1	2	[a]	t			0	Re, Pi						[5]	ss	EC	Secundae
<i>verulosa</i> Epling	24	18	6	7	[ah, d]	t		I	0	Re						6-7	ss	CO	Tubiflorae
<i>verapazana</i> B.L.Turner	20-26	15-20	5-7	5-7	[a]	t		I	0	Re						4-6	p(?)h	GT	Calosphaeae
<i>vestita</i> Benth.	65-67	50-52	11-15	14	[a]	b/t			[1-6]								ss, sh	PE probably	Longiflorae
<i>wagneriana</i> Pol.	18-44	13-34	3-10	2-8	r/bc, also d	t	P, Cb	I	0	Re, Pu, Pi	M70-90 Y20-40 S00-10	whitish/pink area			3	2-10	ph, ss	MX, GT, SV, NI, CR, PA, the Caribbean	Holwaya
<i>weberbaueri</i> Epling	47-48	35	12-13			b/t		I'	0							6-9	sh	PE	Longiflorae
<i>xanthotricha</i> Harley ex E.P.Santos	15-16	13-14	2	1-2	ah, v, lc	t			0	Re						4-5	ss	BR	Secundae
<i>xeropapillosa</i> Fern.Alonso	13-14	11-13	1	2-4	a, also d, v	t	PL?	II H	0	Re						to 5	ph	CO	Rubescentes
mean and SD	34 +/-13	25 +/-9	10 +/-5	9 +/-5					3 +/-4.8				26.2 +/-4.6	18.6 +/-9.8	3 +/-0.7	6 +/-3.3			
minimum and maximum	7-130	5-90	1-35	1-41					0-43				6.8-62	2-53	1-5	0-34(40)			
n	182	181	181	171					172				27	13	70	157			

* refers to the following classification (see Methods): **Lower lip position**: r = reflexed, d = deflexed, a = antrorse (ah = +/- horizontal, not flexed), cu = cup-shaped, v = lateral lobes vertical, lc = lower and upper lips close to each other, bc = basal part of lower and upper lips close to each other. **Flower shape**: b = bilabiate, t = tubular (f = tube funnel-shaped), b/t = in-between. **Nectar retention**: P = papillae, Cl = lateral constriction, Cb = abaxial constriction (sometimes additionally adaxial), RI = lateral ridges, H = hairs, PL = posterior lever arm. **Functional flower types** (see Methods; chapter 5). **Colour**: Bl = blue, Bl(rb) = royal blue; BrOc = brownish-ochre, Lav = lavender, Or = orange, Pi = pink, Pu = purple, Re = red, ReBr = red-brown, Vi = violet, daVi = dark violet, paVi = pale violet, Wh = white, Ye = yellow. CYMK after Küppers (1999). **Nectar volume** (average): m = medium (about 3-10 µl), l = large (>10 µl). **Growth form**: ah = annual herb, ph = perennial herb, ss = subshrub, sh = shrub, tr = small tree, sc = scandent. **Countries**: Argentina: AR, Belize: BZ, Bolivia: BO, Brazil: BR, Chile: CL, Colombia: CO, Costa Rica: CR, Cuba: CU, Dominican Republic: DO, Ecuador: EC, El Salvador: SV, Guatemala: GT, Haiti: HT, Honduras: HN, Mexico: MX, Nicaragua: NI, Panama: PA, Paraguay: PY, Peru: PE, United States of America: US, Uruguay: UY, Venezuela: VE. square brackets: preliminary data.

Appendix 4. Characteristics of selected *Salvia* species not assignable to a distinct syndrome.

<i>Salvia</i> spp.	corolla length [mm]	corolla tube length [mm]	lower lip length [mm]	lower lip position *	flower shape *	exposition of thecae from upper lip [mm]	corolla colour *	nectar guides on corolla	nectar concentration [%]	nectar volume [μ l] *	flower scent	observations of hummingbirds	reports of hummingbirds	observations of insects	reports of insects
<i>purpurea</i> Cav.	(12)19-36	(9)12-21	(3)7-11	a, rarely d	b	0	Pi to Pu or Vi. C20-70 M50-99 S00-10, rarely liPi M10 S00 C00 or Wh M00 S00 C00	absent			no	<i>Selasphorus rufus</i> , <i>Hylocharis leucotis</i> , <i>Archilochus</i> cf. <i>colubris</i> , <i>Cyananthus latirostris</i> (field, Mexico; hovering and perching)	visited by <i>Doricha eliza</i> (Ortiz-Pulido et al. 2002)	visited by various bee species dusted with pollen (e.g. cf. <i>Eulaema</i>), visited by other bees, different butterflies and hawkmoths stealing nectar (field, Mexico)	visited by 5 bee species robbing nectar (Dieringer et al. 1991); visited by <i>Euglossa atrovirena</i> drinking nectar (Ramírez-Martínez 1998)
<i>aspera</i> M. Martens & Galeotti	23-40	13-26	13-17	a, rarely d	b	0	Ye Y70-80 M00-05 S00	absent	28.8 +/-1.3% (24.3-31.5) n=29	l	no				pollinated by bees (possibly only concluded because of corolla colour; Ramamoorthy & Elliott 1998)
<i>concolor</i> Lamb. ex Benth.	22-34	14-27	8-10	a	b	0	daVi C99 M95 S00	absent	21.2 +/-2.8% (15.2-25.8), n=33	m	no		visited and apparently pollinated by hummingbirds (J.H. Beaman 2068: MEXU)		
<i>mexicana</i> L.	major: 28-49; minor: 15-29	major: 18-29; minor: 11-20	major: 9-17; minor: 5-11	major: a or d; minor: a	b	0	major and minor: daVi C90-99 M80-90 S00-20, major: sometimes also meVi and liVi C60-90 M50-80 S00 or whitish C00-10 M00-10 S00; calyx blackish to green and yellowish	absent	major: 18.7 +/-5%, 9-26, n=34; minor: 27.3 +/-3.1%, 20.5-36, n=61	major: mostly l; minor: m to l	no	major: unidentified hummingbirds (field, Mexico; hovering)	both var.: visited/pollinated by hummingbirds (Wagner 1946, Des Granges 1979, Reisfield 1987, Arizmendi et al. 1996, Lara & Ornelas 2001)	major: visited by bees stealing nectar (field, Mexico)	major and minor: pollinated by <i>Deltoptila eieffas</i> , other bee species as robbers (Dieringer et al. 1991); bumble bees as pollinators and robbers (Arizmendi et al. 2007); major: visited by <i>Anthophora</i> sp. (Reisfield 1987); minor: visited by <i>Bombus nigrodorsalis</i> robbing nectar (Reisfield 1987); rarely legitimate bee visits (compared to hummingbirds; C. Lara, pers. comm.)
<i>scutellarioides</i> Kunth	16-25	10-16	8-12	a	b	(4-7)	Bl C99 M80 S00	white	23.7 +/-2.1%, 19-34.4, n=59	4.5 +/-1.2 μ l, 2-7.5, n=29; m	no				visited by <i>Bombus atrata</i> (Rasmussen 2004)
<i>discolor</i> Kunth	20-30	13-19	8-16	a	b	0	daVi (almost black) C99 M90 S80-90; calyx whitish light green	absent	>40%, 19.4->62, n=55	21.3 +/-7.7 μ l, 11-44, n=15; l	no				
<i>retinervia</i> Briq.	21-30	12-20	11-14	a	b	0	daVi C99 M90 S00	absent		l	no			visited/pollinated by large bees, visited by other bees stealing nectar and pollen (field, Bolivia)	
<i>clevelandii</i> (A. Gray) Greene	18-29	12-20	4-6	a, ah	+/-t	5-9	Bl to BiVi C70-90 M60-80 S00	absent	26 +/-2.4%, 20.2-31.6, n=37	m	sweet	<i>Archilochus alexandri</i> (cult.: Rancho Santa Ana BG, California; hovering)	visited/pollinated by hummingbirds (Cox 1981, B. O'Brien, pers. comm.)	visited by different bee species robbing nectar (e.g. <i>Xylocopa</i> sp., <i>Apis mellifera</i>), visited by butterflies (cult.: Rancho Santa Ana BG, California)	visited by hawkmoths (<i>Hemaris thysbe</i>), nectar robbing bees piercing corolla (<i>Xylocopa</i> sp., rarely touching reproductive organs), nectar stealing small bees using these holes (<i>Apis mellifera</i> , <i>Megachile</i> sp.) (Cox 1981)
<i>mohavensis</i> Greene	moh.: 19-30; Pinacate form: 17-25	moh.: functional tube: 16-25; Pinacate form: 16-22	moh.: 4-7; Pinacate form: (3)4-5	moh.: d; Pinacate form: ah, lc	moh.: s; Pinacate form: t	8-13 (both forms)	moh.: liBi M10-30(40) C20-40(50), bracts Wh/whitish, rarely with paVi/yellowish; Pinacate form: liPi/Vi/Lav C10-30 M20-50 S00, lips at their inner part C50 M70 S00, bracts green	absent (both forms)	moh.: 19 +/-6.4%, 8-37, n=32	moh.: m	no (both forms)	moh.: Fullerton Arboretum, California; hovering)	Pinacate form: visited by hummingbirds (A. Sanders, pers. comm.)		moh.: visited by long-tongued flies (B. O'Brien and P. Wilson, pers. comm.; Fenster et al. 2004)
<i>eremostachya</i> Jeps.	18-25	12-17	9-13	a	+/-t	4-6	(pale) ViPi to almost Wh C10 M10 S00, C60 M60 S00	absent	17.4 +/-2.9%, 14.5-21, n=6	m	no		at least occasionally pollinated by hummingbirds (E. Jones, pers. comm.)		
<i>greatae</i> Brandegeee	13-20	8-13	3-7	a	t	0-3	Pi-Lav (lower lip: C40-50 M60-90, tube: C10-20 M20-40 S00)	sometimes pale whitish				hummingbird (cult.: Rancho S. Ana BG, California; hovering)			

* refers to the following classification (see Methods): **Lower lip position**: d = deflexed, a = antrorse (ah = +/- horizontal, not flexed), lc = lower and upper lips close to each other. **Flower shape**: b = bilabiate, t = tubular, s = 'Stielteller'. **Colour**: Bl = blue, Lav = lavender, Pi = pink, liPi = light pink, Pu = purple, Vi = violet, Wh = white, Ye = yellow; da = dark, li = light, pa = pale, me = medium. CYMK after Küppers (1999). **Nectar volume** (average): m = medium (about 3-10 μ l), l = large (>10 μ l).

4.6 SUMMARY

The genus *Salvia* (Lamiaceae) encompasses about 1000 species, thereof approximately two thirds in the New World. Bees and birds are known as pollinators, but a more detailed analysis of the pollination syndromes is lacking. The paper presents a synopsis of all New World *Salvia* species and their pollination syndromes, focussing particularly on bird pollinated species.

The concept of pollination syndromes is used to predict pollinator guilds. The morphological analysis of floral traits is complemented by field investigations largely confirming the previous conclusions. The findings are discussed referring to the recent dispute on generalisation and specialisation in flowers.

Within the 591 New World *Salvia* species, at least 58 % bee pollinated (melittophilous) species and 31 % as bird pollinated (ornithophilous) species are listed. Only *S. whitehousei* appears to be psychophilous (butterflies). A total of 10 % show characters of two or more syndromes and the remaining eight species are not assignable to any group.

Bird pollinated *Salvia* species occur from North America southward to Chile and Argentina. They usually grow as shrubs or perennial herbs (97 %) and have red flowers (at least 49 %) of an average size of 34 mm (7-130 mm). With respect to their floral diversity and systematic affiliation, parallel evolution is evident. The morphological and functional changes during the assumed shift from melittophily to ornithophily are reconstructed and discussed exemplifying so-called 'intermediate' species.

5 Floral diversity and pollen transfer mechanisms in bird pollinated *Salvia* species

5.1 INTRODUCTION

Large genera are model systems that help to reconstruct phenotypic diversification during the course of evolution. This is particularly true for taxa with specific adaptive structures assumed to be 'key innovations' which might have driven speciation (Hodges 1997, Hunter 1998). To reconstruct the genesis of adaptive radiation a phylogenetic framework is needed. This provides us with a hypothesis on the relationship among recent species based on molecular markers. As a complement, developmental, functional morphological and experimental studies as well as field investigations are needed to understand the diversity of characters as a result of developmental and functional constraints. Morphological series which are basically descriptive get their evolutionary direction by combining them with developmental pathways and with assumed selection pressures. The underlying theses are, first, that the later a specific structure is formed during ontogeny the more adaptive it is, and second, that a stable change of the developmental pathway should be caused by an internal or external selection pressure. Summarising, we need at least three sources of knowledge to reconstruct the history of phenotypic diversification: phylogeny, morphology including morphogenesis, and fitness.

In the present paper we are interested in the phenotypic diversification of bird pollinated sages. *Salvia* ('sage', Lamiaceae) is an adequate model system as it is a large genus with approx. 1000 species distributed worldwide (Alziar 1988-1993). It is characterised by the well-known staminal lever mechanism of the flower (see Claßen-Bockhoff et al. 2003). The two monothebic stamens are modified to levers. They have a thin ligament between the connective and the filament, forming a joint, which enables a reversible movement causing pollen transfer. As the latter contributes to sexual reproduction, a high selection pressure on pollen transfer mechanisms is expected.

For most of the bee pollinated species, the lever mechanism is discussed as a key innovation. It may contribute to reproductive isolation due to (precise) pollen deposition, to an increase of fitness by pollen portioning or to the decrease of possible autogamy by herkogamy (Webb & Lloyd 1986, Grant 1994, Claßen-Bockhoff et al. 2004b, chapter 2).

Within the genus *Salvia* at least 186 species mainly from the New World are bird pollinated (chapter 4). They are supposed to have derived from melittophilous species several times in parallel (Grant & Grant 1965, Reisfield 1987, see also Walker & Sytsma 2007). However, little is known about the functional constraints involved in a shift from bees to birds in *Salvia*. To reconstruct the phenotypic changes, the floral diversity in ornithophilous sages is analysed. Based on the general syndrome (see chapter 4), the focus here is on the process of pollen transfer, considering both the morphological construction and the flower-bird interaction.

The process of pollination was addressed in detail by Buzato et al. (2000), Arizmendi (2001) and Lara & Ornelas (2001). They examined several ornithophilous *Salvia* species and illustrated pollen deposition at the bird's body (Buzato et al. 2000, Arizmendi 2001) and recorded seed set after bird pollination (Lara & Ornelas 2001). Recent field studies dealt with the functional significance of the stamens during the process of pollen transfer (chapters 2, 3). At least two different modes of pollen transfer were illustrated, one by means of a staminal lever mechanism as it is known from the bee pollinated species and one without a lever mechanism.

- (1) In the South African *S. lanceolata* pollen is transferred by the staminal lever mechanism. The Lesser Double-collared Sunbird *Nectarinia chalybea* and the Cape White-eye *Zosterops pallidus* were observed to be pollinators (Figs. 5.1A, 5.2A, chapter 3). They inserted their bills into the bilabiate flowers while perching on the branches of the shrub. In this way, they pushed back the posterior connective arms of the stamens (Fig. 5.1A pc) which block access to nectar (Fig. 5.3E). Releasing the staminal lever mechanism, the thecae (Fig. 5.1A t) at the end of the anterior connective arms (Fig. 5.1A ac) came out of the upper lip and were pressed onto the pollinator's head. Visiting a second flower of the same species permitted pollen transfer to the stigma.
- (2) *S. haenkei*, in contrast, represents a bird pollinated species without a working lever mechanism (Figs. 5.1B, 5.2B, chapter 2). Instead, the exerted (projecting) pollen-sacs contact a bird searching for nectar at the base of the narrow tubular corolla. Although the staminal levers are functional they cannot be moved because of the spatial arrangement. The connectives are so closely attached to the upper face of the corolla that they leave no space for a movement.

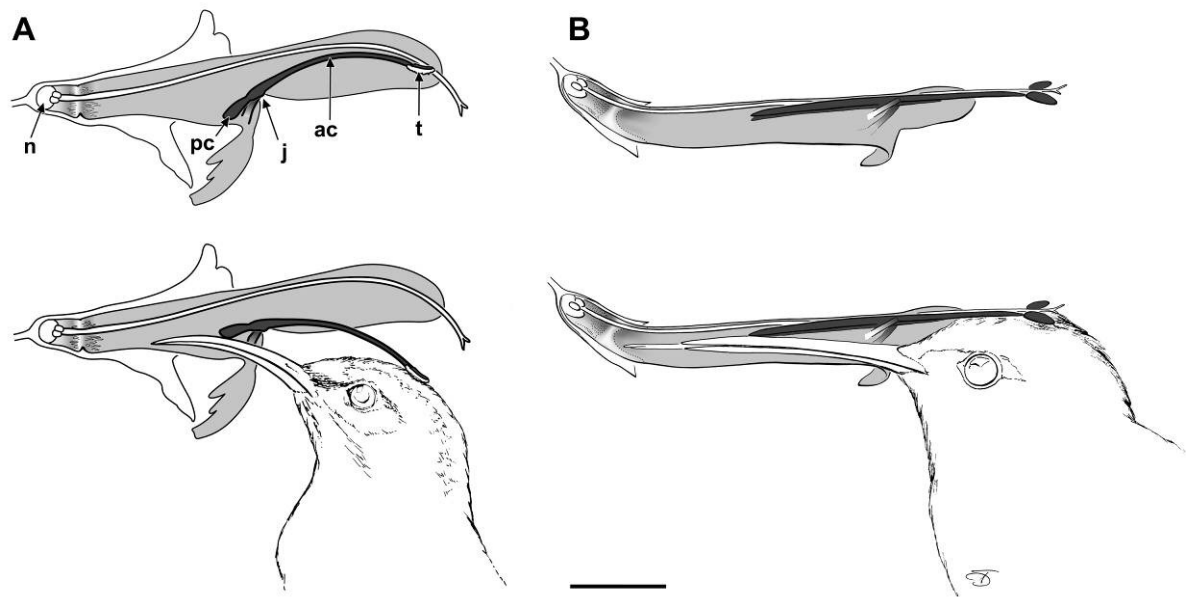


Figure 5.1. Pollen transfer with and without the staminal lever mechanism. (A) *Salvia lanceolata*. In order to access nectar produced by the nectary (n) the bill of *Nectarinia chalybea* pushes back the posterior connective arms (pc). Thereby thecae (t) at the anterior connective arms (ac) move down onto the head of the bird. The movement is enabled by the joint (j) between the filament and the connective. (B) *S. haenkei*. The lever mechanism is inactive with the posterior connective arms closely attached to the upper side of the tubular corolla. Pollen is deposited on the head of *Sappho sparganura*, touching the thecae while entering the flower. Bar = 1 cm. (after chapters 2, 3)

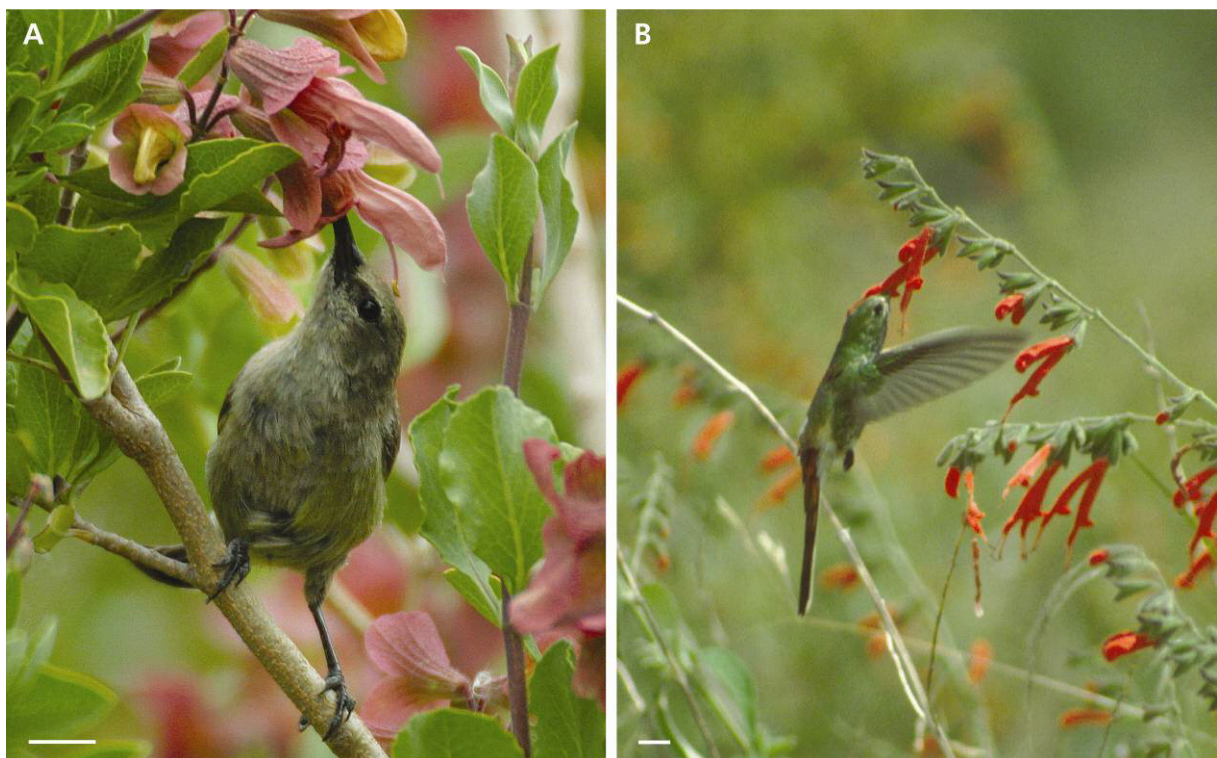


Figure 5.2. Flower-bird interactions. (A) *Salvia lanceolata* visited by a perching *Nectarinia chalybea*. (B) *S. haenkei* visited by a hovering *Sappho sparganura*. Note in both examples the thecae on the bird's heads. Bars = 1 cm. (photo A: R. Groneberg, Mainz)

Immovable stamens and exerted pollen-sacs were also described for *S. heerii*, *S. tubiflora* and *S. coccinea* by Trelease (1882) and Hildebrand (1865). In the latter species, Grases & Ramírez (1998) observed successful pollen deposition at a hummingbird's head, while McGregor (1899) carried out simulation experiments at a *Salvia* species wrongly determined as *S. coccinea*. He inserted a hummingbird skin into a flower, demonstrating the lever movement and the pollen transfer onto the skin and stigma of the flower.

Examination of the diversity of staminal levers and discussion of evolutionary tendencies, based on comparative studies, has already undertaken by Hildebrand (1865), Correns (1891) and Hrubý (1934), Zalewska (1928; >200 spp.) and Himmelbaur & Stibal (1932-1934; >400 spp.). Zalewska (1928) stated that in the Old World, stamens evolved in adaptation to insect pollination and that most of the American ones evolved with hummingbird pollination. Although we generally confirm this statement, we disagree with her in many details (chapter 4). Himmelbaur & Stibal (1932-1934) examined corolla and stamen features. They stated that parallel evolutionary lineages to bilabiate corollas evolved in the New World and in the Old World. Both lineages evolved in adaptation to bees and only few species to birds. Additionally, in a separate lineage in the New World, extremely tubular ornithophilous species evolved. Although the authors suggested parallel evolution in both hemispheres concerning different morphological changes and reductions of the stamens, they never discussed a reduction of the lever mechanism and its correlation to ornithophily.

Parallel evolution of staminal modifications during the shift from bees to birds was also discussed by Reisfield (1987) for the American subgenus *Calosphace*, in which most of the ornithophilous sages occur (chapter 4). The author mentioned a shift from bee pollinated species with hidden pollen-sacs and active lever mechanism to bird pollinated species with exerted thecae and an inoperative lever mechanism. Species which do not fit in those categories, for instance large-flowered species with a lever mechanism, were regarded as possibly being in a transition phase and pollinated by both groups.

Stamen structures were traditionally used for classification, for instance in the revision of the subgenus *Calosphace* by Epling (1939, and supplementary notes:

Epling 1940a, 1941, 1944, 1947b, 1951, 1960, Epling & Mathias 1957, Epling & Játiva 1963, 1966, 1968). In addition to other morphological characters and phytogeographical aspects they formed the base for the sectional arrangement. Walker et al. (2004) and Walker & Sytsma (2007) tested the phylogenetic significance of stamen morphology by mapping selected characters on a molecular tree. Based on about 80 species (<10 % genus coverage) they concluded that *Salvia* is polyphyletic. They supported the hypothesis of parallel evolution in the Old World and the New World (Himmelbaur and Stibál 1932-1934) and their findings correlate with our finding that ornithophilous species evolved several times in parallel (chapter 4). Considering connective widening, theca reduction, different modes of connective fusion and lever functionality they illustrated that the lever mechanism has developed at least three times in parallel.

Ontogenetic studies revealed that the lever-like stamen is the result of specific developmental processes, the most important being inhibition and unilateral growth. Compared to the basic stamen type in Lamiaceae with a bithecate anther and a long filament, the anther in *Salvia* is asymmetric from the early beginning (Troll 1929). The monotheccic anther results from the inhibition of the adaxial theca; the short filament from the inhibited elongation; and the lever arms, from extension of the connective (Claßen-Bockhoff et al. 2004a). From a developmental point of view, a stamen is more derived the earlier the second theca is reduced, the shorter the filament and the more elaborate the joint and lever arms. However, it is necessary to test, in which way these developmental pathways in ornithophilous species interact with the need to adapt to the new pollinator guild.

Based on the pollination syndromes of the New World sages (chapter 4), the present paper deals with floral diversity and pollen transfer mechanisms in 186 *Salvia* species. Considering that ornithophilous species might have derived from melittophilous ones (Grant & Grant 1965) and that inactive levers might have derived from active ones (Werth 1956, Himmelbaur & Stibál 1932-1934, Reisfield 1987, Claßen-Bockhoff et al. 2004a), we test the hypothesis, that due to a pollinator shift, phenotypic changes occur and can even involve the reduction of the 'lever mechanism', an ancestral key innovation.

5.2 MATERIAL AND METHODS

5.2.1 *Salvia* species

Based on the classification of floral syndromes in New World sages (chapter 4), 186 ornithophilous *Salvia* species were included in the present study. 36 species were observed at their natural habitats during field studies in Bolivia (2-4/2002), Mexico and Guatemala (10-12/2003), USA (4-6/2004) and South Africa (1/2004 and 10-11/2005). Plant material was collected from the field and from several botanic gardens and private gardens (chapter 4). Fresh flowers were fixed in 70% ethanol for further investigations. Vouchers of all investigated species are deposited at MJG and some in B, BIGU, JEPS, K, LPB, MEXU and TEX.

The data were complemented by investigating herbarium specimens (only type material and clearly determined specimens) of 132 species and the literature (see chapters 3, 4). For the Madagascan species, data were used from literature (Hedge 1972, 1974, 1998), from herbarium specimens (E: Clement et al. 2001; K: Jongkind 929, Hodgkin & Stansfield 120; MO: Phillipson 2669) and from a photograph provided by P. Phillipson (Missouri Botanical Garden and Muséum National d'Histoire Naturelle, Paris).

Fresh plants and herbarium specimens were determined from the literature (see chapter 3) and with the help of J. Wood (OXF), A. Vázquez (IBUG), A. Espejo (UAMIZ), H. Vibrans (CHAPA), M. Véliz (BIGU) and C. Froissart (Olivet, France). Details of the appropriate nomenclature and systematics are being compiled separately (chapter 3).

5.2.2 Methods

Bird observations of 15 *Salvia* species were made at their natural habitat, in the Botanical Gardens of Berkeley, Rancho Santa Ana, Riverside (California, USA) and in a private garden in Cochabamba (F. Berndt, Bolivia). The birds were identified from Fjeldså & Krabbe (1990), Hilty & Brown (1986) and Schuchmann (1999) and by J.A. Balderrama, J.C. Crespo and V. García (all from Universidad Mayor de San Simón, Cochabamba, Bolivia), J.F. Ornelas and C. González (both from Instituto de Ecología, Xalapa, Mexico), M. Ordano (Universidad Nacional Autónoma de México,

México City, Mexico), O. Reyna (Universidad de Guadalajara, Mexico), G. Stiles (Universidad Nacional de Colombia, Bogotá, Colombia), N. Newfield (Metairie, USA) and A. Weller (University of Bonn, Germany).

To test the fit between flowers and birds and the functionality and movement of the staminal levers, the bird's bill was simulated by inserting either a museum skin or a metal rod into fresh flowers. Simultaneously the area of pollen deposition on the bird's body was determined. The skins were borrowed from the ZFMK (Alexander Koenig Research Institute and Museum of Zoology, Bonn, Germany), the CBF (Colección Boliviana de Fauna, La Paz, Bolivia) and the SAM (South African Museum, Cape Town, South Africa).

Floral structures were morphologically investigated and measured morphometrically by the following: shape and length of the corolla, corolla tube (flower entrance to basal end) and corolla lips; position and stability of the lower lip; structure for nectar retention; and corolla colour. Stamen morphology and functionality was detected by establishing (i) positions of the filament, connective and thecae within the flower; (ii) if thecae were enclosed by either open or closed upper lips, and whether positioned either beneath or exerted from the upper lips; (iii) the functionality of the joint and mobility of the lever arms; (iv) shape, size, stability and flexibility of the filament, connective and joint; (v) the extent of fusion of the connective and thecae and (vi) the number of thecae.

To document the diversity of the joint structures, stamens of representative species were dehydrated through an ascending alcohol-acetone series, critical point dried (BAL-TEC CPD030, Balzar, Switzerland), mounted on SEM stubs, coated with gold (BAL-TEC SCD005) and examined with an SEM (ESEM XL-30, Philips). Colour values were based on the CMYK colour space (Küppers 1999). Floral nectar was measured from cultivated plants in the Botanical Garden of the University of Mainz usually in the morning of the first day of anthesis. Sugar concentration was determined using hand held refractometers (Atago, Honcho/Japan: N1: 0-32 % and N2: 28-62 % sucrose w/w and Bellingham and Stanley, Kent/UK: Eclipse 45-81: 0-50 % sucrose w/w). Volume of nectar was measured with a 25 µl microsyringe (ILS, Stützerbach, Germany).

5.3 RESULTS

Bird pollinated *Salvia* species can be roughly classified into three groups: group I includes those with active levers; group II includes those with inactive levers; and group III is a heterogeneous group including those with different stamen structures. To survey their floral diversity, functionality and pollen transfer mechanisms, eight case studies were selected as representatives of all 186 ornithophilous species.

Salvia fulgens

S. fulgens (Calosphace) represents the species with active staminal levers. The plants, studied at two large populations in Mexico, have large inflorescences bearing several conspicuous flowers each (Fig. 5.3A). The latter were frequently visited by hovering White-eared Hummingbirds (*Hylocharis leucotis*), Blue-throated Hummingbirds (*Lampornis clemenciae*) and Green Violet-ears (*Colibri thalassinus*). Usually the hummingbirds visited the flowers from the front, but sometimes they approached from the side, pulling the flowers to themselves, which is enabled by long (4-6.5 mm) and flexible pedicels. As in *S. lanceolata* (Figs. 5.1A, 5.2A, 5.3E), the birds inserted their bills into the flowers, pushed the posterior connective arms back and causing the anterior connective arms to lower. Thereby, the pollen-sacs, which are oriented parallel to one anther, came out of the upper lip, depositing pollen onto the bird's head and sometimes on its bill. Pollen is deposited at the tip of the lower stigmatic branches (Fig. 5.3B). Nectar robbing was observed by the short-billed Cinnamon-bellied Flowerpiercers (*Diglossa baritula*, Emberizidae), perforating the corolla tube near the base. Bees were never observed at the flowers.

The flowers are typically ornithophilous (Fig. 5.3A, B), being large (about 5-6 cm) and brilliant red (M99 Y70 S10). The corolla has a bilabiate shape with large lips. The lower lips vary in their orientation from antrorse (bent downward less than 90°) to deflexed (bent downward about 90°) and slightly reflexed (bent downward more than 90°) (Fig. 5.3A). In each case, they leave enough space for the birds to enter the flower and touch the stigma. Perching insects would not contact the stigma, except perhaps very large bees. However, bees would never reach the nectar at the base of the 3 to 4-cm-long corolla tubes. Nectar is produced by the nectary at the base of the flower (Fig. 5.3C). Its large volume ($12.7 \pm 3.1 \mu\text{l}$, 9-16.5, $n=7$) and low sugar concentration ($24.4 \pm 2.2 \%$, 20-27, $n=15$) again point to bird pollination. Two papillae near the flower base (Fig. 5.3C: arrow) retain the nectar, preventing the latter from

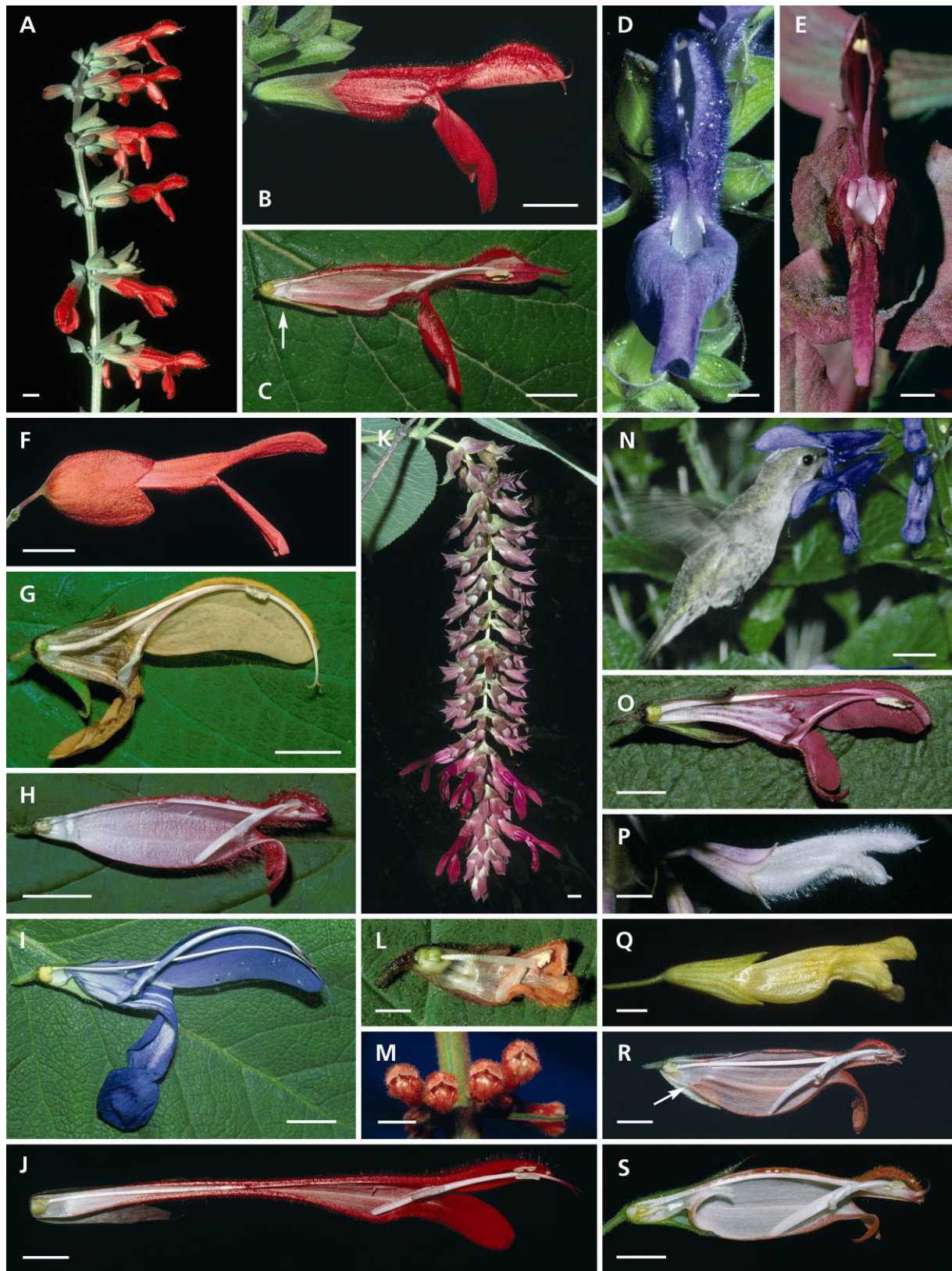


Figure 5.3. Diversity of *Salvia* flowers with active staminal levers and concealed pollen (**group 1**: Lanceolata-type): (A-C) *Salvia fulgens*: (A) inflorescence, (B) flower and (C) longitudinal section: note the lobes at the flower base (arrow); (D) *S. atrocyanea*: front view, note the fusion by hairs of the connective arms; (E) *S. lanceolata*: front view; (F) *S. sessei*: flower with large red calyx; (G) *S. africana-lutea*: longitudinal section with hairs at the flower base and reflexed lower lip; (H) *S. oxyphora*: lateral, basal constriction; (I) *S. patens*: basal constriction from the bottom; (J) *S. dombeyi*: ►

overflowing.

Concerning the staminal lever, the two posterior connective arms are stiff, broadened and fused to each other by hairs (Fig. 5.4B). They reach the lower side of the corolla (Fig. 5.3C), thus blocking the entrance and forming an abutment against the birds' bills. The staminal lever moves easily due to the thin and flexible ligament (Fig. 5.4D: I). Connective and filament outgrowths around the joint (Fig. 5.4B, C: o, ft; compare with A) stabilise the movement. During the release of the lever, the ligament becomes twisted. The movement is reversible. Due to the ligament's tension, the pollen-sacs swing-back into the upper lip when the birds leave the flower.

Within the ornithophilous sages, a total of 92 species correspond to *S. fulgens* in having an active lever movement, a well-functioning joint, hidden pollen-sacs and a blocked flower entrance (Fig. 5.3D, E, see Tab. 5.1). Most of the species belong to the subgenus *Calospatha* (88 spp. in 33 sections) and occur in the USA, Cuba, Mexico, Central America and South America. The North American *S. penstemonoides* is placed in the section *Euspatha* (subg. *Salvia*) whereas *S. africana-lutea* and *S. lanceolata* (South Africa) belong to the section *Hymenopatha* (subg. *Salvia*) respectively 'Species group G'. *S. thamarum* from South Africa is not yet classified to a systematic group.

Besides *S. fulgens*, hummingbirds were observed at nine further species: in Mexico an unidentified species at *S. grandidieri* (Fig. 5.3K) and three unidentified hummingbirds at *S. sessei* (Fig. 5.3F); in Bolivia the Glittering-bellied Emerald *Chlorostilbon aureoventris* at *S. orbignaei*, a Blue-capped Puffleg *Eriocnemis glaucopoides* at *S. atrocyanea* (Fig. 5.3D) and an unidentified hummingbird at *S. grewiiifolia*. Costa's Hummingbirds *Calypte costae* visited cultivated plants of *S. guaranitica* in California (Fig. 5.3N), the Glittering-bellied Emerald *Chlorostilbon aureoventris* visited cultivated plants of *S. leucantha* in Bolivia and an unidentified



► longitudinal section (collapsed tube due to dissection); (K) *S. grandidieri*: pendulous inflorescence with resupinated flowers; (L-M) *S. confertiflora*: (L) longitudinal section and (M) node with flowers in front view, note the cup-shaped lower lip and the small flower entrance; (N) *S. guaranitica* visited by a hovering *Calypte costae* with thecae on the bird's head; (O) *S. penstemonoides*: longitudinal section with hairs at the flower base; (P) *S. divinorum* with white corollas; (Q) *S. madrensis* with yellow corollas; (R) *S. disjuncta*: longitudinal section with lateral ridges at the flower base (arrow); (S) *S. holwayi*: longitudinal section with long nectary and a nectar chamber that is closed by two long and curved papillae. Bars = 1 cm in A-C, F-K, N; 0.5 cm in M, O-S; 0.25 cm in D, E, L.

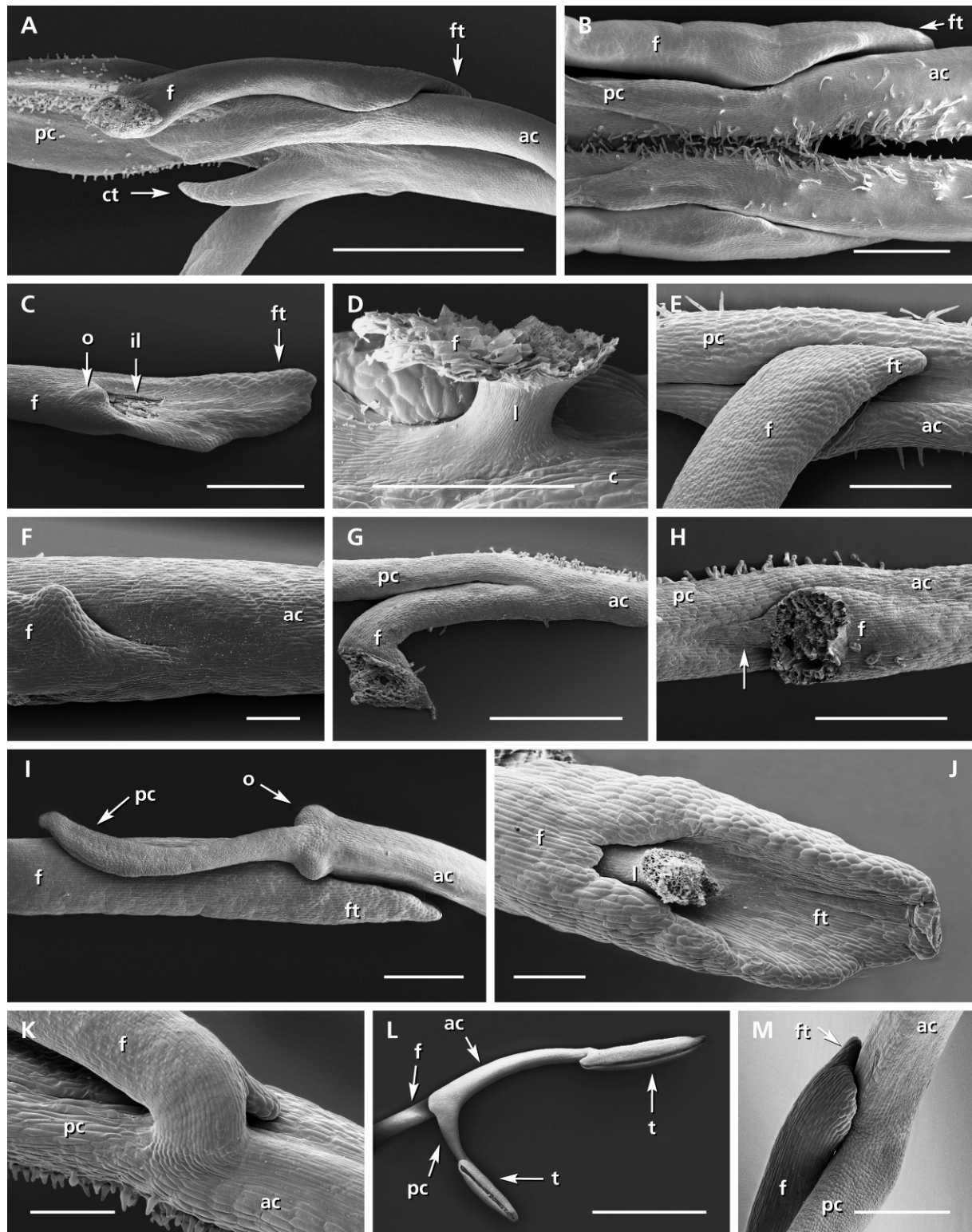


Figure 5.4. Diversity of staminal joints in ornithophilous *Salvia* species. (A) *S. guaranitica*: part of the stamens showing the joint area with well developed filament tip (ft) and tooth-like structures at the connectives (ct, function unknown), (B-D) *S. fulgens*: (B) joint area of the two stamens showing the precise fit between filaments (f) and anterior and posterior connective arms (ac/pc); note the hairs causing the fusion of the two connective arms, (C) filament showing the point of insertion of the ligament (il) and long filament tip, (D) connective (c) with ligament (l) and point of insertion of the filament; (E) *S. cacaliifolia*: joint area with connective and filament; (F): *S. longistyla*: joint area with broad connection between filament and connective; (G-H) *S. elegans*: (G) part of the lever with a broad connection between connective and filament, (H) detail of the 'joint' area showing the tissue joining ►

hummingbird in California also visited cultivated plants of *S. leucantha*. *Calypte costae* was observed at *S. microphylla* var. *wislizenii* and at white cultivars of *S. greggii*, both cultivated in California.

The birds were observed to hover, except in *S. guaranitica* where they also perched on branches or hover-clasped, even on flowers or leaves. Body size and bill length of the hummingbirds observed fit well to the particular flowers, so that successful pollination is to be expected. The birds were observed releasing the lever mechanism in *S. sessei* and being dusted with pollen on the forehead. At *S. guaranitica*, the birds glided along the thecae and got pollen either smeared on their head or precisely deposited at one spot (Fig. 5.3N). When approaching from the side, the birds pulled the flowers to themselves. When flying from below into hanging flowers the birds lifted them up. In general, though entering the flowers from different directions, the birds touched the reproductive organs, either the stigma or the thecae first. *S. grandidis* differs from all other *Salvia* species in having large obligatory pendulous inflorescences (Fig. 5.3K). The flowers resupinate during anthesis. Thereby, they compensate for the hanging position, being pollinated in the usual nototribic way. It was observed that the visiting hummingbird was dusted with pollen on the dorsal side of its head. Nectar robbers were observed at *S. sessei* (butterflies), *S. leucantha* (a large bee and a honeybee), *S. guaranitica*, *S. grewiifolia* (bees) and *S. orbignaei* (bees including *Xylocopa* sp.). At *S. orbignaei*, honeybees also stole pollen.

Although each of the 92 species possesses the specific features of the lever mechanism, they clearly differ in many other floral characters. These aspects are outlined below.

- The **posterior lever arms** always block the flower entrance (Fig. 5.3D, E front view), however they can be short (Fig. 5.3G) or long (Fig. 5.3H), oriented in a diagonal manner (Fig. 5.3H) or rarely in a more or less upright position (Fig. 5.3G). In any case, the posterior lever arms act as an abutment against the bird's bill, a



► the filament and the connective (arrow); (I-J) *S. spathacea*: (I) joint area with connective outgrowths (o) and the short posterior connective arm, (J) filament with ligament and filament tip; (K) *S. exserta*: broad connection between connective and filament; (L-M) *S. roemeriana*: (L) whole lever with two thecae (t) and joint area; (M) joint area showing the precise fit between filament and connective. Bars = 2 mm in L; 1 mm in A-C, G, I; 200 µm in J-K; 500 µm in D-F, H, M. Photo J: Sina Barth, photo M: Norbert Holstein (both University of Mainz, Germany).

function which is optimised by their fusion in most of the species. Epidermal hairs usually cause a fusion, which can be strong (e.g. *S. fulgens*, *S. oxyphora*) or weak (e.g. *S. patens*). The connective arms are free in *S. penstemonoides*, *S. africana-lutea*, *S. lanceolata* and *S. thermarum* and maybe in *S. sessilifolia*. The posterior connective arms are always sterile in the New World (Fig. 5.3C, H, L), but may have a small fertile theca in the Old World species (e.g. *S. africana-lutea*, Fig. 5.3G).

- Simulation experiments showed that in most species **movement** proceeds smoothly (especially in *S. patens*). In several species the release is somewhat hindered by the closely attached or overlapping lobes of the upper lip, which slow down the movement (e.g. *S. oxyphora*, *S. involucrata*, *S. wagneriana*, *S. grewiifolia*). Sometimes the connective arms return slowly into the upper lip. In all species, the birds are easily able to release the levers.
- The **thecae** are usually enclosed by the upper lip but, rarely in some species, they may be slightly exerted (e.g. *S. patens*). The fertile thecae of the upper lever arm are mostly free of each other, except in *S. africana-lutea* and *S. lanceolata* where the fusion contributes to stabilise the lever movement.
- Regarding the **corolla**, the species differ in colour, with more than 50 % of the species being red. They also differ in flower length, being (0.7 cm) - 3.8 cm - (13 cm) (n=92) as well as in the length of the flower tube, being (0.5 cm) - 2.6 cm - (9 cm) (n=91). The latter varies in shape, being mostly tubular (Fig. 5.3F, J), but also funnel shaped (Fig. 5.3G), bellied (Fig. 5.3H) or rarely more or less sigmoid (Fig. 5.3P).
- The **upper lip** varies from being closed by adjacent (e.g. *S. miniata*) or overlapping lobes (sometimes *S. oxyphora*) to being completely open (e.g. *S. confertiflora*, Fig. 5.3M), but the thecae are always covered by the upper lip.
- The **lower lips** are long (Fig. 5.3I) to short (Fig. 5.3P), reflexed (Fig. 5.3G), additionally revolute (*S. lanceolata*, Fig. 5.3E) to antrorse (Fig. 5.3B, F, J-L, P, Q). In the latter case, they may lengthen the corolla tube (Fig. 5.3L). They can be additionally cup-shaped, their front margins oriented upward (Fig. 5.3L, M) and their lateral lobes may be oriented vertically (Fig. 5.3L, Q). The lower lips are weak (e.g. *S. patens*) to firm (e.g. *S. confertiflora*). They often make landing for insects difficult or even impossible.

Table 5.1. Functional flower types in ornithophilous *Salvia* species.

GROUP I (92 spp., 49.5 %)
Lanceolata-type: <i>S. adenophora</i> Fernald, <i>S. africana-lutea</i> L., <i>S. altissima</i> Pohl, <i>S. articulata</i> Epling, <i>S. atrocaulis</i> Fernald, <i>S. atrocyanea</i> Epling, <i>S. balaustina</i> Pohl ¹ , <i>S. benthamiana</i> Gardner, <i>S. betulifolia</i> Epling, <i>S. blepharophylla</i> Brandegee ex Epling, <i>S. buchananii</i> Hedge, <i>S. camarifolia</i> Benth., <i>S. chapadensis</i> E.P.Santos & Harley ¹ , <i>S. confertiflora</i> Pohl, <i>S. curviflora</i> Benth., <i>S. darcy</i> J.Compton, <i>S. diamantina</i> E.P.Santos & Harley ¹ , <i>S. disjuncta</i> Fernald, <i>S. divinorum</i> Epling & Játiva, <i>S. dombeyi</i> Epling, <i>S. dorisiana</i> Standl., <i>S. dugesiana</i> Epling ¹ , <i>S. ernesti-vargasii</i> C.Nelson ¹ , <i>S. erythrostephana</i> Epling ¹ , <i>S. espirito-santensis</i> Brade & Barb.Per., <i>S. falcata</i> J.R.I.Wood & Harley ¹ , <i>S. formosa</i> L'Hér., <i>S. fulgens</i> Cav., <i>S. gesneriiflora</i> Lindl. & Paxton, <i>S. graciliramulosa</i> Epling & Játiva, <i>S. grandis</i> Epling, <i>S. gravida</i> Epling, <i>S. greggii</i> A.Gray, <i>S. grewiifolia</i> S.Moore, <i>S. guaranitica</i> A.St.-Hil. ex Benth., <i>S. harleyana</i> E.P.Santos ¹ , <i>S. hatschbachii</i> E.P.Santos ¹ , <i>S. herrerae</i> Epling ¹ , <i>S. hidalgensis</i> Miranda, <i>S. hilarii</i> Benth., <i>S. holwayi</i> S.F.Blake, <i>S. involucrata</i> Cav., <i>S. juliana</i> Epling ¹ , <i>S. karwinskii</i> Benth., <i>S. lachnostoma</i> Epling, <i>S. lanceolata</i> Lam., <i>S. leucantha</i> Cav., <i>S. leucocephala</i> Kunth, <i>S. libanensis</i> Rusby, <i>S. lineata</i> Benth., <i>S. littae</i> Vis., <i>S. longibracteolata</i> E.P.Santos ¹ , <i>S. macrocalyx</i> Gardner, <i>S. madrensis</i> Seem., <i>S. marci</i> Epling, <i>S. mattogrossensis</i> Pilg. ¹ , <i>S. microphylla</i> Kunth, <i>S. miniata</i> Fernald, <i>S. oaxacana</i> Fernald, <i>S. ombrophila</i> Dusén, <i>S. orbignaei</i> Benth., <i>S. oxyphora</i> Briq., <i>S. patens</i> Cav., <i>S. pavonii</i> Benth., <i>S. peninsularis</i> Brandegee, <i>S. penstemonoides</i> Kunth & C.D.Bouché, <i>S. persicifolia</i> A.St.-Hil. ¹ , <i>S. pringlei</i> B.L.Rob. & Greenm., <i>S. pubescens</i> Benth., <i>S. pulchella</i> DC., <i>S. regla</i> Cav., <i>S. rivularis</i> Gardner ex H.B.Fielding, <i>S. rufula</i> Kunth, <i>S. salicifolia</i> Pohl, <i>S. scabrata</i> Britton & P.Wilson, <i>S. scabrata</i> Pohl, <i>S. scandens</i> Epling, <i>S. sciaphila</i> (J.R.I.Wood & Harley) Fern.Alonso, <i>S. secunda</i> Benth., <i>S. sellowiana</i> Benth., <i>S. sessei</i> Benth., <i>S. stolonifera</i> Benth., <i>S. subhastata</i> Epling, <i>S. thermarum</i> van Jaarsv., <i>S. tolimensis</i> Kunth, <i>S. tomentella</i> Pohl, <i>S. tortuosa</i> Kunth, <i>S. tubulosa</i> Epling ¹ , <i>S. venulosa</i> Epling, <i>S. verapazana</i> B.L.Turner, <i>S. wagneriana</i> Pol., <i>S. weberbaueri</i> Epling ¹
GROUP II (63 spp., 33.9 %)
Haenkei-type (59): <i>S. alborosea</i> Epling & Játiva, <i>S. arbuscula</i> Fernald ² , <i>S. arduinervis</i> Urb. & Ekman, <i>S. ayavacensis</i> Kunth ² , <i>S. bahorucona</i> Urb. & Ekman, <i>S. cacaliifolia</i> Benth., <i>S. coccinea</i> Etl., <i>S. cocuyana</i> Fern.Alonso ² , <i>S. curtiflora</i> Epling, <i>S. cyanocephala</i> Epling, <i>S. florida</i> Benth., <i>S. foveolata</i> Urb. & Ekman, <i>S. fruticetorum</i> Benth. ² , <i>S. funckii</i> Briq. ² , <i>S. gachantivana</i> Fern.Alonso, <i>S. haenkei</i> Benth., <i>S. hapalophylla</i> Epling ² , <i>S. heerii</i> Regel, <i>S. hirta</i> Kunth ² , <i>S. hirtella</i> Vahl, <i>S. integrifolia</i> Ruiz & Pav. ² , <i>S. iodantha</i> Fernald, <i>S. iodophylla</i> Epling ² , <i>S. jorgehintoniana</i> Ramamoorthy, <i>S. lachnaiclada</i> Briq., <i>S. lanicaulis</i> Epling & Játiva ² , <i>S. lavendula</i> Alain ² , <i>S. lobbii</i> Epling, <i>S. longistyla</i> Benth., <i>S. macrophylla</i> Benth., <i>S. medusa</i> Epling & Játiva ² , <i>S. melaleuca</i> Epling, <i>S. neovidensis</i> Benth. ² , <i>S. nervata</i> M.Martens & Galeotti, <i>S. oppositiflora</i> Ruiz & Pav., <i>S. orthostachys</i> Epling, <i>S. palealis</i> Epling ² , <i>S. paryskii</i> Skean & Judd, <i>S. pauciserrata</i> Benth., <i>S. pichinchensis</i> Benth., <i>S. quitensis</i> Benth. ² , <i>S. rhodostephana</i> Epling ² , <i>S. rubescens</i> Kunth, <i>S. rubriflora</i> Epling ² , <i>S. sagittata</i> Ruiz & Pav., <i>S. sigchosica</i> Fern.Alonso ² , <i>S. speirematoides</i> C.Wright, <i>S. splendens</i> Sellow ex Roem. & Schult., <i>S. sprucei</i> Briq., <i>S. squalens</i> Kunth, <i>S. striata</i> Benth., <i>S. subrotunda</i> A.St.-Hil., <i>S. thormannii</i> Urb., <i>S. townsendii</i> Fernald ² , <i>S. trachyphylla</i> Epling ² , <i>S. tubiflora</i> Sm., <i>S. tuerckheimii</i> Urb. ² , <i>S. uncinata</i> Urb., <i>S. xeropapillosa</i> Fern.Alonso
Elegans-type (2): <i>S. cinnabarina</i> M.Martens & Galeotti, <i>S. elegans</i> Vahl
Tubifera-type (1): <i>S. tubifera</i> Cav.
Spathacea-type (1): <i>S. spathacea</i> Greene
GROUP III (7 spp., 3.7 %)
Roemeriana-type (3): <i>S. henryi</i> A.Gray, <i>S. roemeriana</i> Scheele, <i>S. summa</i> A.Nelson
Exserta-type (1): <i>S. exserta</i> Griseb.
Lasiantha-type (3): <i>S. altimitrata</i> Epling, <i>S. lasiantha</i> Benth., <i>S. raveniana</i> Ramamoorthy ³
GROUP I + III (Lasiantha-type) (3 spp., 1.6 %)
<i>S. booleana</i> B.L.Turner ¹ , <i>S. rusbyi</i> Britton ⁴ , <i>S. sessilifolia</i> Baker
Not classifiable because of lacking information (21 spp., 11.3 %)
<i>S. acuminata</i> Ruiz & Pav., <i>S. apparicii</i> Brade & Barb.Per., <i>S. cubensis</i> Britton & P.Wilson, <i>S. cylindriflora</i> Epling, <i>S. itaguassuensis</i> Brade & Barb.Per., <i>S. melissiflora</i> Benth., <i>S. mentiens</i> Pohl, <i>S. nigrescens</i> Alain, <i>S. paramicola</i> Fern.Alonso, <i>S. phaenostemma</i> Donn.Sm., <i>S. plumosa</i> Ruiz & Pav., <i>S. psilantha</i> Epling, <i>S. regnelliana</i> Briq., <i>S. rosei</i> Fernald, <i>S. rubrifaux</i> Epling, <i>S. speciosa</i> C.Presl ex Benth., <i>S. subrubens</i> Epling, <i>S. tenuiflora</i> Epling, <i>S. unguella</i> Epling, <i>S. vestita</i> Benth., <i>S. xanthotricha</i> Harley ex E.P.Santos

¹ classification has to be checked; ² joint has to be checked to exclude the Elegans-type; ³ possibly

affinities to group I; ⁴ possibly also Haenkei-type

- **Nectar** is retained by structures at the base of the corolla, by lateral (Fig. 5.3H) or abaxial constrictions (Fig. 5.3I), by lateral ridges (*S. disjuncta*, Fig. 5.3R, arrow), abaxial papillae (Fig. 5.3S), or by hairs (Fig. 5.3G, O).

Salvia cacaliifolia

S. cacaliifolia (Calosphace; Fig. 5.5A, B) represents the species that transfer pollen without a lever movement. Plants were observed in the Botanic Garden of the University of Riverside (California), where they were frequently visited by Costa's Hummingbird (*Calypte costae*). The birds were dusted with pollen on their heads while hovering at the flowers, hovering-clasping on neighbouring branches or leaves and perching.

The blue (M75 C95 S00), funnel shaped flowers are about 25-30 mm long and have short lower lips (Fig. 5.5A). The latter are often cup-shaped, their front margins oriented upward, making landing difficult for insects. It is unlikely that bees are pollinators because they would hardly touch the exposed reproductive organs. The nectar fits to the ornithophilous syndrome, being large to medium in volume ($7.8 \pm 2.9 \mu\text{l}$, 2-15.5; n=32) and having a low sugar concentration ($22.8 \pm 3.4 \%$, 16.3-30.0; n=45).

Pollen is freely accessible as the thecae are exerted. The posterior connective arms do not block the flower entrance. They partly lean against the adaxial tube wall before they reach the abaxial tube wall at the base of the flower (Fig. 5.5B). Being closely attached to the adaxial tube wall, they leave no space for releasing the lever, although the joint operates freely. The ligament is thin and flexible (Fig. 5.4C, D: o, l). The distal part of the posterior connective arms retains nectar which rises only slightly over it.

There are 59 species corresponding to *S. cacaliifolia* that have freely accessible pollen and lack a lever movement and have a more or less functional joint (Tab. 5.1). The posterior connective arms never block the entrance. The species occur only in the subgenus Calosphace (18 sections) and are distributed from South America, Central America, Mexico to Hispaniola. *Chlorostilbon aureoventris* was observed visiting flowers of the cultivated Brazilian *S. splendens* (Fig. 5.5C) in Bolivia. An unidentified hummingbird visited the flowers of *S. nervata* in Guatemala.

Apart from the specific characters of the lever mechanism, the 59 species are highly

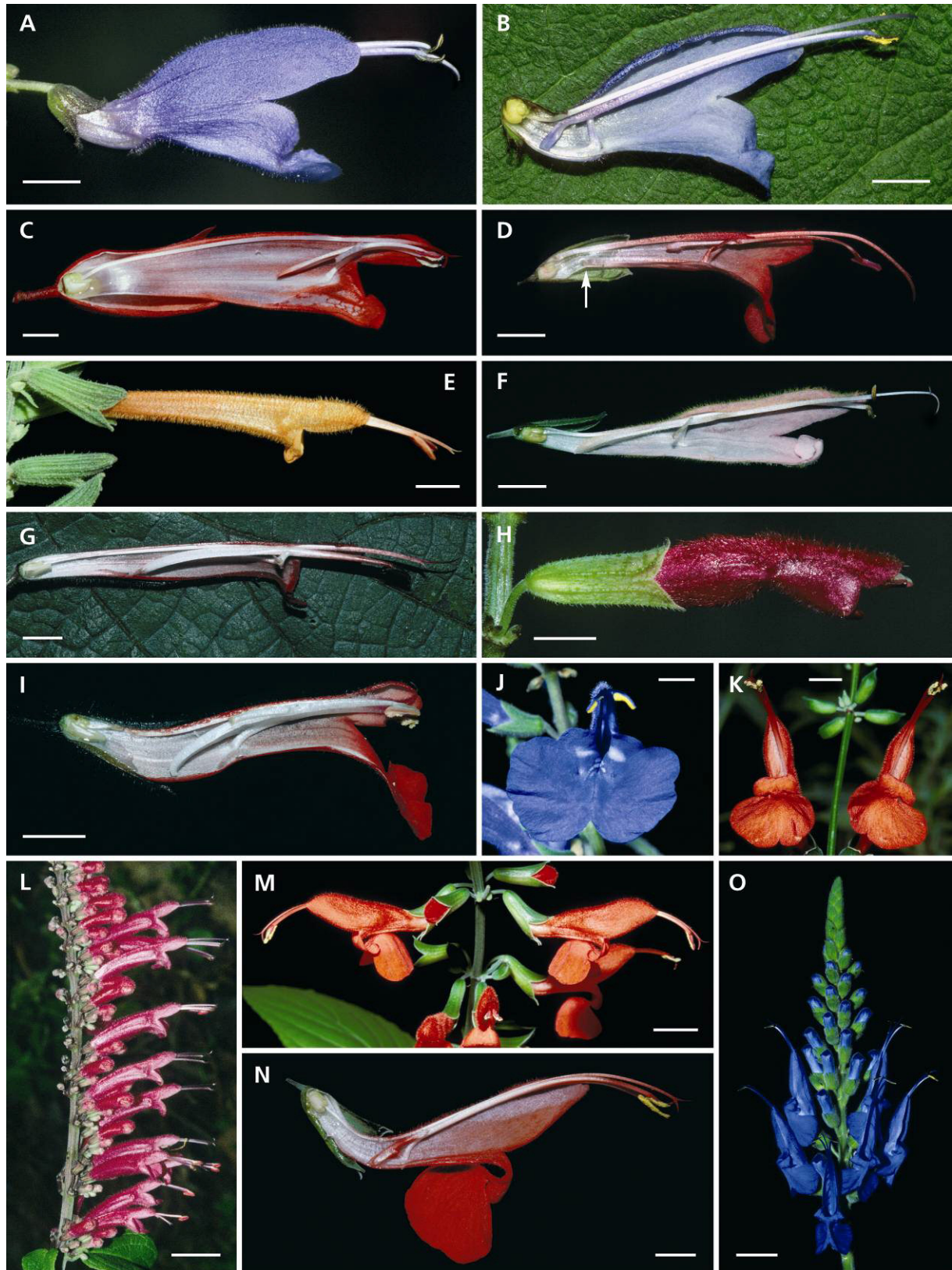


Figure 5.5. Diversity of *Salvia* flowers with freely accessible pollen and lacking a lever mechanism (**group 2**): Haenkei-type: (A-B) *Salvia cacaliifolia*: (A) flower with greatly exerted thecae, (B) longitudinal section with the short posterior lever arm as a nectar cover; (C) *S. splendens*: longitudinal section with the posterior lever arms not reaching the lower side of the flower tube and not blocking the

entrance, (D) *S. hirtella*: longitudinal section with the posterior lever arms attached to the upper corolla wall and papillae at the base of the flower (arrow); (E) *S. haenkei*: tubular flowers with greatly ► diverse in many floral characters, as summarised below:

- The **lever arms** do not block the flower entrance. They are usually attached to the upper tube wall along their whole length (Fig. 5.5D). Their proximal ends may reach the lower side of the corolla either near the base (Fig. 5.5B, F) or about mid-tube (Fig. 5.5G). In *S. splendens*, the posterior connective arms are not closely attached to the upper tube wall but only lie nearby (Fig. 5.5C). In some species such as *S. splendens* and *S. iodantha* the position of the posterior connective arms is variable, sometimes positioned a small distance from the upper tube wall. Simulation experiments illustrated that there is, rarely, a very weak movement depending on the position and direction of the bill insertion.
- As to their **stability**, the connective arms are firm throughout their length as, for instance, in *S. curtiflora* and *S. rubescens* (Fig. 5.5H, I), while their posterior parts at least are thin and relatively flexible, as in *S. striata* (Fig. 5.5F). In this species, a bird's bill may push the posterior lever arms upward, but would never cause lever movement.
- The **posterior connective arms** are usually fused, but in some cases they are only weakly attached to each other (e.g. *S. sagittata*) or even free (*S. cacaliifolia*). They are short (Fig. 5.5B, N) or long (Fig. 5.5G).
- The **joints** differ in their functionality. When they are well developed they are often stabilised by outgrowths, coming from both the filament and the connective (*S. cacaliifolia*: Fig. 5.4E, *S. iodantha*). The ligaments of less functional joints are either more or less easily breakable (e.g. *S. striata*) or are broad and therefore partly stiffened (e.g. sometimes in *S. longistyla*, Fig. 5.4F) often having reduced outgrowths around the joint area (e.g. *S. longistyla*, Fig. 5.4F). The joints are usually located



► exerted thecae; (F) *S. striata*: longitudinal section with posterior lever arms reaching the lower side of the flower tube, note the cup-shaped lower lip; (G) *S. longistyla*: longitudinal section with posterior lever arms reaching the lower side of the corolla tube; (H) *S. curtiflora*: slightly exerted thecae and short lower lip; (I) *S. rubescens*: longitudinal section with long nectary and a large amount of nectar; (J) *S. sagittata*: front view of flower with reflexed, large lower lip; (K, M-N) *S. pauciserrata*: (K) front view of flowers, showing greatly exerted thecae and strongly reflexed, large, lower lips, (M) node with flowers, (N) longitudinal section with strongly curved basal part of the corolla tube and short posterior lever arms reaching the lower side of the tube; (L) *S. iodantha*: part of the inflorescence bearing many

tubular flowers with greatly exerted thecae; (O) *S. macrophylla*: inflorescence of showing flowers with strongly reflexed lower lips. Bars = 0.5 cm in A-K, N; 1 cm in L, M, O.

near the entrance (Fig. 5.5G), but also at the mid of the tube (Fig. 5.5F) or even at its base (Fig. 5.5B).

- **Pollen** is always freely accessible from the thecae, which are either exerted to varying degrees (Fig. 5.5A, D, E, G, J, L, M, O; C, F, H) or positioned beneath the upper lip (Fig. 5.5I). Their position varies within some species (e.g. *S. striata*, *S. nervata*, *S. splendens*, *S. curtiflora*, *S. rubescens*). The thecae are oriented parallel (Fig. 5.5I), diagonal (Fig. 5.5E), across (Fig. 5.5O) or in a variable position (*S. cacaliifolia*, *S. pauciserrata*) relative to one another. They are always free of each other except in *S. hirtella* (Fig. 5.5D).

- In the **corolla**, the species differ in colour (around 50 % red), flower length [(1.2 cm) - 3 cm - (5.9 cm), n=59] and tube length [(1 cm) - 2.3 - (4.6 cm), n=59]. The shape of the flower tube is mostly tubular (Fig. 5.5G), sometimes funnel shaped (Fig. 5.5A) or rarely sigmoid (e.g. in the basal part in *S. pauciserrata*, Fig. 5.5M, N).

- The **lower lip** is long and broad (Fig. 5.5J) to short (Fig. 5.5H), reflexed (Fig. 5.5M, O) to antrorse (Fig. 5.5A, F). In the latter case it might be cup-shaped (Fig. 5.5F) or the lateral lobes of the lower lip might be vertically oriented (e.g. *S. striata*, Fig. 5.5F). The lower lip differs in its stability, ranging from being weak (e.g. *S. sagittata*, *S. hirtella*) to more or less firm (e.g. *S. cacaliifolia*).

- **Nectar** is often retained by basal corolla constrictions (Fig. 5.5C), papillae (*S. hirtella*, Fig. 5.5D: arrow) or by posterior connective arms reaching the lower corolla side (Fig. 5.5B, F).

The species summarised so far represent more than 80 % of the ornithophilous sages. Correspondingly, each of the following case studies represents only relatively few species.

Salvia elegans

In contrast to the above mentioned species, a joint is completely missing in *S. elegans* (Calosphace: Incarnatae, Fig. 5.6A-C) as there is no flexible thin ligament between the connective and the filament (Fig. 5.4G, H). On the contrary, there is even a further stiffening as the filament is fixed to the posterior connective arm by

thin tissue (Fig. 5.4H: arrow). Movement of the lever is impossible. As in *S. hirtella*, the connectives are attached so closely to the upper side of the tubular corolla that there is no space left for any release (Fig. 5.6C). They are fused, very thin and flexible, and do not block the entrance. As in *S. cacaliifolia*, pollen is freely accessible. The thecae, oriented diagonal or across to each other, are either exerted or beneath the open upper lip. Simulation experiments confirmed that the visitor will touch the thecae, on entering the flower.

Plants were studied at different localities in Mexico and in the Botanical Garden of Mainz. Their flowers have typical ornithophilous characters. The slender tubular corollas are long (approx. 3 – 4 cm, their tube: 2 – 3 cm) and bright red (M99 Y80 S20; Fig. 5.6A, B). The lower lips are antrorse or deflexed. The moderate amount of nectar is of low sugar concentration ($17.6 \pm 4.3 \%$, 7.5-24; n=18). The only other species completely lacking a joint is *S. cinnabarina* (Calosphace, Incarnatae). It differs from *S. elegans* in having longer posterior connective arms reaching in or even behind the basal constriction of the corolla tube (Fig. 5.6D). Hovering hummingbirds (*Selasphorus rufus* in Mexico, and an unidentified hummingbird species in Guatemala) were observed visiting the flowers. Occasionally, butterflies and bees were observed stealing nectar and pollen, respectively.

Salvia tubifera

A completely different pollen transfer mechanism operates in *S. tubifera* (Calosphace, Fig. 5.6E). Pollen is totally enclosed by the upper lip (Fig. 5.6F, G: lower flower). As the staminal lever mechanism is lacking, the upper lip has to be opened by the pollinator. Simulation experiments illustrated that a bird has to open the upper lip by pushing the lobes aside with its bill. The movement is facilitated by a weak constriction of the lip lobes at their proximal ends. After removal, the thecae are exposed and pollen is accessible for being deposited onto the bird (Fig. 5.6G: upper flower).

Although the joint of the staminal lever is well developed and thus potentially functional, movement is prevented by the position of the posterior connective arms. Similarly to *S. cacaliifolia*, the latter run parallel to the upper tube wall before reaching the lower wall in the basal part (Fig. 5.6F), leaving no room for any staminal movement. The posterior lever arms contribute to nectar retention.

The plants were studied in Mexico. They have conspicuous red (M99 Y60 S30) tubular flowers (approx. 3 cm) and reflexed lower lips (Fig. 5.6E).

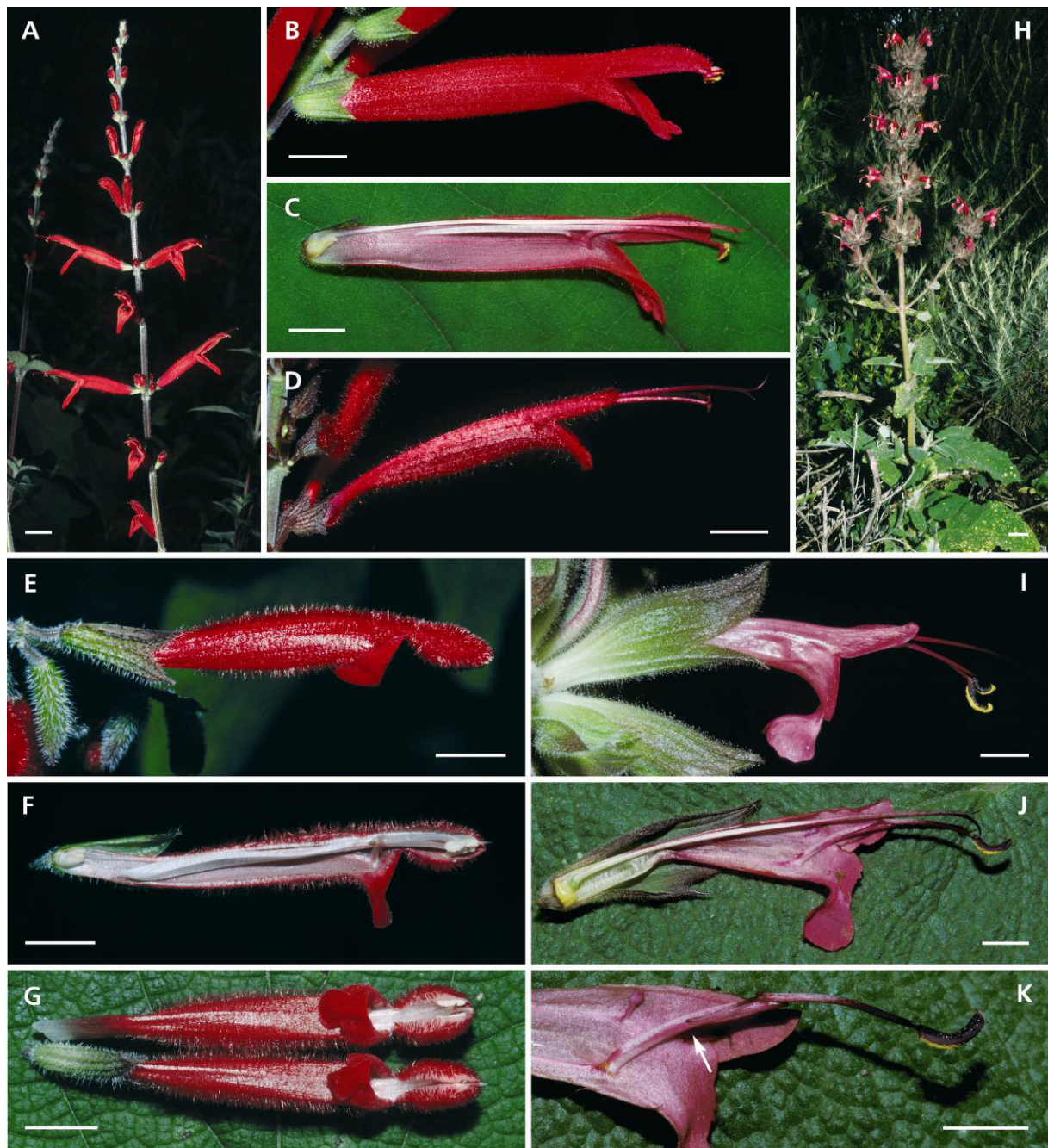


Figure 5.6. Diversity of *Salvia* flowers with freely accessible pollen and lacking a lever mechanism (**group 2, continued**): (A-D) *Elegans*-type, (E-G) *Tubifera*-type, (H-K) *Spathacea*-type. (A-C) *Salvia elegans*: (A) inflorescence with red, conspicuous flowers, (B) flower with slightly exerted thecae, (C) longitudinal section with connective closely attached to the upper side of the corolla tube; (D) *S. cinnabarina*: flower with a narrow basal part of the tube. (E-G) *S. tubifera*: (E) flower with strongly reflexed lower lip and well developed upper lip, (F) longitudinal section and (G) flowers from below showing the thecae enclosed by the upper lip, the upper flower shows the condition after a bird inserts its bill causing a slight opening of the upper lip and making pollen available. (H-K) *S. spathacea*: (H) plant with a richly flowered inflorescence, (I) flower with a large calyx and exerted thecae, (J) longitudinal section with constriction at the flower tube and stamen, (K) stamen with long filament, long anterior connective arm and very short posterior connective arm (note its end: arrow). Bars 1 cm in A;

0.5 cm in B-G, I-K; 3 cm in H.

Salvia spathacea

In *S. spathacea* (Audubertia; Fig. 5.6H) the lever movement is also lacking, in this case due to the extreme reduction of the posterior connective arms (Fig. 5.6J, K). The latter are only few millimetres long, very thin and positioned more or less parallel to the filament (Figs. 5.6J, K, 5.4I: pc). Simulation experiments confirmed that the reduced arms offer no abutment and that there is no movement of the stamens. However, from its construction, the joint is more or less functional, being composed of a thin and flexible ligament and of outgrowths (Fig. 5.4I, J: l, o, ft). The original lateral position of the joint is turned by a right angle, causing a more or less sideways movement (Fig. 5.6K). As the whole lever is exerted by its long and firm filament, pollen is freely accessible.

Hovering *Calypte* sp. were observed visiting the conspicuous flowers of cultivated plants in two botanic gardens in California. The plants were studied in cultivation and at two large populations at the San Bruno Mountain in California. They have large tubular flowers (approx. 3 - 4.5 cm long, tube: 2 - 3.5 cm long; Fig. 5.6I). The flowers show a colour change from salmon pinkish in young flowers (M80 Y40 S30-40) to dark pink (M99 C20 S10 to M99 C50 S00) or dark red (M99 Y30 S50) with age. The lower lips are either deflexed or reflexed and offer no landing platform. Nectar is of low sugar concentration (20 ± 5.34 %, 6.8-25.4, n=23) and its large volume (32.6 ± 16.3 μ l, 13-51, n=10) rises slightly over a basal constriction.

The following three case studies include all species which have both an active lever mechanism and exposed thecae.

Salvia lasiantha

The flowers of *S. lasiantha* (Calosphace, Mitratae) differ from those of *S. fulgens* in having freely accessible pollen (Fig. 5.7A, B). Only in abnormally small flowers the thecae may be enclosed by the upper lip. The posterior connective arms block the entrance (Fig. 5.7B) and have to be pushed away to allow access to nectar.

Although the flowers have relative short corollas (tube: about 10-12 mm; flower about 20 mm), they are regarded as ornithophilous because of their usually deflexed or reflexed lower lips and exerted thecae. Insects which land or hang on

the lower lip would neither become dusted with pollen by the long exerted thecae nor touch the stigma.

The corollas are variable in colour, ranging from orange (M80 Y70 S10 to M60 Y60 S10), orange-ochre (M80 Y99 S50), darkred-orange (M90 Y70 S60) to darkred (M99 Y70 S40), redbrown (M99 Y50 S70), dull pinkred (M60 Y30 S60), dark pink (M90 Y40 S50) and dull pink (M80 Y30 S60). The calyx varies from green to pink-purple.

At the plants examined in Mexico, no birds were observed, instead nectar drinking honeybees hang on the upper lip. They inserted their head into the flower entrance, thereby sometimes touching the thecae and becoming dusted with pollen at the rear part of the abdomen.

Two other species resembling *S. lasiantha* in their floral construction are *S. altimitrata* (Mitratae) and *S. raveniana* (Purpureae). The latter species has slightly exerted thecae.

Salvia exserta

S. exserta (syn.: *S. praeclara*; Calosphace, Mineatae; Fig. 5.7C) is unique within the genus as the easily triggered movement of the lever is not enabled by joints, but by extremely long (up to 9.5 mm), thin and flexible filaments (Fig. 5.7D). The tension of the filaments, which enables reversibility of the movement, becomes apparent when excising the filaments from the corolla tube. Normally heavily curved, the filaments become straight (Fig. 5.7E). Simulation experiments illustrated that a bird's bill will push back the posterior lever arms, thereby increasing the bending of the filaments and forcing the lowering of the thecae.

The joint area is partly stiffened as the connection between the filament and the connective is broad (Fig. 5.4K).

The annual plants, studied in several large populations in Bolivia, bear large conspicuous inflorescences with many flowers (Fig. 5.7C). The flowers were frequently visited and pollinated by various hovering hummingbirds: the Sparkling Violet-ear (*Colibri coruscans*), the White-bellied Hummingbird (*Amazilia chionogaster*) and the Glittering-bellied Emerald (*Chlorostilbon aureoventris*). The birds visited several flowers of an inflorescence before flying to another one. Usually, the hummingbirds visited the flowers from the front, but when coming from the side they pulled the flowers to themselves, which is enabled by long (about 4 mm) and

flexible pedicels. On entering the flowers, the birds were dusted with pollen on their heads and touched the stigma with the same side. Honeybees (*Apis mellifera*) and

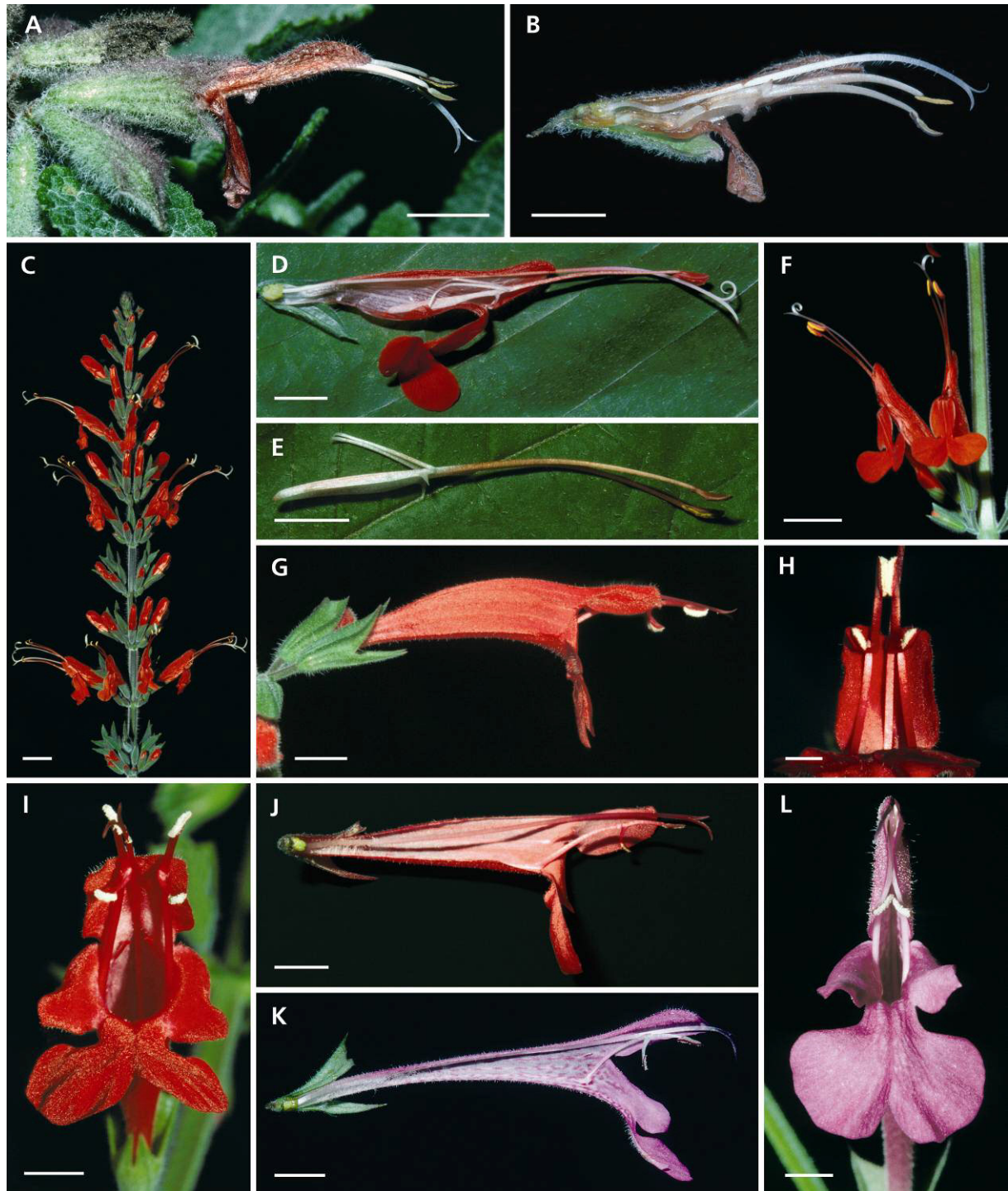


Figure 5.7. *Salvia* flowers with active staminal levers and freely accessible pollen (**group 3**): (A-B) Lasiantha-type, (C-F) Exserta-type, (G-L) Roemeriana-type. (A-B) *Salvia lasiantha*: (A) flower with exserted thecae, (B) longitudinal section with the posterior connective arm reaching the lower side of the corolla tube. (C-F) *S. exserta*: (C) inflorescence, (D) flower longitudinal section with the long curved filament, (E) dissected straight filament, (F) pair of flowers showing the greatly exserted thecae and deflexed lower lip. (G-J) *S. roemeriana*: (G) flower with bithecate stamens, (H) proximal part of the flower from the bottom showing united anterior thecae, (I) front view with non-united thecae, (J)

longitudinal section showing the long filament and hairs at the flower base; (K-L) *S. summa*: (K) longitudinal section also with hairs at the flower base, (L) front view with thecae not blocking the entrance. Bars 0.5 cm in A, B, D, E, G, J, K; 1 cm in C, F; 0.25 cm in H, I, L.

unidentified bee species landed on the exposed connectives, thecae or styles and stole pollen, only occasionally touching the stigma. Carpenter bees (*Xylocopa* sp.) landed on the corolla tube and robbed nectar through holes near the corolla base.

The flowers are brilliant red (M99 Y99 S10) and relatively long (approx. 15-30 mm, tube: 10-20 mm). They lack a landing platform as the lower lip is either reflexed or deflexed (Fig. 5.7C, D, F). The large amount of nectar is of low sugar concentration (25.4 ± 5.9 %, 12-45, n=117). Nectar is prevented from overflowing by lateral corolla constrictions and hairs near the flower base.

Salvia roemeriana

S. roemeriana (sect. *Heterosphace*, subg. *Leonia*) differs from all the above mentioned species in having bithecate anthers (Fig. 5.7G-J). As in *S. spathacea*, the filaments are long and firm, exerting the whole lever from the corolla tube (Fig. 5.7H-J). Thereby, at least the anterior thecae are exerted. The lower thecae do not restrict access to nectar (Fig. 5.7I).

Simulation experiments illustrated that touching the lower thecae causes a relatively weak movement. The joint is functional and well developed with a thin and flexible ligament and with stabilising outgrowths (Fig. 5.4L, M). The thecae of the anterior connective arms may be weakly postgenitally fused (Fig. 5.7H), then often separating after being touched (Fig. 5.7I).

The plants, examined at different localities in Texas and in cultivation (BG Mainz), have brilliant red (M90-99 Y60-80 S20), tubular and long flowers (approx. 3-4 cm, tube 25-30 mm). The weak lower lips are usually oriented downwards (Fig. 5.7G). The large volume of nectar is of low sugar concentration (24.4 ± 3.5 %; 18.8-32.5, n=58). One time a butterfly was observed stealing nectar at cultivated plants (Texas).

Salvia henryi and *S. summa* (Fig. 5.7K, L; both *Heterosphace*) resemble *S. roemeriana* in having bithecate anthers. The thecae are also exposed in front of the upper lip or placed beneath the open upper lip.

Species with varying stamen characters

There are three species which are not represented by the case studies because their

characters were variable.

S. rusbyi (Calosphace, Cylindriflorae) varies in thecae exposition, ranging from greatly exerted (approx. 1 cm) to slightly exerted pollen-sacs which may even be enclosed by the upper lip. The lever mechanism is functional, moving either strongly or sometimes slightly.

The Madagascan *S. sessilifolia* ('Species group B') and the Mexican *S. booleana* have both a functional lever mechanism and thecae, either enclosed by the upper lip or shortly exerted.

5.4 DISCUSSION

5.4.1 Diversity of pollen transfer in ornithophilous *Salvia* species

All *Salvia* flowers have the same organisation (Bauplan) with sympetalous, more or less monosymmetric corollas and development of only the two abaxial stamens, which are modified modifying to act as levers. However, the floral organs greatly differ in their relative proportions, their relative positions and their synorganisation. With respect to the lever mechanism and its necessity for pollen transfer, the case studies have shown that two major constructions can be distinguished: one with a staminal lever mechanism (group I) and those without a staminal lever mechanism (group II). Beside these two groups, some species show unique constructions (group III).

Group I is represented only by the Lanceolata-type, illustrated in *S. lanceolata* (Fig. 5.1A, chapter 3) and here in *S. fulgens*. The lever movement is needed to release the thecae out of the upper lip and to unblock the flower entrance (Tab. 5.2, see also Hildebrand 1865, Ogle 1869, Trelease 1882, Vogel 1954, chapter 3). It is additionally needed to lower further the thecae, as birds also may visit the flowers from below (Fig. 5.2A) without necessarily touching the thecae (chapter 3).

Group II is represented by the Haenkei-type, the Elegans-type, the Tubifera-type and the Spathacea-type. The Haenkei-type (Fig. 5.1B), already illustrated in *S. haenkei* (chapter 2), is here represented by *S. cacaliifolia*. All species are characterised by a lack of lever movement and freely accessible pollen, except in *S. tubifera* (for *S. heerii* see also Trelease 1882; Tab. 5.2). The lever movement is not needed for unblocking the flower entrance or for pollen transfer (Tab. 5.2, see also Hildebrand 1865, Meehan 1871, Himmelbauer & Stibal 1932-1934). The flower tube is often long and narrow, forcing the bird into a specific position whereby the thecae are

touched (compare Werth 1956, Castellanos et al. 2003, Figs. 5.1B, 5.2B,

Table 5.2. Functional flower types of 186 ornithophilous *Salvia* species (OW: Old World, NA: North America, CB: Caribbean, MX: Mexico, CA: Central America, SA: South America). for species specific data see chapter 4

Functional groups and types	species number	stamen movement	position of thecae	lever movement necessary for pollen transfer	lever blocks entrance	position of the posterior connective arm	space for release of the lever mechanism	joint potentially movable	filament extremely long and flexible	strong reduction of posterior connective arm	number of fertile thecae	systematic affiliation (spp./sect.)	distribution ¹
I Lanceolata-type	92	+++	concealed (released by lever mechanism)	+	+	inside tube	+	+	-		1 (in OW: 1-2)	Calospace (88/33), Euspace ³ (1 sp.), Hymenospace/Species group G (2 spp.), <i>S. thamarum</i> not classified; clade I and II ²	OW NA, CB, MX, CA, SA
II Lasiantha-type Exserta-type Roemeriana-type	3	++	exposed			outside tube		+/-	+	-	1	Calospace (4/2); clade II ²	MX, CA
	1												SA
	3	+											
III Haenkei-type Elegans-type Tubifera-type Spathacea-type	59	-		-		inside tube		+	-		1	Calospace (61/19); clade II ²	CB, MX, CA, SA
								+/-					
	2		-					MX, CA					
	1					concealed (released by opening the upper lip)							+
1			exposed			outside tube	+		+		Audibertia (1 sp.); clade II ²	NA	

¹ the widespread *S. coccinea* (Haenkei-type) was not considered as its native distribution is unknown.

² Walker & Sytsma (2007)

³ related to sect. *Salviastrum* per Walker & Sytsma (2007)

chapter 2). In *S. tubifera* pollen is hidden in the upper lip that has to be opened by the visitor (Tab. 5.2).

Group III is heterogeneous, including all species with staminal lever movement as in type I, and freely accessible pollen as in type II (except *S. tubifera*). The staminal lever is not necessary for pollen transfer, but is needed to unblock the flower entrance in the Lasiantha-type and in the Exserta-type (Tab. 5.2). In the Roemeriana-type where the entrance is free (but see Walker & Elisens 2001), the lever has a different morphology with bithecate anthers and a long filament (Tab. 5.2).

The two main types and group III clearly illustrate the functional morphological range of the flowers and their stamens. It is surprising that most species fit to the grouping and only few species vary in the staminal lever construction. For instance in *S. iodantha* and *S. splendens* (type II) stamen movement rarely occurs (see also Trelease 1881, Ogle 1896, Hrubý 1934, Werth 1956, Faegri & van der Pijl 1971, Proctor et al. 1996). In *S. patens* (Type I) the thecae might be slightly exposed (see also Hildebrand 1865, Hrubý 1934). In *S. rusbyi* the thecae are either exserted or enclosed. Thus, this species ranges between the Lasiantha-type and group I. The same is probably true for *S. booleana*, a species separated from *S. fulgens* by Turner (1995a), that is described as having slightly exserted thecae.

Considering the geographical distribution of the different floral constructions in bird pollinated sages, it becomes apparent that group I-flowers, which comprise 50 % of all species, are underrepresented in the Northern Andes (Venezuela to Bolivia: 33 %). They are overrepresented in Southern South America, especially in Brazil (74 %), and in North to Central America (64 %). Only three representatives occur in the Old World. As to group II-flowers, which comprise 34 % of all species, their distribution in the New World is complementary to that of group I: Northern Andes: 51 %, Southern South America and Brazil (11 %), and North to Central America (21 %). Group II is completely absent from the Old World. The distribution is presented in chapter 4.

5.4.2 Phenotypic changes due to pollinator shift from bees to birds

Since ornithophilous *Salvia* species may have been derived from bee pollinated ancestors (Grant & Grant 1965, Reisfield 1987, chapter 4), we have tried to elucidate the adaptational constraints involved in the shift from bee to bird pollination.

Compared to birds, bees often collect pollen for their offspring. This pollen is lost for pollination. Specialised bee flowers often conceal their pollen and reserve it for pollination. In most of the melittophilous *Salvia* flowers, pollen is concealed in the upper lip where it is invisible. This can be regarded as a protection against pollen collecting bees (Müller 1871, Loew 1886, Correns 1891, Westerkamp 1997). By means of the staminal lever mechanism pollen is transferred out of the upper lip and on to the back of the bee. There the bee cannot see the pollen and it is difficult or impossible to reach it with its legs (see also Westerkamp 1996, 1997, Westerkamp & Claßen-Bockhoff 2007).

Compared to bees, birds are regarded as more reliable pollinators; they cover larger distances and are more independent of weather, particularly in highlands (Cruden 1972, Stiles 1978, Thomson et al. 2000). Concealment of pollen is not necessary because birds in general do not seek pollen (Westerkamp & Claßen-Bockhoff 2007, Wolf 1985, see also Stiles 1981, Brice et al. 1989). Although birds occasionally groom their feathers, they do not scrape them selectively in order to obtain pollen. Consequently, pollen adheres longer to the bird and is available to be deposited on the stigmas. It is expected that bees were excluded from bird pollinated flowers in the course of evolution. An optimisation towards birds can be achieved by different modifications. First, the lower lip might be reduced, reflexed or arranged in such a way that landing for bees is impossible (e.g. *S. confertiflora*: Fig. 5.3L, *S. striata*: Fig. 5.5F). Second, the distance between the nectar and the flower entrance, i.e. the corolla tube length, might be increased to such an extent that bees are excluded (Fig. 5.8A, see also Reisfield 1987, but see Himmelbaur & Stibal 1932-1934). The same effect comes about when both the upper and lower lip functionally lengthen the flower tube. A bee's proboscis is too short to reach the nectar in comparison to a bird's bill. The increased distance between the nectar and the flower entrance also increases the distance between nectar and pollen. This might facilitate pollen deposition on the feathered head which is the better vector for pollen transport and delivery on the stigma compared to the smooth bill (Kugler 1970, Faegri & van der Pijl 1971, Johnsgard 1983, Rose 1990, Arizmendi et al. 1996).

The increase of distance between the nectar and the pollen in *Salvia* is caused by various developmental processes (Fig. 5.8). First, the corolla tube may be long, a characteristic for many ornithophilous species (Fig. 5.8A). Second, the filament might be long which is rarely observed in ornithophilous sages, e.g. in *S. exserta*, *S. roemeriana* or *S. spathacea* (Fig. 5.8B). Third, the connectives may

elongate which is very common in bird pollinated sages (Fig. 5.8C). Long filaments and connectives usually appear together with corolla tube elongation (Fig. 5.8B-E), and only seldom with short-tubed flowers (Fig. 5.8F, e.g. *S. lasiantha*, *S. speciosa*). The corolla either elongates in its proximal part (Fig. 5.8A-C) and/or, more rarely, in its distal part displacing the insertion of the filaments towards the flower base (Fig. 5.8D, E). Depending on the position of the filament insertion within the tube, the connectives need to be elongated to make pollen transfer possible or more reliable (compare Fig. 5.8C-E). Often, elongation of the connective and/or the long filaments is associated with exposition of the thecae (and stigma) (Fig. 5.8B-F).

5.4.3 Parallel evolution of floral constructions

Referring to our functional morphological grouping, the flowers of ornithophilous sages range from the typical bilabiate flower with hidden pollen (Fig. 5.1A) to tubular flowers with freely exposed pollen (Fig. 5.2B). The first requires the lever mechanism to lower the thecae and to unblock access to nectar. The latter releases the flower from the need of staminal movement allowing the reduction of the lever mechanism to different degrees. The narrow (and long) corolla often forces the pollinator in a fixed position which is not necessarily the case in the bilabiate construction.

The two main floral constructions are caused by different morphogenetic processes. These occurred several times in parallel, illustrating the broad amplitude of phenotypic responses to a given selection pressure. In detail we distinguish the following analogies.

- **Pollen availability** is usually achieved by the lever movement, which evolved in both hemispheres. A second mode is the exposition of the anthers, which, with only one exception, is an exclusively New World novelty. The rare mechanism of upper lip movement by a pollinator is interpreted as an apomorphy for *S. tubifera*. The latter species may be compared with the bee pollinated *S. verticillata* L. from the Old World, which also has a reduced lever mechanism and a movable upper lip (Hildebrand 1865). In both species a weak tissue at the base of the upper lip enables the reversible movement.
- **Mobility** of the lever mechanism is usually enabled by the flexible ligament of the joint. A completely different mechanism by means of a flexible filament is observed in *S. exserta* (Tab. 5.2), again an apomorphy.

Even the **reduction** or immobilisation of the lever mechanism is effected by different morphological constructions. There is either no space for the release of the lever mechanism (Haenkei-type, Elegans-type, Tubifera-type) or the posterior lever arms are too weak to cause a movement (Elegans-type, Haenkei-type), or they are

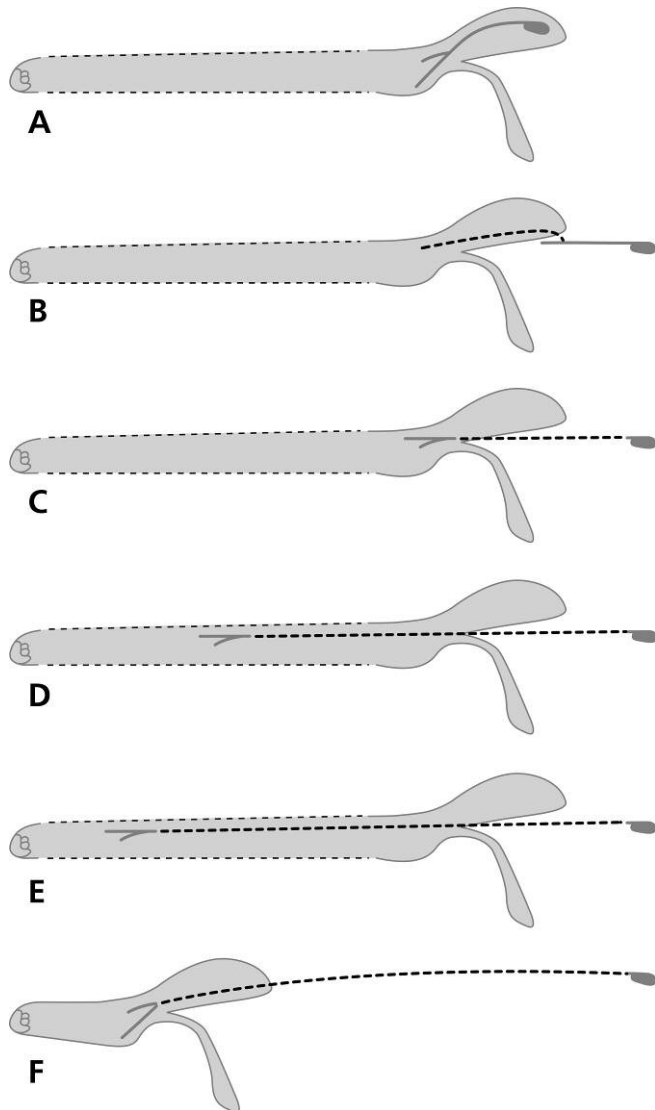


Figure 5.8. Modes to increase the distance between nectar and pollen in *Salvia* flowers. (A-E) elongation of corolla tube: only corolla tube elongated (A), with additional, long filament (B), with additional, long anterior connective arm and different positions of the filament indicating an elongation of the proximal part of the corolla tube (C), of both the proximal and distal parts of the corolla tube (D) or predominantly the distal part of the corolla tube (E) compared to the usual case of an elongated proximal part (A-C); elongation of the anterior connective arm (F). Dashed lines: elements increasing distance in the individual cases.

almost completely reduced (*S. spathacea*). The latter has a parallel in the aforementioned bee pollinated *S. verticillata* (Hildebrand 1865). Furthermore, the joints are reduced (Haenkei-type p.p.), partly stiffened by a broad insertion of the ligament (Haenkei-type p.p.; *S. excelsa*), or the lack of a ligament (Elegans-type, see also Himmelbaur & Stibal 1932-1934).

The diversity of phenotypes following the same functional construction indicates a high degree of parallel evolution towards ornithophily in *Salvia*. As to the staminal lever mechanism - this was already illustrated by the functional-morphological approaches of Zalewska (1928) and Himmelbaur & Stibal (1932-1934). To illustrate evolutionary tendencies within the ornithophilous species, Zalewska (1928) presented a morphological series from species with stiff stamens and free connectives (*S. carduacea*) to those with functional joints and fused connectives (via *S. rhombifolia* to *S. patens* and *S. splendens*). Even though not all the species involved

are ornithophilous, we do not agree with her conclusions because fused connectives and functional joints are also present in almost all New World bee pollinated sages. Himmelbaur & Stibal (1932-1934) emphasised the parallel evolution of the lever mechanism as well as its reduction. In general, we concur with their view, though they never discussed the reduction of the lever mechanism with respect to the shift from bees to birds. However, in this context, Reisfield (1987) mentioned that the reduction of the lever mechanism is likely induced by the ongoing shift from melittophily to ornithophily. He specified 'transition species' between the two syndromes. Although we also found species with character combinations being intermediate between the syndromes (chapter 4), we disagree with Reisfield (1987) who classified large flowers with a working lever mechanism as transitional stages (e.g. *S. patens*, *S. fulgens*).

From the systematic point of view, staminal levers (Lanceolata-group) occur in different groups in the Old World (e.g. *S. lanceolata*) and in the New World (Calospace and *S. penstemonoides*, Tab. 5.2). Thus, parallel evolution in ornithophilous sages becomes apparent. In the New World, it is evident that the reduction of the staminal lever mechanism took place several times in parallel, i.e. in Calospace (Haenkei-type, Elegans-type, Tubifera-type) and in Audibertia (Spathacea-type; Tab. 5.2).

The parallel evolution of the lever mechanism has recently been confirmed by the phylogenetic studies of Walker & Sytsma (2007). The authors found 15 stamen types based on connective widening, theca reduction, different modes of connective fusion and lever functionality and mapped them on a tree based on molecular data. The tree includes three clades with monophyletic lineages and shows that *Salvia* is polyphyletic. Clade I is said to include bithecate anthers (stamen type A) and monothecate anthers with broad fused posterior lever arms (stamen type B), both with a lever mechanism. Clade II, an exclusively New World clade, includes five different stamen types and the Old World clade III includes two stamen types. Though the authors found special stamen types characterising these clades, the grouping does not completely correspond to our classification. Ornithophilous representatives with a lever mechanism occur in two different clades, showing parallel evolution. In the authors' clade I, species are included which belong to our group I (*S. penstemonoides*), to our group I + III (*S. sessilifolia*, Old World) and to our group III (*S. roemeriana*). Their clade II includes two monophyletic lineages of

subgenus Calosphace (e.g. *S. patens* in their stamen type F, *S. oxyphora* in their stamen type E; both our group I). The same is true for species with a reduced lever mechanism, which are found in the two Calosphace lineages (*S. sagittata*, *S. haenkei*) as well as in section Audibertia (*S. spathacea*, see Walker et al. 2004; all group II), again showing parallel evolution. However, we cannot confirm the authors' generalisations. For instance, the authors refer to their stamen type A as being bithecate although e.g. the monothecate *S. penstemonoides* is included.

Although the study by Walker & Sytsma (2007) clearly illustrates the progress of knowledge gained by mapping phenotypic data on a molecular tree, we are far from reconstructing the evolutionary changes in *Salvia* in detail. In view of the great species number and the difficulties in identifying clearly the sister groups, we are only just beginning to understand the functional morphological, morphogenetic and ecological diversity in a phylogenetic way.

Bird pollinated *Salvia* species are not only adequate examples illustrating morphological diversity under functional constraints, but also confirm heterobathmy sensu Takhtajan (1959), i.e. the general view that characters evolve independently.

For instance, in *S. roemeriana*, presumably ancestral bithecate anthers and long filaments appear together with elongated and narrow tubular corollas. Further examples are species in which the joint is functional, but the movement is prevented due to lack of space. Werth (1956) already interpreted inactive levers in *Salvia* as a result of a general tendency in angiosperms to narrow flower tubes. Reisfield (1987) stated that a reduction in tube width (see also Himmelbaur & Stibal 1932-1934) might occur if the lever becomes immovable and that the latter is virtually associated with ornithophily in Calosphace.

5.4.4 The staminal lever mechanism as a lost key innovation in bird pollinated sages

The staminal lever mechanism has been regarded as a key innovation predominantly to release hidden pollen-sacs from the upper lip (Claßen-Bockhoff et al. 2004b). Furthermore, it may contribute to an increase in the range of pollinators by compensating for different body sizes and behaviours (chapters 2, 3). It may influence the breeding system by avoiding possible autogamy by herkogamy, and

increasing male fitness by pollen portioning (Webb & Lloyd 1986, Claßen-Bockhoff et al. 2004b). Finally it may also allow pollinator-sharing among sympatric species by precise pollen deposition on the pollinators' body (Grant 1994, Claßen-Bockhoff et al. 2004b).

As some of the ornithophilous species have reduced the lever mechanism in course of evolution, the question arises how these additional functions may be compensated in these species.

- The active lever mechanism might ensure pollen deposition on flower visitors with **different body sizes and specific behaviour** (chapters 2, 3). This is not necessary in ornithophilous species lacking a lever mechanism, which often have narrow (and long) corolla tubes, forcing the birds into a specific position (compare *S. lanceolata* and *S. haenkei*).
- **Herkogamy** decreases possible autogamy either in species with a lever mechanism or in those lacking one. For *S. greggii*, a species with a working lever mechanism, Webb & Lloyd (1986) described that a pollen-loaded visitor first transfers pollen to the stigma being in front of the thecae. Then the visitor releases the lever mechanism, getting dusted with pollen ('movement herkogamy'). We confirm this observation, but the stigma can also be touched after a dusting with pollen (see *S. guaranitica*; chapter 3). In ornithophilous species lacking a lever mechanism, the approaching birds usually are forced into a specific position. Thus, in general the birds would touch the stigma first, which is usually positioned in front of the thecae (see Webb & Lloyd 1986: 'approach herkogamy', chapter 2).
- Though **pollen portioning** is observed in sages with a working lever mechanism, due to the pollen morphology of the genus, it is also observed in species lacking a lever mechanism (unpubl. data; Claßen-Bockhoff et al. 2004b, compare Vogel & Coccuci 1988, Castellanos et al. 2006).
- **Pollen deposition** in species with a working lever mechanism might be **precise** enough to cause **mechanical isolation** (Grant 1994; Claßen-Bockhoff et al. 2004b). In ornithophilous species, pollen might be transferred precisely, especially in species with a working lever mechanism. Pollen might be also transferred via a 'smear effect' on a larger part of the bird's body, especially in species with long and narrow corolla tubes, lacking a lever mechanism. Both modes might be observed

within the same species (chapters 2, 3; compare *S. guaranitica*). Probably, mechanical isolation is more effective in melittophilous species as the bees' mouthparts are more fixed to a given corolla length in comparison to the birds' tongues that can extend longer to reach the nectar.

5.4.5 Conclusions

The staminal lever mechanism in *Salvia* is a fascinating example of an adaptation that becomes less important and even reduced in some of the bird pollinated species. Once released from the need for pollination, the posterior connective arms might undergo a transfer of function, acting as nectar retaining structures (at least in 28 spp.: Haenkei-type, Elegans-type, *S. tubifera*).

Although *Salvia* illustrates a remarkable reduction of a sophisticated pollination mechanism due to a pollinator shift, it is not an exclusive feature. In the Australian genus *Hemigenia* (Westringieae, Lamiaceae), the bee pollinated species generally have lever-like stamens as in *Salvia* whereas the two ornithophilous species have immovable stamens (Guerin 2005). In Fabaceae, some of the ornithophilous species lack the intricate mechanisms for pollen transfer observed in many bee pollinated keel blossoms (Westerkamp 1997) and instead have simple tubular flowers or brush-like flowers (e.g. *Erythrina* spp.; Westerkamp 1990, 1997). In *Microcorys* (Westringieae, Lamiaceae), the staminodes guide bees into the flower entrance to allow precise pollen transfer in melittophilous species, whereas they are reduced or nonfunctional in the ornithophilous *Microcorys eremophiloides* (Guerin 2005). In melittophilous *Penstemon* species (Plantaginaceae), staminodes contribute to better contact of the pollinator's body with the reproductive organs, whereas in ornithophilous flowers the staminodes lack this function (Walker-Larsen & Harder 2001).

Given that the staminal lever mechanism is a key innovation in *Salvia*, we come to the surprising conclusion that this novelty has undergone many changes due to the pollinator shift from bees to birds. *Salvia* is a large genus that most probably radiated due to this key innovation, which itself evolved and finally became lost.

5.5 SUMMARY

Bird pollinated (ornithophilous) *Salvia* species (sages) transfer pollen either by means of a staminal lever mechanism or by immovable stamens. As the distribution of the two modes within the genus is not known, a survey of all ornithophilous sages is presented. The main focus is given to floral diversity especially with respect to functional lever morphology. Thereby the hypothesis is tested that, due to a pollinator shift from bees to birds, the lever mechanism became unnecessary.

To get a general idea about the diversity of pollen transfer mechanisms, 186 ornithophilous *Salvia* species were classified according to the functional morphology of the stamen and the need for a lever movement. To test the functionality of the staminal levers and the fitting between flowers and birds the process of pollen transfer was examined by pollinator observations and tested by inserting museum skins and metal rods into fresh flowers.

The diversity of pollen transfer mechanisms is represented by eight case studies illustrating three main groups. In group I (approx. 50%) the staminal lever mechanism is necessary to open access to nectar and to enable the transfer of pollen that is hidden in the upper lip. In group II (approx. 34%) pollen is freely accessible and the lever mechanism is reduced in different ways and to different degrees. In group III (approx. 4%) the lever works as in group I, but pollen is freely accessible as in group II. The remaining approx. 13% are not clearly classified.

It is considered that the driving force behind the diverse modes of reduction is the necessity to increase the distance between nectar and pollen, thereby ensuring pollen deposition on the bird's feathered head. This is achieved several times in parallel by corolla elongation and/or exposure of the pollen-sacs. As soon as pollen is freely accessible, the lever movement loses its significance for pollination.

6 General conclusions

The thesis presents the first survey on ornithophilous sages, their distribution, floral characters and possible evolutionary tendencies due to pollinators. It is shown that bird pollinated sages represent about 20 % of the species within the genus, thus a bit more than known from angiosperms in general (10-15 % after Feinsinger 1983).

In the Old World only four species are identified as bird pollinated while in the New World occur at least 182 ornithophilous species. This unexpected distribution may relate to differences in the two hemispheres like different distributions of both sages and pollinating birds, geographical and ecological isolations, habitat diversity and geological and climatic changes during the past. However, the phenomenon is not yet understood.

As already stated by Reisfield (1987), bird pollinated sages evolved several times in parallel. 'Intermediate' species sharing characters of two or more pollination syndromes (e.g. melittophily and ornithophily), might indicate a transition between these syndromes as it is assumed also in other genera (e.g. *Penstemon*, *Pedicularis*; Macior 1986, Wilson et al. 2006). Thereby a shift from bees to birds is more likely than one from birds to bees, but we cannot exclude a reverse shift under certain environmental conditions. In view of the difficulties in identifying clearly the sister groups in *Salvia*, we are only just beginning to understand the functional morphological and ecological diversity in a phylogenetic way.

Floral characters of ornithophilous sages fit to their typical pollination syndrome. As to their prevalence of the red colour and to their flower size, they are in the range of ornithophilous angiosperms in general (Baumberger 1987). However, they differ in some characters like colour composition, corolla shape and stability, showing an enormous diversity in floral characters. They illustrate the broad amplitude of phenotypic responses to a presumed selection pressure.

One of the floral features, also very diverse, is the stamen. As it contributes to sexual reproduction, a high selection pressure on pollen transfer mechanisms is expected. As an innovation compared to its assumed sister genera (e.g. *Rosmarinus*, *Perovskia*, *Meriandra*, *Dorystachys*, *Zhumeria*, *Lepechinia*) *Salvia* has evolved the characteristic staminal lever mechanism. And it shows such a large number of

species that even under the assumption of polyphyly (see Walker & Sytsma 2007) the individual clades are larger than their sister groups. Both findings meet in the conclusion that the staminal lever mechanism is indeed a key innovation that has caused parallel adaptive radiation (Claßen-Bockhoff et al. 2004b, Wester and Claßen-Bockhoff 2004). The most surprising result of the present thesis is that the staminal lever mechanism is lacking in a large part of the ornithophilous species. Whereas in most bee pollinated species transfer of pollen, that is hidden in the upper lip from pollen collecting bees, is enabled by the lever mechanism; in ornithophilous species hiding is not necessary. As soon as pollen is freely accessible, the lever movement loses its significance for pollination and is reduced in a part of the species. Thus, the lever mechanism of *Salvia* gives an example of a structure that may have promoted speciation in bee pollinated species and whose significance got lost due to the shift from bees to birds.

It is surprising that in species lacking lever function, the posterior lever arms, normally acting as abutment against bills, are only rarely reduced. It is unclear whether they really have lost function and might be retained as long as they do not trouble, or whether they change their function to a stabilising structure or for nectar retention.

Relating to pollen transfer, pollen deposition in species with a working lever mechanism might be precise enough to cause mechanical isolation (Grant 1994, Claßen-Bockhoff et al. 2004b). In ornithophilous species, precise pollen deposition, but also a 'smear effect', was observed, not clearly relating to a stamen type. Probably, mechanical isolation is more effective in melittophilous species as the bees' mouthparts are more fixed to a given corolla length in comparison to the birds' tongues that can extend longer to reach the nectar. Considering the rather unprecise pollen removal by the stigma, secure pollen deposition on flower visitors with different body sizes and specific behaviour might be more important. This is not necessary in ornithophilous species lacking a lever mechanism, which often have narrow (and long) corolla tubes, forcing the birds into a specific position.

Concluding, the staminal lever mechanism in *Salvia* shows that a key innovation that commenced as an adaptation to bees through the shift to birds was furthermore either maintained, changed or reduced. All 'versions' still work successfully with birds.

Although in this thesis about 90 % of the New World sages could be clearly assigned to a pollination syndrome and a survey on the ornithophilous sages is given, there are still open questions.

To know more about possible pollinators of species with unclear syndrome and to get deeper insights in the evolutionary significance of the staminal lever mechanism, further studies are needed. Pollinator observations and pollinator choice experiments will help to understand how far differences in floral features reflect selection through pollinators and thus the adaptive significance of these features. Pollination simulation experiments and measurements of pollinator effectiveness, quantified by counting the number of pollen grains received by stigmas after a single visit to an experimental flower, might show whether the differences between sister species or between species differing in stamen types are adaptations that influence the fitting between flowers and visitors, increasing the efficiency of pollen transfer.

7 References

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