

STUDIES ON THE TRICHOMES OF SOME COMPOSITAE I. GENERAL STRUCTURE

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ABSTRACT

Seventy two Compositae belonging to 56 genera representing the thirteen tribes of the family have been investigated in this study. Trichomes are recognised broadly into two categories namely the 'vegetative' and the 'floral' ones. It is the former that have been presently taken up for detailed investigations. In all 35 trichome types are found so far in the family. Of these, 15 have been described by previous workers which the present author has also observed in the species under investigation. Another 13 are the newly established types by the author. The remaining 7 represent types which the author has not come across during the present investigations but are described in the literature.

The general features of the trichomes in the family are discussed in the light of the present study. The trichomes are shown to exhibit in all four patterns in their structure which provide important evidence in the phylogeny of the trichomes.

INTRODUCTION

During the last century, considerable interest seems to have been evinced in studying the plant trichomes leading to accumulation of much data in many families of the angiosperms. The information is, however, mostly piecemeal and often confusing as is seen from the accounts provided by Solereder (1908) in his 'Systematic anatomy of the dicotyledons'. In the recent past, although there appears to be no general interest shown in the study of these structures, certain taxa have, nevertheless, been investigated in detail e.g., the Cactaceae (Hemenway and Allen, 1936), Icacinaceae (Heintzelman and Howard, 1948), *Rhododendron* (Cowan, 1950), *Nicotiana* (Goodspeed, 1954), Madiinae—Compositae (Carlquist, 1958 and 1959 c) and Gramineae (Metcalf, 1960). However, as trichomes are almost universal among the vascular plants (De Bary, 1884; Carlquist, 1961), there is doubtless great need for similar detailed studies in other plant groups.

Compositae is the largest family of the angiosperms with 950 genera and about 20,000 species (Lawrence, 1951). Since it is generally regarded as one of the highly advanced groups, its trichomes were expected to possess great variety and hence form suitable material not only for taxonomic purposes, but also for basic studies concerning themselves. The available literature dealing with studies on the trichomes of the family is not extensive as compared to its large size and further, the observations are mostly incomplete and from stray examples. A resume of the early work is included by Solereder (1908) in his *Systematic*. Subsequent work includes the contributions by Cavillier (1907 & 1911), Lloyd (1901), Kupfer (1903), Holm (1908, 1913, 1917 and 1926), Sabnis (1921), Briquet (1930), Diettert (1938), Astschwager (1943), Volle and Hetzger (1949), Korsmo (1954) and Mirashi (1955 and 1956). Recently Carlquist (1958, 1959 a, b & c) has published

some excellent accounts on the development of the glandular trichomes of the subtribe Madiinae.

The present studies on the trichomes of the family are based on 72 species belonging to 56 genera (cf. Appendix II). The species represent all the thirteen tribes of the family according to Bentham and Hooker's classification (1876). Four aspects of the trichomes namely structure, variations, development and distribution (both the organographic and systematic) have been investigated of which the general structure is presented here.

The trichomes of the family are provisionally recognized into two categories, the 'vegetative' and the 'floral', on the basis of differences in their organographic distribution. The former represents the trichomes so commonly seen on the stems and leaves of plants, but these often also occur on the floral parts viz., calyx (often pappose in the family), corolla, stamens and gynaecium. The latter, on the other hand, are restricted to only the floral parts and they include the papillae (e.g., found both on the outer and inner surfaces of the style-arms), Aseptate Hairs (otherwise collectively called as the anther-tails and characteristic of the Inuleae and Cynareae), Trigger Hairs (cf. Small, 1919, p. 47; the trichomes are found on the filaments in some Cynareae) and the Achenial Hairs (op. cit., p. 101; also called as the 'Zwillingshaare' by Hess, 1938; the trichomes are a characteristic of the ovary in the family). The Laticiferous Hairs which occur on the phyllaries and the axillary bracts of the heads in some Cichoreae (Solereder, 1908, see also his fig. 103 c) is also, however, presently included in the floral trichomes, since it has so far been not observed on the stem and leaves.

TERMINOLOGY

Foot: Part of the trichome lying in the epidermis, usually one cell in thickness. It is recognised into two kinds viz.,

- (a) Simple foot: Consists of as many cells as the number of the cell rows of the immediately overlying part of the trichome.
- (b) Compound foot: Consists of cells which are more in number than the cell rows of the immediately overlying part of the trichome.

In the case of trichomes with wholly multiseriate structure (e.g., in the 26-28 described in the text), often the number of the cells of the foot and that of the cell rows of the overlying portion of the trichome cannot be compared. Consequently, in such instances, the above distinction in the foot is not possible.

Body: Part of the trichome lying above the foot. It is of two categories viz., (a) the differentiated and (b) the entire.

- (a) Differentiated body: Consists of structurally and usually also functionally two different parts i.e., (i) the stalk, representing the proximal region and (ii) the head, representing the distal region.
- (b) Entire body: Consists of a structure without differentiation into the stalk and the head.

The trichomes display the following four kinds of sculpturings on their outer surface.

1. **Ridged:** Bearing fine elevated lines. The latter are usually wavy (fig. 54 a).
2. **Verrucose:** With projections usually circular at the base and not pointed towards the end (fig. 54 c).
3. **Echinulate:** With projections as in the above but with pointed ends (fig. 54 b).
4. **Granulate:** Marked with projections shorter than those characterising the verrucose thickening and irregular in outline (fig. 54 d).

The sculpturings, however, do not rigidly conform to the above definitions in all instances. Often they show intergradations in one and the same trichome. Further, quite commonly they also become reduced on the terminal cells losing their identity.

NOMENCLATURE

All the trichome types observed in the species investigated are given bi- or polynomial names. The names are ended in the epithet 'hair' as they all belong to the category of 'Hairs' according to the classification of trichomes by Cowan (1950) which is followed in the present work.

OBSERVATIONS

In all twenty eight trichome types are observed in the species investigated. Descriptions of their detailed structure in the 72 members presently studied are given elsewhere by the author (1962 a). Based on the above the general structure of the trichomes is as given below:

1. Simple Filiform Hair (figs. 1 & 2).

Foot: Simple or compound. **Body:** Uniseriate, entire, 5 to many-celled, filiform, often cylindrical or tapering above, constricted at the cross walls, pointed or rounded at the apex. Cells of varied lengths, but the basal 1 or 2 usually broader than long or isodiametrical and the terminal relatively long. Contents translucent or dense, usually opaque¹ in 1 to several terminal cells. Cross walls thin. Lateral walls straight or slightly convex, thin or thick, smooth or ridged.

2. Vesicular Filiform Hair (figs. 3 & 4).

Foot: Simple or compound. **Body:** Uniseriate, entire, usually 5 to 10-celled, filiform, cylindrical or slightly tapering above, weakly or prominently constricted at the cross walls, rounded at the apex. Cells of varying lengths, the basal 1 or 2 usually broader than long or isodiametrical. Contents translucent or dense, sometimes opaque in 1 or 2 terminal cells. Cross walls thin. Lateral walls straight or convex, thin or slightly thick, smooth or verrucose. Cuticular vesicle restricted to the apex, persistent or collapsing early.

3. Sclerosed Filiform Hair (fig. 5).

Foot: Simple or compound. **Body:** Uniseriate, filiform, differentiated into stalk and head. **Stalk:** 2 to 5-celled, cylindrical or slightly tapering above, weakly constricted at the cross walls. Cells of varied lengths, the basal 1 or 2 often broader than long or isodiametrical. Cross walls thin. Lateral walls straight or slightly convex, thin and smooth but in the basal 1 or 2 cells sometimes thick, weakly ridged. **Head:** 2 to 6-celled, uniform in breadth, usually larger than the stalk, weakly or prominently constricted at the cross walls, rounded at the apex. Cells so often longer than broad, nearly of the same length. Contents dense, persistent or evanescent. Cross walls thin. Lateral walls usually convex, thick and smooth.

4. Flagellate Filiform Hair (figs. 6 & 7).

Foot: Simple or compound. **Body:** Uniseriate, filiform, differentiated into stalk and head. **Stalk:** 2 to 10-celled, usually cylindrical or slightly tapering above, minutely constricted at the cross walls. Cells of various lengths but the basal 1 or 2 usually broader than long or isodiametrical. Contents translucent or dense. Cross walls thin. Lateral walls straight or slightly convex, thin or thick, smooth. **Head:** unicellular, flagellate, tapering to a pointed tip. Contents translucent or opaque. Lateral walls thin or slightly thick, smooth.

5. Capitate Filiform Hair (fig. 8).

Foot: Simple or compound. **Body:** Uniseriate, filiform, differentiated into stalk and head. **Stalk:** 3 to 6-celled, cylindrical or slightly tapering above, constricted at the cross walls. Cells growing longer

¹ In this and in the next four trichome types, the opaqueness is found to be due to the presence of pectic substances.

above. Contents translucent. Cross walls thin. Lateral walls straight or slightly convex, thin but frequently thick in 1 or 2 basal cells. *Head*: Unicellular, broader than the stalk, swollen to an oblong-ovoid or ovate form. Contents dense. Lateral walls thin and smooth.

6. Cylindrical Hair. The trichome is represented by two subtypes α and β ¹.

Subtype α (cf. Korsmo, 1954, fig. 189 b, 11 a & b, p. 399).

Foot: Simple or compound. *Body*: Uniseriate, differentiated into stalk and head. *Stalk*: 2 to 4-celled, cylindrical, shorter than the head. Contents slightly dense. Cross walls thin. Lateral walls straight or slightly convex, thin and smooth. *Head*: 5 to many-celled, cylindrical, flexuous, constricted at the cross walls, rounded at the distal end. Cells usually longer than broad, growing in their lengths above. Cross walls thin. Lateral walls straight or slightly convex, thin, smooth.

Subtype β (figs. 10 & 11).

Foot: Simple or compound. *Body*: 2 to many-celled, entire, usually cylindrical, slightly constricted at the cross walls, rounded at the apex but at times with a short mucro. Cells usually growing longer above but 1 to 3 basal ones often broader than long. Cross walls thin. Lateral walls straight or slightly convex, thin or slightly thick, smooth, granulate, verrucose or finely ridged.

7. Simple Conical Hair (figs. 17-19).

Foot: Simple or compound. *Body*: Uniseriate, entire, 2 to many-celled, conical, pointed or sometimes rounded at the apex, constricted at the cross walls, often nodulose at the joints. Cells usually growing longer above, the basal 1 to several usually broader than long. Cross walls thin or thick. Lateral walls straight or slightly convex or concave, thick, sometimes growing thinner above, smooth, granulate, verrucose, echinulate or ridged.

8. Wavy Conical Hair (figs. 15 & 16).

Foot: Simple or compound. *Body*: Uniseriate, differentiated into stalk and head. *Stalk*: 2 to many-celled, tapering above, little or not constricted at the cross walls, collapsing early. Cells growing longer above, the basal 1 to 3 usually broader than long. Cross walls thin. Lateral walls straight or slightly convex, thin, smooth. *Head*: 2 to many-celled, continuous with the stalk, tapering above, rounded at the apex, slightly constricted at the cross walls, collapsing early. Cells longer than broad, growing in their lengths above. Contents evanescent. Cross walls thin. Lateral walls irregularly wavy in outline, slightly thick, smooth.

9. Moniliform Hair. The trichome consists of two subtypes, α and β .

Subtype α (fig. 13).

Foot: Simple or compound. *Body*: Uniseriate, differentiated into stalk and head. *Stalk*: 2 to 6-celled, cylindrical or slightly broadening above, flexuous, constricted at the cross walls, collapsing early. Cells varied in their length. Cross walls thin. Lateral walls somewhat convex, thin, smooth. *Head*: 4 to many-celled, larger than the stalk, flexuous, collapsing early. Cells bladder-like, spherical to ovoid, enlarging above, filled with watery sap. Cross walls thin. Lateral walls thin, smooth.

Subtype β (fig. 12).

Foot: Simple or compound. *Body*: Uniseriate, entire, 4 to 10-celled, moniliform, flexuous, collapsing early. Cells spherical to ovoid, of the same or slightly broadening above, filled with watery sap. Cross walls thin. Lateral walls thin, smooth.

10. Capitate Hair (fig. 9).

Foot: Simple or compound. *Body*: Uniseriate, differentiated into stalk and head. *Stalk*: 1 to 4-celled, cylindrical, constricted at the cross walls. Cells longer than broad, growing in their length above. Cross walls thin or slightly thick. Lateral walls straight, thick, finely ridged. *Head*: Unicellular, spherical or slightly drawn below, thick-walled, granulate.

11. Ramose Hair (fig. 14).

Foot: Simple or compound. *Body*: Uniseriate, differentiated into stalk and head. *Stalk*: 4 or more-celled, flexuous, collapsing early, narrower than the head. Cells of various length. Cross walls thin. Lateral walls straight to slightly convex, thin and smooth. *Head*: Few to many-celled appearing unichasially branched, breaking early into its constituent cells. Cells longer than broad, all nearly of the same length, irregularly wavy in outline, attached to one another by their basal ends, the distal end remaining free and rounded. Contents evanescent. Lateral walls slightly thick and smooth.

12. Two-armed Hair (figs. 20-22).

Foot: Simple or compound. *Body*: Uniseriate, differentiated into stalk and head. *Stalk*: 1 or more-celled, cylindrical, tapering above, slightly constricted at the cross-walls. Cells of varying lengths, the basal 1 to few usually broader than long. Cross walls thin. Lateral walls straight to slightly convex, thin or thick, smooth or finely verrucose. *Head*: Unicellular, 2-armed or at times T-shaped. Arms usually flat and channelled at the base, tapering above, pointed or rounded at the apex, straight or bent and folded here and there, placed at an angle to the stalk. Lateral wall thin or thick, smooth or finely verrucose.

13. One-armed Hair (fig. 35).

Foot: Simple or compound. *Body*: Uniseriate, differentiated into stalk and head. *Stalk*: 2 to many-celled, cylindrical or slightly tapering above,

¹ In the same species or in different ones, certain trichomes are found in two conditions, one with the differentiated body (p. 3) and the other with the entire body (p. 4). In such cases, the trichome is recognised to have subtypic differentiation. Trichomes of the first kind are designated as the subtype α and of the second as the subtype β .

weakly constricted at the cross walls. Cells of various lengths, 1 to few basal ones usually broader than long or isodiametrical. Cross walls usually thin. Lateral walls straight to slightly convex, thin or thick but sometimes growing thinner above, smooth or granulate. *Head*: Unicellular, 1-armed. Arm flat, usually channelled at the base, tapering above, pointed or rounded at the apex, placed at an angle to the stalk. Basal and slightly protruded. Basal wall thin. Lateral wall thin or thick, smooth.

14. Septate-flagellate Hair. The trichome consists of two subtypes α and β .

Subtype α (Fig. 23).

Foot: Simple or compound. *Body*: Uniseriate, differentiated into stalk and head. *Stalk*: 2 to 8-celled, usually cylindrical, flexuous, slightly constricted at the cross walls. Cells growing longer above, the basal 1 or 2 often broader than long. Cross walls thin. Lateral walls thin or slightly thick, straight, smooth. *Head*: 3 to 12-celled, slightly broader than the stalk, whip-like, weakly constricted at the cross walls, tapering to a pointed tip. Cells longer than broad, increasing in their length above. Contents translucent or opaque. Cross walls thin. Lateral walls thin or thick, smooth.

Subtype β (fig. 24).

Foot: Simple or compound. *Body*: Uniseriate, entire, 8 to 10-celled, flagellate, tapering above, pointed at the apex, constricted at the cross walls, slightly nodulose at the distal joints. Cells growing longer above, the basal 1 or 2 broader than long. Contents disappearing early from the distal cells. Cross walls thin. Lateral walls thick getting thinner above, smooth.

15. Aseptate-flagellate Hair (fig. 25).

Foot: Simple or compound. *Body*: Uniseriate, differentiated into stalk and head. *Stalk*: 1 to 10-celled, cylindrical or tapering above, constricted at the cross walls. Cells of various lengths, the basal 1 or 2 usually broader than long. Cross walls thin. Lateral walls thin or thick but getting thinner above. *Head*: Unicellular, very long, flagellate, tubular, continuous or sharply delimited from the stalk, collapsing early or remaining intact. Contents evanescent. Lateral wall thin or slightly thick, smooth.

16. Oblique-septate-flagellate Hair (fig. 30).

Foot: Simple or compound. *Body*: Uniseriate, differentiated into stalk and head. *Stalk*: 2 to 4-celled, cylindrical or tapering above, flexuous in the distal region, slightly constricted at the cross walls. Cells growing longer above, but the basal 1 or 2 usually broader than long. Cross walls thick. Lateral walls straight or slightly convex, thick, smooth. *Head*: 3 or 4-celled, quite long, continuous with the stalk, flagellate, constricted at the cross walls, tapering to a pointed tip. Cells many times as long as broad, increasing in their length above. Contents

evanescent. Cross walls oblique, thick, pitted. Lateral walls thick, smooth.

17. Oblique-aseptate-flagellate Hair (figs. 31 & 32).

Foot: Simple or compound. *Body*: Uniseriate, differentiated into stalk and head. *Stalk*: 1 to 5-celled, cylindrical or tapering above, constricted at the cross walls. Cells growing longer above, the basal 1 or 2 usually broader than long. Cross walls thin. Lateral walls straight to slightly convex, thin or thick, smooth. *Head*: Unicellular, very long, flagellate, continuous with the stalk or sharply delimited from it, tapering above, collapsing early or remaining intact, often slightly protruded at the base. Basal wall oblique, thin or thick and pitted. Lateral wall thin or thick, smooth.

18. Bulbiferous Flagellate Hair (figs. 26 & 27).

Foot: Simple or compound. *Body*: Uniseriate, differentiated into stalk and head. *Stalk*: 2 to 10-celled, cylindrical or tapering above, constricted at the cross walls, collapsing early or firm except in the distal portion. Cells growing longer above, the basal 1 to few usually broader than long. Terminal cell swollen, spherical or ovoid-oblong in shape, collapsing early. Contents translucent, but sometimes dense in the terminal cell. Cross walls thin. Lateral walls thin or quite thick but always thin in the terminal cell, smooth or marked with wavy ridges. *Head*: Unicellular, quite long, tubular, flagellate, narrower than the stalk, collapsing early. Contents evanescent. Basal wall thin. Lateral wall thin, smooth.

19. Uniseriate Glandular Hair. (figs. 28 & 29)

Foot: Simple or compound. *Body*: Differentiated into stalk and head. *Stalk*: Uniseriate, 3 to 30-celled, cylindrical or tapering above, slightly constricted at the cross walls. Cells of various lengths, 1 to few basal ones usually broader than long or isodiametrical. Cross walls thin or thick. Lateral walls thin or thick, smooth or marked with prominent ridges. *Head*: 3 to 8-celled, uniseriate, but 1 or more cells often vertically or obliquely subdivided, cylindrical or sometimes capitate, rounded at the apex. Cells mostly broader than long, nearly of the same length. Contents dense, persistent. Cross walls thin. Lateral walls convex, thin or slightly thick, smooth.

20. Simple Biseriate Hair (fig. 34).

Foot: Simple or compound. Cells sometimes much projected above the epidermis. *Body*: Biseriate, entire, 2 to many-celled in each row, uniform in breadth or tapering above, flexuous or stiff. Apex bifurcate with rounded or sharp tips. Cells of the two rows subopposite or alternate, of varied lengths or growing longer above. Inner walls thin or thick, placed at right angles or oblique to the outer walls. Outer walls straight or slightly convex, thin or thick, smooth or finely ridged.

21. Simple Biseriate Glandular Hair. The trichome is found to consist of two subtypes α and β .

Subtype α . (figs. 36 & 37).

Foot: Simple or compound. *Body*: Biseriate, differentiated into stalk and head. *Stalk*: 2 to 4-celled in each row, uniform or slightly tapering above. Cells alternate or subopposite, of various lengths. Contents translucent. Inner walls thin. Outer walls straight or slightly convex, thick and smooth. *Head*: 2 to 5-celled in each row, of varied shapes, emarginate. Cells of the two rows subopposite or opposite, of varied lengths, but those of the terminal tier often relatively long. Contents dense, persistent or evanescent. Inner walls thin. Outer walls straight or slightly convex, thin, smooth.

Subtype β (fig. 38).

Foot: Simple or compound. *Body*: Biseriate, entire, 3 to 8-celled in each row, of varied shapes, emarginate. Cells of the two rows subopposite or opposite, of varied lengths, but those of the terminal tier often relatively long. Contents dense, persistent or evanescent. Inner walls thin. Outer walls usually convex, thin, smooth.

22. Biseriate Vesicular Glandular Hair. The trichome is represented by two subtypes α and β .**Subtype α** (figs. 39 & 40).

Foot: Simple or compound. *Body*: Biseriate, differentiated into stalk and head. *Stalk*: 2 to 5-celled in each row, uniform in breadth or tapering above. Cells of the two rows alternate or subopposite, of various lengths. Contents translucent. Inner walls thin. Outer walls straight or slightly convex, thick and smooth. *Head*: 4 to 8-celled in each row, of varied shapes, emarginate, sharply demarcated from the stalk or continuous with it. Cells of the two rows opposite or subopposite, varied in their length but those of the terminal tier relatively longer. Contents dense, persistent or evanescent. Inner walls thin. Outer walls straight to slightly convex, thin or somewhat thick, smooth. Cuticular vesicle enclosing 1 to 3 tiers or restricted to the apex of the terminal one, persistent or collapsing early.

Subtype β . (figs. 41-44).

Foot: Simple or compound. *Body*: Biseriate, entire, 4 to 10 cells in each row, oblong or cuneate in shape, emarginate. Corresponding cells of the two rows usually subopposite, of various lengths or growing longer above or all nearly of the same length except those of the terminal tier which are often relatively long. Contents dense, commonly persistent. Inner walls thin. Outer walls slightly convex, thin, smooth. Cuticular vesicle enclosing 1 to 4 terminal tiers or restricted to the apex, persistent or collapsing early.

23. Biseriate Rostrate Vesicular Glandular Hair :

This is represented by two subtypes α and β .

Subtype α (fig. 45).

Foot: Simple or compound. *Body*: Biseriate, differentiated into stalk and head. *Stalk*: 2 or 3-celled in each row, oblong or slightly tapering above, smaller than the head. Cells of the two rows alter-

nate, of varied lengths. Contents scanty, translucent. Inner walls thin. Outer walls thin or slightly thick, smooth. *Head*: 5 or 6-celled in each row, oblong but rostrate at the distal end, emarginate. Cells of the two rows alternate or subopposite, broader than long, nearly of the same length. Terminal pair of cells relatively narrow, often longer than the remaining portion of the head, distinct from the latter. Contents dense, persistent or evanescent. Inner walls thin. Outer walls straight or slightly convex, thin, smooth. Cuticular vesicle enclosing the terminal tier.

Subtype β (fig. 46).

Foot: Simple or compound. *Body*: Biseriate, entire, 8 to 10-celled in each row, oblong but rostrate at the distal end. Cells of the two rows alternate, broader than long, all nearly of the same length. Terminal pair of cells shorter than the remaining portion of the body but distinct from it, much longer than broad, opposite to each other. Contents dense, persistent. Inner walls thin. Lateral walls thin, smooth. Cuticular vesicle enclosing the terminal tier.

24. Biseriate Capitate Glandular Hair. (figs. 47-49).

Foot: Simple or compound. *Body*: Differentiated into stalk and head. *Stalk*: Biseriate, 3 to 7-celled in each row, usually tapering above. Cells of the two rows alternate to subopposite, of varied lengths, but of the basal 1 or 2 tiers usually broader than long or isodiametrical. Inner walls thin. Outer walls straight but in 1 or 2 basal tiers slightly convex, thick, smooth. *Head*: 1 to 5-tiered, of varied shapes, continuous or sharply differentiated and shorter than the stalk. Tiers 2 or more-celled in either view but the terminal one usually consisting of the largest number of cells and the basal, minimum 2. Cells of various lengths but in the terminal tier usually palisade-like. Contents dense but more so in the terminal tier, sometimes containing sphaerocrystals. Inner walls thin. Lateral walls straight or slightly convex, thin or thick, smooth.

***25. Biseriate Vesicular Capitate Glandular Hair** (fig. 50).

Foot: Simple or compound. *Body*: Differentiated into stalk and head. *Stalk*: Biseriate, 1 to 5-celled in each row, uniform in breadth or tapering above. Cells of the two rows alternate or subopposite, varying in their lengths but those of the basal 1 or 2 tiers usually broader than long or isodiametrical. Contents translucent. Inner walls thin or thick. Outer walls straight or slightly convex, thick but sometimes growing thinner above, smooth. *Head*: 3 to 7-tiered, of varied shapes, shorter or larger than the stalk. Tiers 2 or more-celled in either view but the basal one often 1-celled in the lateral view. Cells of various lengths or relatively long. Terminal tier palisade-like. Contents dense but more so in the terminal tier, persistent, at times containing sphaerocrystals. Inner walls thin. Outer walls thin or thick, smooth.

Cuticular vesicle enclosing or restricted to the apex of the terminal tier, persistent or collapsing early.

26. M-Simple Multiseriate Glandular Hair¹ (fig. 51).

Foot: Simple or possibly compound. **Body:** Multiseriate, entire, 4 or 5-tiered, as long as broad slightly longer, rounded at the apex. Tiers many-celled. Cells broader than long or isodiametrical, all nearly of the same length. Contents dense, persistent. Inner walls thin. Outer walls straight or slightly convex, thin and smooth.

27. M-Multiseriate Capitulate Glandular Hair¹ (fig. 52).

Foot: Simple or possibly compound. **Body:** Multiseriate, differentiated into stalk and head. **Stalk:** Longer than the head, tapering above. Cells longer than broad but the proximal ones broader than long or isodiametrical. Contents translucent. Inner walls thin or slightly thick. Outer walls straight or slightly convex, thick and smooth. **Head:** 3 to 5-tiered, obconical, truncate, sharply differentiated from the stalk. Tiers many-celled. Cells nearly isodiametrical but in the terminal tier longer than broad and palisade-like in arrangement. Contents dense but more so in the distal 1 or 2 tiers, containing sphaerocrystals. Inner walls thin. Outer walls straight to slightly convex, thick and smooth.

28. P-Multiseriate Capital Glandular Hair² (fig. 53).

Foot: Simple or possibly compound. **Body:** Multiseriate, differentiated into stalk and head. **Stalk:** Several times as long as the head, cylindrical or slightly tapering above. Cells longer than broad, but the basal ones thick and smooth. **Head:** 4 or 5-tiered, broadening above, truncate, sharply differentiated from the stalk. Tiers many-celled. Cells slightly longer than broad in the basal 1 or 2 tiers but isodiametrical in others. Contents dense but more so in the terminal 1 or 2 tiers, persistent. Inner walls thin. Outer walls straight or slightly convex thick and smooth.

Although several workers (see p. 2) in the past have made observations on the trichomes of the family, the data suffers from several discrepancies as incomplete descriptions, absence of uniform terminology, and incorrect interpretations. The details of all these aspects have been discussed elsewhere by the author (1962 a). For the present, therefore, it is considered sufficient to state that among the 28 trichomes described above, 15 (viz., 1, 4, 6, 7, 13, 14, 15, 17, 21, 22, 24, 25, 27 and 28 described above) are those that have been also reported in the literature, while the remaining 13

are newly established in the present work. There are 7 more types reported by the previous workers but they have not been met with in the present species. Hence, they are recognised here as additional types for the family. They are as follows:

29. Stellate Hair (Solereder, 1908, p. 459, cf. also fig. 103 d).

30. Candelabra Hair (op. cit.; Briquet, 1930).

31. Peltate Scale (Solereder, 1908, p. 459).¹

32. Papillate-bulbiferous Flagellate Hair (op. cit., fig. 103 c).²

33. Terminal Glands (Carlquist, 1959 a).

34. Lateral Glands (op. cit.).

35. Hollow-stalked Trichomes (Carlquist, 1959 b).

In all 35 trichome types are so far known in the family. A key for ready identification of all these types is given under Appendix I.

DISCUSSION

a. General features

The trichome types so far known in the family are multicellular. This has been also stated earlier by Solereder (1908).

The foot is either simple or compound. It lies usually embedded in the epidermis except that its distal end is slightly projected above the epidermal level. At times, however, the cells are much projected beyond the epidermis e.g., in the Simple Biseriate Hairs of *Sonchus oleraceus* (fig. 33).

Although, the body when differentiated, consists of the stalk and head, at times, the latter two parts also show further differentiation. For example, in the stalk of the Bulbiferous Flagellate Hair, the terminal cell is quite unlike the other cells (fig. 26 & 27). Likewise, in the head of the Biseriate Rostrate Vesicular Glandular Hair, the terminal two cells are quite different as compared to the others (fig. 45).

The trichomes in their length, except in those which possess long flagellate head, range from a few microns to 0.5 mm. above the epidermis. The Simple Conical Hairs of *Hymenanthemum tenuifolium* are the shortest in length being only a few microns in length, whereas those of *Parthenium alpinum* are the longest so far observed by the present author, being upto 0.5 mm. in length.

Cells of the trichomes are broader than long or

¹ M—as a prefix is used here as an abbreviation for 'Monoantichinal' (a term suggested by Prof. Santapau in a personal communication), because in these trichomes, the first one division is antichinal, a character which is essential for recognising the identity of these trichomes.

² P—is used as the abbreviation of 'Polyantichinal' (also suggested by Prof. Santapau in personal communication), because this trichome is characterised, unlike the above, by more than one antichinal division at the outset in their ontogeny.

¹ The author actually describes as 'Peltate hair'. But since the trichome comes under the category of 'Scales' according to the classification of Cowan (1950) which has been followed in the present work (cf. p. 4), it is named here 'Peltate Scale'.

² Solereder himself does not give the trichome any name but only describes it as 'the upper cell of the bicellular stalk is broadened out above in the shape of a club and produced apically into 4-8 papillae, which are bent inwards and embrace the base of the terminal cell'. From the figure and the description by Solereder, the trichome in general resembles the Bulbiferous Flagellate Hair (p. 12) described in the present work, but differs in that the bulbous cell of the stalk has 4-8 papillae. It is, therefore, recognised as a distinct type and is also given a separate name keeping in view its specific features.

longer. The longest are the unicellular flagella representing the head region in many types of trichomes. It is these flagella which, when quite dense, render the plant surface tomentose e.g. in *Gnaphalium indicum*.

Among the nonflagelliform cells, those of the Simple Conical Hair are found to reach the maximum length e.g. in *Parthenium alpinum* and *Elephantopus scaber*.

Lateral walls may be thin or thick. The thickness also shows a wide range. They are only slightly thick as in the head cells of the Wavy Conical Hairs in *Emilia sonchifolia* (figs. 15 & 16) or markedly thickened as in the Simple Conical Hairs occurring on the leaf-margins in *Solidago velutina* (fig. 17). The secondary thickening is sometimes impregnated with lignin e.g. in the Simple Conical Hairs of *Elephantopus scaber*. Externally, in all trichomes, the surface is covered with a cuticle which may be smooth, ridged, verrucose, echinulate or granulate.

Cross walls are thin although at times they are quite thick e.g., in the Simple Conical Hairs of *Solidago velutina* (fig. 17). In certain cases, the cross wall is also pitted e.g., in the Oblique-aseptate-flagellate Hair of *Senecio corymbosa* (fig. 32).

Contents are translucent or dense. The former condition is common in nonglandular and the latter in the glandular trichomes. Contents may be persistent or evanescent. Although, the latter feature is usually characteristic of the flagella, it is also seen sometimes in certain glandular trichomes, e.g., in the Biseriate Vesicular Glandular Hair of the four species of *Parthenium* presently investigated. At times, the contents also include sphaerocrystals in certain glandular hairs e.g., in the Biseriate Capitate Glandular Hair of *Blumea* spp. investigated (figs. 47 & 48).

b. Patterns of trichome structure

In the species studied, although, as many as 28 trichome types have been recognised on the basis of their specific differences, on a closer comparison they seem to fall into four structural patterns. The patterns of structure and the trichomes belonging to them are as below.

PATTERN I. The trichomes are filiform and consist of a foot and body. The foot is simple or compound. The body is multicellular and uniseriate, entire or differentiated into stalk and head. This is shown by the following trichome types.

1. Simple Filiform Hair 2. Vesicular Filiform Hair 3. Sclerosed Filiform Hair 4. Flagellate Filiform Hair and 5. Capitate Filiform Hair.

PATTERN II. The trichomes are macroform and are differentiated into a foot and body. The foot is simple or compound. The body is multicellular, entire or differentiated. In the case of the former, it is always uniseriate whereas in the latter, the stalk is always uniseriate and the head is uni- or multiseriate (e.g. in Uniseriate Capitate Glandular Hair).

This pattern is exhibited by the following types.

1. Cylindrical Hair 2. Simple Conical Hair 3. Wavy Conical Hair 4. Moniliform Hair 5. Capitate Hair 6. Ramose Hair 7. Two-armed Hair 8. One-armed Hair 9. Septate-flagellate Hair 10. Aseptate-flagellate Hair 11. Oblique-septate-flagellate Hair 12. Oblique septate-flagellate Hair 13. Bulbiferous Flagellate Hair and 14. Uniseriate Glandular Hair.

The types Stellate Hair, Candelabra Hair, Pelate Scale and Papillate-Bulbiferous Flagellate Hair reported in the literature (p. 182) also fall in this pattern.

PATTERN III. The trichomes are differentiated into foot and body. Foot may be simple or compound. The body is entire or differentiated. In the former case it is biseriate, while in the latter the stalk is always biseriate but the head is bi- or multiseriate. This is exhibited by the following trichome types.

1. Simple Biseriate Hair 2. Simple Biseriate Glandular Hair 3. Biseriate Vesicular Glandular Hair 4. Biseriate Rostrate Vesicular Glandular Hair 5. Biseriate Capitate Glandular Hair and 6. Biseriate Vesicular Capitate Glandular Hair.

PATTERN IV. The trichomes are multiseriate throughout their length. The foot is simple or compound. The body may be entire or differentiated. This is shown by the following types.

1. M-Simple Multiseriate Glandular Hair 2. M-Multiseriate Capitate Glandular Hair and 3. P-Multiseriate Capitate Glandular Hair.

The types, Terminal Glands, Lateral Glands, Hollow-stalked Trichomes and Sessile Glands described in the literature (p. 182) also show this pattern.

The patterns of trichome structure are of significance since the trichome types which show the same pattern can be taken as mutually related. Thus, the patterns provide an important evidence in recognising the interrelationships of the trichome types. Accordingly, they are taken into consideration in tracing the phylogeny of the trichomes in the family (Ramayya, 1962 b).

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- do — IV. The stem of *Sphaeranthus indicus* L. *Ibid.* 44 : 177-183, 1956.
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APPENDIX I

KEY FOR THE IDENTIFICATION OF TRICHOMES

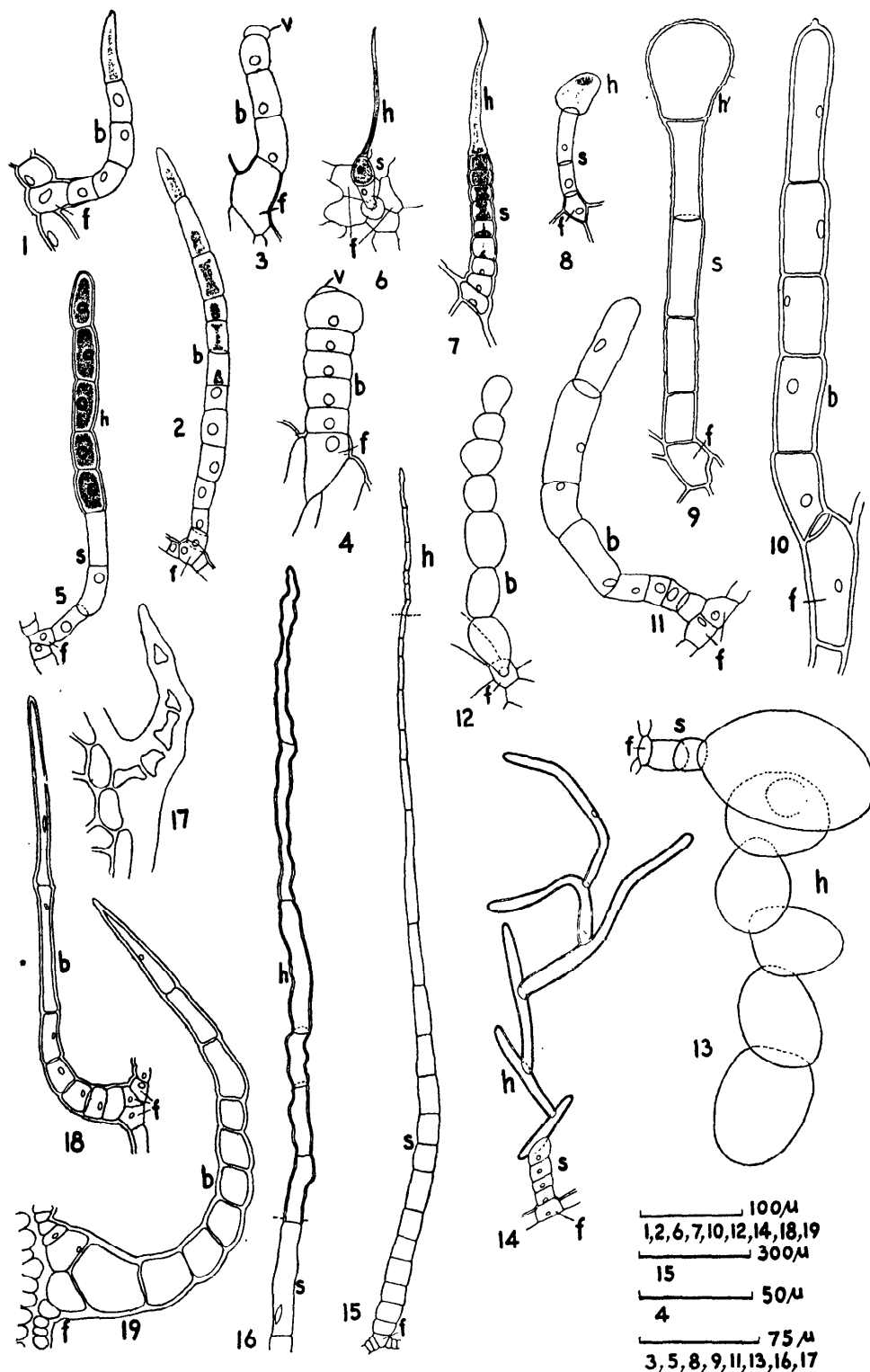
- Body uniseriate ; first division of the initial periclinal.
- Body undifferentiated.
- Trichomes filiform.
- Body cylindrical ... Simple Filiform Hair.
- Body cylindrical with a cuticular vesicle at the apex ... Vesicular Filiform Hair.
- Trichomes macroform.
- Body cylindrical, apex rounded but at times with a short mucro at the tip ... Cylindrical Hair.
- Body conical, apex pointed or rounded ... Simple Conical Hair.
- Body flagellate, apex pointed ... Septate-flagellate Hair.
- Body differentiated into stalk and head.
- Trichomes filiform.
- Head unicellular.
- Head capitate, shorter than the stalk ... Capitate Filiform Hair.
- Head flagellate, much long... Flagellate Filiform Hair.
- Head multicellular.
- Cells of the head thick-walled ... Sclerosed Filiform Hair.
- Trichomes macroform.
- Head unicellular.
- Stalk undifferentiated.
- Head Two-armed ... Two-armed Hair.
- Head One-armed ... One-armed Hair.
- Head capitate ... Capitate Hair.
- Head conical ... Simple Conical Hair.
- Head flagellate ... Aseptate-flagellate Hair.
- Head oblique-flagellate ... Oblique-aseptate-flagellate Hair.
- Head stellate ... Stellate Hair.
- Head peltate ... Peltate Hair.
- Stalk differentiated with bulbous terminal cell.
- Bulbous cell, spherical ... Simple Bulbiferous Flagellate Hair.
- Bulbous cell, spherical with papillae ... Papillate-bulbiferous Flagellate Hair.
- Head multicellular.
- Head glandular with 1 or more 2 to 4-celled tiers ... Uniseriate Glandular Hair.
- Head flagellate ; cross walls at right angle ... Septate-flagellate Hair.
- Head flagellate ; cross walls oblique ... Oblique-septate-flagellate Hair.
- Body conical ; cells of the head with wavy and slightly thick lateral walls, contents evanescent ... Wavy Conical Hair.
- Head moniliform, contents watery ... Moniliform Hair.
- Head ramose, early breaking into constituent cells, contents evanescent ... Ramose Hair.
- Head cylindrical ; lateral walls thin ... Cylindrical Hair.
- Head dendroid ... Candelabra Hair.
- Body bi- or multiseriate ; first division of the initial anticlinal.
- Next few divisions periclinal.
- Body undifferentiated.
- Body biserial.
- Body non-glandular, apex bifurcate with rounded or sharp tips ... Simple Biserial Hair.
- Body glandular, emarginate, cuticular vesicle enclosing 1 to 4 terminal tiers ... Biserial Vesicular Glandular Hair.
- Body glandular, rostrate ; cuticular vesicle enclosing the terminal tier ... Biserial Rostrate Vesicular Glandular Hair.
- Body multiseriate.
- Body globular or slightly cylindrical ; apex rounded ... M-Simple Multiseriate Glandular Hair.

Body differentiated into stalk and head.			19	<i>Laggera aurita</i> (Willd.) Sch.-Bip.	Andhra Pradesh
Stalk biseriate. Head bi-or multiseriate					(India)
Head biseriate.			20	<i>Sphaeranthus indicus</i> L.	-do-
Cuticular vesicle present.			21	<i>Gnaphalium indicum</i> L.	-do-
Head of various shapes ; Biseriate Vesicular			22	<i>Helichrysum bracteatum</i> Andre.	-do-
cuticular vesicle enclosing the Glandular Hair.			23	<i>Caesulia axillaris</i> Roxb.	-do-
distal 1 to 3 tiers			24	<i>Pulicaria foliosa</i> DC.	-do-
Terminal tier rostrate ; Biseriate Rostrate			25	<i>Lagascea mollis</i> Cav.	-do-
cuticular vesicle enclosing Vesicular Glandular			26	<i>Acanthospermum hispidum</i> DC.	-do-
the terminal tier Hair.			27	<i>Parthenium tomentosum</i> DC. var.	Arnold Arboretum
Cuticular vesicle absent.				<i>stramonium</i> (Greene) Rollins.	(U. S. A.)
Head of various shapes ... Simple Biseriate			28	<i>P. incanum</i> H. B. K.	-do-
			29	<i>P. argentatum</i> Gray.	-do-
			30	<i>P. alpinum</i> (Nutt.) T. and G.	-do-
			31	<i>Ambrosia psilostachya</i> DC.	Oklahoma
Head multiseriate.					(U. S. A.)
Cuticular vesicle absent ... Biseriate Capitulate			32	<i>A. artemisiaefolia</i> DC.	-do-
			33	<i>A. trifida</i> L.	Cornell University
Cuticular vesicle present ... Biseriate Vesicular					Campus, (U. S. A.)
					Andhra Pradesh
Stalk and head multiseriate.			34	<i>Xanthium strumarium</i> L.	(India)
Stalk vasculated ... Lateral Glands.			35	<i>Zinnia elegans</i> Jacq.	-do-
Stalk non-vasculated ... M-Multiseriate Capitulate.			36	<i>Z. linearis</i> Bth.	-do-
			37	<i>Eclipta prostrata</i> L.	-do-
			38	<i>Sclerocarpus africanus</i> Jacq.	-do-
			39	<i>Blainvillea latifolia</i> (L. f.) DC.	-do-
			40	<i>Wedelia urticaefolia</i> DC.	-do-
			41	<i>Tithonia rotundifolia</i> (Mill.) Blake.	-do-
			42	<i>T. tagetiflora</i> Desf.	-do-
			43	<i>Helianthus annuus</i> L.	-do-
			44	<i>H. debilis</i> Nutt.	-do-
			45	<i>Verbesina enceloides</i> Gray.	-do-
			46	<i>Gutierrezia abyssinica</i> Cass.	-do-
			47	<i>Synedrella nodiflora</i> Gaertn.	-do-
			48	<i>Glossocardia bosvallea</i> (L. f.) DC.	-do-
			49	<i>Cosmos sulphureus</i> Cav.	-do-
			50	<i>Tridax procumbens</i> L.	-do-
			51	<i>Flaveria australasica</i> Hook.	-do-
			52	<i>Hymenanthemum tenuifolium</i> Cass.	-do-
			53	<i>Gaillardia pulchella</i> Foug. var. <i>picta</i>	-do-
				Gray.	
			54	<i>Anthemis nobilis</i> L.	-do-
			55	<i>Chrysanthemum indicum</i> L. f. var.	-do-
				<i>hortorum</i> Baily	
			56	<i>Artemisia patens</i> Wall.	-do-
			57	<i>A. Absinthium</i> L.	-do-
			58	<i>Emilia sonchifolia</i> (L.) DC.	-do-
			59	<i>Notonia grandiflora</i> DC.	-do-
			60	<i>Senecio corymbosus</i> Wall.	-do-
			61	<i>S. tenuifolius</i> Burm.	-do-
			62	<i>Calendula officinalis</i> L.	-do-
			63	<i>Arctotis stoechadifolia</i> Berg.	-do-
			64	<i>Echinops echinatus</i> Roxb.	-do-
			65	<i>Tricholepis radicans</i> DC.	-do-
			66	<i>Centaurea cyanus</i> L.	-do-
			67	<i>Carthamus tinctorius</i> L.	-do-
			68	<i>Dicoma tomentosa</i> Cass.	-do-
			69	<i>Gerbera jamesonii</i> Hk. f.	-do-
			70	<i>Lactuca sativa</i> L.	-do-
			71	<i>Sonchus oleraceus</i> L.	-do-
			72	<i>Launaea pinnatifida</i> Cass.	-do-

APPENDIX II

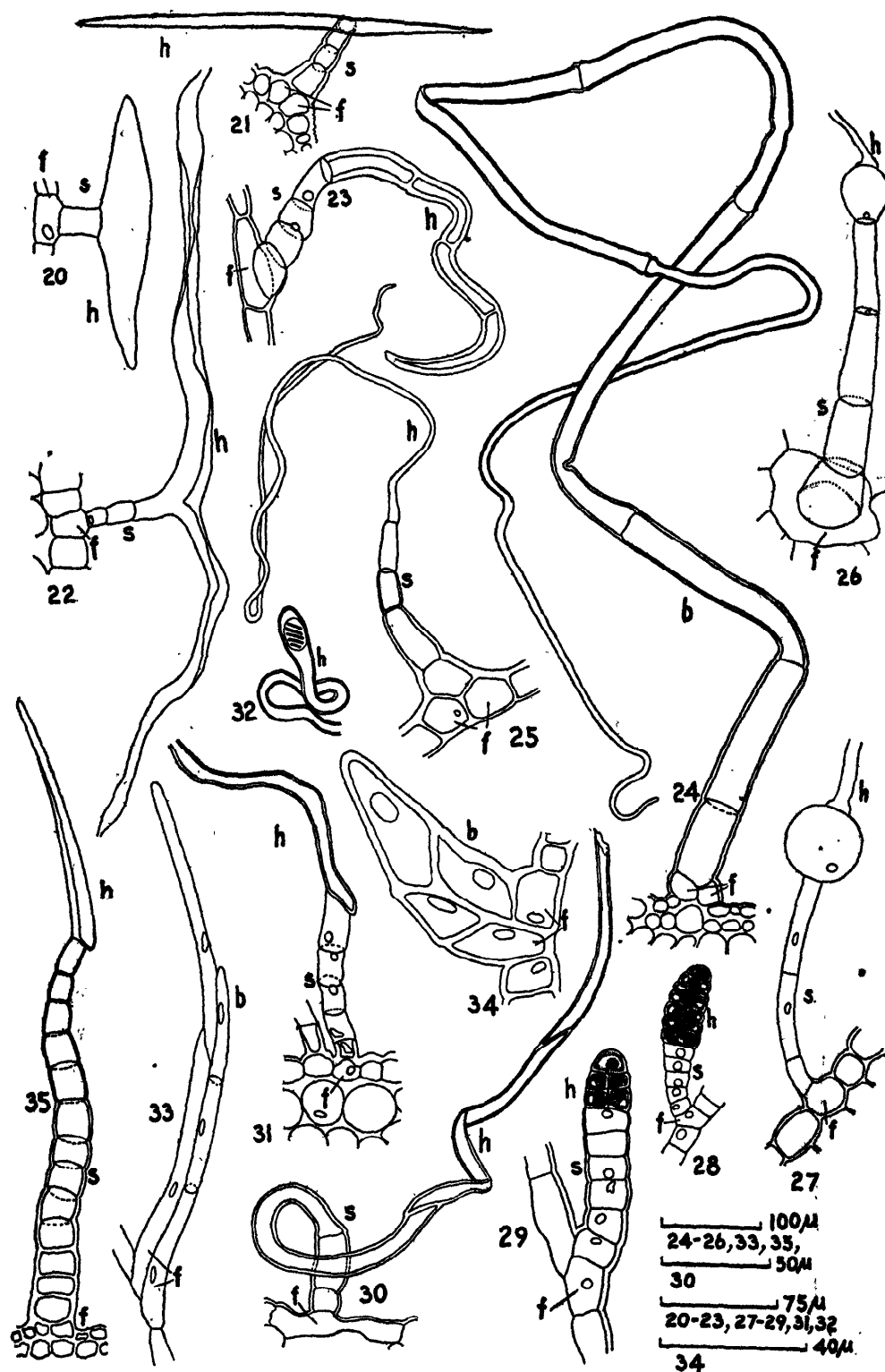
LIST OF THE SPECIES INVESTIGATED

Serial No.	Species	Source of material
1	2	3
1	<i>Vernonia cinerea</i> (L.) Less.	Andhra Pradesh
		(India)
2	<i>V. anthelmintica</i> (L.) Willd.	-do-
3	<i>Elephantopus scaber</i> L.	-do-
4	<i>Adenostemma lavenia</i> (L.) Kuntze	-do-
5	<i>Ageratum conyzoides</i> L.	-do-
6	<i>A. houstonianum</i> Mill.	-do-
7	<i>Eupatorium odoratum</i> L.	-do-
8	<i>Solidago velutina</i> DC.	-do-
9	<i>Grangea madraspatana</i> (L.) Poir.	-do-
10	<i>Bellis perennis</i> L.	-do-
11	<i>Callistephus chinensis</i> Nees	-do-
12	<i>Aster laevis</i> L.	-do-
13	<i>Conyza</i> Sp.	-do-
14	<i>Blumea amplexans</i> DC.	-do-
15	<i>B. bifoliata</i> DC.	-do-
16	<i>B. laciniata</i> DC.	-do-
17	<i>B. oxydonta</i> DC.	-do-
18	<i>B. Wightiana</i> DC.	-do-



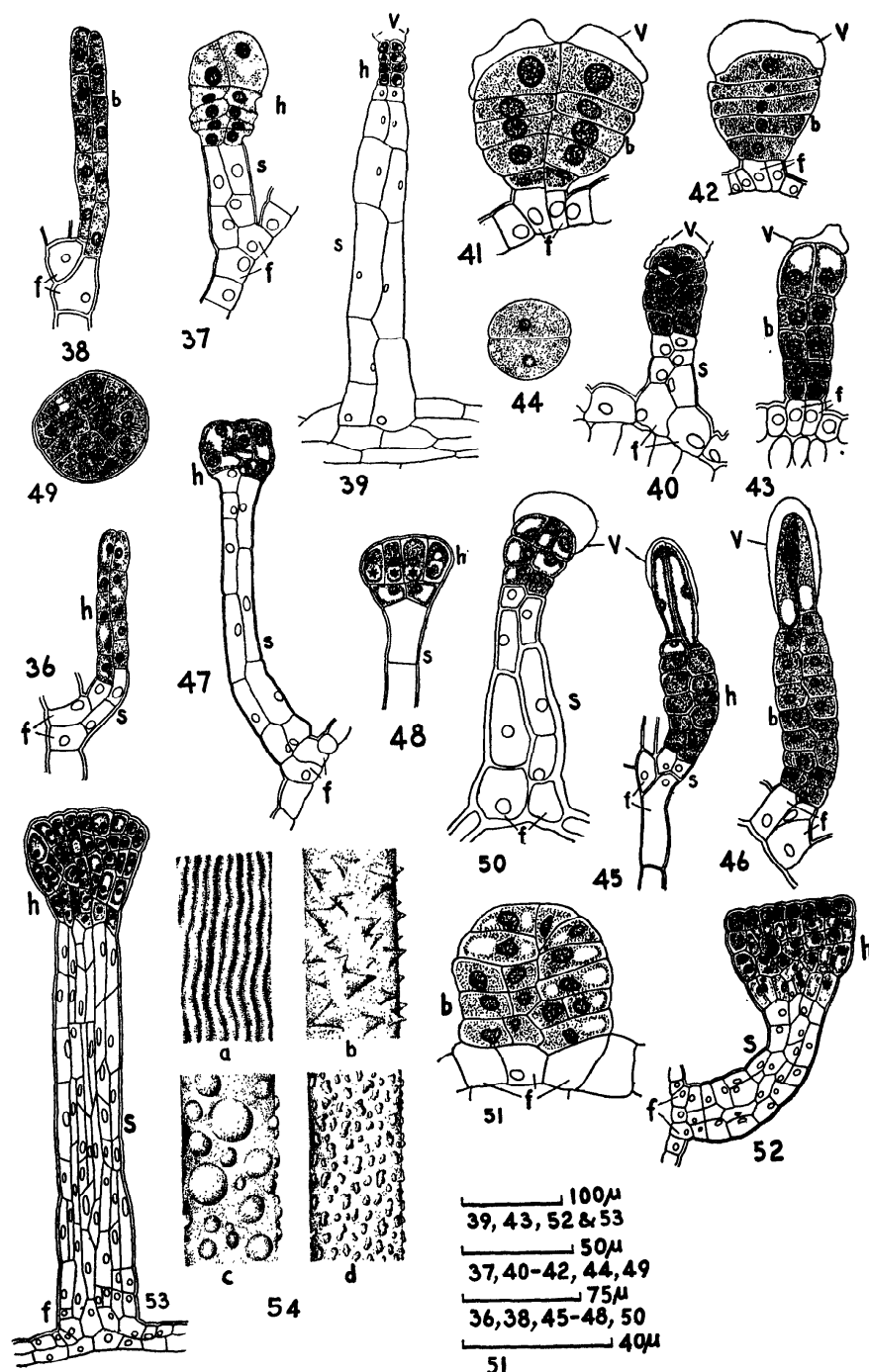
Figs. 1-19

1. from l.s. stem, *Gaillardia pulchella* var. *picta*. 2. from l.s. leaf, *Ageratum conyzoides*. 3. from the margin of phyllary, *Tridax procumbens*. 4. from the margin of a palea, *Helianthus annuus*. 5. from l.s. peduncle, *Flaveria australasica*. 6. from the lower surface of leaf-blade, *Solidago velutina*. 7. from the margin of a phyllary, *Callistephus chinensis*. 8. from the margin of a phyllary, *Eupatorium odoratum*. 9. from the margin of a palea, *Parthenium alpinum*. 10. from the margin of a disc-corolla lobe, *Gaillardia pulchella* var. *picta*. 11. from the adaxial surface of leaf, *Lactuca sativa*. 12. from the abaxial surface of corolla, *Adenostemma lavenia*. 13. from the margin of a young leaf, *Lactuca sativa*. 14. a semi-diagrammatic reconstruction, *Sonchus oleraceus*. 15. from t.s. petiole, *Emilia sonchifolia*. 16. head of the above, enlarged. 17. from the margin of leaf, *Solidago velutina*. 18. from l.s. stem, *Conyza* sp. 19. from t.s. peduncle, *Guizotia abyssynica*. (f = foot ; b = body ; s = stalk ; h = head ; v = cuticular vesicle. The foot is specifically marked where it is quite distinct.)



Figs. 20-35

20. from l.s. stem, *Parthenium argentatum*. 21. from t.s. stem, *Vernonia cinerea*. 22. from t.s. stem, *Artemisia pallens*. 23. from the margin of a leaf, *Senecio tenuifolius*. 24. from t.s. petiole, *Parthenium tomentosum* var. *stramonium*. 25. from the margin of a leaf, *Calendula officinalis*. 26 and 27. from the lower surface of leaf-lamina and t.s. stem respectively *Arctotis stoechadisfolia*. 28 and 29. from l.s. leaf and corolla respectively, *Flaveria australasica*. 30. from l.s. leaf, *Gerbera jamesonii*. 31 and 32. from t.s. stem and an isolated trichome respectively, *Senecio corymbosus*. 33. from the surface of corolla, *Sonchus oleraceus*. 34. from l.s. corolla, *Dicoma tomentosa*. 35. from t.s. stem, *Vernonia anthelmintica*. (f = foot; b = body; s = stalk; h = head; v = cuticular vesicle. The foot is specifically marked where it is quite distinct.)



Figs. 36-54

36. from l.s. disc-corolla, *Callistephus chinensis*. 37. from l.s. corolla, *Vernonia anthelmintica*. 38. from the surface of disc-corolla, *Callistephus chinensis*. 39. from the surface of the leaf mid-rib, *Ageratum houstonianum*. 40. from l.s. stem, *Blumea Wightiana*. 41. from l.s. phyllary, *Acanthospermum hispidum*. 42. from l.s. leaf, *Ageratum conyzoides*. 43. from t.s. stem, *Helichrysum bracteatum*. 44. from a l.s. leaf, *Ageratum conyzoides*; this represents t.s. of the trichome body. 45 and 46. from the surface of ray-corolla and l.s. ovary respectively, *Arctotis stoechadifolia*. 47-49. from l.s. stem (47) and phyllaries (48 & 49), *Blumea Wightiana*; 49. represents the t.s. head of the trichome. 50. from t.s. petiole, *Echinops echinatus*. 51. from l.s. stem, *Cosmos sulphureus*. 52. from l.s. stem, *Blumea laciniata*. 53. from l.s. peduncle, *Sonchus oleraceus*. 54. Diagrammatic representation of the sculpturings.

(f = foot; b = body; s = stalk; h = head; v = cuticular vesicle. The foot is marked out with lines where it is quite distinct.)