Evolution of trichomes and its systematic significance in *Salvia* (Mentheae; Nepetoideae; Lamiaceae)

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We have investigated the trichome characteristics in representative species of *Salvia* and *Pleudia* in order to evaluate this source of morphological evidence for addressing problems regarding generic delimitation and subgeneric classification. Trichomes of 46 *Salvia* spp., representing three subgenera in Iran, were investigated using light microscopy and scanning electron microscopy. General trichome characteristics were constant among different populations of a certain species, but showed a degree of variability useful in the delimitation of taxa, specifically at lower taxonomic levels. Trichome characters of taxonomic interest are as follows: types of glandular hair; number of composing cells (uni-, bi- or multicellular); size and thickness; branching pattern; and presence of papillae on the surface. Non-glandular trichomes can be simple and branched. Glandular trichomes can be stalked, subsessile or sessile. Our investigation reveals the usefulness of such characters in providing fundamental taxonomic criteria for taxon delimitation in these genera at various levels, especially at the specific rank. Furthermore, the data presented here indicate the potential applicability of such characters in the determination of evolutionary trends in *Salvia* and allies. © 2015 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2016, **180**, 241–257.

ADDITIONAL KEYWORDS: classification – light microscopy – *Pleudia* – scanning electron microscopy – trichome morphology.

INTRODUCTION

Salvia L. is the largest genus in the mint family, comprising *c*. 950–1000 species distributed throughout the world: Central and South America (*c*. 500 spp.); western Asia (*c*. 200 spp.); eastern Asia (*c*. 100 spp.); Africa (*c*. 60 spp.); and Europe (*c*. 36 spp.) (Dizkirici *et al*., 2015). In western Asia, the centre of diversity of the genus is found in Turkey with 100 species (Hedge, 1982b; Celep *et al*., 2014a, b; Celep, Dirmenci & Güner, 2015), followed by Iran with 62 species (Hedge, 1982a; Assadi, 1987; Mozaffarian, 1991; Jamzad, 2012). Species diversity in *Salvia* can partly be explained by the occupation of different habitats and adaptation to different ecological conditions, e.g. gravelly slopes, limestone rocks, loamy hills, field sides, banks of steppes, margins of forests and subalpine pastures (Hedge, 1974).

Salvia spp. are mainly herbaceous or suffruticose perennials or, rarely, annuals. The flowers are arranged in variously formed cymes or verticillasters. The calyx is mostly infundibular, campanulate or tubular, but, in some species, it expands. The corolla varies in colour and is characterized by a long and falcate to straight and flattened upper lip. The most important diagnostic feature of *Salvia* as a member of the tribe Mentheae is the presence of two fertile stamens (Harley *et al*., 2004). The presence of nectar in a deep floral tube, pollen sacs and stigma located below the upper lip and a landing place formed by the lower lip of the > 950 *Salvia* spp. are consistent with the bee pollination syndrome (Claßen-Bockhoff, Wester & Tweraser, 2003; Celep *et al*., 2014a, b).

The subgeneric classification of *Salvia* has long been the subject of controversy. The first subgeneric classification of *Salvia* was proposed by Bentham (1832–1836, 1848, 1876), who classified the genus into four subgenera and 12 sections based on stami-

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nal morphology. Briquet (1897) modified Bentham's classification and increased the number of subgenera to eight. Pobedimova (1954) assigned *Salvia* spp. distributed in the former USSR to seven subgenera and eight sections. However, Hedge (1974) considered earlier classifications as artificial and suggested that a worldwide study should be undertaken to elucidate the subgeneric and sectional delimitation in the genus. In Rechingers' *Flora Iranica*, about 70 *Salvia* spp. with 40% endemism are mentioned without assigning them to any subgeneric or sectional rank (Hedge, 1982a).

Recent phylogenetic studies have shown that *Salvia* in its current circumscription is paraphyletic and contains four distinct lineages (Clades I–IV), in which also the genera *Perovskia* Kar., *Rosmarinus* L., *Meriandra* Benth., *Dorystaechas* Boiss. and *Zhumeria* Rech.f. & Wendelbo are nested (Walker *et al*., 2004; Walker & Sytsma, 2007; Will & Claßen-Bockhoff, 2014). Moreover, these studies reveal new aspects concerning the subgeneric classification of *Salvia* (Li *et al*., 2013; Will & Claßen-Bockhoff, 2014). For *Salvia* to be monophyletic, its circumscription must be expanded to include the above-mentioned genera (*Salvia s.l.*) or it could be defined more narrowly (*Salvia s.s.*) by recognizing several new genera (Will & Claßen-Bockhoff, 2014; Will, Schmalz & Claßen-Bockhoff, 2015). As *Salvia* is already highly heterogeneous in species distribution and morphology, Will *et al*. (2015) suggested the division of the genus into molecularly well-supported clades. However, a more extensive taxon sampling is needed in order to evaluate all phylogenetic and taxonomic aspects of *Salvia*.

The taxonomic and phylogenetic significance of trichome characters in different genera of Lamiaceae and related families, such as Verbenaceae, has already been documented (e.g. Cantino, 1990; Marin, Etkovic & Duletic, 1994; Ascensão, Mota & Castro, 1999; Navarro & El Qualidi, 2000; Moon *et al*., 2009). Some genera, e.g. *Stachys* L. (Salmaki *et al*., 2009, 2012) and *Phlomis* L. (Azizian & Cutler, 1982), have been examined explicitly, leading to improved classification systems in these genera. However, trichome micromorphological studies are few in *Salvia* and include one or a few species only (e.g. Singh, Sharma & Jain, 1974; Corsi & Bottega, 1999; Ilçim, Celep & Doğan, 2009; Kahraman, Celep & Dogan, 2010; Kahraman *et al*., 2010; Shirsat, Kokate & Surdakar, 2012; Celep *et al*., 2014a, b; Dizkirici *et al*., 2015).

Here, we perform a detailed micromorphological study of trichomes in *Salvia*, focusing on selected species distributed in Iran and neighbouring countries, to evaluate the significance of indumentum characters for taxonomic purposes and to survey the evolutionary patterns regarding trichome characters according to current phylogenetic hypotheses in the genus. The aims of the present study are: (1) to document trichome characters among *Salvia* spp. representing morphological lineages known in the genus (as many as possible); (2) to determine the most important trichome characters in terms of systematic significance; and (3) to survey the patterns of homoplasy and phylogenetic significance of these characters using phylogenetic frameworks established for this genus.

MATERIAL AND METHODS

SAMPLING

Trichomes of 46 *Salvia* spp. were investigated using light (LM) and scanning electron (SEM) microscopy. Samples for this study were collected in the field and from herbarium material kept at the Central Herbarium of the University of Tehran (TUH) and the Herbarium of Ferdowsi University of Mashhad (FUMH). In order to ensure constancy of trichome characters in the studied species, when available, at least three specimens of each species were examined. Voucher specimens used in this study and the collection data are listed in Table 1. Trichomes were obtained mostly from calyces and leaves.

SEM AND LM STUDIES

For SEM examination, small pieces of dried calyces and leaves were mounted on stubs and coated with a layer of gold–palladium. Some micrographs were taken with a KYKY-EM3200 scanning electron microscope (China) at 2 kV and others were taken with a Leo 962 (Germany) at 15 kV. For LM examination, intact leaves of the observed species were boiled in water and then fixed in 70% ethanol and formalin–acetic acid–alcohol (FAA) solution. Cross-sections of petioles and leaf blades were made by hand. The fine sections were stained with safranin-fast green according to Salmaki *et al*. (2009). After dehydration through an ethanol–xylol gradient, the stained sections were mounted on slides using Canada balsam. Finally, they were studied using a Zeiss Axioskop 40 light microscope (Germany).

Different types of trichomes were classified and compared. The terminology used in this investigation follows Singh *et al*. (1974), Cantino (1990) and Salmaki *et al*. (2009).

RESULTS

Different types of observed trichomes and their distribution among the *Salvia* spp. studied are listed in

Table 1. Collection data of *Pleudia* and *Salvia* specimens examined for micromorphological characters of trichomes

Species	Collection data
***Pleudia* Raf.**	
P. aegyptiaca (L.) M.Will, N.Schmalz & Class. Bockh.	Prov. Bushehr: Tange Zanganeh Gharb, 20 km E. Bushehr, *Mobayen et al. 7679* (TUH)
P. eremophila (Boiss.) M.Will, N.Schmalz & Class. Bockh.	Prov. Yazd: Shirkuh, *28294* (TUH)
P. macilenta (Boiss.) M.Will, N.Schmalz & Class. Bockh.	Prov. Yazd: Taft Kuh, *Dehghanzade 26054* (TUH)
P. santolinifolia (Boiss.) M.Will, N.Schmalz & Class. Bockh.	Prov. Baluchestan: 50 km from Iranshahr to Sarbaz, *Ghahreman, Attar and Sheikh 21601* (TUH)
P. tebesana (Bunge) M.Will, N.Schmalz & Class. Bockh.	Prov. Khorasan: SE to Tabas-Perawde toward Paykuh, *Faghihnia and Zangooi 28196* (FUMH)
***Salvia* L.**	
S. aethiopis L.	Prov. Ardebil: 40 km to Kaleybar from Ahar, *Salmaki, Eijy and Seyedi 45264* (TUH)
S. aristata Aucher ex Benth.	Prov. East Azarbayjan: Yam pass, *7672* (TUH)
S. atropatana Bunge	Prov. East Azarbayjan: Arasbaran Protected Area, 5 km after Oskulu village, *Salmaki, Eijy and Seyedi 45267* (TUH)
S. brachysiphon Stapf	Prov. Hamedan: on the road of Avaj to Razan, 24 km to Razan, *Salmaki, Eijy and Seyedi 45281* (TUH)
S. bracteata Banks & Sol.	Prov. Kordestan: Sardasht, *7665* (TUH)
S. ceratophylla L.	Prov. Ardebil: 50 km to Kaleybar from Ahar, *Salmaki, Eijy and Seyedi 45262* (TUH)
S. chloroleuca Rech.f. & Aellen.	Prov. Semnan: 25 km after Semnan towards Damghan, Ahovan pass, *Salmaki, Seyedi and Eijy s.n.* (TUH)
S. chorassanica Bunge	Prov. Khorasan: Kalat-e Naderi, Zharf village, Sabze Meydan, *s.n.* (FUMH)
S. compressa Vent.	Prov. Tehran: Damavand, Polur to Fioruz kuh, *Lasum, Gahreman and Mozaffarian 9953* (TUH)
S. dracocephaloides Boiss.	Prov. East Azarbayjan: about 16 km after the East of Jolfa, on the road of Jolfa to Hadishahr, Gheshlagh, Kiamaki Dagh, *Salmaki, Eijy and Seyedi 45271* (TUH)
S. glutinosa L.	Prov. East Azarbayjan: Asalem to Khalkhal, 30 km to Khalkhal, *Attar and Dadjou 14672* (TUH)
S. grossheimii Sosn.	Prov. East Azarbayjan: Jolfa to Zonoz , 24 km on the road of Zonoz to Kuhkamar village, *Salmaki, Eijy and Seyedi 45276* (TUH)
S. hydrangea DC. ex Benth.	Prov. Azarbayjan: from Miyaneh to Tabriz near Gharah Chaman, *Ghahreman, Agustin and Shikhaleslami 7673* (TUH)
S. hypoleuca Benth.	Prov. Qazvin: about 7 km after Kuhin village toward Lushan, *Salmaki, Eijy and Seyedi 45254* (TUH)
S. indica L.	Prov. Kermanshah: road to Paveh, *Ghahreman and Agustin 7591* (TUH)
S. leriifolia Benth.	Prov. Khorasan: Torbat-e Heydarieh towards Kashmar before Soltanabad, 4 km to Chenar village, *Salmaki, Seyedi and Eijy 45287* (TUH)
S. limbata C.A.Mey.	Prov. East Azarbayjan: about 16 km after the east of Jolfa, on the road of Jolfa to Hadishahr, Kiamaki Dagh, *Salmaki, Eijy and Seyedi 45294* (TUH)
S. macrochlamys Boiss. & Kotschy	Prov. Azarbayjan: Urmieh, Sirvana, Ghasrik, *Kazempour 8568* (TUH)
S. macrosiphon Boiss.	Prov. Khorasan: about 20 km after Mashhad towards Malekabad (old road), *Salmaki, Seyedi and Eijy 45292* (TUH)
S. mirzayanii Rech.f. & Esfand.	Prov. Bushehr: Bandar-e Taheri, *c.* 3 km from Shirinu to Galedar, *Gahreman and Mozaffarian 9553* (TUH)
S. multicaulis Vahl	Prov. Hamedan: on the road of Avaj to Razan, 24 km to Razan, *Salmaki, Eijy and Seyedi 45283* (TUH)
S. nemorosa L.	Prov. Ardebil: 10 km to Khalkhal from Asalem, *Salmaki, Eijy and Seyedi 45258* (TUH)
S. oligophylla Aucher ex Benth.	Prov. Qazvin: Alamut, *Mehdigholi and Attar 27630* (TUH)
S. pachystachya Trautv.	Prov. Urmieh: Gouran Abad, *Kazempour 13781* (TUH)

Table 1. *Continued*

Species	Collection data
S. palaestina Benth.	Prov. Hamadan: Kangavar to Kermanshah, 2–3 km towards Nahavand, after the deviation from the main road, *Zarre et al. 39499* (TUH)
S. reuteriana Boiss.	Prov. Chaharmahal-e Bakhtiari: Shahr-e Kord to Shalamzar, Agha-Sabz, *Mozaffarian 54583* (TUH)
S. rhytidea Benth.	Prov. Kerman: 40 km Baft, road of Gugher, Yas-Chaman pass, *Ghahreman et al. 28562* (TUH)
S. russellii Benth.	Prov. Kordestan: Marivan to Sanandaj (from old road), Gardane Garan., *Ghahreman and Mozaffarian 18323* (TUH)
S. sahendica Boiss. & Buhse	Prov. East Azarbayjan: on the road of Tabriz to Bostanabad, 5 km from Basmenj toward Lighvan, *Salmaki, Eijy and Seyedi 45277* (TUH).
S. sclarea L.	Prov. Ardebil: 40 km to Kaleybar from Ahar, *Salmaki, Eijy and Seyedi 45265* (TUH)
S. sclareopsis Bornm. ex Hedge	Prov. Lorestan: Khorramabad, Dougar, *Veiskarami 23917* (TUH)
S. sharifii Rech.f. & Esfand.	Prov. Bandar-Abbas: Kuh-e Genu, *Ghahreman and Mozaffarian 5580* (TUH)
S. staminea Montbret & Aucher ex Benth.	Prov. Azarbayjan: NW of Khoy, boundary altitude of Turkey, Zourabad, Ghezelje, *Mozaffarian 69988* (TUH)
S. suffruticosa Montbret & Aucher ex Benth.	Prov. Esfahan: between Esfahan and Shiraz, 7606 (TUH)
S. syriaca L.	Prov. Hamedan: 15 km after Avaj pass toward Razan, *Salmaki, Eijy and Seyedi 45282* (TUH)
S. trichoclada Benth.	Prov. Lorestan: Khorramabad, Tang-e-Tir, *Veiskarami 23919* (TUH)
S. verbascifolia M.Bieb.	Prov. East Azerbayjan: Arasbaran Protected Area, 25 km after Aynalu, 4 km to Asheghlu, *Salmaki, Eijy and Seyedi 45270* (TUH)
S. verticillata L.	Prov. East Azarbayjan: Arasbaran Protected Area, 5 km after Oskulu village, 2 km to Alankosh, *Salmaki, Eijy and Seyedi 45257* (TUH)
S. virgata Jacq.	Prov. Tehran: Qazvin, Alamut, Shahrak to Khoshkechal, *Ghahreman and Mozaffarian 9976* (TUH)
S. viridis L.	Prov. Gilan: Deylaman, *Saidi 18774* (TUH)
S. xanthocheila Boiss. ex Benth.	Prov. Tehran: *Shemshak 7656* (TUH)

Table 2. Selected scanning electron and light micrographs of various trichome types are illustrated in Figures 1–45 and 46–69, respectively.

Characters that could provide adequate variation in discrimination of taxa are as follows: presence or absence of glandular trichomes; cell number (uni-, bi- or multicellular); size of trichomes; presence of extremely long (lanate) trichomes; presence of branched trichomes and the branching pattern; type of glandular trichomes (sessile, subsessile, peltate or capitate); and presence of papillae on the trichome surface. In general, two kinds of trichome (non-glandular and glandular) can be observed on petioles, leaf blades and calyces.

The non-glandular trichomes are categorized as simple [with three subtypes: short (NGI), long (NGII) or extremely long (NGIII)] or branched (NGIV). Glandular trichomes are either capitate (GI–GIII) or peltate (GIV). Capitate glandular trichomes are further either subsessile or sessile (GI), short-stalked (GII) or long-stalked (GIII).

Vegetative and reproductive parts in all *Salvia* spp. are covered by an indumentum of non-glandular and glandular trichomes. The most common type of trichome in most studied species is a short simple trichome (NGI), accompanied by short-stalked capitate glandular trichomes (GI) (Table 2). Moreover, among short simple trichomes, the bi-/multicellular form is more common than the unicellular form.

NON-GLANDULAR TRICHOMES

Simple non-glandular trichomes
Among the non-glandular trichomes, the size, shape, cell number and presence of papillae on the trichome surface are considered to be reliable characters in the determination of taxa. In terms of size, simple non-glandular trichomes might be short (NGI; from 10 μm in *S. sclareopsis* Bornm. ex Hedge to 500 μm in *S. limbata* C.A.Mey., Fig. 62), long (NGII; up to 2000 μm in *S. aristata* Aucher ex Benth., Fig. 44) and

Table 2. Distribution of different types of trichome in the examined *Salvia* and *Pleudia* spp. (non-glandular types: (I), short simple trichomes; (II), long simple trichomes; (III), extremely long simple trichomes; (IV), branched trichomes; glandular types: (I), sessile–subsessile capitate trichomes; (II), short-stalked capitate trichomes; (III), long-stalked capitate trichomes; (IV), peltate trichomes. Arrangements of taxa are according to the latest phylogenetic studies. Those taxa indicated by an asterisk (*) were not classified in previous classifications, but are morphologically similar to species of section *Aethiopi*s. Density is divided arbitrarily into four categories: very dense, dense, sparse and very sparse. The trichomes in most taxa are smooth and bear no projections, but, in some taxa, they are papillate on the surface. Selected scanning electron micrographs of trichomes in *Salvia* are presented in Figures 1–45. Light micrographs in selected *Salvia* spp. are shown in Figures 46–69

| Species | Surface | Density | Non-glandular (NG) | | | | Glandular (G) | | | |
| | | | Simple | | | Branched | Capitate | | | Peltate |
			(NGI)	(NGII)	(NGIII)	(NGIV)	(GI)	(GII)	(GIII)	(GIV)
Salvia* subgenus *Leonia										
S. rusellii	Smooth	Sparse	+	+	–	–	–	+	–	+
S. verticillata	± Papillate	± Dense	+	+	–	–	–	+	+	+
Salvia* subgenus *Salvia										
Section *Salvia*										
S. bracteata	Papillate	Dense	+	+	–	–	+	+	+	–
S. macrochlamys	Papillate	Dense	+	+	–	–	+	+	+	–
S. pachystachya	Smooth	Sparse	+	–	–	–	+	+	+	–
S. suffruticosa	Smooth	Very sparse	+	–	–	–	+	–	–	–
S. trichoclada	Papillate	Dense	+	+	–	–	±	+	+	–
Section *Hymenosphace*										
S. dracocephaloides	Smooth	Sparse	+	+	–	–	–	–	–	+
S. hydrangea	Smooth	Very sparse	+	+	–	–	–	+	–	+
S. multicaulis	Smooth	± Dense	+	–	–	+	–	+	–	+
Salvia* subgenus *Sclarea										
Section *Aethiopis*										
Subsection *Gongrosphaceae*										
S. aethiopis	Smooth	Very dense	+	+	+	–	+	+	+	–
S. atropatana	Smooth	Dense	+	+	±	–	±	+	+	–
S. ceratophylla	Papillate	Very dense	+	+	+	–	–	+	+	–
S. chloroleuca	Smooth	Sparse	+	+	–	–	+	+	+	–
S. chorassanica	Smooth	Dense	+	+	–	–	–	+	+	+
S. grossheimii	Smooth	Dense	+	+	–	–	–	+	–	+
S. hypoleuca	Smooth	Very sparse	+	–	–	–	–	+	+	+
S. indica	Smooth	± Dense	+	+	–	–	–	+	+	–
S. limbata	Papillate	Sparse	+	–	–	–	–	+	–	+
S. oligophylla	Smooth	Very sparse	+	+	–	–	+	+	–	–
S. sahendica	Smooth	Dense	+	+	–	–	–	+	+	+
S. sclarea	Smooth	Dense	+	+	–	–	+	–	+	–
S. verbascifolia	Smooth	Dense	+	+	+	–	–	+	+	±
S. xanthocheila	Smooth	Dense	+	+	+	–	–	–	+	–
Subsection *Homalosphaceae*										
S. compressa	Smooth	± Dense	+	–	–	–	+	+	+	–
S. leriifolia	Smooth	Very dense	+	–	+	–	–	+	+	+
S. macrosiphon	Smooth	Dense	+	–	–	–	–	+	–	±
S. palaestina	Smooth	Dense	+	+	–	–	+	+	–	–
S. reuteriana	Papillate	Dense	+	–	–	–	+	+	–	–
S. rhytidea	Papillate	Dense	+	+	–	–	+	+	–	–
S. syriaca	Smooth	Dense	+	–	+	–	–	+	+	+
*S. brachysiphon	Papillate	Dense	+	–	–	–	–	+	+	–
*S. mirzayanii	Smooth	± Dense	+	–	+	–	–	–	+	±
*S. sclareopsis	Smooth	Dense	+	–	+	–	–	–	+	±
*S. sharifii	Smooth	Dense	+	–	–	–	+	+	–	–
Section *Hormium*										
S. viridis	Smooth	± Dense	+	–	–	–	+	+	–	–
Section *Plethiosphaceae*										
S. nemorosa	Smooth	Sparse	+	+	–	–	–	+	+	+
S. staminea	Papillate	Dense	+	+	–	–	–	+	+	+

Table 2. *Continued*

Species	Surface	Density	Non-glandular (NG)				Glandular (G)			
			Simple			Branched	Capitate			Peltate
			(NGI)	(NGII)	(NGIII)	(NGIV)	(GI)	(GII)	(GIII)	(GIV)
S. virgata	Smooth	Sparse	+	+	−	−	−	+	−	+
Pleudia										
P. aegyptiaca	Papillate	Dense	+	+	±	−	+	+	+	−
P. eremophila	Smooth	Very dense	+	+	−	−	−	+	+	+
P. macilenta	Smooth	Dense	+	+	−	−	+	−	+	−
P. santolinifolia	Smooth	Very dense	+	+	−	−	−	−	−	−
P. tebesana	Smooth	Dense	+	+	+	−	+	+	−	−
Salvia										
S. aristata	Smooth	Sparse	+	+	−	−	−	+	+	+
S. glutinosa	Papillate	Dense	+	+	−	−	−	+	+	+

extremely long (NGIII; > 3000 µm in *S. aethiopis* L., Fig. 9). Moreover, short simple trichomes (NGI) are uni-, bi- or multicellular.

Short simple trichomes (NGI) show some variability on the surface. They can be smooth (e.g. *S. virgata* Jacq., Fig. 38; *S. verbascifolia* M.Bieb., Fig. 25) or papillate (e.g. *S. chorassanica* Bunge, Fig. 13; *S. nemorosa* L., Fig. 34; *S. viridis* L., Fig. 33). Moreover, they can be erect (e.g. *S. sharifii* Rech.f. & Esfand., Fig. 32; *S. syriaca* L., Fig. 30), curved (e.g. *S. limbata*, Fig. 19; *S. verbascifolia*, Fig. 25; *S. virgata*, Fig. 38) or appressed (e.g. *S. dracocephaloides* Boiss., Fig. 6; *S. multicaulis* Vahl, Fig. 7). Short simple trichomes (NGI) vary from acicular or prickly in shape with an acute apex and smooth on the surface (e.g. *S. aristata*, Fig. 69; *S. syriaca*, Fig. 61), to curved towards the tip and blunt at the apex (*S. sharifii*, Fig. 32), to conical in shape, curved at the tip, blunt at the apex and wavy on the surface (e.g. *S. palaestina* Benth., Fig. 28).

Long simple trichomes (NGII) range from erect [e.g. *P. santolinifolia* (Boiss.) M.Will, N.Schmalz & Class. Bockh., Fig. 42; *S. aristata*, Fig. 44] to appressed [e.g. *P. tebesana* (Bunge) M.Will, N.Schmalz & Class. Bockh., Fig. 43; *S. verticillata* L., Fig. 2]. They can be smooth on the surface [e.g. *P. santolinifolia* (Boiss.) M.Will, N.Schmalz & Class. Bockh., Fig. 42; *S. aristata*, Fig. 44] or papillate (e.g. *S. verticillata*, Fig. 2), curved (e.g. *S. verticillata*, Fig. 2) or straight at the tip [e.g. *P. aegyptiaca* (L.) M.Will, N.Schmalz & Class. Bockh., Fig. 40], articulated (e.g. *S. verticillata*, Fig. 2) or non-articulated at their nodes (e.g. *P. santolinifolia*, Fig. 42; *S. aristata*, Fig. 44). In some species, the terminal cell might be much more elongated than the others and the basal cell is broader than long (e.g. *S. chloroleuca* Rech.f. & Aellen, Fig. 12; *S. russellii* Benth., Fig. 1; *S. verticillata*, Fig. 2). Species with

extremely long trichomes (NGIII; e.g. *S. aethiopis*, Fig. 9) are dispersed among different sections.

Branched non-glandular trichomes
Branched papillate trichomes with two or three arms are observed only in *S. multicaulis* (e.g. Figs 7, 8, 52, 53).

GLANDULAR TRICHOMES

Capitate glandular trichomes
Three forms of capitate glandular trichome are recognized in the present study. The first form is composed of subsessile and sessile capitate glandular trichomes (GI), with a basal cell, a stalk cell and a unicellular head, which is observed in most studied species (e.g. *S. aristata*, Fig. 68; *S. atropatana* Bunge, Fig. 54). The second form consists of short-stalked glandular trichomes [GII; up to 10 µm; e.g. *P. eremophila* (Boiss.) M.Will, N.Schmalz & Class. Bockh., Fig. 65] and the last form is of long-stalked glandular trichomes (GIII; up to 150 µm; e.g. *S. ceratophylla* L., Fig. 11).

The stalks of glandular trichomes can be uni- (e.g. *P. eremophila*, Fig. 65), bi- (e.g. *S. leriifolia* Benth., Fig. 57; *S. macrochlamys* Boiss. & Kotschy, Figs 47, 48; *S. sahendica* Boiss. & Buhse, Fig. 56; *S. trichoclada* Benth., Fig. 49) or multicellular (e.g. *S. bracteata* Banks & Sol., Fig. 3; *S. ceratophylla*, Fig. 11; *S. pachystachya* Trautv., Fig. 5). The head of stalked glandular trichomes can be uni- (e.g. *S. macrochlamys*, Fig. 47) or multi-cellular (e.g. *P. leriifolia*, Fig. 58). Moreover, the basal cell of stalks can be of the same size as the other cells (e.g. *S. leriifolia*, Fig. 57) or broader than other stalk cells (e.g. *S. aristata*, Fig. 67; *S. macrochlamys*, Fig. 48).
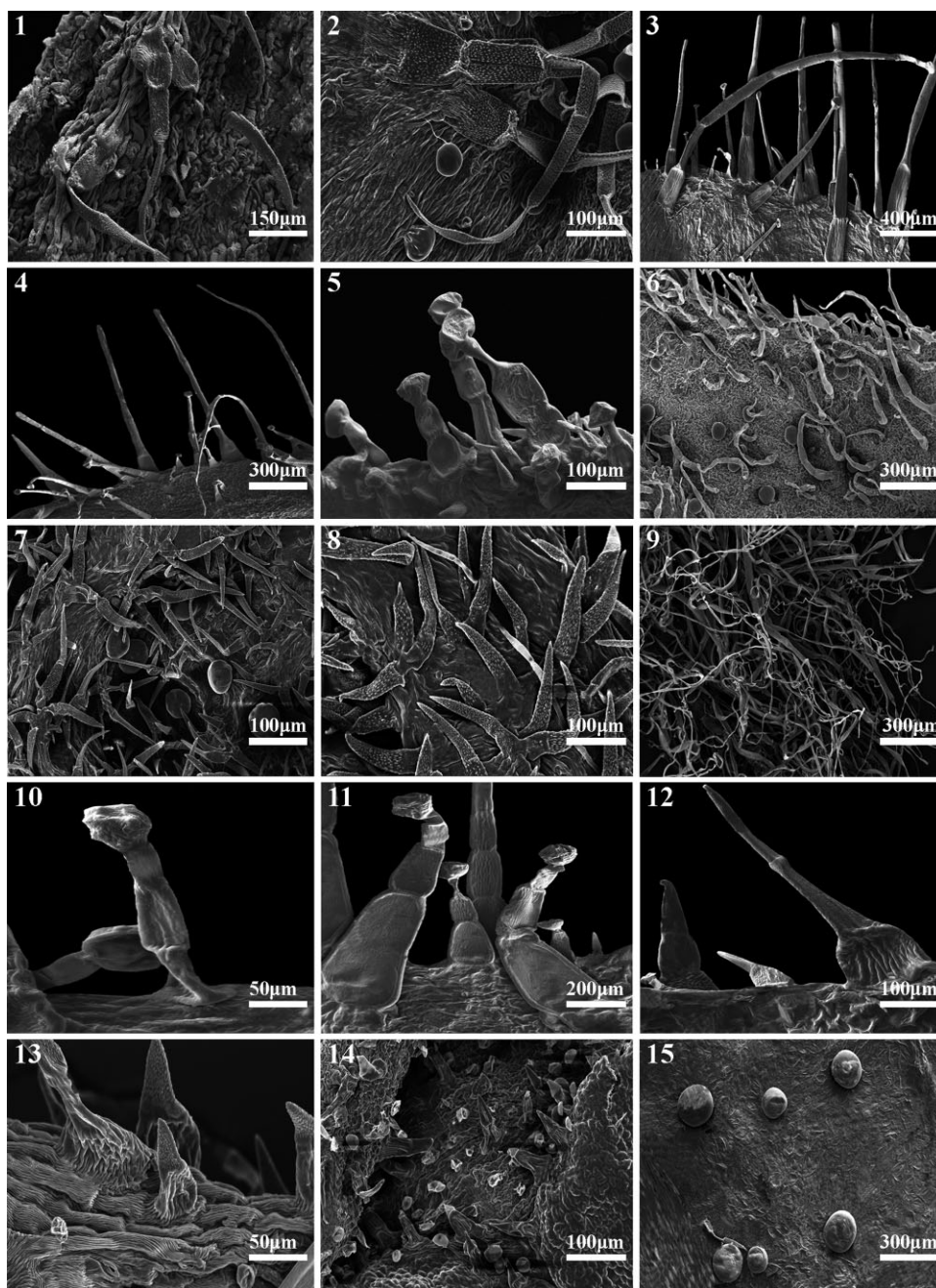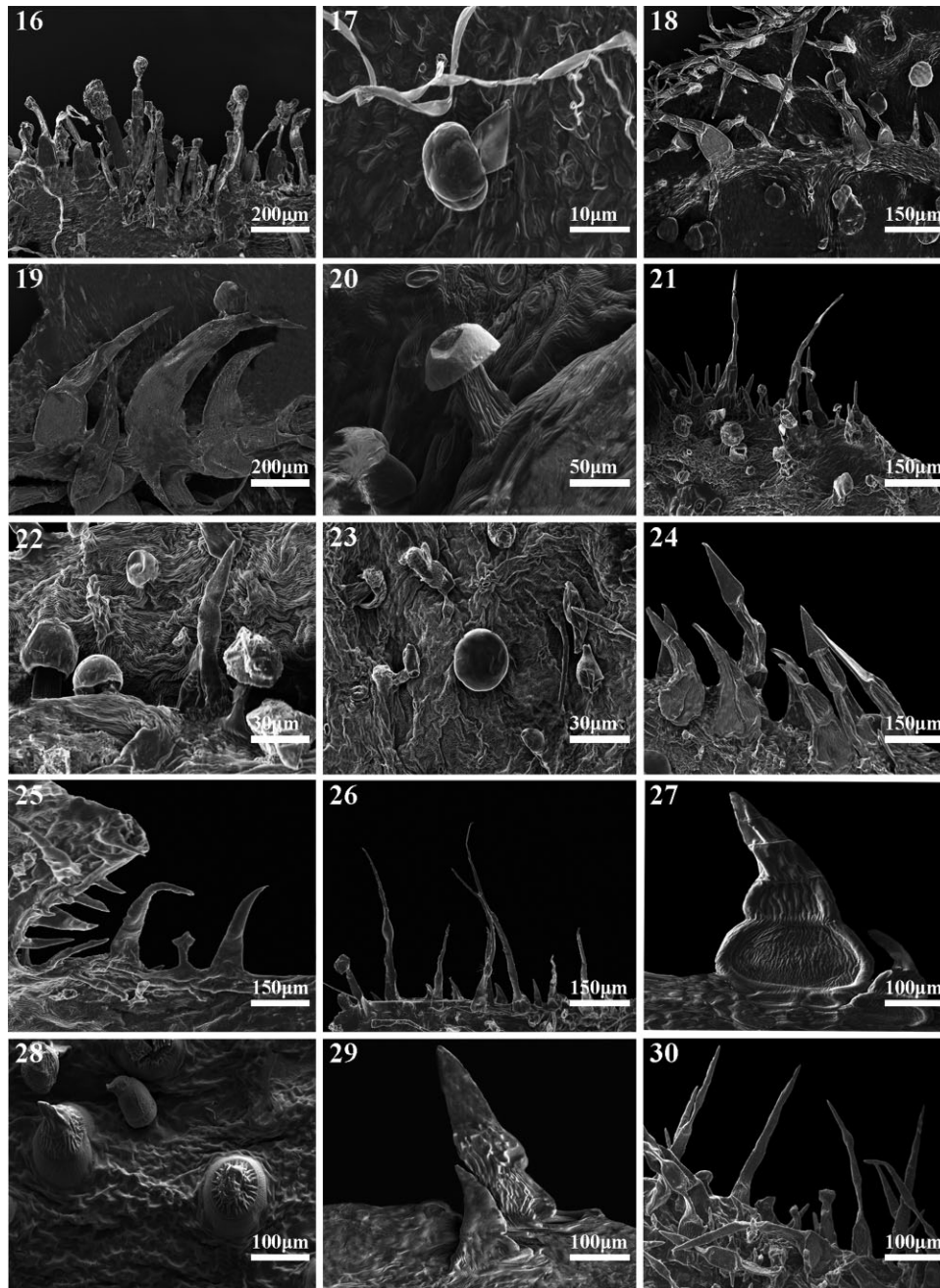
Figures 1–15. Scanning electron micrographs (from calyces and leaves) of trichomes. Fig. 1. *Salvia rusellii*. Fig. 2. *S. verticillata*. Fig. 3. *S. bracteata*. Fig. 4. *S. macrochlamys*. Fig. 5. *S. pachystachya*. Fig. 6. *S. dracocephaloides*. Figs 7, 8. *S. multicaulis*. Fig. 9. *S. aethiopis*. Fig. 10. *S. atropatana*. Fig. 11. *S. ceratophylla*. Fig. 12. *S. chloroleuca*. Fig. 13. *S. chorassanica*. Fig. 14. *S. grossheimii*. Fig. 15. *S. hypoleuca*.

Peltate glandular trichomes

This type of trichome consists of a basal cell, a short stalk cell and a multicellular head (four to eight cells) with subcuticular oil storage cavity (GIV; e.g. *S. chorassanica*, Fig. 55; *S. dracocephaloides*, Fig. 50; *P. eremophila*, Fig. 64; *S. hydrangea* DC. ex Benth., Fig. 51).

DISCUSSION

This study represents the first comprehensive investigation of trichome micromorphology in the genus *Salvia* and its relatives. In accordance with previous studies of trichome morphology in Lamiaceae (Cantino, 1990; Navarro & El Qualidi, 2000; Moon

Figures 16–30. Scanning electron micrographs of trichomes. Figs 16, 17. *Salvia indica*. Figs 18, 19. *S. limbata*. Fig. 20. *S. oligophylla*. Figs 21–23. *S. sahendica*. Fig. 24. *S. sclarea*. Figs 25, 26. *S. verbascifolia*. Fig. 27. *S. macrosiphon*. Fig. 28. *S. palaestina*. Fig. 29. *S. rhytidea*. Fig. 30. *S. syriaca*.

et al., 2009; Salmaki *et al.*, 2009), including *Salvia* (Singh *et al.*, 1974; Bokhari & Hedge, 1977; Corsi & Bottega, 1999; Ilçim *et al.*, 2009; Kahraman *et al.*, 2010; Celep *et al.*, 2014a, b), our investigation reveals the usefulness of such characters in providing fundamental taxonomic criteria in taxon delimitation at various levels, especially at the species level. Furthermore, the data presented here indicate the potential applicability of such characters in the determination of evolutionary trends in indumentum characters in *Salvia* and allies. It has been recognized previously that most epidermal characters, especially hair and stomatal characters, provide large amounts of infrageneric variation, but have little phylogenetic value above the species level (Cantino, 1990). However, Singh *et al.* (1974) defined a detailed terminology of
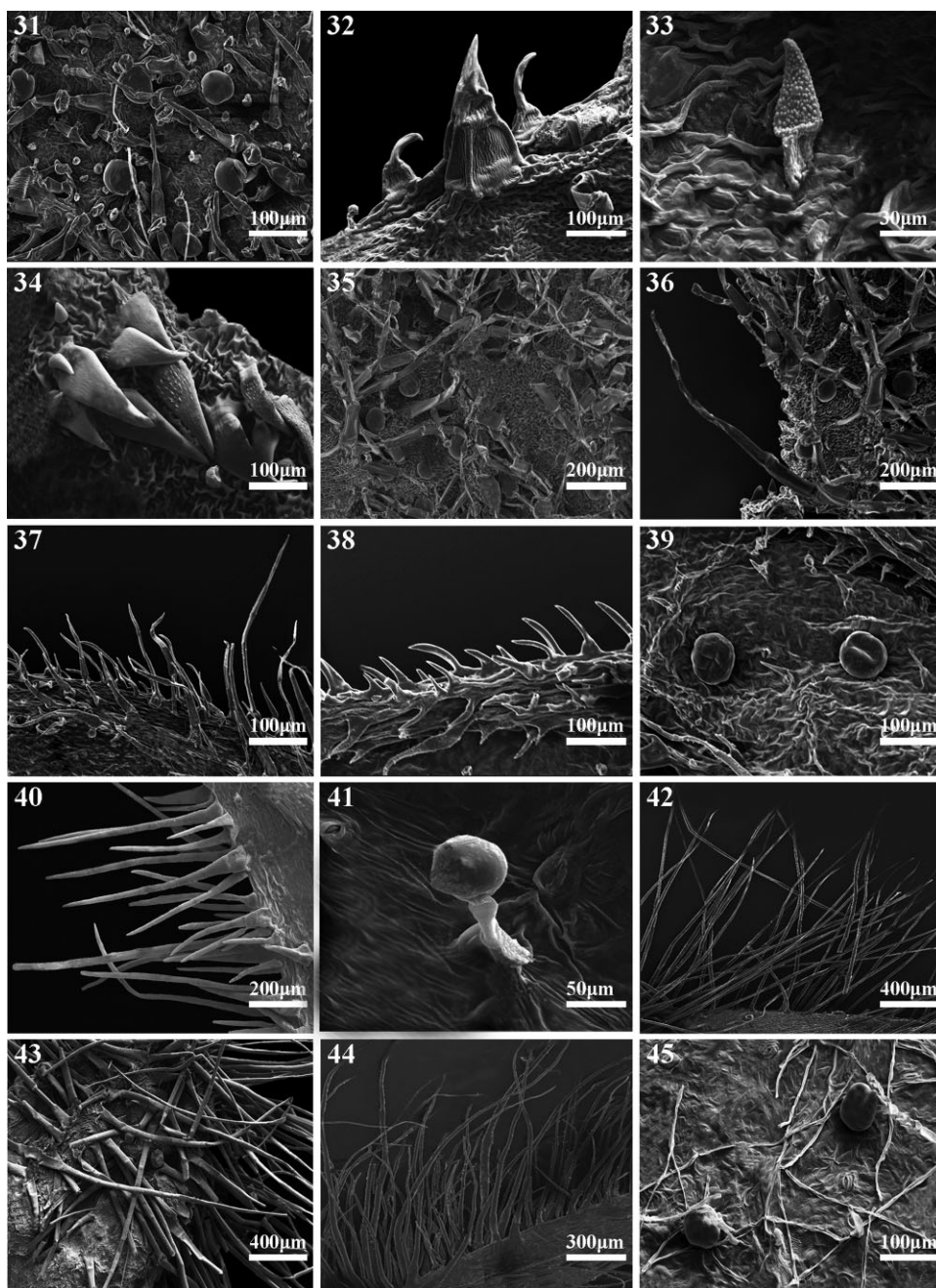
Figures 31–45. Scanning electron micrographs of trichomes in *Salvia* and *Pleudia*. Fig. 31. *Salvia syriaca*. Fig. 32. *S. sharifii*. Fig. 33. *S. viridis*. Fig. 34. *S. nemorosa*. Figs 35, 36. *S. staminea*. Figs 37–39. *S. virgata*. Figs 40, 41. *Pleudia aegyptiaca*. Fig. 42. *P. santolinifolia*. Fig. 43. *P. tebesana*. Fig. 44. *S. aristata*. Fig. 45. *S. glutinosa*.

glandular and non-glandular trichome types in *Salvia* of India which could be used to distinguish 12 species.

The types of glandular trichome and their distribution provide valuable characters for comparison in some genera (Husain *et al*., 1990; Navarro & El Qualidi, 2000; Salmaki *et al*., 2009; Xiang *et al*., 2010). Special attention has been paid to subsessile glandular trichomes in the generic delimitation in Verbenaceae and Lamiaceae, in which 11 types could be distinguished (Abu-Asab & Cantino, 1987; Cantino, 1990). In Lamiaceae subfamily Nepetoideae, which includes *Salvia* and relatives, a glandular trichome with a single large cell at the head is known to be the most common and primitive state (Abu-Asab & Cantino, 1987).
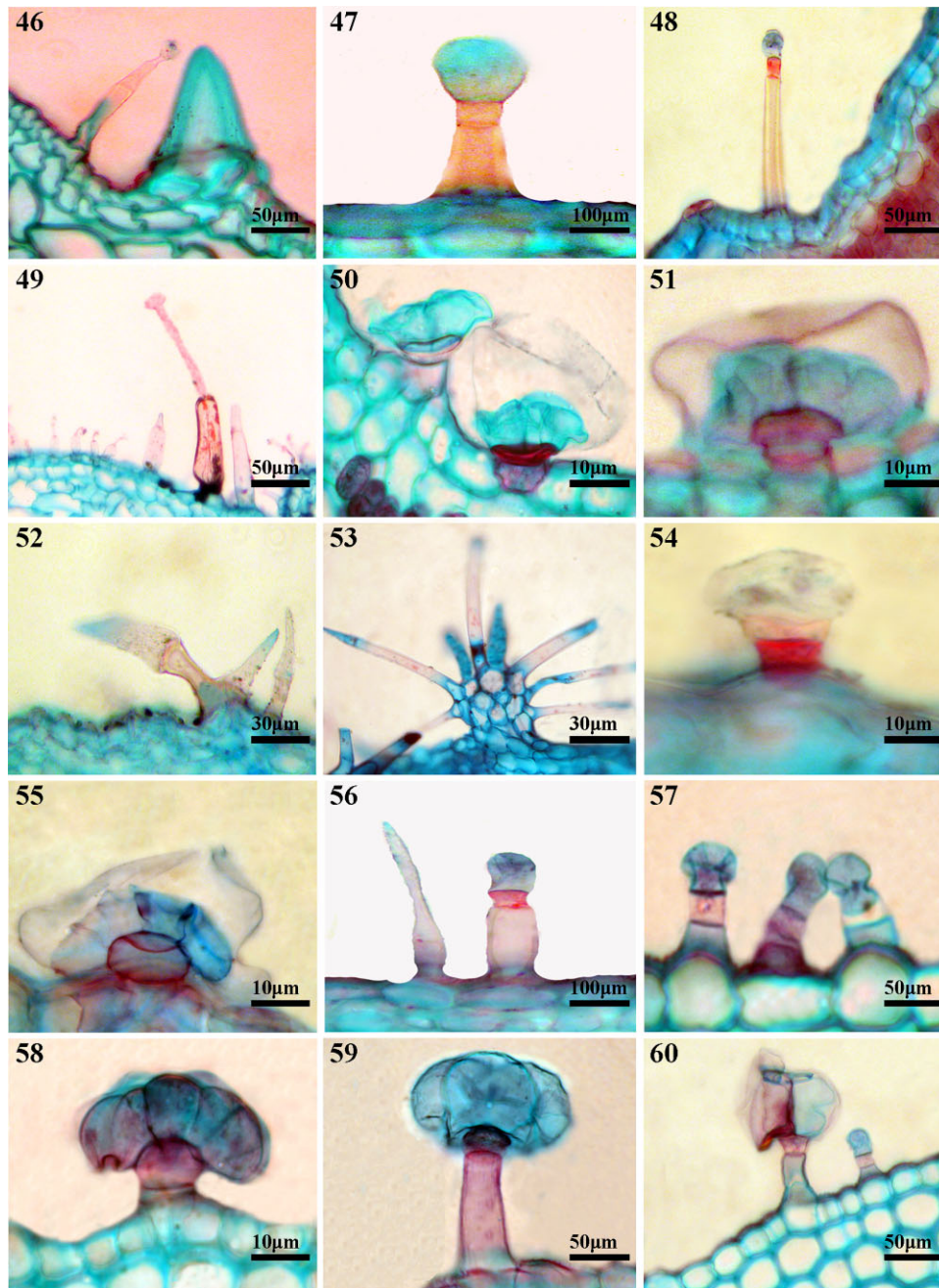
Figures 46–60. Light micrographs of trichomes in *Salvia*. Fig. 46. *Salvia bracteata*. Figs 47, 48. *S. macrochlamys*. Fig. 49. *S. trichoclada*. Fig. 50. *S. dracocephaloides*. Fig. 51. *S. hydrangea*. Figs 52, 53. *S. multicaulis*. Fig. 54. *S. atropatana*. Fig. 55. *S. chrossanica*. Fig. 56. *S. sahendica*. Figs 57–60. *S. leriifolia*.

Previous studies addressing trichome morphology in Lamiaceae have usually only included a limited number of species and have aimed to delimit certain groups in the family or to describe general trends in indumentum evolution in the family (Abu-Asab & Cantino, 1987; Cantino, 1990; Moon *et al.*, 2009). A few studies have dealt with trichome morphology in detail (Ilçim *et al.*, 2009; Celep & Doğan, 2010).

The present study is the broadest of its kind and includes representatives of various groups of *Salvia* and the newly resurrected genus *Pleudia* Raf. Various glandular trichome types are present in most species studied and have taxonomic value at the specific and subspecific levels. For example, *S. suffruticosa* Montbert & Aucher ex Benth. and *S. pachystachya*, which belong to section *Salvia* (Hedge, 1974), differ from
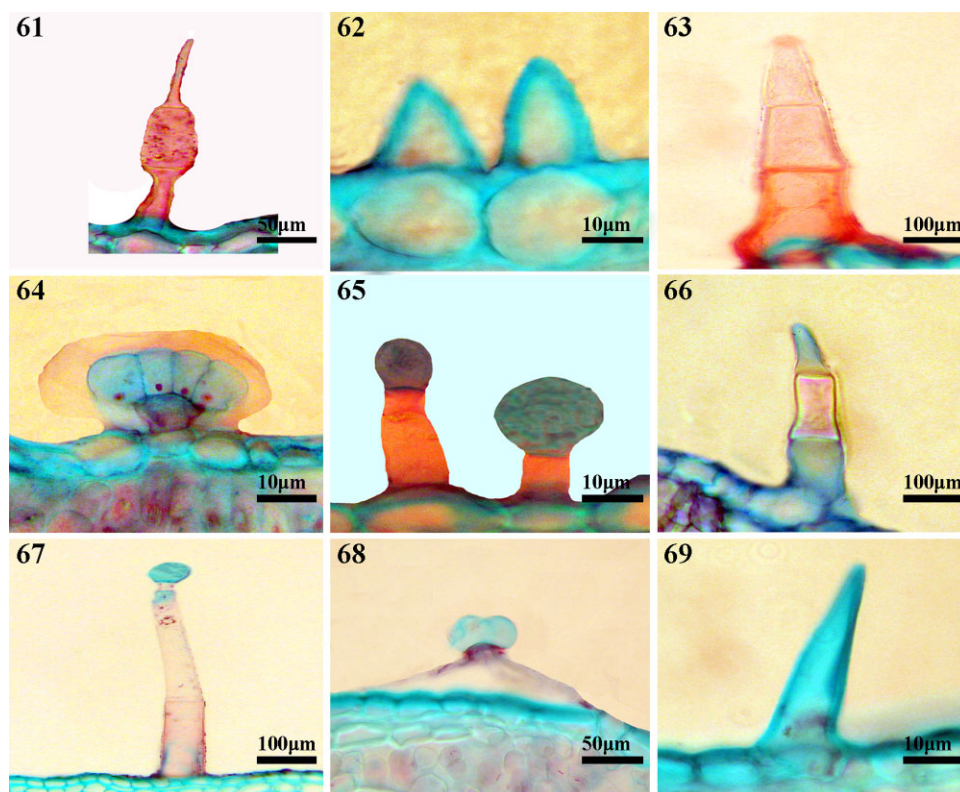
Figures 61–69. Light micrographs of trichomes in *Salvia* and *Pleudia*. Fig. 61. *Salvia syriaca*. Fig. 62. *S. sclareopsis*. Fig. 63. *Pleudia aegyptiaca*. Figs 64, 65. *P. eremophila*. Fig. 66. *P. macilenta*. Figs 67–69. *S. aristata*.

each other by their inflorescence indumentum. *Salvia pachystachya* has glandular trichomes, whereas *S. suffruticosa* does not bear any glandular trichomes on the stem (Hedge, 1982a).

As the taxonomy of the genus is still controversial and under discussion and the available infrageneric classifications do not reflect the current understanding of the supraspecific level in *Salvia*, we evaluated trichome characters based on the clades I–IV derived by molecular phylogenetic studies (*sensu* Walker *et al*., 2004; Will & Claßen-Bockhoff, 2014).

CLADE I

Salvia 'Clade I' appears to include all members of subgenera *Leonia* (La Llave & Lex.) Benth. and *Sclarea* (Moench) Benth. and those members of subgenus *Salvia* not included in *Salvia* 'Clade III' (Walker *et al*., 2004). The type species for the genus is *S. officinalis* L., which belongs to this clade. Our findings agree with those of Corsi & Bottega (1999) in the recognition of various types of peltate and capitate trichomes in *S. officinalis*.

Subgenus Leonia
Salvia russellii and *S. verticillata* are representatives of section *Hemisphace* Benth., which are character-

ized by verticillasters composed of many (20–40) small flowers (Bentham, 1876). *Salvia russellii* is a clear relative of the much more widespread *S. verticillata*, but is more compact in habit with narrowly oblong leaves and acuminate (not mucronate) calyx teeth (Hedge, 1982a). A recent molecular phylogenetic investigation revealed that *S. verticillata* belongs to *Salvia* 'Clade I' with stamen type C (Hedge, 1982a; Walker *et al*., 2004). As these two *Salvia* spp. are morphologically similar, we presume that *S. russellii* also belongs to *Salvia* 'Clade I'. The species has both short and long simple papillate non-glandular (NGI and NGII) trichomes, and sessile and short glandular trichomes (GII). Contrary to *S. russellii*, which is characterized by having only short-stalked capitate-type glandular trichomes on its calyx, *S. verticillata* also possesses long-stalked capitate trichomes (GIII). Thus, the lack of long-stalked capitate trichomes in *S. russellii* is the main difference from *S. verticillata*. Although the indumentum is helpful for the separation of species, it appears uninformative at the subgeneric level.

Subgenus Salvia
According to Bentham's (1832) classification, *S. bracteata*, *S. macrochlamys*, *S. pachystachya*, *S. suffruti-*

cosa and *S. trichoclada* belong to section *Eusphace* Benth., but, later, section *Eusphace* was designated as the type section of *Salvia* by Hedge (1974) (as section *Salvia*). Section *Salvia* is composed of shrubs and herbs that are woody at the base, with staminal connectives relatively equal to filaments and fertile lower thecae. The characteristic features of this section are pinnatisect or simple leaves, herbaceous or suffruticose stems, calyx little enlarging after anthesis, lips not diverging, upper lip of corolla more or less straight, and corolla tube annulate. Staminal connectives are equal or slightly longer than filaments and lower theca are fertile (Hedge, 1974). Most species of *Salvia* section *Salvia* have a European-Mediterranean distribution pattern. The phylogenetic relationships of the species in the genus are still unclear. Our data corroborate a previous study (Kahraman *et al.*, 2010), indicating the presence of multicellular glandular and non-glandular trichomes in *S. macrochlamys*. The delimitation of these species based solely on morphological characters is problematical, and thus this species complex is well known in the literature for its taxonomic difficulties (Hedge, 1982a; Jamzad, 2012). For example, *S. bracteata* and *S. trichoclada* are morphologically similar (Hedge, 1982a; Jamzad, 2012). Although an extraordinary variation of the indumentum was observed among some species in this complex, differentiation among trichome types in this otherwise homogeneous section may provide an effective means for taxon delimitation. All the studied species possess short simple trichomes, but only three have long simple hairs (*S. bracteata*, *S. macrochlamys* and *S. trichoclada*). Species also differ from each other in glandular trichome types. All members contain stalked glandular hairs with the exception of *S. suffruticosa*. The variation of trichomes in section *Salvia* is sufficiently large to provide some evidence for the separation of species, but there is no indumentum character that could be considered as an important synapomorphy of the section.

Salvia section *Hymenosphace* Benth. is represented here by *S. dracocephaloides*, *S. hydrangea* and *S. multicaulis*. Section *Hymenosphace* is distinguishable by its expanded fruiting calyces which are membranous-reticulate in texture (Hedge, 1982a). *Salvia* section *Hymenosphace* is composed of herbaceous and woody semi-shrubby plants (Bentham, 1876). Recently, Dizkirici *et al.* (2015) provided a phylogenetic study of section *Hymenosphace* in Turkey, and reported that taxa in this section are grouped in *Salvia* 'Clade I'. This result was completely congruent with previous molecular phylogenetic studies (Will & Claßen-Bockhoff, 2014). Morphological evidence of the calyx clearly supports the close relationship of *S. hydrangea* and *S. draco-*

cephaloides, but, in trichome micromorphology, they show some differences. *Salvia hydrangea* possesses short-stalked capitate trichomes (GII), whereas *S. dracocephaloides* lacks this kind of trichome. Moreover, *S. multicaulis* has branched trichomes, whereas *S. hydrangea* and *S. dracocephaloides* are similar in having short and long simple trichomes and sessile and subsessile glandular ones. Branched trichomes in *S. multicaulis* are two- or three-armed, and are usually frequent on the leaves rather than the stem and calyx. In addition, the plant shoots are covered with short simple trichomes and different types of glandular trichome.

Subgenus Sclarea

Salvia aristata, *S. aethiopis*, *S. sclarea* L. and *S. verbascifolia*, which have been assigned to section *Aethiopis* (*sensu* Bentham, 1876; Boissier, 1879), have been included in previous molecular phylogenetic studies (Walker & Sytsma, 2007; Will & Claßen-Bockhoff, 2014). These studies placed *S. aristata* in a different clade from the rest of the taxa attributed to this section. This species belongs to a lineage consisting of *Pleudia* spp., a group of western Asian and northern African species including *P. aegyptiaca*, *P. trichocalycina* (Benth.) M.Will, N.Schmalz & Class.-Bockh. and *Zhumeria majdae* Rech.f. & Wendelbo ('Clade III' *sensu* Will & Claßen-Bockhoff, 2014), whereas *S. aethiopis*, *S. sclarea* and *S. verbascifolia* form the well-supported 'Clade I' (Walker & Sytsma, 2007). However, trichome micromorphology does not provide an important synapomorphy supporting the phylogenetic placement of *S. aristata*. In other words, there is no important trichome morphological character placing this species with other members of 'Clade III' (Fig. 70). Although only a limited number of species from this section have been included in previous molecular studies, most species analysed in the present survey belong to this section. Traditionally, members of this section were divided into two subsections: subsection *Gongrosphaceae* Briq. and subsection *Homalosphaceae* (Bunge) Briq. Taking macromorphology into account, the former is characterized by a corolla tube abruptly dilated at the throat, small nectary scales present and staminodes usually absent, whereas, in the latter, the corolla tube is gradually dilated towards the throat, no nectary scales are present and the upper stamens are staminodial. Based on trichome micromorphology, non-glandular and glandular trichomes occur diversely among the studied species. Five species of subsection *Gongrosphaceae* included here (*S. aethiopis*, *S. atropatana*, *S. ceratophylla*, *S. verbasifolia* and *S. xanthochelia* Boiss. ex Benth.) are characterized by extremely long (lanate) trichomes, which also occur in
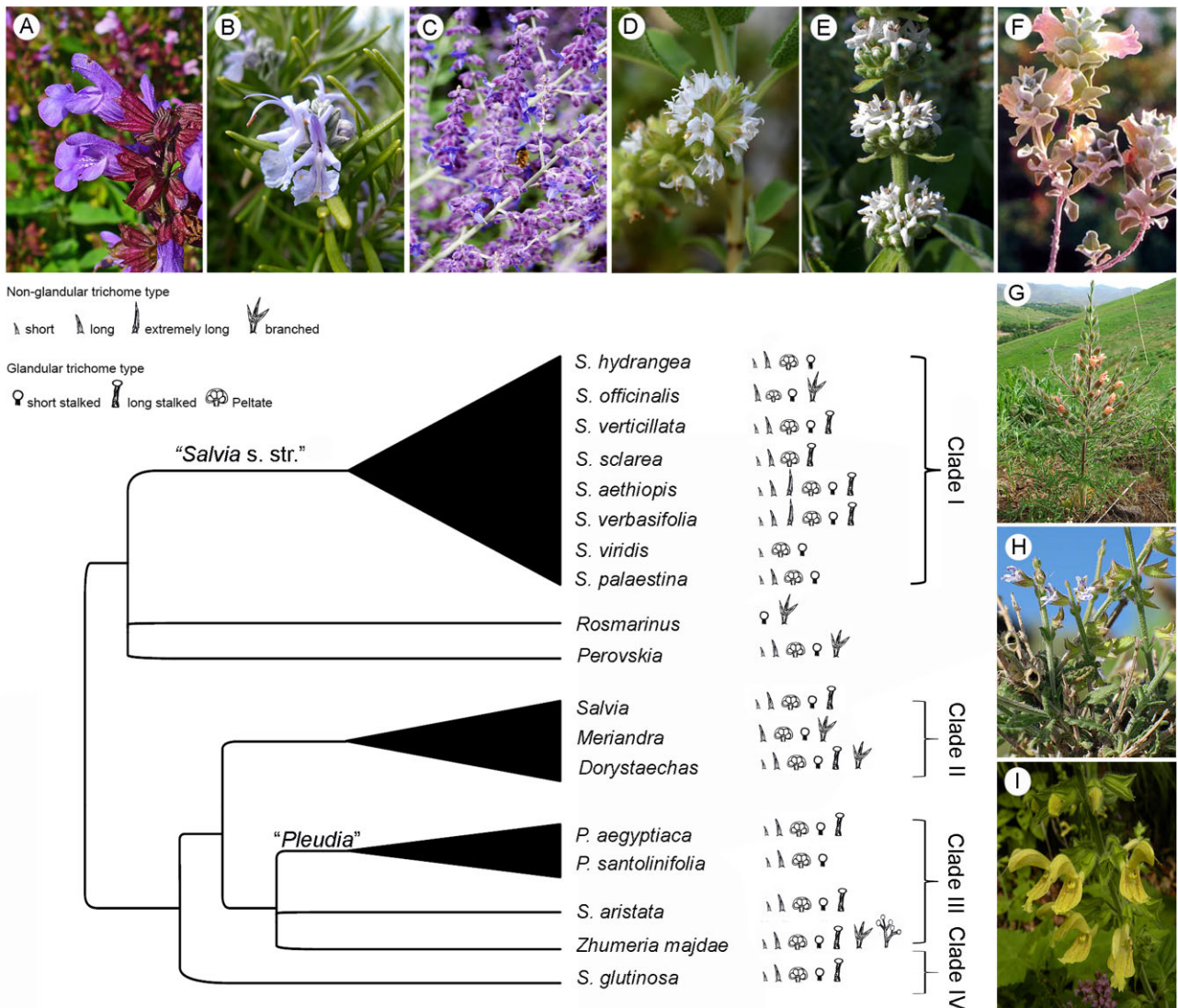
Figure 70. Diagram of trichome types in *Salvia s.l.* and their distribution on the recent phylogenetic tree (simplified tree based on Walker & Sytsma, 2007; Will & Claßen-Bockhoff, 2014; photographer in parentheses). A, *Salvia officinalis* (photograph: H. Zell). B, *Rosmarinus officinalis* (photograph: Kenpei). C, *Perovskia atriplicifolia* (Thames Barrier Park, London). D, *Meriandra strobilifera* (photograph: A. Kasajusaroj). E, *Dorystaechas hastata* (photograph: D. L. Nickrent). F, *Zhumeria majdae* (photograph: http://medplant.ir). G, *Salvia aristata* (photograph: Y. Salmaki). H, *Pleudia aegyptiaca* (photograph: http://www.prota4u.org). I, *Salvia glutinosa* (photograph: Y. Salmaki).

two species of subsection *Homalosphaceae* (*S. palaestina* and *S. syriaca*). Long simple hairs occur in most species of the former subsection, whereas they have been observed only in two species of the latter subsection, i.e. *S. palaestina* and *S. rhytidea* Benth. In contrast with members of *Salvia* subsection *Homalosphaceae*, which contain sessile or subsessile glandular trichomes, this subtype is absent in species belonging to *S.* subsection *Gongrosphaceae*. Moreover, five species of the former possess short-stalked glandular hairs with two- to six-celled heads (*S. aristata*, *S. chorassanica*, *S. indica* L., *S. limbata* and *S. ver-bascifolia*), whereas this subtype of glandular trichomes occurs in three species of the latter (*S. compressa* Vent., *S. leriifolia* and *S. syriaca*). Overall, the trichome variability in this section is sufficiently high to persuade us to accept that the feature might be effective for the separation of species in the section, but not sufficiently informative to diagnose the section.

There are a few unplaced species (e.g. *S. brachysiphon*, *S. sclareopsis* and *S. sharifii*) in our study which were not classified in the previous classifications (Bentham, 1876; Boissier, 1879), but they are

morphologically similar to species of section *Aethiopis* (Hedge, 1982a). According to Hedge (1982a) and Jamzad (2012), *S. brachysiphon* belongs to the *S. aethiopis* species group. Moreover, trichome micromorphology corroborates the similarity of this species with the members of *S.* section *Aethiopis*. *Salvia sclareopsis* is close to the two species of section *Aethiopis*, *S. macrosiphon* and *S. reuteriana* (Hedge, 1982a). Hybridization can occur between *S. sclareopsis* and its close relatives (Hedge, 1982a). *Salvia sclareopsis* differs from *S. macrosiphon* in the much larger and broader bracts, thick leaf texture and the short stem indumentum. Moreover, *S. sclareopsis* is morphologically similar to *S. reuteriana* and shares conspicuous bracts, but differs in height, leaf texture and calyx and corolla dimensions. *Salvia sharifii* is obviously a close ally of the widespread and polymorphic *S. macrosiphon*, but it seems to merit specific separation, especially because of its broadly ovate leaves with entire margins. With regard to trichome micromorphology, *S. sharifii* is generally similar to *S. macrosiphon*, except it lacks the subsessile to sessile capitate trichomes.

The only species of section *Hormium* (Moench) Benth. found in Iran is *S. viridis*. *Salvia viridis* is a distinctive annual species occurring in north-western Africa and the Mediterranean region. It is characterized by a small tubular calyx, a small corolla and linear stipules on its floral leaves. This species belong to the well-supported *Salvia* 'Clade I' (Walker & Sytsma, 2007; Will & Claßen-Bockhoff, 2014), a lineage consisting of *S. aethiopis*, *S. sclarea* and *S. verbascifolia* (Fig. 70). *Salvia viridis* and *S. hormium* L. are closely related and, currently, *S. hormium* is considered as a synonym of *S. viridis* (Jamzad, 2012). Short sessile and short-stalked glandular and short simple trichomes were observed in *S. viridis*.

Salvia nemorosa, *S. staminea* Montbert & Aucher ex Benth. and *S. virgata* are three studied representatives of section *Plethiosphaceae* Benth. These species have similar trichome types. The only difference is observed in *S. virgata* which, unlike the two other species, lacks long-stalked glandular trichomes. Moreover, *S. staminea* is characterized by its densely simple trichomes which are smooth on the surface, whereas the other two possess sparsely simple trichomes that are papillate on the surface. In conclusion, trichome micromorphology cannot be used as an effective tool for the characterization of the section, but supports the separation of the species in this section.

CLADE II

Phylogenetic studies reveal that *Dorystaechas* and *Meriandra* are either sister to *Salvia* 'Clade II' or represent a grade towards a monophyletic *Salvia* 'Clade II', a large lineage of *Salvia* including the New World section *Audibertia* and subgenus *Calosphace* (Walker *et al.*, 2004; Walker & Sytsma, 2007; Will & Claßen-Bockhoff, 2014). The monotypic genus *Dorystaechas* (the only species is *D. hastata* Boiss. & Heldr. ex Benth.), restricted to south-west Anatolia, possesses both non-glandular (NGI, NGII, NGIV) and glandular (GII, GIII, GIV; see Moon *et al.*, 2009) trichomes. *Meriandra* Benth. consists of two species and both glandular and non-glandular trichomes are present in *M. bengalensis* (Roxb.) Benth. (Moon *et al.*, 2009). The presence of simple non-glandular trichomes and different kinds of glandular trichome has been reported for several New World *Salvia* spp. (Siebert, 2004). Among the simple trichomes, the short unicellular trichome is the common type, whereas long simple trichomes are reported rarely among New World *Salvia* spp. (Moon *et al.*, 2009). Moreover, both capitate and peltate glandular trichomes are observed frequently among these taxa (Serrato-Valenti *et al.*, 1997).

CLADE III

According to Walker & Sytsma (2007), *Salvia* 'Clade III' is paraphyletic with respect to *Zhumeria majdae*. Thus, Will & Claßen-Bockhoff (2014) divided the paraphyletic 'Clade III' into two monophyletic clades. They accepted the *S. aegyptiaca* group with *Zhumeria* as a well-supported clade, i.e. 'Clade III', and transferred the remaining species to the fourth independent evolutionary lineage (*Salvia* 'Clade IV'). The plants in 'Clade III' all have somewhat elongated connectives, both thecae producing pollen and the posterior thecae never fused (stamen type M, Walker & Sytsma, 2007). Taking the species groups proposed by Hedge (1974, 1982a, b) into account, *Salvia* 'Clade III' also probably includes *S. macilenta* Boiss., *S. tebesana* Bunge and *S. eremophila* Boiss., all belonging to *S.* section *Notiosphace* Benth. Taxa in *S.* section *Notiosphace* are characterized by their small size (often < 25 cm in height), small revolute leaves and bracts. Based on these characters, this section is distinctly isolated from other groups of the Old World *Salvia* (Bokhari & Hedge, 1977).

Rafinesque (1837) separated *S. aegyptiaca* in the genus *Pleudia* based on differences in corolla shape (contains exclusively small-flowered species) and stamen structure. This treatment remained largely unrecognized until Will *et al.* (2015) resurrected Rafinesque's *Pleudia* to accommodate species of *Salvia* section *Notiosphace*. Altogether, *Pleudia* includes 13 species of low-growing shrubs or suffruticose herbs, often appearing as dwarf shrubs. They are typical elements of the Saharo-Sindian phytogeo-

graphical region, usually locally restricted to arid habitats in North Africa to South-West Asia. The species generally grow on sandy soil, gravel wadi beds and basalt rocks, and on open limestone and basaltic slopes (Will *et al.*, 2015).

Both non-glandular and glandular trichomes are observed among *Pleudia* spp. The common types of non-glandular trichome among the studied species are the short and long trichomes, but the extremely long type is a rare state only observed in *P. tebesana*. Moreover, among different kinds of glandular trichome, subsessile to sessile trichomes are frequent and were observed in almost all members of this section. Short-stalked glandular trichomes are noted in all members of this section, with the exception of *P. macilenta* (Boiss.) M.Will, N.Schmalz & Class. Bockh., which is characterized by long-stalked glandular trichomes. *Pleudia eremophila*, which possesses short-stalked glandular trichomes with two- to eight-celled heads, can be distinguished from those species with short-stalked capitate trichomes. Moreover, among all species in this section, *P. aegyptiaca* is papillate on the surface. Variation in trichome characters appears to have particular value in the separation of different *Pleudia* spp.

Zhumeria majdae is a shrubby species endemic to Iran with historically uncertain affinities (Bokhari & Hedge, 1976), but is placed in molecular phylogenetic analyses as a part of a trichotomy with *Salvia* 'Clade III' (Fig. 70). *Zhumeria* is unusual in having two fertile stamens and two large staminodes (Bokhari & Hedge, 1976). According to Bokhari & Hedge (1976), *Zhumeria* is characterized by a diverse set of glandular and non-glandular hairs, which have not been recorded in combination for any other genus of the family. Non-glandular trichomes might be simple, branched multicellular and multinodal. Moreover, glandular trichomes are also diverse in form and can be simple (with a one-celled stalk and head to multicelled stalk and head) or branched (Bokhari & Hedge, 1976). Our results show that the presence of glandular and non-glandular branched trichomes characterizes this species, which is phylogenetically embedded in 'Clade III'.

CLADE IV

Salvia 'Clade IV' consists of East Asian species loosely corresponding to Bentham's subgenus *Salvia* section *Drymosphace* (Will & Claßen-Bockhoff, 2014). Although this group of species probably includes nearly 100 species with a centre of diversity in China, *S. glutinosa* is the only species distributed in Europe and expanding eastwards to Iran (Walker & Sytsma, 2007; Jamzad, 2012). This species is most probably the best known member of 'Clade IV' and shows a typical stamen morphology of this clade, in which the posterior thecae are rudimentary and produce small amounts of pollen or none at all. This species is further characterized by hastate leaves, six-flowered verticillasters and a pubescent corolla tube. *Salvia glutinosa* is covered with short and long, simple, and sessile and stalked glandular trichomes.

CONCLUSIONS

Trichome characters show levels of variability among species, even when assigned to the same section, but are constant among various populations of a certain species. Therefore, we assess the trichome characters as systematically important. Our results indicate that, although trichome micromorphology provides a source of reliable data in the delimitation of species, this feature has low phylogenetic value in the genus *Salvia*, especially because of the high variation, even among closely related species. The presence of both kinds of trichome is a common condition, and glandular trichomes normally co-occur with non-glandular trichomes (Fig. 70). Our results also show a wide distribution of subsessile glandular trichomes among *Salvia* and allies. Short-stalked glandular trichomes were observed in most taxa. The absence of stalked glandular trichomes is a possible synapomorphy for certain species. For example, four morphologically similar species of section *Homalosphaceae* are characterized by lacking stalked glandular trichomes. Moreover, our results show that branched trichomes are present in almost all clades of Salviinae (Fig. 70), but less frequently in New World taxa. More detailed taxonomic surveys are needed in this widely distributed genus in order to clarify the relationships at different taxonomic ranks.

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