Chapter 3
Morphological Characteristics of *Teucrium* Species: Generative Morphology

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Abstract The generative morphology related with corolla and calyx construction, pollen, inflorescence type and nutlets are of great importance in *Teucrium* L. These characters are the basis for the classic systematic and recent classifications. *Teucrium* has a corolla usually 1-lipped or 2-lipped (bilabiate). *Spartothamnella* Briq., *Oncinocalyx* F. Muell., and *Teucridium* F. Hook, closely related to *Teucrium*, present a corolla 5-lobed in the upper half, lobes slighty spreading, 4 posterior ± similar, anterior lobe larger than the others and not concave. The calyx in these genera is actinomorphic. This is an exceptional corolla conformation in *Teucrium* and only found in these species. The main difference between *Spartothamnella* and *Teucrium* is that the former has drupaceous fruit and between *Teucrium* and *Teucridium* is the ovary form. *Oncinocalyx* differs from *Teucrium* in the conspicuously hooked calyx lobes. *Teucrium* Sections *Pycnobotrys* Benth., *Stachyobotrys* Benth., *Scorodonia* (Hill) Schreb., and *Teucriopsis* Benth., have weakly 2-lipped corolla and zygomorphic calyx. Species of section *Teucrium* have 1-lipped spurred corolla and actinomorphic calyx except for the Australian species with non-spurred corollas. *Teucrium* show a great diversity in floral phenotypic diversity and adaptive significance to pollination and dispersal. Functional redundancy is found in the gullet-shaped corollas with nectar guides and nototribic pollination of the sections *Chamaedrys* (Mill.) Kästner, *lsotriodon* Boiss., subsection *Scordium* (Mill.) Kästner, *Montana* Lazaro Ibiza and subsection *Pumila* (Lazaro Ibiza) Rivas Mart. *Teucrium* is the only genus within the sub family Ajugoideae with two derived pollen characteristics, granulate or verrucate sculpturing and operculate colpi and with a considerable variation in pollen sculpturing. Nototribic pollination of the gullet-shaped corollas with closed gullet mechanism (by a palate of hairs associated to a slight pouch in the corolla tube) are exclusive of the section *Teucrium.* The sternotribic pollination of the brush-shaped corollas closed by a tuft of hair in the entrance of the corolla tube (base of the anterior lobe), are specific of the ginodioecious species of section *Polium* (Mill.) Schreb. Resupinate flag-shaped corollas with sternotribic pollination

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is present in subsection *Spinularia* (Boiss.) Kästner and *Stachyobotrys*. The main dispersal modes in section *Chamaedrys, lsotriodon* and *Polium* is the semachory. Sections *Teucrium* and *Teucriopsis* are wind-dispersal by pogonospores, subsection *Spinularia*, section *Scorodonia* and *Teucrium betonicum* and *Teucrium abutiloides* L'Hér from section *Teucriopsis* are ballospores.

Keywords *Teucrium* · *Spartothamnella* · *Oncinocalyx* · *Teucridium* · Corolla and calyx construction · Inflorescence · Nutlets · Pollen · Pollination · Dispersal · Lamiaceae

3.1 Introduction

The "bilabiate blossom" characterizing the Lamiaceae is a floral construction for nototribic (dorsal) pollen deposition (Claßen-Bockhoff 2007). The floral construction is a syndrome of adaptive characters from generative structures needed for pollen transfer that have evolved under phylogenetic developmental and environmental constraints. The floral construction allows understanding of the ecological and morphogenetic constraints of flower evolution in Lamiaceae (Claßen-Bockhoff 2007) and it is particularly interesting in *Teucrium* because most of the species have one-lipped flowers except for the section *Pycnobotrys, Stachyobotrys, Scorodonia* and *Teucriopsis* with weakly bilabiate (two-lipped) flowers. The *Teucrium* phylogenetic related genera, such as *Spartothamnella* Briq., *Oncinocalyx* F. Muell., and *Teucridium* F. Hook, do not have one-lipped or two-lipped (bilabiate) flowers; they own flowers with corolla of five-lobed, four posterior ± similar, and anterior lobe larger.

Some studies have also investigated the variation of floral construction in different flower morphs related to the breeding system and the evolution of separate sexes in gynodioecius *Teucrium* species (Puech 1978; El Oualidi 1987; Alados et al. 1997; Rodríguez-Riaño and Dafni 2007) and *Teucridium* genus (Merrett 2005).

Teucrium and its related genera show a great phenotypic diversity and adaptive significance in the morphological generative characters related to breeding system, pollination and other functional generative traits such as dispersal. *Teucrium* is melittophilous and pollinated mainly by bees (van der Pijl 1972) and wasps (Petanidou 1996), it is a good example of a sympetal, tubular, hermaphrodite and gynodioecious, proterandrous flower. In particular, this flower type is interesting in *Teucrium*, because it has mainly one-lipped corollas with bilateral symmetry, slightly campanulate tube and the lower lip with five asymmetrical lobes; this corolla type also occurs in related genera of the Ajugoideae. The lower lip acts as a landing platform and provides an easier access to the nectar, but in some sections, a barrier in the tube may still act as a selective device. The variations in the corolla construction, size, lobes symmetry, specialized features of lower lip, resupination of the tube are the result of a selection by pollinators, which leads an adjustment in floral forms to efficient pollen transfer and fruit set. The most common *Teucrium*

calyx is five-lobed and persistent, except when falls with the diaspores inside and plays a part in seed dispersal (van der Pjil 1972; Bouman and Meeuse 1992; Paton 1992; Navarro et al. 2009). The variation in the calyx symmetry, morphology of the tube and teeth while as functioning of the pedicel, express the adaptation to a certain kind of seed dispersal mechanisms and a protection of immature nutlets (Navarro and El Oualidi 1999). The sculpturing and size of the nutlets have an important role in dispersal mechanisms (Bouman and Meeuse 1992). Most of the species show a flowering peak at the end of spring but may also extend their flowering season into the summer and autumn (Navarro and Cabezudo 1995).

Teucrium pollen grains are trizonocolpate, isopolar and radiosymmetric. They are circular to circular-lobulate in polar view and sinuaperturate; in equatorial view they are elliptic and usually subprolate to prolate. Pollen surface is minutely perforated with granules, less often with verrucae and with a supractectal reticulum or with an intermediate sculpturing composed of short, discontinuous supratectal ridges (Navarro et al. 2004). *Teucrium* is the only genus within the sub family Ajugoideae in the Mediterranean region with two derived pollen characteristics, granulate or verrucate sculpturing and operculate colpi. Abu Asab and Cantino (1993) pointed to the considerable variation in pollen sculpturing within *Teucrium*, distinguishing three sculpturing types: the verrucate sculpturing (bearing supratectal wart-like projections), which is considered as a derived pollen character in Lamiaceae, the suprareticulate exine (supratectal ridges forming a reticulate pattern), a plesiomorphic condition within the subfamily Nepetoideae (Wagstaff 1992), and an intermediate sculpturing type transition from the verrucate to the suprareticulate composed of short discontinuous supratectal ridges. The first type is considered as the norm in *Teucrium*, while the last two are less common. Nabli (1970, 1976), El Oualidi (1987), Diez et al. (1993), Abu-Asab and Cantino (1993) and Navarro et al. (2004) described the pollen morphology of many species of section *Polium*. The pollen morphology supports the phylogenetic relationships between these genera and *Teucrium* (Abu Asab and Cantino 1993), forming the *Teucriina* clade (Cantino et al. 1997), based on the operculate and verrucate pollen.

The generative characters related with corolla and calyx construction, pollen, inflorescence type and nutlet morphology are of great importance in *Teucrium.* These characters are the basis for the classic and recent systematic classifications, the great useful for delimiting and structuring the most problematic taxonomic groups. In order to examine the floral phenotypic diversity, a sample of 341 specimens of 97 *Teucrium* taxa and its close related phylogenetic genera *Spartothamnella*, *Oncinocalyx* and *Teucridium* from throughout the world have been studied in addition to whose examined in previous works (Navarro and El Oualid 1999; Navarro 1995, 2010). This study based on the field, herbarium specimens and bibliographic references of the regional Floras. Flowers and nutlets were collected in the field or from authorized Herbarium specimens (see Appendix in Chap. 1). The main floral features, such as the inflorescence type, corolla size, corolla colour, flower sexuality and main flowering season were measures or observed. The flower form related to the pollination based on Faegry and van der Pjil (1979). The primary dispersal mode follows van der Pijl (1972), Zohary (1937) and Bouman and Meeuse (1992) and the

diaspore type is described in accordance with Dansereau and Lems (1957) and Jenny (1995). The sectional delimitation of *Teucrium* is according to Bentham (1833), Boissier (1879) and Navarro (2010). The examined specimens are listed in the Appendix included in the Chap. 1.

The aim of this study is described the phenotypic diversity and adaptive significance of the *Teucrium* flower construction to carry out an overview of the diversity of the generative characters, especially floral features related to pollination and dispersal mechanisms, providing a synthesis of the predominant generative strategies and their infrageneric diversity.

3.2 Floral Phenotypic Diversity and Adaptive Functional Significance in *Teucrium* and Related Genera

Teucrium has a corolla usually 1-lipped or 2-lipped, 5-lobed (with the anterior lobe much larger than the others), concave, occasionally unequal 5-lobed in the upper half; lobes slightly spreading, 4 posterior ± similar (anterior lobe larger than the others). *Oncinocalyx betchei, Spartothamnella teucriiflora* and *Teucridium parvifolium* present a corolla 5-lobed in the upper half, lobes slighty spreading, 4 posterior ± similar, anterior lobe larger than the others and not concave, with an annulus of hairs at the middle part of insertion of stamens in the corolla tube (Table 3.1). The calyx in these genera is actinomorphic. This is an exceptional corolla conformation in *Teucrium* and only found in these species. The main difference between *Spartothamnella* and *Teucrium* is that the former has drupaceous fruit and between *Teucrium* and *Teucridium* is the ovary form, unlobed or lobed up to a quarter part of its length in *Teucridium* and usually lobed from a quarter to half its length in *Teucrium*. *Oncinocalyx* differs from *Teucrium* in the conspicuously hooked calyx lobes. Variation in corolla construction is show in Table 3.1 and corolla characters related with pollination in Table 3.2. A schematic drawing of the general conformation of the *Teucrium* flower is shown in Fig. 3.1.

Teucrium and its close related genera also differs from the other members of Lamiaceae based on non-gynobasic style. The ovary is bicarpellary, syncarpous, 4-lobed, 4-locular, with one ovule in each cell attached to an axile placenta, the style terminal, exserted, filiform, with 2 stigmatic lobes at the top. Fruit dry, schizocarpic, splitting into 4 mericarps (nutlets), enclosed in the persistent calyx, except for the drupaceous fruit in *Spartothamnella*.

The basic inflorescence is a raceme derived from a tyrse of verticillasters by floral reduction, originating contracted verticillasters, grouping into heads (Navarro and Cabezudo 1995). The infrageneric variation from axillary flowers or lax verticillasters (2–8 flowers) to simple dense terminal or branched raceme of contracted verticillasters is show in Table 3.1.

The calyx is tubular or campanulate, urceolate (gibbous) in plate or obconical, ventral, dorsiventral or dorsally pedicellated, 10-nerved, zygomorphic (bilabiate),

Table 3.1 Floral construction of the infrageneric taxa of *Teucrium* and its related genera *Oncinocalyx, Spartothamnella* and *Teucridium*

Teucrium infrageneric taxa	Broad upper calyx lip	Calyx construction	Corolla construction	Internal indumentum of corolla	Calyx pedicellum insertion	Corolla tube short apically broadly
Teucrium (Mediterranean area)	Absent	Actinomorphic Calyx	1-lipped, llp. not forming angle with the tube	Annulus of hairs at the base of the ct.	Ventral	Present
Teucrium (*T. racemosum* group)	Absent	Actinomorphic Calyx	1-lipped, llp. not forming angle with the tube	Annulus of hairs at the middle part of the ct.	Ventral	Present
Teucrium (Austral areas)	Absent	Actinomorphic Calyx	5-lobed,4 posterior ±similar, anterior lobe larger	Annulus of hairs at the middle part of the ct.	Ventral	Present
Teucriopsis	Absent	2-lipped 1/4	2-lipped 2/3, llp. emarginated or two lobed,	Without indumentum	Dorsi-ventral	Absent
Scorodonia	Present	2-lipped 1/4	2-lipped 2/3, ul. developed	Without indumentum	Dorsi-ventral	Absent
Pycnobotrys	Present	2-lipped(1/4)/ zygomorphic (1/2/2)/ Sub-actinomorphic (3/2)	Sligth 2-lipped (pseudo-2-lipped)	Without indumentum	Dorsi-ventral	Absent
Stachyobotrys	Present	Zygomorphic (1/2/2)	Sligth 2-lipped (pseudo-2-lipped)	Without indumentum	Dorsal	Absent
Isotriodon	Absent	Zygomorphic (1/2/2)	1-lipped, llp forming angle with the ct.	Hairs at the base of ml. forming two guides	Dorsi-ventral	Absent
Chamaedrys subsection *Chamaedrys*	Absent	Sub-actinomorphic (3/2)	1-lipped, llp forming angle with the ct.	Hairs at the base of ml. forming two guides	Dorsi-ventral	Absent
Chamaedrys subsection *Marum*	Absent	Sub-actinomorphic (3/2)	1-lipped, llp forming angle with the ct.	Hairs at the base of ml. forming two guides	Dorsi-ventral	Absent

(continued)

Table 3.1 (continued)

Teucrium infrageneric taxa	Broad upper calyx lip	Calyx construction	Corolla construction	Internal indumentum of corolla	Calyx pedicellum insertion	Corolla tube short apically broadly
Montana	Absent	Sub-actinomorphic (3/2)	1-lipped, llp forming angle with the tube,	Hairs at the base of ml. forming two guides	Dorsi-ventral	Absent
Polium subsection *Polium*	Absent	Sub-actinomorphic (3/2)	1-lipped, llp not forming angle with the ct.	Hairs at the base of the ml. forming a tuf	Dorsi-ventral	Present
Polium subsection *Pumila*	Absent	Sub-actinomorphic (3/2)	1-lipped, llp forming angle with the ct.	Hairs at the base of ml. forming two guides	Dorsi-ventral	Absent
Polium subsection *Simplicipilosa*	Absent	Sub-actinomorphic (3/2)	1-lipped, llp not forming angle with the ct.	Hairs at the base of the ml. forming a tuf	Dorsi-ventral	Present
Scordium	Absent	Sub-actinomorphic (3/2)	1-lipped, llp forming angle with the ct.	Hairs at the base of ml. forming two guides	Dorsi-ventral	Absent
Scordium subsection *Botrys*	Absent	2-lipped (1/4)	1-lipped, llp forming angle with the ct.	Hairs at the base of ml. forming two guides	Dorsal	Absent
Scordium subsection *Spinularia*	Absent	2-lipped (1/4)	1-lipped, llp forming angle with the ct.	Hairs at the base of ml. forming two guides/ without indumentum	Dorsal	Absent
Oncinocalyx genus	Absent	Actinomorphic Calyx	5-lobed,4 posterior ±similar, anterior lobe larger	Annulus of hairs at the middle part of the ct.	Ventral	Present
Spartothamnella genus	Absent	Actinomorphic Calyx	5-lobed,4 posterior ±similar, anterior lobe larger	Annulus of hairs at the middle part of the ct.	Ventral	Present

(continued)

Table 3.1 (continued)

Teucrium infrageneric taxa	Broad upper calyx lip	Calyx construction	Corolla construction	Internal indumentum of corolla	Calyx pedicellum insertion	Corolla tube short apically broadly
Teucridium genus	Absent	Actinomorphic Calyx	5-lobed,4 posterior ±similar, anterior lobe larger	Annulus of hairs at the middle part of the ct.	Ventral	Present

ct corolla tube, *ml* middle lobe, *llp* latero-posterior corolla lobes

sub-actinomorphic or actinomorphic, tube within glabrous or pilose at throat, the 5 teeth, equal or unequal, some times mucronate to hooked at end or cucullate (Table 3.1).

The infrageneric adaptive functional significance of floral features to pollination and dispersal is summarized below. Very detailed illustrations of the inflorescence type, corolla and clayx construction and nutlets morphology can be consulted in Navarro (2010).

The corolla of section *Teucrium* is one-lipped, gullet-shaped and slightly personate (with a slight pouch) and shortened tubuled, lilac or white with closed gullet mechanisms by a palate of hairs; the lateral and latero-posterior lobes are developed. Flowers are axillary in the leaves or in lax verticillasters (Fig. 3.2) and the flowering occurs in spring or multi-seasonal floration in winter-spring-summer. In this group, the most important factor for attracting pollinators is presumably the strong visual signal of their large flowers described by Shmida and Dafni (1989) as flowers engaged in a "discovery advertisement" (Fig. 3.2). The campanulate actinomorphic calyx does not have a closed mechanism to protect the immature seed. They are wind-dispersal species with a big hairy nutlet, ancestral character in the genus (Marin et al. 1994; Navarro and El Oualidi 2000b). The diaspore type is pogonospore. Section *Teucrium* is a basal group within *Teucrium* (Marin et al. 1994; Navarro and El Oualidi 2000a; Navarro et al. 2004; Salmaki et al. 2016). This section has widespread floral characters in the structurally simple states, including the actinomorphic calyx and unclearly lipped corollas (Austral species of section *Teucrium*) such as *Spartothamnella, Oncinocalyx* and *Teucridium* present in geologically ancient areas.

Section *Teucriopsis* comprise endemic species from Macaronesian region. The flowers are in verticillasters or in lax axillary cymes in the upper leaves. The corolla blue, orange or cream is weakly bilabiate, wide and shortly tubular; the calyx is campanulate, actinomorphic, some with an annulus of hairs inside; the nutlets are large and haired.

Species from section *Scorodonia* have one-lipped gullet-shaped corollas with long and narrow tube and a lower lip and latero-posterior lobes well-developed without nectar guides; the calyx is bilabiate with an annulus of hairs inside. Flowers

Table 3.2 Main inflorescence type, corolla size (mm), corolla colour, main flowering season and pollinators in the infrageneric taxa of *Teucrium* L

Teucrium infrageneric taxa	Inflorescence	Corolla size (mm) Length of tube and lower lip	Corolla colour	Main flowering season	Pollinators
Teucrium	Axillary flowers or lax verticillasters	(10)12.5–14.5(22)	Lilac/white	End winter-spring-summer (III–VI)	Large solitary bees
Teucriopsis	Axillary flowers or lax verticillasters	(7.5)9.5–11.5(13.5)	Blue/orange/white	Summer (V–VI)	Large solitary bees
Chamaedrys	Lax verticillasters/sub-spirally racemes	(9.5)11.5–12.5(14.5)	Purple/pink/yellow	Summer (V–VI)	Small solitary bees, flies
Montana	Sub-spirally raceme	(8)10.5–12.5(17)	Cream/white-pink/purple/yellow	Summer (V–VII)	Solitary bees, ants, flies
Scorodonia	Verticillasters	(5.5)7–8(11)	Cream/pink	End spring-summer (IV–VI)	Long-tongued butterflies, bees
Scordium	Axillary flowers/verticillasters (2–8) flowered	7.5–8.5	Cream/pink	Summer (V–VII)	Small solitary bees
Stachyobotrys	Dense Verticillasters like spike	7.5–9.5	Cream/cream-yellow	End spring-summer (IV–VI)	Small solitary bees, flies
Scordium subsection *Spinularia*	Verticillasters (2–4) flowered	(6.8)8.5–9(15.5)	Cream/cream-pink	Summer (V–VIII)	Solitary bees
Isotriodon	Sub-spirally racemes	(5.5)8–10(14.5)	Cream/pink-purple/yellow	Spring (IV–V)	Solitary bees, flies
Polium subsection *Polium*	Simple dense terminal or branched raceme	(3)3.5–4.5(6.5)	White/cream-pink/yellow	End spring-end summer (IV–VIII)	Small solitary bees, wasps, ants, flies
Polium subsection *Simplicipilosa*	Simple dense terminal or branched raceme	(3)3.5–4.5(6.5)	White/cream	Summer (VI–VII)	Small solitary bees, wasps, ants, flies

(continued)

Table 3.2 (continued)

Teucrium infrageneric taxa	Inflorescence	Corolla size (mm) Length of tube and lower lip	Corolla colour	Main flowering season	Pollinators
Polium subsection *Pumila*	Simple dense terminal or branched raceme	5.5–6	White/ purple	Summer (V–VII)	Solitary bees, long-tongued butterflies, ants

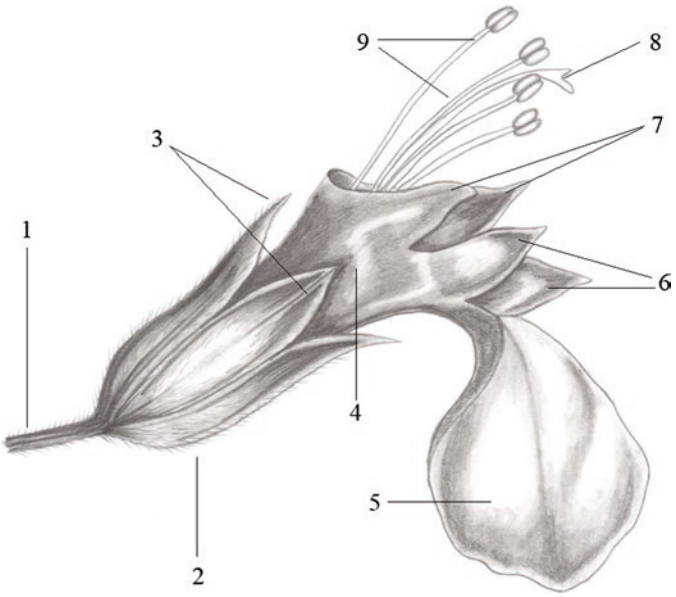

Fig. 3.1 Schematic drawing of the general conformation of the *Teucrium* flower. 1 – Flower pedicel; 2 – Calyx; 3 – Calyx lobes; 4 – Corolla tube; 5 – Anterior corolla lobe; 6 – Lateral corolla lobes; 7 – Latero-posterior corolla lobes; 8 – Style; 9 – Stamines

are disposed in verticillasters and the main flowering season is the summer Fig. 3.3. They are wind-ballistic or/and rain-ballistic species with glabrous and smooth nutlets. These features are in accordance with the ones described by Paton (1992) in *Scutellaria*.

Section *Isotriodon* includes species with infloreseence in a sub-spiral raceme; the calyx is tubular-campanulate, sub-actinomorphic, gibbous at the base, ±pedicellate with the upper tooth shorty ovate, the lower teeth narrower and acute; the corolla has long tube with well-developed lobes and two nectar guides of hairs on the lower lip; the nutlets have glandular hairs. In the species of section *Chamaedrys,* the flowers are placed in lax verticillasters or in sub-spirally lax racemes; the corolla has

Fig. 3.2 *T. fruticans* L. (section *Teucrium*)

Fig. 3.3 *T. oxylepis* Font Quer (section *Scorodonia*)

long latero-posterior lobes, acute and haired and the lower lip has two clear nectar guidelines of hairs; the calyx is tubular-campanulate and actinomorphic (Fig. 3.4) with an annulus of hairs inside and the nutlets are haired.

The greatest convergence of floral features is show in the species of section *Isotriodon*, the rocky species of section *Chamaedrys* and the rocky species of section *Montana* indicating a higher incidence of functional redundancy. The corolla is one-lipped, gullet-shaped and with regular tube (tube >5 mm), with two clear nectar guides in the lower lip, without closed gullet mechanisms and with well-developed

Fig. 3.4 *T. webbianum* Boiss. (section *Chamaedrys*)

Fig. 3.5 *T. charidemi* Sandwith (section *Polium* subsection *Simplicipilosa*)

and specialized latero-posterior lobes acting as guiding visitors. Flowers are purple, white or cream, rarely yellow, flowering mainly at the end spring and summer. They are wind dispersal species with campanulate, sub-actinomorphic calyx generally without annulus of hairs inside. They are also wind-ballistic species, or seed-dispersal inside the calyx. In this last case, the calyx is easily detached and generally dry and papery. In some species such as *Teucrium charidemi* Sandwith (Fig. 3.5), *T. compactum* Clemente ex Lag., and *T. yemense* Deflers, the inflated calyx ensure long distance dispersion by the wind, this type is found by Zohary (1937) and

Fig. 3.6 *T. scordium* L. (section *Scordium*)

Navarro et al. (2009) in desert species. This group of species shows a highly convergence exemplified by the lax inflorescence in sub-spirally simple racemes.

Species from the section *Scordium* have one-lipped, gullet-shaped corollas with nectar guides. Flowers are placed in verticillasters (2–8) flowered axillary in upper leaves; the calyx is tubular-campanulate, and sub-actinomorphic; the corolla has two nectar guides on lower lip and the nutlets are glandular haired (Fig. 3.6).

The species of section *Scordium* subsection *Spinularia* have corolla one-lipped, gullet and flag-shaped with a long and narrow tube, resupinate in some species. The strongly zygomorphic, gibbous calyx have an annulus of hairs inside. They are wind-ballistic species and possibly epizoochores, since most of the species show spinescent calyx teeth. The flowers (2–4) placed in axillary verticillasters in the upper leaves; the nutlets are small and glabrous. The species flowering mainly in spring and summer (Fig. 3.7).

In the section *Stachyobotrys,* the flowers are in dense verticillasters like spikes; the lateral lobes of the corolla are reduced or absent, in some cases, the tube is resupinate; the calyx is campanulate, bilabiate often-gibbous al the base with spinescent teeth, upper tooth weakly broad, 2 lower teeth lanceolate and the nutlets have glandular hairs. Some species from section *Stachyobotrys* such as *Teucrium collincola* Greuter & Burdet show a particular resupinate corolla without nectar guides and with a well-developed lower lip, the latero-posterior lobes are almost totally reduced and the lateral lobes are very short. The calyx is strongly zygomophic and campanulate. They are rain-ballistic or/and wind-ballistic species, some of them show the long mucronated calyx teeth, perhaps related to the epizoochory.

Species belonging to section *Polium* subsections *Polium* and *Simplicipilosa* are ginodioecious species (Fig. 3.8) with one-lipped brush-shaped corollas shortened tubuled with closed gullet mechanisms by a tuft of hairs to exclude inefficient

Fig. 3.7 *T. spinosum* L. (section *Scordium* subsection *Spinularia*)

Fig. 3.8 *T. teresianum* Blanca, Cueto & J. Fuentes (section *Montana*)

visitors and limit pollinator diversity. Flowers are compacted in the dense racemes forming the branched inflorescence (Figs. 3.8 and 3.9). Flowering mainly in spring, the ginodioecious system imposes limitations in pollination and rewards partitioning between females, generally pink and with nectar reward flowers and hermaphrodite flowers (white or cream). The calyx is sub-actinomorphic. They are wind-dispersal species and the calyx falls with the nutlet inside. Some species from arid regions have cucullate calyx teeth that close the calyx tube and protect the nutlets. In other species like *Teucrium charidemi* (Fig. 3.5) or *T. musimonum* Humbert, the dense vermiform hairs cover the calyx outside to facilitate the dispersion by the air that pushes them hovering over the ground.

Fig. 3.9 *T. lusitanicum* Schreb. (section *Polium*)

3.3 Corolla Construction and Pollination Adaptive Significance

Teucrium exhibit a great diversity in flower construction. Table 3.1 show the main infrageneric generative traits in *Teucrium* related to the pollination. *Teucrium* has with white, cream, pink and purple flowers. The orange and blue flowers are exclusive from section *Teucriopsis* and the lilac from section *Teucrium*. The most common flower construction related to pollination in *Teucrium* are the gullet-shaped corollas with nototribic pollen deposition; this type occurs in all sections of the genus except in section *Polium* subsection *Polium.* The flag-shaped corollas with sternotribic pollen deposition are rare and exclusive of the species with resupinate corollas from subsections *Spinularia* (Fig. 3.7) and section *Stachyobotrys*. In these cases, the gullet-shaped corollas are reversed and function like a flag-shaped and there may be a simple resupination through torsion of the corolla tube, and the lower lip only acts as an attraction and the lateral and latero-posterior lobes are reduced or absent (Fig. 3.7). The brush-shaped corollas with diffuse pollen deposition are exclusive of the ginodioecious flowers of the section *Polium.* The bilateral symmetric flowers such as those of the section *Teucrium* induce a more specific behavior to ensure that stigma and anthers are touched effectively (Fig. 3.2). Sternotribic and nototribic pollen deposition occur in this last section.

Teucrium species have corollas closed to ineffective insect visitors. We observed two closed gullet mechanisms related to pollination: (1) A barrier, which offers resistance and demands precision on the part of the pollinator. This barrier formed by a palate of hairs in the region of the common basal part of the latero-posterior lobes and stamine insertion, which is associated to a slight pouch (Navarro and El Oualidi 1999). When the insect poses on the lower lip, its force makes the lip bend down and the tube closed with an annulus of hair. This mechanism is specific of the species from the section *Teucrium.* (2) A barrier to exclude the inefficient visitors,

formed by an annulus of hairs from the base of the stamine insertion to the basal part of the anterior lobe. This basal part is cover densely by hair forming a tuft, which also serves as a foothold for the pollinator visitors. This mechanism is exclusive of the unspecialized ginodioecious species of section *Polium* subsections *Polium* and *Simplicipilosa* and section *Montana* (Navarro and El Oualidi 1999) and *Teucridium* genus (Merrett 2005).

The gullet-shaped corollas without closed gullet mechanism show the guiding of visitors such as the nectar guides formed by two clear rows of hairs in the adaxial side of the lower lip extending to the entrance of the corolla tube. These guidings are common in the species of the sections *Chamaedrys, lsotriodon, Scordium, Montana* and *Polium*. The calyx does not play an important role in the pollination syndromes because it does not have a known semaphyll function, but has glandular hairs emitting scent adding to the attraction for visitors.

3.4 Calyx Construction, Nutlet Morphology and Dispersal Adaptive Significance

Table 3.3 show the main infrageneric generative traits in *Teucrium* related to the dispersal. The predominant primary dispersal mode in *Teucrium* is the semachory and ballautochory. Wind-dispersal or wind-ballistic species (semachores or ballospores) are found in *Teucrium heterophyllum* L'Her from section *Teucriopsis* and in the species of the sections *Teucrium, Chamaedrys, Scordium*, *Isotriodon* and *Polium*. Ballautochory, wind-ballistic or rain-ballistic species (ombrochory) found in the section *Scorodonia, Stachyobotrys*, subsection *Spinularia* and in *Teucrium abutiloides* and *T. betonicum* from the section *Teucriopsis.* Epizoochory is rare in the genus, found in some species with spinescent calyx from subsection *Spinularia*. Meteo-anemochory only found in the section *Polium.*

The sculpturing and size of the nutlets (diaspore) have an important role in dispersal mechanisms (Bouman and Meeuse, 1992). Pericarp surface of the nutlets in *Teucrium* are variously ornamented (Marin et al. 1994); smooth (section *Scorodonia*); haired (section *Teucrium*, *Teucriopsis* and *Chamaedrys*) (Fig. 3.10); with glands (sections *Chatnaedrys, Isotriodon* and *Montana*) and very reticulated (section *Polium* subsection *Polium*) to maximize the dispersion by the wind. The variation in the type of indument of the nutlets are described in Navarro and El Oualidi (2000b).

The main diaspore type present in *Teucrium* are the semaspores associated to the species with actinomorphic or sub-actinomorphic, pedicelled calyx. This dispersal mode characterized *Thymus* (Bouman and Meeuse 1992). Ballospores are associated to species with bilabiate or strongly zygomorphic calyx and pogonospores (diaspores largest than 2 mm) with the actinomorphic and campanulated calyx.

The calyx morphology vary in relation to the protection of the immature nutlets by two type of system: (1) an annulus of hairs inside the calyx tube, considering its presence as a derived state character (Abu-Asab and Cantino 1993) frequent in other

Table 3.3 Main dispersal mode, diaspore type and diaspore size (mm) in the infrageneric taxa of *Teucrium* L

Teucrium infrageneric taxa	Dispersal mode	Diaspore type	Diaspore size (mm) length × width
Teucrium	Semachory wind-dispersal	Pogonospore	(1.5)2 × 3(3.5)
Teucriopsis	Semachory wind-dispersal	Pogonospore	(1.5)1.8 × 2.5
Chamaedrys	Semachory wind-dispersal	Semaspore/ pogonospore	(0.7)1.5 × 1.8(2.5)
Montana	Ballautochory semachory wind dispersal	Semaspore/calyx with seed inside	(0.5)1.2 × 1.3(2.5)
Scorodonia	Ballautochory semachory wind-dispersal	Ballospore	(1)1.3 × 1.5(1.8)
Scordium	Ballautochory semachory wind-dispersal	Semaspore	(0.8)1 × 1.3
Stachyobotrys	Ballautochory epizoochory	Ballospore	(1)1.3 × 1.8
Scordium subsection *Spinularia*	Ballautochory epizoochory	Semaspore/ ballospore/ sclerospore	(0.1)1 × 1 × (1.5)
Isotriodon	Ballautochory/ semachory wind-dispersal	Semaspore	(0.7)1.3 × 1.5(2.5)
Polium subsection *Polium*	Meteo-anemochory wind-dispersal	Calyx with seed inside	(0.8)1.3 × 1.5(2.5)
Polium subsection *Simplicipilosa*	Meteo-anemochory wind-dispersal	Calyx with seed inside	(0.6)1.2 × 1.5(1.7)
Polium subsection *Pumila*	Meteo-anemochory	Calyx with seed inside	(0.6)0.8 × 1(1.5)

Lamiaceae genera such as *Marrubium, Origanum, Sideritis, Ocimum* and *Scutellaria*; (2) the mature cucullate teeth closing completely the calyx tube (El Oualidi and Puech 1993). The last is exclusive of some species of section *Polium* subsection *Polium* as *Teucrium lusitanicum* Schreb., or (3) a gibbous in the base of the calyx like *Teucrium botrys* L., covered inside by long hairs, making difficult the exit the nutlets, this mechanisms is exclusive of the subsection *Spinularia.*

The pedicel of the calyx and the upper tooth in strongly zygomorphic calyces plays a role in the dispersal mechanism of *Teucrium.* The pedicel is present in all *Teucrium* flowers except in the section *Polium* subsection *Polium* and some rocky and arid species from section *Montana*. The pedicel is not rigid and acts in the ballistic mechanisms contracting itself to eject the mature nutlets (subsections

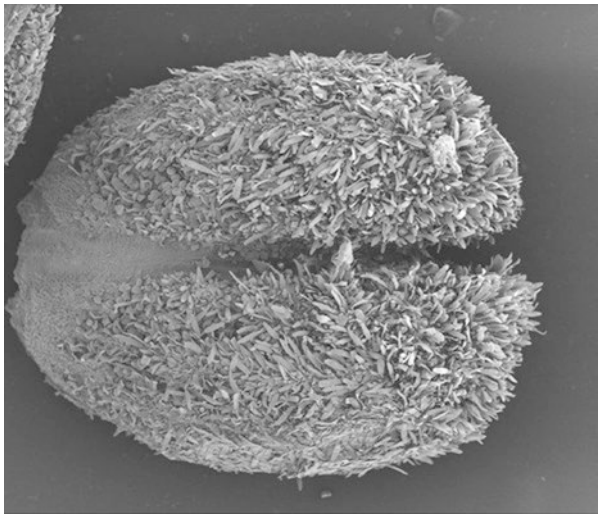

Fig. 3.10 Haired nutlet of *T. racemosum* R.Br. (section *Teucrium*)

Spinularia, section *Scorodonia,* some species from section *Stachyobotrys* and in *Teucrium abutiloides* and *T. betonicum* from section *Teucriopsis*). The broad and more or less horizontally upper lobe tooth of the calyx reinforces this ballistic action.

3.5 Conclusions

The most important discriminant generative characters within *Teucrium* are the corolla and calyx construction. Sections *Pycnobotrys, Stachyobotrys, Scorodonia* and *Teucriopsis* have species with wrakly 2-lipped corolla and zygomorphic calyx (2-lipped calyx that in the majority of cases present an upper broad lip). Sections *Polium, Chamaedrys, Montana, Isotriodon, Pumila* and *Scordium* have 1-lipped corolla and mainly sub-actinomorphic calyx. Section *Polium* is separate into two groups: species of the subsection *Simplicipilosa* with 1-lipped corolla, tube apically broading and a tuft of hairs inside, and species of subsection *Pumila,* with 1-lipped corollas and latero-posterior lobes forming an angle with the corolla tube, which has two guides of hairs at the base of the anterior corolla lobe. Section *Teucrium* is the most heterogeneous and distinctive group within *Teucrium.* Species of section *Teucrium* subsection *Fruticantia* (Kästner 1989) have 1-lipped corolla and actinomorphic calyx. Species of section *Teucrium* subsection *Cretica* (Kästner 1989) have 1-lipped spurred corolla with an annulus of hairs in the base and actinomorphic calyx and the Australian species of section *Teucrium* are characterized by their longer pedicellate flowers, 1-lipped non-spurred corollas with an annulus of hairs in the middle part of the tube.

Flower shapes in the genus range from weakly bilabiate corollas to one-lipped gullet shaped corollas with guiding visitors; gullet shaped slightly personate corollas closed by a palate of hairs and rare flag-shaped resupinate corollas with poorly developed lateral lobes and finally the brush-shaped corollas closed by a tuft of hairs at the base of the anterior lobe. All corolla forms exemplify the evolutionary potential of tubular one-lipped corollas. A personate corolla is universally present in all the species of section *Teucrium* and totally absent from other sections. This type occurs in species of *Anthirrhitteae, Gratioleae* and *Cheloneae* and considered as derived characters in *Scrophulariaceae* (Kampny 1995). Bilabiate corollas is the common type in Lamiaceae (Bouman and Meeuse 1992), weakly bilabiate corollas are only present in the species of the sections *Pycnobotrys, Stachyobotrys, Scorodonia* and *Teucriopsis.* The tuft of hairs at the entrance of the corolla tube is present in the species from section *Polium* subsection *Polium* but is absent in the rest of the sections. The species of this section are mainly ginodioecious with white or cream corollas and brush-shaped pollination such as the typical thymoideas of the Mediterranean maquis (Dafni and O'Toole 1994).

Seed dispersal inside the calyx is exclusive of the section *Polium*. This suggests that the above are characters, which may be of use in phylogenetic studies and an additional taxonomic use at infrageneric level. The pogonospores is the unique diaspore type in the section *Teucrium, Teucriopsis* and in some species of section *Chamaedrys.* The presence of the annulus of hairs on the inner side of the calyx in all species of the section *Scorodonia* and in some ones of the sections *Chamaedrys* and *Stachyobotrys,* suggests that these two characters express the intersectional taxonomic boundaries.

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