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Observation on the Cotyledonary Stomata and Trichomes and their Ontogeny in some Genera of *Lamiaceae*

By

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With 85 Figures (4 plates)

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Summary

NAIDU A. C. & SHAH G. L. 1981. Observations on the cotyledonary stomata and trichomes and their ontogeny in some genera of *Lamiaceae*. — *Phyton* (Austria) 21 (1): 137—152, 85 figures (4 plates). — English with German Summary.

The structure and ontogeny of cotyledonary stomata and trichomes are described in 34 species of *Lamiaceae*. Stomata are diacytic, anomocytic, haplocytic, transitional form, tetracytic, paracytic and tricytic, different types often occurring side by side even on the same surface. The most frequent type is diacytic on both surfaces in most of the taxa, but it is anomocytic on adaxial surface or both surfaces in some. Rarely anisocytic, transitional form or haplocytic stomata are also dominant types on the adaxial surface. More than one type of ontogenetic patterns are observed on the same surface in different taxa. Anomocytic stomata are perigenous. Other types are mesogenous or mesoperigenous. The ontogeny of tetracytic is not traced. Fourteen types of unusual stomatal forms occurring under natural conditions are described. Most of them are rare to very rare and therefore taxonomically they are not significant.

Trichomes are present on both surfaces. They are glandular or eglandular. The former are capitate sessile and short stalked or long stalked. The later are uniseriate or stellate. The trichomes are classified into five major types and their ontogeny is also described. The taxonomic significance of stomata and trichomes to delineate genera and species is also suggested.

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Zusammenfassung

NAIDU A. G. & SHAH G. L. 1981. Beobachtungen an Spaltöffnungen und Haaren und deren Entstehungsweise an den Keimblättern einiger Lamiaceen-Gattungen. — *Phyton* (Austria) 21 (1): 137—152, mit 85 Figuren und 4 Tafeln. — Englisch mit deutscher Zusammenfassung.

An 34 Lamiaceen-Arten (aus dem Botanischen Garten Berlin—Dahlem, BRD, erg. vom Editor) werden Bau und Entstehungsweise der Spaltöffnungsapparate und der Haare der Keimblätter untersucht. Es kommen die unterschiedlichsten Stomatatypen vor, bei einigen Arten finden sich an ein und derselben Blattoberfläche mehrere Typen. Vierzehn unter normalen Wachstumsbedingungen auftretende ungewöhnliche Stomatatypen konnten beschrieben werden. Wegen ihres sporadischen Auftretens kommt ihnen aber kein systematischer Wert zu. — Trichome finden sich an beiden Blattseiten. Es werden fünf Hauptgruppen unterschieden. Der Bau der Stomata und der Haare wird als taxonomisch wertvolles Merkmal zur Abgrenzung von Gattungen und Arten angesehen.

(Editor transl. and abbrev.)

1. Introduction

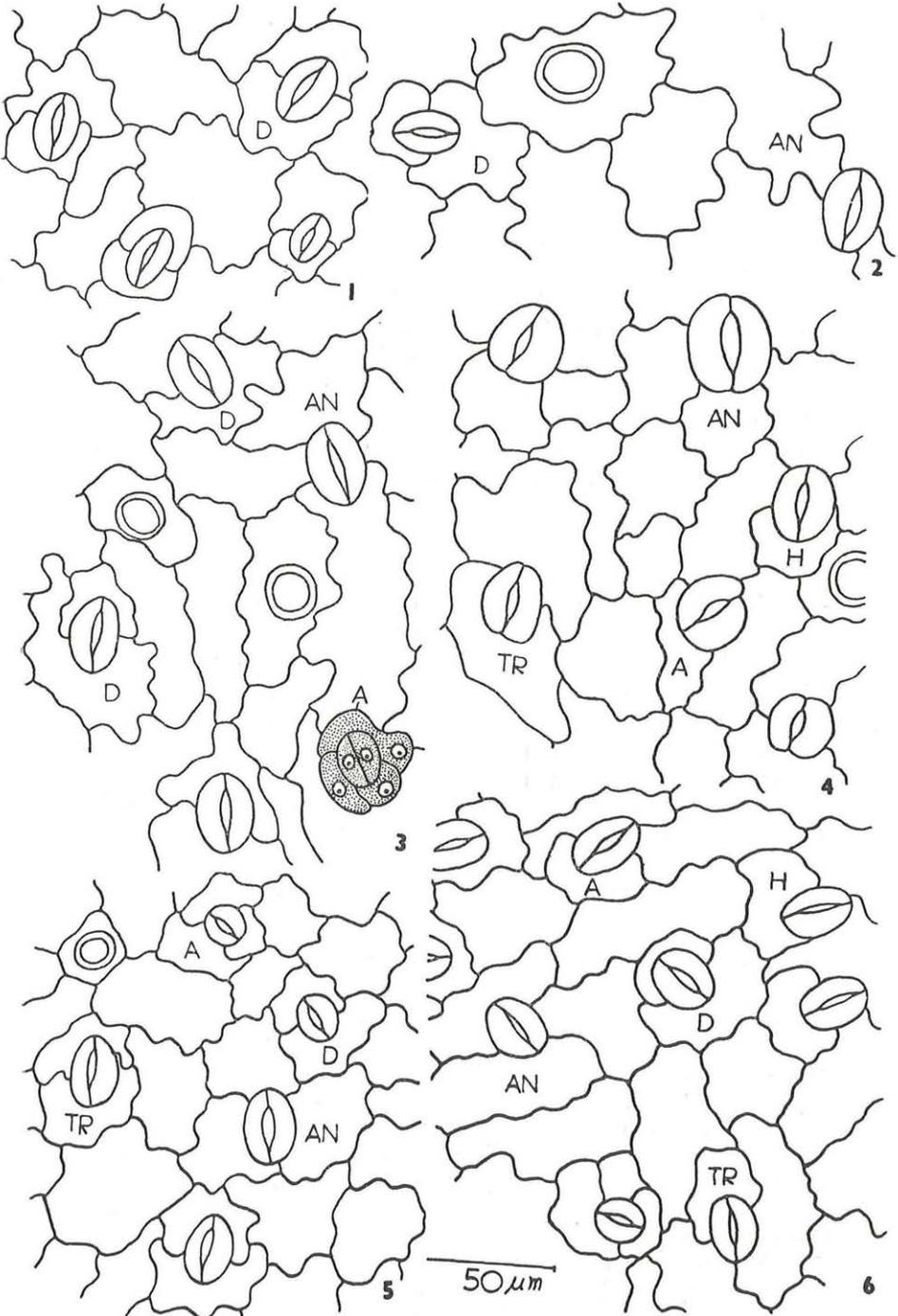
Stomata and trichomes are described on the leaves of some *Lamiaceae* by METCALFE & CHALK (1950), MATHUR (1961), INAMDAR & BHATT (1972), EL-GAZZAR & WATSON (1970), SINGH *et al.* (1975) and GUPTA & BHAMBIE (1978), but there is no report about them on the cotyledons except in three species of *Ocimum* (RAMAYYA & RAO, 1969). Therefore, our observations on their structure and ontogeny in thirty four species are presented here to supplement the existing data and assess their taxonomic significance.

2. Materials and Methods

34 species of *Lamiaceae*, obtained from the Botanical Garden Berlin—Dahlem (University of Berlin, FRG) were investigated. The species are listed in Table 1 alphabetically. The seeds are grown in earthen pots in the Botanical Garden of this University. Seedlings are fixed in formalin — acetic acid — ethanol on the tenth day after germination and stored in 70% alcohol after 48h. The peels from the middle region of the cotyledons are stained with Delafield's hematoxylin and temporarily mounted in glycerine jelly. Trichomes are studied from safranin stained preparations of free hand transverse sections.

The relative frequency of different types of stomata are calculated from the camera lucida drawings of five different peels from each surface.

Figs. 1—6. Stomata as viewed in epidermal peels from adaxial (figs. 2, 4, 6) and abaxial surface (figs. 1, 3, 5) showing diversity. *Prunella vulgaris*: Fig. 1. — *Lavandula angustifolia*: Figs. 2, 3. — *Stachys officinalis*: Fig. 4. — *Salvia patens*: Fig. 5. — *Stachys grandiflora*: Fig. 6



The terminology and circumscription of stomata adopted in this paper are by METCALFE & CHALK (1950), METCALFE (1961), PANT & BANERJI (1965) and SHAH & KOTHARI (1975). Stomata with three unequal subsidiary cells incompletely surrounding the guard cells are here understood as tricytic. The ontogeny of stomata is termed and described after PANT (1965).

3. Observations

3.1 Aspects of mature epidermis

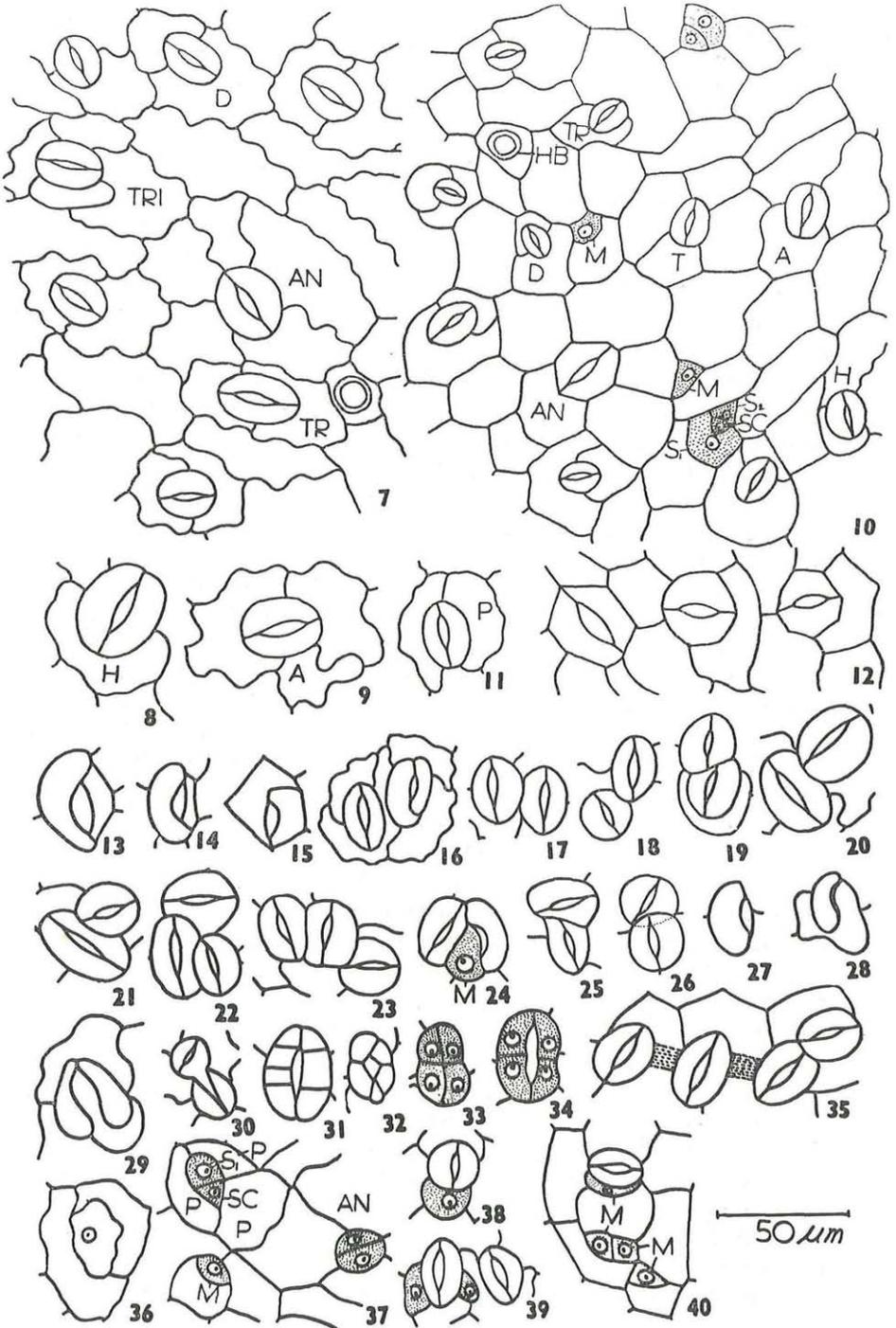
Epidermal cells are variously shaped with sinuous walls on both surfaces (Figs. 1–7) except in *Salvia argentea*, *S. nemorosa* and *S. triloba* where they are nearly straight or slightly wavy on the adaxial surface (Fig. 10). Stomata are evenly distributed throughout the epidermis without any definite pattern of orientation on both surfaces (Figs. 1–7, 10). Trichomes are present on both surfaces. They are glandular or eglandular, the former type is present on abaxial surface or both surfaces or both the types occur on adaxial surface or both surfaces.

3.2 Mature stomata

From Table I it will be also seen that the stomata are anomocytic (AN), anisocytic (A), diacytic (D), haplocytic (H), paracytic (PA), transitional forms (TR), tetracytic (T) and tricytic (TRI). Only diacytic stomata occur on the adaxial surface of *Nepeta cataria* var. *citriodora* and *Prunella vulgaris* (Fig. 1). In other species there are more than one type on the same surface in different combinations. The combinations are in number and types of stomata (Figs. 2–11) and differ on the two surfaces.

In spite of the diversity, the most frequent type is (i) diacytic on both surfaces in many species, (ii) anomocytic on both surfaces of *Leonurus cardiaca*, *Stachys officinalis* and *St. palustris*, and on adaxial surface of

Figs. 7–40: Stomata as viewed in epidermal peels (Figs. 13, 14, 22, 24, 25, 28, 31, 39 from adaxial surface, rest from abaxial surface). *Salvia nemorosa*: Figs. 7–9. — *S. argentea*: Figs. 10, 11, 25, 26. — *S. cleistogama*: Fig. 12. — *S. triloba*: Figs. 15, 21–24, 35. — *S. sclarea*: Figs. 28, 38–40. — *Stachys macrostachys*: Fig. 17. — *Si. montana*: Figs. 20, 27. — *St. officinalis*: Figs. 13, 14, 31. — *St. olympica*: Fig. 16. — *St. recta*: Fig. 37. — *Physostegia virginiana*: Figs. 19, 32. — *Dracocephalum moldavica*: Figs. 18, 30, 36. — *Prunella vulgaris*: Fig. 29. — *Marrubium supinum* Figs. 33, 34. — Figs. 7–11 showing diversity in stomatal types; Fig. 12: polygonal stomata; Figs. 13–15: unequal guard cells; Fig. 16: stomata with common subsidiary cell; Figs. 17–25: contiguous stomata; Fig. 26: overlapping stomata; Figs. 27, 28: stomata with one guard cell; Fig. 29: stoma with very oblique guard cell and horse shoe shaped pore; Fig. 30: contiguous wall between two stomata ruptured; Figs. 31–34: septate guard cells; Fig. 35: cytoplasmic connection; Fig. 36: arrested development; Fig. 37–40: stages of ontogeny



Agastache rugosa, *Lavandula angustifolia*, *Leonurus cardiaca* var. *crispa*, *Marrubium vulgare*, *Nepeta cataria*, *Sideritis macrostachyos*, *Stachys alpina*, *St. macrostachys* and *St. recta*, (iii) anisocytic on abaxial surface of *Marrubium supinum*, (iv) haplocytic on the abaxial surface of *Salvia triloba* and *Stachys recta* and (v) transitional form on the adaxial surface of *St. olympica*. Rarely the two dominant types have an equal frequency on the adaxial surface of *Si. montana*. It is interesting to note that, where the diacytic is the most frequent type, anomocytic is the next abundant type and vice-versa. In case of other dominant types the second type may be anomocytic, transitional or haplocytic.

During the course of the present investigation a few unusual stomatal forms are encountered.

(1) Though the stomata in general are circular, oval or oblong in outline, rarely one or both the guard cells show angularities, so that the stoma at times is polygonal in *Moschosma polystachyum*, *S. argentea*, *S. cleistogama*, *S. triloba* and *St. officinalis* (Figs. 12—15).

(2) Two guard cells of a stoma are unequal (Figs. 13—16).

(3) It is common to observe two stomata with a common subsidiary cell (Fig. 16).

(4) Various positions, equal or unequal, contiguous stomata (Figs. 17—23) are rare in most of the taxa, but they frequently occur in *S. cleistogama*, *S. nemorosa* and *S. triloba*.

(5) In *S. triloba* a complete stoma is very obliquely contiguous with half stoma (i. e. with one guard cell and pore) and the space between them is occupied by a triangular, deeply stained meristemoid like cell (Fig. 24).

(6) Sometimes the contiguous wall of two stomata is almost flat (Fig. 25).

(7) Seldom the contiguous wall between two stomata is broken (Fig. 30).

(8) Two overlapping stomata are rare (Fig. 26).

(9) Stomata with one guard cell and well developed or undeveloped pore (Figs. 27, 28) are sparingly met with in many taxa.

(10) In *Prunella* very rarely the two guard cells are much separated at one end and the pore projects out in the form of a horse shoe (Fig. 29).

(11) The guard cells are sometimes septate due to secondary wall formation in *Physostegia virginiana*, *S. argentea*, *S. sclarea* and *St. palustris* (Fig. 31). In extreme cases the stoma looks like a ring of cells surrounding the pore (Fig. 32).

(12) At times two superimposed stomata (Fig. 33) are so arranged that a common pore is bounded on either side by a pair of superimposed guard cells (Fig. 34). They are observed in *M. supinum*.

(13) Cytoplasmic connections between the guard cells of adjacent stomata are rarely observed in *S. triloba* (Fig. 35).

(14) The development of a stoma ceases at various stages. The cells are devoid of contents. This is an arrested development (See PANT & KIDWAI, 1964). It is rarely met with in *Dracocephalum moldavica*, *M. vulgare*,

Lavandula angustifolia, *Leonurus*, *Prunella vulgaris* and *S. nemorosa* (Fig. 36).

3.3 Ontogeny of stomata

The stomata follow a mixed sequence of ontogeny since the ontogenetical stages are found along with the mature stomata (Figs. 3, 10, 37, 41).

Meristemoids (M) can be distinguished by their smaller size, denser contents and various shapes (Figs. 10, 37, 40, 41). They are scattered throughout the epidermis, or they occur in groups of two to three (Fig. 40). At times they are contiguously lateral or polar to a mature stoma (Figs. 38—40).

A meristemoid increases in size and transforms into a guard cell mother cell without cutting of any subsidiary cell. The guard cell mother cell divides by a vertical wall to produce two guard cells. This is an anomocytic stoma (Fig. 37) and the ontogeny is perigenous. More commonly it divides by one to three curved walls to cut off larger segments S_1 — S_3 and the smaller segment SC (Figs. 3, 10, 41). The later produces guard cells and the former the subsidiary cells. These result into stomata which are haplocytic, paracytic, diacytic or transitional, anisocytic or tricytic (Fig. 41). Since the guard cells and subsidiary cells are the products of the same meristemoid, the ontogeny is mesogenous. However, after the meristemoid has cut off S_1 and S_2 , the neighbouring perigene also assumes the form of subsidiary cell in diacytic, transitional and anisocytic stomata. This type of ontogeny is mesoperigeneous. Even in a mature stoma it is possible to observe clear differences between mesogenous and perigenous subsidiary cells (cf. Figs. 1, 41).

Contiguous stomata may arise due to two or more adjacently placed meristemoids or meristemoid(s) cut off contiguous to a mature stoma developing into stomata (cf. Figs. 38—40).

3.4 Trichomes

They are glandular and eglandular. The former type differs from the latter in having dense contents in all the cells or at least in head cell(s) and neck cells when present. The following are the types of *glandular trichomes*.

Type I — Capitate long stalked:

(a) Foot cell forming a stalk: The trichomes are uniseriate consisting of a foot and the body. Foot one celled, much elongated, projecting beyond the epidermal cells, bluntly wedge shaped, polygonal (Fig. 50), conical with obtuse tips (Figs. 51—52), flask shaped (Figs. 53—55), or ovate with angularities at the base (Fig. 56). Body is thin walled with smooth, seldom rough cuticle (Fig. 54). It consists of only a head cell (H) (Figs. 50, 51) or

differentiated into a head cell (H) and rectangular stalk cell (SC) (Figs. 53, 55). The stalk cell is derived from the head cell by a transverse wall (cf. Figs. 52, 53); very seldom the division is oblique (Fig. 54).

(b) Stalk cells forming a stalk: The stalk is contributed by the stalk cells. In this type, foot is one celled or rarely juxtaposed two celled (Figs. 67, 68), cells polygonal, squarish or trapezoidal, projecting or not beyond the cells of the epidermis. Body uniseriate, straight or slightly curved (Fig. 64), with smooth, seldom rough cuticle (Fig. 65), consisting of 1–3 elongated stalk cells (SC), 1–2 neck cells (NC) and a spherical, oblong or obovate head (H). The stalk cells are rectangular, trapezoidal, or squarish, generally much longer than broad with thin contents (Figs. 62, 63, 66, 67) or without contents (Figs. 64, 68). Head (H) is unicellular or bi-celled. Neck cells (NC) are subterminal, rectangular or trapezoidal.

Type II — Capitulate sessile or very shortly stalked:

Foot (F) one-celled, squarish or polygonal projecting or not, without contents. Body differentiated into a short rectangular, trapezoidal or polygonal stalk cell (SC) and spherical head (H). The stalk cell and head cells are smooth and thin walled, cuticularized, each with dense cytoplasm and a nucleus. Type IIa: head unicellular (Fig. 71), Type IIb: head 2—many celled (Figs. 72—75).

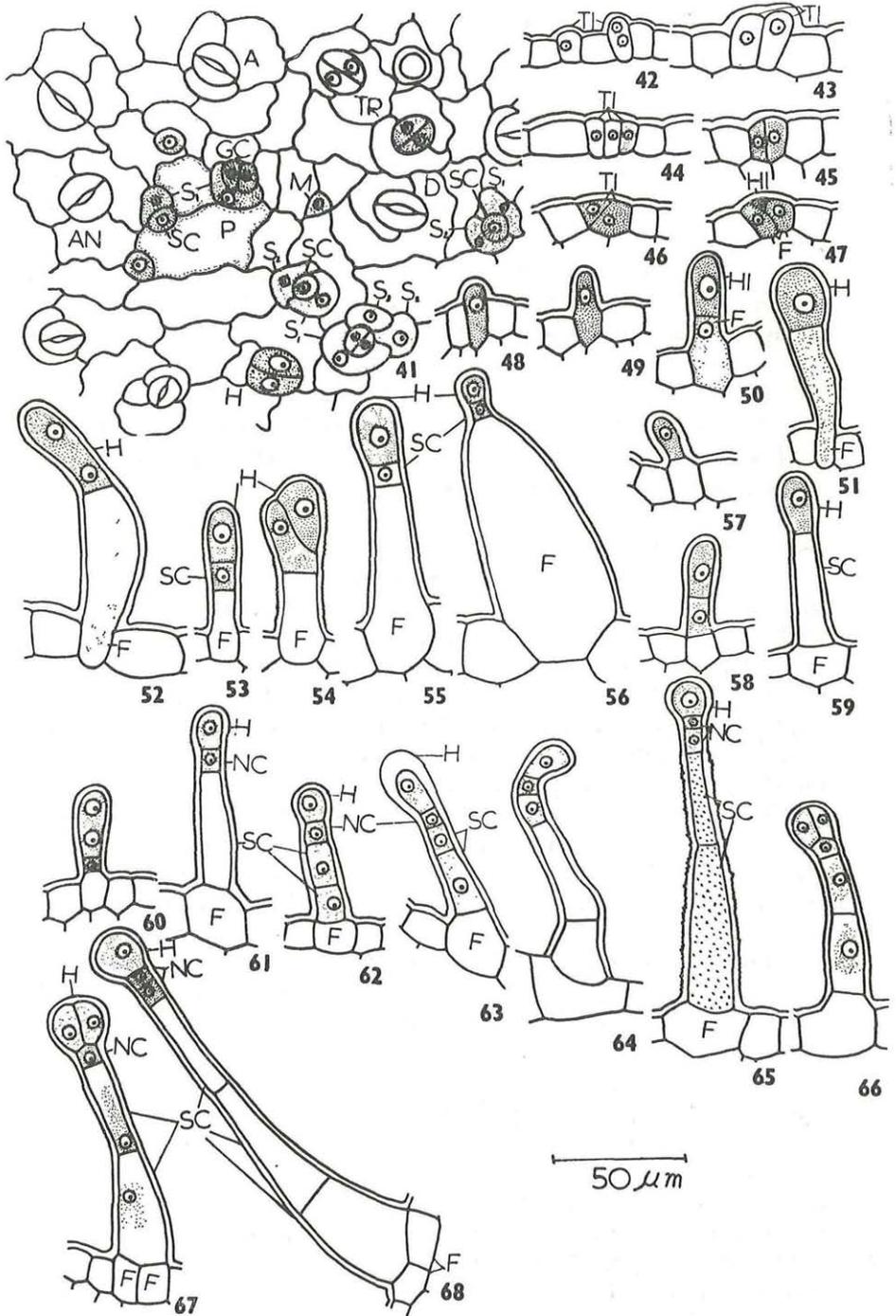
Eglandular trichomes are uniseriate, differentiated into foot and body. Foot (F) one-celled, squarish (Fig. 78), rectangular (Figs. 80, 83), trapezoidal (Fig. 80) or polygonal (Fig. 82), at times slightly projecting beyond the epidermal cells, usually devoid of contents, seldom contents faint (Fig. 79). The body is thin walled; cuticle smooth (Figs. 78—80, 82) or tubercled (Figs. 81, 83, 84).

Type III — Body unicellular:

Body conical with acute or subacute tip, straight or bent (Figs. 78—81).

Fig. 41. Epidermal peel showing stages in stomatal ontogeny. (*Stachys cretica* ssp. *bulgarica*)

Figs. 42—68: Glandular trichomes in transverse sections (Figs. 43—47, 54—56, 58, 61, 64, 65, 67, 68 from adaxial surface, rest from abaxial surface). — *Stachys recta*: Figs. 45—47. — *St. macrostachys*: Fig. 56. — *St. palustris*: Figs. 41, 67. — *St. cretica* ssp. *bulgarica*: Fig. 65. — *St. olympica*: Fig. 68. — *Salvia argentea*: Figs. 42, 50. — *S. patens*: Figs. 43, 44, 51, 52. — *S. cleistogama*: Fig. 53. — *S. sclarea*: Fig. 62. — *S. triloba*: Figs. 63, 66. — *Lallemantia iberica*: Figs. 48, 49, 58, 60. — *Marrubium supinum*: Figs. 59, 61. — *Hyssopus officinalis*: Fig. 57. — *Nepeta cataria*: Figs. 54, 55. — *N. cataria* var. *citriodora*: Fig. 64. — Figs. 42—51: Stages in the ontogeny of glandular trichomes



Type IV — 2—3 celled body:

(a) Acuminate conical hair: This type of hairs are rarely seen in *M. supinum* and *St. officinalis*. Foot (F) one celled. Body is smooth walled, thinly cuticularized, basal cell cylindrical, terminal one narrowly acuminate (Fig. 82).

(b) Non-acuminate conical hair: It is frequent in many taxa. The body is straight or slightly bent, acute at tip; cuticle smooth or tubercled (Figs. 80, 83).

(c) Non-acuminate cylindrical branched hair: It is found on both surfaces only in *Lavandula*, body cylindrical, rounded or obtuse at tip, thinly cuticularized, tubercled (Fig. 84).

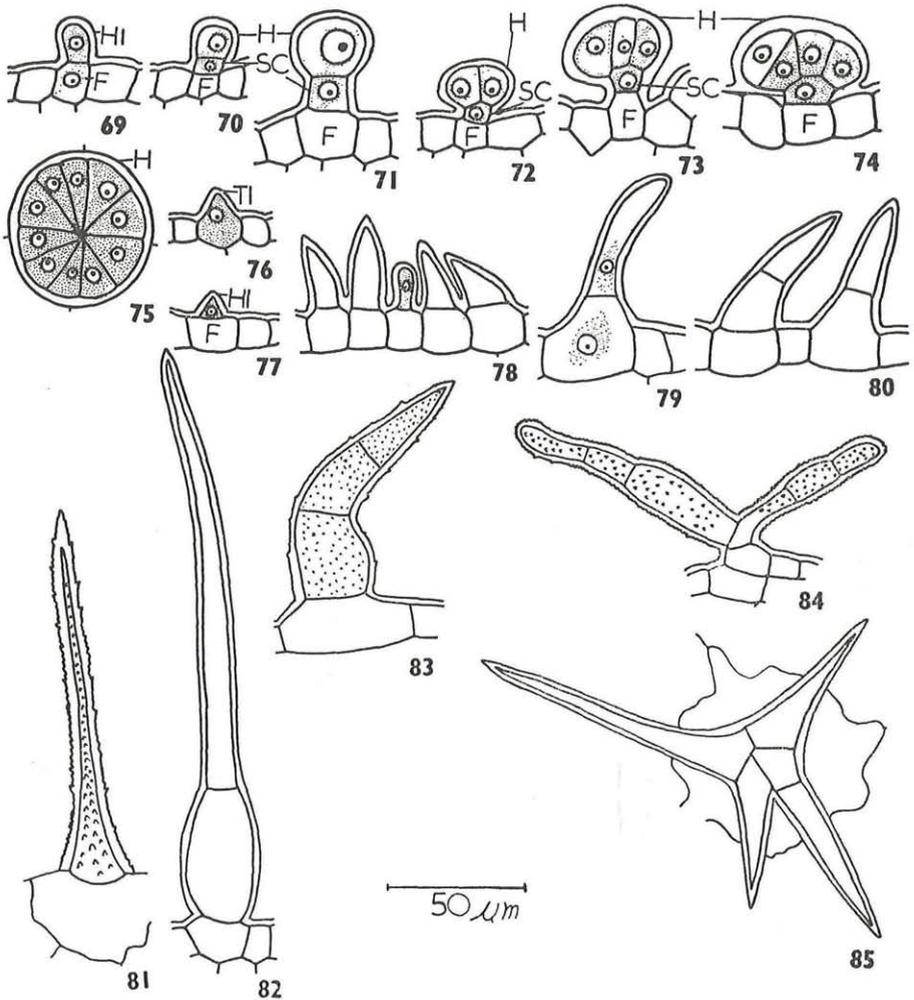
Type V — Stellate hair:

Foot (F) 1-celled, rectangular or polygonal devoid of contents. Body 2—4 armed, arms conical, smooth walled, with acute tip (Fig. 85). It is sparingly found in *Sideritis macrostachyos*.

3.5 Ontogeny of trichomes

3.5.1 Glandular trichomes: A trichome initial (TI) develops from a single epidermal cell which can be distinguished from other, epidermal cells by its size, dense cytoplasm, relatively larger nucleus and rounded outer wall (Fig. 42). Sometimes 2—3 trichome initials are found side by side and they may be of the same size or different sizes (Figs. 43, 44). At times in *Salvia patens*, *Stachys palustris* and *St. recta*, the trichome initial increases in size and may divide by a vertical or an oblique wall so that two unequal initials are produced (Figs. 45, 46). A trichome initial (TI) increases in size and becomes oblong, cylindrical or flask shaped (Figs. 42, 48, 49). It divides by a transverse wall to cut off an upper cell, the hair initial (HI), and the lower the foot (F, cf. Figs. 42, 50). The foot initial in some cases increases very much in size and forms a stalk whereas the hair initial enlarges into a spherical head (cf. Fig. 51). The nucleus of the head cell divides into two nuclei (Fig. 52), followed by a transverse wall to produce two unequal cells, the lower smaller, rectangular or squarish is the stalk cell (SC) and the larger upper one the head cell (Fig. 53, 55, 56). Very seldom the wall between the two nuclei is oblique (cf. Fig. 54).

The foot cell remains at the same level as other epidermal cells or it slightly projects beyond them (Fig. 57). The hair initial then increases in size and divides by a transverse wall to form an upper head cell and the lower stalk cell, which becomes very much elongated and loses its content (cf. Figs. 58, 59). Sometimes, before the stalk cell elongates, the head cell nucleus divides into two nuclei (Fig. 60), followed by a transverse septum cutting off two unequal cells, the smaller the neck cell and the upper head cell. By this time the stalk cell, considerably increases in length and is



Figs. 69—75: Glandular trichomes. Figs. 76—85 eglandular trichomes, as observed in transverse section (except figs. 85 and 81 from epidermal peels). Figs. 69, 71, 73, 74, 78—80, 82 from adaxial surface, rest from abaxial surface. — *Calamintha nepeta*: Fig. 69. — *Lallemantia iberica*: Figs. 70, 72, 73. — *Sideritis hyssopifolia*: Fig. 71. — *Si. macrostachyos*: Fig. 85. — *Salvia argentea*: Figs. 76, 77. — *S. sclarea*: Fig. 78. — *S. triloba*: Figs. 74, 79, 80. — *Stachys officinalis*: Fig. 81. — *Marrubium supinum*: Fig. 82. — *Dracocephalum moldavica*: Fig. 75. — *Nepeta cataria*: Fig. 83. — *Lavandula angustifolia*: Fig. 84. — Figs. 69, 70: Stages in development of glandular trichomes; Fig. 76, 77: Stages in development of eglandular trichomes

devoid of contents (cf. Fig. 61). In some cases the stalk cell simultaneously divides to form two to three stalk cells, of which one or two cells become elongated. The head in most of the taxa is unicellular (Figs. 62—65, 68) or seldom bicellular by a vertical wall formation (Figs. 66, 67). When such hairs mature, they develop usual cuticular thickenings.

Where there are two or more trichome initials, generally only one of them divides by an oblique wall to cut off a hair initial and foot cell. The remaining initials contribute to form a compound foot (cf. Fig. 47).

In capitate sessile or very shortly stalked hairs, the trichome initial cuts off the foot cell (F), stalk cell (SC) and the head cell (H) (Fig. 70). The later increases in size and becomes spherical without undergoing any division (cf. Fig. 71) or it may variously divide to produce 2 — many celled head (cf. Figs. 72—75).

3.5.2 Eglandular trichomes: The trichome initial (TI) of an eglandular trichome differs from that of glandular one by its papillate outer wall (Fig. 76). A transverse wall is formed in the trichome initial to cut off the hair initial (HI) and foot cell (F, Fig. 77). The hair initial increases in size and produces an unicellular or uniseriate body by transverse division (Figs. 78—80, cf. Figs. 80, 82, 83). As the hair assumes the final shape it develops usual cuticular thickenings. The ontogeny of stellate hair is not traced.

4. Discussion

According to METCALFE & CHALK (1950), the stoma in *Lamiaceae* are diacytic with a few anomocytic intermixed and these observations are confirmed by RAMAYYA & RAO (1969) on the cotyledons of three species of *Ocimum*. INAMDAR & BHATT (1972) reported diacytic, transitional and anomocytic stomata in thirty three species of this family with the first type as the most frequent in all taxa, with perigenous and mesogenous ontogenetic patterns. On the other hand EL-GAZZAR & WATSON (1970), from their study of this family, reported that the stomata are predominantly diacytic, predominantly anomocytic, predominantly anisocytic and a mixture of anomocytics and anisocytics. Our study is in agreement with those of these authors because, though diacytic is most frequent type in many taxa, anomocytic replaces diacytic on both surfaces in a few taxa and on adaxial surface in some more taxa, at times making up more than 50% of the total number of stomata in *Lamium* (71%), *Le. cardiaca* var. *crispa* (68%), *M. supinum* (92%) and *N. cataria* (55%). The other dominant types are anisocytic on the abaxial surface of *M. supinum* (59.5%), haplocytic in *S. triloba* (56%), *St. recta* (32.5%) and transitional in *St. olympica* (36%). These results clearly indicate a taxonomic delineation of the genera and species on the basis of the most frequent type, already indicated earlier in general by EL-GAZZAR & WATSON (1970). The present study and earlier

report of the last authors also show that *Lamiaceae* are not predominantly diacytic as hitherto understood.

The supplementary information to the published literature is the occurrence of (i) haplocytic, paracytic, tetracytic and tricytic stomata, (ii) twelve more abnormalities in addition to contiguous stomata and stoma with one guard cell and (iii) mesoperigenous ontogeny of some diacytic and anisocytic stomata.

Though the foliar trichomes are described in some members of *Labiatae* (METCALFE & CHALK 1950, EL-GAZZAR & WATSON 1970, SINGH *et al.* 1975, GUPTA & BHAMBIE 1978), their ontogeny is not traced by any of these authors. We have described it for different types.

The importance of trichomes in determining the relationships of families, genera or species has been recognised in the literature (METCALFE & CHALK 1950, CARLQUIST 1961, METCALFE 1961, 1969, RAMAYYA & RAJAGOPAL 1971, RADFORD *et al.* 1974, SINGH *et al.* 1974, 1975, RAO & RAMAYYA 1977, GUPTA & BHAMBIE 1978, SHAH & PARABIA 1979). A critical study of the distribution of different types of trichomes suggests that they provide a useful criterion to delineate various species and genera in the present study.

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