A CONTRIBUTION TO THE VASCULAR ANATOMY OF THE FLOWER OF CERTAIN SPECIES OF THE SALVADORACEAE

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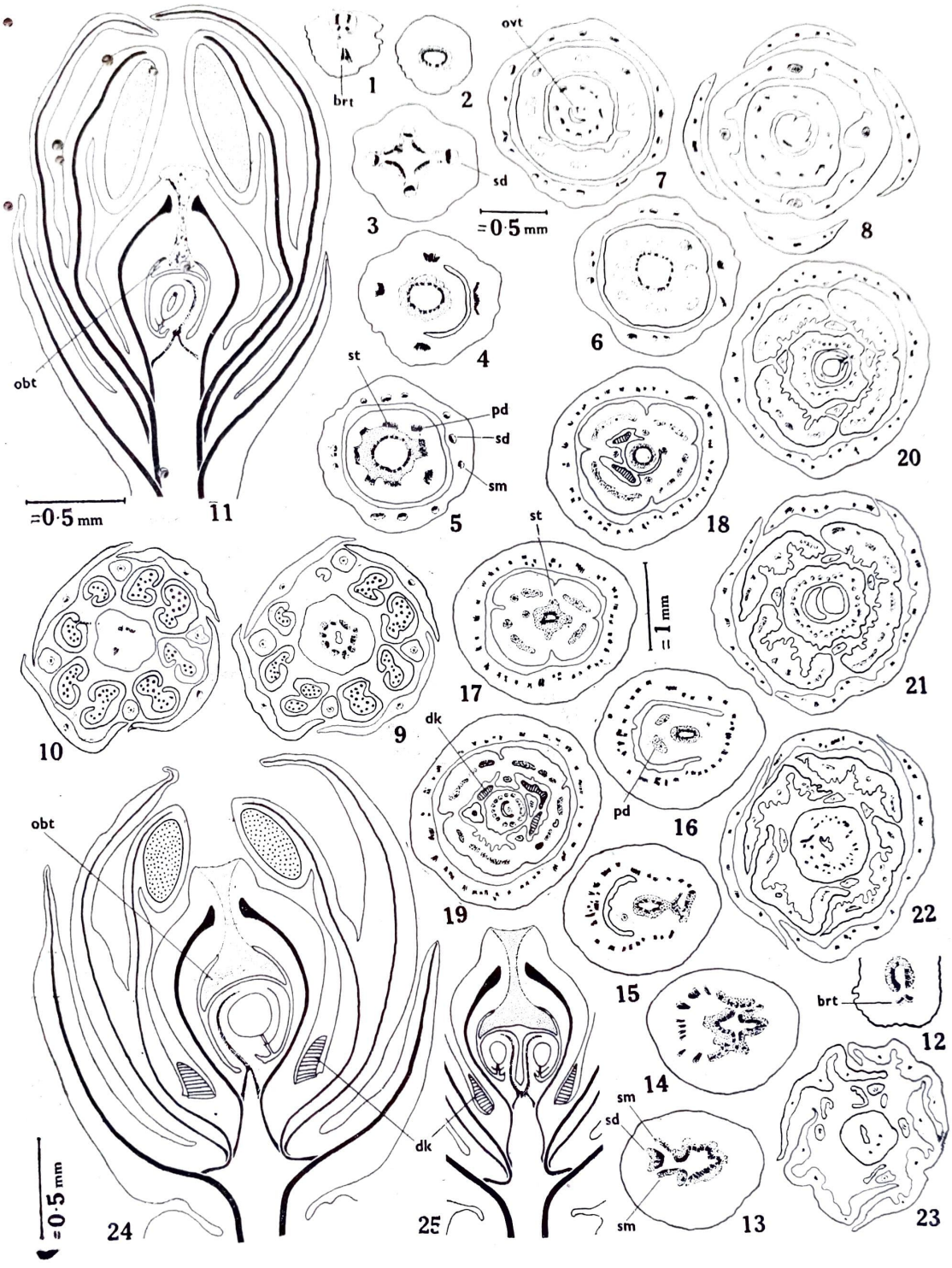
Salvadoraceae is a small family of three genera and about twelve species, occurring in Africa, Madagascar and Asia. *Azima* and *Salvadora* occur in India while *Dobera* is African. In spite of its controversial systematic position, there has been no work on the floral anatomy of Salvadoraceae. Earlier, Tiagi (1954) worked out the embryology of *Salvadora persica* and suggested that the Salvadoraceae belongs to the Choripetalae. Mauritzon (1936) earlier expressed a similar opinion.

In the present work vascular anatomy of the flower of *Salvadora persica*, *S. oleoides* and *Azima tetracantha* has been described. Material of *Salvadora* species was sent to me from Agra by Dr. J. S. Gupta and that of *Azima* from Gudivada by Dr. B. S. M. Dutt. Customary methods of microtechnique were employed. Floral buds were also cleared with 10% aqueous potassium hydroxide and lactic acid for understanding the 3-dimensional plan of vasculature.

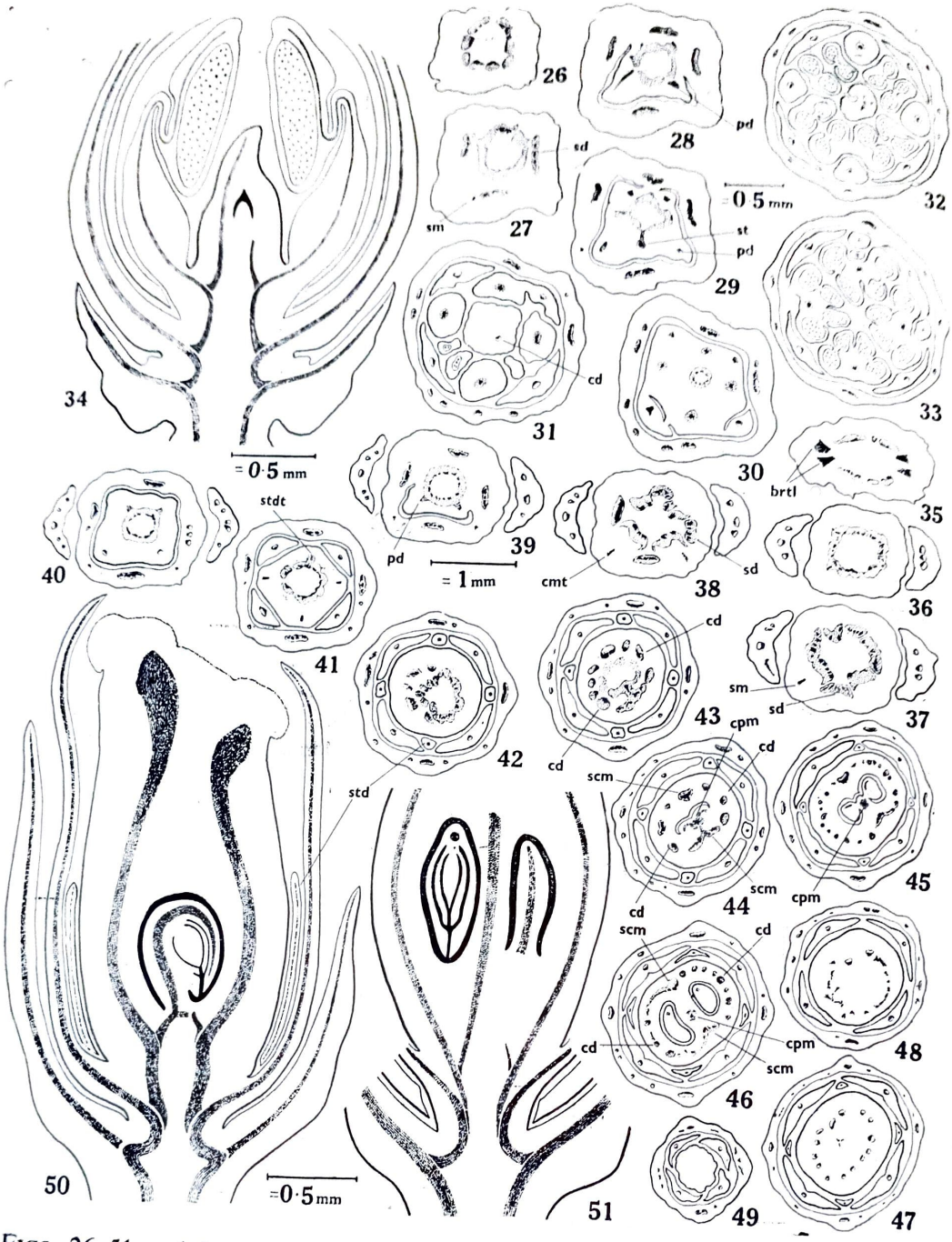
Observations

External Morphology.—The flowers are borne in racemose panicles in *Salvadora* and in axillary cymes in *Azima*. In the former genus, they are bisexual but in the latter unisexual, dioecious. The flower is tetramerous. In *Salvadora*, the corolla is gamopetalous but it is polypetalous in *Azima*. The ovary is unilocular, usually with a single, sometimes two basal ovules in *Salvadora* (Figs. 8, 11, 20, 24, 25) where the glandular transmitting tissue of the style expands in the top of the



FIGS. 1–25. Figs. 1–11. *Salvadora persica*. Figs. 1-10. Serial transections of a flower-bud from below upward showing the origin and subsequent behaviour of the vascular supply of the different floral whorls. Fig. 11. Median longisection of a flower-bud (diagrammatic) showing course of vascular traces. Figs. 12–25. *Salvadora oleoides*. Figs. 12–23. Serial transections of a flower-bud from below upward showing the origin and subsequent behaviour of the vascular supply of the different floral cycles. Figs. 24, 25. Median longisections of flower-buds showing course of vascular traces and uni- and biovulate ovaries respectively.

• *brt*, bract trace; *dk*, disk; *obt*, obturator; *ovt*, ovular trace; *pd*, petal dorsal trace; *sd*, sepal dorsal trace; *sm*, sepal marginal trace; *st*, staminal trace.



FIGS. 26–51. *Azima tetracantha*. Figs. 26–33. Serial transections of a staminate flower-bud showing the origin and subsequent behaviour of the vascular traces of the different floral cycles. Fig. 34. Median longisection of a staminate flower-bud showing course of vascular traces. Figs. 35–49. Serial transections of a pistillate flower-bud showing origin and subsequent behaviour of the vascular supply of bracteoles and the different floral cycles. Fig. 50. Median longisection of a pistillate flower-bud showing vascular traces and the ovule of one of the two loculi. Fig. 51. Same but in a different plane passing through the body of the ovule of one loculus and through the funiculus of the ovule in the other loculus.

brtl, bracteole trace; *cd*, carpellary dorsal trace; *cmt*, compound marginal trace; *cpm*, carpellary marginal trace; *pd*, petal dorsal trace; *scm*, secondary marginal trace; *sd*, sepal dorsal trace; *sm*, sepal marginal trace; *st*, staminal trace; *std*, staminode; *stdt*, staminodal trace.

loculus into a hood-shaped stylar obturator which closely fits on the chalazal side of the ovule. In *Azima*, the ovary is unilocular in the lower but bilocular in the upper region and the stylar obturator is lacking (Figs. 45, 46); a single basal anatropous ovule is attached on either side of a placenta which is parietal, the other similar placenta being sterile (Figs. 45, 46, 50, 51).

Salvadora persica Linn. and *S. oleoides* Decne.—*Vascular anatomy of the flower.*—A single trace for the bract and two for its axillary flower diverge out from the stele of the peduncle (Figs. 1, 12). Inside the pedicel the two bundles become laterally united to form a continuous ring of xylem surrounded by phloem (Fig. 2). In *Salvadora oleoides* which has sessile flowers, the receptacular stele is slightly evaginated (Figs. 24–25). Two of the four sepals are median and the other two lateral in disposition. In *Salvadora oleoides*, the sepals are 3-traced (Figs. 3–4, 13–15) but in *S. persica* 1-traced. However, in the latter species, the single bundle of a sepal quickly forks into three in the basal part of the calyx tube, followed by further divisions higher up; in *S. oleoides*, divisions of the three main traces of the sepals are rather precocious (Figs. 4–8, 14–22). In any case only a few bundles reach up to the apex of the calyx lobes (Figs. 9–10, 23).

After furnishing the traces of the calyx, the receptacular stele gives out a set of four traces each for the corolla and the androecium in quick succession (Figs. 5–6, 15–17). In *S. persica*, the single bundle of a petal remains unbranched throughout its course (Figs. 6–10) but in *S. oleoides*, it undergoes radial splitting (Figs. 17–23). The staminal bundles remain unbranched throughout their course. The four scales (disk) which are present only in *S. oleoides* in positions alternating with the stamens are without any vascular supply. After furnishing the vascular supply of the stamens, the receptacular stele again becomes a continuous ring. Ten or more traces now diverge out into the ovary wall, ascend upward inside it, some of them branching once and finally terminate below the top of the stigma (Figs. 6–11, 18–25). The residual portion of the receptacular stele now consists of a few strands of provascular tissue; these ascend upward and inward and establish connection with a small mass of vascular tissue in the base of the ovary from which the single ovular trace rises up into the raphe, finally terminating in the chalaza (Figs. 11, 24–25).

Azima tetracantha Lamk.—The stele of the pedicel consists of a ring of discrete collateral bundles (Fig. 26). The lateral bracteoles, like the leaves, are furnished with paired traces (Fig. 35). In the basal region of a bracteole, the two traces unite to form a single strand which quickly forks into three bundles, of which the lateral ones undergo one more division (Figs. 36–39).

In the male flowers, the sepals, petals and stamens are all 1-traced (Figs. 27–33) but in the female flower, two compound marginal traces are furnished to the calyx (Figs. 36–40). The petals and staminodes

are 1-traced (Figs. 40–42). After supplying the androecium, the stele becomes a continuous ring. In the male flower, a single bundle ascends up in the pistillode, terminates near its apex while the residual stele disappears in its base (Figs. 30–31, 34). In the female flower, about ten bundles diverge out from the receptacular stele into the ovary wall. On one side some of these bundles remain adnated to the receptacular stele (Figs. 41–43). It is here that a strong vascular cord develops which furnishes an ovular trace on either side (Fig. 44). The ovular bundle traverses upward in the raphe up to the chalaza and then extends beyond it into the outer integument (Fig. 50). A perusal of Figs. 44–46 shows that the two ovules are borne on a placenta formed by the fusion of adjacent margins of different carpels and the other similar placenta is sterile. Higher up, the fertile placenta unites with the sterile one and the ovary becomes bilocular (Fig. 46). The oblique placement of the two carpels in this genus is also clear from these figures. The placental cord terminates in the apical region of the septum while most of the bundles of the ovary wall disappear in the tip of the stigma (Figs 47–51).

Discussion

The oblique placement of the carpels in *Azima* has already been mentioned (Figs. 44–46). In *Salvadora* due to the indistinguishability of the carpellary dorsals from the other bundles of the ovary wall, it is not possible to decide this point conclusively. However, the oblique placement of the ovule inside the loculus (Figs. 8, 20) is indicative of similar disposition of the two carpels.

Salvadoraceae present a primitive type of vascular ground plan in having practically no adnation and cohesion among the vascular traces of different floral cycles. Like the leaf (Kshetrapal and Tiagi, 1967 *b*), the vascular supply of the bract and bracteoles in *Azima* belongs to the unilacunar 2-traced type; in *Salvadora*, the leaves and bracts are unilacunar 1-traced and bracteoles are wanting. In *Salvadora oleoides*, the sepals are ostensibly 3-traced. In the female flower of *Azima*, some compound marginal bundles are present in the calyx while in *Salvadora persica* and the male flowers of *Azima*, the sepals have become 1-traced.

According to the definition given by Puri (1952), placentation in Salvadoraceae is basal. Detailed discussion exists on the morphological nature of basal placenta in the works of Puri (1952) and Eames (1961). The placental condition in *Azima* is helpful in interpreting the nature of basal placentation in this family. It will be recalled that the ovary in this genus is unilocular in the lower region and the two ovules remain attached one on either side of the placenta which is borne on the junction of the two carpellary margins belonging to different carpels, the second similar placenta being sterile (Fig. 45). This is typical parietal placentation, topographically as well as anatomically. Suppression of one of the two ovules would give rise to the usual

condition in the genus *Salvadora*. Basal placentation in the Salvadoraceae, therefore, seems to have been derived from parietal.

Relationships of the Salvadoraceae

Wide divergence of opinion exists regarding the phylogenetic placement of the Salvadoraceae among the systems of angiosperms. According to one school of thought (Wettstein, 1935; Melchior, 1964; Hutchinson, 1959; Takhtajan, 1966), the family belongs to the polypetalae while according to the other (Bentham and Hooker, 1876; Rendle, 1938), it belongs to the gamopetalae. Further, the interrelationships of the three genera of the Salvadoraceae also merit some comments. Little is known about *Dobera*. Available information (Metcalfe and Chalk, 1950) indicates that *Dobera* is like *Salvadora* in having interxylary phloem which is lacking in *Azima*. The latter genus differs from *Salvadora* in its rambling habit, first pair of leaves of axillary shoot modified into spines, stele of the stem and pedicel consisting of a ring of discrete bundles, unilacunar, 2-traced type of node, dioecious unisexual flowers in cymes, presence of bracteoles, polypetalous, valvate corolla, reclinate tips of staminal filaments and ovary with two ovules, unilocular below, bilocular above and without a stylar obturator. *Salvadora* and *Azima*, however, resemble each other in the oblique placement of their carpels and in their embryology. Further, similarity in the structure of their embryos is remarkable. The cotyledons in both the genera are produced downward into prominent obtuse lobes on either side of their attachment to the embryonic axis. In the author's opinion, the Salvadoraceae may be divided into two subfamilies, the Azimoideae to include *Azima* and the Salvadoroideae to include *Salvadora* and *Dobera*.

Regarding the phylogenetic placement of the Salvadoraceae among the systems of angiosperms, Kshetrapal (1967) in her recent detailed study of the phylogenetic morphology of the Gentianales concluded that in the following characters taken collectively, the family stands completely isolated in this order: lack of intraxylary phloem and squamellae; presence of both cymose and racemose inflorescences; unilacunar 2- or 1-traced type of node; lack of adnation among the vascular traces of the various floral cycles; petals free or united, valvate, imbricate or twisted, their bundles often remaining undivided; gynoecium syncarpous with basal placentation; ovule bitegminal and crassinucellar; non-endospermic seed and cotyledons with basal lobes. Further, Mauritzon (1936) and Tiagi (1954) who worked on the embryology of *Salvadora persica* concluded that in the possession of bitegminal, crassinucellar ovules, nuclear endosperm and absence of integumentary tapetum, the Salvadoraceae are unlike most of the Gamopetalae. On the other hand, Salvadoraceae and the Celastraceae have the following common characters: flowers greenish-white in cymes or racemes, tetramerous, bisexual or unisexual; sepals generally persistent; petals free but with a tendency to union; stamens as many as the petals, alternating with them and often with an associated disk and each loculus

of the ovary with one or two anatropous ovules with an inferior micropyle. Occurrence of polyembryony in several taxa of the Celastraceae (Davis, 1966) and *Salvadora* (Tiagi, 1954) further corroborates this affinity. Biochemical data by Gibbs (1958) suggest relationship of Salvadoraceae to the Aquifoliaceae. The latter family with its pendulous unitegmic ovules with a dorsal raphe, superior micropyle and minute embryo differs conspicuously from the Salvadoraceae. The placement of Salvadoraceae in the Celastrales near the Celastraceae appears, therefore, to rest on a sound footing.

Summary

The pedicel stele in *Salvadora* is a continuous ring of xylem surrounded by phloem; in *Azima*, it consists of a ring of collateral bundles. Bract and bracteoles in *Azima* are supplied with paired traces from a single gap. In *Salvadora*, bracteoles are wanting and the bracts are 1-traced. Sepals are 3-traced in *Salvadora oleoides* but 1-traced in *S. persica* and usually so in *Azima*. Petals and stamens are 1-traced. The two carpels are obliquely placed in this family and they are many traced. In *Salvadora*, the ovular bundle ends in the chalaza but in *Azima* it continues further into the outer integument. There is no adnation among the traces of the different floral cycles. Basal placentation in Salvadoraceae appears to be derived from a parietal condition. Sum total of evidence from floral structure and vasculature and embryology indicates that the Salvadoraceae belongs to the Celastrales.

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