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VASCULARIZATION OF COROLLA OF THE COMPOSITAE[1]

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Abstract

The vascular anatomy of the corolla of 66 species of the family Compositae is described. The petals in this family are basically 3-traced. The members of this family exhibit all grades from the full development of all the vascular bundles in the corolla in certain species to their complete elimination in others. A greater degree of variation in the vasculature is found in the ray-corollas than in the disk-corollas. The corollas of the ray-florets in certain species of the tribe Asteroideae are entirely devoid of vascular bundles while those in certain species of the tribe Helianthoideae have all their vascular bundles fully developed. In general the reduction in the vascular bundles of the corolla has been faster than the organ itself. The tubular, ligulate and bilabiate corollas exhibit the same fundamental vascular pattern. The ligulate and bilabiate corollas are mere modifications of the tubular type.

Introduction

The corolla of the Compositae presents interesting features concerning the reduction and amplification of its vascular supply in their various taxa. Except for the work of Koch (1930a 1930b) no attempt seems to have been made to explain on an anatomical basis the evolutionary trends seen in corolla of Compositae. The present paper is based on a comparative study of 54 genera and 66 species belonging to 12 tribes of the family compositae.

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Material and Methods

The following species have been studied :

Tribe I. Vernonieae.—*Vernonia cinerea* Lees, *V. patula* (Dryand.) Merrill.

Tribe II. Eupatorieae.—*Ageratum conyzoides* Linn., *Eupatorium triplinerve* vahl., *Mikania cordata* (Burm. f.) B. L. Robinson.

Tribe III. Asteroideae.—*Solidago virgaaurea* Linn., *S. odora* Ait., *Cyathocline purpurea* (Don) Kuntze, *Brachycome assamica* Clarke, *Aster molliusculus* wall. *A. thomsoni* Clarke, *A. asperulus* Nees, *A. amellus* var. *bassarabicus* DC., *Erigeron canadensis* Linn., *Conyza stricta Willd.*

Tribe IV. Inuloideae.—*Blumea oxyodonta* DC., *B. eriantha* DC., *Laggera flava*

Benth. *L. aurita* schultz-Bip., *Sphaeranthus indicus* Linn., *Anaphalis adnata* DC., *Gnaphalium indicum* Linn. *G., pulvinatum* Delile, *Caesulia axillaris* Roxb., *Inula cuspidata* Clarke, *I. indica* Linn., *Pulicaria angustjfolia* DC.

Tribe V. Helianthoideae.—*Lagasca Mollis* Cav., *Acanthospermum hispidum* DC., *Xanthium strumarium* Linn., *Siegesbeckia orientalis* Linn., *Eclipta prostrata* (Linn.) Linn., *Sclerocarpus africanus* Jacq., *Blainvillea acmella* (Linn.) Philipson, *Spilanthes acmella* Linn., *Ximensia encelioides* Cav., *Verbesina oncophora* Robinson & Seaton, *Helianthus annuus* Linn., *H. annuus* (var. Russian giant), *Tithonia diversi folia* Gray., *Zinnia elegans* Jacqu., *Glossocardia bosvallea (*Linn. f.*)* D.C., *Bidens biternata* (Lour.) Merr. & Sherff., *Chrysanthellum indicum* DC., *Galinsoga parviflora* Cav., *Tridax procumbens* Linn.

Tribe VI. Helenieae.—*Flaveria repanda* Lag., *Gaillardia pulchella* var. *picta* Gray, *Tagetes erecta* Linn.

Tribe VII. Anthemideae.—*Cotula anthemoides* Linn., *Artemesia scoparia* Waldst. & Kit., *A. vulgaris* Linn.

Tribe VIII. Senecionideae.—*Emilia sonchifolia* DC.

Tribe IX. Calenduleae.—*Calendula officinalis* Linn.

Tribe X. Cynaroideae.—*Echinops echinatus* Linn, *Cnicus wallichii* Hook, *Tricholepis glaberrima* DC., *Volutarella ramosa* (Roxb.) Santapau.

Tribe XI. Mutisieae.—*Gerbera jamesonii* Hook.

Tribe XII. Cichorieae.—*Cichorium intybus* Linn., *Taraxacum officinale* Wigg., *Lactuca macrorhiza* Hook., *Prenanthes brunoniana* Wall., *Sonchus oleraceus S. arvensis* Linn., *Launaea aspleniifolia* DC.

The materials were fixed in 70% ethyl alcohol or F. A. A. Customary methods of microtechnique were followed. Serial transverse sections of florets were cut at thicknesses ranging from 12–30 μ and stained with crystal violet and erythrosin. vascular supply of the corolla was also studied by clearing in lactic acid or 5 per cent solution of potassium hydroxide.

Observations

In Compositae there are 3 types of corollas, viz., tubular, bilabiate and ligulate. Typically the tubular 5-fid corolla has at its base five vascular traces. Each of these is compound (VV), formed by the fusion of adjacent marginal bundles of the adjoining petals. They run upward through the corolla tube and separate into their constituents just below the sinuses of the petal lobes. The marginal bundles of a petal may unite at its apex to form an arch as in *Vernonia* (Fig. 1) *Solidago, Brachycome, Aster, Conyza, Blumea, Inula, Sphaeranthus, Anaphalis, Caesulia, Lagasca, Xanthium, Siegesbeçkia, Sclerocarpus, Bidens, Galinsoga Tridax, Zinnia, Ximensia, Acanthospermum, Flaveria, Tagetes, Cotula* (bisexual florets), *Emilla, Calendula, Echinops, Tricholepis* and *Volutarella* or may not unite at the apex as in *Eupatorium* (Fig. 2), *Mikania, Solidago, Cyathocline, Aster moliusculus, Blainvillea* and *Chrysanthellum.* In *Ageratum* (Fig. 3), *Laggera, Gnaphalium & Spilanthes* the marginals remain more or less suppressed or the compound marginals bundles fail to separate into their constituents ending blindly below the sinuses of the petal lobes.

The tubular 5-fid corolla of *Cnicus* (Fig. 4) also has five compound vascular bundles which separate into their consti-

tuents below the sinuses of the petal lobes, the marginal of each petal lobe uniting at its apex. The petals in this separate from each other at different levels ; as a result different petal lobes are unequal in their length. Usually one of the lobes is much longer than the others.

The tubular corolla is 4-fid in *Eclipta* (Fig. 5), *Glossocardia* and *Erigeron* and is supplied with four compound bundles which divide below the sinuses of the corolla lobes. The 2 marginals of a petal lobe unite at its apex.

In *Helianthus*, *Tithonia*, *Gaillardia* and *Verbesina* the tubular corolla has 10 vascular bundles. Of these, five are the dorsal bundles of the petals (D). The other five are compound marginal bundles of the petals (VV) which separate into their constituents (V) below the sinuses of the corolla lobes. The two marginals and the dorsal bundle in a petal lobe in *Helianthus* unite at its apex (Fig. 6) while in *Verbesina* (Fig. 9) the dorsals disappear at various levels in the corolla tube. The compound marginal bundles may give out several secondary marginal bundles (SM) in the basal region of the corolla as in *Helianthus* (var. Russian giant) and *Tithonia* (Fig. 7) or at the apical region as in the outer florets of *Gaillardia* (Fig. 8).

In several disk-florets of *Sclerocarpus* (Fig. 10), *Acanthospermum* and *Artemesia* (Fig. 11), apart from the five compound marginal bundles the corolla may possess 1 or 2 fully or partially developed petal dorsals.

In *Gerbera*, the corolla of both the disk and ray florets is bilabiate. In the disk-corolla, the 2-lobed posterior lip is as long as the 3-lobed anterior lip and has five compound bundles which divide below the sinuses of the petal lobes. The marginals of a petal lobe unite at its apex (Fig. 12). In the ray-corolla the 2-lobed posterior lip is much smaller than the 3-lobed anterior lip. It is supplied with eight vascular bundles, five compound marginal bundles and three anterior petal dorsal. The dorsal and the two marginal bundles of a petal lobe unite at its apex. A few secondary marginal bundles given off by the compound marginals may also join them at the apex (Fig. 13).

The ligulate corollas of *Ximensia* (Fig. 14) and *Helianthus* and several ray-corrollas of *Tridax* have 11 vascular bundles five dorsal bundles of the petals, four compound marginals and two marginal bundles of the posterior petals.

The odd posterior compound marginal bundle in these species separates into its constituents before it enters the corolla, at the top of the ovary-wall. The splitting of the ligulate corolla occurs between these two free marginals (Fig. 14). The remaining four compound marginals also divide near the apex of the corolla. In the apex of the middle lobe of the corolla its dorsal bundle fuses with its two marginals while the bundles in either of the flanking lobes variously unite with one another.

The ray-corollas of *Tithonia* (Fig. 15) and *Helianthus annuus* var. Russian gaint may have more than 11 vascular bundles. The extra bundles in these are the secondary marginals of the compound ventral bundles.

In the ray-corollas of *Brachycome*, *Galinsoga* and *Zinnia* also, the posterior compound bundle separates into its constituents before it enters the corolla with the other 4 compound bundles. Apart from these bundles three petal-dorsals are present in *Brachycome* (Fig. 16), while 1 anterior petal dorsal alone is seen in *Galinsoga* (Fig. 17). In *Zinnia* (Fig. 18)

the ligulate corolla has no dorsal bundle. In these taxa all or some of the compound ventrals may divide near the apex of the corolla. The marginals of a petal lobe generally unite at its apex (Figs. 16, 18).

The ray-corollas of *Aster*, *Cichorium*, *Taraxacum*, *Lactuca*, *Prenanthes*, *Launaea* and *Sonchus* have five vascular bundles all of which are compound. The posterior compound bundle divides just below the split of the ligule. Other bundles may divide near the apex. In *Cichorium* (Fig 19), *Taraxacum*, *Lactuca*, *Prenanthes* and *Launaea* the free marginals of a petal lobe unite at its apex, while in *Aster* (Fig. 20), and *Sonchus* (Fig. 21), they usually fail to do so.

In the ray florets of *Seigesbeckia*, *Sclerocarpus*, *Verbesina*, *Blainvillea*, *Bidens* and *Flaveria* the corolla has five compound bundles. In *Sigesbeckia* and *Sclerocarpus* the dorsals of one or two anterior petals may also be present. The corollas in these split on one side of the posterior compound bundle (Figs. 22-24). In *Siegesbeckia* (Fig. 22) and *Sclerocarpus* some of the compound bundles divide near the apex of the corolla. The marginal bundles of a petal lobe may unite at its apex or remain free. In *Verbesina* the two compound bundles near the margins of the ligule, after entering the corolla immediately separate into their constituents (Fig. 23). In *Blainvillea* (Fig. 24) *Bidens* and *Flaveria* none of the five compound bundles do so.

In the ray-corolla of *Glossocardia* there are only four compound bundles and three dorsal bundles (Fig. 25). The odd posterior compound bundle is lost and the corolla splits at this region. All these seven bundles terminate blindly near its apex.

In the ray-florets of *Pulicaria*; *Inula*, *Calendula*, *Acanthospermum* and several ray-florets of *Aster* and *Solidago* the corolla has four compound bundles only (Figs. 26-30). The odd posterior compound bundle is lost and the corolla spilts at this region.

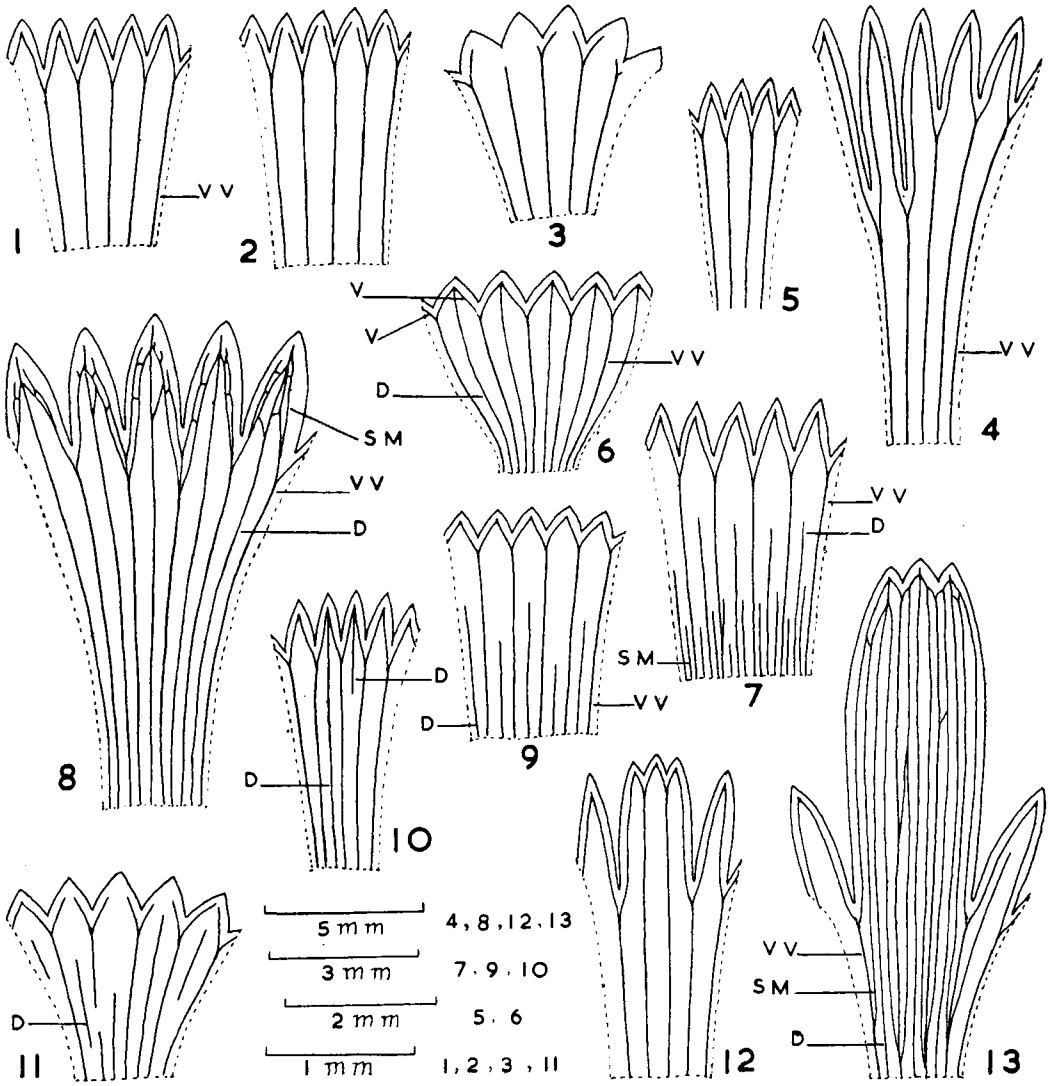
In *Calendula* the two compound bundles nearest to the marginals of the ligule divide immediately after entering the corolla (Figs. 28-29). The other two divide near the apex. The two marginals of a petal lobe may unite at its apex in *Pulicaria* (Fig. 26) and *Inula*. Although the petal dorsals are generally missing in these taxa, isolated pieces of dorsal bundles unconnected above and below are observed in some ray-corollas of *Inula* (Fig. 27) and *Calendula* (Fig. 29). In *Acanthospermum* (Fig. 30) and several florets of *Aster* and *Solidago* all the four compound bundles terminate without splitting.

The corolla of most of the ray-florets of *Aster* (Fig. 31) and *Eclipta* have just three compound bundles. These terminate without splitting. The ligulate corolla in *Chrysanthellum* (Fig. 32) has two compound bundles only while in *Artemesia* (Fig. 33) it has a solitary compound bundle. The ligulate corolla of *Solidago*, *Erigeron* and *Artemesia* may have one or two compound bundles. No dorsal bundles are present in them.

In the ray-florets of *Cyathocline* (Fig. 34), *Conyza*, *Gnaphalium* (Fig. 35), *Laggera*, *Sphaeranthus*, Anaphalis and *Blumea* (Fig. 36) the corolla is completely devoid of any Vascular bundles. In the ray (female) floret of *Cotula* the corolla itself is absent (Fig. 37)

Discussion

The petals in the family Compositae are fundamentally 3-traced in contrast to the general 1-traced condition in the



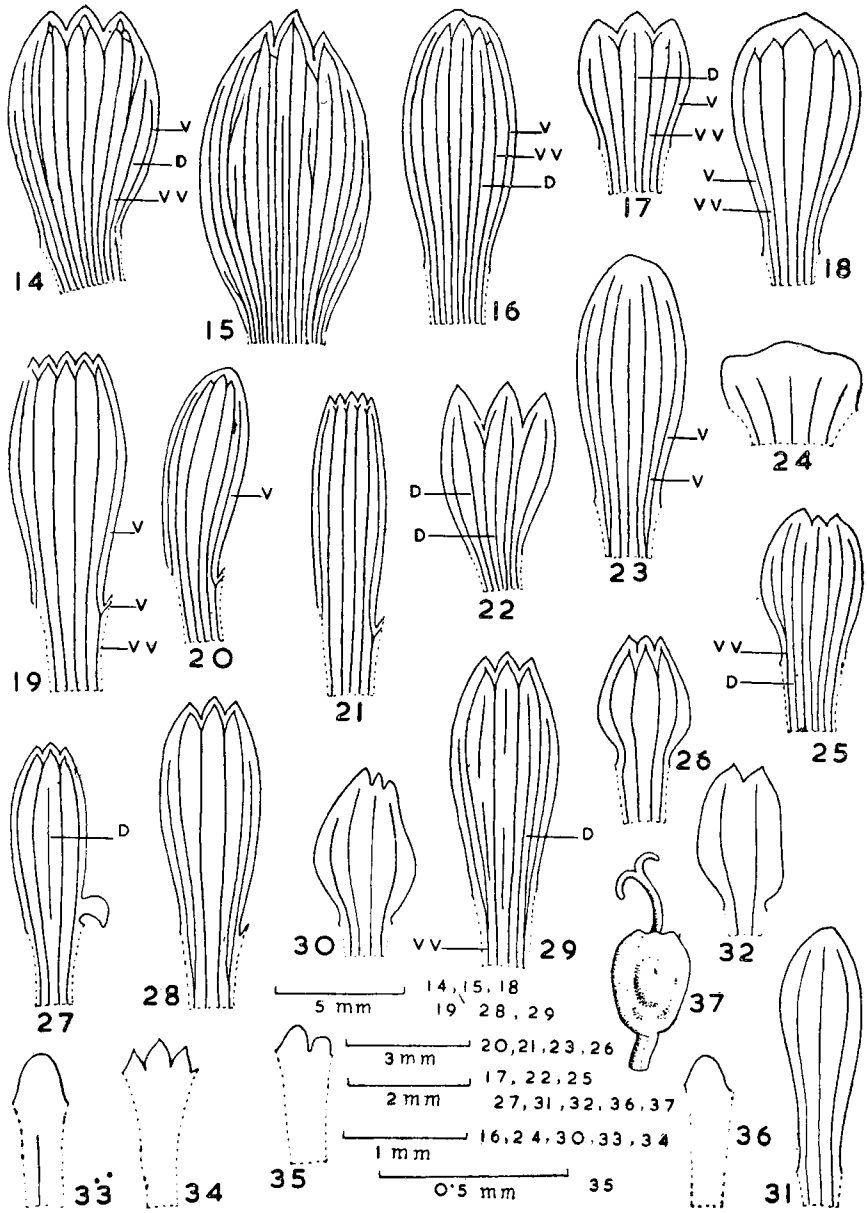
FIGS. 1–13. Cleared disk-corollas cut longitudinally and spread open to show their vasculature. Fig. 1. *Vernonia cinerea.* Fig. 2. *Eupatorium triplinerve.* Fig. 3. *Ageratum conyzoides* Fig. 4. *Cnicus wallichi.* Fig. 5. *Eclipta prostrata.* Fig. 6. *Helianthus annuus.* Fig. 7. *Tithonia diversifolia.* Fig. 8. *Gaillardia pulchella.* Fig. 9. *Verbesina oncophora.* Fig. 10. *Sclerocarpus africanus.* Fig. 11. *Artemesia vulgaris.* Figs. 12, 13. *Gerbera jamesonii.* Cleared bilabiate-corollas cut longitudinally and spread open to show their vasculature. Fig. 12. A disk-corolla. Fig. 13. A ray-corolla.

D, Dorsal bundle ; *SM*, Secondary marginal bundle ; *V*, Ventral bundle ; *VV*, Compound ventral bundle.

angiosperms. In the various species of this family all transitions from a condition in which all the three bundles are present in a petal to their total absence are seen. The adjacent marginal bundles of the adjoining marginals of the petals have without exception become fused at least in the lower region, more commonly up to the sinuses of the corolla lobes to form compound marginal bundles (cf. Koch, 1930a; Eames, 1931). Generally, the two marginal bundles of a petal unite at its apex to form an arch.

The reduction and suppression of the bundles in the corolla exhibit varied trends. In Helianthoideae, the bundles in the corolla in general are well developed, more so in the ray-florets than in the disk. Thus, in the disk-and ray-florets of *Helianthus* and *Tithonia* the dorsal and marginal bundles of the petals are fully developed. In the ray-florets the marginal bundles even give out a number of secondary branches (Fig. 15). In *Siegeskeckia, Sclerocarpus, Glossocardia, Galinsoga, Tridax, Ximensia,* etc., although the dorsal bundles are fully developed in the ray-corollas they are almost absent in the disk-corollas. Further, all stages of reduction of the dorsal bundles leading to their total elimination are met with in the ray-corollas of different species. Thus the ray-corolla of *Ximensia* (Fig. 14) *Helianthus, Tithonia* and *Tridax* possesses all the five dorsal bundles while that of *Brachycome* (Fig.16) has three and that of *Siegesbeckia* (Fig.22) and *Sclerocarpus* has only two of them. In *Galinsoga* (Fig. 17) the ray corolla has a solitary dorsal bundle. All the dorsal bundles are missing in the ray-corolla of *Zinnia* (Fig.18) and *Aster* (Fig.20). On the other hand in *Solidago, Erigeron Artemesia, Chrysanthellum, Conyza, Blumea, Laggera, Gnaphalium, Cyathocline* etc., the reduction of the vascular bundles in the corollas of the peripheral florets has been much greater than in those of the disk-florets. All the five compound bundles are fully developed in the disk-corollas of *Acanthospermum,* etc. but only four of them are seen in their ray-corollas (Fig. 30) while only 3 of them are found in most of the ray-corollas of *Aster molliusculus* (Fig. 31). Their number is reduced to two or one in *Chrysanthellum* (Fig. 32), *Solidago, Erigeron, Artemesia* (Fig. 33) etc. In *Cyathocline* (Fig. 34), *Gnaphalium* (Fig. 35), *Blumea* (Fig. 36), *Conyza, Laggera, Anaphalis, Sphaeranthus* etc., the corolla of the ray-floret is entirely devoid of vascular bundles. Evidently the suppression of the vascular bundles here has been faster than the organ itself. It is only after so much reduction of vascular bundles that the corolla itself has become almost completely suppressed in certain forms like the female florets of *Xanthium* and the ray-florets of *Cotula* (Fig. 37). The suppression of the vascular bundles of the corolla before the suppression of the corolla itself is in conformity with the condition in other floral organs in Compositae (Manilal, 1963). The relative conservatism of vascular bundles *versus* the organ it supplies was discussed at length by Puri (1951) who stressed the need for a judicial approach to tackle such problems of evolutionary morphology.

The presence of three types of corollas in this family, namely tubular, ligulate and bilabiate was anatomically confirmed by Small (1917) and Koch (1930a). Small (1917) expressed the opinion that the three types of corollas could be distinguished from each other by the variability of their anatomical characters alone. The present study



FIGS. 14–37. Cleared ray-corollas cut longitudinally and spread open to show their vasculature. Fig. 14. *Ximensia enceloides.* Fig. 15. *Tithonia diversifolia.* Fig. 16. *Brachycome assamica.* Fig. 17. *Galinsoga parviflora.* Fig. 18. *Zinnia elegans.* Fig. 19. *Cichorium intybus.* Fig. 20. *Aster amellus.* Fig. 21. *Sonchus oleraceus.* Fig. 22. *Siegesbeckia orientalis.* Fig. 23. *Verbesena oncophora.* Fig. 24. *Blainvillea acmella.* Fig. 25. *Glossocardia bosvallea.* Fig. 26. *Pulicaria angustifolia.* Fig. 27. *Inula indica.* Figs. 28, 29. *Calendula officinalis.* Fig. 30. *Acanthospermum hispidum.* Fig 31. *Aster molliusculus.* Fig. 32. *Chrysanthellum indicum.* Fig. 33. *Artemesia vulgaris.* Figs. 34–36. Cleared ray-corollas cut longitudinally and spread open to show the absence of vascular bundles. Fig. 34. *Cyathocline purpurea.* Fig. 35. *Gnaphalium pulvinatum.* Fig. 36. *Blumea eriantha.* Fig. 37. *Cotula anthemoides.* A ray-floret.

D, Dorsal bundle; *SM*, Secondary Marginal bundle; *V*, Ventral bundle; *VV*, Compound ventral bundle.

does not subscribe to such a view but shows that the ligulate and bilabiate types of corollas are mere modifications of the tubular type.

A single deep sinus on the posterior side in the tubular corolla preceded by the division of the compound marginal bundle below gives rise to the ligulate type as exhibited not by the members of the tribe Cichorieae alone (Fig. 19, 21) but also by several species belonging to other tribes (Fig. 20, cf. Figs. 14, 16). A more advanced type of formation of the ligulate corolla is exhibited by those species where the posterior compound marginal bundle of the petal fail to divide and the splitting of the corolla occurs between two posterior compound marginals (Figs. 22-24).

Similarly, the splitting of the corolla by the two main sinuses one on each side of a posterior and a lateral petal preceded by the splitting of the compound marginal below, results in the bilabiate types as in *Gerbera* (Figs. 12-13 cf. *Cnicus*). Therefore it can be concluded that the bilabiate and ligulate corollas are modifications of the basic tubular type. This is also borne out by the similarity in their fundamental vascular pattern.

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