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# STUDIES ON THE TRICHOMES OF SOME COMPOSITAE II. PHYLOGENY AND CLASSIFICATION

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ABSTRACT

On the basis of the evidences from structural patterns, modes of development and metamorphic variations, the vegetative trichomes of the Compositae are shown to consist of four systems viz., I. Filiform System II. Macroform System III. M-Multiseriate System and P-Multiseriate System.

As Trichomes comprise more than one system, their phylogeny and classification needs to be studied separately within each system.

Evidences from the metamorphic variations and from the trichomes of the hybrids are shown to be of value in tracing the relationships. Netolitzky's (1932) phyletic dicta—which in general conform to the evolutionary principle 'simple to complex'—are considered to be useful in recognising the general primitive or advanced condition of a trichome within its system.

Within the systems, trichomes are shown to be classifiable into the three morphological groups 'Papillae', 'Scales' and 'Hairs' adopted by Cowan (1950) for the trichomes in *Rhododendron*.

Studies on the trichomes of vascular plants in general are emphasized so that information could be available on the total number of their systems and distribution which will not only be of morphological value but also of taxonomic significance.

## INTRODUCTION

Goebel (1900) seems to be the first to have visualised the possibility of the existence of relationships among the trichomes differing from one another and he himself showed the 'water-secreting hairs of Rhinantheae (to) arise from glandular hairs' (p. 16). Subsequently, Fedorowicz (ex Netolitzky, 1932) presented the phylogeny for the 'lower' glands of the whole of the Rhinanthoideae (Scrophulariaceae). Regarding the dermal appendages of the ferns, Bower (1926) suggests that, 'the simple hair should be held as primitive and the scale or bristle derivative from it'. Recently, Cowan (1950) and Carlquist (1961) have also dealt with the relationships of the trichomes of *Rhododendron* leaf and the glandular hairs of the Madiinae (Compositae) respectively.

Trichomes of the vascular plants have been classified by several workers in the past, and a review of the different classifications is given by Netolitzky (1932) in his 'Der Pflanzenhaare'. Weiss (ex Netolitzky, 1932) divides trichomes primarily into three groups viz., those with (a) 'All Zellen gleichartig', (b) 'Zellen nicht alle gleichwertig' and (c) 'epidermiszellen umschleissen Einen in Trichomkorper gelegenen sekretraum'. De Bary (1884) recognizes four major categories viz., (1) Bladders (Papulae), (2) Hairs (Pili, Setae), (3) Scales (Squamae, Lepides, Paleae) and (4) Shaggy Hairs (Villi). Solereder (1908) divides trichomes into two principal groups, (1) the clothing hairs and (2) the glandular hairs. Recently, Cowan (1950) has classified the foliar trichomes of *Rhododendron* into three groups: (1) Papillae, (2) Scales and (3) Hairs. Cowan's classification seems to be based on that of De Bary given above except that the 'Shaggy Hairs' is merged into the 'Hairs'.

## TRICHOME SYSTEMS

In the present paper phylogeny and classification of the 'vegetative' trichomes of the Compositae, which the author has studied (Ramayya, 1962b), is dealt with. The concepts of phylogeny and classification presented below are based upon evidences from three aspects of the trichomes namely, their structural patterns (op. cit.), modes of development (Ramayya, 1963) and metamorphic variations[1]. In the light of these, the trichomes in the Compositae suggest to represent four distinct 'Systems' as described below:

[1] Trichomes in the Compositae often show variations of qualitative nature which on a comparative study are found to be of three kinds viz., the 'metamorphic', 'reductional' and 'irregular' (Ramayya, 1962a). The first one represents changes in which two trichome types intergrade through transitionary forms (e.g., the Simple Conical Hair and Uniseriate Capitate Glandular Hair on the stem in *Cosmos sulphureus* Cav.). In the second, the trichomes become progressively reduced so that ultimately they are one-celled (e.g., the Simple Conical Hair becomes one-celled on the margin of the phyllaries in *Blumea Wightiana* DC.). In the third, the trichomes become irregular in structure either partly or wholly, so that the variants do not resemble the typical forms and further, they also do not resemble one another (e.g., the Cylindrical Hair is represented by increasingly bizarre forms on the tips of the phyllaries in *Lactuca sativa* L.). For illustrations of the trichome types above mentioned *see* Ramayya, 1962b.

**I. Filiform Trichome System.**

**II. Macroform Trichome System.**

**III. M-Multiseriate Trichome System.**[2]

**IV. P-Multiseriate Trichome System.**[2]

I. *Filiform Trichome System*: These trichomes have Pattern I type of structure (Ramayya, 1962b) and in their ontogeny the first division of the mother-cell is periclinal (Ramayya, 1963). Interrelationships among several of these types are also indicated by their metamorphic variations in several of the species studied (Ramayya, 1962a). The types falling under this system are:

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

II. *Macroform Trichome System*: These show Pattern II type of structure (Ramayya, 1962b). In their development, the mother-cell first divides by a periclinal wall (Ramayya, 1963). Although, the division of the mother-cell is similar to in the trichomes of the preceding system, still they are consistently different from them in their pattern of structure in the species investigated. Further, in the metamorphic variations so far observed in the species studied, never these trichomes are found to intergrade with those of the preceding system (Ramayya, 1962 a). The similarity in the mode of development in these two systems, therefore, seems to be of homoplastic nature. The types belonging to this system are:

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-aseptate-flagellate Hair 13. Bulbiferous Flagellate Hair 14. Uniseriate Glandular Hair.

According to Rollins (1944), the hybrids of *Parthenium incanum* and *P. argentatum* possess trichomes which look like transitionary between the Septate-flagellate Hair of the former species and the Two-armed Hair of the latter. Thus, genetically also, the relationship of these types is confirmed.

The trichomes, Stellate Hair, Candelabra Hair, Papillate-bulbiferous Flagellate Hair and Peltate Scale described in the literature (*see* Ramayya, 1962b, p. 19) belong to this system, as these also have Pattern II type of structure (op. cit., p. 23). Further, the Stellate Hair and Two-armed Hair show intergradation in *Santolina Chamaecyparissus* (Solereder, 1908, p. 459), thus confirming their relationship.

III. *M-Multiseriate Trichome System*: These are characterised by Pattern III or IV type of structure (Ramayya, 1962b). In their development, the first division of the initial is anticlinal (Ramayya, 1963). Interrelationships among several of these types are also indicated by their metamorphic variations (Ramayya, 1962a). The types of this system are:

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 6. Biseriate Vesicular Capitate Glandular Hair 7. M-Simple Multiseriate Glandular Hair 8. M-Multiseriate Capitate Glandular Hair.

The Lateral Glands and Hollow-stalked Trichomes reported in the literature (*see* Ramayya, 1962b) also belong to this system as they possess Pattern IV type of structure (op. cit.) and in their development the first division of the initial is anticlinal as in the above (Carlquist, 1959a & b).

IV. *P-Multiseriate Trichome System*: These are characterised by Pattern IV type of structure similar to some of the trichomes of the above system (Ramayya, 1962b), but the first two or more divisions of their initial are anticlinal (Ramayya, 1963). Thus, the similarity in the structural pattern of these trichomes and of some of the preceding system is of homoplastic nature (op. cit.).

Only one type P-Multiseriate Capitate Glandular Hair studied by the author (Ramayya, 1962b) belongs to this system.

The Terminal Glands described in the literature (Ramayya, 1962b) also belongs to this system being similar to the above type in its pattern of structure (op. cit.) and mode of development (Carlquist, 1959a).

## DISCUSSION

Concerning the phylogenetic relationships of trichomes, Netolitzky (1932) offers several dicta which as summarised by Carlquist (1961) are presented in the foot note below.[1] From a perusal of these dicta, it is obvious that they conform in general to the evolutionary principle 'simple to complex', and hence, according to Netolitzky trichome relationships are to be recognized on this basis. Cowan's (1950) phyletic tree of the trichomes of

[2] As explained by the author elsewhere (1962 b), M- and P- are used here in the sense of 'Monoanticlinal' and 'Polyanticlinal' respectively. Accordingly, the System III represents such trichomes in the development of which the first division of the initial is anticlinal, whereas the System IV, such trichomes where the first two or more divisions of the initial are anticlinal.

[1] 1. Trichomes have originated from papillate epidermal cell. 2. A one-celled trichome, unless shown to be reduction, is more primitive than a several-celled hair ; in the latter types, differentiation among the various component cells (for example, a glandular trichome) for special functions can occur. 3. Trichomes without radial symmetry or with mechanisms for becoming upright in relation to the surface on which they are borne are derived from those with radial symmetry or those that originate perpendicular to the surface on which they are borne. 4. If cells of a trichome acquire contents different from those of surrounding epidermal cells, this should be regarded as a specialisation. 5. Every epidermal cell has the potentiality of becoming a trichome ; this potentiality is affected by various influences. 6. Cells adjacent to a trichome may participate in the specialisation of a trichome if they acquire structure and cell contents resembling those of the trichome but differing from those of ordinary epidermal cells'.

*Rhododendron* is based on a similar consideration for he observes: 'Such information as we have suggests an evolutionary progression from the simple papilla as the rudimentary form, to an undifferentiated hair or scale rudiment, leading to the ultimate appearance of specialised, distinctive types,' (p. 92 ; *see* also fig. 8, p. 93). Carlquist (1961) seems to trace the relationships of the glandular trichomes of the Madiinae on the same principle for he states 'that from a simple biseriate glandular trichome, capitate types (multiseriate head portion) have been derived ; these, in turn, have given rise to hollow-stalked glands, tack-shaped glands and sessile glands' (pp.33-34). It is also evident in the phyletic relationships set forth by Bower for the trichomes of the ferns (*see* p. 1). Apart from this, it may be noted that in all these attempts on phylogeny, trichomes have been treated as a single category of dermal appendages. Even in the different trichome classifications which have been earlier reviewed (p. 1), they have been considered as a single group.

From the present study, it is obvious that trichomes in the Compositae do not represent a single category of structures. They consist of four systems.[1] Consequently, the problems of phylogeny and classification do not arise regarding trichomes as a whole as considered in the past. The trichomes of each system require to be studied of their phylogeny and classification separately. Regarding the recognition of the systems themselves, as presently shown, evidences from three aspects of trichomes namely, their structural patterns, modes of development and metamorphic variations (evidence from the last aspect wherever available) are necessary: the evolutionary principle 'simple to complex' followed by previous workers is not of any use here.

In tracing the phylogeny of trichomes within the systems, the metamorphic variations are again very important. For example, in *Cosmos sulphureus* the Simple Conical Hair and the Uniseriate Glandular Hair often grade over into each other through transitionary forms and hence the two types can be taken as related (*see* footnote on p. 189). Genetical evidence also helps in recognising the relationships e.g., as shown between the Septate-flagellate Hair and the Two-armed Hair of the Macroform Trichome System in *Parthenium* (*see* p. 4). The principle 'simple to complex' is useful here in so far as understanding the primitive and advanced condition of the trichomes. For example, in the Filiform Trichome System, the Simple Filiform Hair as compared to the others could be considered in general primitive, because of its simple structure. The principle, however, cannot be applied in all taxa since the Simple Filiform Hair in some of them may have been derived through reduction, and hence, is not primitive in them.

Regarding the classification within each system, Cowan's (1950) division of the trichomes into the 'Papillae', 'Scales' and 'Hairs' seems to be of value, though types representing the three categories are so far not known under each system in the family. In the Filiform Trichome System all the known types represent only the 'Hairs'. In the Macroform Trichome System, seventeen belong to the 'Hairs' and one to the 'Scales'. Under both the M-Multiseriate and P-Multiseriate Trichome Systems the known types belong to the 'Hairs' only.[2] But in the trichomes of *Rhododendron,* scales are present in both these systems (*see* footnote [1] on p. 191). Trichomes representing the 'Papillae' have so far been not observed under any of the systems. Further work within the Compositae and in other angiosperms may throw light on the validity of this category.

Since trichomes consist of more than one system, there is much need for information about the number (both in the vegetative and floral types) and distribution of their system among the different taxa of the vascular plants. Like the individual trichome types, the systems are also found to show differences in their distribution from one taxon to the other in the Compositae (Ramayya, 1962a). Therefore, a knowledge of the trichome systems in general will not only be of morphological value, but also of taxonomic significance.

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[1] In other taxa also, trichomes seem to consist of more than one system. It is illustrated here in the trichomes of *Rhododendron* studied by Cowan (1950). In *R. lapponicum,* there is a scale with a biseriate stalk and a multiseriate head and in its development the first division of the initial is anticlinal (p. 84). Similarly, in *R. fictolacteum,* there are Funnel-shaped and Rostrate Hairs with multiseriate structure and in these also the initial divides by an anticlinal wall for it is stated that they originate 'from two cells on each side of a median wall' (p. 87). Thus the above trichomes provide examples of M-Multiseriate System. On the other hand, in *R. Dalhousiae* and *R. Griaersonium* there is a scale and a dendroid hair of multiseriate structure respectively. In these the first two divisions of the initial are described to be anticlinal (p. 85). These trichomes obviously belong to P-Multiseriate System.

[2] The names of trichomes presently adopted, therefore, end either in 'Hair' or 'Scale' keeping in view the category to which they belong (Ramayya, 1962b).

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