

TRICHOME MORPHOLOGY IN *TEUCRIUM* L. (LABIATAE). A TAXONOMIC REVIEW

by

TERESA NAVARRO¹ & JALAL EL OUALIDI²

Resumen

NAVARRO, T. & J. EL OUALIDI (2000). Morfología de los tricomas en *Teucrium* L. (Labiatae). Una revisión taxonómica. *Anales Jard. Bot. Madrid* 57(2): 277-297 (en inglés).

La micromorfología de los tricomas de las hojas, cáliz, corola y semillas de 56 especies de *Teucrium* L. pertenecientes a las 9 secciones del género en el área mediterránea ha sido analizada mediante microscopía electrónica de barrido (MEB). Se describen 25 tipos de tricomas, 12 de ellos, nuevos. Los pelos simples con células de paredes delgadas constituyen el único tipo encontrado en la corola y el más ampliamente distribuido en la cara abaxial de las hojas. Los pelos glandulares subsésiles, con 2-4 células, son exclusivos de las semillas y hojas de las especies saxícolas y paleoendémicas. La presencia de pelos simples, cónicos, con células de paredes gruesas, cortos o elongados y generalmente adpresos, proporciona un carácter adicional para clarificar los límites entre la sección *Chamaedrys* (Mill.) Schreb. y la sección *Polium* (Mill.) Schreb. Los pelos ramificados no glandulares solamente aparecen en la sección *Polium* subsección *Polium*, con excepción de los pelos ramificados de ramas cónicas y células de paredes gruesas encontrados solo en *Teucrium barbarum* Jahand. & Maire (sección *Chamaedrys*) y *T. heterophyllum* L'Hér. (sección *Teucrium*). Esta última sección está bien definida por la ausencia de pelos simples cónicos con células de paredes gruesas y pelos glandulares en la corola. La sección *Teucropsis* Benth. es de particular interés por la presencia exclusiva de pelos glandulares ramificados y peltados en las semillas. La sección *Chamaedrys* es un grupo homogéneo que se distingue de las otras secciones por un indumento formado sólo por pelos desarrollados a partir de pelos simples cónicos con células de paredes gruesas. Esta sección tiene en común con las secciones *Isotriodon* Boiss. y *Polium* subsección *Rotundifolia* Cohen ex Valdés Berm. & Sánchez Crespo la presencia de pelos glandulares en la superficie de las semillas. El tipo de tricomas de los dientes del cáliz, de la cara abaxial de la hoja y de los lóbulos látero-posteriores de la corola pueden ser usados como un carácter taxonómico distintivo a nivel específico y subspecífico. Este estudio apoya la delimitación de secciones de Bentham con las posteriores adiciones de Boissier.

Palabras clave: *Labiatae*, *Teucrium*, taxonomía, microcaracteres, indumento de la hoja, cáliz, corola y superficie de las semillas.

Abstract

NAVARRO, T. & J. EL OUALIDI (2000). Trichome morphology in *Teucrium* L. (Labiatae). A taxonomic review. *Anales Jard. Bot. Madrid* 57(2): 277-297.

The micromorphology of trichomes of 56 *Teucrium* L. species belonging to the 9 sections of the genus in the Mediterranean area was surveyed by scanning electron microscopy (SEM) of leaves, calyx, corolla and nutlets. 25 trichome types are described, 12 of them are new. Thin-

¹ Departamento de Biología Vegetal, Facultad de Ciencias, Universidad de Málaga. E-29018 Málaga (Spain). e-mail: tnavarro@uma.es

² Institut Scientifique, Département de Botanique et d'Ecologie Végétale, Université Mohammed V. BP 703 Rabat (Morocco). e-mail: eloualidi@israbat.ac.ma

walled hairs are the exclusive type found in the corolla and are the most widespread type on the abaxial side of the leaves. Subsessile glandular hairs, 2-4-celled, are found on the nutlet and leaves of the semi-shrubby and paleoendemic species. The presence of short or elongated, generally adpressed simple thick-walled slightly conical hairs provides an additional character to clarify the boundaries between sect. *Chamaedrys* (Mill.) Schreb. and sect. *Polium* (Mill.) Schreb. Branched non-glandular hairs are confined to sect. *Polium* subsect. *Polium*, except for the rare branched hair conical and thick-walled type found in *Teucrium barbarum* Jahand. & Maire (sect. *Chamaedrys*) and *T. heterophyllum* L'Hér. from sect. *Teucrium*. This last section is well defined by the absence of simple slightly conical thick-walled hairs and the glandular hairs in the corolla. Sect. *Teucriopsis* Benth. is of particular interest for the exclusive presence of branched and peltate glandular hairs on the nutlets surface. Sect. *Chamaedrys* is a homogeneous group, distinguished from the other sections by an indumentum formed only by trichomes types evolved from the simple slightly conical thick-walled hairs. This section overlaps, in the presence of glandular sub-sessile hair on the nutlets surface, with sects. *Isotriodon* Boiss. and sect. *Polium* subsect. *Rotundifolia* Cohen ex Valdés Berm. & Sánchez Crespo. The trichomes type of the calyx teeth, abaxial side of the leaf and latero-posterior corolla lobes can be used as a distinctive taxonomic character at specific and infra-specific level. This study supports Bentham's delimitation of sections with the additions subsequently made by Boissier.

Key words: *Labiatae*, *Teucrium*, taxonomy, microcharacters, leaf, calyx and corolla indumentum, nutlet surface.

INTRODUCTION

The taxonomic value of the indumentum and its importance in systematic and phylogenetic relationships is well known in *Lamiaceae* and such related families as *Verbenaceae* and *Scrophulariaceae* (ABU ASSAB & CANTINO, 1987; CANTINO, 1990; METCALFE & CHALK, 1950).

Trichomes are among the most useful taxonomic characters in *Teucrium* L. Their absence or presence, their typology on the nutlet surface can be used as taxonomic markers in the infrageneric classification of the genus (MARÍN & *al.*, 1994), while the infrasectional classification of sect. *Polium* is based almost totally on the typology of the trichomes (PUECH, 1984; NAVARRO, 1995).

The dependence on micromorphology for the correct characterization of trichome type, diversity and distribution in plant structures leaves, calyx and corolla and their taxonomic value as an additional marker at specific and subspecific level has been demonstrated in some Italian, Polish, Slovakian and Moroccan species from sect. *Chamaedrys*, *Scorodonia* and *Polium* subsect. *Rotundifolia* (BINI-MALECI & SERVETTAZ, 1991; BINI-MALECI & *al.*, 1992; SERVETTAZ & *al.*, 1992; SERVETTAZ & *al.*, 1994; ANTUNES & SEVINATE-PINTO,

1991; GRZYBEK, 1967; EL OUALIDI & *al.*, 1997).

However, in spite of their stability as a character (DAVIS & HEYWOOD, 1963), there are no reports on the infrageneric value of the stability, distribution patterns and diversity of trichomes in leaves, calyx and corolla, particularly in regard to the floral features for pollination such as attraction vectors, nectar guides and closed gullet selective mechanism. Furthermore, the taxonomic value of trichomes in *Teucrium* is confused because of the varying terminology used in the past and because none of the previous classifications accommodate the full diversity of the *Teucrium* trichome spectrum.

Teucrium is a large and polymorphic genus mainly in Europe, North Africa and in the temperate parts of Asia. The basic sectional arrangement of the genus (BENTHAM, 1835) is based mainly on the calyx and inflorescence type undertake both very variable characters. The difficulty of classifying some species into sections and the uncertainty over the affinities of some of their sections would led us to a micromorphological study of the leaf, calyx, nutlets and corolla in the hope that it clarify the confusion sectional boundaries and inter-specific relationships (ABU-ASAB & CANTINO, 1993) and demonstrate the taxonomic value of these micro-characters.

In this study, *Teucrium* sections are recognized in accordance with BENTHAM's delimitation (1835) with the additions made by BOISSIER (1879).

MATERIAL AND METHODS

This present study is based on field studies as well as herbarium specimens housed at the following institutions (abbreviations following HOLMGREN & *al.*, 1990): B, BC, E, G, MA, MGC, MPU, ORT, RAB and TFC. The list of species and their origin is given in the Appendix. Light and SEM microscope were used. For SEM studies, several samples were prepared, minimum three, the flowers and calyces being fixed whole after critical point technique in a Balzers CPD-020, while the nutlets were mounted directly on aluminium stubs and covered with 24k gold in an ion sputter JFC-1100. After coating, they were observed and photographed by a scanning microscope JEOL JSM-840.

Flowers. We studied the adaxial side of the lower lip, principally the central zone (CZ) located between the basal part of anterior lobe (AL) and the entrance of the corolla tube. The lobes (AL; LL, lateral lobes; LPL, latero-posterior lobes) of the lower lip and the inner side of the corolla tube including the stamen base were analysed and trichome types forming part of the floral features for pollination such as the vector of attractions or nectar guides and closed gullet mechanism were described. The epidermal sculpturing of the corolla lobes were also described. The trichomes of the outer and inner side and margin lobes were described, including the type forming part of the closed tube mechanism in immature calyces. For gynodioecious species the calyx and corolla of male-sterile and cosexuals were observed.

Nutlets. Nutlets were previously observed using a light microscope to ensure that they were of normal size and maturity.

Trichomes. Trichome micromorphology and the structure of leaves, calyx, corolla and nutlets were described and classified. The

general classification scheme is based on ROE (1971), but the typological classification of glandular hairs is based on CANTINO (1990), and for most of the categories described, thin-walled and thick-walled groups (HARDIN, 1976) were segregated.

The characters of taxonomic interest in the classification were: presence or absence of the secretory cells, glandular and non-glandular; shape of wall of basal and stalk cells, thin-walled and thick-walled, and presence of the transverse wall cells; number and length of the cells in uniseriate trichomes, unicellular or multicellular; presence or absence of few-armed hairs, stellate hairs, dendritic hairs, vermiform hairs and twisted hairs. In addition, the orientation of the trichomes in relation to the epidermal surface (erect, adpressed), the shape (flexuose, curved, hooked, triangular, conic) and finally the presence/absence of micro-papillae in wall cells were analysed.

RESULTS

The trichome micromorphology of the leaf, calyx and corolla of the following taxa was analysed in 5 species of the sect. *Teucrium*; all species comprising the sect. *Teucriopsis*; 4 previously uninvestigated species of sect. *Chamaedrys*; 5 unstudied species of sect. *Scorodonia*; 2 of sect. *Stachybotrys* Benth.; 2 of sect. *Scordium*; 5 of sect. *Spinularia*; 4 of sect. *Isotriodon*; 26 of sect. *Polium*. Sect. *Pycnobotrys* Benth. was not studied. The surfaces of 41 nutlets corresponding to otherwise unstudied species were also studied.

Synopsis of trichomes types in Teucrium

Figures 1-4 shows the common trichomes types in the studied species.

1. Glandular trichomes

These constitute an important taxonomic character of the *Lamiaceae* and *Verbenaceae* and form part of the floral specialized features for pollination. For each type, the most significant variation is described. Some of

these types are present in other genera of *Lamiaceae* whose citation is included. The thin-walled and thick-walled groups are also represented in the clavate glandular trichomes.

1.1. Simple glandular trichomes

A: Clavate glandular trichomes. Reported as long/short-stalked gland or capitate trichomes (BINI MALECI & SERVETTAZ, 1991). Variations in the size and morphology of clavate glandular trichomes are decided by the number, size and disposition of the stalk cell. The number of cells in the secretory head has not been observed. The presence of micro-papillae is rare.

A1: Short clavate glandular trichomes. Reported in *Rosmarinus* L. (WERKER & *al.*, 1985), generally with two, large and thin stalk cells or three stalk cells, with reduced neck and usually without micro-papillae (fig. 1a, b).

A2: Long clavate glandular trichomes with 3(5)-cells. With thick-walled cells (fig. 1c), with long thin-walled 3(4)-cells (fig. 1d) illustrated in *Scutellaria* L. (ABU ASSAB & CANTINO, 1987), with short large thin-walled cells (fig. 1e), with large thin-walled basal cell with micro-papillae (fig. 1f), with elongated, transverse thin-walled cells (fig. 1g) illustrated in *Nepeta* L. (HUSEIN & *al.*, 1989).

B: Subsessile glandular trichomes. Reported as short-stalked bladder-like glands, sunken glandular dots, glandular scales, glandular capitate sessile trichomes or peltate hairs (BINI-MALECEI & SERVETTAZ, 1991). Following the description and typology of ABU-ASSAB & CANTINO (1987) and based on the number of cells and the cell-wall configuration, the subsessile glandular trichomes correspond to types 1, 2 and 4. Type 1, named B1 (fig. 1h), was the most frequently observed types, while type 2, named B2 (fig. 1i) and type 4, named B4 (fig. 1j, k) were less common.

1.2. Branched glandular trichomes

C: Few 2(5)-armed trichomes with lateral glands (fig. 1l). BOKHARI & HEDGE (1971) noticed their presence in *Meriandra* Benth.

2. Non-glandular trichomes

2.2. Simple, unbranched trichomes

D: Prick-less-hairs. These are the unicellular epidermal appendages (fig. 2a).

E: Conical thin-walled unicellular hairs, also called papillate long cells. More or less elongated with or without micro-papillae (fig. 2b).

F: Thin-walled trichomes.

F1: Triangular, large and very thin-walled unicellular hairs, with ridges (fig. 2c).

F2: Large, very thin-walled, 2(5)-celled trichomes with an acute apical cell. With ridges and marked internodes (fig. 2d); rare with the crumpled apical cell (fig. 2e); without micro-papillae (fig. 2f).

F3: Short, thin-walled, 2-3-celled trichomes with micro-papillae; the apical cell is erect triangular, acute (fig. 2g).

F4: Short, thin-walled, 2-celled trichomes densely covered by micro-papillae, with the apical cell elongated (fig. 2h), slightly crumpled or falcate and with a smooth basal cell (fig. 2i).

F5: Elongated and flexuose, thin-walled 3-7(11)-celled trichomes with internode distinct, the apical cell acute with micro-papillae, the basal cell smooth, each cell transverse to the preceding one; when the apical is very elongated it looks like the vermiform type (fig. 2j); illustrated as tuberculate hairs by MARÍN & *al.* (1994) and reported in *Origanum* L., *Clinopodium* L. and *Calamintha* Mill. by HUSEIN & *al.* (1990) (fig. 2k, l).

G: Thick-walled trichomes.

G1: Short and slightly conical, thick-walled, 2-celled or rarely 3-celled trichomes, with a pointed short or elongated apical cell and the basal cell without micro-papillae, erect or sometimes slightly curved, some of them illustrated as flask-shaped by BINI-MALECI & SERVETTAZ (1991); BARTHLOTT (1980) (fig. 3a, b).

G2: Elongated, generally adpressed, thick-walled 3(5)-celled trichomes, folded with rounded micro-papillae, hooked (fig. 3c); curved (fig. 3d); with falcate and slight thin

elongated apical cell (fig. 3e); with the apical cell elongated (fig. 3f) reported in *T. chamaedrys* L. by MANZANARES & al. (1983) and in *T. marum* L. by BINI-MALECI & SERVETTAZ (1991).

G3: Elongated, thick-walled (3)5-7(8)-celled trichomes, erect with rounded epidermal cell and marked internode. Erect, 3-celled (fig. 3g), with elongated stalk cells and slightly flexuose (fig. 3h); in a developing

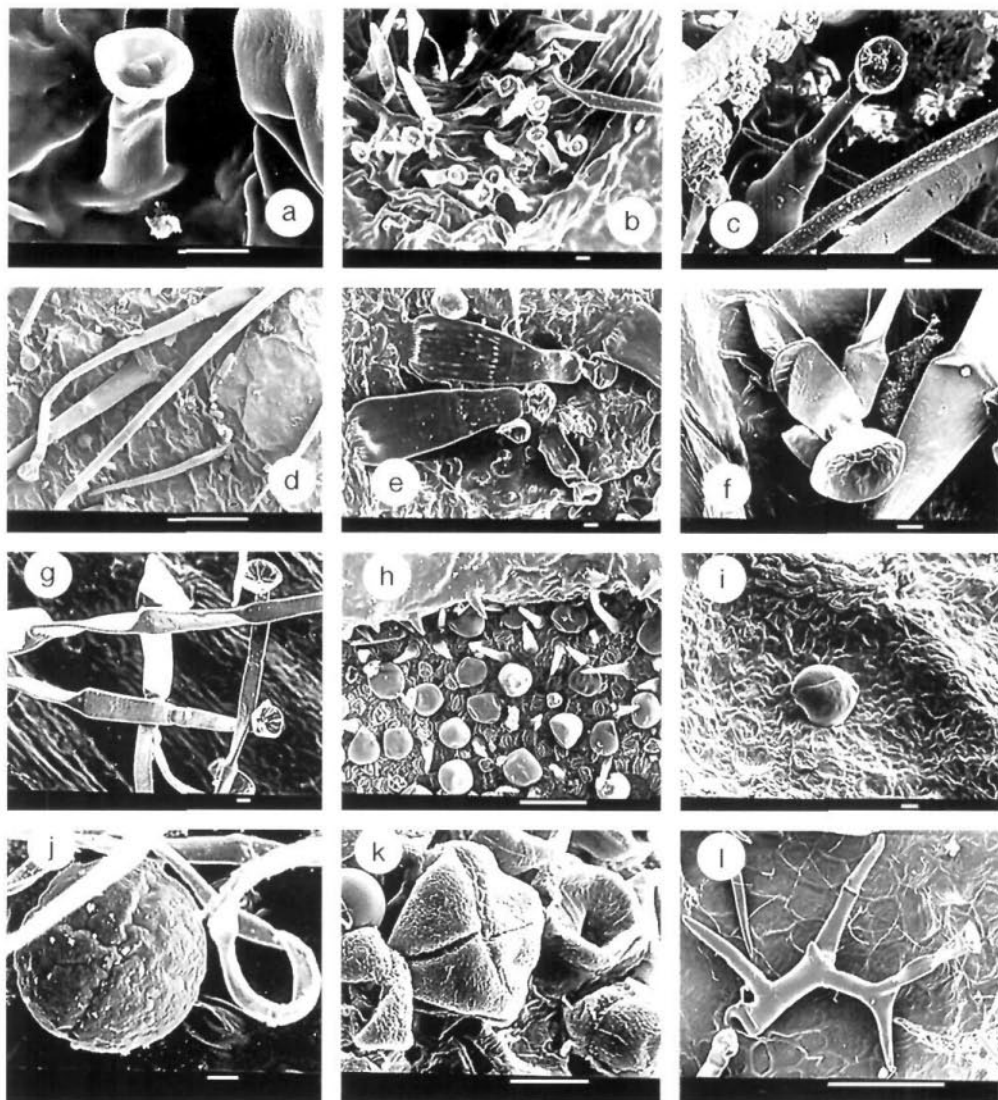


Fig. 1.—SEM glandular trichomes: a, b, A1 short clavate: a, *Teucrium carolipau* subsp. *carolipau*, MGC 6207; b, *T. fragile*, MGC 42191. c-g, A2 long clavate: c, with thick-walled cells, *T. persicum*, G 8347/73; d, with thin-walled, long cells, *T. maghrebinum*, BC 811317; e, with thin-walled, large cells, *T. odontites*, G 8347/21; f, without micropapillae, *T. bracteatum*, BC 47399; g, with transverse wall cells, *T. botrys*, BC 811319. h, i, B subsessile: h, B1 one-celled, *T. pseudochamaepestis*, MGC 48026; i, B2 two-celled, *T. rupestre*, BC 802723. j, k, B4 four-celled: j, *T. eriocephalum*, MGC 10900; k, *T. tananicum*, BC 82723. C branched: l, *T. heterophyllum*, ORT 2940. [Scale = 100 μ m (d, h, l); 10 μ m (a-c, e-g, i, j, k).]

state (fig. 3i), reported in *T. chrysotrichum* Lange by MANZANARES & *al.* (1983).

H: Very long inter-twined trichomes, fibrous-like, sometimes coalescent (fig. 3j).

I: Vermiform (lanate) hairs, essentially thick-walled with elongated cells (fig. 3k).

2.3. Branched trichomes

It is known that the same hair type can have

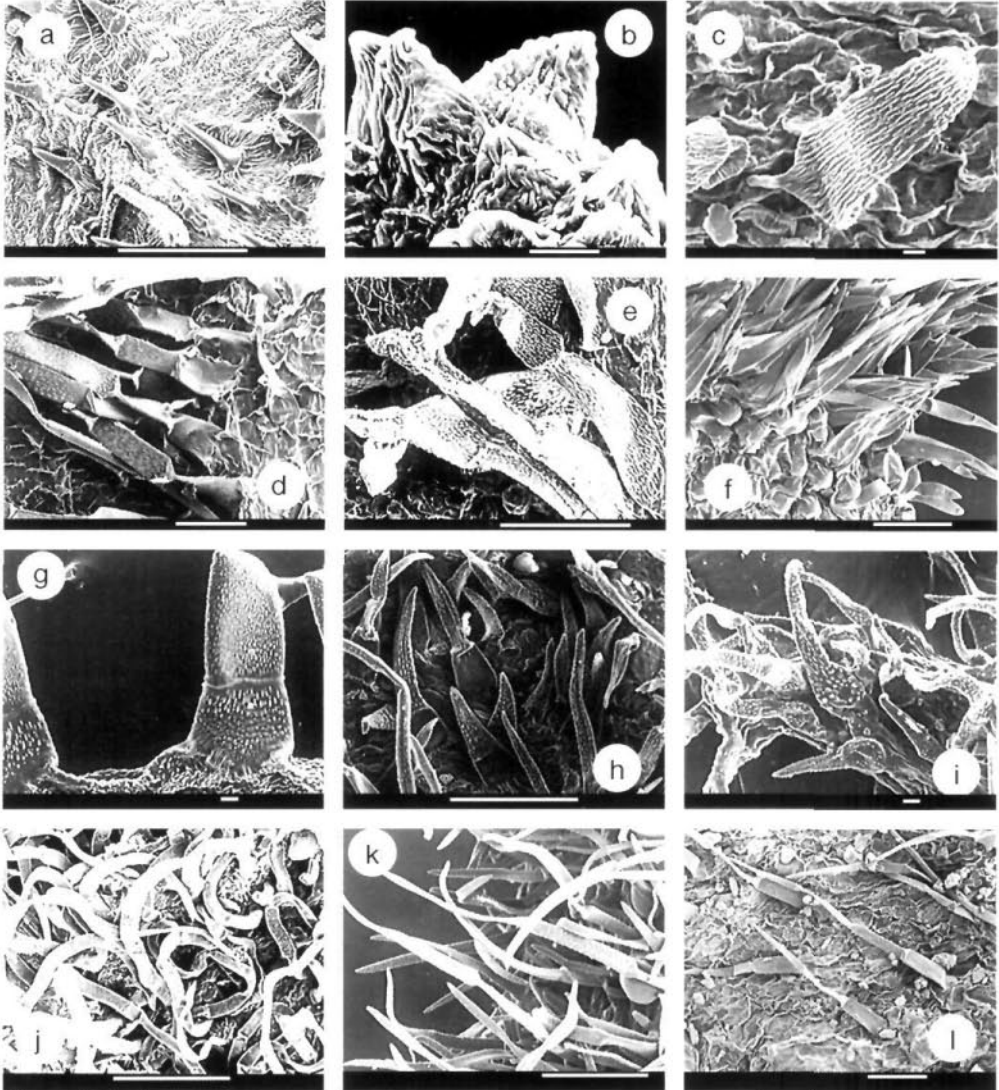


Fig. 2.- SEM non-glandular unbranched trichomes: a, D prick-less-hairs, *Teucrium afrum* subsp. *afrum*, BC 827294. b, c, E-F1 unicellular: b, conic (long cells), *T. maghrebinum*, BC 811317; c, larger with micro-papillae, *T. rupestre*, BC 802723. d-f, F2 multicellular larger, thin-walled: d, *T. fragile*, MGC 42191; e, with crumpled apical cell, *T. decipiens*, BC 82742; f, without micro-papillae, *T. pseudochamaepitys*, MGC 48026. g, F3 short with triangular apical cell, *T. rotundifolium*, MGC 20627. h, i, F4 with elongated apical cell: h, triangular, *T. collincola*, BC 807513; i, crumpled, *T. betonicum*, TFC 13888. j, F5 long, flexuose, *T. maghrebinum*, BC 811317. k, with elongated apical cell, *T. scorodonia* subsp. *scorodonia*, MGC 20986. l, without micro-papillae, *T. spinosum*, BC 814270. [Scale = 100 μ m (a, d-f, h, j-l); 10 μ m (b, c, g, i).]

evolved independently in different lines (METCALFE & CHALK, 1950); for example, the O type corresponds to the branched F4 type and the J type corresponds to the branched G1 type exemplified in *T. heterophyllum* (ANTUNES & *al.*, 1997).

2.3.1. Stellate

J: Few (2-5) thick armed hairs (fig. 3l). Corresponds to branched type of G1.

K: Two-rayed stellate, multiangular biramous hairs with thick-walled and curved

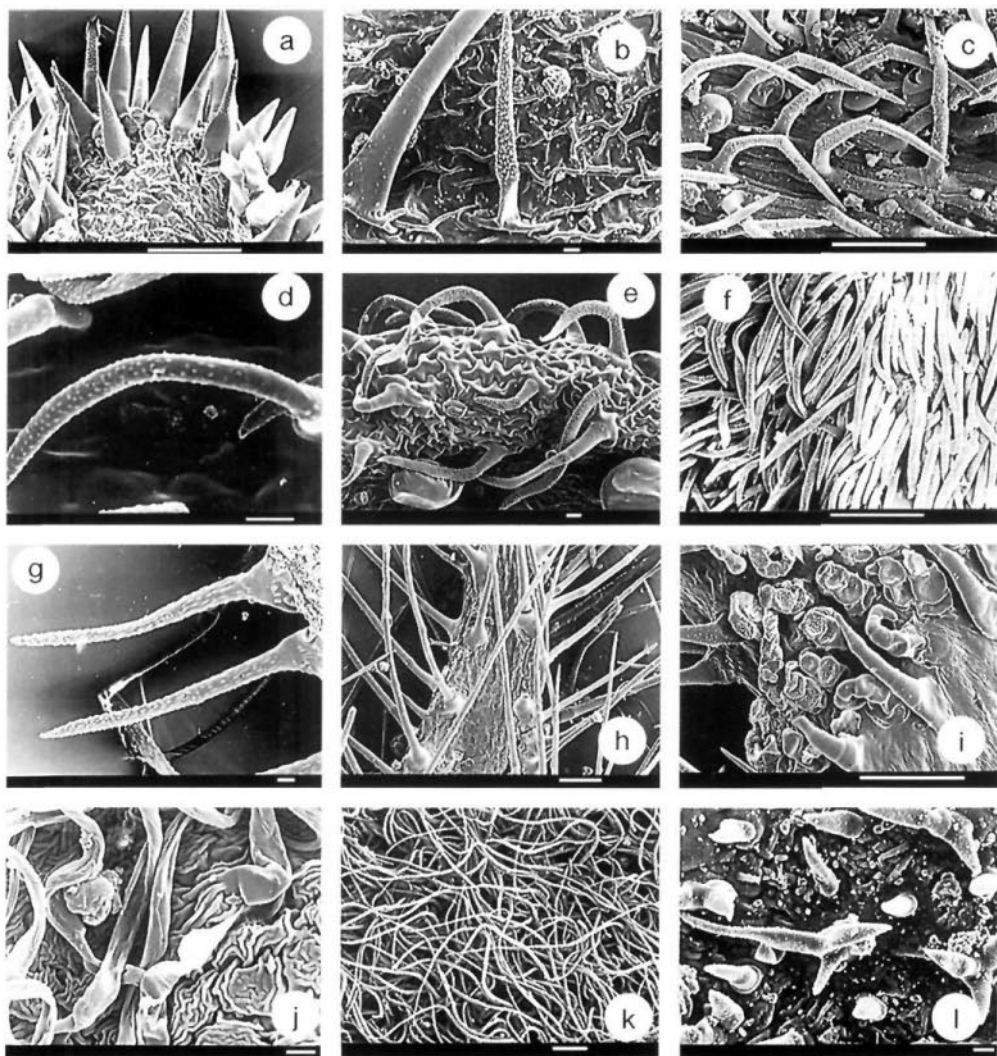


Fig. 3.—SEM non-glandular unbranched and branched trichomes: a, b, G1 conic thick-walled: a, *Teucrium barbarum*, BC 827275; b, *T. magrhebinum*, BC 827175. c-f, G2: c, hooked, *T. chamaedrys* subsp. *chamaedrys*, BC 811281; d, curved, *T. thymifolium*, MGC 46274; e, with falcate apical cell, *T. cincinnatum*, E 49029; f, with elongated apical cell, *T. rivas-martinezii*, MGC 46270. g-i, G3 elongated thick-walled: g, short, *T. eriocephalum*, MGC 10900; h, long, slightly flexuose, *T. compactum*, B 7399; i, in developing state, *T. resupinatum*, BC 827175. j, H inter-twined, *T. fruticans*, MGC 48025. k, I vermiform, *T. yemense*, MGC 37049. l, J branched stellate few-armed, *T. barbarum*, BC 827275. [Scale = 100 μ m (a, c, d, f, h, i, k); 10 μ m (b, e, g, j, l).]

arms (fig. 4a). Also considered as furcate hairs divided into two branches.

L: Stipitate-stellate hairs, thin-walled (fig. 4b).

2.3.2. Dendroid or dendritic

M: Dendritic hairs, with well-developed axis and thick-walled and short acute arms, reported in *T. carthaginense* Lange by MANZANARES & *al.* (1983) (fig. 4c).

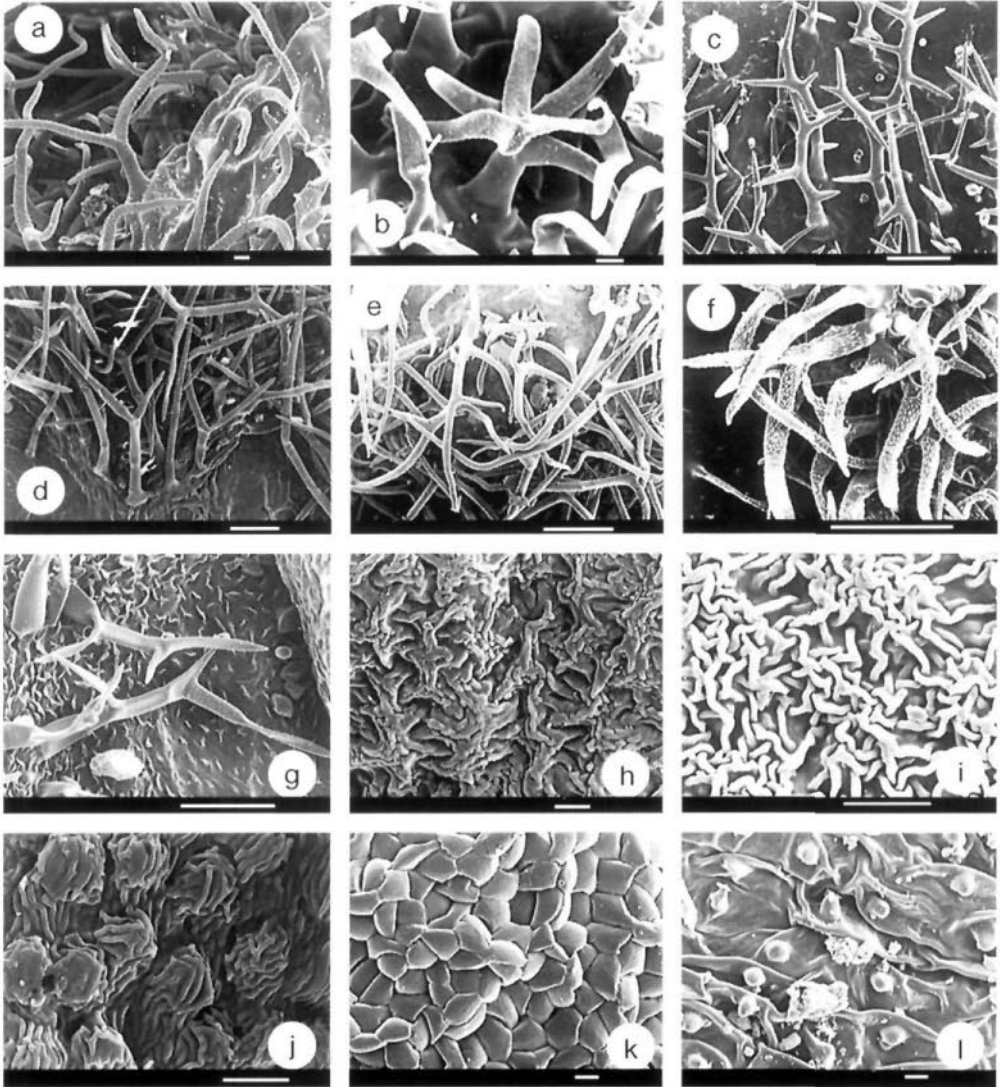


Fig. 4.—SEM non-glandular branched trichomes and epidermal sculpturing: a, K stellate two-rayed, *Teucrium hieronymi*, MGC 46232; b, L stipitate-stellate, *T. capitatum* subsp. *capitatum*, MGC 4374; c, M dendritic, *T. homotrichum*, MGC 38766; d, N long branched; thick-walled, *T. dunense*, MGC 9030; e, with long axis, *T. lusitanicum* subsp. *lusitanicum*, MGC 20571; f, O with crumpled branches, *T. capitatum* subsp. *capitatum*, MGC 4374; g, P with thin-walled branches, *T. homotrichum*, MGC 3876; h-l, ES epidermal sculpturing: h, ES1 with thin ridges, *T. yemense*, MGC 37049; i, ES2 with prominent fields, *T. charidemi*, MGC 6191; j, ES3 with high prominent ridges, *T. dunense*, MGC 9030; k, ES4 with crossed ridges, *T. compactum*, B 7399; l, ES5 with protusion field, *T. abutiloides*, TFC 28401. [Scale = 100 μ m (c-g); 10 μ m (a, b, h-l).]

N: Long branched hairs, with short axis and very long thick-walled arms (fig. 4d) with long axis (fig. 4e).

O: Branched hairs, with short axis, thin-walled slightly crumpled arms densely covered with micro-papillae, correspond to the branched type of F4 (fig. 4f).

P: Elongated branched hairs, with well-developed axis and thin-walled arms, the basal cell without micro-papillae (fig. 4g).

Diagnostic SEM features. The micro-morphological characters observed were the following:

PP: Papillae, protusions from outer walls of epidermal cells in the main part of the trichomes (named micro-papillae) (figs. 2c, 4e).

ES: Epidermal sculpturing of the lobes of the corolla, principally the latero-posterior lobes. Drawings of specialized arrangement of epidermal cells: ES1 (thin ridges in crossing fields; fig. 4h); ES2 (coalescent thin ridges in prominent fields; fig. 4i); ES3 (high prominent ridges; fig. 4j); ES4 (high prominent ridges crossed; fig. 4k); ES5 (thin ridges in protusion field; fig. 4l).

Distribution of trichomes

The morphology and distribution of trichomes in calyx, leaves and pericarp of the nutlets is shown in table 1, while table 2 shows the same characters from the corolla. Nutlet sculpturing is shown in figure 5.

Section *Teucrium*. The five species examined fall into two groups, one formed by *T. fruticans* L. and *T. brevifolium* Schreb. with H trichomes in the calyx and leaves and another group formed by *T. chardonianum* Maire & Wilczek, *T. pseudochamaepitys* L. and *T. orientale* L. subsp. *taylori*. (Boiss.) Rech. with mainly F4 and F5 trichomes in the calyx and leaves. This is the only section studied with no glandular trichomes in the corolla.

T. orientale subsp. *taylori* show hairy nutlets with sessile glandular hairs and reticulate ridges (fig. 5a).

Section *Teucriopsis* Benth. This section is

very heterogeneous. In *T. betonicum* L'Hér. the main trichome type is F5. *T. heterophyllum* show a homogeneous indumentum of J type branched trichome in the calyx and leaves and, of great interest, C 2(3)-armed trichomes in the inner margin of calyx lobes. Sometimes, the many-branched J type can be similar in the shape to the dendroid type (M). *T. abutiloides* L'Hér., it is the only species studied which shows a predominance of glandular hairs over all structures this results is according to ANTUNES & al. (1995).

The nutlets of *T. heterophyllum* (fig. 5b) show reticulate ridges and the distal part is densely covered by 3(4)-celled long branched thin-walled P type trichomes. This is the only species analysed in the genus in which the branched trichomes are present in the nutlets while *T. betonicum* (fig. 5c) is the only species examined with clavate glandular trichomes A1 in the nutlet surface.

Section *Chamaedrys* (Mill.) Schreb. The species studied in sect. *Chamaedrys* are characterized by the high degree of homogeneity of trichome type, structure and distribution.

The principal trichome type G2, covers all structures. In *T. barbarum*, the annulus of the inner side of the calyx is formed of branched P type trichome, as occurs in nowhere else in the genus, *T. barbarum* represents an exception in relation to the other species with J and G1 on the leaves.

The surface of the nutlets in *T. barbarum* shows deep fields bordered with thick ridges, more or less completely covered by thin-walled 2(3)-celled F5 trichomes and B2 glandular trichomes, while *T. fragile* Boiss. and *T. webbium* Boiss. (fig. 5d) display bordered fields, thin ridges and presence of B2.

Section *Scorodonia* (Mill.) Schreb. In this section, trichome type varies between species and within the different structures of the same species. The horizontal position of the broad upper lobe of the calyx, leads to an inversion of the indumentum, so that the previous lobes show the same trichomes as the external side of the calyx although in greater abundance.

T. afrum (Emb. & Maire) Pau & Font Quer

subsp. *afrum* (fig. 5e) possesses nutlets without glandular trichomes and tends to have a smooth surface.

Section *Spinularia* Boiss. Trichome type and distribution structure vary between species and within structures. Only *T. resu-*

pinatum Desf. and *T. maghrebinum* Greuter & Burdet show similar distribution of the trichomes. And only *T. decipiens* has F5 in the annulus of the inner side of the calyx like *T. betonicum*. In these species, on the base of mucron or spine of the lobe, the developing

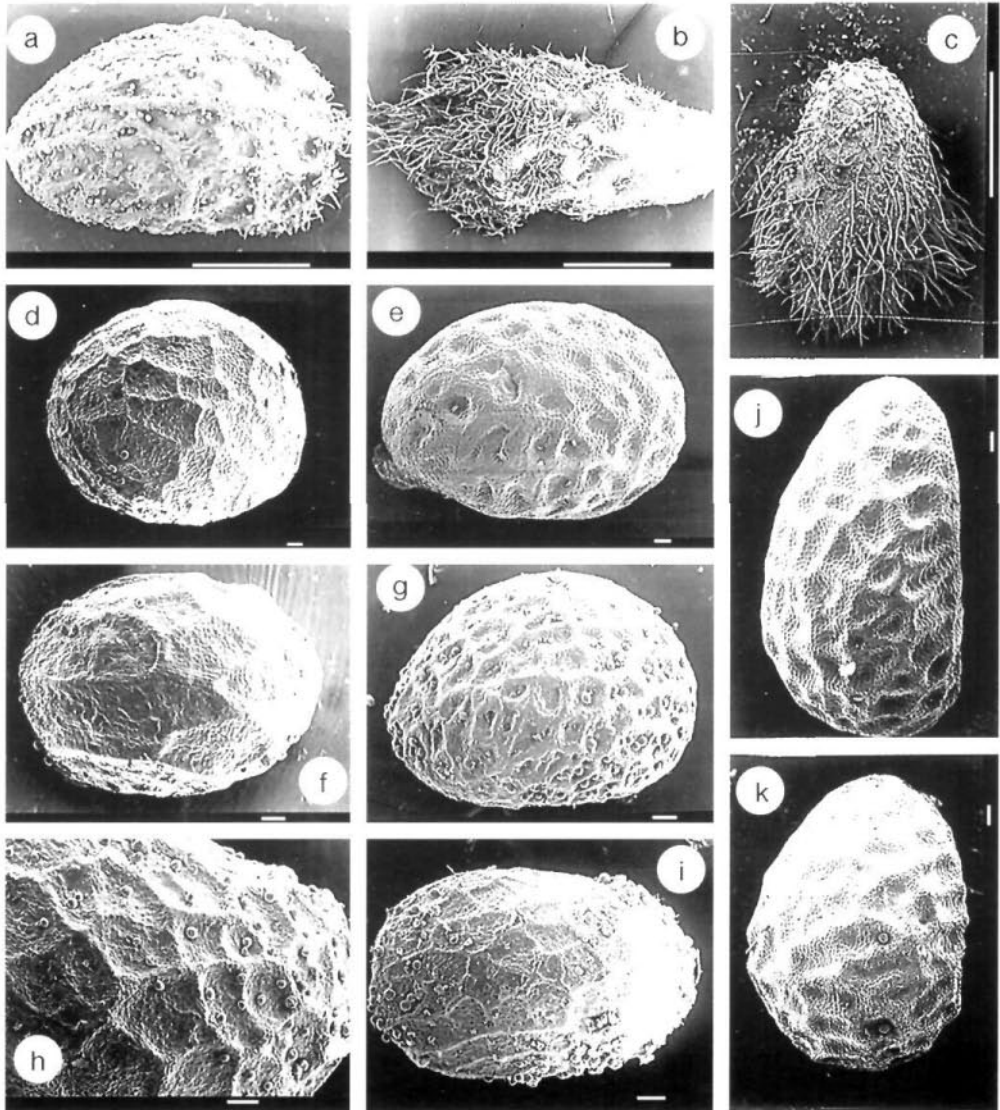


Fig. 5.—SEM nutlets surface: a, *Teucrium orientale* subsp. *taylori*, G 8347/33; b, *T. heterophyllum*, ORT 2940; c, *T. betonicum*, TFC 13888; d, *T. webbium*, MGC 8180; e, *T. afrum* subsp. *afrum*, BC 827294; f, *T. melissoides*, G 8347/18; g, *T. collincola*, BC 827186; h, *T. rupestre*, BC 802723; i, *T. odontites*, G 8347/21; j, *T. persicum*, G 8347/73; k, *T. yemense*, MGC 37049. [Scale = 1 mm (a-c); 100 μ m (d-k).]

G3 hairs observed may be regarded as playing a role in strengthening the spine (fig. 4h).

Two corolla types are observed. A resupinate corolla in *T. resupinatum*, *T. decipiens* and *T. maghrebinum* with the patches of F2 in the and a corolla without resupination is *T. botrys* L., which shows a reduced patch. In most of the species, the base of the long corolla tube is densely covered F2 hairs, which is an exception in the genus.

Section *Scordium* (Mill.) Rchb. The two species studied show the same type of non-glandular F5 type trichomes covering the outer side of the calyx and leaves, although *T. melissoides* Boiss. shows thick-walled G2 type hairs in the lobes of the calyx.

The nutlets of *T. melissoides* (fig. 5f) show sessile glandular B4 trichomes and tend to have a smooth surface.

Section *Stachyobotrys* Benth. A great diversity of trichomes was observed in the two species studied. F4, G1 and B1 were found on the outer side of the calyx in both species and F4, B1 and A2 with G1 on the leaves of *T. collincola* Greuter & Burdet. In this species too, G3 in a developing state is seen on the base of mucro or spine of the lobes, as in sect. *Spinularia*.

T. collincola shows nutlets with reticulate ridges and sessile glandular hairs (fig. 5g).

Section *Isotriodon* Boiss. The main non-glandular trichomes covering all structures are of the G3 type.

T. rupestre Coss. & Balansa (fig. 5h) and *T. odontites* Boiss. (fig. 5i) have no reticulated nutlets with the undulating fields and sessile glandular trichomes distributed on the surface and one or more in the centre of the sunken fields. *T. persicum* Boiss. (fig. 5j) has the surrounding fields and thick ridges quite deep in these three species. The sculpturing of sect. *Isotriodon* is similar to that of sect. *Strachyobotrys* although the ridges in the latter are thick and deep. The presence of B2 in *T. rupestre* is of interest.

Section *Polium* (Mill.) Schreb. Trichome type, structure and distribution show high heterogeneity in sect. *Polium*. In subsect. *Polium* thick-walled trichomes are the

predominant type on the calyx, while stipitate-stellate thin-walled types predominate on leaves. The presence of G3 or F5 is more frequent in hermaphrodite plants than their cosexual counterpart.

T. homotrichum (Font Quer) Rivas Mart. and *T. bicolorum* Pau have M hairs. Dendritic trichomes type are present in some species from sect. *Polium* subsect. *Polium* from N Africa as *T. aureum* subsp. *gabesianum* S. Puech, *T. nablii* s. Puech (PUECH, 1985, 1990) and *T. mideltense* (Batt.) Maire, endemic species of the high Moroccan Atlas (EL OUALIDI & al., 1996). In the gynodioecious species, the bisexual plants show more dense tufts of F5 trichomes in the entrance of the corolla tube than male-sterile ones.

The nutlets have no hairs and their sculpturing shows reticulated fields in contact with the inside part of the calyx.

In the species of subsect. *Rotundifolia* Cohen ex Valdés Berm. & Sánchez Crespo except in *T. pyrenaicum* L. subsp. *pyrenaicum* G3 type 6(11)-celled are the most common hairs on the outer side of the calyx and leaves, generally mixed with A2 of proportional length as occurs in sect. *Isotriodon*, except in the case of *T. yemensis* Deflers and *T. musimonum* Humbert, where the leaves and calyx are covered by vermiform trichomes. *T. rivas-martinezii* Alcaraz & al., *T. cincinnatum* Maire, *T. thymifolium* Schreb. and *T. sokotranum* Vierh. are the only species from this subsection with G2 type hairs in the calyx and leaves, as occur in the species of sect. *Chamaedrys*. The leaves of *T. thymifolium* and *T. sokotranum* also show the same G2 type with apical cells elongated on the adaxial side and thick-walled vermiform trichomes on the abaxial side.

The presence of the sessile glandular trichomes in the nutlets of *T. yemensis* (fig. 5k) and the presence of G2 trichomes in *T. thymifolium* represents a rare character within sect. *Polium*.

In the species studied from subsect. *Simplicipilosa* S. Puech, only *T. charidemi* Sandwith shows vermiform trichomes. *T. leucocladum* Boiss. and *T. charidemi* has slightly reticulated nutlets and bordered fields

TABLE 1
TRICHOME DISTRIBUTION ON THE CALYX (OUTER, INNER SIDE AND LOBES), ON THE LEAF (ADAXIAL AND ABAXIAL SIDE) AND ON THE NUTLET SURFACE OF THE *TEUCRIUM* SSP. INVESTIGATED

[Symbols: a, cells with transverse walls; b, cells without transverse walls; c, without micro-papillae; d, trichome composed of two cells; e, trichome composed of three cells; f, trichome composed of (3)5 cells; g, trichome with more than five cells; +, surface completely covered; ?, presence uncertain; TA, trichomes absent; ns, no investigated]

Sect. / Subsect.	calyx outer side	calyx inner side	calyx inner annulus	calyx upper lobe	calyx lateral lobes	calyx lower lobes	leaves adaxial side	leaves abaxial side	nutlets surface
<i>Teucrium</i>									
BREVI	H	TA	TA	H	H	H	H+B1?	H+A1	ns
RDONI	F4fa	F4fa	TA	TA	TA	TA	F4eb	F4eb	ns
MAEPI	A2e F5g D	TA	TA	TA	TA	TA	F5f A1 D	B1+ F5f	F1 B1
FRUTI	H	TA	TA	H	H	H	H+B1?	H+B1	ns
ORIEI	F4 A1	TA	TA	E	E	E	F4 B1 A2d	B1 A1 F4	F5 B1
<i>Teucriopsis</i>									
ABUTI	A2g+	A1 A2f	TA	A2e	A2e+	A2e+	A1 E A2g	A2e B1 E	ns
BETON	F5fb	TA	F5c	F4	F4	F4	F5f B1 D	F5f B1	F5 B1 A2
HETER	Jc	Cc	TA	Jc	Jc	Jc	Jc	Jc B1	P
<i>Chamaedrys</i>									
CHAMA	G2 B1 A1	G3f A1	TA	G2 A1	G2 A1	G2 A1	G2	G2 B1	ns
BARBA	G1 B1 A2	TA	Pc A1	A2e G1	A2e G1	A2e G1	J G1	J B1+	F2 B2
FRAGI	G1 G2 A2e B1	TA	G3fc A2	G2 A1	G2 A1	G2 A1	G2 G3f A2e	A2e B1 G3f D	B2
WEBBI	G2 A1 B1	A2e	G3fc A2e	G2	G2	G2	G2	G2 A1 B1	B2
<i>Scorodonia</i>									
SCORO	D E A1	E A2e	TA	TA	TA	TA	F5e B+	B1+	ns
PSESC	D B1 A1 E	TA	G3 D B1 A1	A1 D F5	D A1 F5	D A1 F5	G1+ F5 B2	G1+ F5 B2	ns
AFRUM	TA	D	G3fc D B1? A1	A1	A1	A1	A1+ G3f B1	G F5 G3f B1	TA
RIPHA	TA	D	G3gc D E	A1	A1	A1	TA	B1	ns
RUBIF	G2 B1	D	G3fc A1	G2	A1	A1	A1	G2	ns
<i>Stachybotrys</i>									
COLLI	F4+ G1 B1 G3 A2e	D	G3fc A1+ B1	A1 A2 B1 E	D G3f	A2 D G3f	F4g G1 A2 B1	G1 F4g A2 A1 B1	B1
BRACT	G1 F4 D B1	E	G3fc A2f	D A2f G3f E	D G3f	D A2f G3f E	F4g A2g	F4g A2g B1	ns
<i>Scordium</i>									
MELIS	F5 A1 B1	A1	G3fc A1	G2	G2	G2	TA	B1+ F5	B4
RDIUM	F5f B1?	TA	TA	TA	TA	TA	F5e A2e	F5 B1	ns
<i>Spinularia</i>									
SPINO	E A2e B1	A1	G3fc A2	A2+	A2	A2	F5f B1	B1+	ns
BOTRY	A2e F5 D	G3g A2 B1	G3fc B1	A1 D	G3f A2b	G3f A2b	F5 B1+ A2e+	TA	ns

RESUP	A2g G3 B1	TA	G3c A2e	G3 A1	G3 A1	G3 A1	G3 A1	G3 A1	G3 A1	F5f B1	ns
MAGRE	A2e G3f B1	A2 D	TA	G3f A2f	G3f A2f	G3f A2f	G3f A2f	G3f A2f	G3f A2f	F5f G1 A2e	ns
DECIP	F5g A2f	F5g A2e	F5dc	A2f F5f	A2f F5f	A2f F5f	A2f F5f	A2f F5f	A2f F5f	F5e A1 G1	ns
<i>Isotriodon</i>											
RUPES	G3g	D	TA	D G3g A2e	D G3g A2e	D G3g A2e	D G3g A2e	D G3g A2e	D G3g A2e	B+ K7	B2+
TANAN	G3g B1	TA	TA	G3g A2e+	G3g A2e	G3g A2e	G3g A2e	G3g A2e	G3g A2e	A2e B4+	ns
PERSI	G3g A2e B1	AI	TA	TA	TA	TA	TA	TA	TA	G3f B2+ A2+	TA
ODONT	G3g A2e F4 B	A2e	TA	G3f A2e	G3f A2e	G3f A2e	G3f A2e	G3f A2e	G3f A2e	F5f B1+ A1	B1+
<i>Potium / Potium</i>											
DESCA	G3f B1 A1 A2e	E A2f	TA	G3f	G3f	G3f	G3f	G3f	G3f	A2f B1 G3f N	TA
HOMOT	M+ B1?	M+ A1	TA	M	M	M	M	M	M	M A1 P B1	TA
DUNEN	N B1	F5 N A1	TA	F5f	F5f	F5f	F5f	F5f	F5f	N B1	TA
BICOL	M B1? A1	A1 K	TA	M	M	M	M	M	M	M B1 A2d	TA
LUSIT	N4 B1	EN K	TA	N	N	N	N	N	N	A2d Lg B4	TA
CAPIT	L B1?	LE A1	TA	L O	L O	L O	L O	L O	L O	F5 G1 L B1	TA
GRACI	L B1	AI	TA	F5f	F5f	F5f	F5f	F5f	F5f	K L A1 B1	TA
MURCI	N B1?	A1+ G3f	TA	N A1	N A1	N A1	N A1	N A1	N A1	K Lg B1+	TA
HIERO	N B?	A1 G3f	TA	G3f A1	G3f A1	G3f A1	G3f A1	G3f A1	G3f A1	K Lg G3f B+	TA
<i>Potium / Rotundifolia</i>											
FREYN	G2 A1 B1	A2e	TA	G2	G2	G2	G2	G2	G2	G2 B1	TA
SOKOT	G3f A2g B1	TA	TA	G3g	G3g	G3g	G3g	G3g	G3g	G2+	TA
THYMI	G2 B1	TA	TA	TA	TA	TA	TA	TA	TA	G2 B2	G2+
ROTUN	G3g A2e B1	G3g A2 B1	TA	G3g	G3g	G3g	G3g	G3g	G3g	F5 B1 A2e	TA
PYREN	A2e D B1	D	TA	G3f A2 G1	G3f A2 G1	G3f A2 G1	G3f A2 G1	G3f A2 G1	G3f A2 G1	A2 F5f B1?	TA
MUSIM	I+ A2e B1	D	TA	I+	I+	I+	I+	I+	I+	I+ B1	TA
HUAZ	G3g B1	A2	TA	G3g	G3g	G3g	G3g	G3g	G3g	G3g B1	TA
CYPRI	G3g A2f B1	A2e D E	TA	G3g+	G3g+	G3g+	G3g+	G3g+	G3g+	G3f A2e B1	TA
COMPA	G3e A2e B1? D	A2e	TA	G3e	G3e	G3e	G3e	G3e	G3e	G3e A2e B1	TA
YEMEN	I+ B1+	E	TA	I+	I+	I+	I+	I+	I+	I+ B1	B1
CINCI	G2 B1	G2 A2e	TA	G2 A2e	G2 A2e	G2 A2e	G2 A2e	G2 A2e	G2 A2e	B1 A1 A2d G3	TA
RIVAS	A2e B1?	G2 D	TA	G2 A2e	G2 A2e	G2 A2e	G2 A2e	G2 A2e	G2 A2e	TA	G2
STOCK	G3f A2e B1	E A2e	TA	G3f	G3f	G3f	G3f	G3f	G3f	G3f B2 A2	TA
<i>Potium / Simpliciflora</i>											
ERIOC	G3g B1	E A2e	TA	G3g A2e	G3g A2e	G3g A2e	G3g A2e	G3g A2e	G3g A2e	A1 B4	TA
LEUCO	F5g+ A1	G3g	TA	F5g	F5g	F5g	F5g	F5g	F5g	F5g+ B1?	TA
RIDEM	I* F5 B1?	E A2e B1	TA	I+ A2e	I+ A2e	I+ A2e	I+ A2e	I+ A2e	I+ A2e	A1 B2	TA
<i>Potium / Pumilum</i>											
CAROL	G2 B1?	A1 E	TA	G2	G2	G2	G2	G2	G2	G2 B1	TA

TABLE 2
TRICHOME DISTRIBUTION ON THE COROLLA (LOBES AND ADAXIAL SIDE OF LOWER LIP, CLOSED COROLLA TUBE MECHANISMS AND STAMEN BASE) OF THE *TEUCRIUM* SSP. INVESTIGATED
[Symbols as in Table 1 except for: (two)-, two rows of trichomes; (three)-, three rows of trichomes]

Sect. / Subsect.	anterior AL	Lower lip laterals LL	lobes latero-posteriors LPL	Adaxial base AL patch	side of central zone patch	lower lip base AL nectar	central zone guides	Corolla closed tuft	tube by annulus	Base stamen
<i>Teucrium</i>										
BREVI	ES5	ES5	ES5						F2c	F2
RDONI	E	E F4f	F4f						F2c	F5
MAEPI	E	E	E						F2c	F2
FRUTI	ES5	ES5	ES5						F2c	F1
ORIEN	ES5	ES5	ES5						F2c	F2
<i>Teucriopsis</i>										
ABUTI	ES5	ES5	ES5 A2f	A2fE	F2d					F2
BETON	TA	TA	TA	A2fE	F5f					F5
HETER	TA	TA	TA	A2fE						TA
<i>Chamaedrys</i>										
CHAMA	E	E	A1 G1		E	twoF2f	twoF2d			E
BARBA	E	TA	A1 G1		F2d E	threeE	threeE			E
FRAGI	E	A1	A1 G3e		F2d E	twoF2g	twoF2d			E
TWEB	E	A1	G1 A1 G3e		E	twoF2d	twoF2d			E
<i>Scorodonia</i>										
SCORO	A1	A2e	TA	E						E
PESC	A1 E	A1	ES2		E	twoF2e	threeE			TA
AFRUM	TA	TA	TA		E					TA
RIPHA	TA	A1 G1	G1	E						TA
RUBIF	A1	A1	G1	E						TA
<i>Stachybotrys</i>										
COLLI	TA	TA	TA	A1	TA					TA
BRACT	E	E	E+	twoA1 E	A1 F4g					TA
<i>Scordium</i>										
MELIS	E	A1 F2	G3e A1			twoF2g	twoF2g			TA
RDJUM	E	E	E G3e			twoF2g	twoF2g			TA

with small and very thin ridges. This sculpturing type is rare in sect. *Polium*.

In subsect. *Pumilum* (Lázaro Ibiza) Rivas Mart., *T. carolipau* Vicioso ex Pau has mainly G2 trichomes over all vegetative structures as do *T. rivas-martinezii*, *T. thymifolium* and *T. cincinnatum*.

DISCUSSION

For the standard classification of trichome type in *Teucrium*, differentiation into thin and thick-walled provides an excellent taxonomic help. Trichome type, distribution and cover vary widely in the different sections of the genus and in the different structures of the same individual plant, as occurs in others *Lamiaceae* genera (HUSAIN, 1983; DOROSZENKO, 1986; HUSAIN & *al.*, 1990). Variations exist between the outer and inner side of the calyx and between the adaxial and abaxial surfaces of the leaves, and, within the same individual plant, the cover is always more diverse and dense on the outer side of the calyx and abaxial surface of the leaves.

The micro-papillae are irregularly distributed over the epidermal cell of the trichomes as slight ridges or globose shapes. They are always present on all non-glandular hairs in the non-functional trichomes.

The diversity observed in the calyx structures is correlated with zygomorphy; strictly symmetrical or bilabiate calyces showing lesser indumentum variability, while strongly zygomorphic calyces show high variability.

In the adaxial surface of the lower lip and corolla tube, trichomes type and their distribution are extremely homogeneous in all species of the same section and provide a additional character at sectional and sub-sectional level. A specialised arrangement of the epidermal cells on the inner side of the lateral and latero-posterior lobes of the corolla is rare in the genus, and has only been observed in the species with well-developed lobes from sects. *Polium* and *Scorodonia*, as has been reported in *Melissa* L. genus (FAHN, 1979). It is assumed that they play a role in the visual attraction of the visiting insects.

Glandular and non-glandular trichomes from the same plant structure always belong to only one group, thin or thick-walled, although the clavate glandular trichomes of the floral specializations are always of the thin-walled type.

The distribution of the glandular trichomes is clearly correlated with their role in pollination. A1 type is frequent in the axils and upper part of the inner side of the calyx lobes and in the apical part of the corolla lobes. B1 are totally absent from the adaxial side of the lower lip of the corolla, but appear on the outer side of the calyx and less frequently on the inner side from the insertion of the annulus of hairs to the margin of lobes. B2 and B4 are only observed on the outlet surface and leaf surface (adaxial and abaxial side, but more frequently on the latter) but never on the calyx structures, and are most frequent in chasmophyte and paleo-endemic species. B4 is the most common type in *Scrophulariales* and probably represents an ancestral condition in *Lamiaceae* (CANTINO, 1990). Branched glandular hairs are rare in the genus, only being found in *T. heterophyllum*. Glandular trichomes have a taxonomic value at specific and a subspecific level (MRÁZ, 1998) and their presence or absence in the corolla structures can be used as a phylogenetic character.

The presence of branched hairs in vegetative structures has a high systematic value, since they are only universally present in the species of sect. *Polium* subsect. *Polium*. They are also present in one rare endemic species of sect. *Chamaedrys* from Morocco, *T. barbarum* and another isolated endemic species of the Canary Islands, *T. heterophyllum*. The branched hairs in *T. barbarum* and *T. heterophyllum* are both type J, a type not present in sect. *Polium*.

In sect. *Polium* subsect. *Polium*, the branched hairs are generally mixed with simple hairs on the leaves and less frequently on the outer side of calyx. RYDING (1998), comments that the species related to *T. polium* L. group from the Arabian Peninsula show a clear mixture of the simple and branched hairs, which reflects our findings in *T. des-*

caisnei C. Presl. The presence or absence of branched hairs in the genus has an important infrageneric phylogenetic significance.

Simple thin-walled trichomes are universally present in the genus, forming part of the floral features for pollination, such as attraction vectors or nectar guides, including a closed gullet mechanism, except in sect. *Polium* subsect. *Polium* and subsect. *Simplicipilosa*. F2 hairs form part of the closed gullet mechanism of sect. *Teucrium* and the nectar guides in sects. *Chamaedrys*, *Scordium*, *Isotriodon* and sect. *Polium* subsect. *Rotundifolia*. F5 and G3 form the trichome tuft of the closed gullet mechanism in sect. *Polium* subsect. *Polium* and subsect. *Simplicipilosa*.

Thin-walled trichomes are the most widespread type on the abaxial side of leaves, occurring commonly in every section except sect. *Chamaedrys* and only occasionally in sect. *Polium* subsect. *Polium*. It is also worth noting that thin-walled trichomes on the adaxial side of the lower lip of the corolla and the abaxial side of the leaves exhibit less intra-sectional variation than other trichome types and are therefore of particular value in assessing intra-generic phylogenetic relationships. F5 type trichomes are present in *Calamintha*, *Clinopodium*, *Nepeta* and are widely distributed through the sections studied except sect. *Chamaedrys* and less frequent, in sects. *Isotriodon* and *Polium* subsect. *Polium*.

The basic type simple thick-walled hairs (G1 and G2) are the only type present in all the species from sect. *Chamaedrys* and are completely absent in sect. *Teucriopsis* and *Teucrium*. This type provides a good additional taxonomic marker for delimiting the sect. *Chamaedrys*. The widespread presence of G type trichomes (G1, G2 and G3) in all the sections except in sects. *Teucriopsis* and *Teucrium* may have some phylogenetic significance in *Teucrium*. This basic type also formed the annulus of hairs on the inner side of the calyx in all the species studied except *T. betonicum* and *T. barbarum*.

Nutlets with trichomes represent a primitive character in *Teucrium* according (MARÍN & al., 1994), showing little infra-

generic variation. Trichomes are universally present in sects. *Teucrium* and *Teucriopsis* and in some European species of sect. *Chamaedrys* and only in some species from sect. *Polium* subsect. *Rotundifolia* from N Africa and SE of Spain. It can therefore reasonably be considered as a character of phylogenetic value at an infrageneric level.

The systematic relationship between sects. *Chamaedrys* and *Teucrium* established by MARÍN & al. (1994) on the basis of the presence of the hairy nutlets in the *T. marum* group, is confirmed by the results obtained in this study of *T. barbarum*, which has a combination of the taxonomic characters of the sect. *Teucrium*, such as the symmetrical campanulate calyx and *T. creticum* L. inflorescence type (NAVARRO & EL OUALIDI, 1997). In accordance with the results of MARÍN & al. (1994), *T. barbarum* of sect. *Chamaedrys* belongs to the group of species of *T. marum* with trichomes on the nutlets, while *T. fragile* and *T. webbium* belong to the *T. flavum* L. group. The presence of glandular trichomes in the Mediterranean chasmophytic of sect. *Isotriodon*, *T. rupes-tre* and *T. odontites*, and the presence of glandular trichomes in *T. yemense* and non-glandular trichomes in *T. thymifolium* of sect. *Polium* subsect. *Rotundifolia*, established, in accordance with MARÍN & al. (1994), a relationship between these sections and sect. *Chamaedrys*.

BENTHAM (1835) considered that sects. *Teucrium*, *Teucriopsis* and *Pycnobotrys* are the most distinct of the genus. MARÍN & al. (1994) and HARBONNE & al. (1986) suggest that sect. *Teucrium* is totally separate from the other sections of the genus. Our investigation of micro-morphological characters makes us agree with these authors and also reveals the distinctness of the sect. *Polium* subsect. *Polium*, sect. *Chamaedrys* and sect. *Teucriopsis* from the other sections.

Sect. *Polium* is the most heterogeneous section as regards trichome type and distribution. Branched trichomes are the only non-glandular trichomes present in the subsect. *Polium*. Despite this, the morphological diversity is high and acts as

an excellent taxonomic marker at different taxonomic levels. KÄSTNER (1989) combined the sect. *Polium* under the sect. *Chamaedrys*, but our results agree with Bentham's delimitations of the sections.

Sect. *Teucriopsis* is a polymorphic section. BENTHAM (1835) included two species, *T. hetrophyllum*, described under the genus *Polyodendron* Noë and *T. betonicum*. KÄSTNER (1989), added *T. abutiloides*, a species considered by Bentham under sect. *Pycnobotrys*. The affinity between *T. betonicum* and the species of sect. *Scorodonia* has been mentioned by several authors (BENTHAM, 1848; LINK, 1829). Our results reflect the affinity between *T. abutiloides* and the species of sect. *Scorodonia* studied, based on the similar distribution patterns of the glandular trichomes and similar patterns in the nutlets sculpturing.

New infrageneric relationships are demonstrated between sect. *Chamaedrys* and sect. *Polium* subsect. *Rotundifolia*, based on the presence of the same type G2 trichome in *T. freynii*, *T. thymifolium*, *T. cincinnatum* and *T. rivas-martinezii*. The taxonomic relationship between the *T. sokotranum* and *T. buxifolium* Schreb. groups from the Iberian Peninsula and between *T. hijazicum* Hedge & King and *T. cyprium* Boiss. subsp. *cyprium* mentioned by KING (1988) are confirmed by our study of trichome micro-morphology, while a new taxonomic affinity is observed between *T. yemense* and *T. compactum* Clem. ex Lag., on the basis of trichome micro-morphology and others morphological characters: inflated calyx, elongated spike-like inflorescence and growth habits.

The varied combination of taxonomic characters in sect. *Polium*, according to NAVARRO (1995), and the observation of trichome micro-morphology strongly suggest taxonomic affinities between *T. cyprium* subsp. *cyprium*, *T. hijazicum*, *T. stocksianum* Boiss. subsp. *stocksianum*, *T. yemense* and *T. sokotranum* with the eastern Mediterranean species of the sect. *Polium* subsect. *Rotundifolia*. In the case of *T. leucocladum*, a species similar to those of the Mediterranean region (KING, 1988) there are close affinities

to the Iberian species from sect. *Polium* subsect. *Simplicipilosa*.

A study of trichome micro-morphology permits a better understanding of the relationships between the sections investigated. In most cases, character combinations could easily be used as a means of taxonomic identification at different infra-generic levels. The classification of trichome micro-morphology adopted here considerably enhances the value of this character within the genus and makes it possible to establish systematic relationships with others genera of Lamiaceae or related families. Variation in the distribution of trichome type in the different sections are of phylogenetic use. This study also supports Bentham's system with the additions made by BOISSIER (1879).

ACKNOWLEDGMENTS

We would like to express our special thanks to I. Hedge (Royal Botanic Garden, Edinburgh, UK) for his constructive remarks on the manuscript and the loan of specimen from E. We acknowledge P. Cantino (Ohio University, USA) for his comments. Thanks are due to A. Charpin (Conservatoire et Jardin Botanique de la Ville de Genève) for the loan of specimens from G. The help provided by J.M. Montserrat (Instituto Botánico de Barcelona, Spain) in the study of BC specimens is gratefully appreciated. Thanks also to Mr. Gayo and Mr. Canca for their technical assistance in SEM and the Directors of the following herbaria: B, MA, MPU, ORT, RAB and TFC.

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APPENDIX

Alphabetical list of the codes and complete names of the *Teucrium* investigated and their most frequent synonyms. Abbreviated localities and collection data for voucher specimens are given. Nomenclature follows KING (1988), NAVARRO (1995), NAVARRO & EL OUALIDI (1997) and RYDING (1997).

- ABUTI *Teucrium abutiloides* L'Hér.: Madeira, Pico Ruivo, TFC 28401.
- AFRUM *T. afrum* (Emb. & Maire) Pau & Font Quer subsp. *afrum* (*T. salviastrum* subsp. *afrum*): Morocco, Chefchaouen, BC 827294; Spain, Málaga, MGC 22978.
- BARBA *T. barbarum* Jahand. & Maire: Morocco, Fès, BC 827275; Khenifra, Maire 314, MPU.
- BETON *T. betonum* L'Hér.: Madeira, San Jorge, TFC 13888; Eiva do Serrado, TFC 28354.
- BICOL *T. bicolorum* Sennen: Spain, Jaén, MGC 39850.
- BOTRY *T. botrys* L.: Morocco, Tazaut, BC 811319; Spain, Huesca, MGC 37966.
- BRACT *T. bracteatum* Desf.: Morocco, Xauen, BC 47399.
- BREVI *T. brevifolium* Schreb.: Morocco, Fés, SEV 827231; Lybia, Maire & Weiller 1263, MPU.
- CAPIT *T. capitatum* L. subsp. *capitatum*: Spain, Madrid, MGC 4374.
- CAROL *T. carolipau* Vicioso ex Pau subsp. *carolipau*: Spain, Alicante, MGC 6207.
- CHAMA *T. chamaedrys* L. subsp. *chamaedrys*: Morocco, Tazaout, BC 827186; Aknoul, BC 827285; Spain, Soria, MGC 2850.
- CINCI *T. cincinnatum* Maire: Morocco, Ouarzazate, Davis 49029, E; Morocco, Jarro, Emberger 43627, RAB.
- COLLI *T. collincola* Greuter & Burdet (*T. collinum*): Morocco, Agadir, BC 807513; Safi, BC 807549.
- COMPA *T. compactum* Clem. ex Lag.: Tunisia, Matmata, Vogt 13136 & Oberprieler 7441(B); Spain, Almería, MGC 39595.
- CYPRI *T. cyprum* Boiss. subsp. *cyprum*: Cyprus, Röthlisberger, G 834715.
- DECIP *T. decipiens* Coss. & Balansa: Morocco, Zerhoum, BC 82742; Fés, BC 827221.
- DESCA *T. descasnei* C. Presl. (*T. polium* var. *pilosum*): Arabia, Jeddah, G 8437/101.
- DUNEN *T. dunense* Sennen: Spain, Almería, MGC 9030.
- ERIOC *T. eriocephalum* Willk.: Spain, Málaga, MGC 10900.
- FRAGI *T. fragile* Boiss.: Spain, Granada, MGC 42191.
- FREYN *T. freynii* Willk.: Spain, Murcia, MGC 46532-MA 25676.
- FRUTI *T. fruticans* L.: Morocco, Tizi Ousli, BC 811322; Tazzeke, MGC 48025; Spain, Málaga, MGC 45375.
- GRACI *T. capitatum* L. subsp. *gracillimum* (Rouy) Váldez Berm.: Spain, Alicante, MGC 6197.
- HETER *T. heterophyllum* L'Hér.: Canary Islands, Tenerife, ORT 2940; Gran Canaria, ORT 8586; Hierro, ORT 18801.
- HIERO *T. hieronymi* Sennen: Spain, Almería, MGC 46232.
- HIJAZ *T. hijazicum* Hedge & King: Saudi Arabia, Jabal Radwa, (E5941)
- HOMOT *T. homotrichum* (Font Quer) Rivas Mart. (*T. aureum* subsp. *latifolium*): Spain, Valencia, MGC 38766.
- LEUCO *T. leucocladum* Boiss.: Arabia, Wadi Hebran (G 8347/16).
- LUSIT *T. lusitanicum* Schreb. subsp. *lusitanicum*: Spain, Málaga, MGC 20571.
- MAEPI *T. pseudochamaepitys* L.: Morocco, Tazzeke, MGC 48026; Spain, Málaga, MGC 45375.
- MAGRE *T. maghrebinum* Greuter & Burdet (*T. mauritanicum* de Noë): Morocco, Nador, BC 811317; Al Hoceima, BC 827219.
- MELIS *T. melissoides* Boiss.: Iraq, Erbil, G 8347/18.

- MURCI *T. murcicum* Sennen (*T. polium* subsp. *aguilasense*): Spain, Murcia, MGC 46018.
- MUSIM *T. musimonum* Humbert: Morocco, Djbel Ayachi, MGC 39019; Tichnika, Emberger 44808, RAB.
- ODONT *T. odontites* Boiss.: Libano, Raz Chekka, G 8347/21; Karadouranne, G 8347/24.
- ORIEN *T. orientale* L. subsp. *taylori* (Boiss.) Rech.: Iran, Khorramabad, G 8347/33; Jahram, G 8347/29.
- PERSI *T. persicum* Boiss.: Iran, Jahrom, G 8347/73.
- PSESC *T. pseudoscorodonia* Desf.: Morocco, Al-Hoceima, BC 827277; Ketama, BC 827278.
- PYREN *T. pyrenaicum* L. subsp. *pyrenaicum*: Spain, Huesca, MGC 37970.
- RDIUM *T. scordium* L. subsp. *scordioides* (Schreb.) Arcangeli: Morocco, Djbel Zem-Zem, BC 811278; Spain, Huelva, MGC 18238.
- RDONI *T. chardonianum* Maire & Wilczek: Morocco, Agadir, BC 13683.
- RESUP *T. resupinatum* Desf.: Morocco, Taza, BC 827147; Kenitra, BC 827175.
- RIDEM *T. charidemi* Sandwith: Spain, Almería, MGC 6191.
- RIPHA *T. afrum* (Emb. & Maire) subsp. *riphaeum* (Font Quer & Pau) Castrov. & Bayon (*T. oxylepis* var. *riphaeum*): Morocco, Djbel Lerz, BC 811086.
- RIVAS *T. rivas-martinezii* Alcaraz, Garre, Mart. Parras & Peinado: Spain, Murcia, MGC46270.
- ROTUN *T. rotundifolium* Schreb.: Spain, Granada, MGC 20627.
- RUBIF *T. afrum* (Emb. & Maire) subsp. *rubriflorum* (Font Quer & Pau) Castrov. & Bayon (*T. afrum* var. *rubriflorum*): Morocco, Tazza, BC 827150.
- RUPES *T. rupestre* Coss. & Balansa: Morocco, Safi, BC 802723.
- SCORO *T. scorodonia* L. subsp. *scorodonia*: Spain, Huesca, MGC 20986.
- SOKOT *T. sokotranum* Vierh. (*T. petiolare*): Socotra (E 10407).
- SPINO *T. spinosum* L.: Morocco, Meknes, BC 814270; Al-Hoceima, BC 827251; Spain, Sevilla, MGC 10463.
- STOCK *T. stocksianum* Boiss. subsp. *stocksianum*: Pakistan, Baluchistan, G 8347/102.
- TANAN *T. tananicum* Maire: Morocco, Agadir, BC 82723.
- THYMI *T. thymifolium* Schreb. (*T. buxifolium* subsp. *thymifolium*): Spain, Murcia, MGC 46274-MA 97924.
- WEBBI *T. webbium* Boiss.: Spain, Almería, MGC 8180.
- YEMEN *T. yemense* Deflers (*T. spicastrum*): Djibouti, Ali-Sabieh, MGC 37049.

Editado por Ramón Morales
Aceptado para publicación: 26-IV-1999