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Delimitation and revision of the genus *Thymbra* (Lamiaceae)

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Abstract

The importance of comprehensive species sampling in phylogenetics and revisions of taxonomically complex groups is outlined using an example from Lamiaceae. To render the genus *Thymbra* into a well circumscribed, natural and monophyletic group, three species are transferred from *Satureja* to *Thymbra.* A run down of the classification history is provided along with an updated generic circumscription for *Thymbra.* Important diagnostic characters are discussed and a key to the species of *Thymbra* is presented. Notes on both types and distribution are provided for each species accompanied by illustration of representative herbarium specimens. Finally, *Thymus cephalotos*, a name currently placed in the synonymy of *Thymbra capitata*, is typified to fix its exclusion from *Thymbra*.

Dedication: This work is dedicated to the memory of Avinoam Danin (1939–2015) for his contribution to our knowledge on the Flora of the Near East and his encouraging support of my work on *Thymbra*

Introduction

In Lamiaceae, the ecologically and economically important mint family, taxonomic controversials have a long tradition. This resulted in a considerable number of recent efforts to reevaluate existing classification concepts using molecular phylogenetic analyses (e.g. Paton *et al.* 2004, Pastore *et al.* 2011, Salmaki *et al.* 2013, 2016, Li *et al.* 2017). Among the notoriously difficult taxa, subtribe Menthinae (Lamiaceae, Nepetoideae, Mentheae), including such well known plants as peppermint, oregano, savory and thyme (see Bräuchler *et al.* 2010 for overview), probably is the most prominent example. The two fundamentally contrasting treatments of Briquet (1896) and Bentham (1848, 1876) have been differently followed in local revisions and floristic treatments over time. This led to an enormous number of names (Govaerts 2018) with many synonyms under different generic names and in consequence to considerable taxonomic confusion.

A genus previously considered rather isolated in this group is *Thymbra* Linnaeus (1753: 569) comprising four species of primarily Mediterranean subshrubs (Morales 1987, Harley *et al.* 2004). The recent molecular phylogenetic analysis of both nuclear ribosomal and plastid markers (Bräuchler *et al.* 2010) reveals that genus as a distinct lineage dissociated from both *Thymus* Linnaeus (1753: 590) and *Satureja* Linnaeus (1753: 568) s.str. Based on a comprehensive sampling at species level in all genera of Menthinae, *Thymbra*, however, could be revealed as paraphyletic with respect to a group of three species currently placed in *Satureja* (Bräuchler *et al.* 2010) and hereafter informally called the "Euhesperida group". They are morphologically similar and occur very scattered from Israel and Jordan to Saudi Arabia and Lybia in highly specialized habitats on limestone or sandstone formations.

In absence of a conclusive, comprehensive revision of generic delimitations in the *Satureja* alliance, the generic placement of *S. thymbrifolia* Hedge & Feinbrun (1969: 213), the first of these three species to be described, was considered problematic from the beginning. It was originally placed in *Satureja* sect. *Zatarioideae* Boissier (1879: 567) with doubt. Similarities to *Thymbra spicata* Linnaeus (1753: 569) were pointed out, but the much closer affinities to *T. calostachya* (Rechinger 1943: 122) Rechinger (1962: 64), endemic to Crete, remained unnoticed. *Satureja linearifolia* (Brullo & Furnari 1979: 434) Greuter (1986: 422) was described later and originallly placed in the monotypic genus *Euhesperida* Brullo & Furnari (1979: 434; as *Euhesperida linearifolia* Brullo & Furnari 1979: 434). Neither mentioning *S. thymbrifolia* nor *T. calostachya*, the genus was considered intermediate between *Satureja* (habit) and *Origanum* Linnaeus (1753: 590; floral features). The above-mentioned uncertainties in generic delimitation among

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Satureja and allies lead to the radical lumping approach by Greuter *et al.* (1986) resulting in a broadly circumscribed vast genus *Satureja*, now including *Euhesperida linearifolia*. Rejecting this broad view, Doroszenko (1986) was the first to recognize the close resemblence of *S. linearifolia* and *S. thymbrifolia*. Not considering *T. calostachya*, he included both species in *Euhesperida* in his PhD thesis, but did not formally publish the necessary new combination for *S. thymbrifolia*. Thus, when describing *S. nabateorum* Danin & Hedge (1998: 135) as distinct species closely related to the latter, the authors missed on *S. linearifolia* of which no herbarium material was available to them.

Continuing the efforts to clarify generic boundaries in Menthinae (Bräuchler *et al.* 2005, Bräuchler *et al.* 2006, Bräuchler *et al.* 2008a, Bräuchler *et al*. 2008b, Bräuchler *et al.* 2010), I here present a new generic concept for *Thymbra* in order to satisfactorily address its delimitation especially towards *Satureja* s.str. In consequence I transfer the species of the "Euhesperida group" to *Thymbra*, provide the first comprehensive treatment of the genus in a modern context and discuss characters used for generic delimitation.

Materials and Methods

This study was based on extensive examination of herbarium specimens, field work and literature survey allowing the first comprehensive overview of the group. Characteristics and distributional data were extracted from previous treatments on the genus (species descriptions, revisions and floristic treatments). Specimens for all species were made available by several herbaria (BM, E, HUJ, JE, K, M, W, WU) during visits or on loan, and as gifts from colleagues (S. Brullo, A. Danin, I. Künne; currently kept at TUM). This allowed to re-evaluate morphological features using stereo microscopes and to clarify the generic delimitation of *Satureja* and *Thymbra*. Some additional characters were observed on living plants in the field and cultivated at the Botanical Garden Munich. A list of representative material investigated in addition to the types is provided in Table 1.

Results

Taxonomic treatment

Using previous circumscriptions of the genus as a base (Davis 1982, Morales 1987), extracting information from taxonomic descriptions (Bornmüller 1912, Brullo & Furnari 1979, Danin & Hedge 1998, Davis 1949, 1980, Hedge & Feinbrun 1969, Rechinger 1943) and adding data from own observations on types, the specimens listed above and plants in the field, I here give an updated description of the genus *Thymbra*. Due to the new combination of three species names into this genus an updated identification key is necessary and provided. For each species type information is given and a representative specimen illustrated. Not to repeat information already published and readily available I refer to the original treatments listed above for detailed species descriptions.

Thymbra Linnaeus (1753: 569)

Type (designated by Green 1929): *Thymbra spicata* Linnaeus (1753: 569).

= *Coridothymus* Reichenbach (1857: 160) ≡ *Thymus* subgen. *Coridothymus* (Rchb.f.) Borbás (1890: 48) ≡ *Thymus* sect. *Coridothymus* (Rchb.f.) Boissier (1879: 560).

Type: *Coridothymus capitatus* (Linnaeus 1753: 568) Reichenbach (1857: 161) ≡ *Satureja capitata* Linnaeus (1753: 568)

= *Euhesperida* Brullo & Furnari (1979: 434).

Type: *Euhesperida thymbrifolia* Brullo & Furnari (1979: 434).

= *Satureja* Linnaeus (1753: 568) et sensu Harley *et al.* (2004: 239).

Description

Subshrubs, 10–60 cm, aromatic; branches ascending, erect or intricate; young leaves in axillary fascicles, leaves entire, sometimes with few cilia at margin, obovate, elliptic, lanceolate or linear, conduplicate to caniculate or flat, sessile, sometimes slightly succulent, punctate by sessile to shortly stalked globular glands, secondary veins tiny and not visible,

glabrous to densely villose; inflorescence a terminal spiciform or capituliform thyrse, condensed to lax, composed of congested verticillasters; bracts leaf like or not, oblong-ovate to ovate-lanceolate or lanceolate, sometimes coloured; bracteoles not leaf like, elliptic to lanceolate, acute or mucronate; calyx 3–6.5 mm long, 2-lipped (sometimes appearing almost actinomorphic due small dimensions and dense indumentum), 5-lobed (3/2), cylindrical to curved, with two +/-conspicuous lateral keels (produced by the veins ending in the lateral lobes of the upper calyx lip), more or less dorsiventrally compressed, scarcely accrescent, 12–23-nerved, lobes never spreading or following the tube outline, either subequal, triangular to acicular, or unequal with posterior lobes short, triangular, anterior lobes lanceolate, upcurved, throat sometimes constricted, never wide, bearded or not; corolla 2-lipped, 4-lobed (1/3), 4–12 mm long, cream or almost white to purple, posterior lobe +/-rounded, straight, emarginate, anterior lip with lobes suborbicular, median lobe downcurved; stames 4, inserted in middle of tube, filaments curved, exserted, thecae divaricate, confluent; stigma-lobes equal to subequal; disc entire; mericarps ovoid, +/-smooth. 2n = 30; seven species, Mediterranean, and in adjacent areas (W: Portugal; E: Anatolia, Iraq and Iran to N Arabian Peninsula).

TABLE 1. Voucher information for specimens examined for this study in addition to the types

Thymbra calostachya	GREECE. E Crete, 1 km W of Monikapsa, rocks close to the sea, 10 m, 15 June 1990, *Ulrich s.n.* (M); Crete, Sitia, W Kapsa Monastery, 31 March 2007, *Tillich 5231* (M, TUM); ibid., 01 April 2007, *Tillich 5265* (M, TUM)
T. capitata	CULTIVATED. [origin: GREECE. Crete, *Bräuchler 2526*] Botanical Garden Munich, 03 June 2005, *Bräuchler 3403* (TUM); [origin SPAIN] Palmengarten Frankfurt, 25 September 2003, *Bräuchler 2519* (TUM); GREECE. Crete, Prov. Rethymnon 35°11‘44.0“N 24°24‘21.1“E, 116 m, 26 March 2004, *Bräuchler 2526* (TUM); Peloponnes, Taygetos, 15 July 2007, *Kattari SK07/Pel046* (TUM); ITALY. Sardinia, 39°03‘00.0“N 8°21‘30.0“E, 81 m, 11 June 1999, *Bräuchler 97* (TUM); MALTA. *Meimberg 05* (TUM),
T. linearifolia	LIBYA. Wadi Belbarabides, 09 May 1974, *Brullo & Furnari s.n.* (TUM); Wadi el-Chresci (Tocra), 21 May 1981, *Brullo & Furnari s.n.* (TUM)
T. nabateorum	SAUDI ARABIA. Off the Dula-Tabuk road,10 km NE of Ruafah, 4.500 ft., 16 May 1994, *Collenette 9059* (E00102242); 72 km S of Tayma, Madinah road, 17 April 1991, *Collenette 7814* (E); JORDAN. 12 km SSW of Petra (type locality), 11 May 1995, *Danin s.n.* (TUM; HUJ980701); Edom, Ras Raibid, 640 m, 03 October 1988, *Künne 3368* (TUM); 1.5 km SW of Taiyiba, 1000 m, 28 September 1993, *Künne 93-123-02* (TUM); Siq Qseir al Anajil (NW Taiyiba), 1100 m, 30 September 1995, *Künne 95-122-01* (TUM); Edom, El-Hesma, 22 km N. of Queira, Nubian sandstone, about 800 m, 30 March 1936, *Eig,Zohary & Feinbrun s.n.* (K000193589, paratype of *Satureja thymbrifolia*)
T. sintenisii subsp. *isaurica*	TURKEY. Antalya, Alanya, 36°45´N, 32°28´E, 1290 m, 18 July 1998, *Güner et al. 12628* (E00075637)
T. spicata subsp. *spicata*	CULTIVATED. [origin TURKEY. Taurus, *Erben s.n.*] Botanical Garden Munich, 23 June 2008, *Bräuchler 4548* (TUM); ibid., 26 July 2007, *Bräuchler 4197*; LEBANON. Above Matara on the road to reserve, 33°39‘49.3“N 35°38‘06.4“E, 1025 m, 24 July 2010, *Bräuchler 5207* (TUM); TURKEY. Antalya, Alanya , 36°41‘25.6“N 31°53‘26.0“E, 522 m, 12 August 2007, *Bräuchler 4420* (TUM); Antalya, Kemer, 36°40‘1.16“N, 30°32‘25.62“E, 40 m, 11 August 2007, *Bräuchler 4161* (TUM); Karabük, Safranbolu, 41°13‘53.3“N 32°40‘21.5“E, 363 m, 04 August 2007, *Bräuchler, Dirmenci & Yildiz 4344* (TUM)
T. thymbrifolia	ISRAEL: Judean Desert, 11 km S of Jericho, 29 April 1994, *Danin s.n.* (TUM); Judean Desert, Near Khirbet el Mird Hill, 02 April 1932, *Eig & Feinbrun s.n.* (HUJ 315080)

Key to the species

1 Leaves generally glabrous, ciliate at margin, sometimes few cilia also on lamina, not revolute, inflorescence condensed, forming a capitulum or a more or less condensed spike ("sectio *Thymbra*") 2
- Leaves densely white eglandular pubescent on both sides, margin not ciliate, usually revolute, inflorescence a lax spike ("sectio *Neothymbra*") 4
2 Winter leaves 4–10 × 1–1.5 mm; inflorescence usually capituliform (rarely oblong-conical); bracts imbricate, concealing calyces ..... *T. capitata*
- Winter leaves 11–18 × 2–3 mm; inflorescence usually spike like; bracts not imbricate, not concealing calyces 3
3 Bracteoles usually purplish, always narrower than the bracts; calyx with upper lobes < 0.5 mm, calyx throat glabrous; corollla white, 8–9 mm, upper lip equal or shorter than lower lip ..... *T. sintenisii*
a) Leaves and bracts shortly ciliate or not ciliate, bracts glabrous, bracteoles shortly ciliate ..... subsp. *sintenisii*
b) Leaves, bracts and bracteoles with large cilia, bracts frequently pilose on lower surface ..... subsp. *isaurica*
- Bracteoles green, roughly as wide as bracts; calyx with upper lobes > 0.5 mm, calyx throat bearded; corolla purplish, 12–16 mm, upper lip much longer than lower lip ..... *T. spicata*
a) Branches pilose on 2 opposite sides, alternating at the nodes, bracteoles densely ciliate with short cilia ..... subsp. *spicata*
b) Branches pilose on all sides, bracteoles sparsely ciliate with large cilia ..... subsp. *intricata*
4 Leaves obovate-lanceolate to oblong-lanceolate, indumentum of straight hair (sometimes slightly curved to tip), < 0.3 mm long. Occurring on Crete ..... *T. calostachya*
- Leaves linear to elliptic linear and narrowly oblong, indumentum of frequently slightly curled hair, > 0.5 mm long 5
5 Intricately branched, branches spreading, leaves shorter than internodes, bracteoles mucronate, shorter than calyx. Occurring from Jordan to Saudi Arabia ..... *T. nabateorum*
- Not intricately branched, branches ascending/erect, leaves at least as long, but mostly longer than internodes, bracteoles not mucronate, as long as or slightly longer than calyx 6
6 Branch indumentum composed of straight spreading or antrorse hairs. Occurring in Libya ..... *T. linearifolia*
- Branch indumentum composed of retrorse hairs. Occurring in Israel ..... *T. thymbrifolia*

List of species including notes on types and distribution

1. *Thymbra calostachya* (Rech.f.) Rech.f., Kulturpfl., Beih. 3, 64 (1962); Figure 1. a

≡ *Micromeria calostachya* Rech.f., Akad. Wiss. Wien, Math.-Naturwiss. Kl., Denkschr. 105(2): 122 (1943).

Type : GREECE. Ost-Kreta, Prov. Sitia: Steile Felshänge der Schlucht unterhalb Achladi gegen die Südküste, 09 May 1942, *Rechinger 12734* (lectotype, designated by Rechinger (1962: 65), W 1960-0012710!, isolectotypes BM!, K000494968!, M!, E00207260!, G, WU!).

Distribution: Endemic to the SE coast of Crete.

2. *Thymbra capitata* (L.) Cavanilles (1803: 37), Figures 2. a–c

≡ *Coridothymus capitatus* (L.) Rchb.f., Oesterr. Bot. Wochenbl. 6: 161 (1857).

≡ *Origanum capitatum* (L.) Kuntze (1891: 528).

≡ *Satureja capitata* L., Sp. Pl.: 568 (1753)

≡ *Thymus capitatus* (L.) Hoffmannsegg & Link (1809: 123).

≡ *Thymus creticus* Brotero (1804: 174), nom. illeg.

Type: PORTUGAL. Thymus creticus off., Satureja mat. med. […] Lisboa vulgaris [*Loefling*] (lectotype, designated by Siddiqi (1985: 90), LINN 723.11!)

Distribution: Mediterranean Basin, Portugal; the most widespread species of the genus.

Note: Brotero (1804: 175) gives "in collibus calcareis de Alcantara prope Olisiponem, et prope Sacellum S. Luciae circa Conimbricam, et alibi in Lusitania meridionali" as localities for his *Thymus creticus*. I was not able to trace authentic specimens, but since he cites the earlier legitimate *Satureja capitata* L. in the synonymy, his name is illegitimate anyway.

3. *Thymbra linearifolia* (Brullo & Furnari) Bräuchler, *comb. nov.*; Figure 1. c

≡ *Euhesperida linearifolia* Brullo & Furnari, Webbia, 34(1): 434 (1979).

≡ *Satureja linearifolia* (Brullo & Furnari) Greuter, Willdenowia 15: 422 (1986).

Type: LIBYA. Uadi el-Cresci, 07 May 1974, *Brullo & Furnari s.n.* (holotype CAT, isotypes K000193384!, M!, herb. Bräuchler!).

Distribution: Endemic to Libya and only known from three collections in the Gebel el-Akhdar between Bengasi and Taucheira (see material studied).

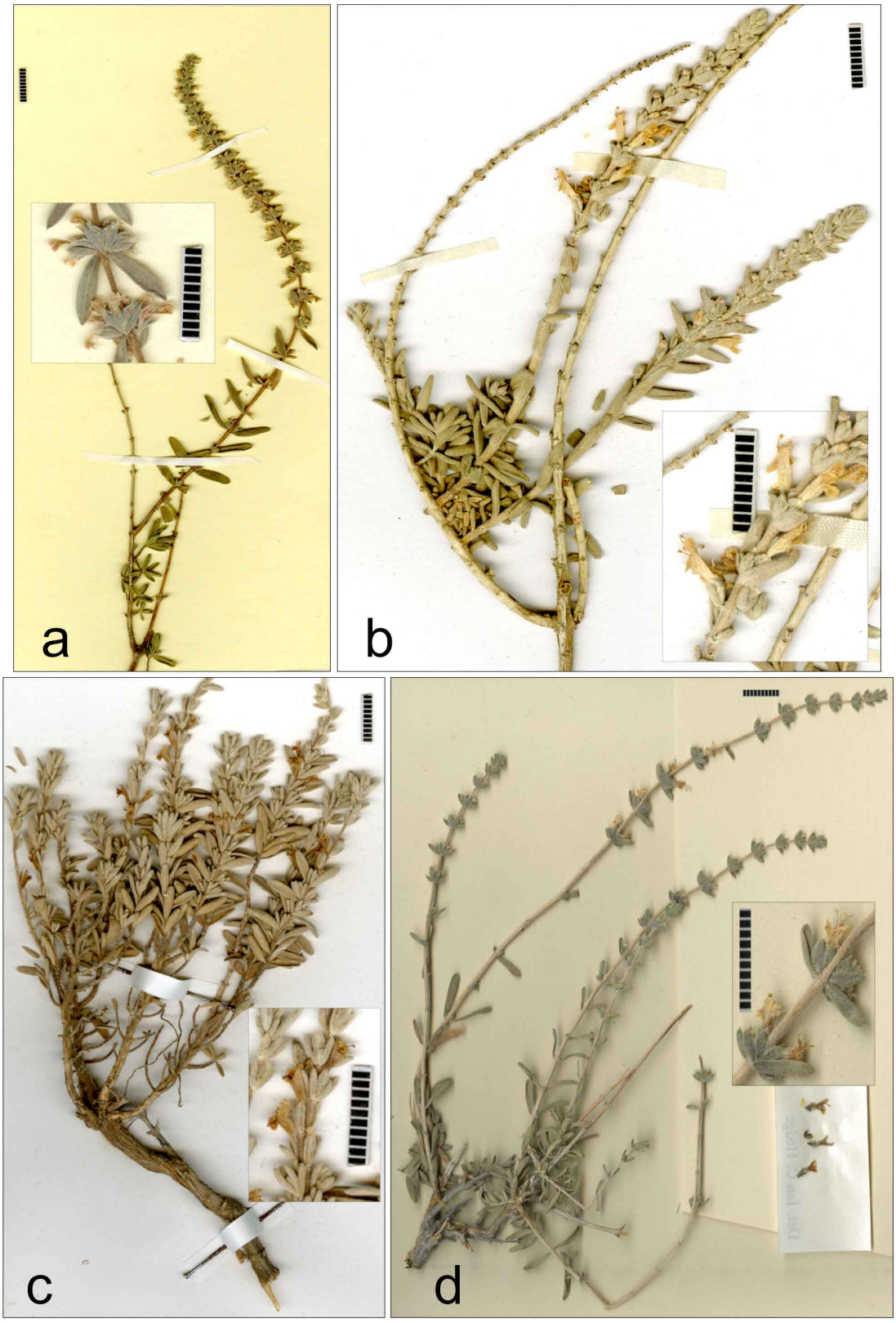

FIGURE 1. Representative specimens of *Thymbra* species with close-ups of the inflorescence; scale bar = 10 mm;-**a**) *T. calostachya* (*Ulrich*, M);-**b**) *T. thymbrifolia* (*Danin*, TUM);-**c**) *T. linearifolia* (isotype TUM); **d**) *T. nabateorum* (isotype E00208104)

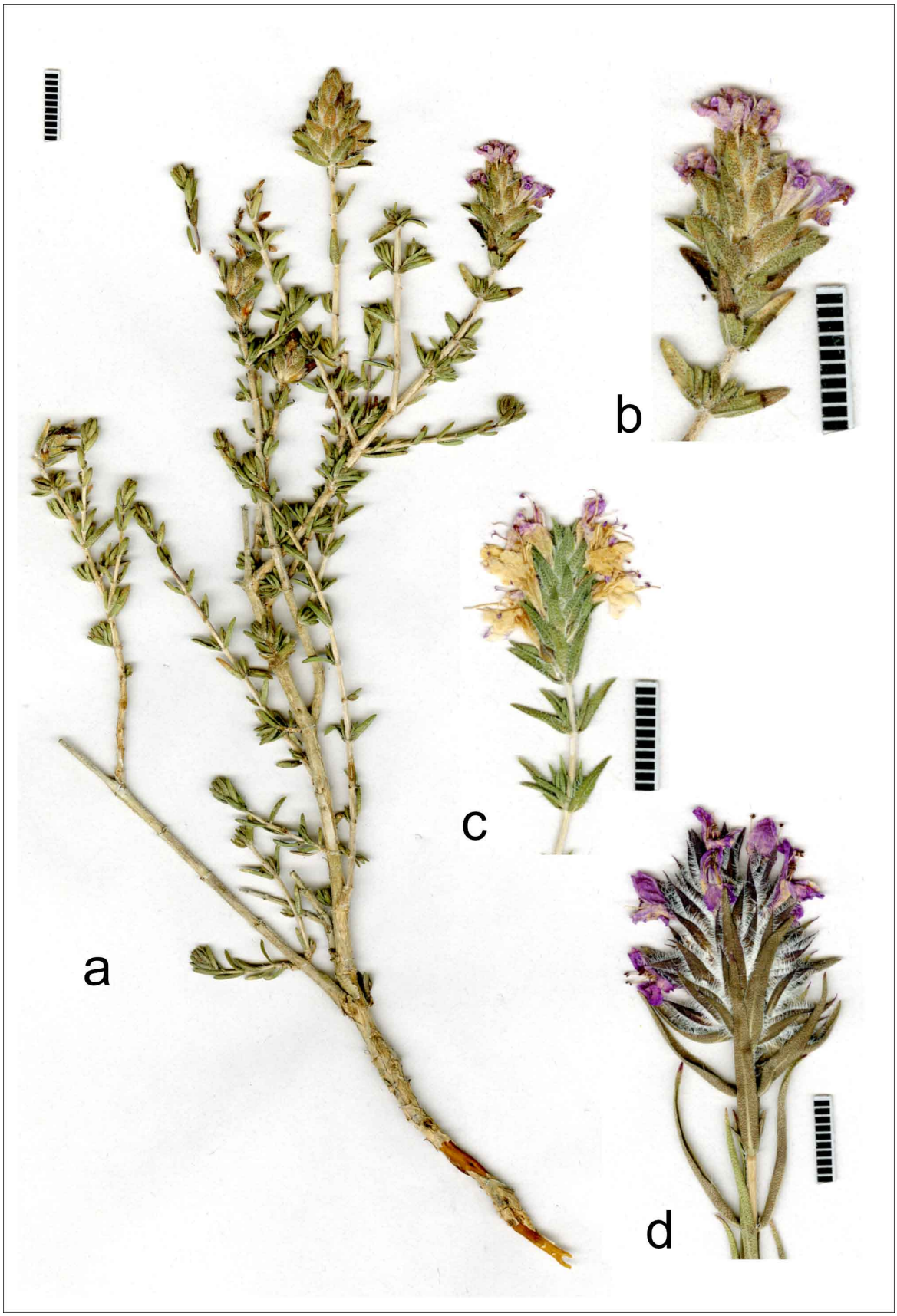

FIGURE 2. Representative specimens of *Thymbra* species; scale bar = 10 mm;-**a**) *T. capitata*, branch of a wild plant (*Kattari SK07/Pel046*, TUM),-**b**) inflorescence of *T. capitata* (*Kattari SK07/Pel046*, TUM);-**c**) inflorescence of a cultivated plant of *T. capitata* (*Bräuchler 2526*, TUM), note the narrower bracts compared to the wild plant, that are however never as long and narrow as in *T. spicata*;-**d**) inflorescence of a cultivated plant of *T. spicata* subsp. *spicata* (*Bräuchler 4548*, TUM).

4. *Thymbra nabateorum* (Danin & Hedge) Bräuchler, *comb. nov.*; Figure 1. d

≡ *Satureja nabateorum* Danin & Hedge, Willdenowia 28: 135 (1998).

Type: JORDAN. Edom, 10 km E of Risha to Jabal Masonda, in crevices of smooth-faced white sandstone (Disi Formation), 650 m, 19 May 1997, *Danin 970201* (holotype HUJ; isotype B!, E00208104!, K!)

Distribution: Restricted to the far W of Jordan and the adjacent N of Saudi Arabia, but apparently the most widespread species of the "Euhesperida group".

5. *Thymbra sintenisii* Bornm. & Azn., in Bornmüller (1912: 471).

For a detailed anatomical and morphological study of the subspecies see Erken (2005).

subsp. *isaurica* Davis (1980: 59); Figures 3. c & f

Type: TURKEY. Vil. Antalya: Kargi chai in Isaurian Taurus, between Durbanas & Desinje derry, rocky slopes, 25 July 1947, *Davis 14464* (holotype E00208086!, isotype E00208085!, G, K, JE 00002710!, W 1983-0008299!)

Distribtuion: SW Turkey, endemic to the Isaurian Taurus.

subsp. *sintenisii*; Figures 3. d & g

Type: TURKEY. Kurdistan: Mardin; Bakakri; 28 June 1888, *Sintenis [Iter Orientale 1888, no. 1176]* (lectotype, designated by Morales (1987: 367), B!, isolectotype E00208087!, JE 00005901!, K000494969!, K000494970!, LD, WU 0059329!)

Distribution: E Turkey to N Iraq.

Note: The lectotype represents a duplicate of Sintenis´ exsiccate without printed label and most likely coming from Bornmüller´s private herbarium. Duplicates probably are present in numerous other herbaria.

6. *Thymbra spicata* L., Sp. Pl.: 569 (1753).

For a detailed anatomical and morphological study of the subspecies see Erken (2001).

subsp. *intricata* (P.H. Davis) Morales (1987: 377); Figure 3. a

≡ *T. spicata* var. *intricata* Davis (1949: 424)

Type*:* TURKEY. Prov. Denizli, distr. Acipayam (Caria): Boz Dag, near Geyran

Yayla, 1220–1520 m, 16 July 1947, *Davis 13328* (holotype K000193688!, isotype E00208084!, G).

Distribution: Restricted to the SW of Turkey and the island of Rhodos.

subsp. *spicata*; Figures 2. d, 3. b & e

Type*: "Thymum majus longifolium, Staechadis foliaceo capite purpurascente, pilosum"* (lectotype, designated by Morales & López in Jarvis *et al.* (1993: 94), t. 116, f.5 in Plukenet (1691))

Note: According to Jarvis (2007: 887), the sheet 724.1 (LINN!), designated as lectotype by Morales (1987: 371) "lacks a *Species Plantarum* number and is a post-1753 addition to the herbarium, and not original material for the name". Since identity of the lectotype is unambiguous, I refrain from formally selecting 724.1 as epitype.

= *Thymbra verticillata* Linnaeus (1753: 569).

Type: Thymbra verticillata, s.d. (lectotype, designated by Morales in Jarvis *et al.* (2001: 521), LINN 724.2!)

= *Thymbra ambigua* Clarke (1814: 239).

Type: "Defile of the Thermopylae, at the hot springs, in the narrowest part of the pass, close to the Via Militaris" (whereabouts unknown, maybe at CGE or OXF)

Note: Although no original material for this name has been traced so far, both description and location leave no doubt about the synonymy.

Distribution: East Mediterranean, costal areas from Greece to Israel, extending to Iraq and Iran.

7. *Thymbra thymbrifolia* (Hedge & Feinbrun) Bräuchler, *comb. nov.*; Figure 1. b

≡ *Satureja thymbrifolia* Hedge & Feinbrun, Israel J. Bot. 17: 213 (1969).

Type: ISRAEL. Palestine, Judean Desert, Khirbet el Mird (Horkaniye), 3 km NE of the Mar Saba Monastery, 240 m, hard limestone, N. exposure, 27 October 1967, *Danin s.n.* (holotype HUJ, isotype E00208033!)

Distribution: Endemic to an 18 km long strip in the Judean Desert (see Danin, 1969 and Danin & Hedge, 1998 for further details).

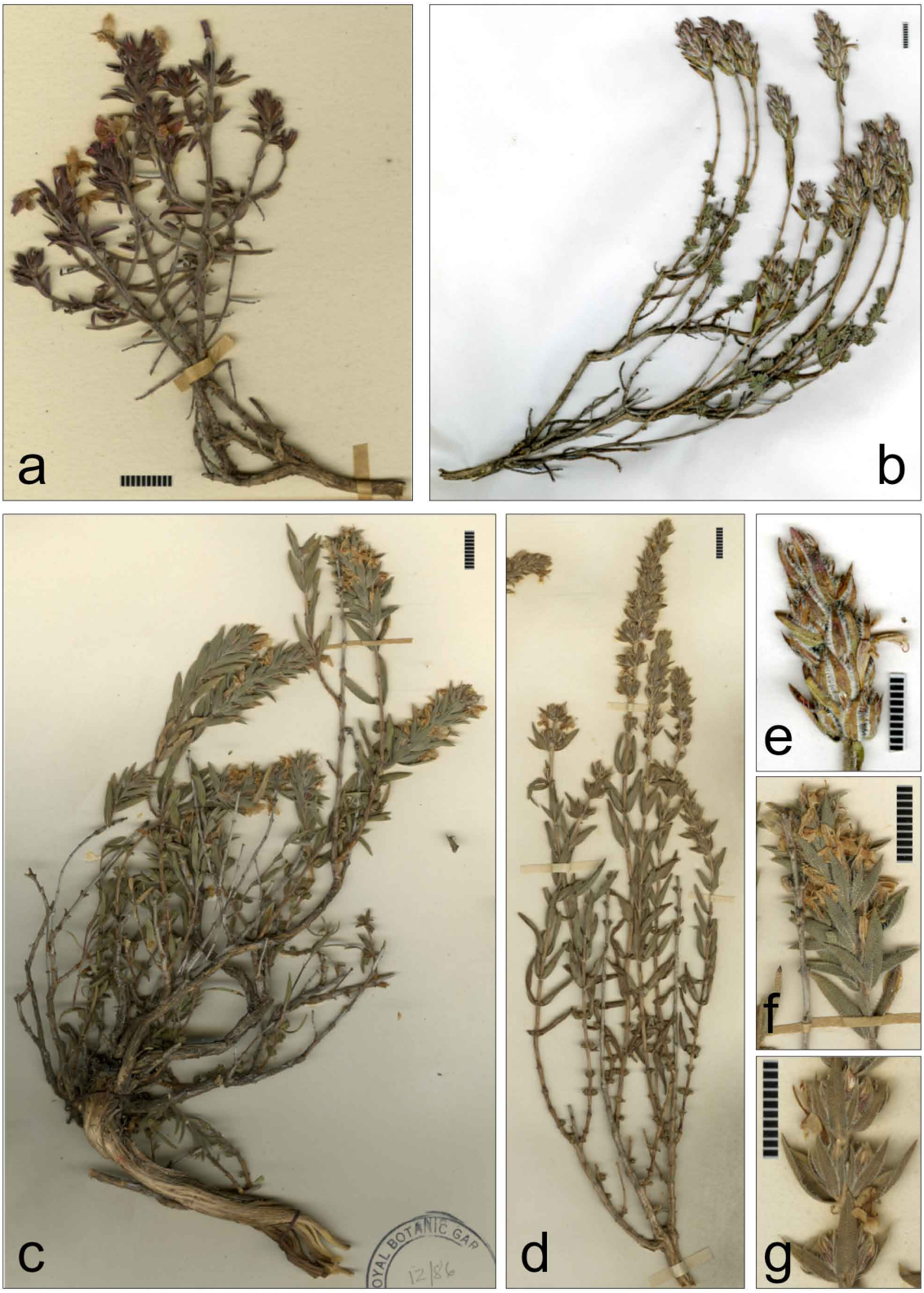

FIGURE 3. Representative specimens of *Thymbra* species; scale bar = 10 mm;-**a**) branch of an isotype of *T. spicata* subsp. *intricata* (E00208084);-**b**) branch of *T. spicata* subsp. *spicata* (*Bräuchler et al. 4344*; TUM);-**c**) holotype of *T. sintenisii* subsp. *isaurica* (E00208086);-**d**) branch of an isolectotype of *T. sintenisii* subsp. *sintenisii* (E00208087);-**e**) inflorescence of *T. spicata* subsp. *spicata* (*Bräuchler et al. 4344*; TUM);-**f**) inflorescence of the holotype of *T. sintenisii* subsp. *isaurica* (E00208086);-g) inflorescence of an isolectotype of *T. sintenisii* subsp. *sintenisii* (E00208087).

List of names previously included in *Thymbra*, but excluded here

Thymbra cephalota (Linnaeus 1753: 592) Desvaux (1831: 64)
≡ ***Thymus cephalotos* L., Sp. Pl.: 592 (1753)**
≡ *Origanum cephalotos* (L.) Kuntze (1891: 528)
Type: "Tragoriganum dictami capite hispanicum" (lectotype, designated here, t. 43 in Boccone (1697)).
= ***Thymus moroderi* Pau ex Martinez (1934: 465)**

Note: The sheet 247.5 (S-LINN!) previously designated as lectotype of *Thymus cephalotos* by Morales (1986: 179) clearly represents *Thymbra capitata*. This resulted in placing the former name into the synonmy of the latter. According to Jarvis (2007: 887) the intended lectotype, however, is not to be considered original material of *Thymus cephalotos*, since it lacks any Linnean annotation. To fix correct application of this name, I here designate the oldest illustration cited by Linnaeus (1753) as lectotype. The second figure cited ("Tragoriganum dictami capite hispanicum" in Barrelier 1714: t. 788) actually represents a later (flipped) reproduction of the former. Morales & López (1984) state that the lectotype represents the taxon currently known as *Thymus moroderi* Pau ex Martinez.

Thymbra caroliniana Walter (1788: 162)
≡ ***Macbridea caroliniana* (Walter) Blake (1915: 132)**
Thymbra ciliata Desfontaines (1798: 10)
≡ ***Thymus munbyanus* subsp. *ciliatus* (Desf.) Greuter & Burdet in Greuter & Raus (1985: 82)**
Thymbra hirsuta Persoon (1806: 114)
= ***Satureja thymbra* Linnaeus (1753: 567)**

Thymbra hirsutissima Persoon (1806: 114), *nom. invalid. (pro syn.)*
= ***Satureja thymbra* Linnaeus (1753: 567)**
Thymbra neurophylla Rechinger (1979: 107)
≡ ***Thymus neurophyllus* (Rech.f.) Morales (1989: 562)**
Thymbra zotas Willd. in Bentham (1837: 328), *nom. invalid. (pro syn.)*
= ***Thymus munbyanus* Boissier & Reuter (1852: 96) subsp. munbyanus**

Discussion

Generic delimitation of *Thymbra*

All three species transferred here from *Satureja* to *Thymbra*, *T. linearifolia, T. nabateorum* and *T. thymbrifolia* (the "Euhesperida group"), have superficial morphological similarities with some species of *Satureja* (in first place *S. bachtiarica* Bunge (1873: 37) and *S. popovii* Fedtschenko & Gontscharov (1929: 117)-the latter once placed in the monotypic genus *Gontscharovia* Borissova (1953: 321)), particularly in inflorescence shape, leaf arrangement, and calyx structure. Molecular analyses clearly place the three species in *Thymbra*, a lineage well distant from *Satureja* s.str. (Bräuchler *et al.* 2010). Due to data gaps *T. nabateorum* has not been included in the published phylogenetic tree, but an unpublished *trn*L-F sequence confirms its placement. With respect to morphology, especially the characteristic (comparatively) lax inflorescence, the three species are further linked to *Thymbra* by the geographically close *T. calostachya* (endemic to Crete) and to a lesser extent also by *T. sintenisii*. Of all relevant species, *T. calostachya* by far is the closest match and there are several characters linking it to the "Euhesperida group" that are either not found or rather uncommon in *Satureja*: very dense indumentum, only the midvein of the leaves visible (whereas in *Satureja* secondary veins are generally strongly developed and usually visible at least in herbarium specimens).

When including the "Euhesperida group", the most important character distinguishing *Thymbra* from all representatives of *Satureja* and in fact all other members of Menthinae, however, is the calyx shape and the orientation of the calyx lobes (Figure 4). In *Satureja* the calyx is obconical and wide at throat with the calyx lobes following the calyx throat outline and frequently bending outwards towards the tip (Figure 4. a). In *Thymbra* the calyx is dorsiventrally compressed (Figure 4. b) even though only very slightly in *T. calostachya* (Rechinger, 1962) and the "Euhesperida group". In the latter group this has not been reported-or been overlooked-due to the small dimensions and the very inconspicuous nature of the compression, but was verified here based on observation of types and the

additional herbarium material cited. The calyx is frequently slightly curved (Figure 4. b) and never obconical, with the lobes either converging or tightly appressed to the corolla tube, but not spreading (Figure 4. c).

Infrageneric division

As outlined above, both molecular data and morphological characters favour transfer of the Euhesperida group to *Thymbra*. The corresponding characters have been included in the generic recircumscription above and the necessary new combinations were provided. Rechinger (1962) accommodated the three species known to him in two sections, sectio *Thymbra* (type: *T. spicata*; *T. sintenisii*) and sectio *Neothymbra* Rech.f. (type: *T. calostachya*). Since none of the sections has been indicated as a cluster in the phylogenetic analysis (Bräuchler *et al.* 2010), the sections may not represent natural groups and in consequence are only provisionally mentioned in the identification key provided above. Morphologically, however, *T. capitata* would clearly fall into the typical section, while the "Euhesperida group" shares characters with the only species previously included in *Neothymbra*. Even when considered natural, the sections should be redefined rather based on characteristics of leaves and inflorescences as indicated in the key as well.

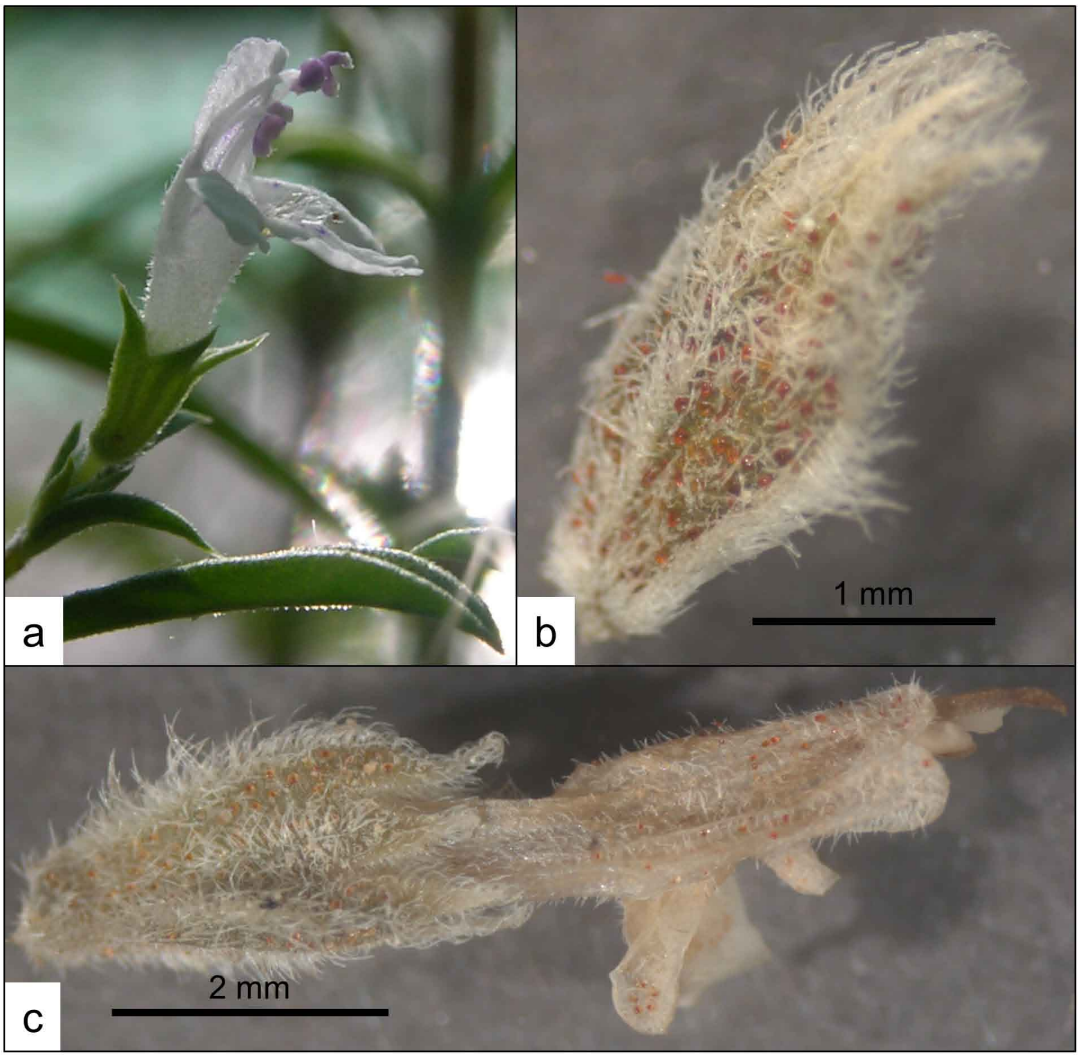

FIGURE 4. a) Flower of *Satureja cuneifolia* (cultivated at the Botanical Garden Munich, origin Italy) illustrating the characteristic features of a wide calyx throat, and spreading calyx lobes;-**b**) flower bud of an isotype of *T. nabateorum* (E00208104), showing the typical dorsiventral compression of the calyx;-**c**) flower of an isotype of *T. nabateorum* (E00208104), showing the narrow calyx throat with lobes tightly attached to the corolla, but not spreading.

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