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# LEAF ANATOMY AND HAIRS OF TURKISH *Satureja* L. (LAMIACEAE)

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There are some taxonomic uncertainties within the Turkish members of *Satureja*. It is extremely difficult to distinguish some *Satureja* species because of their great morphological similarity. *Satureja* species are used as herbal teas and spices, and for this reason they are important commercial and medicinal plants. In this study, the leaf anatomy and hair features of species were examined by LM and SEM. The investigated species can be divided into two main groups, as bifacial and equifacial leaves according to mesophyll structure. They can be secondarily divided into two types based on the midrib region in cross section, as projecting or nonprojecting. Thirdly, two main vascular bundle types can be identified in transverse section according to the presence or absence of sclerenchyma. All species have glandular, peltate and capitate, and nonglandular hairs and diacytic stomata, but the covering hairs differ between species. The leaves of fifteen *Satureja* L. species were studied in order to assess anatomical variations that may serve as distinguishing characters, and to evaluate their significance for the taxonomy of the genus.

**Key words:** Lamiaceae, *Satureja*, leaf anatomy, glandular hairs, nonglandular hairs, Turkey.

## INTRODUCTION

The genus *Satureja* L. (Lamiaceae) includes about 200 species of herbs and shrubs, often aromatic, widely distributed in the Mediterranean area, Asia and boreal America (Rustaiyan et al., 2004). *Satureja* is represented by 15 species in Turkey (Davis, 1982; Tümen et al., 2000). The endemism ratio of the genus is 33% in Turkey, where *Satureja* species are grown mainly in south and west Anatolia.

*Satureja* species have economic and medicinal importance because of their high essential oil content. There are many studies on the essential oil of *Satureja* species in Turkey (Tümen and Baser, 1996; Tümen et al., 1997, 1998; Baser et al., 2000). With their pleasant fragrance, *Satureja* species are widely used as herbal teas and spices in Turkey. Members of this genus are called *kekik* in Turkish, and some species are exported as thyme (Satil et al., 2002a). In folk medicine, *Satureja* species, especially *S. cuneifolia*, *S. thymbra* and *S. hortensis*, are traditionally used as digestives and diuretics in various regions of Turkey (Baytop, 1999).

Glandular hairs are widely distributed over the aerial reproductive and vegetative organs of plants of

the Lamiaceae, a family of great economic importance, and their structure has been investigated by many researchers (Bosabalidis, 1990; Maleci and Servettaz, 1991; Servettaz et al., 1992; Bourett et al., 1994; Serrato-Valenti et al., 1997; Kolalite, 1998; Ascensao et al., 1999; Rapisarda et al., 2001; Kaya et al., 2003). Little is also known of hair and gland structure in *Satureja* (Bosabalidis, 1990; Husain et al., 1990; Bezic et al., 2001). The morphology and anatomy of some *Satureja* species have been described by Kaya et al. (1994) and Satil et al. (2002b, 2003).

There are taxonomic uncertainties within the *Satureja* species. In this paper we report a comparative study on leaf anatomy and hairs of the genus *Satureja* in order to improve our knowledge of its anatomy for systematics and to help separate similar species.

## MATERIALS AND METHODS

### PLANT MATERIAL

The plant material was collected from different localities in Turkey (Tab. 1). Voucher specimens are deposited at the Herbarium of the Science and Arts Faculty of Balikesir University, Turkey.

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TABLE 1. Collection data of studied *Satureja* species

| Taxon  | Collection data   | Herbarium No. |
|--|---|---------------|
| <i>S. thymbra</i> L.   | B1 Izmir: Kiraz-Sarıgöl 15 km, 20.06.2001                   | FS1046        |
|  | C4 Antalya: Gazipaşa to Anamur, 22.06.2001                  | FS1048        |
| <i>S. cuneifolia</i> Ten.  | C2 Denizli: Babadağ, Taşdelen plateau, 1600 m, 22.08.2001   | FS1043        |
|  | B1 Izmir: Kiraz, 17.09.2001                                 | FS1042        |
| * <i>S. cilicica</i> P.H.Davis   | C6 Kahramanmaraş: Andırın-Geben plateau, 1400 m, 27.08.2000 | FS1180        |
| * <i>S. amani</i> P.H.Davis  | C5/6 Hatay: Hassa, Amanos mountain                          | TD1221        |
| <i>S. icarica</i> P.H.Davis  | A1 Çanakkale: Gökçeada, Keklik hill, 250 m, 22.09.2002      | FS1024        |
| * <i>S. wiedemanniana</i> (Lalem.) Velen.  | A5 Amasya: Kral grave vicinity, 400-500 m, 24.07.2002       | TD2033        |
| * <i>S. parnassica</i> Heldr. & Sart. ex Boiss. subsp. <i>sipylea</i> P.H. Davis | B1 Manisa: Spil Mountain, 1500 m, 17.08.2001                | FS1382        |
|  | A1 Balıkesir: Marmara Island, 400 m, 11.08.2001             | FS1383        |
| <i>S. spinosa</i> L.   | C2 Muğla: Fethiye, Babadağ 1750 m, 10.08.2001               | FS1381        |
| <i>S. coerulea</i> Janka   | A1 Kırklareli: Dereköy 23 km 600 m, 29.10.2001              | TD1625        |
| <i>S. spicigera</i> (C. Koch) Boiss.   | A7 Ordu: Akkuş-Aybastı plateau, 11.08.2001                  | TD1403        |
|  | A7 Trabzon: Beşikdüzü, Yeşilköy, 850 m, 14.10.2005          | FS1421        |
| <i>S. boissieri</i> Hausskn. ex Boiss.   | B7 Adıyaman: Yazıbaşı village, 2000 m, 30.09.2001           | FS1027        |
| <i>S. macrantha</i> C.A.Mayer  | A9 Erzurum: Şenkaya-Akşar 5 km, 08.08.2002                  | FS1040        |
| * <i>S. aintabensis</i> P.H. Davis   | C6 Gaziantep: Dülükbaba, 900 m, 14.07.2001                  | FS1012        |
|  | C7 Urfa: Akabe place, 700 m, 19.07.2001                     | FS1004        |
| <i>S. pilosa</i> Velen.  | B1 Balıkesir: Edremit, Kazdağ-Kapıkule, 1400 m, 15.09.2004  | FS1385        |
| <i>S. hortensis</i> L.   | A9 Erzurum: Şenkaya-Akşar 5. km, 08.08.2002                 | FS1042        |
|  | C6 Kahramanmaraş: Andırın plateau, 1500 m, 26.07.2001       | FS1016        |

FS – Dr. Fatih Satil, Balıkesir University; TD – Dr. Tuncay Dirmenci, Balıkesir University; \* – Endemic

#### LIGHT MICROSCOPY (LM)

Living material was stored in 70% alcohol for anatomical studies. All sections were taken from leaves in the middle parts of plants. Transverse sections of lamina and the midrib, and surface preparations of leaves were prepared manually. All sections were embedded in glycerine-gelatine and mounted on microscope slides with Canada Balsam, and examined with an Olympus BX50 phase contrast binocular microscope with a camera lucida.

#### SCANNING ELECTRON MICROSCOPY (SEM)

Leaves, stems and calyces were fixed with 3% glutaraldehyde in 0.1 M sodium phosphate buffer (pH 7.2) for 4 h at 4°C. After washing, the material was dehydrated in acetone and then critical-point dried. The specimens were mounted on stubs with double-sided adhesive tape and coated with gold. Photographs were taken with a scanning electron microscope (Cam Scan S4).

### RESULTS

The lamina, hair and midrib of *Satureja* species were examined in transverse sections and surface preparations.

The adaxial and abaxial epidermises of the leaf consist of uniseriate oval, square and rectangular cells in transverse section. The upper walls are thicker than the lower and lateral ones. Both epidermises are covered with a cuticle 0.6–2.5 µm thick (Tab. 2).

Covering hairs consist of nonglandular and glandular types in both epidermises. Light and scanning electron microscopy showed details of the anatomy of these hairs (Figs. 1, 2). The glandular hairs include peltate and capitate types.

The peltate hairs, yellow to red in color, consist of a basal cell, a short unicellular stalk and a secretory head, usually composed of 12–16 cells. The latter secretes an essential oil which accumulates in a large space formed at the tip of the head between the raised cuticle and the apical cell walls. Four of these head cells are small and occupy the central area of the head, and 8–12 are large and peripheral (Fig. 1). The head is composed of only 12 cells in *S. cilicica*, *S. cuneifolia*, *S. amani*, *S. wiedemanniana*, *S. parnassica* subsp. *sipylea*, *S. coerulea*, *S. spinosa* and *S. pilosa*. In the other species the number of cells is 12–16 (Tab. 3). The peltate hairs in *S. spicigera* are easily distinguished from the others because they are almost at the same level with the epidermis. The peltate glandular heads show a smooth or wrinkled

TABLE 2. Anatomical characteristics of studied *Satureja* species

| Taxon   | Cuticle thickness ( $\mu\text{m}$ )<br>mean $\pm$ SD | Lamina thickness ( $\mu\text{m}$ )<br>mean $\pm$ SD | Mesophyll type | Palisade cell layers | Spongy cell layers | Sclerenchyma in VB* | VB diameter ( $\mu\text{m}$ )<br>mean $\pm$ SD |
|---|--|---|----------------|----------------------|--------------------|---------------------|--|
| <i>S. thymbra</i>                             | 2.5 $\pm$ 0.0  | 396 $\pm$ 14.3                                      | Equifacial     | 1–2                  | 2–4                | Absent              | 83.9 $\pm$ 8.9                                 |
| <i>S. cuneifolia</i>                          | 1.0 $\pm$ 0.1  | 312 $\pm$ 9.6                                       | Equifacial     | 1–2                  | 2–4                | Absent              | 111.6 $\pm$ 8.5                                |
| <i>S. cilicica</i>                            | 0.8 $\pm$ 0.0  | 278 $\pm$ 16.4                                      | Equifacial     | 1–2                  | 1–4                | Absent              | 131.8 $\pm$ 8.4                                |
| <i>S. amani</i>                               | 1.0 $\pm$ 0.0  | 220 $\pm$ 11.5                                      | Equifacial     | 1–2                  | 2–3                | Absent              | 71.5 $\pm$ 3.3                                 |
| <i>S. icarica</i>                             | 0.8 $\pm$ 0.0  | 269 $\pm$ 15.2                                      | Equifacial     | 1–2                  | 1–4                | Absent              | 82.5 $\pm$ 5.8                                 |
| <i>S. wiedemanniana</i>                       | 1.9 $\pm$ 0.4  | 367 $\pm$ 19.9                                      | Equifacial     | 2                    | 2–3                | Present             | 128.8 $\pm$ 10.0                               |
| <i>S. pamassiaca</i><br>subsp. <i>sipylea</i> | 1.2 $\pm$ 0.0  | 282 $\pm$ 19.9                                      | Equifacial     | 1–2                  | 2–4                | Present             | 99.9 $\pm$ 9.6                                 |
| <i>S. spinosa</i>                             | 0.6 $\pm$ 0.0  | 219 $\pm$ 19.4                                      | Equifacial     | 1–2                  | 2–3                | Absent              | 50.0 $\pm$ 0.0                                 |
| <i>S. coerulea</i>                            | 2.5 $\pm$ 0.0  | 301 $\pm$ 19.7                                      | Equifacial     | 1–2                  | 2–3                | Present             | 93.9 $\pm$ 5.7                                 |
| <i>S. spicigera</i>                           | 1.9 $\pm$ 0.4  | 166 $\pm$ 17.9                                      | Bifacial       | 1–2                  | 2–5                | Absent              | 73.0 $\pm$ 2.7                                 |
| <i>S. boissieri</i>                           | 1.2 $\pm$ 0.0  | 362 $\pm$ 12.5                                      | Equifacial     | 1–2                  | 2–5                | Absent              | 122.5 $\pm$ 6.6                                |
| <i>S. macrantha</i>                           | 1.2 $\pm$ 0.0  | 380 $\pm$ 11.7                                      | Equifacial     | 2–3                  | 2–3                | Absent              | 162.1 $\pm$ 9.2                                |
| <i>S. aintabensis</i>                         | 1.2 $\pm$ 0.0  | 372 $\pm$ 16.9                                      | Equifacial     | 2–3                  | 2–3                | Absent              | 95.0 $\pm$ 3.5                                 |
| <i>S. hortensis</i>                           | 0.8 $\pm$ 0.0  | 227 $\pm$ 18.6                                      | Equifacial     | 1                    | 2                  | Absent              | 93.5 $\pm$ 4.3                                 |
| <i>S. pilosa</i>                              | 0.8 $\pm$ 0.0  | 327 $\pm$ 15.5                                      | Equifacial     | 1–2                  | 2–3                | Absent              | 91.0 $\pm$ 4.6                                 |

\*VB – vascular bundle

surface (Fig. 2) in SEM micrographs. The cells of the secretory head also have a thick cuticle which lifts to form a large subcuticular chamber for the secretory material. The density of peltate hairs in different species varies (2–12 per  $\text{mm}^2$ ). In some species these hairs are sparse (in *S. coerulea* 2 or 3 per  $\text{mm}^2$ , *S. spicigera* 3 or 4, *S. hortensis* 4, *S. macrantha* and *S. spinosa* 5), while in others they form a dense covering (*S. thymbra* 9 or 10, *S. boissieri* 8–10, *S. cuneifolia* 10 or 11, *S. amani* 7–12, *S. aintabensis* 9 or 10). Peltate hairs have large heads 82.8–118.0  $\mu\text{m}$  in diameter. Some characteristics of peltate hairs in *Satureja* species are given in Table 3.

The capitate hairs are quite simple in morphology. They have a short unicellular stalk, rarely bicellular in *S. aintabensis*, and a head (Fig. 1). They are located on both surfaces of the leaf.

The nonglandular hairs are uni- or multicellular, with cuticular micropapillae, unbranched and consisting of elongated cells (Fig. 1). While unicellular (rarely 2-celled) hairs are found in *S. cilicica*, *S. wiedemanniana*, *S. coerulea* and *S. spicigera*, they are 1–5-celled in the other species (Tab. 3). The density of the nonglandular hairs in *Satureja* leaves varies. In some species they are sparser, as in *S. amani*, *S. boissieri*, *S. cilicica* and *S. spicigera*, while in others they form a dense covering. Nonglandular hairs in *S. coerulea* are almost absent from both leaf surfaces, and they are located at the leaf margins (Figs. 2e<sub>1</sub>, e<sub>3</sub>).

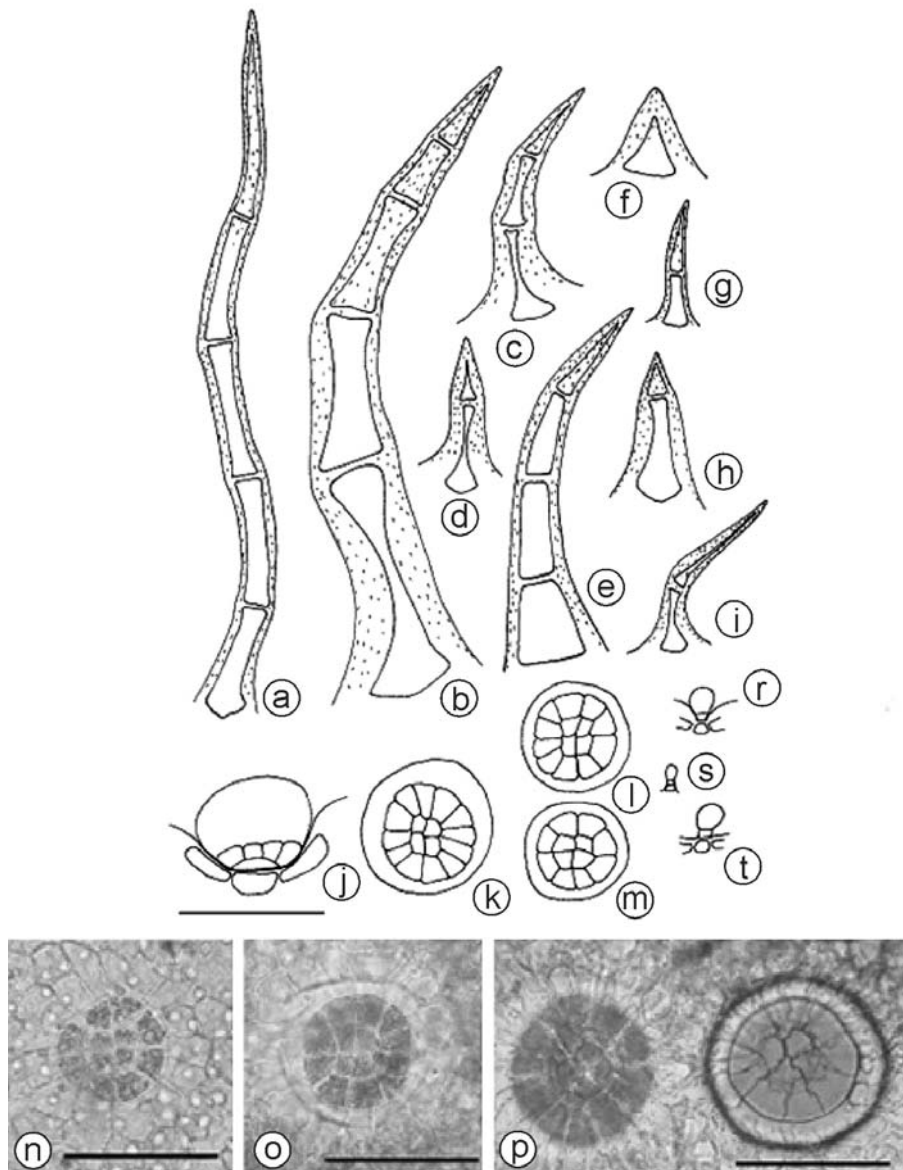
The stomata are diacytic and occur on both leaf epidermises (amphistomatic leaf). They are located a little higher than the epidermal level (hygromorph type) and they appear oval-shaped in surface preparations (Fig. 2).

*Satureja* species exhibit obvious differences in lamina thickness, which ranges from 166  $\mu\text{m}$  to 396  $\mu\text{m}$ . The lamina are thinnest in *S. spicigera* (166  $\mu\text{m}$ ) and thickest in *S. thymbra* (396  $\mu\text{m}$ ).

*Satureja* leaves are ordinarily equifacial, but they may be bifacial as observed in *S. spicigera* (Fig. 3). The mesophyll is differentiated into a usually 1- or 2-seriate palisade parenchyma (rarely 2- or 3-layered in *S. macrantha* and *S. aintabensis*) and a 2–4-seriate spongy parenchyma (rarely 1–4-layered in *S. cilicica* and *S. icarica*; 2–5-layered in *S. spicigera* and *S. boissieri*) (Tab. 2). A single-layered palisade parenchyma and a 2-layered spongy parenchyma are recorded only in the mesophyll of *S. hortensis*. The palisade parenchyma cells are cylindrical and the spongy parenchyma cells are circular or ovoid in transverse section.

The leaf midrib region can be divided into two groups: not projecting (type I), identified only in *S. coerulea*; and projecting (type II), observed in all other *Satureja* species (Fig. 4).

The vascular bundles are of collateral type and usually occur in a narrow area surrounded by a bundle sheath. The xylem faces towards the adaxial leaf surface while the phloem faces the abaxial epi-



**Fig. 1.** Brightfield micrographs of Turkish *Satureja* leaf hairs. (a-t) nonglandular hairs, (j-p) peltate hairs (n – *S. icarica*, o – *S. macrantha*, p – *S. thymbra*), (r-t) capitate hairs. Bar = 100  $\mu$ m.

dermis. The midrib in transverse section is round in half of the *Satureja* species, and nearly round in some *Satureja* species. Transversely it is elliptical only in *S. macrantha*, whose vascular bundle is well developed (Fig. 5). The vascular bundles are between 50.0  $\mu$ m and 162.1  $\mu$ m in diameter.

The bundles in *S. wiedemanniana*, *S. parnassica* subsp. *sipylea* and *S. coerulea* are sclerenchymatous in the xylem of the midrib region; this structure can be identified as type I, but it is found in the midrib area of the other *Satureja* species (Fig. 5).

## DISCUSSION

In this study, leaf anatomy and hairs of Turkish *Satureja* species were examined, and structural features of the hairs, midrib, vascular bundles and mesophyll were determined to be useful characters.

All *Satureja* species have nonglandular hairs and two types of glandular hairs, peltate and capitate. In the Lamiaceae, glandular hairs are generally classified as either capitate (clavate) or peltate (sessile), based on morphological characteristics (Fahn, 2000). The peltate hairs are composed of one

TABLE 3. Hair characteristics of studied *Satureja* species

| Taxon  | Peltate hairs     |   |          |                                 | Nonglandular hairs |
|--|-------------------|---|----------|---------------------------------|--------------------|
|  | No. of head cells | Hair density per mm <sup>2</sup> leaf surface |          | Head diameter (µm)<br>mean ± SD | No. of cells       |
|  |                   | adaxial                                       | abaxial  |                                 |                    |
| <i>S. thymbra</i>                              | 14–16-celled      | 9 ± 0.7                                       | 10 ± 0.7 | 118.0 ± 8.5                     | 1–5-celled         |
| <i>S. cuneifolia</i>                           | 12-celled         | 10 ± 0.7                                      | 11 ± 0.7 | 100.0 ± 8.8                     | 1–4-celled         |
| <i>S. cilicica</i>                             | 12-celled         | 8 ± 0.0                                       | 10 ± 0.7 | 94.0 ± 4.4                      | 1–2-celled         |
| <i>S. amani</i>                                | 12-celled         | 7 ± 0.0                                       | 12 ± 0.0 | 100.0 ± 4.0                     | 1–3-celled         |
| <i>S. icarica</i>                              | 12–14-celled      | 5 ± 0.7                                       | 9 ± 0.7  | 100.0 ± 9.2                     | 1–4-celled         |
| <i>S. wiedemanniana</i>                        | 12-celled         | 5 ± 0.7                                       | 11 ± 0.7 | 95.0 ± 6.4                      | 1–2-celled         |
| <i>S. parnassiaca</i><br>subsp. <i>sipylea</i> | 12-celled         | 7 ± 0.7                                       | 8 ± 0.7  | 90.0 ± 7.6                      | 1–5-celled         |
| <i>S. spinosa</i>                              | 12-celled         | 5 ± 0.0                                       | 5 ± 0.0  | 88.3 ± 6.9                      | 1–5-celled         |
| <i>S. coerulea</i>                             | 12-celled         | 2 ± 0.0                                       | 3 ± 0.5  | 85.0 ± 2.8                      | 1–2-celled         |
| <i>S. spicigera</i>                            | 14-celled         | 3 ± 0.7                                       | 4 ± 0.7  | 82.8 ± 5.9                      | 1–2-celled         |
| <i>S. boissieri</i>                            | 14-celled         | 8 ± 0.9                                       | 10 ± 0.7 | 105.0 ± 4.7                     | 1–3-celled         |
| <i>S. macrantha</i>                            | 14-celled         | 5 ± 0.7                                       | 5 ± 0.5  | 110.0 ± 6.4                     | 1–4-celled         |
| <i>S. aintabensis</i>                          | 12–14-celled      | 9 ± 0.7                                       | 10 ± 0.7 | 98.5 ± 8.4                      | 1–5-celled         |
| <i>S. hortensis</i>                            | 14–16-celled      | 4 ± 0.7                                       | 4 ± 0.5  | 114.2 ± 7.5                     | 1–3-celled         |
| <i>S. pilosa</i>                               | 12-celled         | 8 ± 0.7                                       | 9 ± 0.5  | 90.0 ± 3.7                      | 1–5-celled         |

basal cell, one stalk cell and a broad 12–16-celled head, 8–12 of which are large and peripheral, and 4 of which are small and occupy the central area of the head.

The nutlet, leaf surfaces and hair features of five *Satureja* species were investigated by Husain et al. (1990), who observed that the stomata are densely distributed and diacytic (Group I: *S. montana* L., *S. cuneifolia* and *S. subspicata* Bartl. ex Vis.). They found that nonglandular hairs of *S. montana* are unicellular, with small granules. Such hairs were not observed in *S. subspicata*. The hairs of *S. cuneifolia* are large and 4-celled, as also found in our study. In group II (*S. horvatii* Silic and *S. pilosa*) the hairs are long and 3-celled (1–5-celled in our *S. pilosa* samples). According to Husain et al. (1990), small unicellular hairs are also observed and are not abundantly distributed. Diacytic stomata are found on the abaxial surface of the leaves.

According to Bosabalidis (1990), glandular hairs on *S. thymbra* leaves are of two different forms: short glandular hairs (capitate hairs) and glandular scales (peltate hairs) having heads of 12 cells, 4 of which are small and centrally located and 8 of which are large and peripheral. In our samples, *S. thymbra* has 14–16 cells in the head, with 4 cells in the center and 10–12 cells at the periphery. In other species of the same family, such as *Origanum* (Bosabalidis and Tsekos, 1984), *Salvia officinalis*

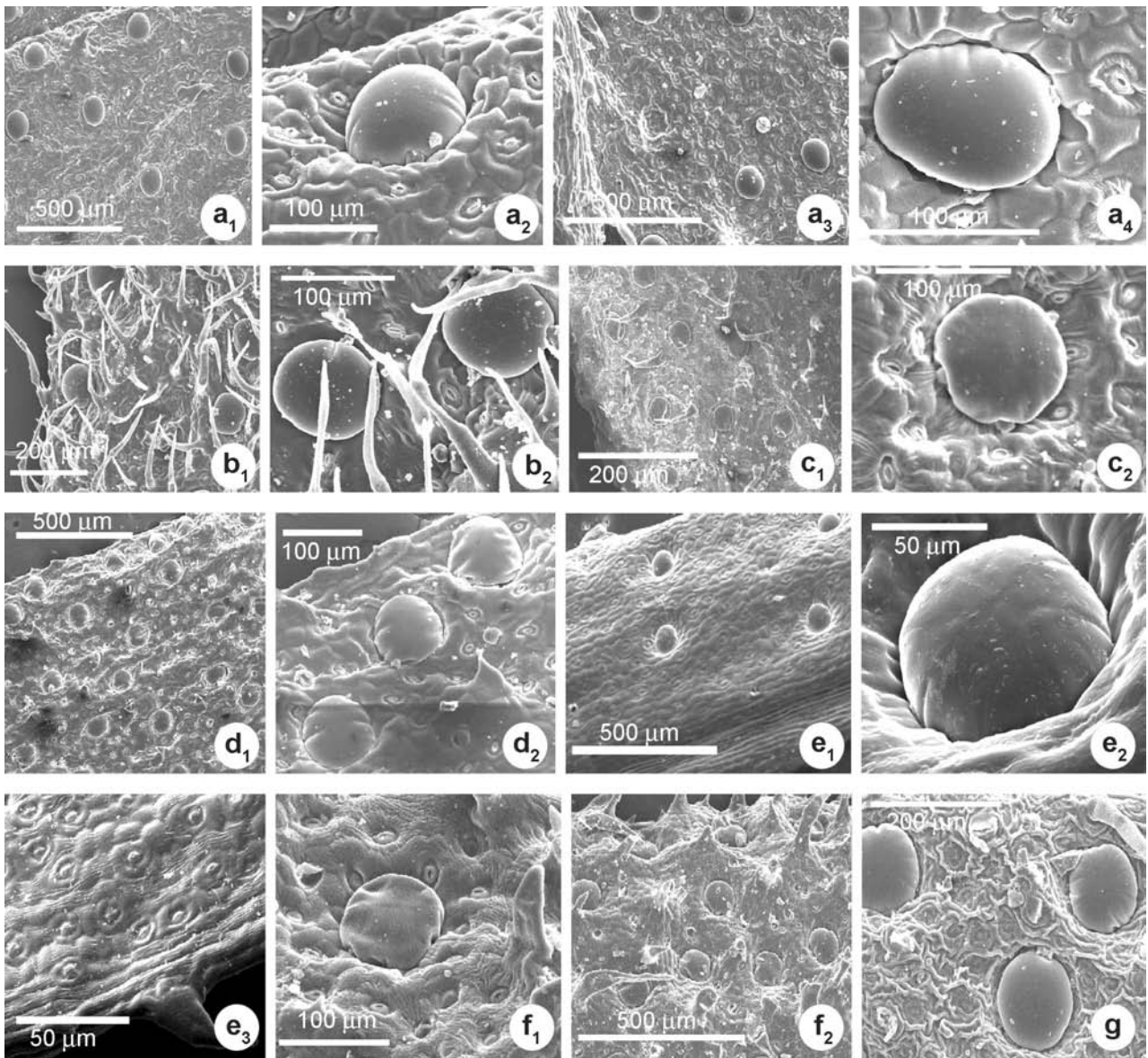
(Corsi and Bottega, 1999), *Plectranthas ornatus* Codd (Ascensao et al., 1999) and some species examined by Werker et al. (1985), a higher number of head cells are arranged in two concentric circles.

Bezic et al. (2001) examined the anatomical structure of the glandular apparatus in *S. cuneifolia* and reported that a glandular scale consists of a unicellular base, a unicellular stalk and a 12-celled head. Their results for *S. cuneifolia* are similar to ours.

In *Satureja* species, the apical surface of the glandular scales appears either smooth or wrinkled. This is probably because the cuticle is entirely detached from the upper walls of the secretory cells, thus forming an oil-accumulating chamber. The wrinkled surface of the peltate hair head indicates that the cuticle is still closely attached to the secretory cells, emphasizing the cell outlines (Bosabalidis, 1990).

The density of peltate hairs differs between species. The hairs are very densely distributed in *S. thymbra*, *S. cuneifolia*, *S. amani*, *S. boissieri* and *S. aintabensis*. These species are important because of their high essential oil content (1.0–4.3% in *S. thymbra*, 0.6–3.6% in *S. cuneifolia*, 2.1% in *S. boissieri* and 2.8% in *S. aintabensis*) (Kürkcüoğlu et al., 2001).

Capitate hairs are widespread in the Lamiaceae. They vary greatly in structure and size, but in the



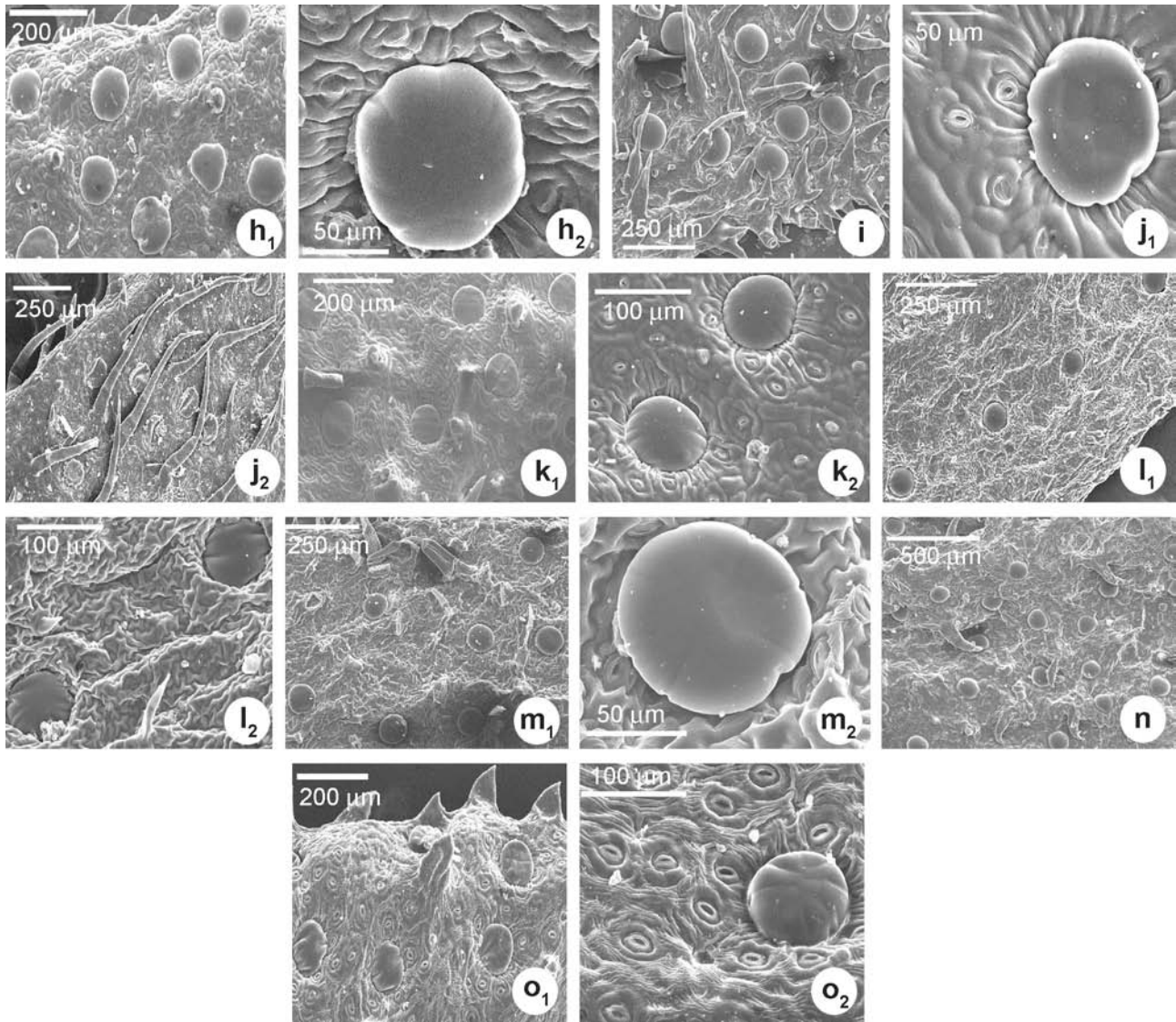
**Fig. 2.** Scanning electron micrographs of Turkish *Satureja* leaf hairs. (a<sub>1</sub>-a<sub>4</sub>) *S. amani* (adaxial, abaxial, respectively); (b<sub>1</sub>, b<sub>2</sub>) *S. aintabensis* (adaxial); (c<sub>1</sub>, c<sub>2</sub>) *S. boissieri* (adaxial); (d<sub>1</sub>, d<sub>2</sub>) *S. cilicica* (adaxial); (e<sub>1</sub>-e<sub>3</sub>) *S. coerulea* (abaxial, abaxial and adaxial, respectively); (f<sub>1</sub>, f<sub>2</sub>) *S. cuneifolia* (adaxial, abaxial, respectively); (g) *S. hortensis* (abaxial).

studied *Satureja* species they usually displayed one morphological type: a unicellular secretory head, a unicellular stalk and a foot cell. This type is similar to that previously described in *S. thymbra* (Bosabalidis, 1990) and other Lamiaceae species such as *Salvia blepharophyll* Brandege ex Epling (Bisio et al., 1999) and *Salvia glutinosa* (Kaya et al., 2003). Rarely we observed capitate hairs with a small bicellular stalk in *S. aintabensis*.

All the studied species were found to have amphistomatic leaves with diacytic stomata, which are common in the Lamiaceae. In an extensive sur-

vey of stomatal position in 127 genera of Labiatae, Cantino (1990) remarked that both hypostomatic and amphistomatic leaves are found in the members of the family, the latter type being slightly more frequent. The stomata in all *Satureja* species are of hygromorph type or sometimes of hygromorph to mesomorph type.

The genus *Satureja* has equifacial leaves except for *S. spicigera*, which has bifacial leaves. The mesophyll is differentiated into a 1-3-seriate palisade parenchyma and 2-5-seriate spongy parenchyma in all of the species. There are some differences in the



**Fig. 2** (continued). (**h<sub>1</sub>**, **h<sub>2</sub>**) *S. icarica* (adaxial, abaxial, respectively); (**i**) *S. macrantha* (abaxial); (**j<sub>1</sub>**, **j<sub>2</sub>**) *S. parnassica* subsp. *sipylea* (adaxial, abaxial, respectively); (**k<sub>1</sub>**, **k<sub>2</sub>**) *S. pilosa* (abaxial); (**l<sub>1</sub>**, **l<sub>2</sub>**) *S. spicigera* (abaxial, adaxial, respectively); (**m<sub>1</sub>**, **m<sub>2</sub>**) *S. spinosa* (adaxial, abaxial, respectively); (**n**) *S. thymbra* (adaxial); (**o<sub>1</sub>**, **o<sub>2</sub>**) *S. wiedemanniana* (adaxial).

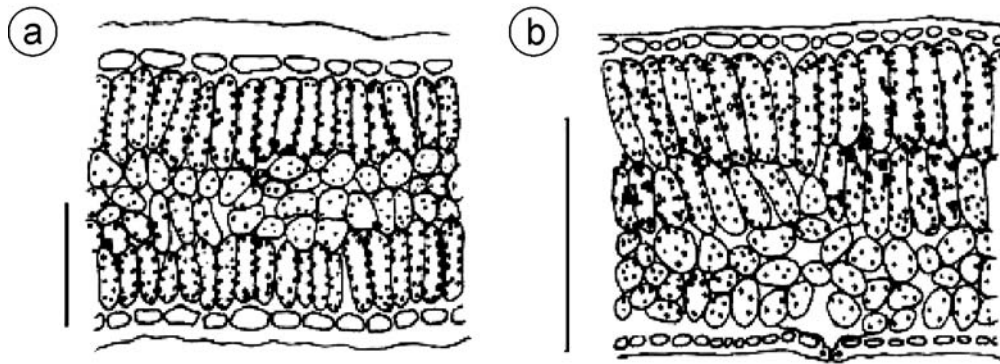
number of the mesophyll cells. For example, it is differentiated into a 1-seriate palisade parenchyma and a 2-seriate spongy parenchyma in the mesophyll of *S. hortensis*, which is an annual plant according to *Flora of Turkey* (Davis, 1982).

The vascular bundles usually occur in a narrow area surrounded by a bundle sheath. The midrib region forms a projecting part in all species except for *S. coerulea*. This diagnostic difference has also been observed in the leaf vascular bundles of some other Lamiaceae members (Ozdemir and Senel, 1999; Kandemir, 2003). In leaf transverse sections

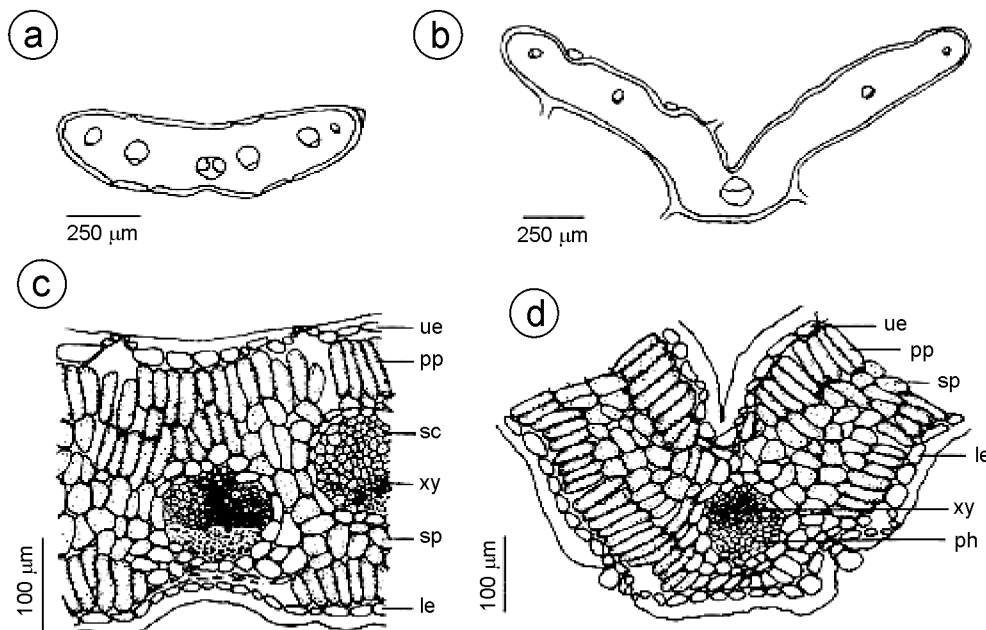
of *Satureja* species, vascular bundles can be identified as of two main types based on the presence or absent of sclerenchymatous cells. Sclerenchymatous cells are located in the xylem of *S. parnassica* subsp. *sipylea*, *S. wiedemanniana* and *S. coerulea*. We did not observe this feature in other species.

According to *Flora of Turkey* (Davis, 1982), *S. cuneifolia* and *S. wiedemanniana* are very similar morphologically. Our anatomical results show clear differences between *S. cuneifolia* and *S. wiedemanniana*. The presence of sclerenchymatous tissue in the vascular bundles is a diagnostic





**Fig. 3.** Mesophyll types in *Satureja* species. (a) Type I, equifacial (in 14 *Satureja* species), (b) Type II, bifacial (in *S. spicigera*). Bar = 100  $\mu\text{m}$ .



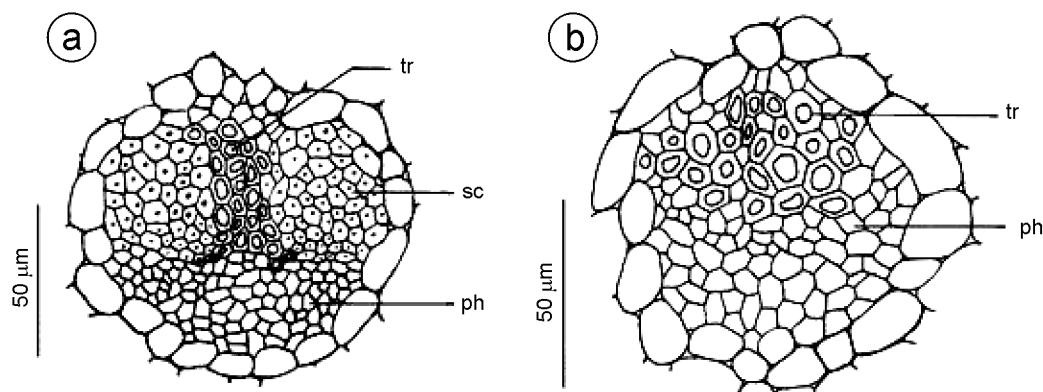
**Fig. 4.** Midrib region types in *Satureja* species. (a,c) Type I, with no projecting midrib (in *S. coerulea*), (b,d) Type II, projecting (in the other species). le – lower epidermis; ph – phloem; pp – palisade parenchyma; sc – sclerenchyma; sp – spongy parenchyma; ue – upper epidermis; xy – xylem.

characteristic to distinguish the two species. *S. cuneifolia* is also morphologically similar to *S. amani* and *S. cilicica* according to *Flora of Turkey*, but we found evident differences in vascular bundle diameter and in cuticle and lamina thickness between these species. Cuticle thickness is 0.8  $\mu\text{m}$  in *S. cilicica* and 1.0  $\mu\text{m}$  in *S. cuneifolia* and *S. amani*. Vascular bundle diameter is 71.5  $\mu\text{m}$  in *S. amani*, 111.6  $\mu\text{m}$  in *S. cuneifolia* and 131.8  $\mu\text{m}$  in *S. cilicica*; and lamina thickness is 220  $\mu\text{m}$  in *S. amani*, 278  $\mu\text{m}$  in *S. cilicica* and 312  $\mu\text{m}$  in *S. cuneifolia*. In *S. aintabensis*, which is nearest to *S. macrantha* in *Flora of Turkey*, peltate hair density and vascular bundle diameters distinguish the two species:

5 peltate hairs per  $\text{mm}^2$  (adaxial/abaxial) in *S. macrantha* and 9 (adaxial) and 10 (abaxial) per  $\text{mm}^2$  in *S. aintabensis*; and 162.1  $\mu\text{m}$  vascular bundle diameter in *S. macrantha*, more than in *S. aintabensis* (95.0  $\mu\text{m}$ ).

Anatomically, however, *S. parnassica* subsp. *sipylea* and *S. wiedemanniana* are very similar (Davis, 1982). Moreover, RAPD-PCR studies of *Satureja* species showed *S. parnassica* subsp. *sipylea* and *S. wiedemanniana* to be very similar in molecular structure (Oz Aydin, 2004). Our study supports those anatomical results.

Davis (1982) described *Satureja* as a very difficult genus, and according to Husain et al. (1990) it



**Fig. 5.** Vascular bundle types in *Satureja* species. (a) Type I, with sclerenchyma (*S. wiedemanniana*, *S. parnassica* subsp. *sipylea*, *S. coerulea*), (b) Type II, without sclerenchyma (the remaining species). ph – phloem; sc – sclerenchyma; tr – trachea.

is a polymorphic genus which is not divided into sections in the current classification system. The anatomical features of *Satureja* species are complex, so the species have not been separated with great precision. Needed are useful distinguishing characters such as the ones we determined: hair characteristics, protrusion (or lack thereof) of the midrib, vascular bundle structure and mesophyll structure.

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