Milan Stanković *Editor*

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Foreword

Nature is a major source of our current medicines, and many (semi)synthetic medicines have been developed from natural products. These compounds have been found by studying traditional medicines and by screening extracts from various organisms, particularly plants and microorganisms. In fact, about 25% of all western drugs are from plants. Microorganisms are particularly the source of antibiotics and antitumor medicines. In the meantime, for most ailments, good medicines are available; however, in the field of antibiotics and parasitic diseases, the resistance of microbes and parasites against available medicine is causing a major problem. New drugs are urgently needed, drugs that particularly should be available for the poor in developing countries at a reasonable price. As it concerns drugs cure a patient, the use is only for short periods. Consequently, the market is small if compared to, for example, an antihypertension drug that a patient takes every day for many years. Therefore, it is difficult to earn back the high costs for developing a new drug. The big pharma is thus not investing effort in developing such drugs, but if good leads are available, they may develop these further, as we can learn from the Nobel Prize of 2015. That prize shows the interest from the medical field for nature as a source of medicine, either by bioprospecting or by studying traditional medicines.

There is thus a unique opportunity for governmental and academic research institutes to look for novel leads from Nature for infectious and parasitic diseases. Particularly in Asia, with a well- documented traditional use of medicinal plants to treat patients, there is host of projects aiming at evidence-based traditional

medicines and new leads for drug development. With the enormous biodiversity, with plants only having a rather small number of species (estimations run from 250,000 to 350,000) if compared with the largest group that of the insects (some 30 million species), there are ample materials to choose from. Concerning plants, I wrote in the year 2000 that only about 15% were studied phytochemically and 6% for one or more biological activities. At that time, the Dictionary of Natural Products had 139,000 entries. At present, the Dictionary of Natural Products claims to have now more than 300,000 entries (September 2019), which means an average increase of about 8000 compounds per year. That is quite a lot, but when we assume that each biological species can make one unique compound, there should be 10–100 million natural products, that means compared with the number of known ones, there must be many more compounds waiting to be discovered. Obviously, we will not be out of work for the coming years. But at the same time, it is clear that we must make choices for the goals of our research. The choices are made on the basis of previously reported results and the needs of the society for novel medicines and other sustainable products. Also, we will have to choose what approach to use, for example, to focus on evidence-based traditional uses or at random screening of extracts, which plant species or genera should be prioritized, and what type of activity does one focus on. Many questions and few answers, only a thorough study of the literature can help us make choices.

Publications like the present book are very helpful in making our choices, as one can learn about what type of activity is already shown and if that is of sufficient interest to warrant further studies. What kind of compounds may one expect, are they novel, and do they look like good candidates for further development from hit to lead, or is it already clear from other studies that the compounds are not promising. The editor have done an excellent job in compiling all the information and making this book a good navigator for further studies, as all aspects of the plants from the genus *Teucrium* are dealt with in this book. It will be an excellent guide for making new discoveries.

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Robert Verpoorte

Preface

Species of the genus *Teucrium* (Lamiaceae) are widespread in different climates as well as on different habitat types especially in the Mediterranean region. With more than 300 species, *Teucrium* is one of the largest genera of the Lamiaceae family. Some species have been used in folk medicine since Antiquity—the name *Teucrium* refers to the Achaean hero Teucros (Teucer), a great archer during the Trojan War. Species of this genus are commonly known as germanders. The species of genus *Teucrium* are mainly perennial herbaceous plants, shrubs, or subshrubs, while only a small number are annual species.

Known medicinal species belonging to the genus *Teucrium* are used as sources of natural therapy and beneficial bioactive compounds. Also, some *Teucrium* species are useful as spices, for the preparation of teas and bitter drinks. The species of the genus *Teucrium* are very rich in a variety of secondary metabolites with very significant biological activities. For medicinal purposes, these species are used in the treatment of digestive and respiratory disorders, abscesses, gout, and conjunctivitis as well as in the stimulation of fat and cellulite decomposition; they also possess anti-inflammatory, antioxidative, anticancer, antimicrobial, antidiabetic, and anthelminthic properties. However, their most significant therapeutic effect is the elimination of some digestive and respiratory problems.

Teucrium species are an interesting object of research in the numerous scientific projects from various aspects of science, with multiple applications. Numerous studies on the biological activity and phytochemical composition of plant extracts and essential oils, as well as biotechnological applications of *Teucrium* species, are based on ethnobotany as a primary source. All of these influenced the need for a book publication that will integrate such aspects. On that basis, the book *Teucrium Species: Biology and Applications* includes 15 systematically grouped chapters which highlight recent advances in exploring the unique features of *Teucrium* species. The chapters describe the systematics, morphology, ecology, biogeography, ethnobotany, and phytochemistry—secondary metabolites diversity; genotoxic, antioxidant, antibacterial, antifungal, antiviral, anticancer, anticholinesterase, and antidiabetic and anti-inflammatory activity of *Teucrium* secondary metabolites; as well as applications in biotechnology, food industry, and pharmacy, including

current challenges and further perspectives. Excessive use of some medicinal plants of this genus can cause liver inflammation. This phenomenon and precaution are described in detail in a separate chapter in order to promote the safe use of certain species.

A book about *Teucrium* species will have several advantages as a literary material. First of all, this book is a comprehensive overview of the scientific information on the current achievements of research and their application of *Teucrium* species, as well as a rich source of the up-to-date bibliography of all scientific and practical fields related to *Teucrium* genus. The book will also provide the current list of the species of *Teucrium* genus, as well as color photographs of many species. Scientists in the field of biology, biotechnology, and pharmacy will have all the information and current literature in one place about *Teucrium* species from all aspects of science. The book would be initial literature review for beginners in the investigations of *Teucrium* species. Science enthusiasts and practitioners involved in medicinal plant applications will have the opportunity to get to know everything about the *Teucrium* species used in everyday life in Ethnomedicine for the treatment of various diseases and as the sources of additives as well as preservatives. The book can be used as a course literature at the university level. It is suitable for PhD students who focus on research on *Teucrium* species or other types of plant biological activity and applications.

Kragujevac, Serbia Milan Stanković

Acknowledgments

The book *Teucrium Species: Biology and Applications* includes 15 chapters written by 32 scientists in the field of Plant Biology and Ecology, Systematics, Morphology, Physiology, as well as Chemistry, Genetics, Microbiology, Molecular Biology, Pharmacognosy, Biotechnology, Food Sciences, Medicine and Pharmacy. Many of them are leading scientists in their field, my colleagues from the University, associates from foreign institutions, as well as laboratory colleagues from my research team working on the investigations of *Teucrium* species. I am highly grateful to all the chapter authors for their professional contributions and productive collaboration.

I am grateful to my colleague Prof. Dr. Teresa Navarro del Aguila (University of Malaga, Spain) for the expertise, effort, and valuable time devoted, as well as to other colleagues Prof. Dr. Trinidad Ruiz Tellez, Dr. Jose Blanco Salas (University of Extremadura, Spain) and Dr. Abhay Mishra (HNBG University, India) for friendly support.

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I would like to specially thank Professor Emeritus Dr. Robert Verpoorte (Leiden University, The Netherlands) for supporting the book concept and idea in his Foreword to this book.

Book Editor
Prof. Dr. Milan Stanković

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About the Editor

Milan Stanković (1984) is an Associate Professor of Plant Science in the Department of Biology and Ecology, Faculty of Science, University of Kragujevac, Republic of Serbia, and Head of Department of Biology and Ecology. He earned his BSc in Biology from the Faculty of Science and Mathematics at the University of Niš, in 2007. Dr. Stanković began his scientific and teaching career as an Assistant in the Department of Biology and Ecology, Faculty of Science, University of Kragujevac (2008). He acquired PhD degree in Plant Science (2012) from the same University with the thesis "Biological activity of secondary metabolites of *Teucrium* L. species from Serbian flora." He completed Postdoctoral Research at the Université François-Rabelais de Tours, France. In the Faculty of Science, he was appointed as an Assistant Professor (2013) as well as Associate Professor (2019) and taught several BSc, MSc, and PhD courses on Plant Science as well as supervised thesis and dissertations in this field. His current research is focused on the biology, ecology, and applications of *Teucrium* species. Dr. Stanković is (co-)author of over 300 references including articles in peer-reviewed journals, edited books, book chapters, conference papers, meeting abstracts, etc. He is an editor, editorial board member, and reviewer of several scientific journals. Currently, he works as an Associate Editor of *Plants* (2012-) and *Rangeland Ecology and Management* (2015–). He was a member of the scientific and organizing committee of several conferences, congresses,

and symposia in the fields of Biology and Plant Sciences. During his university career, he was a member of various scientific and professional associations such as the Society for Experimental Biology—Italy, Society for Medicinal Plants and Natural Product Research, Société Botanique de France, Organization for the Phyto-Taxonomic Investigation of the Mediterranean Area, and Serbian Biological Society. Currently he is a member of the State Commission for Expertise in the publication of school textbooks in Biology. In scientific collaboration, Dr. Stanković has published co-authored papers with colleagues from 23 various international universities from 17 countries. During his scientific career, he participated in the realization of over 30 scientific projects and studies.

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Chapter 1
Systematics and Biogeography of the Genus *Teucrium* (Lamiaceae)

Teresa Navarro

Abstract *Teucrium* L. is the second-largest genus of subfamily Ajugoideae with a subcosmopolitan distribution and 434 taxa (Govaerts RA, Paton A, Harvey Y, Navarro T, Del Rosario Garcia Pena M, World checklist of Lamiaceae. The Board of Trustees of the Royal Botanic Gardens Kew, Kew. www.kew.org/wcsp/, 2013). The Mediterranean region and surrounding floristic areas are the main center of diversity with around 90% of the total *Teucrium* species in the world. We describe the systematic of *Teucrium* following Bentham (Labiatarum genera et species. Ridgeway Sons, London, 1833), Boissier (Flora Orientalis IV. H. Georg, Geneva/Basel, 1879) and Kästner (Übersicht zur systematischen gliederung der gattung *Teucrium* L. Biocosme Mésogéen 6:63–78, 1989) with the recognition of the independent status of the section *Montana* Lazaro Ibiza (Navarro, *Teucrium* L. In: Castroviejo S et al (eds) Flora Iberica, VerbenaceaeLabiataeCallitrichaceae, vol 7. Real Jardín Botánico, CSIC, Madrid, pp 30–166, 2010). 341 herbarium specimens of 97 *Teucrium* taxa from throughout the world were studied, three taxa of its phylogenetic related genera *Spartothamnella* Briq., *Oncinocalyx* F. Muell., and *Teucridium* F. Hook, and two taxa of its segregated genera *Rubiteucris* Kudô and *Leucosceptrum* Smith. Based on the species biogeographical distribution and the main discriminant systematic characters, almost five major biogeographic and taxonomic species groups can differentiate. The group of species with 2-lipped corolla and zygomorphic calyx (sections *Pycnobotrys* Benth., *Stachyobotrys* Benth., *Scorodonia* (Hill) Schreb. and *Teucriopsis* Benth.) which provide a clear example of the Eurasian pattern of radiation from C Asia and China. The group of species with 1-lipped corolla and subactinomorphic calyx (sections *Polium* (Mill.) Schreb., *Chamaedrys* (Mill.) Schreb., *Montana* Lazaro Ibiza, *Isotriodon* Boiss., *Scordium* (Mill.) Schreb., and subsection *Pumila*), which represent the Mediterranean pattern of radiation, with a high degree of recent diversification. The typical Mediterranean species with 1-lipped corolla and actinomorphic calyx, consistent with the bulk of species of section *Teucrium* (Kästner, Übersicht zur systematischen gliederung der gattung *Teucrium* L. Biocosme Mésogéen 6:63–78, 1989). The Australian and S America 1-lipped corolla species with actinomorphic calyx, (*Teucrium* subsection

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Cretica (pro part)) (Kästner, Übersicht zur systematischen gliederung der gattung *Teucrium* L. Biocosme Mésogéen 6:63–78, 1989). Finally, the species with unclear 1-lipped corolla and actinomorphic calyx (Australian and Cape Region species belong to section *Teucrium*). The section *Teucrium* is the most heterogeneous and distinctive group within *Teucrium* with three different geographical distribution in Australian, N America and Mexico *Teucrium* while as other Ajugoideae genera closed to *Teucrium* such as Schnabelia Hand.-Mazz. All the sections occurs in the Mediterranean area, NW Africa, N Sahara Desert (Morocco, Algeria, Tunisia and Libya), N Egypt to the Ethiopia mountains, SW Arabian mountains, the Sinai Peninsula and through the arid regions up through W Asia and Europe. Section *Teucriopsis* is exclusive of Canary and Madeira islands, section *Pycnobotrys* distributed only in SE Asia and section *Leucosceptrum* Smith., exclusive from India.

Keywords *Teucrium* · *Teucrium* sections · Systematics · Biogeography · *Spartothamnella* · *Oncinocalyx* · *Teucridium* · *Rubiteucris* · Lamiaceae

1.1 Introduction

Teucrium L. is a polymorphic and widespread genus of Lamiaceae family including about 434 taxa (Appendix I) currently recognised species (Navarro and El Oualidi 2000a; Govaerts et al. 2013). They are shrubs, subshrubs and perennial herbs (rarely annuals or biennials) (Appendix II) with a subcosmopolitan distribution occurring mainly in the Mediterranean region and in the temperate parts of Asia (King 1988; Hedge 1992; Navarro and El Oualidi 2000a; Harley et al. 2004; Navarro 2010). *Teucrium* has an unusual distribution in the Lamiaceae family, only 7% of its species are present in the southern hemisphere (Australia, New Zealand, Cape Region and Argentina), while 93% are present in the north (Hedge and Miller 1977; Navarro and El Oualidi 2000a). The Mediterranean region, without doubt represents the major area of distribution, since it is represented by more of the 90% of the total of species in the world (Navarro and El Oualidi 2000a; Blanca et al. 2017) being the only genus of the subfamily Teucrioideae in the area (Cantino et al. 1992).

Teucrium has been divided into several sections mainly based on calyx shape, inflorescence structure and plant habitat. Bentham (1833) made the most relevant taxonomic classification with additions of Boisser (1879), and the most recent is whose of Kästner (1989). *Teucrium* is a paraphyletic genus (Salmaki et al. 2016) based on the placement of *Spartothamnella*, *Oncinocalyx* and *Teucridium* within it. All the sections, following Bentham (1833), occurs in the Mediterranean area, NW Africa, N Sahara Desert (Morocco, Algeria, Tunisia and Libya), N Egypt to the Ethiopia mountains, SW Arabian mountains, the Sinai Peninsula and through the arid regions up through W Asia and Europe. *Teucridium* is exclusive of Canary and Madeira islands, section *Pycnobotrys* distributed only in SE Asia and section *Leucosceptrum* exclusive from India.

The most recent hypothesis on evolutionary relationships within *Teucrium* have been proposed based on phylogenetic and chromosomatic studies, Salmaki et al. (2016) and Massoud et al. (2018) respectively. These authors proposed two main hypotheses, one of them considering the *Teucrium* section *Teucrium* (*Teucrium* core clade), as an old lineage within the genus as well as the Australian and S African lineages. The second and most speculative, consider the probable origin of the genus was the Mediterranean region, likely with the first aneuploidy originated in the Old World and dispersed in the New World (Massoud et al. 2018).

Due to the size of the taxa under study, a sample of 341 specimens of 97 *Teucrium* taxa from throughout the world have been studied in addition to the previous biosystematic revisions (Navarro and El Oualid 2000a; Navarro 1995, 2010). Species was taken to represent the total taxonomic variation and geographical distribution of *Teucrium*. For geographical regions where no infrageneric divisions of *Teucrium* have hitherto been recognised, representative species were chosen from the regional Floras. The monotypic genera *Oncinocalyx* and *Teucridium* were both examined. In *Sparthotamnella*, *Leucosceptrum* and *Rubiteucris* one member from each genera was chosen (Appendix III). The studied specimens are housed at: (Spain) MA, MAF, BC, SEV, MGC, GDAC, VAL, ABH, JACA; (Portugal) LISU; (United Kingdom) KEW, EDI; (Australia) NE, CANB; (New Zealand) CHR; (Italy) CAG; (France) MPU (for herbarium abbreviations see Holmgren et al. 1990).

In this chapter, we will discuss the systematic and biogeography of *Teucrium* focusing in the relationships within *Teucrium* infrageneric taxa and between *Teucrium* and its close related phylogenetic genera *Spartothamnella*, *Oncinocalyx* and *Teucridium*.

1.2 Systematic of *Teucrium* Genus and Its Infrageneric Delimitation Taxa

Teucrium has a corolla usually 1-lipped or 2-lipped, 5-lobed (with the anterior lobe much larger than the others), concave, most rarely unequal 5-lobed in the upper half; lobes slightly spreading, 4 posterior ± similar, (anterior lobe larger than the others). *Spartothamnella*, *Oncinocalyx* and *Teucridium* are the closest taxonomically related genera to *Teucrium* (Harley et al. 2004) and forming a phylogenetic clade (Salmaki et al. 2016). *Spartothamnella* is an endemic Australian genus that contains three species: *Spartothamnella teucriiflora* (F. Muell.) Moldenke, *S. juncea* Briq. Engl. and Prantl and *S. puberula* (F. Muell.) Maiden and Betchei. The main morphological difference between *Spartothamnella* and *Teucrium* is that the former has drupaceous fruit. *Teucridium*, is an endemic New Zealand genus represented by *T. parvifolium* F. Hook, which differs from *Teucrium* mainly in 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,* also an endemic genus from E Australia (represented by *Oncinocalyx betchei* F. Muell), differs from *Teucrium* in the conspicuously hooked calyx lobes. 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 phylogenetic analysis based on DNA sequence data has confirmed the affinities between *Teucrium* (throughout *T. fruticans* L.), *Teucridium* and *Oncinocalyx* (Wagstaff and Olmstead 1997; Wagstaff et al. 1998; Lindquist and Albert 2002) and *Spartothamnella* (Steane et al. 2004). *Teucridium*, *Oncinocalyx*, *Spartothamnella* and *Teucrium fruticans* L. form a morphologically recognised species group. They are erect or straggly shrubs with many branches with entire leaves, often-axillary cymes, actinomorphic calyx, and fruit in a schizocarp of four big haired reticulate-ridged nutlets.

The delimitation of infrageneric taxa in *Teucrium* is difficult because of the great variation in most morphological characters in many of the species. Bentam's (1833) system is the most traditional classification based on floral features that divides the genus into nine sections: *Leucosceptrum*, *Teucropsis*, *Teucris*, *Pycnobotrys*, *Stachyobotrys*, *Scorodonia*, *Scordium*, *Chamaedrys* and *Polium*. Bentham noted that the most distinct section is *Teucris*, recognising three distinct species (*Teucrium fruticans*, *T. corymbosum* R. Br. and *T. pseudochamaepitys* L.) which show different ways in this section. *Scorodonia*, *Pycnobotrys*, *Stachyobotrys*, *Leucosceptrum* and *Teucropsis* would, when considered together, form a well characterised group based on the broad upper lip of the calyx, which is usually but not always accompanied by less reticulate achenia. As well, section *Teucropsis* is similar to section *Scorodonia* in calyx morphology. Boissier (1879) described two new sections, *Spinularia* from species included by Bentham in *Scordium* and *Isotriodon* for the Asian species unknown to Bentham. Briquet (1895-1897) retained Bentham's circumscription but segregated *Leucosceptrum*, at present included in the subfamily Lamioideae (Harley et al. 2004). Lazaro Ibiza (1896) described two new sections, *Montana* and *Pumila*, for the Iberian species segregated from section *Polium*, based on leaf morphology. Rouy (1909) created a new monospecific section; section *Botrys* based on *Teucrium botrys*, a species included by Bentham in *Scordium*. Kudô (1929) segregated *Kinostemon* based on *Teucrium* section *Pleurobotrys*. *Kinostemon* included three species: *Kinostemon pernyi* (Franch.) Kudô, *K. bidentatum* (Hemsl.) Kudô and *K. ornatum* (Hemsl.) Kudô. Kästner (1989) and Harley et al. (2004) retained all *Kinostemon* within *Teucrium*. Cohen (1956) described the subsection *Rotundifolia* under *Polium*, based on the *Teucrium rotundifolium* species group. Rivas Martinez (1974) treated *Pumilum* (*Pumila*) as a subsection under *Polium*. Valdés Bermejo and Sánchez-Crespo (1978) recognised three subsections under *Polium*; *Polium*, *Pumilum* and *Rotundifolia*. Puech (1978) described the subsection *Simplicipilosa* for a *Polium* species group with simple hairs, endemic to the Iberian Peninsula. The most commonly used infrasectional arrangement of *Polium* is the one proposed by Valdés Bermejo and Sánchez-Crespo (1978), with an addition made by Puech (1980). As a result, *Polium* is one of the largest (50% of the total species, following Gobaerts et al. 2013) and most complex groups within *Teucrium*. Finally, Kästner (1989) produced the first substantial revision of the genus based on corolla, inflorescence and leaf characters. However, the taxonomic sampling of section *Polium* was poor, and many critical species have not been investigated. Kästner included *Polium* as a subsection under *Chamaedrys*, *Spinularia* and *Botrys* under *Scordium*,

Pycnobotrys under *Isotriodon* and *Stachyobotrys* under *Scorodonia*. This author suggested new subsections; *Cretica* under *Teucrium*, *Canadensia* under *Scorodonia* and *Marum* under *Chamaedrys* and retained *Rubiteucris* palmata as *Teucrium palmatum* in the section *Pycnobotrys*. However, pollen morphology (Abu-Asab and Cantino 1993) and phylogenetic research segregate this genus.

The infrageneric taxonomic relationships within *Teucrium* have been investigated by different authors, karyology by Valdés Bermejo and Sánchez-Crespo (1978), growth form (Kästner 1985), chemical analyses (Harbone et al. 1986) and nutlet morphology (Marin et al. 1994) show *Teucrium* as the most distinctive section. The results of the study on trichome morphology (Manzanares et al. 1983; Navarro and El Oualidi 2000b) concluded that sections *Teucrium* and *Polium* are two well-differentiated groups. Navarro and El Oualidi (1999) investigated floral features and concluded that *Teucrium* and *Scorodonia* are the most distinct sections within *Teucrium*. A molecular study based on ITS analyses (El Oualidi et al. 1999) shows that *Polium* can be differentiated from the rest of the sections. The results obtained from pollen morphology (Abu Asab and Cantino 1993; Diez et al. 1993; Navarro et al. 2004) support Bentham's delimitation and agree with the distinctiveness of the sections *Teucrium* and *Spinularia* and establishing new taxonomic relationships between *Chamaedrys* and *Montanum*. Juan et al. (2004) studied seed amino acids and showed that sections *Scordium*, *Botrys* and *Spinularia* are different.

1.3 Systematic and Biogeographic Relationships Within *Teucrium* Infrageneric Taxa and Close Related Genera

Taxonomic relationships are established between *Oncinocalyx*, *Teucridium*, *Oncinocalyx*, *Spartothamnella* and the Austral *Teucrium* (section *Teucrium*) based on the no clearly lipped corolla. These relationships have been proven with results of phylogenetic analysis (Wagstaff and Olmstead 1997; Wagstaff et al. 1998; Lindquist and Albert 2002; Steane et al. 2004; Salmaki et al. 2016). Among them, *Spartothamnella* is the most morphologically close genus to *Teucrium*, differing substantially only based on it drupaceous fruit.

The primitive forms of subfamily Ajugoideae, such as section *Teucrium*, may have appeared in Australia (Chengyih and Hsiwen 1982). Section *Teucrium* is a basal group within *Teucrium* (Marin et al. 1994; Navarro and El Oualidi 1999; Navarro et al. 2004). This section has widespread floral characters in the structurally simple states, including the actinomorphic calyx and unclearly lipped corollas (Austral species of section *Teucrium*) present in geologically ancient areas. *Teucrium* is also the most worldwide spread section found in regions with a Mediterranean climate. As a result of climatic change (Pliocene/Pleistocene), closed forests started to open up and arid areas were established in Australia (Mummenhoff et al. 1992; Cox and Moore 1993) and in the Mediterranean (Quezel 2000). Therefore, it is not surprising to find two different centres of diversification of this section in Australia and in the Mediterranean region.

Section *Teucrium* can be separated from the rest of the sections mainly based on the actinomorphic ventral calyx (Bentham 1833; Kästner 1989; Marin et al. 1994; Navarro and El Oualidi 1999, 2000a). Three distinct groups can be recognized on the basis of corolla conformation. The first includes the 1-lipped species with spurred corollas, an annulus of hairs in the base, adpressed simple hairs in the stems and big nutlets. These are the much branched divaricate evergreen shrubs, including *Teucrium fruticans*, *T. brevifolium* Schreb., *T. malenconianum* and *T. chardonianum* Maire and Wilczek which form the most typically Mediterranean *Teucrium* with convergent traits of woody plants that belong to pre-Mediterranean lineages (Herrera 1987, 1992; Specht 1988; Verdú 2000; Verdú et al. 2003). The second is composed of the Australian *Teucrium racemosum* group characterized by their longer pedicellate flowers, 1-lipped non- spurred corollas with an annulus of hairs in the middle part of the tube. This group includes *Teucrium racemosum* R.Br., *T. corymbosum* R.Br. and *T. cubense* Jacq., and possibly, *T. integrifolium* Benth., *T. depressum* Small and *T. laciniatum* Torr. The third and most distinctive group is composed of the S African species *T. africanum* Thunb, *T. capense* Thunb., and *T. fililobum* F. Muell. ex Benth. Section *Teucriopsis* is discriminate from the rest of the sections according to previous morphological studies (Bentham 1833; Kästner 1989; Marin et al. 1994; Navarro and El Oualidi 2000a).

Trichome morphology (Bini-Maleci and Servettaz 1991; Servettaz et al. 1992) support the systematic affinities between the sections *Chamaedrys* and *Isotriodon* (Kästner 1985, 1986), both distributed in open forest, shrublands and rocky slopes and fissures in arid and sub-humid regions, mainly in the E Mediterranean area. Nevertheless, species of *Isotriodon* section are weel differenciated to be herbaceous often with a broad upper lip to the calyx and fruit in a schizocarp of four smooth or slightly reticulate coherent nutlets. An annulus of hairs in the calyx tube, a derived character (Abu Asab and Cantino 1993), also unites the species of this section.

The independent status of section *Stachyobotrys* is supported by pollen morphology (Abu Asab and Cantino 1993; Navarro et al. 2004) by chemical studies (Harbone et al. 1986) and floral features (Kästner 1989; Navarro and El Oualidi 1999). The Irano–Turanian and Mediterranean species of this section (*Teucrium lamiifolium* D'Urv., *T. hircanicum* L., *T. bracteatum* Desf. and *T. collincola* Greuter and Burdet) have a gibbous calyx, which is absent from the American species (*Teucrium canadense* L., and *T. vesicarium* Mill.). The Moroccan subshrubs, *Teucrium collincola*, seem to be the most different as regards hair type, corolla conformation and reticulate nutlets (Navarro and El Oualidi 1999). The N American and Mexican *Teucrium canadense* differs from the Mediterranean species on the basis of its tubular calyx, curved hairs and slightly reticulate nutlets, while the temperate S American *Teucrium vesicarium* differs in its rare sacciform calyx and reticulate-rugose nutlets.

The Mediterranean species of section *Scorodonia* with 2-lipped (1/4) calyx with a broad upper lip, 2-lipped corolla with straight stamens, the two last characters being the autopomorphies relative to *Teucrium* (Abu Asab and Cantino 1993). The two Chinese species, *Teucrium pernyi* (*Kinostemon pernyi*) and *T. bidentatum* (*K. bidentatum*), both with zygomorphic calyx (1/2/2), broad upper lip and slightly 2-lipped corollas, the five SE Asian species; *Teucrium veronicoides* Maxim., *T.*

stoloniferum Roxb., *T. viscidum* Blume and *T. japonicum* Will., with slightly 2-lipped corollas and zygomorphic calyx (3/2). *T. plectranthoides* Gamble appears to be separate group inside this section based on its 2-lipped calyx. The two SE Asian species, *Teucrium quadrifarium* Buchanan-Hamilton ex D. Don and *T. argutum* R. Br., and the Iberian *T. salviastrum* Schreb., all with 2-lipped corollas, calyx 1/2/2 with broad upper lip, are considered by Bentham (1833) as species belonging to the section *Scorodonia*. This author noted the strong affinity between *Teucrium quadrifarium* and *T. argutum* and the doubtful position of *T. salviastrum*.

Section *Polium* subsection *Polium* and *Simplicipilosa* were clearly different from the rest of the sections because they are the only group with sessile flowers and leaves, short corolla tube with a tuft of hairs inside. Close affinities between them have been reported (Puech 1978; Navarro and Rosúa 1988; Navarro and El Oualidi 1999, 2000b).

Species of section *Montana* can be differenciated based on the calyx, stem hair type, erect in the *Teucrium rotundifolium* group, and curved in *T. montanum* group. Systematic relationships between sections *Montana* and *Chamaedrys* are shown based on nutlet ornamentation (Marin et al. 1994) and trichome morphology (Navarro and El Oualidi 1999). Affinities between sections *Teucrium*, *Chamaedrys* and *Montana* were shown based on nutlet morphology (Marin et al. 1994), and trichome morphology (Navarro and El Oualidi 2000b).

The relationships between the 1-lipped taxa with subactinomorphic calyx, as occurs in the sections *Chamaedrys*, *Montana* and *Pumila* was shown by Kästner (1989), El Oualidi et al. (1999), Navarro and El Oualidi (2000b), Navarro et al. (2004) and between sections *Scordium* and *Polium* (on the basis of pollen morphology) by Diez et al. (1993), Navarro et al. (2004) and seed amino acids (Juan et al. 2004).

1.4 Biogeography of the Infrageneric *Teucrium* Taxa

Section *Teucrium* is distributes in the Mediterranean region, Europe, Africa, Australia, Asia and America (Fig. 1.1). Most species are perennials or short-lived herbs found in the E Mediterranean. They are branched shrubs like *Teucrium fruticans* looking like the relict elements from the old tropical Mediterranean flora. Section *Teucriopsis* comprises the semi-sclerophyllous shrub: *Teucrium heterophyllum* L'Hér from Canary Islands, and two perennial herbs; *T. abutiloides* L'Hér and *T. betonicum* L'Hér from Madeira Islands. It is an endemic section from the Macaronesian region distributed in forest, open habitats and rocky slopes. Section *Stachyobotrys* is distributed in America, Australia, Mediterranean region and Asia. The species are the perennials or short-lived herbs and half-shrubs. This section is distributed mainly on shady walls, rocky slopes and sandy areas in the semi-arid and sub-humid climate regions. It is represented by only two species in the W Mediterranean area, *Teucrium bracteatum* Desf. (Morocco and Spain) and *T. collincola* Greuter & Burdet endemic from Morocco. Section *Scorodonia* is distributed

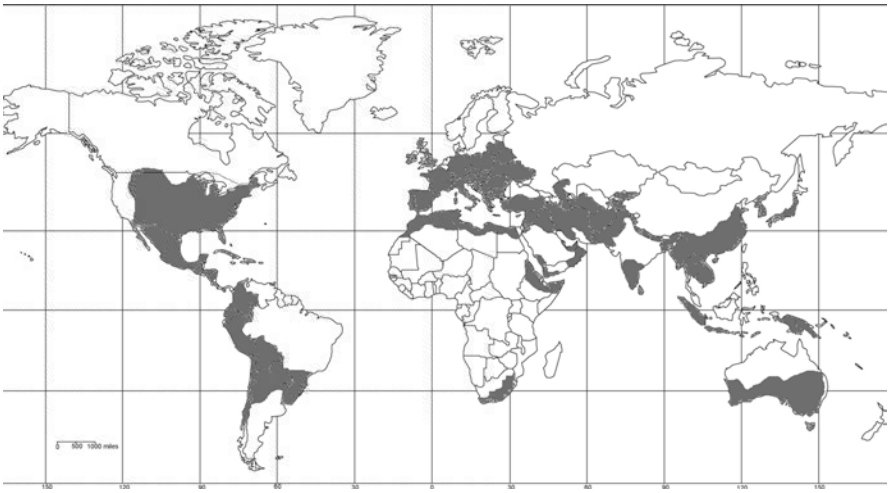

Fig. 1.1 Distribution map of *Teucrium* genus

in the Mediterranean, Europe and Asia but mainly in the humid climate of the W Mediterranean. This section includes half-shrubs and perennial herbs with asexual reproduction. Section *Scordium* is distributed in the Mediterranean, Europe and Asia. This section includes the stoloniferous erect and prostrate short-lived herbs. This is a widespread section in the meadows of the humid habitats. The most important species is the Saharo–Sindian *Teucrium scordium* L. Section *Scordium* subsection *Spinularia* is distributed in the Mediterranean, Europe and Africa and includes erect, prostrate and spinescent annual and short-lived herbs. This section is distributed mainly in the semi-arid and sub-humid regions of the W Mediterranean region (NW Africa). Section *Isotriodon* includes half-shrub species restricted to cliffs, rocky slopes and fissures in the Mediterranean semi-arid regions. Section *Chamaedrys* mainly occurring in the Mediterranean region, Europe, Africa and Asia. They are small half-shrubs and perennial herbs with asexual reproduction. The most important species is *Teucrium chamaedrys* L., distributed through the Mediterranean region. It is the only section of the genus found in the W Mediterrancan islands. Section *Polium* includes a difficult systematic group of vary diverse Mediterranean widespread species with adaptative radiations by polyploidy. The species of this section are common in exposed and disturbed areas of the Mediterranean area, N Africa (Morocco, Algeria and Tunisia). *Polium* is the most diversified section into the genus due its adaptative radiation in the Mediterranean region (Cohen 1956; Puech 1984; Navarro 1995, 2010; Navarro and El Oualidi 1999, 2000a, b; El Oualidi et al. 2002).

Section *Polium* comprises the subsection *Polium* that includes erect, prostrate, cushion-like, half-shrubs or scrubs and perennial herbs. The most important species are *T. polium* L. and *Teucrium capitatum* L., occur throughout the Mediterranean and Irano–Turanian regions. 70% of species are found in the W Mediterranean area

(SE Spain and N Morocco). Subsection *Simplicilpilosa* includes often endemic species from SE Spain, Ethiopia, and SE Arabian Peninsula and subsection *Pumila* is endemic to the Iberian Peninsula. Section *Montanum* is a diverse section throughout the Mediterranean area, NE Africa and E Mediterranean (Turkey, Greece and Cyprus), Ethiopia, E of the Arabia peninsula and W Asia mainly in from rocky slopes, fissures and cliffs.

1.5 Conclusions

Based on the biogeographical distribution of the species of *Teucrium* and the main discriminant systematic characters in the genus, such as corolla and calyx lobes structure (zygomorphy) as well as their indumentum type, almost five major biogeographic and taxonomic species groups can be differentiate. The group of the perennial herbs with 2-lipped corolla and zygomorphic calyx (sections *Pycnobotrys*, *Stachyobotrys*, *Scorodonia* and *Teucropsis*) which provide a clear example of the Eurasian pattern of radiation from C Asia and China. A group integrate for the subshrubs and half-shrubs with 1-lipped corolla and mainly subactinomorphic calyx (sections *Polium*, *Chamaedrys*, *Montana*, *Isotriodon*, *Pumila* and *Scordium*), that clearly represent the Mediterranean pattern of radiation, with a high degree of recent diversification (Hedge 1986). A third group composed by the typical Mediterranean shrubs with 1-lipped corolla and actinomorphic calyx, consistent with the bulk of species of section *Teucrium* subsection *Fruticantia* (pro part.) (Kästner 1989). A fourth group that includes the Australian and S America subshrubs and perennial herbs with 1-lipped corolla and actinomorphic calyx, which seem to be the most distinctive group (*Teucrium racemosum* group), which corresponds to the section *Teucrium* subsection *Cretica* (pro part) (Kästner 1989). This last group confirms the connection between Australasia and S American (through *Teucrium cubense*), the sole pattern of radiation in Lamiaceae in the southern hemisphere (Hedge 1992). Finally, the group formed of the perennial herbs and subshrubs with unclear 1-lipped corolla and actinomorphic calyx (Australian and Cape Region species belong to section *Teucrium*). The section *Teucrium* is the most heterogeneous and distinctive group within *Teucrium* with three different geographical distribution in Australian, N America and Mexico *Teucrium* while as other Ajugoideae genera closed to *Teucrium* such as *Schnabelia* and *Pseudocaryopteris*.

Teucrium genus is widespread in the Mediterranean, Macaronesian, Irano–Turanian and Saharo–Arabian regions with 434 taxa (Govaerts et al. 2013) in the world. The genus shows two centres of richness located in the E and W region of the Mediterranean Sea. This fact is exemplified by the geographical distribution of sections *Stachyobotrys*, *Isotriodon* and section *Polium* subsection *Simplicipilosa*. However, other sections, such as *Scordium*, have an homogeneous distribution in all the areas but are mainly represented by Saharo–Sindian species. The sections *Teucrium*, *Chamaedrys*, *Isotriodon* and *Stachyobotrys* mainly occur in the E Mediterranean and Irano–Turanian region. *Polium*, *Scorodonia* and *Spinularia* are

predominantly in the W Mediterranean area. The E Mediterranean region, the S of the Arabian Peninsula and NE Africa are centres of floristic diversity of the section *Polium*. *Teucriopsis* is restricted to the Macaronesian region. Part of the floristic richness of *Teucrium* genus is the high number of endemic species in the Mediterranean region (63% of total species in the world). The main part of them (c. 50%) in the lberian Peninsula and Morocco and a high number (c. 18%) in Turkey and Greece.

Stachyobotrys (through *Teucrium canadense* and *T. inflatum*), *Pycnobotrys* (through *Teucrium vesicarium*) are the only taxonomic groups with amphiatlantic relationships, in which the basalmost members of these are largely Mediterranean and C Asian in origin. This pattern of distribution can be explained based on the Boreotropics hypothesis (Wolfe 1975). In this sense, *Teucrium* species have a distinct distribution in the Old and in the New World, among arid regions of S Africa, N America, N Africa and Asia (Mabberly 1997). All these sections can be considered as a remnant of widespread early Tertiary flora. Finally, section *Polium* is an example that reflects a rapid radiation and speciation with a high number of species in the Mediterranean region (Navarro and El Oualidi 2000a; El Oualidi et al. 2002).

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Appendices

Appendix I: List of Teucrium *Infrageneric Taxa in the World*

Teucrium L., taxa list of the accepted names from WCSP World Checklist of Selected Plant (WCSP) (familieshttp://wcsp.science.kew.org/qsearch.do). Govaerts RA, Paton A, Harvey Y, Navarro T, Del Rosario Garcia Pena M (2013) World Checklist of Lamiaceae. Kew. The Board of Trustees of the Royal Botanic Gardens, Kew.www.kew.org/wcsp/

***Teucrium* L., Sp. Pl.: 562 (1753).**

Teucrium abolhayatensis Ranjbar & Mahmoudi, Novon 25: 304 (2017).
Teucrium abutiloides L'Hér., Stirp. Nov.: 84 (1788).
Teucrium africanum Thunb., Prodr. Pl. Cap.: 95 (1800).
Teucrium afrum (Emb. & Maire) Pau & Font Quer in P.Font i Quer, Iter Marocc. 1927: n.° 510 (1928).

Teucrium afrum subsp. *afrum*.
Teucrium afrum subsp. *rhiphaeum* (Font Quer & Pau) Castrov. & Bayon, Anales Jard. Bot. Madrid 47: 513 (1989 publ. 1990).
Teucrium afrum subsp. *rubriflorum* (Font Quer & Pau) Castrov. & Bayon, Anales Jard. Bot. Madrid 47: 513 (1989 publ. 1990).

Teucrium aladagense Vural & H.Duman, Turkish J. Bot. 39: 319 (2015).
Teucrium albicaule Toelken, J. Adelaide Bot. Gard. 7: 296 (1985).
Teucrium albidum Munby, Bull. Soc. Bot. France 2: 286 (1855).
Teucrium alborubrum Hemsl., J. Linn. Soc., Bot. 26: 311 (1890).
Teucrium* × *alexeenkoanum Juz. in V.L.Komarov, Fl. URSS 20: 506 (1954).
Teucrium algarbiense (Cout.) Cout., Esboco Fl. Lenh. Portug., ed. 2: 262 (1936).
Teucrium alopecurus de Noé, Bull. Soc. Bot. France 2: 585 (1855).
Teucrium alpestre Sm. in J.Sibthorp & J.E.Smith, Fl. Graec. Prodr. 1: 395 (1809).
Teucrium* × *alvarezii Alcaraz, Sánchez-Gómez, De la Torre & S.Ríos, Datos Veg. Murcia: 144 (1991).
Teucrium alyssifolium Stapf, Denkschr. Kaiserl. Akad. Wiss., Wien. Math.-Naturwiss. Kl. 50: 104 (1885).
Teucrium amplexicaule Benth., Labiat. Gen. Spec.: 687 (1835).
Teucrium andrusi Post, Bull. Herb. Boissier 5: 758 (1897).
Teucrium angustissimum Schreb., Pl. Verticill. Unilab. Gen. Sp.: 49 (1774).
Teucrium anlungense C.Y.Wu & S.Chow, Acta Phytotax. Sin. 10: 338 (1965).
Teucrium annandalei Mukerjee, Rec. Bot. Surv. India 14: 219 (1940).
Teucrium antiatlanticum (Maire) Sauvage & Vindt, Bull. Soc. Sci. Nat. Maroc 35: 286 (1956).
Teucrium antilibanoticum Mouterde, Saussurea 4: 25 (1973).
Teucrium antitauricum Ekim, Notes Roy. Bot. Gard. Edinburgh 38: 58 (1980).
Teucrium apollinis Maire & Weiller, Bull. Soc. Hist. Nat. Afrique N. 30: 86 (1939).
Teucrium aragonense Loscos & J.Pardo in H.M. Willkomm (ed.), Ser. Inconf. Pl. Aragon.: 85 (1863).
Teucrium arduinoi L., Mant. Pl. 1: 81 (1767).
Teucrium argutum R.Br., Prodr. Fl. Nov. Holland.: 504 (1810).
Teucrium aristatum Pérez Lara, Anales Soc. Esp. Hist. Nat. 18: 90 (1889).
Teucrium aroanium Orph. ex Boiss., Diagn. Pl. Orient., ser. 2, 4: 55 (1859).
Teucrium asiaticum L., Mant. Pl. 1: 80 (1767).
Teucrium atratum Pomel, Nouv. Mat. Fl. Atl.: 304 (1874).
Teucrium aureiforme Pomel, Nouv. Mat. Fl. Atl.: 113 (1874).
Teucrium aureocandidum Andr., Ind. Horti Bot. Univ. Budapest 5: 18 (1941).
Teucrium aureum Schreb., Pl. Verticill. Unilab. Gen. Sp.: 43 (1774).

Teucrium aureum subsp. *aureum*.
Teucrium aureum subsp. *turdetanum* Devesa & Valdés Berm., Anales Jard. Bot. Madrid 41: 88 (1984).

Teucrium* × *badiae Sennen, Bol. Soc. Aragonesa Ci. Nat. 11: 230 (1912).
Teucrium balearicum (Coss. ex Pau) Castrov. & Bayon, Anales Jard. Bot. Madrid 47: 508 (1989 publ. 1990).
Teucrium balfourii Vierh., Denkschr. Kaiserl. Akad. Wiss., Wien. Math.-Naturwiss. Kl. 71: 436 (1907).
Teucrium balthazaris Sennen, Diagn. Nouv.: 95 (1936).
Teucrium baokangensis C.L.Xiang, Taxon 67: 390 (2018).
Teucrium barbarum Jahand. & Maire, Bull. Soc. Hist. Nat. Afrique N. 19: 85 (1928).
Teucrium barbeyanum Asch. & Taub. ex E.A.Durand & Barratte, Fl. Libyc. Prodr.: 191 (1910).
Teucrium* × *bergadense Sennen, Bol. Soc. Aragonesa Ci. Nat. 11: 214 (1912).
Teucrium betchei (F.Muell.) Kattari & Salmaki, Taxon 65: 818 (2016).
Teucrium betonicum L'Hér., Stirp. Nov.: 83 (1788).
Teucrium bicolor Sm. in A.Rees, Cycl. 35: n.° 25 (1817).
Teucrium bicoloreum Pau ex Vicioso, Bol. Soc. Esp. Hist. Nat. 16: 142 (1916).
Teucrium bidentatum Hemsl., J. Linn. Soc., Bot. 26: 312 (1890).
Teucrium bogoutdinovae Melnikov, Novosti Sist. Vyssh. Rast. 45: 81 (2014).
Teucrium botrys L., Sp. Pl.: 562 (1753).
Teucrium brachyandrum Puech, Naturalia Monspel., Sér. Bot. 21: 209 (1970 publ. 1971).
Teucrium bracteatum Desf., Fl. Atlant. 2: 7 (1798).
Teucrium brevifolium Schreb., Pl. Verticill. Unilab. Gen. Sp.: 27 (1774).
Teucrium* × *bubanii Sennen, Bol. Soc. Aragonesa Ci. Nat. 11: 229 (1912).
Teucrium bullatum Coss. & Balansa, Bull. Soc. Bot. France 20: 260 (1873).
Teucrium burmanicum Mukerjee, Notes Roy. Bot. Gard. Edinburgh 19: 306 (1938).
Teucrium buxifolium Schreb., Pl. Verticill. Unilab. Gen. Sp.: 42 (1774).
Teucrium campanulatum L., Sp. Pl.: 562 (1753).
Teucrium canadense L., Sp. Pl.: 564 (1753).

Teucrium canadense var. *canadense*.
Teucrium canadense var. *hypoleucum* Griseb., Cat. Pl. Cub.: 214 (1866).
Teucrium canadense var. *occidentale* (A.Gray) E.M.McClint. & Epling, Brittonia 5: 500 (1946).
Teucrium canadense var. *virginicum* (L.) Eaton, Man. Bot., ed. 5: 415 (1829).

Teucrium canum Fisch. & C.A.Mey., Index Seminum (LE, Petropolitanus) 1: 40 (1835).
Teucrium capitatum L., Sp. Pl.: 566 (1753).

Teucrium capitatum subsp. *capitatum*.
Teucrium capitatum subsp. *gracillimum* (Rouy) Valdés Berm., Acta Bot. Malac. 4: 40 (1978 publ. 1979).
Teucrium capitatum subsp. *majoricum* (Rouy) Nyman, Consp. Fl. Eur., Suppl. 2: 246 (1889).

Teucrium* × *carmelitanum Roselló, P.P.Ferrer, A.Guillén, Gómez Nav., Peris & E. Laguna, Flora Montiber. 55: 102 (2013).

Teucrium carolipaui Vicioso ex Pau, Bol. Soc. Ibér. Ci. Nat. 20: 185 (1921 publ. 1922).

Teucrium carolipaui subsp. *carolipaui*.

Teucrium carolipaui subsp. *fontqueri* (Sennen) Rivas Mart., Anales Inst. Bot. Cavanilles 31: 88 (1974).

Teucrium carthaginense Lange, Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn 1881: 97 (1882).

Teucrium* × *carvalhoae A.F.Carrillo, A.Hern., Coy, Güemes & Sánchez-Gómez, Acta Bot. Malac. 22: 221 (1997).

Teucrium caucasigenum Melnikov, Novosti Sist. Vyssh. Rast. 45: 72 (2014).

Teucrium cavanillesianum Font Quer & Jeronimo, Anales Jard. Bot. Madrid 6(2): 488 (1946).

Teucrium cavernarum P.H.Davis, Kew Bull. 6: 113 (1951).

Teucrium chamaedrys L., Sp. Pl.: 565 (1753).

Teucrium chamaedrys subsp. *albarracinii* (Pau) Rech.f., Bot. Arch. 42: 385 (1941).

Teucrium chamaedrys subsp. *algeriense* Rech.f., Bot. Arch. 42: 364 (1941).

Teucrium chamaedrys subsp. *chamaedrys*.

Teucrium chamaedrys subsp. *germanicum* (F.Herm.) Rech.f., Bot. Arch. 42: 379 (1941).

Teucrium chamaedrys subsp. *gracile* (Batt.) Rech.f., Bot. Arch. 42: 389 (1941).

Teucrium chamaedrys subsp. *lydium* O.Schwarz, Repert. Spec. Nov. Regni Veg. 36: 132 (1934).

Teucrium chamaedrys var. *multinodum* Bordz., Mat. Fl. Kavk. 4(3): 57 (1916).

Teucrium chamaedrys subsp. *nuchense* (K.Koch) Rech.f., Bot. Arch. 42: 370 (1941).

Teucrium chamaedrys subsp. *olympicum* Rech.f., Bot. Arch. 42: 368 (1941).

Teucrium chamaedrys subsp. *pectinatum* Rech.f., Bot. Arch. 42: 366 (1941).

Teucrium chamaedrys subsp. *pinnatifidum* (Sennen) Rech.f., Bot. Arch. 42: 383 (1941).

Teucrium chamaedrys subsp. *sinuatum* (Celak.) Rech.f., Bot. Arch. 42: 378 (1941).

Teucrium chamaedrys subsp. *syspirense* (K.Koch) Rech.f., Ann. Naturhist. Mus. Wien 51: 427 (1941).

Teucrium chamaedrys subsp. *tauricola* Rech.f., Bot. Arch. 42: 376 (1941).

Teucrium chamaedrys subsp. *trapezunticum* Rech.f., Bot. Arch. 42: 369 (1941).

Teucrium chardonianum Maire & Wilczek, Bull. Soc. Hist. Nat. Afrique N. 26: 130 (1935).
Teucrium charidemi Sandwith, Cavanillesia 3: 38 (1930).
Teucrium chasmophyticum Rech.f., Pl. Syst. Evol. 134: 287 (1980).
Teucrium chlorocephalum Celak., Bot. Centralbl. 14: 186 (1883).
Teucrium chlorostachyum Pau & Font Quer in P.Font i Quer, Iter Marocc. 1929: n.° 370 (1930).

Teucrium chlorostachyum subsp. *chlorostachyum*.
Teucrium chlorostachyum subsp. *melillense* (Sennen ex Maire) Ouqlidi, Mathez & T.Navarro, Fl. Medit. 7: 23 (1997).

Teucrium chowii Y.H.Tong & N.H.Xia, Phytotaxa 349: 99 (2018).
Teucrium chrysotrichum Lange, Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn 1881: 96 (1882).
Teucrium cincinnatum Maire, Bull. Soc. Sci. Nat. Maroc 13: 272 (1933 publ. 1934).
Teucrium clementiae Ryding, Edinburgh J. Bot. 55: 210 (1998).
Teucrium coahuilanum B.L.Turner, Lundellia 8: 7 (2005).
Teucrium* × *coeleste Schreb., Pl. Verticill. Unilab. Gen. Sp.: 49 (1774).
Teucrium compactum Clemente ex Lag., Gen. Sp. Pl.: 17 (1816).
Teucrium coniortodes Boiss. & Blanche in P.E.Boissier, Fl. Orient. 4: 818 (1879).
Teucrium* × *conquense M.B.Crespo & Mateo, Fl. Medit. 1: 197 (1991).

Teucrium × *conquense* nothosubsp. *conquense*.
Teucrium × *conquense* nothosubsp. *siyasense* A.F.Carrillo & Sánchez Gómez, Acta Bot. Malac. 21: 285 (1996).

Teucrium* × *contejeanii Giraudias, Bull. Soc. Études Sci. Angers 1888: 16 (1888).
Teucrium corymbiferum Desf., Fl. Atlant. 2: 8 (1798).
Teucrium corymbosum R.Br., Prodr. Fl. Nov. Holland.: 504 (1810).
Teucrium cossonii D.Wood, Bot. J. Linn. Soc. 65: 261 (1972).
Teucrium creticum L., Sp. Pl.: 563 (1753).
Teucrium cubense Jacq., Enum. Syst. Pl.: 25 (1760).
Teucrium cuneifolium Sm. in J.Sibthorp & J.E.Smith, Fl. Graec. Prodr. 1: 395 (1809).
Teucrium cyprium Boiss., Diagn. Pl. Orient. 5: 43 (1844).
Teucrium cyrenaicum (Maire & Weiller) Brullo & Furnari, Webbia 34: 167 (1979).
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