

FLOWER AND LIFE STRATEGY DIVERSITY IN *TEUCRIUM* L. (LAMIACEAE)

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ABSTRACT. *Flower and life strategy diversity in Teucrium L. (Lamiaceae).* The flowers of *Teucrium* L., show a great diversity in form, floral features and floral mechanisms related to pollination. Functional redundancy is found in the gullet-shaped corollas with nectar guides and nototribic pollination shown in the sections *Chamaedrys* (Mill.) Schreb., *Isotriodon* Boiss., *Scordium* (Mill.) Rchb. and *Polium* subsections *Rotundifolia* (Cohen) ex Valdés Berm. & Sánchez Crespo and *Pumilum* Rivas Mart. 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 is 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 the section *Polium* (Mill.) Schreb. subsection *Polium* and subsection *Simpliciplosa* S. Puech. The presence of flag-shaped corollas with sternotribic pollination are found in the resupinate flowers from sections *Spinularia* (Boiss.) Kästner and *Stachyobotrys* Boiss. These floral features provide a systematic use at sectional level and exemplifies the evolutionary potential of the tubular sympetal corollas. *Teucrium* has five different life strategies established. The dominant life strategy are the chamaephyte half-shrubs summer semi-deciduous with sexual reproduction and wind-dispersal with diaspores adapted to the semachory shown by the sections *Chamaedrys*, *Isotriodon* and *Polium*. Clearly less frequent are the nano-phanerophytes, shrub-branched, summer semi-deciduous, wind-dispersal by pogonosporos which correspond to sections *Teucrium* and *Teucriopsis* Benth. And the perennial herbs winter deciduous with asexual reproduction and semachory. In some cases, these are rizhomatoses as in the section *Chamaedrys* or stoloniferous as in the section *Scordium* Kästner. The annual, erect, prostrate or spinescent herbs winter or summer deciduous dispersal by ballospores and sclerosporos are exclusive from the section *Spinularia* and finally, the perennial herbs and half-shrubs winter or summer deciduous species, ballospores with bilabiate calyces characteristics of the section *Scorodonia* (Hill) Schreb., and the *T. betonicum* L'Hér and *T. abutiloides* L'Hér from section *Teucriopsis*.

Key words. Flower, life strategy, diversity, *Teucrium* L., *Lamiaceae*.

RESUMEN. *Diversidad floral y de estrategia de vida en Teucrium L. (Lamiaceae).* Las flores de *Teucrium* L., muestran una gran diversidad en formas, características florales y mecanismos de polinización. Existe una redundancia funcional en las corolas con forma "tubular", con guías para el néctar y polinización nototribal de las secciones *Chamaedrys* (Mill.) Schreb., *Isotriodon* Boiss., *Scordium* (Mill.) Rchb. y *Polium* subsecciones *Rotundifolia* (Cohen) ex Valdés Berm. & Sánchez Crespo y *Pumilum* Rivas Mart. La polinización nototribal de las corolas con forma "tubular" y mecanismos de cierre del tubo, mediante un paladar de pelos asociado a una ligera giba, son exclusivos de la sección *Teucrium*. La polinización esternotribal de las corolas con forma de "cepillo" y tubo cerrado mediante un "mechón" de pelos situado en la entrada del tubo de la corola (base del lóbulo anterior), son específicas de las especies ginodioécicas de la sección *Polium* (Mill.) Schreb. subsecciones *Polium* y *Simpliciplosa* S. Puech. Las corolas con forma de "bandera" y polinización esternotribal se encuentran en las flores resupinadas de las secciones *Spinularia* (Boiss.) Kästner y *Stachyobotrys* Boiss. Estas características florales proporcionan un uso sistemático seccional y ponen de manifiesto el potencial evolutivo de las corolas tubulares simpétalas.

Teucrium tiene cinco diferentes estrategias de vida establecidas. La estrategia de vida dominante está representada por los caméfitos semidecíduos de verano y con reproducción sexual, dispersión por el viento y diásporas adaptadas a la semacoría que muestran las secciones *Chamaedrys*, *Isotriodon*, y *Polium*. Claramente menos frecuentes son los nanofanerófitos, arbustos bajos y ramificados, semidecíduos de verano que dispersan por acción del viento, mediante poganosporas con cálices actinomorfos de las secciones *Teucrium* y *Teucriopsis* Benth., y las hierbas perennes decíduas de invierno con reproducción asexual y semacoría. En algunos casos, son rizomatosas como en la sección *Chamaedrys* o estoloníferas como en la sección *Scordium* Kástner. Finalmente, las hierbas anuales postradas o espinescentes decíduas de invierno o de verano que dispersan mediante balosporas y esclerosporas con cálices zigomórficos, y las hierbas perennes y matas decíduas de invierno o verano, que dispersan por balosporas y tienen cálices bilabiados de la sección *Scorodonia* (Hill) Schreb., y de *T. betonicum* L'Hér y *T. abutiloides* L'Hér de la sección *Teucriopsis*.

Palabras clave. Flores, estrategia de vida, diversidad, *Teucrium* L., *Lamiaceae*.

INTRODUCTION

Teucrium L., is a polymorphic and cosmopolitan genus (Hedge, 1992), the largest of the *Lamiaceae* in the Mediterranean area, and one of most typical genera of the Mediterranean shrub-land communities. Species of *Teucrium* usually form part of the vegetation in open, dry, rocky places, slopes and disturbed areas and tend to occupy exposed habitats. Most of the species are chamaephytes and which do not exceed 50 cm, and show a flowering peak at the end of spring-summer but may also extend their flowering season into the autumn and winter, like most typical Mediterranean species, (Kummerov, 1983).

Teucrium is melittophilous and is pollinated mainly by bees (Stebbins, 1974 and van der Pijl, 1972a) and wasps (Petanidou, 1996) and 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 one-lipped corollas with bilateral symmetry and a zygomorphic lower lip. The corolle tube is slightly campanulate and the lower lip has five asymmetrical lobes; this corolle type also occurs in related genera of the tribe *Ajugeae*. 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 morphology, size, lobes symmetry, specialized features of lower lip, resupination of the tube and presence of the gynodioecious species are the result of a selection by pollinators which leads an adjustment in floral forms to efficient pollen transfer and fruit set. Nowadays, very little is known about the diversity of floral forms including aspects of pollination in Mediterranean species of *Lamiaceae* (Herrera, 1986; Brabant *et al.*, 1980; Dafni & O'Toole, 1994; Shmida & Dukas, 1990 and Petanidou, *op. cit.*).

The most common *Teucrium* calyx is five-lobed and persistent, except when it is shed with the diaspores inside and plays a part in seed dispersal (van der Pijl, 1972b; Bouman & Meeuse, 1992 and Paton, 1992). The variation in the calyx symmetry, morphology of the tube and teeth and functioning of the pedicel, express the adaptation to a certain kind of seed dispersal mechanisms and a protection of immature nutlets.

The sculpturing and size of the nutlets have an important role in dispersal mechanisms (Bouman & Meeuse, *op. cit.*). Pericarp surface of the nutlets in *Teucrium* are variously ornamented (Marin *et al.*, 1994); smooth (section *Scorodonia*); haired (section *Teucrium*, *Teucriopsis* and *Chamaedrys*); with glands (sections *Chamaedrys*, *Isotriodon* and

Polium subsection *Rotundifolia*) and very reticulated (section *Polium* subsection *Polium*) to maximize the dispersion by the wind.

The synthetic analysis of the sectional life strategies in *Teucrium* based on the significant positive relationship between the life form diversity, drought adaptative strategies, adaptative dispersal mechanisms and reproduction behaviour contribute to the characterization of the species richness in *Teucrium* and provide information about the diversity of the groups of species characterized by the similar ecological adaptative mechanisms to the different environments.

The aim of this study is: an overview of the diversity of the floral features, floral forms and pollination mechanisms, a synthesis of the predominant life strategies in *Teucrium* and finally, an analysis of their sectional diversity and value in the Mediterranean area.

The sectional delimitation of *Teucrium* is according to Bentham (1832-36) with the additions made by Boissier (1879). Nomenclature following Navarro (1995) and Navarro & El Oualidi (1997).

MATERIAL AND METHODS

This study is based on the field studies, herbarium specimens and bibliographic references of the regional Floras from the Mediterranean area.

Flowers were observed in the field and collected from determined and authorized herbarium specimens of the following institutions; B, E, G, MGC, RAB, TFC and ORT. The list of the analysed species and their origin is given in Appendix.

Light and SEM were used. For SEM analysis at least three samples were prepared. The flowers were fixed whole after critical point technique in Balzers CPD-020 and were mounted on aluminium stubs and covered with 24K gold in an ion sputter JFC-1100 and

studied with a JEOL JSM-840.

The main floral features, such as the inflorescence type, corolla size, corolla colour, flower sexuality and main flowering season were noted. The flower form related to the pollination is based on Faegry & van der Pijl (1979). The most frequent pollinators are indicated based on bibliographic references and field observations.

Life forms are described according to Raunkaier (1905), the primary dispersal type following van der Pijl (1972b), Zohary (1937) and Bouman & Meeuse (1992) and the diaspore type in accordance with Dansereau & Lems (1957), Jenny (1995) and Gutterman (1993).

RESULTS AND CONCLUSIONS

Floral features, Floral forms and Pollination mechanisms

Teucrium flowers exhibit diversity in forms, especially oin the corolla. The main sectional floral features are shown in table 1 and the floral forms and pollination mechanisms in table 2.

The bilateral symmetric flowers such as those of the *Teucrium* induce a more specific behaviour to ensure that stigma and anthers are touched effectively. Sternotribic and nototribic pollen deposition occur in *Teucrium*. In this way, nectar guides on the adaxial side of the lower lip and corolla tube are orientation cues to which bees and wasps respond.

There are *Teucrium* 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 forms in *Teucrium* related to pollination 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

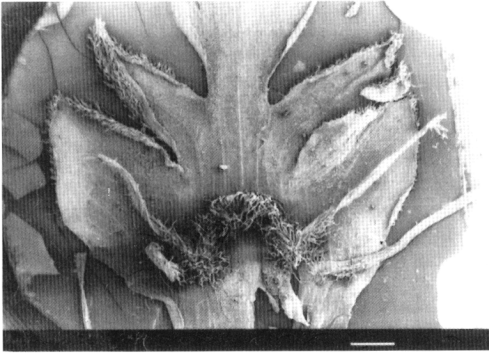


Fig. 1. Adaxial side of the lower lip and entrance of the corolla tube with closed gullet mechanism by a palate of hairs associated to a slight pouch of *Teucrium malenconianum* Maire L. (Section *Teucrium*) (RAB 24877). (Scale= 1mm).

rare and exclusive of the species with resupinate corollas from sections *Spinularia* and *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. The brush-shaped corollas with diffuse pollen deposition, are a characteristic of the section *Polium* and include corollas closed to ineffective insect visitors.

Two closed gullet mechanisms related to pollination are observed: (1) A barrier which offers resistance and demands precision on the part of the pollinator formed by a palate of hairs in the region of the common basal part of the latero-posterior lobes and staminal insertion associated to a slight pouch (fig. 1), when the insect poses on the lower lip, its force makes the lip bend down and the tube is 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 staminal insertion to the basal part of the anterior lobe of the lower lip (fig. 2.1). Its

basal part is more densely covered, forming a tuft of hairs, 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*.

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 (fig. 2.2); these guidings are common in the species of the sections *Chamaedrys*, *Isotriodon*, *Scordium* and *Polium* subsections *Rotundifolia* and *Pumilum*.

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.

Life strategies diversity, Life forms and Seed dispersal mechanisms

The synthetic analysis of life strategies in *Teucrium* is based on the characteristics shown in table 3.

The most striking variation in life strategy in *Teucrium* is exhibited by the life form and general habit of the plant and its adaptive response to the environmental condition, mainly to the drought adaptive strategy.

The biological spectrum of *Teucrium* includes the nano-phanerophytes species from section *Teucrium* forming part of the Mediterranean garrigue and the Atlantic branched-shrubs from the section *Teucriopsis*, to the summer or winter therophytes from disturbed areas characteristic of the section *Spinularia* or the hemi-cryptophyte, stoloniferous, winter semi-deciduous herbs typical of the meadows belong to the section *Scordium*.

The predominant life form is the summer semi-deciduous, chamaephyte, half-shrubs

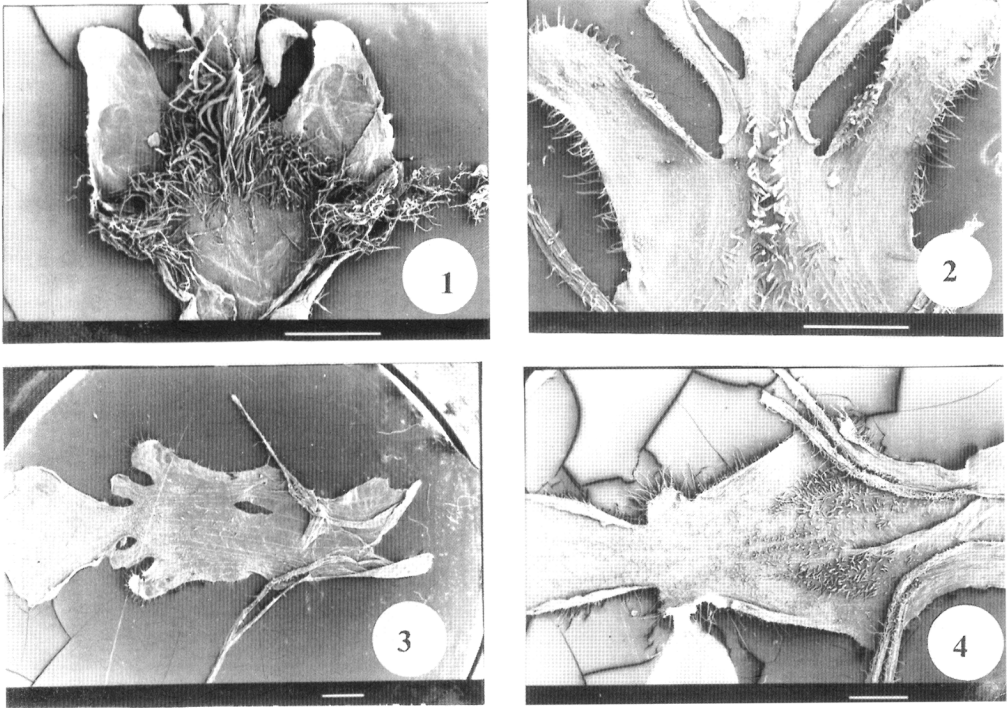


Fig. 2. Adaxial side of the lower lip and entrance of the corolla tube: 1.- With closed gullet mechanism by a tuft of hairs of *Teucrium lusitanicum* Schreb. L. (Section *Polium* (Mill.) Schreb. subsection *Polium*) (MGC 15744). 2.- With the nectar guides formed by two rows of hairs of *T. rotundifolium* Schreb. L. (Section *Polium* subsection *Rotundifolia* Cohen ex Valdés Berm. & Sánchez Crespo) (RAB 43626). 3.- Without nectar guides and without closed gullet mechanism of *T. spinosum* L. (Section *Spinularia* (Boiss.) Kästner) (MGC 19303). 4.- With short lateral lobes and absent latero-posterior lobes of *T. collincola* Greuter & Burdet (Section *Stachyobotrys* (Benth.) Kästner) (RAB 47292). (Scale= 1mm).

forming part of the Mediterranean exposed areas and degraded scrubland.

The primary dispersal type described in some *Teucrium* species do not necessarily correlate with the properties of diaspores or diaspore types. The predominant primary dispersal type in *Teucrium* is the semachory and ballautochory, wind-dispersal or wind-ballistic species (semachores or ballospores) found in *T. heterophyllum* L'Hér from section *Teucriopsis* and in species of the sections *Teucrium*, *Chamaedrys*, *Scordium*, *Isotriodon* and *Polium*. Ballautochory, wind-ballistic or rain-ballistic species (ombrochory) in the

section *Scorodonia*, *Spinularia* and *Stachyobotrys* and in *T. abutiloides* and *T. betonicum* of the section *Teucriopsis*. Epizoochry, rare in the genus, can be found in some species with spinescent calyx from section *Spinularia*. Meteoranemochory, aestatiphory (Zohary, op. cit.) and secondary dispersal by ants is only found in the section *Polium*.

The main diaspore type present in *Teucrium* are the semaspores related to the species with actinomorphic or sub-actinomorphic, pedicelled calyx and related to species which disperse the nutlets into the sub-

<i>Sections and Subsections</i>	<i>Plant size (cm)</i>	<i>Inflorescence</i>	<i>Corolla size (mm)</i>	<i>Corolla colour</i>	<i>Flower sexuality</i>	<i>Main flowering season</i>	<i>Pollinators</i>
<i>Teucrium</i>	80-120	Axillary flowers or lax verticillasters	(10)12,5-14,5(22)	Lilac/white	Hermaphrodite rare male sterile	End winter-spring-summer (III-VI)	Large solitary bees
<i>Teucriopsis</i>	(30) 40/ 80-150	Axillary flowers or lax verticillasters	(7,5)9,5-11,5(13,5)	Blue/orange/white	Hermaphrodite	Summer (V-VI)	Large solitary bees
<i>Chamaedryas</i>	(10)25-30(45)	Lax verticillasters /sub-spirally racemes	(9,5)11,5-12,5(14,5)	Purple/pink/yellow	Hermaphrodite	Summer (V-VI)	Small solitary bees, flies
<i>Scorodonia</i>	(25)30-35(40)	Verticillasters	(5,5)7-8(11)	Cream/pink	Hermaphrodite	End spring-summer (IV-VI)	Long-tongued butterflies, bees
<i>Scordium</i>	25-35	Axillary flowers/verticillasters (2-8) flowered	7,5-8,5	Cream-pink	Hermaphrodite	Summer (V-VII)	Small solitary bees
<i>Stachyobotrys</i>	(25)30-45(50)	Dense verticillasters like spike	7,5-9,5	Cream/cream-yellow	Hermaphrodite	End spring-summer (IV-VI)	Small solitary bees, flies
<i>Spinularia</i>	(10)25-35	Verticillasters (2-4) flowered	(6,8)8,5-9(15,5)	Cream/cream-pink	Hermaphrodite	Summer (V-VIII)	Solitary bees
<i>Isotriodon</i>	(10)25-35	Sub-spirally racemes	(5,5)8-10(14,5)	Cream/pink-purple/yellow	Hermaphrodite	Spring (IV-V)	Solitary bees, flies
<i>Polium Polium</i>	(10)25-35(45)	Simple dense terminal or branched raceme	(3)3,5-4,5(6,5)	White/cream-pink/yellow	Gynodioecious	End spring-end summer (IV-VIII)	Small solitary bees, wasps, ants, flies
<i>Polium Simplicipilosa</i>	20-35	Simple dense terminal or branched raceme	(3)3,5-4,5(6,5)	White/cream	Hermaphrodite/gynodioecious	Summer (VI-VIII)	Small solitary bees, wasps, ants, flies
<i>Polium Rotundifolia</i>	(10)25-35	Sub-spirally raceme	(8)10,5-12,5-(17)	Cream/white-pink/purple/yellow	Hermaphrodite	Summer (V-VII)	Solitary bees, ants, flies
<i>Polium Pumilum</i>	20-35	Simple dense terminal or branched raceme	5,5-6	White/purple	Hermaphrodite/gynodioecious	Summer (V-VII)	Solitary bees, long-tongued butterflies, ants

Table 1. Main floral features and pollinators in the sections of the genus *Teucrium* L. in the Mediterranean area.

Sections and subsections	Pollination type	Flower form	Closed gullet mechanism of corolla tube	Nectar guides on the lower lip of the corolla	Resupination of the corolla tube
<i>Teucrium</i>	Nototribic	Gullet-shaped-tubular/short-tubular	By a palate of hairs		
<i>Teucriopsis</i>	Nototribic	Gullet-shaped-short-tubular			
<i>Chamaedrys</i>	Nototribic	Gullet-shaped-tubular		+	
<i>Scorodonia</i>	Nototribic	Gullet-shaped-tubular/short-tubular			
<i>Scordium</i>	Nototribic	Gullet-shaped-tubular/short-tubular		+	
<i>Stachyobotrys</i>	Nototribic/sternotriby	Gullet-shaped-tubular/flag-shaped-tubular			+
<i>Spinularia</i>	Nototribic/sternotriby	Gullet-shaped-tubular/flag-shaped-tubular			+
<i>Isotriodon</i>	Nototribic	Gullet-shaped-tubular		+	
<i>Polium</i>	Sternotriby	Brush-shaped-short-tubular	By a tuft of hairs		
<i>Polium</i>	Sternotriby	Brush-shaped-short-tubular	By a tuft of hairs		
<i>Simplicipilosa</i>	Nototribic	Gullet-shaped-tubular		+	
<i>Rotundifolia</i>	Sternotriby	Gullet-shaped-tubular		+	
<i>Pumilum</i>	Sternotriby	Gullet-shaped-tubular			

Table 2. Pollination type, flower forms and mainly floral pollination mechanisms in the sections of *Teucrium* L., in the Mediterranean area.

actinomorphic calyces such as *Thymus* (Bouman & Meeuse, 1992) exclusive from the section *Polium*; ballospores are related to bilabiated or strongly zygomorphic calyx and pogonosporos with large sizes (>2mm long) associated with the actinomorphic and campanulate calyx. The calyx morphology mainly represents a protection system for the immature nutlets formed by: (1) an annulus of hairs inside the calyx tube, considering its presence as a derived state character (Abu-Asab & Cantino, 1993) and frequent in other *Lamiaceae* genera such as *Marrubium*, *Origanum*, *Sideritis*, *Ocimum* and *Scutellaria*; (2) the cucullate teeth convergent in maturity closing the calyx tube perfectly (El Oualidi & Puech, 1993), is exclusive of some species of section *Polium* subsection *Polium* as *T. lusitanicum* Schreb.; or (3) a gibbous in the base of the calyx as in *T. botrys* L., covered inside by long hairs, making difficult the exit of the nutlets, exclusive of the section *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 *Polium* subsection *Rotundifolia*. The pedicel is not rigid and acts in the ballistic mechanisms contracting itself to eject the mature nutlets (sections *Spinularia*, *Scorodonia*, some species from section *Stachyobotrys* and in *T. abutiloides* and *T. betonicum* from section *Teucriopsis*), this ballistic action is reinforced by the broad and more or less horizontally upper lobe tooth of the calyx.

Synthetic Analysis of the Sectional Diversity

The section *Teucriopsis* (Kästner, 1989) comprises three species: an erect branched shrub, *T. heterophyllum* and two perennial herbs, *T. abutiloides* and *T. betonicum*. They

have weak bilabiate corollas, which is their main taxonomic diagnostic character and is exclusive for the genus. The flower form is gullet-shaped, shortened tubuled with poorly developed lateral lobes, the anterior lobe is sub-auriculated at the base. Flowers are axillary in the leaves or in lax verticillasters. There are wind-ballistic and rain-ballistic species and the diaspore is pogonospore type.

Section *Teucrium* is formed by semi-sclerophyllous shrubs and perennial branched herbs. The corolla is one-lipped, gullet-shaped and slightly personate (with a slight pouch), shortened tubuled, lilac or white with closed gullet mechanisms by a palate of hairs (fig. 1); the lateral and latero-posterior lobes are developed. Flowers are axillary in the leaves or in lax verticillasters 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 & Dafni, 1989 as flowers engaged in a "discovery advertisement". The nano-phanerophyte species are elements of the Mediterranean maquis (Quezel, 1985). 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). The diaspore type is pogonospore.

Species from section *Scorodonia* (Hill) Schreb., are perennial herbs or half-shrub species with one-lipped gullet-shaped corollas with long and narrow tube and a lower lip with well developed latero-posterior lobes without nectar guides. Flowers are disposed in verticillasters and the main flowering season is the summer. They are wind-ballistic or/and rain-ballistic species with glabrous and smooth nutlets and bilabiate calyx with annulus of hairs inside. These features are not in accordance with the ones described by Paton (1992) in *Scutellaria*, who shows that the

Sections and Subsections	Life form and general habit	Drought adaptive strategy	With asexual reproduction	Main primary dispersal type	Diaspore type	Diaspore size (mm)	With aestat-phory	Calyx morphology
<i>Teucrium</i>	<i>Ph-Hm</i> shrub branched and perennial herbs	Semi-sclerophyllus summer semi-deciduous/ winter deciduous		Semachory wind-dispersal	Pogonospore	(1.5)2x3(3.5)		Campanulate actinomorphic pedicelled
<i>Teucriopsis</i>	<i>Ph-Hm</i> shrub branched and perennial herbs	Semi-sclerophyllus summer semi-deciduous/ winter deciduous		Semachory wind-dispersal	Pogonospore	(1.5)1.8x2.5		Campanulate actinomorphic/ bilabiate
<i>Chamaedrys</i>	<i>Ch-Hm</i> rhizomatose, rocky-small half-shrub and perennial herbs	Winter deciduous/ summer semi-deciduous	+	Semachory wind-dispersal	Semaspore/ pogonospore	(0.7)1.5x1.8(2.5)		pedicelled Tubular-campanulate actinomorphic with annulus of hairs inside
<i>Scorodonia</i>	<i>Ch-Hm</i> half-shrub and perennial herbs	Winter deciduous/ summer semi-deciduous	+	Ballautochory/ semachory wind-dispersal	Ballospore	(1)1.3x1.5(1.8)		Campanulate bilabiate pedicelled gibbous at the base with annulus of hairs inside
<i>Scordium</i>	<i>Hm</i> erect, prostrate and stoloniferous paucennial branched herbs	Summer deciduous /winter semi-deciduous	+	Ballautochory/ semachory wind-dispersal	Semaspore	(0.8)1x1.3		Tubular campanulate sub-actinomorphic sub-pedicelled
<i>Stachybotrys</i>	<i>Ch-Hm</i> perennial herbs and cushion like half- shrub	Winter deciduous/ summer semi-deciduous	+	Ballautochory epizoochory?	Ballospore	(1)1.3x1.8		Campanulate zygomorphic spinescent
<i>Spinularia</i>	<i>Hm-Th</i> erect, prostrate and spinescent annual or paucennial branched herbs	Winter and summer deciduous		Ballautochory epizoochory?	Semaspore/ ballospore/ sclerospore	(0.1)1x1(1.5)		pedicelled Campanulate zygomorphic bilabiate spinescent pedicelled
<i>Isotriodon</i>	<i>Ch</i> rocky half-shrub	Summer semi-deciduous		Ballautochory/ semachory wind-dispersal	Semaspore	(0.7)1.3x1.5(2.5)		pedicelled gibbous at the base Tubular campanulate
<i>Potium</i> <i>Potium</i>	<i>Ch-Hm</i> erect, prostrate, cushion like and rocky half-shrub and perennial herbs	Summer and winter semi-deciduous	+	Melcoaranemochory wind-dispersal	Calyx	(0.8)1.3x1.5(2.5)	+	sub-actinomorphic sign gibbous sub-pedicelled Tubular
<i>Potium</i> <i>Simpliciflora</i>	<i>Ch</i> erect and cushion like half-shrub	Summer-deciduous and summer semi-deciduous		Melcoaranemochory wind-dispersal	Calyx	(0.6)1.2x1.5(1.7)	+	non pedicelled Tubular
<i>Potium</i> <i>Rotundifolia</i>	<i>Ch-Hm</i> rocky half-shrub, cushion like and perennial herbs	Summer deciduous and summer semi-deciduous		Ballautochory/ semachory wind-dispersal	Semaspore/ calyx	(0.5)1.2x1.3(2.5)	+	non pedicelled Tubular campanulate some inflated
<i>Potium</i> <i>Pumilum</i>	<i>Ch</i> erect half-shrub	Summer deciduous and summer semi-deciduous		Melcoaranemochory	Calyx	(0.6) 0.8x1(1.5)	+	sub-actinomorphic sub-pedicelled Tubular sub-actinomorphic

Table 3. Synthetic analysis of sectional life strategy diversity of the genus *Teucrium* L., in the Mediterranean area. Life forms; Ph= Phanerophyte; Ch= Chamaephyte; Hm=Hemicriptophyte; Th=Therophyte.

ballistic species have very ornamented surfaces to maximize their contact with the calyx.

The greatest convergence of floral features is shown by the half-shrub species from the rocky slopes indicating a higher incidence of functional redundancy. The corolla is one-lipped, gullet-shaped and regular-tubed (tube >5mm), with two clear nectar guides in the lower lip (fig. 2.2) without closed gullet mechanisms and with well developed 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 and wind-ballistic species, or seed-dispersal in the calyx. In this last case, the calyx is easily detached and generally dry and papery. In some species such as *T. compactum* Clemente ex Lag. and *T. yemense* Deflers, the inflated calyx ensure long distance dispersion by the wind, this type is found by Ryding (1998) and Zohary (1937) in desert species. This group comprises, the species of section *Isotriodon* the rocky species from section *Chamaedrys*, and the rocky species from section *Polium* subsection *Rotundifolia*. On the other hand, this group shows a highly convergence exemplified by the lax inflorescence in sub-spirally simple racemes; leaves flat, villous and petiolated may be due to the adaptation to the same habitat and probably convergent evolution to use similar limited resources (Cody & Mooney, 1978).

The section *Scordium* are the perennial herbs with one-lipped, gullet-shaped corollas with nectar guides. Flowers are axillary or in lax verticillasters and they are wind ballistic species from humid Mediterranean climates.

The species of section *Spinularia* are winter and summer-deciduous, predominantly well-branched annual or paucennial herbs. Corolla is one-lipped, gullet and flag-shaped with a long and narrow tube (fig. 2.3) and some

with resupination. Flowers in verticillasters flowering mainly in spring and summer. The strongly zygomorphic, gibbous calyx have an annulus of hairs inside. They are wind-ballistic species and possibly epizoochore, since most of the species show spinescent calyx teeth.

Some species from section *Stachybotrys* such as *T. 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 (fig. 2.4). The calyx is strongly zygomorphic and campanulate. They are rain-ballistic or/and wind-ballistic species, some of them show the long mucronated calyx teeth, perhaps related to the epizoochry.

Species belonging to section *Polium* subsections *Polium* and *Simplicipilosa* are the half-shrub polyploids and ginodioecious chamaephytes with one-lipped brush-shaped corollas shortened tubed with closed gullet mechanisms by a tuft of hairs to exclude inefficient visitors and limit pollinator diversity (fig. 2.1). Flowers are compacted in the dense racemes forming the branched inflorescence. Flowering mainly in spring, the ginodioecious system imposes limitations in pollination and rewards partitioning between females, generally pink and with nectar reward flowers (Herrera, 1987), and hermaphrodite flowers (white or cream). The calyx is sub-actinomorphic without an annulus of hairs inside. They are wind-dispersal species and the calyx is shed with the nutlet inside. Some species from arid regions show cucullate calyx teeth that close the calyx tube and protect the nutlets, and in other species like *T. charidemi* Sandwith or *T. musimonum* Humbert, the calyx is densely covered by vermiform hairs to facilitate the ground. The species of section *Polium* belong to the brush-shaped pollination such as the typical thymoides of the Mediterranean maquis (Dafni & O'Toole, 1994).

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 *Anthirrhineae*, *Gratiroleae* and *Cheloneae* and are considered as derived characters in *Scrophulariaceae* (Kampny, 1995). Bilabiate corollas is the common type in *Lamiaceae* (Meeuse, 1992), weakly bilabiate corollas are only present in the three species of the section *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. Seed-dispersal in the calyx is only seen in section *Polium* and absent from the other sections. This suggests that the above are characters which may be of use in phylogenetic studies and an additional taxonomic use at infrageneric level.

The comprehensive presence of pogonosporae as an unique diaspore type in section *Teucrium*, *Teucriopsis* and in some species of section *Chamaedrys*, while the presence of the annulus of hairs on the inner side of the calyx in all species of the section *Scorodonia* and only in some of the sections *Chamaedrys* and *Stachybotrys* suggests that these two characters express the intersectional taxonomic boundaries.

APPENDIX

List of the sections and species of the

Teucrium L., studied. Origin and number of the herbarium collection are given.

Sect. *Teucrium*

T. chardonianum Maire & Wilczek: Morocco (RAB 24317-61090)

T. fruticans L.: Morocco (RAB 00202-01329); Spain (MGC 44908)

T. malenconianum Maire: Morocco (RAB 24877-48523)

T. oliverianum Gingins ex Benth.: Iran (G 8347/34)

T. pseudo-chamaeptytis L.: Spain (MGC 45375)

Sect. *Teucriopsis* Benth.

T. abutiloides L'Hér.: Madeira Islands (TFC 28354-28401)

T. betonicum L'Hér.: Madeira Islands (TFC 13888-28354)

T. heterophyllum L'Hér.: Canary Islands (ORT 2940); Madeira Islands (TFC 6551)

Sect. *Scorodonia* (Hill.) Schreb.

T. pseudo-scorodonia Desf.: Morocco (RAB 24862-23947)

T. scorodonia subsp. *baeticum* (Boiss. & Reuter) Tutin: Spain (MGC 32166)

T. wernerii Emb.: Morocco (RAB 46947-45205)

T. zaianum Emb. & Maire: Morocco (RAB 24880-02008).

Sect. *Scordium* (Mill.) Rchb.

T. melissoides Boiss.: Iran (G 8347/19)

Sect. *Stachybotrys* Benth.

T. bracteatum Desf.: Morocco (RAB 29512-45205)

T. collincola Greuter & Burdet: Morocco (RAB 47292-48945)

Sect. *Spinularia* Boiss.

T. botrys L.: Spain (MGC 37966)

T. decipiens Coss.: Morocco (RAB 46942-04608)

T. resupinatum Desf.: Morocco (RAB 6176-8444)

T. spinosum L.: Morocco (RAB 23740-23977); Spain (MGC 10463-19303)

Sect. *Polium* (Mill.) Schreb. subsect. *Polium*

T. bicolorum Pau: Spain (MGC 39850)

T. capitatum L.: Morocco (E-DAVIS 68117; B-VOGT & OBERPRIELER 8619; RAB 47964-47960)

T. cylindraceum Greuter & Burdet: Morocco (RAB 61259; B-VOGT & OBERPRIELER 4815)

T. doumerguei Sennen: Morocco (B-VOGT & OBERPRIELER 5880; RAB 6178-7177)

T. gypsophilum Maire: Morocco (MGC 28023)

T. lusitanicum Schreb: Spain (MGC 15744)

T. luteum subsp. *flavovirens* (Batt.) Greuter &

Burdet: Morocco (B-VOGT & OBERPRIELER 6213; RAB 46943-44022)

T. polium L. Morocco (RAB 44839)

T. vinctinum Rouy: Portugal (MGC 27964)

Sect. Polium subsect. **Rotundifolia** (Cohen) ex Valdés Berm. & Sánchez Crespo

T. buxifolium Schreb.: Spain (MGC 6951)

T. cincinnatum Maire: Morocco (RAB 43627- RAB-SAUVAGE 2533-12092)

T. compactum Clemente ex Lag.: Tunicia (B-VOGT & OBERPRIELER 7399-7441)

T. cypricum Boiss.: Cyprus (G 8347/3)

T. hijazicum Hedge & R. A. King: Arabia (E 60898)

T. musimonum Humbert. Morocco (RAB 44530)

T. nummularifolium Baker: Oman (E 60909-60911)

T. rotundifolium Schreb. subsp. *rotundifolium*: Morocco (RAB 43626)

T. rotundifolium subsp. *trasatlanticum* Emb. ex Greuter, Burdet & Long: Morocco (RAB 43626-49962-19306)

T. sokotranum Vierh.: Socotra (E 60905-60906)

T. yemensense Deflers: Yemen (E 60901)

Sect. Polium subsect. **Simplicipilosa** S. Puech

T. charidemi Sandwith: Spain (MGC 38810)

T. eriocephalum Willk.: Spain (MGC 35859)

T. haenseleri Boiss.: Spain (MGC 39132)

Sect. Polium subsect. **Pumilum** Rivas Mart.

T. pumilum L. Spain (MGC 34256)

T. turredanum Losa & Rivas Mart.: Spain (MGC 43322)

Sect. Chamaedrys (Mill.) Schreb.

T. barbarum Jahand. & Maire: Morocco (RAB 24873-00133)

T. chamaedrys L.: Morocco (RAB 61090-07176)

T. fragile Boiss.: Spain (MGC 7450)

T. webbiana Boiss.: Spain (MGC 8180)

Sect. Isotriodon Boiss.

T. odontites Boiss.: Libano (G 8347/23)

T. rupestre Coss. & Balansa: Morocco (RAB 46946-24879)

T. tananicum Maire: Morocco (RAB 29502-48933)

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