ABSTRACT - (Morphology and floral anatomy of Struthanthus vulgaris Mart. (Loranthaceae). The flowers are imperfect and arranged in pairs of triads. Each flower is subtended by a bract; in the lateral flower of the triad the bract is inserted below the ovary and, in the central one, at the base of the pedicel. The floral organs arise in acropetal succession, that is, calyx, corolla, androecium and gynoecium. Along with the floral organs a collective ovule develops at the base of the ovary cavity. The vascular supply of the flower is based on a hexamerous plano. The corolla tube, androecium and gynoecium receive six bundles each, and these bundles remain undivided. The calyx is inconspicuous and devoid of any vascular supply, while the bract receives a single trace. The ovary is inferior and, probably, of receptacular origin. The noncarpellary tissue enclosing the gynoecium has nontypical amphicribal bundles which might be the result of the fusion of the ascendent bundles with the recurrent ones. Anomalous formations, resembling galls were also observed.

Key words: floral vascularization, Loranthaceae, Struthanthus.

Introduction

Studies on floral anatomy, especially those focused on vascularization, have long provided data for the resolution of taxonomic and evolutionary problems, in addition to those related to morphology.

With regard to the Loranthaceae, embryologists have made some observations about the floral anatomy of certain family members; however, it has not received due attention from morphologists. Among the various problems of morphology in this family, the nature of the calyx and the extracarpal wall are outstanding. The calyx is used by taxonomists as a character to separate the Loranthaceae from the Viscaceae, being present in the first and absent in the second family. Its nature has been the subject of controversy. It is considered as a calyx (Roxburg 1874, Haines 1924 and Danser 1931 apud Johri & Bhatnagar 1972, Narayana 1956, Kuijt 1969, Johri & Bhatnagar 1972), as an axial structure (Eichler 1878 apud Johri & Bhatnagar 1972, Engler & Krause 1935, Schaeppi & Steindl 1942), as a vestigial whorl of flower bracts suppressed from the lateral axis of the inflorescence (Rao 1963, Singh & Ratnakar 1974), and even as a “sui generis” organ (Maheshwary & Singh 1952). The nature of the extracarpellary wall has also been much discussed. According to some authors, the ovary is of receptacle origin (Smith & Smith 1942), but is considered appendicular by others (Narayana 1956, Rao 1963). Singh & Ratnakar (1974), however, are of the opinion that the vascular anatomy alone can not elucidate the infertile nature of the Loranthaceae. Struthanthus vulgaris Mart. is described by Eichler (1866/68) and by Rizzini (1968) as a bract. However, the authors do not refer to the position occupied by the bracts.
Through histological studies and the floral vascularization plan, the present work will seek to contribute to the elucidation of the aspects of external morphology mentioned above, which constitute controversial motifs.

Material and methods

The material of *Struthanthus vulgaris* Mart., used in this work, comes from Pereiras, SP, Brazil, from which exsicates are deposited in the Herbarium of the Department of Botany of the Institute of Biosciences of the University of São Paulo, under number SPF16078.

Floral buds, at stages of development close to the anthesis, were fixed at FAA 50% (Johansen 1940). Afterwards, they were dehydrated in alcoholic ethanol series and included in paraffin according to the usual anatomy techniques, and the serial sections 10-12 μm thick were stained with safranin (Sass 1951). Complementing this study, part of the flowers was diaphanized and stained with safranin, according to the technique indicated by Foster (1949).

Results

Morphology - The inflorescence is a compound dichasium. The flowers originate in triads that are arranged in pairs; each pair attaches to the leaf axil by a peduncle of variable length, which does not exceed 1.2 cm (Figures 1 and 2). The flower is actinomorphic and imperfect, possessing staminodia and a pistilodium (Figures 3 and 6). The bract is deciduous; in the lateral flowers of the triad is below the ovary and in the central flower at the base of the floral pedicel (Figures 4 to 7). The flower is hexameric. The calyx is inconspicuous (Figures 5 and 8); such structure persists in the fruit. The yellow-white corolla is constituted by petals fused at the base; in the open flower the petals are reflected with inflected apexes (Figures 5 and 8). In the buds, the petals remain attached to each other; it has been observed that this occurs because the epidermal cells of contiguous petals show to be intermingled. The flower has an inferior ovary, which is less developed in the staminate flower. The styles of both flowers are long, the stigmas are capitate and papillary (Figures 3 and 6). The style persists for some time after the corolla falls and its residence time is greater in the pistillate flower. The drop of the style is made thanks to a tissue of abscission; this one installs itself in the fruit, just below the base of the stylus. In the staminate flower the stamens are partially congruent with the elements of the corolla, and three of them are longer, and completely cover the stigma (Figures 6 and 8). In the pistillate flower, the six staminodia are also epipetalous, being arranged as in the staminate flower, but the difference in size between them is not so marked; in these flowers the anthers do not cover the stigma (Figures 3 and 5). In fertile stamens an undeveloped connective separates the two thecae, which exhibit longitudinal dehiscence. The two thecae present in the staminodes are separated by a more developed connective, which protrudes into the tip. The staminodes differ from the stamens on the insertion of the filaments on the anthers. In the first, the anther is basifixed and in the second, dorsifixed. The style is seated on a nectary in the shape of a six-lobed ring (Figures 3 and 6). The floral buds with fertile gynoecium can be easily recognized by being thinner and slightly smaller. This can be seen by comparing Figures 1 and 2.

On two occasions, among the staminate flowers, the presence of anomalous, gall-like buds was observed. These had a general increase in their volumes and their petals were more or less coriaceous and were largely concentrated with the filaments. The anthers were misshapen; the pollen sacs were present, however, their contents presented diverse alterations.
**Organogenesis** - The development of the two types of flowers, up to a certain stage, follow a single pattern. The following description refers to the lateral flowers of the triad, which present either the androecium (Figures 9-11), or the fertile gynoecium (Figures 12-14).

The floral primordium appears as a protuberance in the axil of a bract and the various floral elements appear in acropetal sequence. The bract develops faster and covers the young floral bud. The calyx, of the flower whorls, is the first to develop, on a small margin, above which originate the beginnings of the corolla and the androecium, which remain united from the beginning; the consequence of this fact is the epigynous condition. The gynoecium is the last to develop and this occurs as the androecium matures. In the early stages of development of the gynoecium there is formation of the locule, which is continuous with the style channel. This initially is ample but, with the development, becomes obliterated by the presence of the transmitting tissue. Simultaneously with the development of the floral parts, a conical projection can be distinguished at the base of the ovarian cavity, which corresponds to the collective ovule. At the base of this structure the pelvis is differentiated. The locus, which at the beginning is at the same level as the floral elements, starts to occupy a lower position as development takes place. Microspore stem cells and megaspore stem cells form in pistillate and staminate flowers, respectively.

**Vascularization** - The sequence described refers to a lateral flower of the triad, in the case of a pistillate flower. The vascularization of the flower derives from a ring formed by seven bundles, which are arranged in the pedicel of the flower. Of these, one irrigates the bract and the others go to the ovary (Figures 15-17). At the base of this structure, these bundles bifurcate so that the stellar ring is in this region composed of twelve bundles, six of which are more developed, alternating with six smaller ones. Two circles are formed above (Figures 18-21). The outer circle, formed by the larger bundles, represents the vascular supply traces for the perianth and androecium. The inner is formed by the smaller bundles, corresponding to the traces of dorsal carpellary bundles, which are directed, without branching, to the style, extending to the base of the stigma. In some cases one or more traces do not reach the described regions and, in cross-section, are then detected in the number of four or five (Figures 22-28). The bundles of the outer ring enter the portion formed by the fusion of the androecium and corolla. In this region each of these bundles forks; the external branch will vascularize the petals and the internal branch will vascularize staminodes (Figures 24-28). The calyx receives no vascular supply (Figures 23-25).

The vascularization of the central flower of the triad is the same as the lateral pattern (Figures 29-34). There is, however, a difference in the number of bundles present in the floral pedicel, in relation to the lateral flower. This difference is related to the position occupied by the bract, as already shown in the chapter referring to morphology. Thus, in the pedicel of the central flower, the trace that is destined to the bract is not present; the same is found below, being part of the vascular system of the peduncle of the triad.

The vascular anatomy was studied in the central flower of the triad, in the case of a staminate flower (Figure 35-48). The vascular tissue of the pedicel is represented by seven collateral vascular bundles, with the phloem facing the periphery of the organ (Figures 35 and 39). At the base of the ovary, these bundles are arranged in two circles. The outer is now made up of amphicribal bundles. In these, the phloem tissue is arranged in groups, around the xylem, or is located, preferably, in the lateral regions of the same and toward the center of the organ. The inner ring consists of collateral bundles, usually oriented (Figures 36 and 40). The bundles of the
inner ring are intended for the style, while those of the outer ring bifurcate (Figures 37 and 41, 38 and 42), giving rise to a collateral bundle that will irrigate the petal in its free portion and a partially amphicribral bundle, which will vascularize the filament (Figure 43 and 46, 44 and 47, 45 and 48). The ovary wall of the pistillate flower shows the same vascular structure as the staminate flower described, however, the filament is irrigated by a collateral bundle.

**Discussion**

The flowers of *Struthanthus vulgaris* are imperfect, however, in the staminates occurs the formation of mother cells of megasporocytes and in the pistils, of mother cells of microspores (Venturelli 1981). There is agreement with Rizzini (1952) regarding dioecy. A cross section through the pedicel of the lateral flower of the triad reveals that from the central vascular system leaves the trace that will constitute the bundle and vascularization of the bract. This bundle is located far from the central part at the apex of the pedicel, and this could indicate a pedicel-to-bundle contraction as described by Johri & Bhatnagar (1972) for the Loranthaceae. In the pedicel of the central flower, the tract of the bract is absent, being observed, however, in the peduncle of the triad; at apical levels of the peduncle, the trace moves away from the central vascular trunk; in this case, the bract is not fused to the floral pedicel. The fusion of the bract with the pedicel, in the lateral flowers of the dichasia of *S. vulgaris*, is a subject that may be of phylogenetic interest, which is why it would be advisable for future research to devote more attention to it. The observations made in the species under study are in disagreement with those of Eichler (1866/68), since that author mentions that in the lateral flowers of the triad of species belonging to section II of *Struthanthus*, bracteoles are at the apex of the pedicel and, in the central flower, at the base. Regarding *S. vulgaris*, Eichler states that he did not observe the bracteoles and bracts, but he mentions their occurrence based on the scars left by them. The same terminology is adopted by Rizzini (1968), although this author also does not refer to the position occupied by such structures.

The calyx of *S. vulgaris* is not vascularized, as is common among Loranthaceae. However, it is a true calyx, once it has been shown to be vascularized in *Nuytsia floribunda* (Labill.) R. Br. and *Atkinsonia ligustrina* (A. Cunn., Ex F. Muell.) F. Muell. (Garg 1958, Narayana 1958b), the latter, according to Prakash (1961), represents the link between the distinct vascular supply of *Nuytsia* and other members of Loranthaceae, where the calyx is devoid of vascular supply.

One problem that is studied in close relation with the vascularization of the gynoecium is the nature of the extracarpellar wall, in the ovary of epigynous flowers. With regard to Loranthaceae and Viscaceae, few data are found in the literature. Smith & Smith (1942) studied the floral anatomy of *Phoradendron villosum* Nutt. and *Arceuthobium americanum* Nutt. and concluded that the ovary was probably receptacular in nature. However, Singh & Rhatnakar (1974) analyzing *A. americanum* did not observe recurrent bundles, i.e. bundles with reverse orientation, referred by those authors and concluded, therefore, that it is not possible to consider such ovary as receptacular. With respect to the Loranthaceae, Narayana (1956), in describing the embryology of *Dendrophthoe neelgherrensis* (W. & A.) Van Tiegh, mentions that the ovary is appendicular and also cites that *Lysiana exocarpi* (Berth.) Van Tiegh. and *N. floribunda* present this same type of ovary, but the author does not refer to this subject again when describing the embryology of these two species (Narayana 1958 a, b).

The study of the floral anatomy of *S. vulgaris* showed that the extracarpellary wall of the ovary is vascularized by amphicribral bundles representing the vascular surface of the petals and
androecium, while the dorsal carpellary bundles that irrigate the gynoecium are normally oriented, with the phloem facing toward the periphery of the organ and the ventral are absent. Smith & Smith (1942) also refer to the occurrence of amphicribral bundles in the ovary of some Santalaceae and consider that they result of the phylogenetic fusion of the normally oriented upward receiving bundles with the inverted recurrent bundles and represent the vascular supply for the sepals and stamens. The presence of such bundles indicates, according to the aforementioned authors, the receptacular nature of the ovary. With respect to S. vulgaris, what has become known, as already mentioned above, was the occurrence of bundles identified as amphicribral, although they do not fit the known pattern, since the phloem is arranged in groups, sometimes around the entire bundle, now predominating in the region facing the center of the organ. The presence of this type of bundle, described for the first time for the Loranthaceae, and the confirmation of the deepening of the gynoecium during organogenesis, leads us to suppose that such ovary is of receptacular origin. However, a definite position can only be taken when other genera are studied in this respect.

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References


Figures 1-8. Floral morphology. 1-2. Inflorescences of pistillate and staminate flowers, respectively. 3. Flower pistil, showing one of the staminodes, whose filament is attached partially to the petal. 4. Triad of pistillate flowers, showing the position occupied by the bract of the central and lateral flowers. 5. Flower pistillode. 6. Staminate flower, showing one of the stamens, whose filament is partially fused to the petal. 7. Triad of staminate flowers. 8. Staminate flower (B - bract, C - calyx, N - nectary).
Figures 15-28. Vascularization. 15. Diagrammatic representation of the longitudinal section of a lateral flower of the triad, showing the path of the vascular bundles that supply the various floral whorls. The dotted central region represents the embryo sac: 16-28. Diagrammatic representation of successive cross sections through the pistilate bud, from the pedicel, showing the origin and the modifications suffered by the bundles that irrigate the floral whorls. The heights at which these sections were made are marked in Figure 15, by the numbers 16 to 28, respectively. (TB - dash for the bract, TCD - dorsal carpellary trace, TPA - dash for the perianth and androecium).
Figures 29-34. Vascularization. 29. Young triad of pistillate flowers, showing the position occupied by the bract of the central flower and the lateral flowers. 30-34. Diagrammatic representation of successive cross sections through a triad, from the peduncle. The bundle indicated with TBC, in figure 30, constitutes the trace that will form the bract bundle of the central flower; is from the peduncle of the triad (figure 30). The heights at which these cuts were made are marked in Figure 29, by the numbers 30 to 34, respectively.
Figures 35-48. Vascular anatomy. 39, 40, 41, 42, 46, 47, 48. Diagrammatic representation of cross-sections made from the pedicle of a staminate flower; 35, 36, 37, 38, 43, 44, 45. Details of the cross-sections shown in Figures 39, 40, 41, 42, 46, 47, 48, respectively. The changes undergone by the vascular bundles are visible along the way. Figure 35 shows the collateral bundle of the pedicel and in Fig. 36 there are visible bundles that will vascularize the perianth and androecium and, more internally, the dorsal carpels. (ESC - sclerenchyma, F - filament, FI - phloem, P - petal, X - xylem).