

FLORAL ANATOMY OF *ACTINOMERIS SQUARROSA* AND *BIDENS BITERNATA* (ASTERACEAE)

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Floral anatomy of *Actinomeris squarrosa* and *Bidens biternata* have been described. The presence of pappus is an important structural feature of the Asteraceae. It has been considered by some as phyllome and by others a trichome structure. The presence of vascular supply to the pappus scales shows that it is a phyllome structure. Once the pappus is considered as a phyllome structure, two major lines of specialization can be established in this family from a primitive type of five vascular scales. In one line of evolution there has been increase in the number of pappus from five to twenty and finally indefinite in number and the vascular supply is totally suppressed. In another line of evolution there has been a reduction in the number of pappus scales from five to two and finally total reduction of the scales.

The disc-florets of *Bidens biternata* are pentamerous but occasionally tetramerous florets are also observed. In *Actinomeris squarrosa* disc-florets are tetramerous. Tetramerous florets are derived from pentamerous floret by complete fusion of the two anterior alternipetalous strands is discussed.

In the Asteraceae, the pistillate ray-florets are derived from disc-florets by formation of a deep sinus in the corolla on the posterior side, followed by gradual suppression of the androecium. The neutral ray-florets are derived from ray-florets by complete reduction of an ovule, loculus and style along with its vascular supply is also discussed.

Key words: *Actinomeris squarrosa*, *Bidens biternata*, floral anatomy, neutral ray-floret, pappus, tetramerous

INTRODUCTION

The Asteraceae, comprising about 1,600 genera and 25,000 species, is one of the largest family of the flowering plants. The great homogeneity of the Asteraceae is displayed by their possession of the capitulum inflorescence, as well as the peculiar plan of their florets which even when divorced from the mother plant could in no case be mistaken from anything else (Good 1956, Leppik 1960). To a student of evolutionary morphology of Angiosperms, the Asteraceae flower presents several thoughts provoking problems. The nature and evolution of flower, corolla, pappus, placentation and inferior ovary are subject of acrimonious debate, which has

already been reviewed in the earlier papers (Tiagi and Singh 1972, 1981, Singh 1994, 1998, Singh and Kaur 1998*a, b*).

MATERIALS AND METHODS

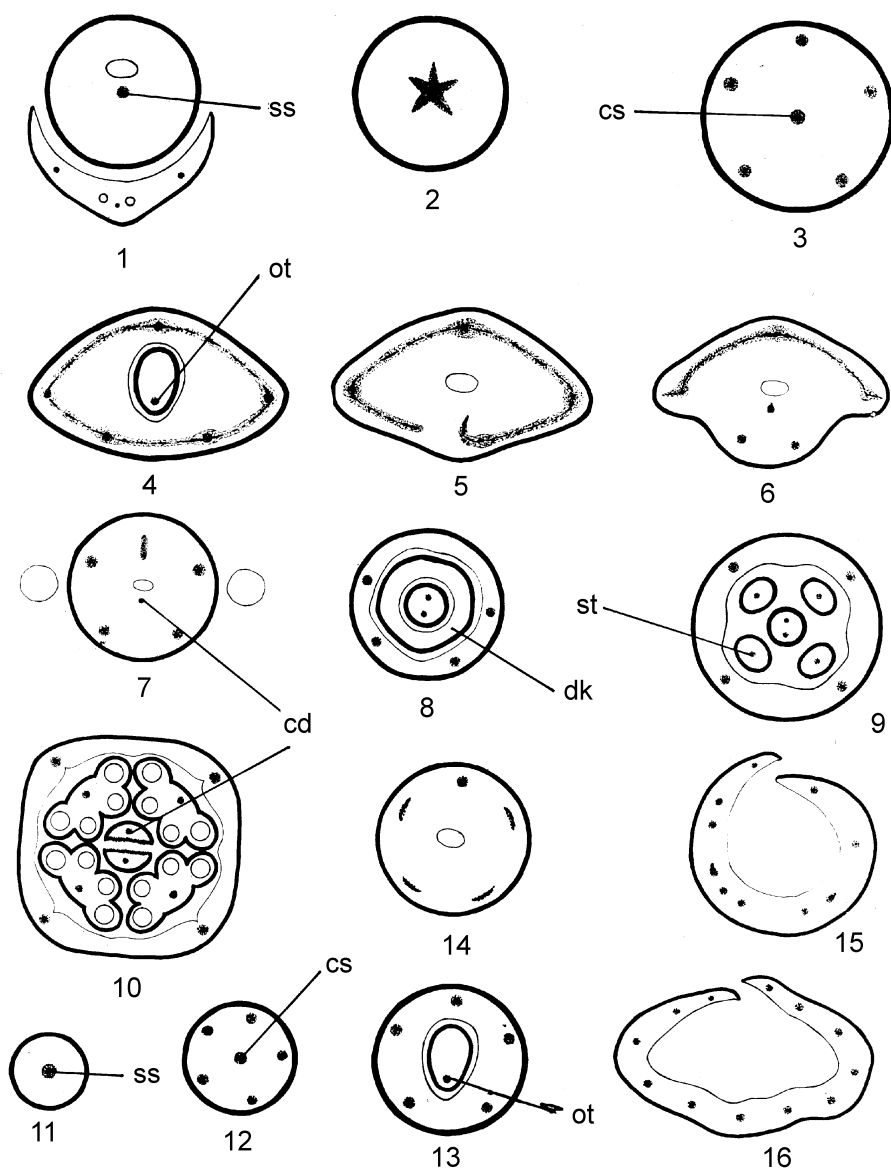
In the present work, vascular anatomy of the flowers of *Actinomeris squarrosa* and *Bidens biternata* have been investigated. Customary methods of microtechnique were used. Serial transverse and longitudinal sections of the florets and capitula were cut at the thickness ranging from 7–15 µm. Double staining with crystal violet and erythrosin gave satisfactory results. In all cases the floral buds were cleared by warming in 10% solution of potassium hydroxide and subsequently in colourless lactic acid. The cleared buds were dissected under a stereoscope. This was found to be very useful in understanding 3-dimensional picture of the vascular skeleton.

Observations

Actinomeris squarrosa Nutt.

Disc-floret. The single vascular strand in the base of the floret gives out five alternipetalous strands into the wall of the inferior ovary and then itself *in toto* becomes the ovular trace (Figs 1–3). Inside the wall of inferior ovary, the five strands become connected laterally by girdle shaped vascular band (Fig. 4). In the top of the inferior ovary, the anterior stylar trace arises from the anterior position of the circular vascular girdle (Fig. 5). The circular vascular girdle also gives out two smaller traces, one on either side and then breaks up into five separate strands. The lateral strands traverse a little outward but terminate blindly in the base of the pappus scales (Figs 6–7). The posterior vascular strands turn inward and *in toto* become the posterior stylar trace and only the other four alternipetalous traces are left to enter the corolla tube (Fig. 8). The usual tangential splitting of these four bundles gives rise to the inner staminal and outer compound marginal bundles of the petals, the latter breaking up into their constituents a little higher up (Figs 9–10).

Ray-floret. In the pistillate ray-floret, the single vascular strand in the base of the floret gives out five alternipetalous traces into its wall and then itself *in toto* becomes the ovular trace (Figs 11–13). The floret has no style

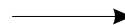


Figs 1–16. *Actinomeris squarrosa*. Figs 1–10: Serial transverse sections of a disc-floret from below upward, showing the origin and subsequent coursing of the vascular supply of the different floral cycles (for explanation, see text). – Figs 11–16: Serial transverse sections of a ray-floret from below upward, showing the origin and subsequent coursing of the vascular supply of the different floral cycles (for explanation, see text). – Explanation of lettering: cd = carpellary dorsal, cs = central strand, dk = disc, ot = ovular trace, ss = stelar strand, st = staminal

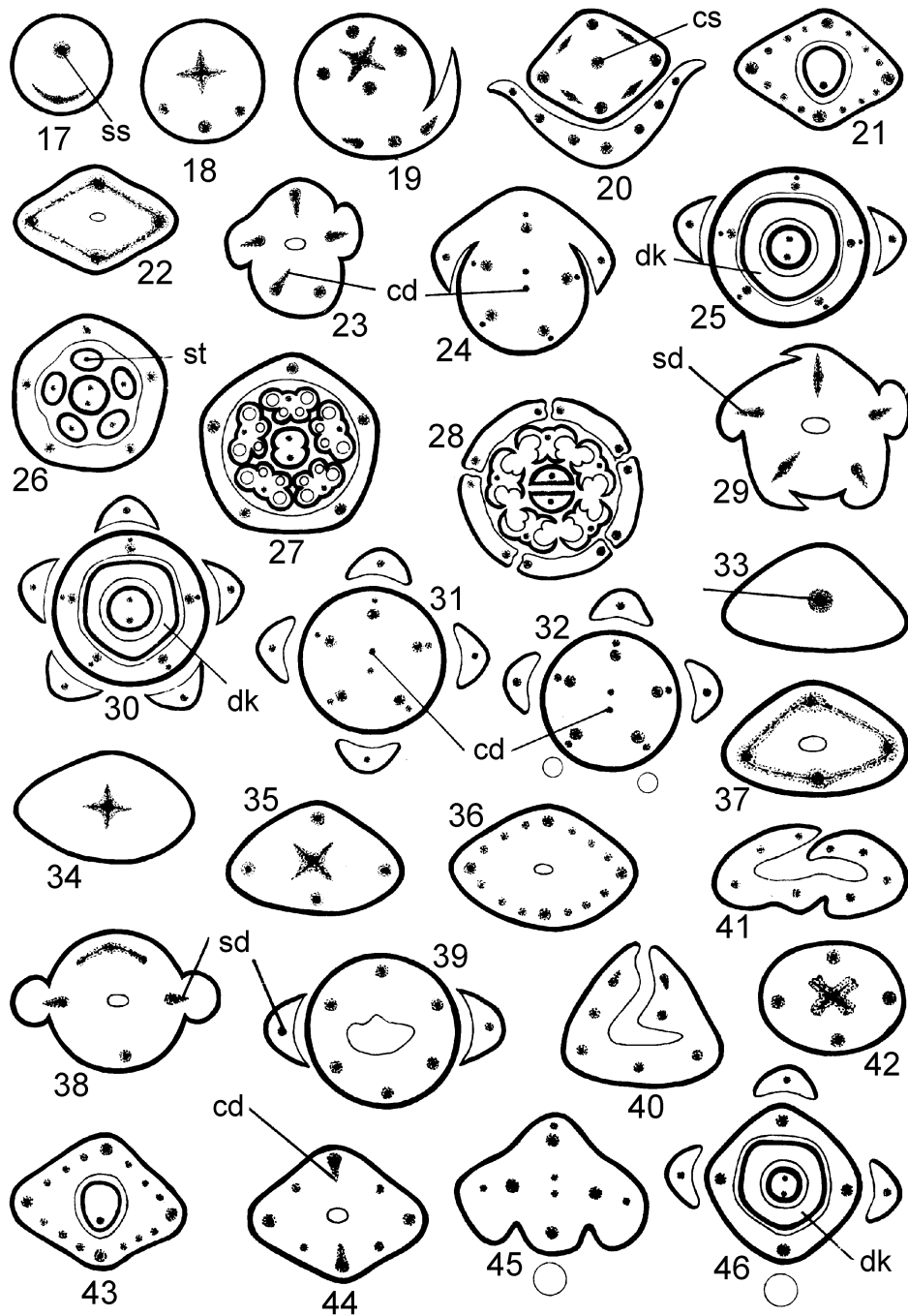
and stamens. The five bundles directly enter the corolla and undergo radial division to form an arc of ten or more bundles (Figs 14–16).

***Bidens biternata* (Lour.) Merr. et Sherff**

Disc-floret. The palea is three traced and its bundles undergo radial division to form an arc of several bundles. The single vascular strand in the base of the floret gives out four traces, two on the median and two on the lateral plane, soon followed by another four in the diagonal positions (Figs 17–18). The former remain undivided while each of the latter forks into three so that a ring of sixteen strands, four strong strands with four triplets of traces each in alternating positions is observed in the base and wall of the inferior ovary (Figs 19–20). After furnishing all these peripheral strands, the central strand *in toto* becomes the ovular trace. In the top of the inferior ovary, first the two lateral strands of the triplets terminate blindly, so that a ring of four strong strands with four weak strands in alternating positions is observed (Fig. 21). A little higher up, the four weak strands totally disappear totally and the strong strands give out small traces on their outer side. Simultaneously, the anterior strand splits up radially onto two, so that the five strong alternipetalous strands become organized. By now all of them have given rise to a smaller trace on their outer side and the posterior and one of the anterior has also given rise to the styler traces on their inside (Figs 22–23). Thus two concentric rings of vascular traces in the peripheral part and two medianly situated styler traces are seen in a transverse section in the top of the inferior ovary (Fig. 24). The outer five weak traces enter the five spiny pappus scales on the top of the inferior ovary (Figs 24–25, and 35), whereas the inner five traces enter the corolla tube and by the usual tangential splitting furnish the vascular supply of the stamens and the corollas (Figs 25–27).



Figs 17–46. *Bidens biternata*. Figs 17–28: Serial transverse sections of a disc-floret from below upward, showing the origin and subsequent coursing of the vascular supply of the different floral cycles (for explanation, see text). – Figs 29–30: Same, showing five pappus scales. – Fig. 31: Same, showing only four pappus scales. – Fig. 32: Same, showing three massive and two small pappus scales. – Figs 42–46: Same, showing tetramerous floret with three massive and one small pappus scales. – Figs 33–41: Serial transverse sections of a ray-floret from below upward, showing the origin and subsequent coursing of the vascular supply of the different floral cycles (for explanation, see text). – Explanation of lettering: als = alternipetalous strand, cd = carpellary dorsal, cpm = compound petal marginal, cs = central strand, ot = ovular trace, sd = sepal dorsal, ss = stelar strand, st = staminal



The above specimen which has been described is a slightly unusual one since in most florets of *Bidens biternata* there are only four epigynous scales of the pappus and in such cases the anterior strand furnishes a trace to the pappus scale of the same side before dividing into two. In such cases, though four pappus scales are present, five compound marginal traces are seen in the top of the inferior ovary (Fig. 29). Occasionally in some specimens, no vascular supply is furnished by the anterior strand to the anterior pappus scale (Figs 30–34). In still other cases two of the five pappus scales occurring in antero-lateral position are totally devoid of any vascular supply and are conspicuously smaller in size (Fig. 28).

Ray-floret. The vascular anatomy of the inferior ovary of the neutral ray-floret (Figs 36–38) is similar to that of the disc-floret. In the apical region, these vascular strands become jointed laterally to form a girdle (Fig. 39). Only two pappus scales in the lateral positions are present and a single trace is given to each (Figs 40–42). The ovary is solid and the style is reduced to an insignificant structure. Some of the five alternipetalous strands which enter the corolla tube may undergo a division (Figs 43–44).

DISCUSSION

The present work on the vascular anatomy of the florets of *Actinomeris squarrosa* and *Bidens biternata* and certain other taxa of the Asteraceae studied elsewhere (Singh 1973) has brought out certain features whose significance is discussed in the following pages.

Evolution of pappus. The pappus is an important characteristic structural feature of the family Asteraceae. Its morphological nature has remained enigma for quite a long time. There are two schools of thought regarding the morphological nature of the pappus. According to one school of thought, they have been considered as a more or less modified calyx (Bentham 1873, Rendle 1938, Lawrence 1951, Cronquist 1955, Carlquist 1961, Singh 1973). This is also sometimes known as phyllome theory of the morphological nature of the pappus. According to another school of thought, the pappus does not represent a modified calyx but is of the nature of trichomes (McNab 1873, Warming 1873, Hanlein 1874, Masters 1878, Small 1919, Tiagi and Taimni 1963). The author believes that the pappus is a calyx which has undergone modifications in several ways. The following stages and lines of evolution in the pappus can be recognized in this family.

Primitive types. In *Bidens biternata* (Fig. 25) the pappus represents the least modified calyx and is characterized by the following features. (i) Five in number with the odd member on the posterior side. (ii) The general appearance of the pappus members is sepal-like. (iii) Each member possesses a well developed vascular supply. (iv) The aestivation is valvate. The only uncommon thing about the sepals (pappus) of this type is that they are one traced. This is understandable in view of the reduction, the calyx in the Asteraceae has undergone. Similar type of pappus scales are also observed in *Ageratum conyzoides*, *Adenostemma lavenia* and wild form of *Tagetes erecta* (Singh 1973). From this type of calyx as seen in *Bidens biternata* the calyx has undergone modifications in several ways and the derived types are discussed below. They can be classified into two categories, one is the result of reduction and the other of amplification.

Reduction series. In *Bidens biternata* quite often the two anterior pappus scales are fused, so that the pappus scales are reduced to only four members (Fig. 29). Occasionally in some tetramerous specimens, no vascular supply is furnished by the anterior strand to the anterior pappus scale (Fig. 34). In still other case two of the five pappus scales occurring in antero-lateral positions are totally devoid of vascular supply (Fig. 28), and are conspicuously smaller in size. All the types are derived from primitive type. In the ray-floret of *Bidens biternata* the pappus scales, though sepal-like, are reduced to only two members (Fig. 42). This type can be visualized to have been originated, from the *Bidens biternata* having four pappus members, by suppression of the posterior and anterior pappus members. The pappus type of *Actinomeris squarrosa* can be easily derived from that seen in ray-floret of *Bidens biternata* by reduction of the size of two laterally placed pappus members though the vascular supply is still present in the form of vascular stubs (Fig. 6). By further suppression of both the pappus members, as well as their vascular supply will give rise to the condition seen in taxa like *Cyathocline purpurea*, *Sigesbeckia orientalis*, *Artemisia scoparia*, *A. vulgaris* and many other taxa of the family Asteraceae (Singh 1973), where pappus are non-existent.

Amplification series. From the condition seen in *Bidens biternata* and other similar types, we can visualize the origin of two whorled calyx that Schaffner (1934) called as "duplicate evolution", or by common process known as doubling. A pappus consisting of two whorls of members is known to occur in *Cymbia occidentalis* in which the odd member of the inner whorl is anterior in position. On purely morphological grounds, Cronquist (1955) believed that the pappus in several genera of Helianthoideae like

Dysodia, has originated by longitudinal splitting of sepal-like members. From the *Cymbia occidentalis* type of pappus, further amplification by choris (longitudinal splitting) of each members would give rise to the condition of pappus reported in *Tridax procumbens*, where there are ten members in each whorl with well developed vascular supply (Singh 1973). By further amplification, gradual loss of vascular supply and assumption of setose form would give rise to the condition seen in *Eupatorium triplinerve*, *Emilia sonchifolia* and in vast majority of the taxa of the family Asteraceae.

To conclude, therefore, we can say that the pappus in the ancestral Asteraceae consisted of five sepal-like members. In one line of evolution there has been reduction in the number of pappus members from five to total loss of pappus along with its vascular supply. In the other line of evolution there has occurred an amplification of the number of whorls and number of members in the whorls of the pappus and which assumed the setose form.

Evolution of flower. The chief evolutionary processes which have been operative in the modification of the vascular ground plan of the flower of the Asteraceae are cohesion, reduction and rarely amplification. In the present investigation the structure, vascular anatomy and evolution of tetramerous and neutral ray-florets are discussed.

Tetramerous floret. The vascular anatomy of the florets of *Actinomeris squarrosa* and *Bidens biternata* presents anatomical facts that tetramerous florets are derived from pentamerous florets in the family Asteraceae. In *Actinomeris squarrosa*, *Eclipta prostrata*, *Chrysanthellum indicum*, *Dicrocephala latifolia*, *Erigeron canadensis*, *Glossocardia bosvallea* and *Vicoa auriculata*, the disc-florets are tetramerous (Singh 1973). The tetramerous florets in all cases are derived from pentamerous florets by cohesion or reduction of alternipetalous strands.

In the capitulum of *Bidens biternata* majority of the disc-florets are pentamerous but occasionally tetramerous florets are also observed. In pentamerous florets the two anterior alternipetalous strands fuse to form a single strand, which however, in the top of the inferior ovary splits up into its (original) constituents. So at the top of the inferior ovary are present only the five alternipetalous strands which rise up and all the remaining strands disappear. These five alternipetalous compound strands supply vascular traces to five pappus scales, five petals, five stamens and two medianly placed carpels. In tetramerous florets the two anterior alternipetalous strands are completely fused, so at the top of the ovary are present four alternipetalous strands, the two antero-posterior and two lateral in

position. The four alternipetalous compound strands supply vascular traces to four pappus scales, four petals, four stamens and two carpels which are medianly placed. So the floret in this case has become tetramerous.

In all the taxa of the family Asteraceae studied so far, the tetramerous florets are derived from pentamerous condition either by fusion of the two anterior alternipetalous strands or by suppression of the posterior alternipetalous strand (Singh 1973). In *Actinomeris squarrosa* the posterior strand turns inward and *in toto* becomes the posterior styler trace and the floret is tetramerous.

Neutral ray-floret. The disc-florets are actinomorphic, bisexual with tubular corollas. The stelar strand in the base of the disc-floret gives out peripheral strands into the wall of the inferior ovary. The central strand *in toto* becomes the ovular trace which enters the basal ovule. The peripheral strands at the top of the inferior ovary furnished traces to sepals (pappus), petals, stamens and medianly placed two carpels. There can be hardly any doubt that the actinomorphic disc-florets are most primitive among the family from which the ray, ligulate and neutral florets are derived.

The ray-florets are derived from disc-florets by formation of a deep sinus in the corolla on the posterior side followed by gradual suppression of the androecium along with its vascular supply. Ray-florets with five, four, three and two staminodes are reported, respectively in *Gerbera jamesonii*, *Aster thomsoni*, *Inula cappa* and *Erigeron multicaulis* (Singh 1973).

In next step of evolution towards neutral florets, the style, stigma and the styler bundles are completely suppressed, a condition seen in *Actinomeris squarrosa*. In the final stage of evolution that can be seen in the neutral ray-floret of *Bidens biternata*, the ovary is solid without ovules and loculus, and the central strand has been completely suppressed.

The nature of the inferior ovary, evolution of corolla in the Asteraceae has already been discussed in the earlier papers (Tiagi and Singh 1972, 1981, Singh 1994) and since no more additional information has added, the subject is not repeated here.

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