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A MONOGRAPH OF THE GENUS MALVASTRUM A. GRAY (MALVACEAE: MALVEAE)^{1,2}

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ABSTRACT

Malvastrum, a genus of yellow-flowered annual or perennial tropical and subtropical herbs in the Malvaceae, was described by Asa Gray in 1849 to include members of *Sida* and *Malva* that did not quite fit into those genera. During the next century the rather ill-defined genus became a repository for over 300 names. Subsequent monographic work brought about refinements in its circumscription that resulted in generic segregates and a core of so-called "true" *Malvastrums*. After morphological, karyological, phenological, and numerical analyses, the present study accepts seven sections, 14 species, six subspecies, and two varieties in *Malvastrum*.

The following contributions have been made: 1) the citation of all of the names published in *Malvastrum* together with their present placement and disposition of types; 2) an analysis of the geographic distribution of *Malvastrum* together with an hypothetical account of the origin and subsequent dispersal of the species; 3) a comparison of the morphology, chromosome numbers, limited hybridization data, and floral behavior within *Malvastrum* resulting in a proposal of infra- and intergeneric relationships; 4) the inclusion of a revised generic description and diagnostic key to the taxa; and 5) the inclusion of a detailed description, synonymy, and illustration for each taxon, several of which have never previously been illustrated.

The Malvaceae, placed within the order Malvales, is a moderately large family of flowering plants occurring throughout the tropical

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and temperate regions of the world but with its greatest diversity in the American tropics. Composed of more than 1500 species, the family is characterized by alternate and usually primarily palmately-veined leaves with well-developed but occasionally deciduous stipules, a superior ovary with generally three to ten or up to an indefinite number of carpels, an actinomorphic corolla with usually clawed asymmetric distinct petals united to the stamen tube, an androecium composed of monadelphous stamens with mostly unilocular anthers bearing echinate pollen, and by capsular, baccate, or schizocarpic fruits. The family is currently subdivided into five tribes: Gossypieae, Hibisceae, Decaschistieae, Malvavisceae, and Malveae, characterized by differences in the fruit type, the number of carpels, the degree of connation of the styles, the ratio of style to carpel number, the characteristics of the apical region of the stamen tube, and by the presence or absence of gossypol glands. Of these five tribes, the most species-rich and also one of the least understood is the tribe Malveae. This diverse tribe can be distinguished from the other four by the lack of apical teeth on the stamen tube, by its schizocarpic or pseudo-capsular fruits consisting of rarely one or two, usually three to many carpels, by the styles which are apically free at least one-fourth their length, by the ratio of one style per carpel, and by the lack of gossypol glands. Revisionary work within this tribe has been rapid in the last decade, increasing the number of its accepted genera from 53 (Bates, 1968) to the present total (1979) of 65.

The genus *Malvastrum* was described in 1849 by Asa Gray. His original intention was to segregate out certain members of *Sida* and *Malva* to leave those two genera more "natural" and clearly defined. The generic characters that he used to circumscribe *Malvastrum* were later found to encompass several otherwise dissimilar groups of species, and so *Malvastrum* became an artificial assemblage. During subsequent years over 300 names were published in *Malvastrum*. Major assemblages of related species have previously been removed into previously published genera or have been given generic status (particularly the genera *Acaulimalva* Krapovickas, *Anisodontea* Presl, *Malacothamnus* Greene, *Monteiroa* Krapovickas, *Nototriche* Turczaninow, *Tarasa* Philippi, and *Urocarpidium* Ulbrich). Revisions of these genera have left the remaining true *Malvastrums* without a complete treatment, and that has been the subject of the present study.

Taxonomic decisions have been based upon herbarium specimens examined at and loaned by the major domestic and foreign herbaria, upon examinations of locally cultivated individuals of most of the taxa, and upon field observations of the three *Malvastrum*s in Texas. During this examination, the morphological characters of the specimens were recorded and compared, karyological preparations were made, and the phenology of living individuals was studied. After the range of variation in the samples had been determined, a numerical analysis was undertaken to aid in constructing relationships among the taxa. The result has been to accept seven sections, 14 species, six subspecies, and two varieties in *Malvastrum*.

Taxonomic and nomenclatural order has been brought to the five most variable species or species-complexes. The exceedingly variable *Malvastrum bicuspidatum* in Mexico has been divided into four well-defined subspecies and one additional variety, the subspecies corresponding to major geologic subdivisions of that region. Evidence is presented that suggests that *Malvastrum corchorifolium* is an allopolyploid (octoploid) derivative of the tetraploids *M. americanum* and *M. coromandelianum*. The variable *M. tomentosum* in South America has been divided into two geographically and morphologically distinct subspecies. The variation in *M. americanum* in Australia is interpreted to have resulted from a long history in that region, and one distinctive new variety is included. Finally, *M. coromandelianum* has been divided into three subspecies that are morphologically, geographically, and phenologically isolated from one another.

As a result of this study, *Malvastrum* is now considered to be a small, clearly defined, mostly American genus with 14 species, and is considered to be isolated from all of the other genera in the tribe Malveae (Malvaceae) but with probable affinities with the larger *Abutilon* alliance.

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LITERATURE AND HISTORICAL SURVEY

Etymology

The name *Malvastrum* was derived from *Malva*, the generic name for the True Mallows and from the latin substantival suffix "-astrum" which indicates an incomplete resemblance, thus the frequently used common name of False Mallow for members of the genus.

Early treatments of *Malva*

The history of the taxa later transferred to the genus *Malvastrum* is inseparable from that of the genus *Malva* Linnaeus. Linnaeus (1753, p. 687-688) first ordered the members of the genus *Malva* into two informal but coherent assemblages based upon leaf shape, the first being "*Foliis indivisis" with three species and the second termed "*Foliis angulatis" containing the remaining twelve species. This arrangement, adequate for the few species known at the time, was subsequently followed with little change except for the addition of new species by Aiton (1789), Willdenow (1800, 1809), and by R. Brown (in Aiton, 1812).

Cavanilles in his extensive treatment of *Malva* (1786) placed all of the uniovulate species known to him in "Sectio II. Capsulae monospermae", further dividing this section into two subsections

based upon bracteole number: "I. Calyx exterior diphyllus" with six species and "II. Calyx exterior triphyllus" with 37 species. Within subsection II the taxa were placed into two groups according to bracteole shape, the first "A. Laciniae capillares aut angustissimae" with 13 species and a second "B. Laciniae ovatae, aut lanceolatae" with 24 species. Desrousseaux in Lamarck's *Encyclopédie* (1792) chose to follow Cavanilles' arrangement almost exactly, treating 12 "diphyllus" and 42 "triphyllus" species of *Malva* which included several new taxa. The 42 tribracteolate species were placed in two groups corresponding to those of Cavanilles based upon bracteole shape. There were no further innovations introduced beyond his many useful observations on the taxa.

Medicus (1787, p. 37-38) treated 11 species of *Malva* and divided them into two groups based upon the morphology of the mericarps ("Saamen-Kapseln"). The first six species listed by Medicus were said to possess notched and somewhat dehiscent mericarps, and the second five species were said to have stony-layered, indehiscent, and (presumably) unnotched mericarps. It is interesting to note that the first six species (*M. coromandelina* (sic), *M. gangetica*, *M. peruviana*, *M. limensis*, *M. capensis*, and *M. fragrans*) were all later transferred to *Malvastrum* while the latter five species (*M. sylvestris*, *M. veneta*, *M. mauritiana*, *M. verticillata*, and *M. crispa*) remain in the genus *Malva*. No formal status was given to the two groups at this time, however, and the usefulness of this character was largely ignored until again pointed out by Garcke (1857).

Link (1822, p. 209-211) grouped the 39 species of *Malva* known to him into two primary assemblages based upon flower color. His first informal group "A. Cor. flavis" with eight species corresponded in content to the grouping "*Foliis indivisis" used by Linnaeus and his followers, though relying on a different diagnostic character. The second grouping "B. Corollis rubris, albis miniatisve", with 31 species, was further subdivided into "a. Calyce exteriori triphyllor-separato" with 28 species, "b. Calyce exteriori diphyllor" with two species, and "Cal. exteriori triphyllor cum interiori connato" with a single species (*Malva anomala* Link & Otto). The lattermost division was an important innovation for it would later serve as one of the bases for Presl's genera *Anisodontea* and *Malveopsis* (Presl, 1845; Bates, 1969).

The section *Malvastrum* DC.

The epithet *Malvastrum* first appeared in the literature in De Candolle's treatment of the Malvaceae in his *Prodromus* (1824, p. 430) as the first of four sections of *Malva* and contained all of the then known species of *Malva* with the following characteristics: herbaceous or fruticose stems, 2-3-phyllous epicalyx, and monospermous unilocular carpels. The remaining three sections, *Maluchia* DC., *Sphaeroma* DC., and *Modiola* (Moench) DC., differed in one or more respects from these characters. The section *Malvastrum* DC. contained the majority of the 82 species of *Malva* listed by De Candolle, 67 in all, including the well-known European herbs (such as *Malva sylvestris* L., later the lectotype of *Malva* L.) and was subdivided into seven rather well-defined subsections. De Candolle treated all 43 of the taxa contained in Cavanilles' "Sectio II" within *Malva* section *Malvastrum* (with the exception of *M. angustifolia* Cav. which was placed in section III, *Sphaeroma*). Cavanilles' informal subsection I corresponded to De Candolle's formal subsection "3. *Bibracteolatae*" while his more inclusive subsection II was regrouped into the remaining six subsections proposed by De Candolle within the section *Malvastrum*.

The first subsection of the section *Malvastrum*, *Chrysanthae* DC., roughly corresponded to both the Linnaean grouping "*Foliis indivisis" and Link's grouping "A. Cor. flavis" as mentioned above, its diagnostic characters being a combination of undivided leaves and yellow axillary or spicate flowers. It was this subsection as well as the subsection *Capenses* DC. that contained species later treated as members of the genus *Malvastrum* A. Gray. It should be noted here that, in addition, De Candolle included within *Sida* Linnaeus section *Malvinda* (Medicus) DC. and in the "Species non satis notae" of *Sida* several taxa that would also be included within the genus *Malvastrum* at a later date.

The genus *Malvastrum* A. Gray

In 1849, the American botanist Asa Gray published the new generic name *Malvastrum* in a footnote on page 21 of his paper "Plantae Fendlerianae" with the comment (p. 15) that the name itself was borrowed from De Candolle's section bearing the same name. There has been some debate as to whether or not it was the intention of Gray to elevate De Candolle's section to generic rank

(Fryxell & Hill, 1977; Bates, 1978). It would seem, however, that this was not the case, as evidenced by Gray's own statement (p. 15) that the name was "no longer required now that the corresponding divisions are admitted genera". Gray actually proposed a new genus for which he used the De Candolle sectional name. Gray's stated purpose in proposing the new genus was to leave *Malva* and *Sida* more "natural" and clearly defined. Unfortunately, Gray stated that his "set of ambiguous, perhaps all American, species" were distinguished from *Malva* only by their capitate stigmas, and from *Sida* by their ascending ovule and inferior radicle, useful diagnostic characters, but ones shared by a great number of species that were certainly not congeneric. A summary of the characters used by Gray to circumscribe *Malvastrum* follows: American herbs, flowers axillary or in racemes, calyx with one to three caducous or three persistent bracteoles or these lacking, corolla reddish, orange-yellow, or golden-yellow, stamen tube simple, stigmas terminal and capitate, ovules peritropous-ascending, embryo semi-circular and with an inferior radicle, and carpels muticous or rostrate. Gray expressed particular confidence that his first informal section "Flores miniati" was a natural and essentially the typical one. He also indicated that numerous Andean species for which he did not propose new combinations belonged here. In the second section "Flores flavi" were enumerated only the North American species known to Gray. In fact, his comments on the South American yellow-flowered species indicated his uncertainty as to their proper disposition. His statement that more species were to be included as well as the rather poor circumscription of the genus later led to a large number of new combinations proposed by Gray and others resulting in a taxonomic miscellany of mostly unrelated plants.

The changing concept of *Malvastrum*

Clarification and a strict definition of *Malvastrum* was a gradual development. Walpers (1851) was the first European botanist to accept and treat the new genus and to adhere to Gray's two groupings based upon flower color, involucrel-composition, and mericarp characteristics, but only hesitantly transferred two more species into it. Gray himself greatly expanded the concept of *Malvastrum* in 1854 while treating specimens collected in South America by the United States Exploring Expedition. At this time he

made fourteen new combinations and described seven new species, including within the genus the annual blue-flowered malvas (now *Urocarpidium* Ulbrich and *Tarasa* Philippi), the acaulescent malvas (now *Acaulimalva* Krapovickas), and the phyllanthophorous malvas (now *Nototriche* Turczaninow). The latter group of species was placed in a formal new section of the genus, the section *Phyllanthophora* A. Gray ("*Malvastra phyllanthophora*"). This inclusive treatment allowed a more critical review of the infrequently collected and often overlooked South American taxa and clearly indicated that the yellow-flowered South American species were indeed to be considered members of *Malvastrum*. Nevertheless, it weakened the coherence of an already heterogeneous group.

In 1857, Garcke presented a detailed consideration of *Malvastrum* and *Malva* and reviewed the literature, treating every species with which he was familiar. This treatment was particularly important since there was the question among European botanists of the period as to the validity of *Malvastrum*, especially since it was delineated from *Malva* only by its capitate stigmas. Garcke also reviewed the validity of Presl's genera *Malveopsis* and *Anisodonteia*, which were also said to have capitate stigmas, and concluded that they were the same entity, yet not necessarily the same as *Malvastrum*. Garcke also noted that *Malvastrum coccineum* more nearly resembled members of the genus *Sphaeroma* (DC.) Schlectendal with respect to its mericarps and so should not be included in *Malvastrum*. Garcke's discussion continued with a review of treatments of *Malva* by De Candolle and by others, indicating which species belonged in *Malvastrum* but in most cases not making the proper combinations. His greatest contributions in this paper were his discussions of specimens now lost, his completeness in indicating synonyms, and his acceptance of Gray's intent in proposing *Malvastrum*.

The species of *Malva* growing at the Cape of Good Hope, treated by De Candolle as *Malva* L. section *Malvastrum* DC. subsection *Capenses* DC., were transferred with additions into *Malvastrum* by Gray and Harvey in Harvey and Sonder (1860). At that time, 18 species were accepted. This group of plants, which included Presl's concepts of *Malveopsis* and *Anisodonteia*, has been fully discussed by Bates (1969) in his revision of *Anisodonteia* Presl, in which work they were transferred to that genus. The inclusion in 1860 of these

South African species in *Malvastrum* continued to make it unwieldy and contributed towards its reputation as a repository for diverse elements.

The next significant change in the concept of *Malvastrum* appeared in Weddell's *Chloris Andina* (1861). In Weddell's *Conceptus* (p. 273) *Malva* was characterized by a usually bibracteolate or tribacteolate involucl with peduncles that were axillary or basally attached to the stem, while *Malvastrum* was said to possess exinvolucellate flowers with its peduncles more or less adnate to the petioles. Therefore, Weddell considered *Malvastrum* to be equivalent to Gray's section *Phyllanthophora* alone (all of the 17 species listed are now included in *Nototriche* Turczaninow). Among Weddell's eleven species of *Malva*, eight had been removed from *Malvastrum*, to which they had been transferred in 1854 by Gray. *Malva* as treated by Weddell contained species now referred to as *Tarasa*, *Urocarpidium*, and *Acaulimalva*. Neither a true *Malva* nor a true *Malvastrum* was included among the 28 species treated by Weddell.

In 1887, while preparing a Flora of North America, Gray again presented a discussion of *Malvastrum* in an attempt to distinguish it more clearly from *Sphaeralcea* A. St.-Hil. He concluded (p. 287-288) "to retain in *Malvastrum* the species with cell of the carpels conformed to the solitary ovule and seed, therefore with no empty terminal portion; and to refer to *Sphaeralcea* those with solitary or occasionally two ovules, which, when the upper ovule is either abortive or wanting, have the upper part, usually the whole upper half, of the mature carpel empty, and of a different texture from the lower [reticulate] part . . .". A treatment of the North American species of *Malvastrum* followed as a footnote to this discussion, and was later presented again and with additions and formal sectional names by Robinson (in Gray, 1897). For the first time, two annual species with elongated peduncles and rose petals, *M. rotundifolium* and *M. exile*, appeared grouped together as the section *Pedunculosa* Gray. The second group of six species in the 1897 treatment with short peduncles and yellow petals, the section *Sidoides* Gray, consisted of what are now treated as the true *Malvastrums*, while the third and last group of twelve species with short peduncles and scarlet, copper-color, or rose-color petals, the section *Sphaeralceoides* Gray, contained, as currently understood, members of both

the genus *Sphaeralcea* and the genus *Malacothamnus*. *Malvastrum leptophyllum* and *M. coccineum* were retained in *Malvastrum* in spite of Gray's own clarification of *Sphaeralcea*, perhaps because of a previous statement (Gray, 1849, p. 25) that *M. coccineum* was "one of the typical species".

Malvastrum received one of its most complete and important treatments in E. G. Baker's synopsis of the genera and species of the tribe Malveae (1890, 1891, 1894). In this summary a critical examination of all of the names and species then known in the tribe was undertaken, allowing for the first time since Garcke's 1857 paper an extensive appraisal of the species of *Malva* that actually belonged within Gray's concept of *Malvastrum*. In Baker's treatment, (1891, p. 164) *Malvastrum* was again a very inclusive genus characterized by: one to three distinct bracteoles or these absent, stigmas capitellate or clavate, carpels conforming to the seeds, without an empty apical portion. With the last character, Baker clearly followed Gray's final treatment in excluding *Sphaeralcea*. *Malvastrum* was treated in two groups, not given formal rank, the first of which, the "Capensia", corresponded to those species mentioned above that were treated by Gray and Harvey in 1860, and are now included within the South African genus *Anisodonteia* Presl (Bates, 1969). The second, the "Americana", contained 79 species and nine varieties along with their synonymy. Only eight of these names are still in *Malvastrum*, the others having been distributed primarily among ten other genera (*Acaulimalva*, *Eremalche* Greene, *Kearnemalvastrum* Bates, *Malacothamnus* Greene, *Modiolastrum* Schumann, *Monteiroa* Krapovickas, *Nototriche*, *Sphaeralcea*, *Tarasa*, and *Urocarpidium*) discussed in this literature review. As in Gray's 1887 treatment, the true *Malvastrums* were placed in a single group characterized by yellow petals and a peduncle that was short or absent. Although exceedingly useful as a synopsis, Baker's treatment did not contribute toward a more natural circumscription of the genus.

In the same year that the major portion of Baker's synopsis appeared, 1891, Kuntze resurrected the generic name *Malveopsis* Presl (1845) and treated it as an earlier name for *Malvastrum*, transferring 56 names from *Malvastrum* into that genus. In 1898 he transferred four more names into *Malveopsis* and described two new species. Kuntze's work disturbed several contemporary botanists such as Baker and Schumann (1890, 1891) who had recently

exerted great effort to bring taxonomic order and stability to the group. Rules concerning conservation and rejection of names were demanded at the international level, and as early as 1892 Ascherson published the first list of generic names proposed for conservation, in which *Malvastrum* A. Gray was proposed for conservation against *Malveopsis* Presl. This proposal was undoubtedly submitted by Schumann, who was on the commission responsible for the list. The proposal was acted upon favorably by the International Botanical Congress at Vienna in 1905 (Wettstein et al., 1906) and was included in all subsequent editions of the Code. However, as Bates has pointed out (1969, p. 231), since the name *Malveopsis* applied to a South African genus not congeneric with *Malvastrum*, the proposal for conservation need never have been advanced.

Generic segregates

The process of removing related species-groups from *Malvastrum* as coherent genera, begun to a limited extent by Gray in treating *Sphaeralcea*, soon gained impetus after the synopses of Baker (1890, 1891, 1894) and Robinson (in Gray, 1897) appeared. Greene (1906, p. 208) segregated two groups of species from *Malvastrum* as the new genera *Eremalche* and *Malacothamnus*.

Eremalche Greene consisted of two desert annual species of the Southwestern United States treated as the section *Pedunculosa* A. Gray by Robinson (*Malvastrum rotundifolium* and *M. exile*) and also included the more recently described *M. parryi* Greene. This is a coherent group of species but its generic status was not accepted for many years. In 1936 Jepson referred the species to *Sphaeralcea* (for reasons to be detailed below), and Kearney (1951b) treated the genus as *Malvastrum* section *Eremalche* (Greene) Kearney. However, its generic integrity was accepted by Abrams (1951) and subsequently by Kearney (1955, 1956), as the significance of chromosomal evidence was realized (for *Eremalche*, $n = 10, 20$) and as other generic segregates were defined.

The proposed segregate genus *Malacothamnus* Greene (1906) consisting of the shrubby Californian species did not gain acceptance for many years. Prior to 1906, the eleven species were distinguished from the other *Malvastrums* by their shrubby habit, their canescent or tomentose foliage (thus the name meaning "soft-shrub"), and their suborbicular, thin-walled, and completely dehiscent two-valved mature carpels, but the group was not given any

formal status (Robinson in Gray, 1897). Greene's useful but brief treatment was not widely circulated and did not gain acceptance at first as a result of Gray's and Robinson's pervasive influence, except that Abrams (1910) at least temporarily accepted the genus without comment. The first exhaustive treatment of the shrubby Californian *Malvastrums* by Estes (1925) did not accept *Malacothamnus*, nor did the later more comprehensive treatments by Eastwood (1936) and McMinn (1939). Jepson (1936) transferred all of the species to *Sphaeralcea* (for reasons detailed below). Kearney (1951a), while preparing his review of the American Malvaceae, revived Greene's genus, recognized 21 species and six varieties, and designated *Malva fasciculata* Nuttall as the lectotype species. A haploid chromosome number of $n = 17$ was established for the genus (Webber, 1936). Kearney's treatment stands essentially unchanged today. An unpublished treatment was prepared by Bates (1963), who accumulated data that led him to conclude that several species within *Malacothamnus* should be given subspecific status.

Another important treatment that also helped to clarify the circumscription of *Malvastrum* was that of A. W. Hill (1906, 1909b) who resurrected, amended, and revised the nearly forgotten genus *Nototriche* Turczaninow (1863). Hill's intent was to raise Gray's section *Phyllanthophora*, containing the exinvolucellate Andean species of *Malvastrum* with pedicels and petioles adnate, to generic status. The generic name *Nototriche* Turcz. was available, having been applied to several members of this group previously described as species of *Malvastrum*. About 35 names previously under *Malvastrum* were thereby removed.

In addition, Hill (1909a, p. 218) treated the involuclate acaulescent Andean species of *Malvastrum* as the new section *Acaules* A. W. Hill. The name "acaules" may have been borrowed from Weddell's (1861) informal group within *Malva* under that name, also utilized by Triana and Planchon (1862). The section *Acaules* A. W. Hill was later the basis for the new genus *Acaulimalva* described by Krapovickas (1974a), a genus presently considered to contain 19 Andean species distinguished from *Malvastrum* not only by a series of morphological characters, but also by its different base chromosome number, $x = 5$.

As part of a series of studies on the Rocky Mountain flora, Rydberg (1913) again raised the problem of the status of *Sphaeralcea*. His decision was to merge *Malvastrum* within *Sphaeralcea*

since he felt that the type of the genus must be "the first given binomial under *Malvastrum*, which is *M. coccineum*" (p. 57). His interpretation of *M. coccineum* as a *Sphaeralcea* was correct, but his arbitrary selection of Gray's first species was inappropriate and also violated Article 8 of the Code (Stafleu et al., 1972) in not following Schumann's original choice of lectotype (1890, p. 41). The choice of *M. coccineum* as the lectotype would also necessitate a new name for the yellow-flowered species presently treated as *Malvastrum*. Although Rydberg's lectotype was unofficially published in several editions of the Code in its appended list of conserved genera, the choice was never formally adopted. Instead, Schumann's choice of *Malvastrum wrightii* A. Gray as lectotype has now been formally accepted by the Committee for Spermatophyta (Taxon 27: 545, 1978). Nevertheless, Rydberg's proposal encouraged numerous transfers of *Malvastrum* species into *Sphaeralcea* (Arthur, 1921, Jepson, 1925, 1936; Metz, 1934). Kearney (1935) clarified the true *Sphaeralceas* and included still another discussion on the relationships of *Sphaeralcea* and *Malvastrum*. He pointed out for the first time in a footnote (p. 5) and in the text (p. 16) that the *Sphaeralceas* differed from *Malvastrum* in their basic chromosome number of $x = 5$, a fact later elaborated on by Webber (1936).

Krapovickas (1945), while studying the South American Malvaceae, reviewed the small genus *Modiolastrum*, proposed by Schumann (in Martius, 1891, p. 276). This genus, clearly distinguished from *Malvastrum* by its procumbent habit, its palmately-parted leaves, usually rose-colored flowers, and by the transversely two-chambered mericarps, nevertheless had two names residing in *Malvastrum*, which were removed. Furthermore, Krapovickas (1951) segregated three more species from *Malvastrum* into a new genus, *Monteiroa*, and included two additional new species. He based the separation on the ventrally and apically dehiscent mericarps, the cymose inflorescences, and a different base chromosome number, $x = 10$. In addition, the chromosomes were seen to be much larger than those of *Malvastrum*, and the flowers were shades of rose rather than yellow.

Continuing his studies of *Malvastrum* and related genera, Krapovickas revised the major portions of the genera *Tarasa* Philippi and *Urocarpidium* Ulbrich. These genera had been accepted since their first publication as being allied to *Malvastrum*, but neither had been comprehensively surveyed until this time. *Tarasa* was distinguished

from *Malvastrum* by its auriculate lilac or blue petals, mostly cymose inflorescences, dehiscent mericarps bearing two apical plumose or pilose cusps, and by its basic chromosome number $x = 5$ (Krapovickas, 1954a). Krapovickas accepted 24 species in *Tarasa*, shifting 20 names from *Malvastrum* to 14 of the species of *Tarasa*. In his study of the genus *Urocarpidium* Ulbrich, Krapovickas (1954b) described the new section *Anurum* containing ten species, a section equivalent to *Malvastrum* section *Peruviana* Kearney (1951b). In doing so, he distinguished *Urocarpidium* from *Malvastrum* by its irregularly rugose mericarps, its cymose (concinuate) inflorescences, annual herbaceous habit, often lobed leaves, lilac to rose flowers, and by its chromosome number of $n = 10, 15$. In this treatment 11 more names were transferred from *Malvastrum* into seven of the species of *Urocarpidium*.

Malvastrum was redefined by Kearney in 1955 (p. 239), taking into account the new information. His definition follows: "the genus comprises only perennial, often somewhat woody species of tropical and subtropical America having a persistent, triphyllous involucre, yellow corollas, and nearly indehiscent dorsally smooth, laterally smooth or rugose carpels." The chromosomal integrity, $n = 6, 12, 18$, was also indicated and 12 species were enumerated, nine of which are presently maintained exactly as cited.

A particularly useful treatment of the five Argentinian species of *Malvastrum* section *Malvastrum* as circumscribed by Kearney was presented by Krapovickas (1975b). In addition a list of 38 excluded species was appended, which was the model for Appendix III in the present work.

Ten years later, Bates added two important studies to the still changing genus *Malvastrum*. In segregating the genus *Kearnemalvastrum*, Bates (1967c) removed two species and seven names from *Malvastrum*, noting that Kearney's revised circumscription could no longer encompass these entities. *Kearnemalvastrum* became a small but coherent genus characterized by white flowers, by black glabrous (or nearly so) unarmed mericarps, and by a chromosome number $n = 16$. His discussion of the two genera clearly indicated a lack of any close relationship between the two.

In contrast to the general trend to segregate species from *Malvastrum*, Bates (1967a) merged the monotypic *Sidopsis hispida* (Pursh) Rydb. back into it. He provided a reasonable argument for doing so (which is accepted in the present treatment) although by

doing so he somewhat extended the generic limits of *Malvastrum*. A redefinition was again provided, this being the most complete description of the genus to that time (Bates, 1967a, p. 16–17).

Since 1967 the two important treatments concerning *Acaulimalva* Krapovickas (1974a) and *Anisodonteia* (Bates, 1969) referred to above have appeared. The publication of these two treatments left the remaining true *Malvastrum*s without a complete treatment. The present monograph is intended to fill this gap.

Table 1 summarizes Appendix III in the number of validly published binomials that have been removed from consideration in *Malvastrum* and transferred to genera listed in the left-hand column. Several minor transfers to genera not discussed above have been added for completeness. The reference in which the majority of transfers or new combinations were made is listed in the right-hand column. Appendix III lists all of the names both included and excluded from *Malvastrum* and their current taxonomic placement.

The historical survey presented above has demonstrated that the concept of *Malvastrum* has changed considerably since Gray's original intention to clarify *Sida* and *Malva*. The conception of the genus has changed from a repository for nearly every involuclate

Table 1. Nomenclatural changes in *Malvastrum*

Genus	Binomials removed from <i>Malvastrum</i>	Primary Reference
<i>Acaulimalva</i> Krap.	23	Krapovickas, 1974a
<i>Anisodonteia</i> Presl	26	Bates, 1969
<i>Eremalche</i> Greene	4	Greene, 1906
<i>Kearnemalvastrum</i> Bates	7	Bates, 1967c
<i>Lecanophora</i> Speg.	1	Spegazzini, 1926
<i>Malacothamnus</i> Greene	33	Kearney, 1951a
<i>Malvella</i> Jaub. & Spach	1	Krapovickas, 1970
<i>Melochia</i> L.	1	Krapovickas, pers. com.
<i>Modiolastrum</i> K. Schum.	7	Krapovickas, 1945
<i>Monteiroa</i> Krap.	4	Krapovickas, 1951
<i>Nototriche</i> Turcz.	33	Hill, 1909b
<i>Palaua</i> Cav.	1	Kearney, 1952
<i>Phymosia</i> Desv. ex Ham.	1	Kearney, 1949
<i>Sida</i> L.	2	Gray, 1862
<i>Sphaeralcea</i> St.-Hil.	24	Kearney, 1935
<i>Tarasa</i> Phil.	24	Krapovickas, 1954a
<i>Urocarpidium</i> Ulbr.	10	Krapovickas, 1954b
	Total	202

uniovulate mallow with capitate stigmas, to its present status as a small, clearly delimited, mostly American genus of only 14 species.

DISTRIBUTION AND HABITAT

Contemporary distribution

Members of the genus *Malvastrum* are found primarily in the New World in tropical, subtropical, and warm temperate latitudes between 35°N and 35°S (Fig. 1). The single exception is *M. hispidum*, found between 41°N and 34°N latitudes in the central United States. With the exception of *M. hispidum*, the species are restricted to regions lacking a prolonged period (over three months) of temperature below 0°C and, in fact, most of the species are sensitive to even a brief exposure to this temperature.

Although usually encountered at 0–500 meters elevation at the northern and southern extremes of its range, *Malvastrum* may be found at increasing altitudes of up to 2600–2700 meters towards the equator. *Malvastrum interruptum* and *M. spiciflorum* reach the uppermost altitude limits for the genus. Several species are restricted to the slopes of Central and South American highlands or ranges of moderate elevation (500–2500 m), namely *M. bicuspidatum* (in part), *M. guatemalense*, *M. scoparioides*, and *M. tomentosum* subsp. *pautense*. The three species that have been introduced into tropical and subtropical regions of the Old World, *M. americanum*, *M. corchorifolium*, and *M. coromandelianum*, are most frequently found in coastal regions at low elevations. Subsequent expansion in lands with extensive human or animal disturbance (such as India) has been extensive.

A species considered to be both indigenous in and endemic to the Old World, *Malvastrum chillagoense*, occurs in a small area of limestone outcrops at an altitude of 300–400 meters in northern Queensland, Australia. This disjunct distribution remains an enigmatic phytogeographical feature of the genus, along with the distributions of *M. hispidum*, *M. aurantiacum*, *M. americanum* var. *stellatum*, and some Australian populations of *M. americanum* var. *americanum*.

One of the greatest concentrations of *Malvastrum* species occurs in a region consisting of northern and northwestern Argentina, southeastern Bolivia, and Paraguay, where half (seven) of the species are to be found. A second area of concentration of species is

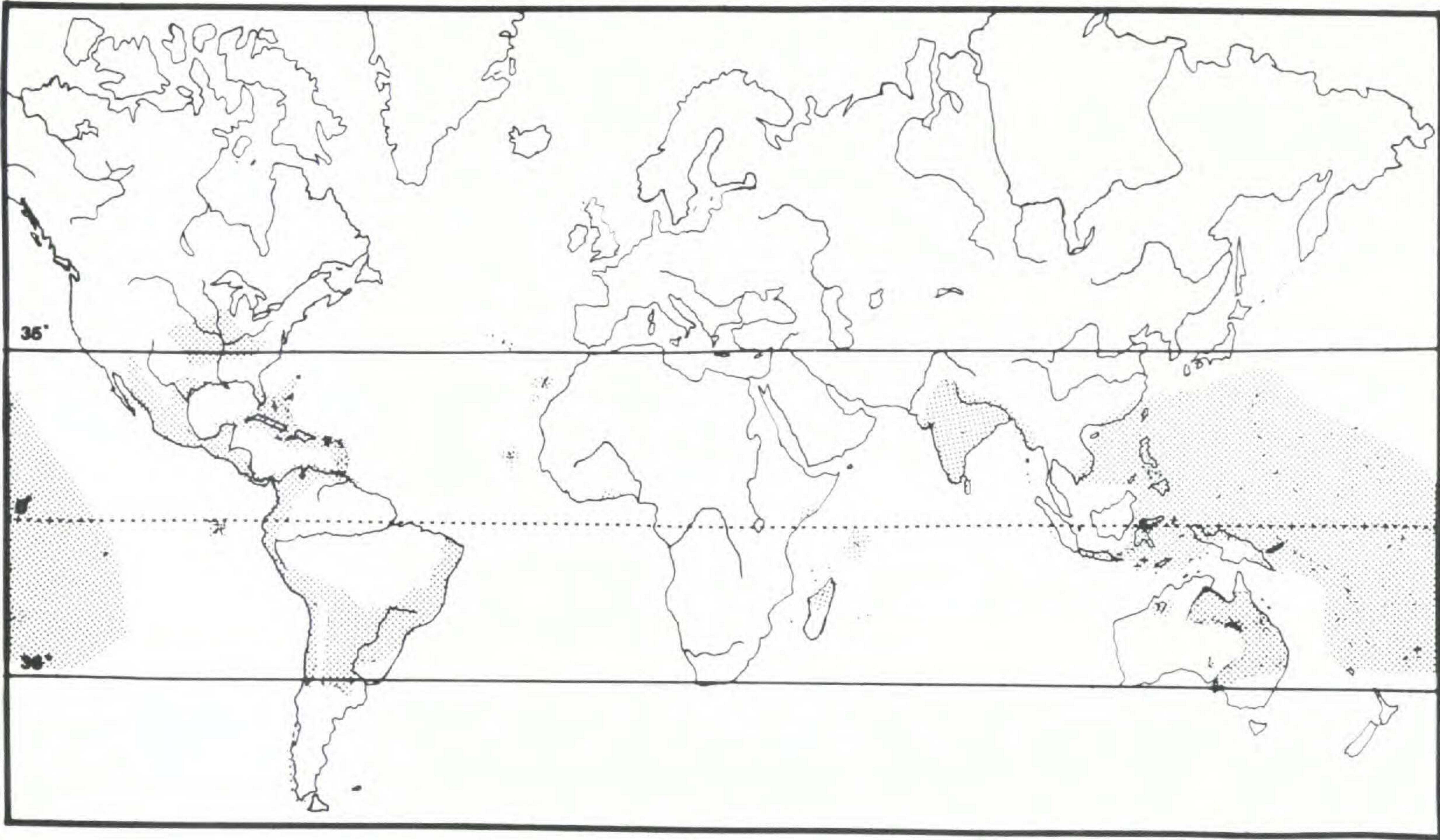


Figure 1. Distribution of *Malvastrum*.

in a larger region extending from northwestern and coastal Peru and coastal Ecuador northward into central Mexico where, again, seven of the species occur. Of the 14 species, all but five (*M. americanum*, *M. bicuspidatum*, *M. corchorifolium*, *M. coromandelianum*, and *M. tomentosum*) have rather restricted ranges, but only three (*M. chillagoense*, *M. grandiflorum*, *M. guatemalense*) are here considered to be narrowly distributed endemics. A summary of the taxa and the political regions in which they occur is presented as Appendix I.

Habitat

Although data are not available on every taxon, several species occur in calcareous or alkaline soils varying in texture from loose rock or gravel to fine clay. Populations of the most obvious calciphiles (*Malvastrum chillagoense*, *M. corchorifolium*, and *M. hispidum*) are best developed and usually restricted to the immediate vicinity of limestone outcrops and their associated thin rocky soils. The preference shown by *M. corchorifolium* for disturbed calcareous gravels and clays is seen in its frequency on the coastal limestones of southern Florida, the Caribbean islands, and the Yucatan. Bates (1967a) has noted in his study of *M. hispidum* that its populations were frequently restricted to a few square meters in the vicinity of limestone outcrops. Herbarium notes for *M. chillagoense*, and to a lesser extent *M. tomentosum* (in Paraguay and southwestern Brazil), also indicate a restriction to limestone outcrops. My own observations on the three species occurring in Texas (*M. americanum*, *M. aurantiacum*, and *M. coromandelianum*) indicate that the largest populations appear on the alkaline clays and loams of river bottoms and in the agricultural lands bordering those sites, as well as on the calcareous (caliche) soils of low hills, clay pits, road fill, and residential sites.

Other species in the genus do not seem to have such an obvious preference for limestone and may occur in volcanic or granitic soils. This seems to be particularly true of *M. bicuspidatum*, *M. guatemalense*, and *M. tomentosum* (in Ecuador and Peru), which are not infrequently found in the unstable volcanic zones of Central and South America. A knowledge of the pH requirements of each species, beyond the scope of this study, might further aid in understanding the more subtle points of their distribution patterns.

The adaptation of *M. americanum* and *M. coromandelianum* to the disturbed soils of lowlands and river valleys has apparently allowed them to invade successfully and colonize areas of human environmental disturbance, resulting ultimately in their present wide distributions.

Water requirements and tolerances vary considerably among the species. *Malvastrum aurantiacum* represents one extreme, as it most frequently occurs in wet clay or in periodically marshy areas in full sun along rivers and streams. These poorly drained and often slightly saline flats, while occasionally flooded, are usually dry in the summer to a parched, rock-hard condition. *Malvastrum aurantiacum* is able to survive the periodic semi-aridity by storing water as mucilaginous sap in its elongated and somewhat enlarged taproot and becomes dormant at that season. *Malvastrum americanum* also grows well in an abundance of moisture and may be found in rainforest clearings, slopes, dooryards, and roadsides in areas of heavy rainfall but, in contrast to *M. aurantiacum*, it requires a well-drained soil. *Malvastrum corchorifolium* and *M. hispidum* are quite sensitive to an over-abundance of water. In greenhouse culture these two species are easily attacked by fungi and will not flower when given the same amount of water as *M. americanum* but will produce flowers when the water amount is reduced and the soil is allowed to dry. The remaining species cultured all show their best growth when moderate amounts of water and well-drained soils are provided.

Hypothetical geographical origin and dispersal

The interpretation of the origin and subsequent dispersal of *Malvastrum* is not aided by the fossil record. Even today, none of the species are frequent in areas of sedimentation. On the contrary, many are found on mesic to semi-xeric slopes or outcrops, or in disturbed land where preservation is highly unlikely. A leaf impression discovered in Oligocene ash deposits at Florissant, Colorado, was named *Malvastrum exhumatum* by Cockerell (1906), but an examination of the photograph and description indicates that this is the leaf fragment of a *Sphaeralcea* (see Appendix III).

In reconstructing the geographical history of the genus, I have considered: 1) the present distribution of clearly indigenous or endemic species; 2) the geologic history of the region thought to be its area of origin; 3) the relative number of specialized and

unspecialized characters shown by taxa; and 4) examples of other genera with similar distributions, ecology, and dispersal mechanisms.

Of the 14 accepted species, six are endemic to South America and two more have their greatest frequency and diversity there (*Malvastrum americanum*, *M. coromandelianum*). Of the remaining six not found in South America, one is of probable hybrid origin (*M. corchorifolium*), two are clearly derived from South American members of the section *Tomentosum* (*M. cuspidatum*, *M. guatemalense*), and three (*M. aurantiacum*, *M. chillagoense*, *M. hispidum*) will be treated individually as phytogeographic problems. With respect to the primary generic distribution pattern, however, a proposal indicating South America as the ancestral home for *Malvastrum* seems reasonable.

Among the major geologically stable regions known in South America are three pre-Cambrian shields (Guyana shield, Central Brazilian shield, East Brazilian shield) and several massifs (Pampean Ranges, Patagonian, Deseado) (Haffer, 1974). *Malvastrum* is most diverse on the Pampean Ranges massif, the region consisting of the subtropical and warm temperate chaco and Paraná basin as well as the comparatively low eastern foothill ranges of northwestern Argentina and Bolivia. This diversity of habitats supports the greatest number of species (seven) in the smallest area for the genus as a whole. Based upon this contemporary distribution and known geologic changes in South America, one can be confident that the genus has had a long history in that region. It is not a component of the Guyana shield nor Amazonian basin floras but, instead, it is a component of the highland arc that is nearly continuous in either direction from the pampean ranges around the Amazon basin (Fig. 1).

If one follows the assumption that the present center of diversity for a genus indicates not only its long history but also its center of origin (Willis, 1922, 1949) then this Pampean region would be that area for *Malvastrum*. However, such a diversity center may also simply reflect the geologic stability of this region as compared to the instability of other areas of South America, thus allowing the persistence of the species. This would be the 'museum hypothesis' of Stebbins (1974, p. 166). The third hypothesis would be that the area of greatest diversity indicates a region of secondary speciation. For

this last hypothesis to be reasonable, one must demonstrate that all of the species involved are closely related.

One can examine the characteristics of the taxa inhabiting the possible area of origin to evaluate the hypotheses. The process of secondary radiation or speciation does seem to explain subspeciation in *M. bicuspidatum* in Central America, but this same subspeciation cannot be demonstrated in the pampean region. Instead, in this region are found several of the most distinctive and divergent species of the genus. One of these, *M. spiciflorum*, is the only diploid extant ($n = 6$) and has scarcely modified mericarps, autogamous flowers, and other unique features (cf. Appendix II). This diploid shares its range with the tetraploid *M. grandiflorum* ($n = 12$) which has elaborately ridged, winged, and cuspidate mericarps, and entomophilous flowers that are self-sterile. Also present and overlapping in range is the hexaploid *M. interruptum* ($n = 18$). Furthermore, *M. coromandelianum* and *M. americanum* have less weedy and somewhat restricted morphotypes here (some given formal rank) that do not occur where the more widespread pantropical forms live, suggesting a long history for those species in this region.

To understand better the history of *Malvastrum* in the context of geologic change it is important to present a brief overview of these events in South America (Haffer, 1974; Vuilleumier, 1971).

Proponents of plate tectonics have supplied data indicating that until the late Cretaceous portions of northeastern South America and western Africa remained in close proximity while the southern portions of the two continents had separated much earlier. While the new continent sloped gently westward into the Andean geosyncline upon separation from Africa, there was a subsequent pronounced emergence of the Brazilian shields and a gentle subsidence of the middle Amazon basin during the late Cretaceous that continued into the Tertiary. The lack of indigenous *Malvastrums* or even close relatives in western Africa or on the ancient Guyana and Brazilian shields suggests that the genus appeared in more recent times.

According to McLean and Iveney-Cook (1967), during the Eocene the flora of latitude 38° S in central Argentina (in the vicinity of the present *Malvastrum* diversity center) was fully tropical, while 4° farther south at latitude 42° S the surface was probably covered

by a subtropical woodland with surrounding pampas, a vegetation type more suitable for the genus. Cooling occurred during the Oligocene, and by the Miocene temperate elements of the Antarctic-Tertiary flora replaced the tropical floras of southern Chile and Argentina, indicating northward migration. The climate in northwestern South America was probably more humid than during the early Tertiary and permitted the existence of luxuriant plant life, as documented by thin coal seams in Miocene deposits there. This humid flora would have been generally unsuitable for *Malvastrums*. It would seem, then, that by the Miocene the genus or its ancestors could have been centered in the pampean ranges.

From the mid-Tertiary onward, open savannas, patches of rain forest, and vast mud flats probably were found in the eastern foothill belt of the present Andes, while the upper part of the Amazon valley was filled by a large inland sea. The central and southern Andes were still low-lying islands and permitted the strong drying influence of the Humboldt Current to reach far inland to the east. This correlated with an expanse of semi-xeric vegetation for which such taxa as *Malvastrum tomentosum* would have been well-suited.

In the late Pliocene a continuous land-bridge was finally formed as the Central American system became continuous with the Andean system. Not until the continuous land connection formed did major faunal and floral exchange of northern and southern forms take place. Since the Andes were much lower at that time, and since dense forests were by then limited by the aridity of the epoch, various north-south invasion routes allowed migration through northwestern Colombia, more than at any other period prior to the final uplift of the Andes and prior to the expansion of the tropical lowland forests. Since most *Malvastrums* have fur-attachment mechanisms, this would have been the most significant period in its dispersal.

The events of the Pleistocene epoch brought about present topography and distribution patterns. First, the main uplift of the Andes during the late Pliocene and early Pleistocene led to extensive eastern rains and the expansion of humid forests onto the emerging Amazon basin. Second, the uplift must have forced a rapid adaptation, evolution, or extinction of species inhabiting the elevating Andean belt. Third, the periods of mountain building eventually led to climatic deterioration and temperature decrease during the cold

periods of the Pleistocene (Barghoorn, 1964) that would have forced migration. During the peak phases of glaciation, rainfall decreased and strong arid conditions again prevailed in many regions, restricting humid forests to refugia. During warm phases the humid forests expanded. Damuth and Fairbridge (1970) have traced the westerly air flow against the southern and central Andes that during peak glaciations led to extensive cool deserts east of the mountains.

While glacial climates lowered both the snowline and timberline in the high plateau of southern Peru, western Bolivia, and northwestern Argentina, there is no evidence of radical climatic changes in the eastern pampean foothills that would have decimated the flora. In addition, there were no barriers to migration in that area to warmer regions of the north or east except, perhaps, for the occasionally submerged Paraná basin. Since the last glaciation (ca. 15,000 yrs b.p.) humid forests have again expanded and recolonized the basins, leaving isolated remnants of the formerly widespread semi-arid woodlands and savannas on the highlands and sands surrounding the Amazon.

My hypothesis is, then, that *Malvastrum* first appeared and diversified in the diverse habitats of the pampean massif and the mesic to semi-xeric regions that were apparently continuous in a western coastal band reaching from this region north to Colombia and Venezuela and east to the Brazilian coastal highlands before the Andes orogeny. The submerged Paraná basin may have isolated the genus from the eastern Brazilian shield in its earliest phases. As the Andes arose, *Malvastrum* populations were probably able to persist and migrate along lower elevations until aridity and cold exterminated them. The present discontinuous distribution of *M. tomentosum* (Fig. 37) would appear to be evidence of a greater range during the periodic xeric phases of the Pleistocene or earlier. The formation of the Central American landbridge in the Pliocene resulted in the transport of those species adapted to mammalian transport out of South America and, in at least the section *Tomentosum*, secondary speciation in the new environment. The several species in the Argentinian-Bolivian foothills that were not adapted for animal transport or that could not migrate along xeric lowlands remained in their general area of origin. The result was a southern center of diversity and a northern center of lesser diversity separated by a vast inhospitable Andean and rainforest terrain. The final event in *Malvastrum* dispersal occurred in man's accidental

transport of the clinging seeds to areas of the Old World tropics.

Malvastrum is only one of several genera of the Malvaceae with similar distributions. For example, *Tarasa*, found in northwestern Argentina north and west to Chile, Bolivia, and Peru, has a disjunct distribution in Mexico. Members of that genus have colonized higher elevations in the Andes than *Malvastrum* and this correlates with changes in ploidal level (Krapovickas, 1960). *Sphaeralcea* is a genus with semixerophytic tendencies with its center of distribution in western South America and then again in northern Mexico and western North America. *Urocarpidum* also has a very similar distribution, occurring from northwestern Argentina, Bolivia, and Chile in the south, northwards nearly continuously to Colombia and Venezuela along the Andes and again in Mexico at high elevations. The species, like *Tarasa*, are better adapted to high elevations and cold than *Malvastrum*, occurring up to 3800 m in the southern latitudes and as far south in Chile as 30° S latitude. The distribution of the American species of *Cienfuegosia* is also remarkably similar to that of *Malvastrum* (Fryxell, 1969). Several of its species are found in the Pampean ranges and Chaco region as well as in the Paraná basin. The distribution of *C. argentina* closely matches those of *M. amblyphyllum*, *M. interruptum*, and *M. spiciflorum*; that of *C. tripartita* matches that of *M. tomentosum* in western South America. In general, the ranges of the two genera coincide except that some species of *Cienfuegosia* are more frequent in the Planalto of south-central Brazil and at least one (*C. affinis*) is present in the Guyana highlands. *Cienfuegosia* seems to be a much older genus than *Malvastrum*, as one subgenus is also indigenous in Africa, its distribution providing some evidence for the former connection and proximity of the two continents. Other genera in other families also show the pattern of distribution shown by *Malvastrum*; some of these distributions are summarized by Rzedowski (1978, Chapter 6) and Raven (1963).

Long distance dispersal

There remain three species in their entirety (*Malvastrum aurantiacum*, *M. chillagoense*, and *M. hispidum*) and two species in part (certain forms of *M. americanum* var. *americanum* in Australia, *M. americanum* var. *stellatum*, and *M. coromandelianum* in Texas and northern Mexico) that may have been distributed by means of long distance dispersal. Long distance dispersal by birds has often been

proposed for such disjuncts. Sound evidence that this may actually occur has been presented by Cruden (1966) and Proctor (1968). Raven (1963) summarized the known and suspected amphitropical disjuncts and presented several important observations summarized here: 1) the plant communities involved are relatively recent in origin; 2) the amphitropical disjuncts are plants that occur in open or weedy habitats such as seasonally moist places where establishment would be relatively easy; 3) nearly all of the plants are autogamous or self-compatible; and 4) many of the disjunct patterns correspond with the migration routes of birds, which must occasionally carry seeds between one hemisphere and the other.

Most populations of *Malvastrum coromandelianum* subsp. *coromandelianum* in Texas and northern Mexico are morphologically very similar to those of the lowlands of Paraguay and northeastern Argentina, particularly with regard to their ascending stems and the appressed 4-rayed bilateral rather than simple hairs on the upper leaf surfaces. These two disjunct populations in their natural state occupy similar environments, i.e., typically low, periodically wet, loamy or clay areas along river floodplains, from which they may spread to other disturbed areas. Since the Texas and northeastern Mexico populations differ from those of southern Mexico and the Caribbean but yet resemble again those of the South American Paraná basin, I feel that they represent a separate introduction. Applying Raven's principles to *M. coromandelianum* subsp. *coromandelianum* in Texas: 1) the populations occur in the coastal plain and central and southern river systems of Texas and northern Mexico east of the Edwards plateau, an area mostly under water during the late Tertiary and so floristically rather young; 2) the populations occur in disturbed river bottoms and seasonally wet areas; 3) greenhouse observations have shown that the Texas (and all other) populations are autogamous; and 4) the disjunction corresponds with the western branch of the Mississippi flyway. A proposed fifth principle is that the disjuncts often have smaller flowers than those of the source population. An alternative explanation for the occurrence of the Texas population with Paraná basin affinities would be through human introduction. While its range has undoubtedly been expanded in Texas by man's destruction of the environment, the form has been present at least since the earliest days of botanical exploration in the state in the early and mid 1800's (Berlandier and Lindheimer collections) when it occurred in areas

relatively undisturbed by man. In more recent times, the adventive Central American-Pan Caribbean (and Pan-Tropical) form with simple upper leaf hairs has become established particularly near Houston and in other scattered southern Texas localities, and now intergrades freely with the indigenous population.

Malvastrum aurantiacum is found in similar often low lying, wet habitats in Texas, particularly near the coast, often with the indigenous *M. coromandelianum* population. The species is also autogamous but maintains a well-developed outcrossing potential. Unlike *M. coromandelianum*, however, this species is not known to occur in South America, and has no known close relatives. It is a morphologically distinct and specialized hexaploid species ($2n = 36$). Its distribution and habitat correspond to a major extent with that of other disjuncts in the region, such as *Cienfuegosia drummondii* (A. Gray) Lewt. which is found in similar habitats in the Paraná basin in South America. Fryxell (1967) has presented a case for the likelihood of long-distance dispersal in that species. It is my opinion that *M. aurantiacum* also reached Texas in ancient times in this manner and that its ancestors have become extinct in South America since that introduction. Migration seems unlikely since no other populations exist. Its fruits just previous to maturity are rose-red and probably attractive to birds. Evidence for its ancient occurrence in Texas is provided by the presence of an undescribed species of the Anthonomid weevil genus *Macrorhoptus* whose life cycle depends entirely (as far as is known) on this plant (Burke, 1973). Other genera and species found in Texas in the same general region as *M. aurantiacum* that show the same pattern of disjunction, are: *Bothriochloa exaristatus* (Nash) Henr., *Chloris pluriflora* (Fourn.) Clayton, *Cressa nudicaulis* Griseb., *Desmanthus brevipes* B. L. Turner, *Gaillardia* spp., *Hedeoma* spp., *Hymenoxys* spp., *Leptochloa dubia* (HBK) Nees, *Lycium* spp., *Menodora* spp., *Phyla* spp., *Prosopis reptans* Benth., *Salvia* spp., *Sida* spp., and *Xanthocephalum* spp. (Raven, 1963).

The distributions of the remaining 3 disjuncts do not fit the general pattern presented by Raven (1963). *Malvastrum hispidum*, *M. chillagoense*, and *M. americanum* var. *stellatum* seem to belong to old vegetation communities, and do not occur in open, moist, or weedy habitats.

While *Malvastrum hispidum* occurs near the Mississippi bird migration route, *M. chillagoense* seems isolated from such routes.

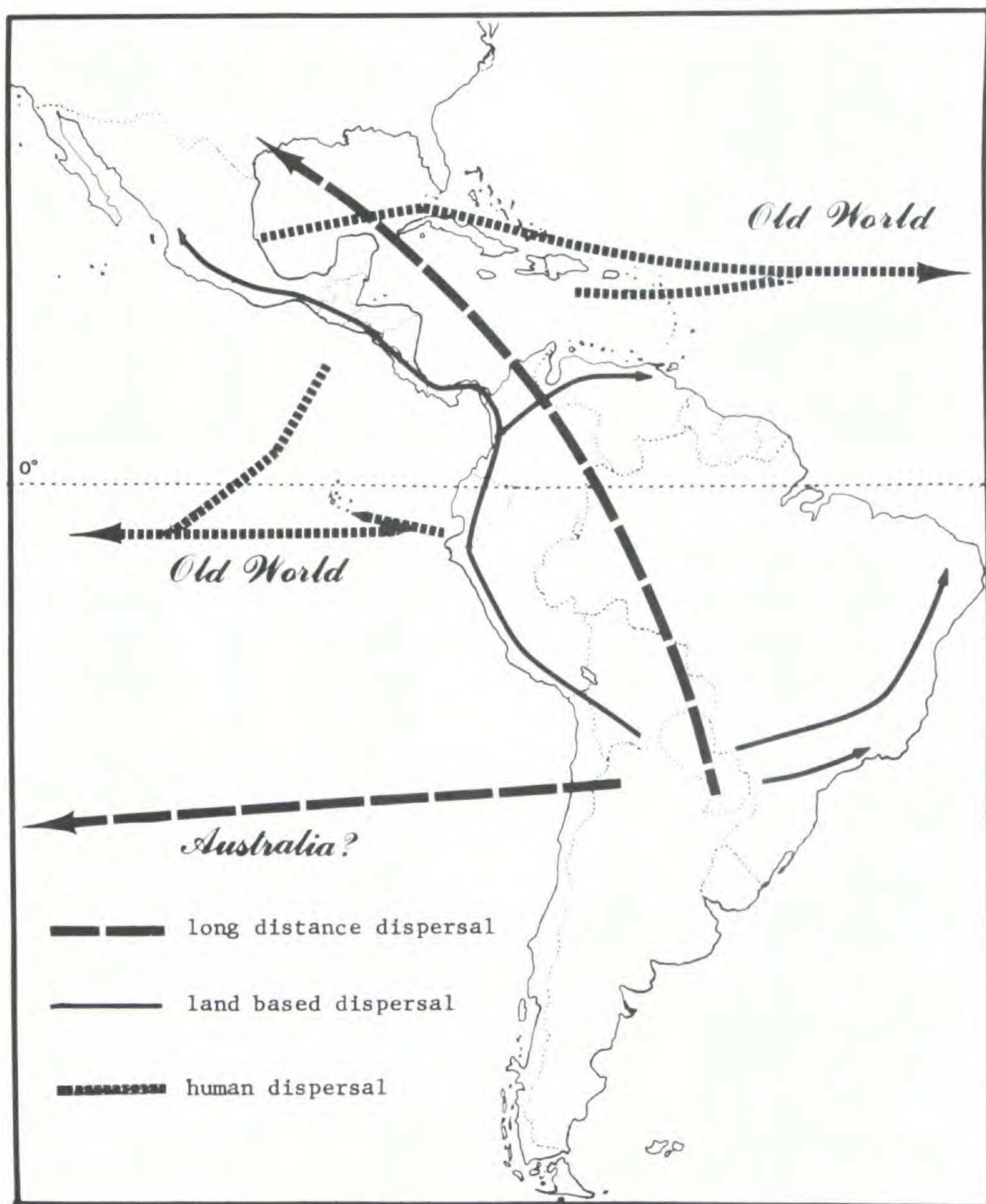


Figure 2. Hypothetical dispersal routes for *Malvastrum*.

However, both seem to be autogamous species, *M. hispidum* not infrequently being also cleistogamous. While each is primitive in some respects, each is specialized in others. *Malvastrum hispidum* is a hexaploid ($n = 18$), and is assumed not to be relictual or particularly ancient within the genus. There are no additional data that might lead to a distributional history for either species. My opinion is that *M. hispidum* is an ancient long-distance disjunct that survived the glacial epochs in the Ozark refuge. *Malvastrum*

chillagoense may also be a long-distance disjunct, although considering the distance involved this seems unlikely. It would be easily explained if eastern Australia and western South America had been joined in the past. An alternative explanation is that it is a more recent derivative form from *M. americanum* (once thought to have been solely introduced to Australia and distributed widely by grazing mammals) since the two species have a significant number of morphological characters in common and nearly identical pollen grains. This presents a problem, namely, has there been sufficient time for its divergence from *M. americanum*? Also, what would explain the retention of several primitive characters, such as the free bracteoles? The fact that it is restricted to limestone is also a unique feature. There are no chromosome counts for this infrequently collected species.

Judging by the great diversity in *Malvastrum americanum* in Australia and its presence in native vegetation types, there is some reason to suspect that this species also has a far longer history on that continent than previously thought. It has been collected in rather inaccessible areas since at least the 1830's. Nevertheless, evidence suggests that at least some Australian populations of *M. americanum* could have been recently introduced since: 1) several collection labels indicate that sheep, cattle, and horses are fond of the old dried seed heads, and since sheep are not only a very early introduction but also nearly ubiquitous, a rapid range extension could have resulted from a chance introduction, and 2) the range of variation of most populations fits into the periphery of the range of variation shown by *M. americanum* in the American tropics. Until a chromosome count has been made and it has been studied in greenhouse culture, conclusions as to the origin of *M. chillagoense* and the Australian variants of *M. americanum* remain very speculative.

Figure 2 illustrates the hypothetical dispersal routes discussed in this section. The primary routes include: 1) long-distance dispersal as in *M. aurantiacum*, *M. coromandelianum* subsp. *coromandelianum* in part, *M. chillagoense*, and *M. americanum* in part; 2) land-based animal dispersal by means of ornamented or cuspidate fruits as in *M. tomentosum* and its allies, *M. coromandelianum* in part, and *M. americanum*; and 3) dispersal by man as in the cases of *M. americanum*, *M. corchorifolium*, and *M. coromandelianum* subsp. *coromandelianum*.

ETHNOBOTANY

While species of *Malvastrum* have never been of great importance to man, several have been companion plants to man in the tropics. As a result, they have been generally recognized, named, and examined for possible uses.

The use of *Malvastrum* species as brooms is well documented. L'Heritier (1786) described *Malva scoparia* (= *Malvastrum tomentosum*) from Peru and stated that the inhabitants of the region made cheap brooms from this bushy plant ("Scopas sat viles e ramis conficiunt incolae", p. 54). The common names attributed to the plant were "balai sauvage" (French) and "escoba cimarrona" (Spanish). In the following year, Jacquin (1787, p. 59) described a different *Malva scoparia* (= *Malvastrum corchorifolium*) from Haiti which he said the inhabitants called "herbe a balay" for the same reason. "Escoba" or "broom" is a general name applied to several unrelated dooryard plants used in this manner, such as *Parthenium*, *Sida*, *Melochia*, and *Scoparia*, as well as *Malvastrum*. In addition to the two species named above, *M. americanum* and *M. coromandelianum* are also called "Escoba" or "Escobilla."

Other names, often somewhat descriptive, have also been applied to the weedy species: e.g. *M. americanum*, "Olotillo" ("little corn cob", El Salvador), "Mozote" ("stickseed"), "sheepmallow" (Australia); for *M. coromandelianum*, "Wild Okra" (Bahamas), "wire weed" (Virgin Islands). The general name "Malva" is also encountered in Latin America for the weedy species.

Malvastrum coromandelianum (and probably *M. corchorifolium* in Yucatan) has had medicinal uses. A specimen collected in Coahuila, Mexico (Gregg 337) bore the notation that the plant was used for emollient poultices and against headaches. Standley (1930, p. 349) stated that "The plant has emollient properties. Its decoction is employed to cleanse sores and as a remedy for dysentery." In Haiti, *M. corchorifolium* is occasionally used in a similar manner for the stomach (label data, Leonard 13497). The only clinical laboratory of which I am aware concerning *Malvastrum's* medicinal value was conducted by Vermeersch et al. (1972). *Malvastrum coromandelianum* infusions were used for their hypotensive properties by the inhabitants of parts of Madagascar. Results indicated a slight hypotensive result, and histological studies of test animals indicated a histaminic effect on the smooth muscle fiber of the blood

vessels and intestines. Although this hypotensive effect is somewhat unusual, the emollient quality due to foliar mucilage is a characteristic of many members of the Malvaceae.

In Australia, *M. americanum* has been thought to cause illness in livestock (*Gessler s.n.* (BRI): "Reported that it is eaten by sheep and causes them to have a hump in the back and lose their ability to walk"; *Grummitt s.n.* (BRI): "Suspected of being responsible for a sickness in sheep"). The animals, nevertheless, are reported to eat the plant eagerly. The poisoning may actually be the result of a high concentration of selenium in the soil (*Murphy s.n.* (BRI): "Voucher for selenium determination. Collected from a known poison strip") since poisoning from this species is not known to occur elsewhere in its range.

PHENOLOGY AND REPRODUCTIVE BIOLOGY

Of the 22 taxa presently recognized in *Malvastrum*, individuals of 16 were grown to maturity in the greenhouse (11 of the 14 species) and their growth characteristics were observed. Three species (*M. americanum*, *M. aurantiacum*, and *M. coromandelianum*) were also studied in naturally occurring populations in Texas. The remaining entities are known from very few collections and were not observed in the living state. The data on phenology and reproductive biology summarized in this section result from these greenhouse and field observations as well as from inferences based upon preserved materials. The features discussed here include: 1) seed longevity and germination, 2) plant-maturation and seasonality, 3) the duration and pattern of anthesis (floral phenology), 4) fruit-maturation, and 5) pollination-mechanisms and vectors.

Seed longevity and germination

Malvastrum seeds are extremely durable. The seed coat is thick (0.1–0.3 mm) and composed primarily of radially elongated, narrow, densely-packed, highly lignified cells (see Fig. 15). Greenhouse plantings have shown that seeds as much as 46 years old can be viable (e.g., seeds from *Steere 1010*, *M. corchorifolium*, collected in 1932), and germination of seeds 20–40 years old is not infrequent. The seeds can pass through the digestive systems of birds and cattle without damage, as personal observations of the Texas species

attest. I have observed *M. coromandelianum* seedlings in old fecal matter in Texas pastures, and have seen sparrows eating and scattering the seeds of the same species in the greenhouse. The seeds may germinate a few days after being shed from the plant in some species (particularly *M. coromandelianum*) or may undergo a dormancy period and germinate the following spring or during favorable periods of subsequent years (as observed in *M. aurantiacum*). Most seeds examined, except those of *M. coromandelianum*, seemed to require a dormancy period and did not germinate simultaneously, but differentially over as much as a year or more. Seeds of *M. amblyphyllum*, *M. americanum*, *M. corchorifolium*, *M. coromandelianum*, and *M. grandiflorum* generally germinated in 3–5 days after planting. The other species usually required 14–30 days for germination under the same conditions. It seems significant that seeds of the three weedy species germinated rapidly and had particularly long-lived seeds. Members of the section *Tomentosum* as well as *M. aurantiacum* required the longest period before seed germination, from 7 to more frequently 14–30 days. Perhaps this is a result of the unstable environmental conditions where these occur.

Maturation and seasonality

In the greenhouse the taxa, planted simultaneously in March, matured at quite different rates. *Malvastrum coromandelianum* subsp. *coromandelianum* is, compared to the other *Malvastrum*s, a precociously flowering taxon and produces its first flowers after 50–60 days of growth, often at the sixth leaf node above the cotyledons. Several individuals produced flowers when only 7–10 cm tall. This is interpreted as being correlated with its weedy habit, and may reflect a neotenus developmental pathway. *Malvastrum coromandelianum* subsp. *capitato-spicatum* also required 50–60 days of growth before anthesis but first flowered at heights of 20 cm or more. The warm-temperate species *M. aurantiacum* requires 60–65 days before anthesis, followed by *M. hispidum* requiring about 60 days. The southern hemisphere warm-temperate *M. grandiflorum* requires 60–70 days of growth before flowering. Next to attain reproductive capability were *M. americanum* (90 days) and *M. corchorifolium* (90–120 days). The remaining plants required 100–180 days from germination to the first flower, these being *M. bicuspidatum* (all three subspecies grown), *M. scoparioides*, and *M.*

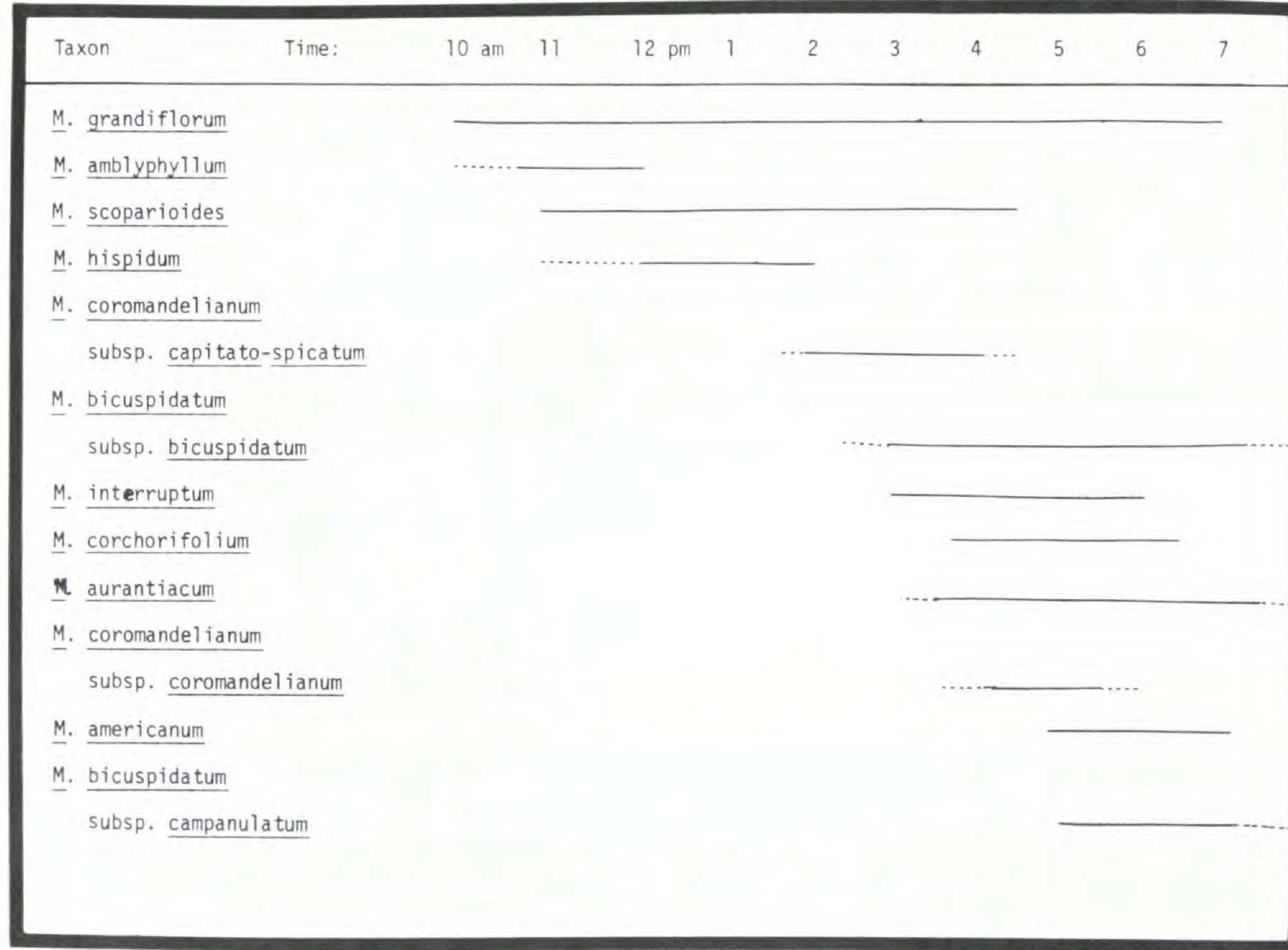
tomentosum (both subspecies). Specific periods required for each taxon for maturation and other processes are included in the individual taxonomic treatments. Several trends were seen: 1) the weedy species were among the first to flower, 2) the temperate species also flowered early, and 3) taxa from semi-xeric and tropical regions were among the last to flower.

Floral phenology

Most of the taxa examined flowered in the greenhouse in the autumn months (September–December) and continued through the early winter if not cold-damaged. *Malvastrum coromandelianum* subsp. *coromandelianum* and subsp. *capitato-spicatum* flowered continuously from spring through to the early winter. The Texas populations of *M. americanum* occasionally flowered in the early summer, but all tropical populations of the species grown in the greenhouse did not flower until the autumn. The Texas *M. aurantiacum* flowered in the late spring (May, June), became dormant during the driest summer months, flowered again in the early autumn, and became completely dormant by the end of November. The pattern of flowering in the spring and autumn with dormancy in the summer was also shown by *M. grandiflorum* and *M. bicuspidatum* subsp. *bicuspidatum*. The remaining taxa flowered only in the autumn. Data from herbarium specimens indicate that the seasonal pattern seen in greenhouse plants is more or less typical of patterns in native populations.

Flowers were produced for periods of time varying from one to two months (*M. amblyphyllum*, *M. bicuspidatum* subsp. *campanulatum* and subsp. *tumidum*, *M. grandiflorum*, *M. scoparioides*) to over 9 months (*M. coromandelianum* subsp. *coromandelianum* and subsp. *capitato-spicatum*). The remaining taxa were intermediate in inflorescence duration and flowered for 3–7 months out of the year. Each flower typically was open for only a few hours on a single day.

Figure 3 presents data on the daily flowering periods that were observed in this study (the times have been adjusted to local standard time). The solid lines indicate the usual duration of open flowers and the dashed lines indicate exceptional flower periods. The following trends were observed: 1) flowers opened at various times of day but more frequently in the late afternoon; 2) taxa with mostly autogamous flowers (*M. amblyphyllum*, *M. americanum*, *M. corchorifolium*, *M. coromandelianum*, and *M. hispidum*) bore

Figure 3. Daily flowering periods in *Malvastrum*. Local standard time.

open flowers for only 1.5–2 hours, while those with outcrossing or potentially outcrossing flowers bore open flowers for 3–9 hours (*M. aurantiacum*, *M. bicuspidatum*, *M. grandiflorum*, *M. interruptum*, *M. scoparioides*). Infrequently during cooler weather, flowers of several individuals of *M. bicuspidatum* subsp. *bicuspidatum* and subsp. *campanulatum* remained open through the night and most of the next day. This may also be true in the wild populations of those taxa since the latitude at which these were cultivated did not differ greatly from that of the seed sources.

Flowering periodicity has aided taxonomic conclusions. Within *M. coromandelianum*, the individuals referred to subsp. *capitato-spicatum* bore flowers that opened and closed earlier than those of subsp. *coromandelianum* even when the seed sources were from the same geographic area. This would isolate these from crossing where their ranges might overlap, and so has aided in defining the subspecies. A second observation was that the flowers of *M. corchorifolium* closed after those of *M. coromandelianum* subsp. *coromandelianum* and before those of *M. americanum*. This not only suggests the importance of genetic controls on flowering but also gives further support for belief in the hybrid origin of that taxon from the latter two (see Table 4). Support for the close relationship of *M. amblyphyllum* with *M. grandiflorum* (members of the section *Amblyphyllum*) is seen in the late morning or midday anthesis shown by those two taxa. The sequence of flowering remained constant from day to day and was a useful taxonomic character.

Variation in the flowering schedule occurred only on cool or overcast days and also followed seasonal daylength changes. Several taxa flowered earlier in the day on cool overcast days than on warm sunny days. Wild populations of *M. aurantiacum* infrequently produced open flowers at noon or else failed to blossom in such weather. In those taxa that had long flowering periods, flowers opened and closed as much as 2 hours earlier in the winter months (December–February) than in the summer (June–September). Nevertheless, the sequence of flowering among the taxa remained constant, e.g. flowers of *M. coromandelianum* subsp. *capitato-spicatum* were always closed by the time those of subsp. *coromandelianum* opened.

Fruit maturation

The time required for fruit maturation (anthesis to the dry fruit) was also recorded for several of the taxa. *Malvastrum americanum* and *M. coromandelianum* fruits ripened the most rapidly, in 15–19 days and 17–22 days after pollination, respectively. The speed of fruit maturation is correlated with the weedy habit in both species. Of the remaining taxa observed, ripening occurred as follows, the taxa listed in the order of increased ripening time: *M. interruptum* (21–26 days), *M. bicuspidatum* subsp. *bicuspidatum* (23–29 days), *M. corchorifolium* (24–36 days), *M. amblyphyllum* (29–33 days), *M. bicuspidatum* subsp. *campanulatum* (ca. 30 days), *M. grandiflorum* (30 days) and *M. aurantiacum* (33–34 days). The order of ripening follows directly from the fruit size; smaller fruits matured more rapidly than larger ones. Since the maturation times overlap to such a significant extent in this second group of taxa, the character is not of great diagnostic value.

Pollination mechanism

The flowers of *Malvastrum* are perfect and homogamous, that is, the stigmas and stamens mature at the same time. However, this can be affected by environmental conditions. In *M. interruptum*, a species from temperate high altitudes, the anthers did not dehisce at all during the warmest (29–35°C) late summer days. On the cooler days of autumn, normal anther dehiscence occurred. In those taxa that were primarily autogamous (*M. amblyphyllum*, *M. bicuspidatum* subsp. *campanulatum*, *M. chillagoense*, *M. corchorifolium*, *M. coromandelianum* subsp. *capitato-spicatum*, *M. hispidum*) pollen was shed directly onto the stigmas as the petals opened making natural crossing difficult. In contrast the remaining taxa, at least in early flower, had exerted stigmas that prevented early self-pollination and promoted outcrossing. With the exception of *M. grandiflorum* and *M. scoparioides*, the stigmas of members of this group recurved into the anther cluster and self-pollinated, usually as the flower began to wilt. The species were seen to be, for the most part, self-compatible and produced high percentages (80–90%) of viable seed. Exceptions include *M. grandiflorum*, *M. interruptum*, *M. scoparioides*, and *M. bicuspidatum* subsp. *tumidum*, all of which produced very low percentages (ca. 10% or less) of viable seed when self-pollinated and which may have incompatibility mechanisms not

yet understood. Since seeds failed to develop on flowers that were emasculated, apomixis does not seem to be involved, nor is it suspected in any taxon.

In *M. hispidum* the extreme condition of cleistogamy can occur and fruits are produced as a result of pollen shed on the stigmas in bud. Apparently the stigmas are recurved into the anther cluster precociously. Seed set is ca. 90% in this species. The reduced number of carpels and stamens in this and other taxa is correlated with autogamy and cleistogamy, reflecting the greater efficiency of this pollination system.

While autogamy predominates in the genus, morphological evidence and field observations demonstrate that outcrossing also occurs. In the outcrossing taxa, the petals are conspicuous, nearly planar at anthesis, and may provide a suitable platform for insects. The large number of anthers and the echinate pollen insures that any suitable insect visitor will receive some grains. In addition, the stigmas are generally papillose and this may aid in the efficient attachment of the grains when they are transferred. The generally large number of apertures on the grains perhaps insures germination at various orientations on the stigma. Since nectar is produced in minute amounts, the flower visitors are apparently attracted to the large amounts of pollen. This is supported by observations of pollen-gatherers on local species (see below).

Insect vectors

The three Texas species *M. americanum*, *M. aurantiacum*, and *M. coromandelianum* were observed in the field, and flower visitors were captured. In my two years of observation, insect pollinators or potential pollinators were never seen in the flowers of *M. coromandelianum* in Texas, but *M. americanum* flowers were occasionally visited by a large number and variety of insects. In mid-October, 1978, I collected a group of insects from flowers of the northernmost population of this species known in Texas (at Corpus Christi). A list of these insects as well as others appears in Table 2. All are widespread generalized foragers except for the weevil *Anthonomus solarii* which is also known from *M. coromandelianum* along with *A. squamans* which appears to feed upon the flower buds (Burke, 1968). The former not only feeds upon the pollen but also completes its life cycle as a larval parasite in the fruits. The ants and butterfly

Table 2. Pollinators and Predators

Insect	Species utilized	Part utilized	Voucher plant or reference
<i>Acanthoscelides</i> cf. <i>aequalis</i> Sharp (Coleoptera: Bruchidae)	<i>M. americanum</i>	mericarps	<i>Seymour 2362</i>
<i>Anthonomus solarii</i> Champion (Coleoptera: Curculionidae)	<i>M. americanum</i>	pollen, buds	<i>Hill 8093; Burke, 1968</i>
<i>Anthonomus squamans</i> Champion (Coleoptera: Curculionidae)	<i>M. americanum</i> and <i>M. coromandelianum</i>	young mericarps, buds	<i>Hill 6054; Burke, 1968</i>
<i>Apion</i> sp. (Coleoptera: Curculionidae)	<i>M. americanum</i>	mericarps	<i>Chippendale 7148;</i> <i>Johnson 2116</i>
<i>Celotes limpia</i> Burns (Lepidoptera: HesperIIDae)	<i>M. americanum</i>	foliage	<i>Burns, 1974</i>
<i>Cochliomyia macellaria</i> Fabr. (Diptera: Calliphoridae)	<i>M. americanum</i>	pollen	<i>Hill 8093</i>
<i>Halictus ligatus</i> Say (Hymenoptera: Halictidae)	<i>M. aurantiacum</i>	pollen	<i>Hill 4514</i>
<i>Lerodea eufala</i> Edw. (Lepidoptera: HesperIIDae)	<i>M. americanum</i>	nectar?	<i>Hill 8093</i>
<i>Macrorhoptus</i> sp (undescr.) (Coleoptera: Curculionidae)	<i>M. aurantiacum</i>	pollen, mericarps	<i>Hill 4514; Burke, 1973</i>
<i>Megabombus pennsylvanicus</i> De Geer (Hymenoptera: Apidae)	<i>M. americanum</i>	pollen	<i>Hill 8093</i>
<i>Megachile montivaga</i> Cresson (Hymenoptera: Megachilidae)	<i>M. americanum</i>	pollen	<i>Hill 8093</i>
<i>Monomorium minimum</i> Buckley (Hymenoptera: Formicidae)	<i>M. americanum</i>	nectar?	<i>Hill 8093</i>
<i>Strymon melinus</i> Hubner (Lepidoptera: Lycaenidae)	<i>M. coromandelianum</i>	young mericarps, foliage?	<i>Hill 5112</i>
<i>Vanessa caryi</i> (Lepidoptera)	<i>M. tomentosum</i>	foliage	<i>Smyth 48</i>

collected on the flowers were apparently the only insects feeding upon the nectar. Flowers of *M. aurantiacum* were visited by fewer individuals and fewer species of insects (listed in Table 2). The insects observed were feeding upon and gathering the pollen and made no attempt to search out the poorly-developed nectaries. The undescribed species of *Macrorhoptus* was seen in Brazos County and Goliad County on *M. aurantiacum* and completes its life cycle as a larval seed-parasite within the fruits. Some benefit may be gained by both members of this symbiosis, since pollen may be transferred by the insect. I feel that it is significant that *Macrorhoptus* is also known from Argentina (Burke, 1973) where *M. aurantiacum* is thought to have originated, suggesting an ancient association.

Several Bruchid weevils have been found as parasites in the fruits of *M. americanum* in Central America and Australia. While lepidopterids are infrequent visitors to *Malvastrum*, several are known to utilize the foliage. *Vanessa caryi* larvae feed on the foliage of *M. tomentosum* in Peru (field notes from Smyth 48) and *Celotes limpia* will feed upon *M. americanum* in the laboratory (Burns, 1974). Other larval predators were collected on *M. coromandelianum*.

In summary, primary pollination-vectors seem to be pollen-gathering solitary bees and Anthonomid weevils.

COMPARATIVE MORPHOLOGY

Although several of the species of *Malvastrum* have been well known (under various names) for a considerable time, descriptions of certain morphological details that are of diagnostic value are usually lacking in the literature. In particular, vesture characters, seen to be exceedingly useful diagnostic features in this study, have been detailed only infrequently, such general terms as 'strigose', 'hispid', and 'tomentose' being the only commonly used terms. No detailed study of stamen number in the genus has come to my attention except for those pointing out unusually low numbers in some taxa (see Krapovickas, 1957b). Petal-shape, vesture of the stamen column, and mericarp number have been only cursorily examined in the past in the genus. I have examined the variation in over 80 characters for this study and have used 60 of these in a numerical analysis to prepare a graphic presentation of the cladistics of *Malvastrum* using the Wagner Groundplan/Divergence Method

(see Fig. 18). This section summarizes the variation within *Malvastrum* and is based upon data obtained from herbarium specimens, field observations, and cultivated individuals grown at College Station, Texas.

Habit and duration

Members of the genus *Malvastrum* are mostly characterized by a suffrutescent or nearly fruticose perennial habit with herbaceous stems that may become soft-woody in age. Several species are annuals in disturbed situations, and one (*M. hispidum*) is always annual. Nevertheless, all the taxa produce strong fibrous to soft-woody tissues as they mature. The perennials occasionally die back or are grazed back to a ligneous branched caudex at ground level and produce new growth from it. Other perennial species may produce new growth from erect woody stems. While it is not known precisely how long the plants may live, I have collected *M. americanum* wood samples in Texas (Hill 7640) that bore six annual rings. All of the taxa under cultivation reached reproductive maturity in a single year with a constant adequate water supply. Vegetative growth is seasonal in the greenhouse due in part to a normal dormancy exhibited by the species. The individuals grown locally in the greenhouse equalled or exceeded heights attained by individuals in the wild in a single season, varying from 20 cm (*M. coromandelianum* subsp. *coromandelianum* and *M. hispidum*) to nearly 3 meters (*M. americanum*). Most of the species grow to a height averaging 1 meter.

Roots

Malvastrum roots take the form of a single or branched elongated taproot which may develop several somewhat fibrous lateral branches. The length of the root varies from 5–10 cm in the annuals to 0.5–1 meter below the soil surface in the strong perennial *M. aurantiacum* in which the length equals or exceeds that of the above ground parts.

The root system of *M. aurantiacum* is among the most rapid to elongate in the seedling stage (of those taxa examined) and at maturity consists of a single thickened somewhat fleshy taproot with a few small primary branches (Fig. 4c) and has a distinctive salmon-pink internal color. Some collections of *M. coromandelianum*

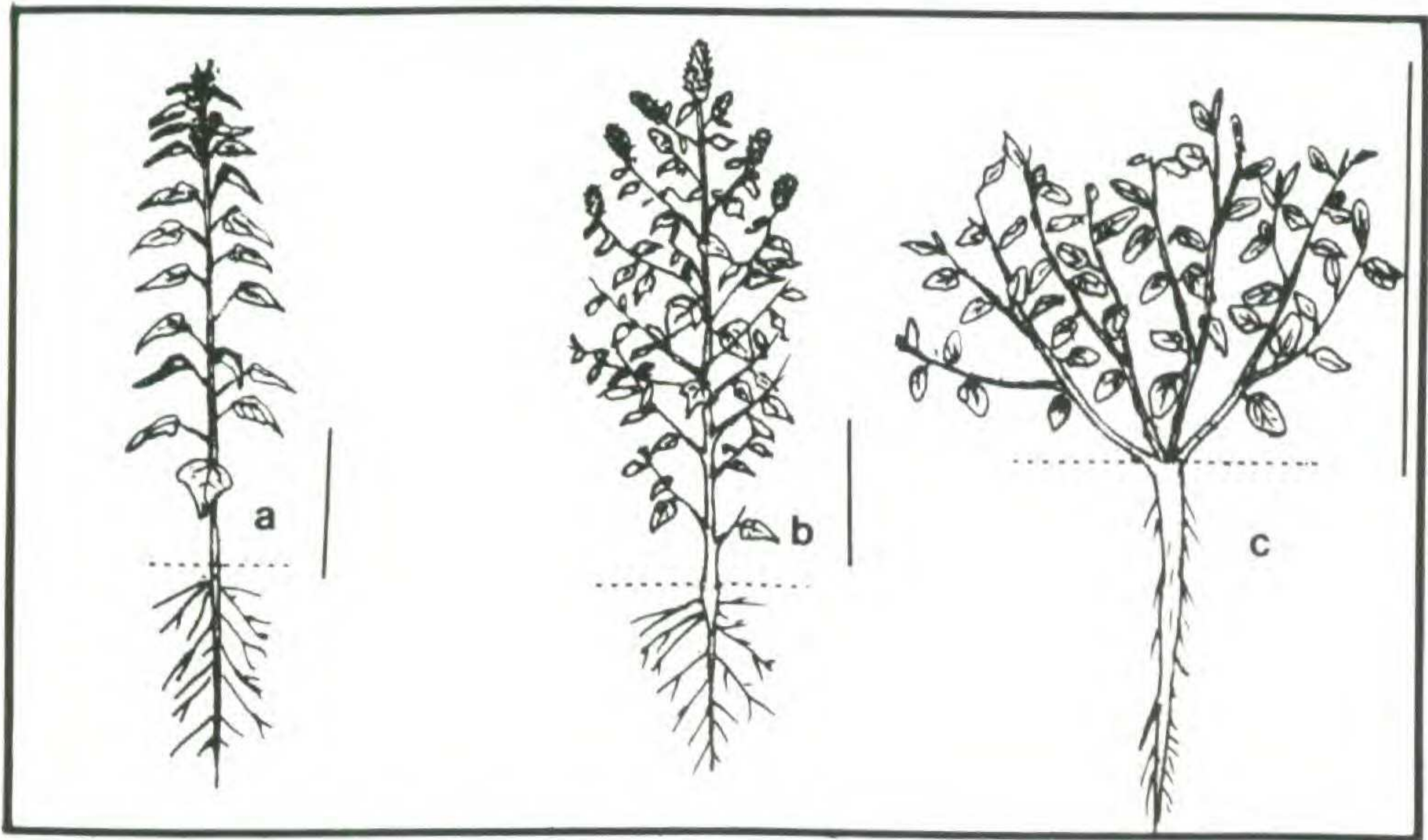


Figure 4. Habit variation in *Malvastrum*. a. *M. interruptum*, b. *M. americanum*, c. *M. aurantiacum*. Scale = 0.5 m.

subsp. *coromandelianum*, especially those from Texas and northern Mexico from semi-xeric or grazed areas, occasionally bear a similar but less fleshy unpigmented taproot. The other taxa for which roots are available have rather tough, ligneous, and more highly branched taproots that are usually less than half the length of the above ground parts (Fig. 4a & b). The root morphology in *Malvastrum*, then, falls into two basic categories which correlate loosely with habitat: 1) taxa with somewhat thickened, elongated, sparsely branched taproots (in periodically wet and poorly drained soils, which may seasonally dry to a parched state), and 2) those with less thickened, comparatively short, and more highly branched taproots (in well-drained soils). Except for the limited variation discussed above, the root-systems are of little diagnostic value in *Malvastrum*.

Vesture

The variation in hair types and their distribution is second in importance only to characters of the mericarp in recognizing the taxa of *Malvastrum*. The usual multiradiate stellate hair of the Malvaceae has been modified in various ways and usually independently within the genus. While not very useful in separating genera within the family, variation in vesture can aid in distinguishing species within genera when each taxon has a unique combination of

hair types. While variable in other genera (such as *Malvaviscus* Adanson and *Anisodonteia* Presl, see Bates, 1969) general patterns of vestiture are nearly constant within the species of *Malvastrum* allowing the determination of vegetative specimens with a degree of confidence.

Modification of the basic stellate hair has apparently proceeded in several directions within the genus (Fig. 5). The basic or primitive hair type in the genus is taken to be the 5–8-rayed, somewhat tufted to nearly rotate, actinomorphic, multicellular, slightly tuberculate stellate hair (Fig. 5a) found in all of the taxa but nearly lacking in some (*M. aurantiacum*, *M. coromandelianum*). From the primitive hair can be derived the 10–12-rayed, often biseriate, tufted stellate hair (Fig. 5b), perhaps by the multiplication of basal precursor cells during development. Probably functioning in semi-arid regions as a windscreen, this hair type in *Malvastrum* is most frequent on abaxial leaf surfaces, a surface where the stomata are concentrated. This 10–12-rayed hair is absent from *M. aurantiacum*, *M. bicuspidatum* (except subsp. *oaxacantum*), *M. chillagoense*, *M. corchorifolium*, *M. coromandelianum*, and *M. hispidum*. Probably also from the basic type has been derived the appressed (6) 8–10-rayed pseudo-lepidote stellate hair. This hair type with basally coalesced rays is found only in *M. aurantiacum* (Fig. 5c).

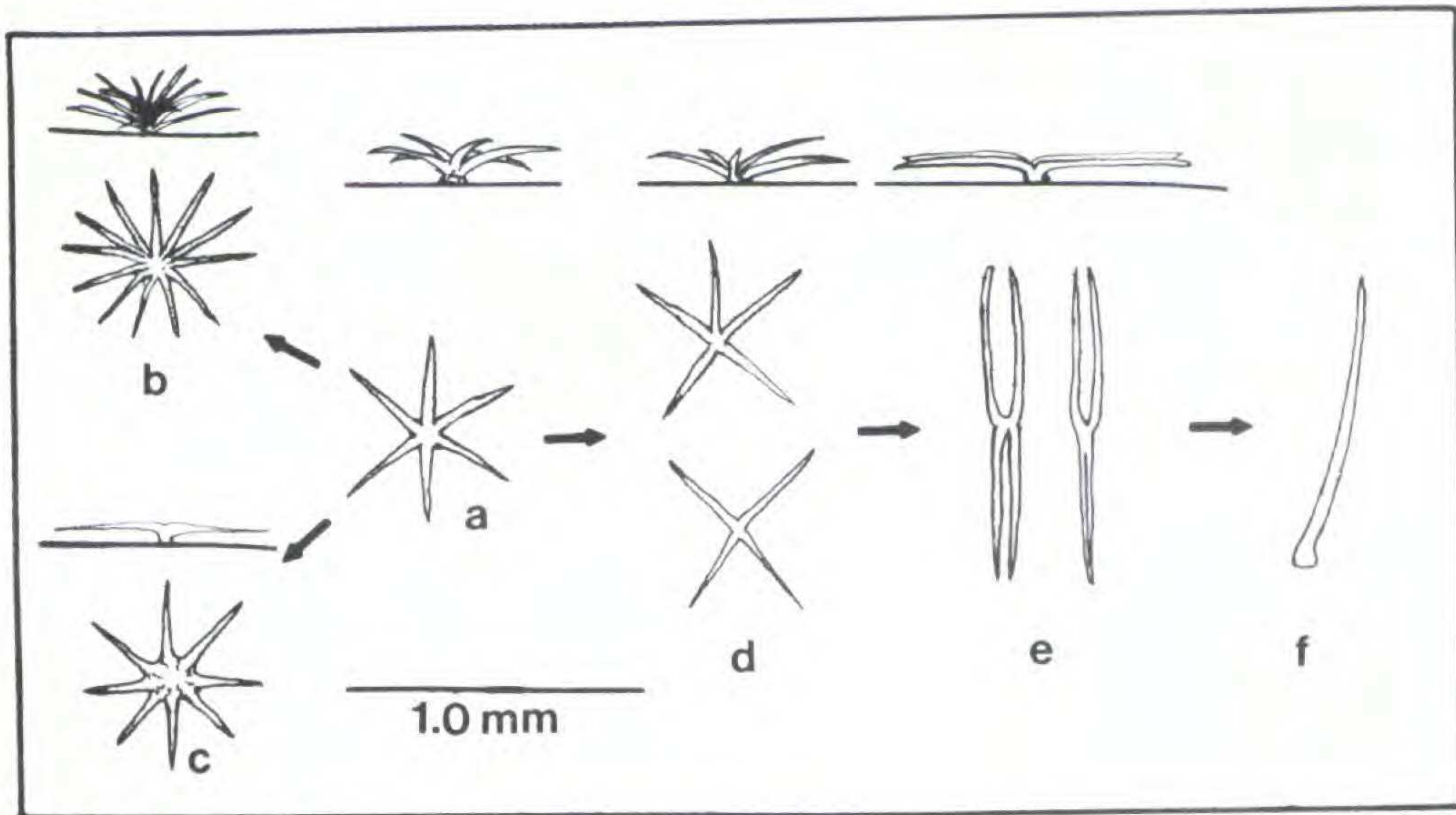


Figure 5. Elaboration or reduction of stellate hairs in *Malvastrum*. a. Unspecialized tufted 6-rayed hair. b. Multiplication of rays. c. Planation and coalescence of rays. d. Reduction of rays. e. Reduction, planation, and change in symmetry. f. Simple hair.

A third derivation pattern involves a reduction in the number of rays and a subsequent change in the symmetry of the hair. Several taxa have 4–5-rayed actinomorphic stellate hairs with equally divergent rays (Fig. 5d) and others have hairs which show a trend towards bilateral symmetry. This trend reaches its peak development in *M. corchorifolium* and *M. coromandelianum*. These two species bear closely appressed, bilateral, thickened, 4-rayed stellate hairs (the “H-shaped stellate hair” of Rao and Ramayya, 1977), which often have contiguous parallel rays directed longitudinally on plant parts (Fig. 5e). Similar hairs occur in other Malvaceae such as *Hibiscus coulteri* Harv. ex Gray and *Sida ciliaris* L. These hairs are infrequently reduced to submalpighiaceous hairs with 2 or 3 rays.

The final reduction of the basic stellate hair to a simple hair has occurred independently in several taxa and on various plant parts. The simple hairs may arise from a multicellular base or may be unicellular but in both cases arise from the epidermis (Fig. 5f).

Rao and Ramayya (1977), in describing the trichomes of *M. americanum* and *M. coromandelianum* in India, point out several hairs that they term “flagellate hairs”, which are restricted to the adaxial surface of the calyx lobes. In my species descriptions I have referred to these as arachnoid hairs. These are all minute (ca. 150–250 μm) simple or stellate hairs with thin walls and flexible rays and are found in most of the taxa on the adaxial surface of the calyx lobes and bracteoles, and less frequently on the adaxial surface of the stipules.

Glandular hairs are lacking in *Malvastrum* except for the multicellular nectar-secreting hairs of the internal basal surface of the calyx. These are found in restricted regions beneath and between the petal claws.

The vestiture attributes to the plant parts a texture varying from velvety to scabrous to nearly smooth. Most of the hairs are colorless, vitreous, and rigid at maturity (with the exception of the glandular and arachnoid hairs) but do not penetrate skin. In one taxon of the genus (*M. bicuspidatum* subsp. *tumidum* var. *glabrum*) all vestiture has been lost on the fruit. In the other taxa the above-ground vegetative and reproductive parts with the exception of the anthers, style, and stigma, and occasional exception of the filament tube have at least some vestiture.

The size of the hairs in *Malvastrum* is quite variable. The smallest glandular nectary hairs measure ca. 50–150 μm and the largest

simple and 4-rayed bilateral hairs of *M. coromandelianum* may reach a length of 2.0 mm. Most hairs are 0.5–1 mm in diameter in the genus. Hairs of different sizes are often mixed.

There are probably several important functions attributable to the hairs. In addition to protecting the plant from water loss, the hairs on the flower buds, ovaries, and soft vegetative parts may discourage insect predation. In *Gossypium* it is known that resistance to leafhoppers (family Jassidae) is dependent upon the density of the vesture on the abaxial surface of the leaf (Knight, 1952). In rice (Martins et al., 1977) it is known that more pubescent varieties discourage oviposition by predators. The bristle-like hairs on the mericarps in some taxa may aid in their adherence to fur and so in their dispersal.

The density of the vesture of any given plant depends not only on genetics, but also upon the age of the plant part and the habitat. Young herbaceous plant parts bear a very dense indument of overlapping hairs that becomes less dense as the tissues enlarge and lignify. Plants growing in moist areas and in shade have a more sparse vesture than those in dry or exposed areas. This suggests that hairs may also function to decrease the incident light to the leaf surface as well as to protect it from water loss. The vesture in *Helianthus*, *Tussilago*, and *Encelia* is known to reflect selectively as much as 56 percent of certain light spectra (Gousman et al., 1977; Eller & Willi, 1977; Ehleringer et al., 1976).

Stems

The stems have a moderate pith, a siphonostelic vascular cylinder, a chlorenchymatous cortex in youth, and a well-developed epidermis from which the vesture arises. The stem increases as secondary tissues are produced to a basal diameter of 1–15 mm. The green pigment is lost for the most part as secondary tissues such as cork arise and the stem becomes narrowly furrowed longitudinally. The hairs may or may not persist. In regions of seasonal variation, annual growth rings may be produced, while in temperate regions the stems generally die back to ground level or to the main stem in winter.

The branching pattern is monopodial. In the seedling stage all species in cultivation produce a single actively growing main stem that later produces few to several primary branches. In some taxa the main stem retains its dominance and primary branching occurs

only after injury, as inflorescences are produced, or in the second year (as in *M. interruptum* and *M. spiciflorum*, Fig. 4a). In a second group of taxa (such as the sections *Amblyphyllum* and *Tomentosum*, *M. americanum*, and *M. coromandelianum* subsp. *capitato-spicatum*) branches are regularly produced as the plant reaches maturity but the main axis retains its dominance and secondary branching is infrequent (Fig. 4b) unless the main axis is damaged. The third branching pattern is seen in *M. aurantiacum* and *M. coromandelianum* subsp. *coromandelianum* in which the main axis in the young plant soon loses its dominance and several primary branches, often basal, achieve the same stature. In these two taxa secondary branching is frequent (Fig. 4c). In each succeeding year several main stems are produced from the ligneous crown.

Cotyledons

The cotyledons of those taxa examined are ovate with a subcordate truncate to wide-cuneate base and a retuse to rounded apex. The margins are entire, but in *Malvastrum amblyphyllum* and *M. grandiflorum* (Fig. 6a) the cotyledon has a tendency to be very briefly three-lobed in the apical third. The petiole in all of the taxa examined is puberulent with simple to 2-rayed erect hairs less than 0.5 mm long and the blade is glabrous to minutely ciliate at the basal margin. Each cotyledon has a midnerve and 2 or 4 additional palmately arranged veins and few secondary veins. While subequal in length and width or even wider than long in most taxa, the blades of *M. aurantiacum* (Fig. 6b) and *M. hispidum* cotyledons are slightly longer than wide and easily recognizable. The three cotyledon types are presented in Fig. 6, the most frequent form represented by *M. coromandelianum* (Fig. 6c). The cotyledons measure (6)7–18 mm in length, (7)8–13 mm in width, and their petioles are 3–9 mm long.

Leaves

As in many genera of the Malvaceae, the leaves of *Malvastrum* are spirally arranged, petiolate, basically ovate with a tendency to be briefly 3-lobed, cordate truncate to wide-cuneate at the base, and acute acuminate or rounded at the apex, have a single midvein and several associated palmate veins, are marginally dentate to dentate-serrate, and bear paired lateral stipules at each node. The leaf form

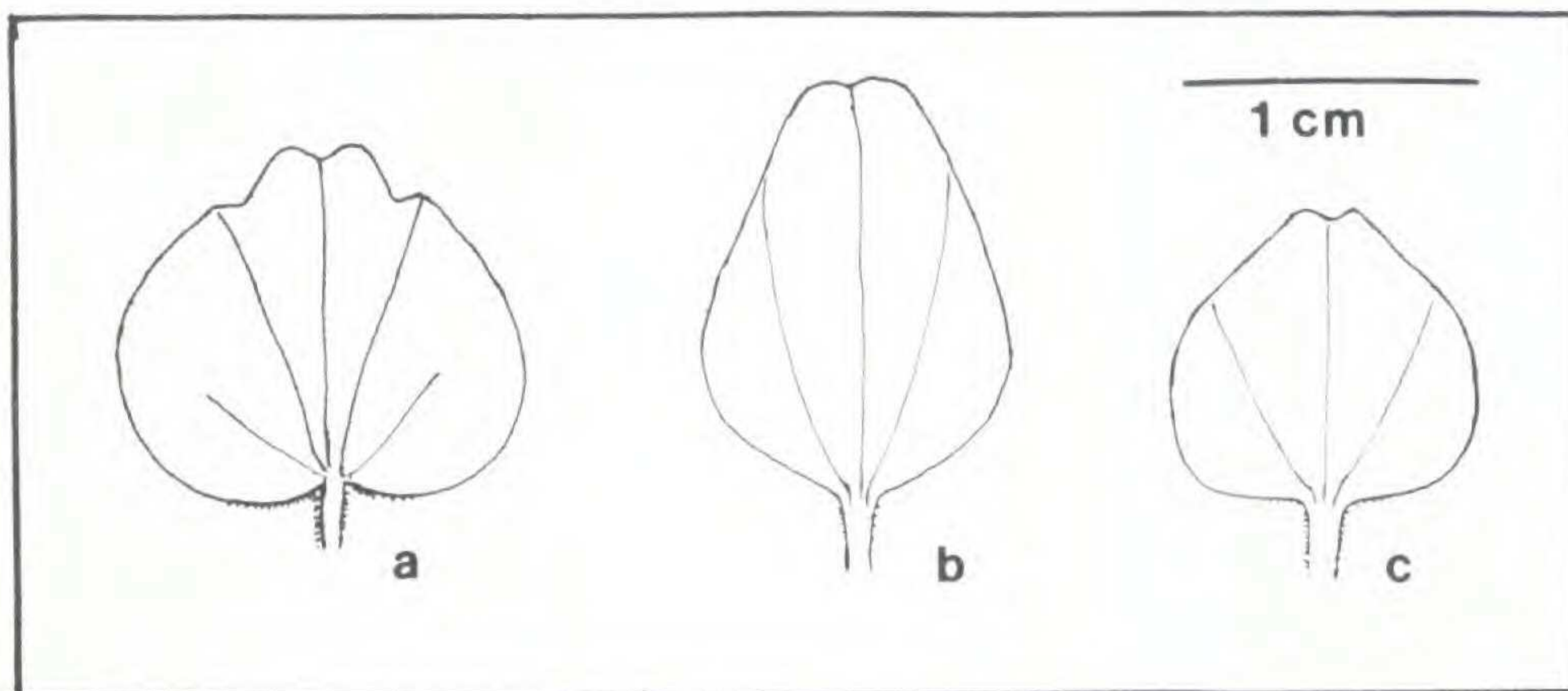


Figure 6. Cotyledon variation in *Malvastrum*. a. *M. grandiflorum* (Krapovickas 19300). b. *M. aurantiacum* (Hill 6430). c. *M. coromandelianum* (Hill 4579).

varies according to the taxon and the placement on the stem. Figure 7 exhibits some of the variation in leaf morphology found in the genus.

The petioles, (3)5–50 (100) mm long, are longest in early vegetative leaves, reduced apically, and are pubescent with hairs resembling those of the stem. They may subequal the blades or be 1/6 their length or less. The blades may or may not vary in form corresponding to their placement on the plant. In *Malvastrum amblyphyllum* (Fig. 7a), *M. aurantiacum*, *M. corchorifolium*, and *M. hispidum* (Fig. 7b), the blades scarcely vary with placement except that the earliest blades are often slightly larger or wider than those produced late in the season. In addition, the blades of these four species are almost always unlobed. Leaves of the remaining taxa are variable to a limited degree in size and shape in a manner similar to those of *Anisodonteia* Presl studied by Bates (1969). The mature vegetative leaves produced on the main stems during the periods of most active seasonal growth are the largest, particularly in first-year plants. These early vegetative leaves vary from 2.5–3.5 cm long \times 0.5–0.9 cm wide in *M. hispidum* to 5.0–11.5 cm long \times 4.0–10.0 cm wide in *M. americanum* (Fig. 7c). In mature plants the blades and petioles are smaller and narrower, especially in *M. americanum* (Fig. 7d), *M. bicuspidatum*, and *M. coromandelianum* subsp. *capitato-spicatum*. The final leaves produced with the inflorescence are the smallest, nearly sessile in some cases (petioles 5 mm or less in length), and often unlobed or with highly reduced lobes. At the time of

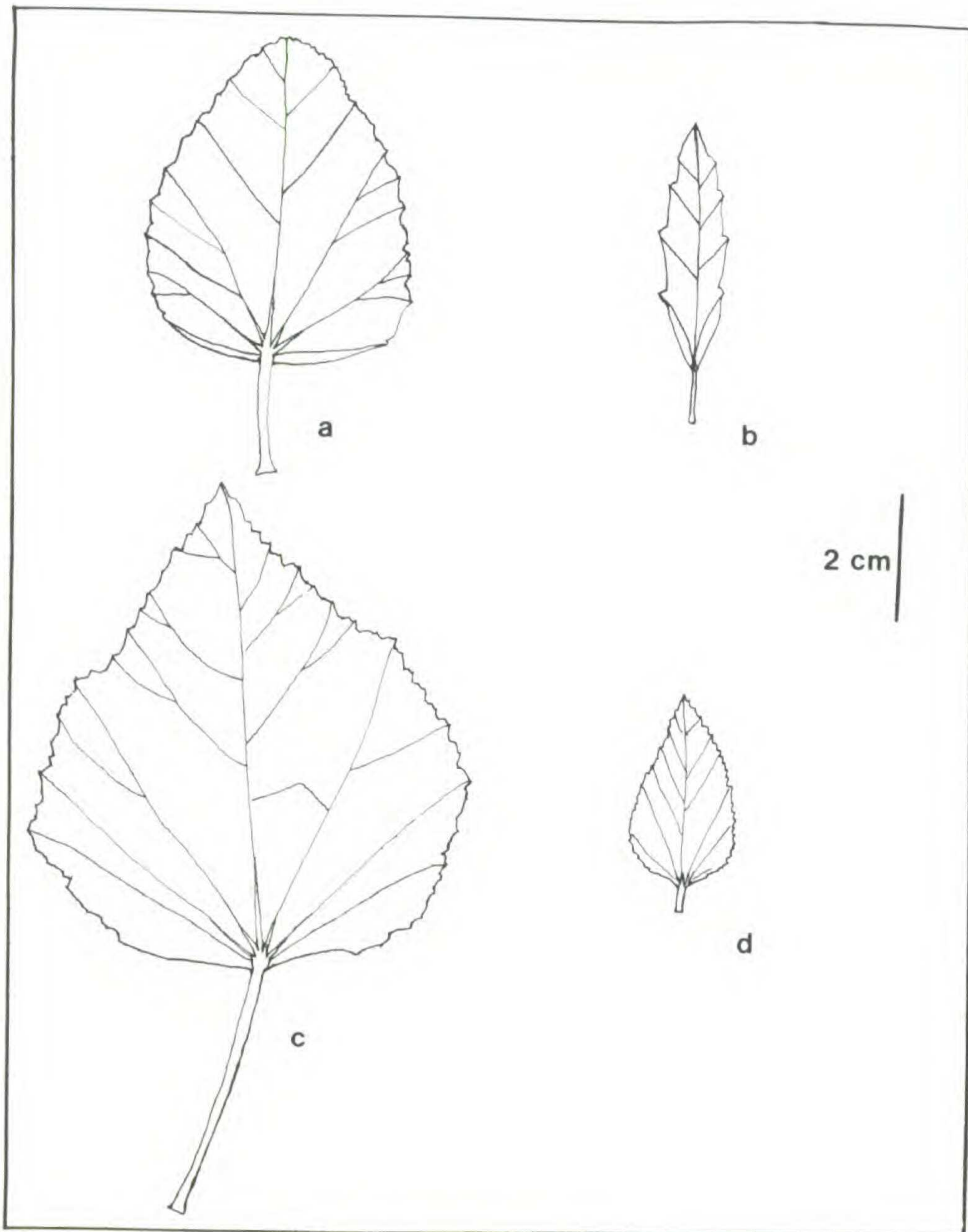


Figure 7. Leaf variation in *Malvastrum*. a. *M. amblyphyllum* (Krapovickas 19127). b. *M. hispidum* (Bates 2691). c. & d. *M. americanum* (Krapovickas 15566).

reproductive maturity nearly all of the large main stem leaves have fallen, probably as an adaptation to drying conditions and a result of lessened metabolic activity. As also noted in *Anisodonteia* Presl (Bates, 1969, p. 260–265) immature individuals of *Malvastrum* are different in appearance from those at reproductive maturity due to changes in both the branching pattern and in leaf morphology.

The orientation of the leaves on the midstem region of the main stem was examined for potential diagnostic value. Measurements of the angle formed between the petiole and the stem above were taken from cultivated specimens at midday since it was noted that the leaves droop at night as well as in age, changing the angle. This study was undertaken after the narrow angle specific to *M. interruptum* (and possibly also *M. spiciflorum*) was observed. The angle was seen to vary from 30°–60° in *M. interruptum*, to 90° in *M. amblyphyllum*, and to the usual 110°–113° in *M. americanum*. While of some diagnostic value in living vegetative plants, this character is not useful in pressed specimens.

The vesture of the leaves can be used to distinguish not only species but also subspecies, as in *M. bicuspidatum*, and in delineating specific populations, as in *M. coromandelianum*. All of the hair types described earlier in this work except for the arachnoid and glandular hairs are present in various combinations on *Malvastrum* leaf surfaces. The hairs are often best developed over the veins and these often have a greater number of rays than those in intercostal zones. The hairs may be reduced in size and number of rays towards the leaf margins.

The leaf venation is basically palmate in *Malvastrum*. The midnerve is the most strongly developed, and there are one to three additional pairs of nerves radiating from the base of the blade. The primary veins extend to the margins and terminate in the marginal teeth. Secondary veins branch from the primary veins and may terminate in the teeth. The smallest reticulate veins occur throughout the remainder of the leaf. The primary veins are conspicuously raised on the abaxial surface of the leaf in both fresh and dried specimens and slightly impressed above (except in *M. interruptum* in which they are deeply impressed on the adaxial surface).

The leaf-margins are typically dentate but may be crenate-dentate, nearly serrate, or denticulate. There is a tendency for the teeth to be relatively large and few in number/cm in the early main stem leaves and in leaves from shaded plants. The later leaves have

relatively smaller teeth and a larger number/cm of margin (e.g., in *Malvastrum americanum* var. *americanum* main stem leaves have 2 teeth/cm, increasing to 7 teeth/cm in apical leaves). Taxa from more arid regions show a tendency towards serrate leaf margins particularly on those leaves produced late in the season (e.g. *M. bicuspidatum* and certain populations of *M. coromandelianum*).

Lobing of the blade is poorly developed in *Malvastrum*. The lobes are less than 1 cm deep and often appear as a pair of enlarged teeth about 1/2 to 2/3 the distance from the base of the blade, each with the terminus of an elongated palmate vein. Most of the taxa retain leaf lobing only in the juvenile leaves, if at all, suggesting that lobing is a primitive feature within the genus.

Stipules

Malvastrum stipules are found paired at the base of the petioles or, less frequently, subtending the flowers. The shape varies from wide-lanceolate (Fig. 8a) to narrowly triangular (Fig. 8b) to nearly linear (Fig. 8c), and the stipules are usually falcate, widest at the base, and have a long-acuminate to subulate apex. They are completely free from the petioles. The length varies from 2–16 mm and the width from 0.2–1.5 mm. The stipules are often reduced in the congested axillary inflorescences of *M. coromandelianum* subsp. *capitato-spicatum*, *M. interruptum*, *M. spiciflorum*, and *M. tomen-*

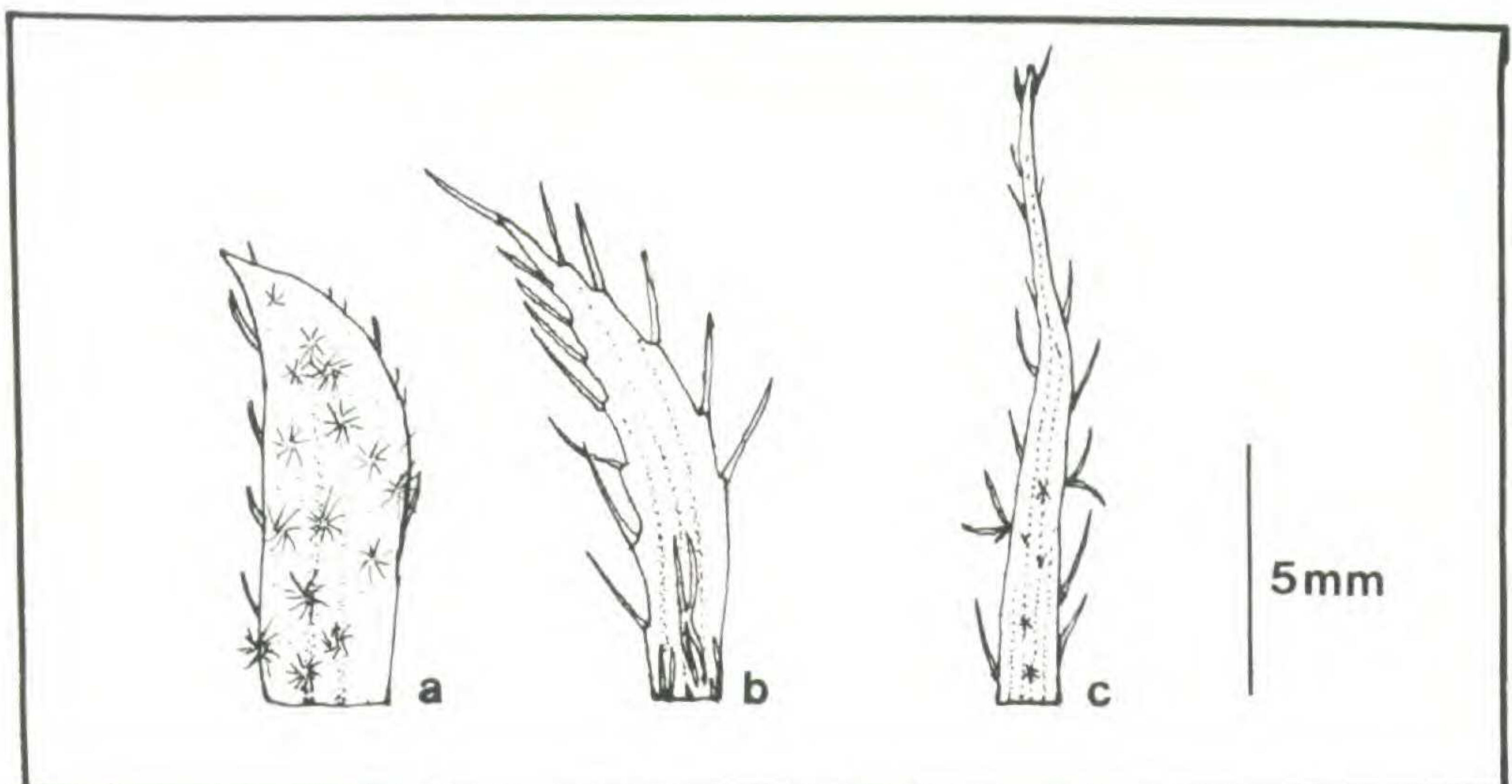


Figure 8. *Malvastrum* stipules. a. *M. aurantiacum* (Hill 6430). b. *M. coromandelianum* (Hill 4579). c. *M. grandiflorum* (Krapovickas 19300). Abaxial surface views.

tosum, but are retained unchanged or as modified floral bracts in the other taxa. The stipules remain green or may dry within a few days. They may be early deciduous, may fragment gradually, or may persist, but this character can vary within a taxon. The stipules are appressed to the stem, perpendicular to the stem, or slightly reflexed. The stipular margin is entire to irregularly toothed, the dentition resulting from the development of large marginal multicellular based simple hairs (e.g. *M. coromandelianum*, Fig. 8b). The vestiture of the stipule surface resembles that of the stem, usually consisting of appressed stellate and marginally simple hairs, and the adaxial surface is glabrous or has a few scattered stellate or arachnoid hairs. The venation of the stipules is usually obscure or consists of 1–5 palmate veins that become parallel immediately above their base.

Inflorescence

There are four related inflorescence-types in *Malvastrum*, the simplest consisting of solitary flowers in the axils of leaves and their associated stipules (Fig. 9a). The flowers produced late in the season may appear congested at the apices of the stems when the internodes are reduced. Taxa with this inflorescence-type exclusively include *M. amblyphyllum*, *M. aurantiacum*, *M. coromandelianum* subsp. *coromandelianum*, *M. grandiflorum*, and *M. hispidum*. In young

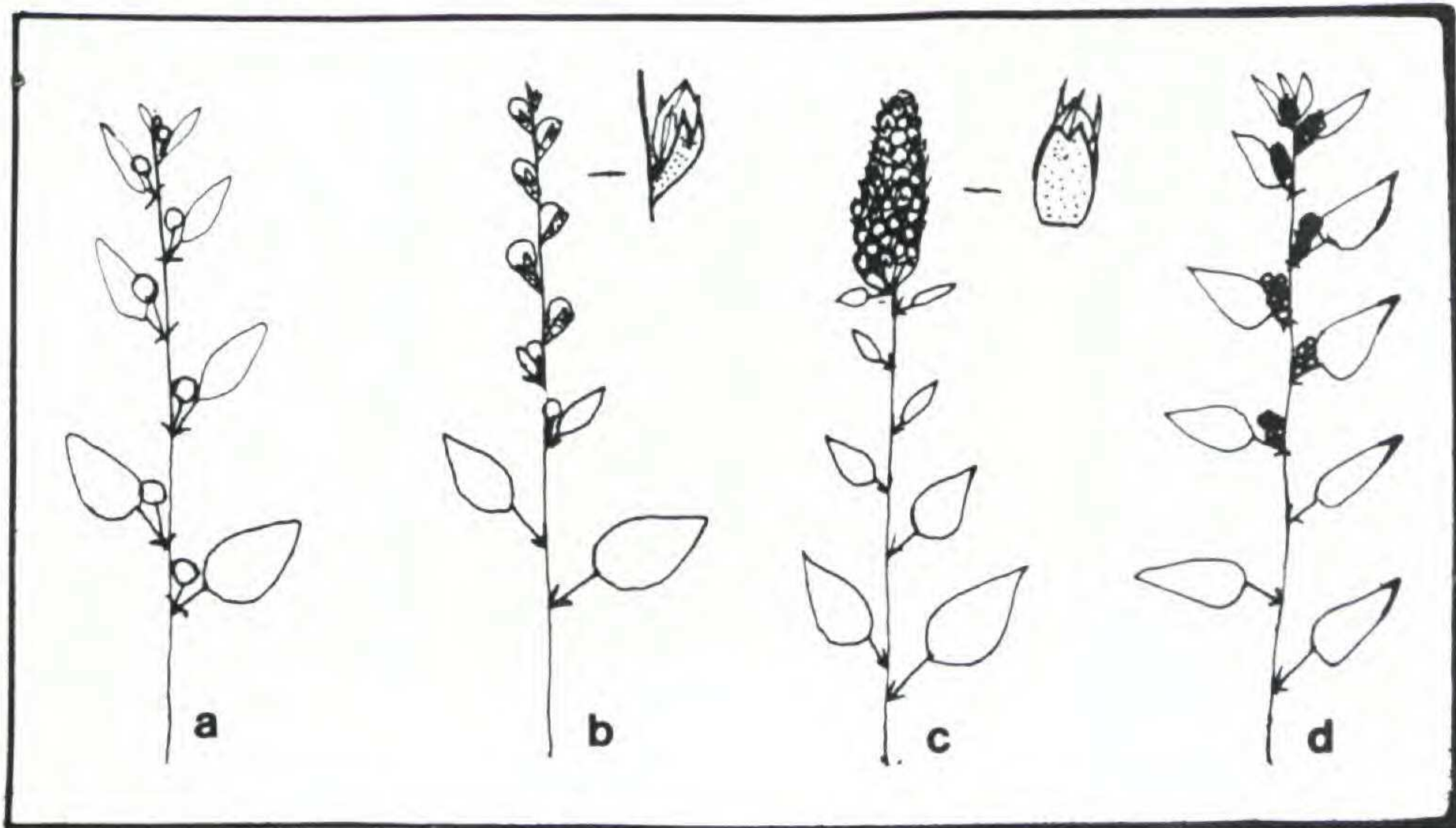


Figure 9. Inflorescence types in *Malvastrum*. a. Solitary, axillary. b. Terminal raceme. c. Terminal spike. d. Axillary spicate racemes. Schematic.

plants of most other taxa the first flowers are produced in this manner, but the inflorescence soon becomes more complex.

The second inflorescence-type is a simple terminal raceme (Fig. 9b). This raceme, if present, generally terminates every branch-apex and the flowers are either non-continuous with long (0.5–2 cm) internodes or congested and subspicate. The flowers are pedicellate (pedicels 0.5–2 mm long in flower) and at least a few lack subtending leaves. They are usually subtended instead by a sessile bifid bract derived by partial connation of the paired stipules. This inflorescence type is found exclusively in *M. bicuspidatum* (all subspecies), *M. chillagoense*, *M. coromandelianum* subsp. *fryxellii*, *M. guatemalense*, and *M. scoparioides*.

The third inflorescence-type is closely allied to the last and can be called a congested terminal spike (Fig. 9c). The flower pedicels are nearly absent, the flowers are densely congested at the apex of all upper branches (which are leafy below), and each flower is subtended by a bifid bract. This type is found exclusively in *M. americanum* and in mature individuals of *M. corchorifolium*. Several other taxa have congested inflorescences that superficially resemble those of *M. americanum*, but these can easily be distinguished by the lack of bifid bracts, the presence of subtending floral leaves, or by the lack of leaves in the lower part of the reproductive branch.

The fourth type of inflorescence consists of a number of short (1–4 cm) leafless axillary spicate racemes located in the upper half to third of the plant (Fig. 9d). This inflorescence-type probably has been derived independently in several taxa. The floral bracts usually consist of reduced, paired stipules that are rarely united in their basal half to form a bifid bract. The pedicels are 0.5–1.0 mm long. Each inflorescence unit is in the axil of an upper or midstem leaf that usually exceeds it. A terminal congested spicate inflorescence composed of several of the smaller inflorescence units with reduced leaves and internodes between is usually present in fully mature individuals. This type of inflorescence is found exclusively in *M. coromandelianum* subsp. *capitato-spicatum*, *M. interruptum*, *M. spiciflorum*, and *M. tomentosum*. To a certain extent, *M. bicuspidatum* subsp. *tumidum* and *M. guatemalense* have a reduced but basally leafy racemose inflorescence approaching this type.

Ideas concerning trends in the evolution of the inflorescence in *Malvastrum* are based on inductive reasoning. I have assumed that

the most primitive type is that consisting of solitary axillary flowers as in most other members of the Malvaceae and that the other types with reduced internodes, united stipules, or reduced to absent leaves have been derived from this. Evidence for this is seen in the fact that every taxon has at least one or two early solitary axillary flowers before the inflorescence becomes more complex. However, there is the possibility that through neoteny, a delay in the development of adult characteristics, the solitary axillary inflorescence can recur. This may explain, in particular, the solitary axillary flowers in *M. coromandelianum* subsp. *coromandelianum* which produces somewhat congested terminal inflorescences only at full maturity or senescence. Therefore, there is no reason to suppose that inflorescence evolution is unidirectional in *Malvastrum*.

The bifid floral bracts that have been used in the past (Krapovickas, 1957b) to distinguish *M. americanum* from other taxa with congested inflorescences are actually found in several other species as well. Morphological and developmental evidence from both herbarium specimens and greenhouse plants shows that the bifid floral bracts found in members of the genus are derived from paired leaf stipules. In many individuals a progression can be clearly seen from well-developed leaves with their associated stipules, to reduced leaves with stipules, stipules with a leaf remnant attached, and finally to a bifid bract (Fig. 10). The bracts are best developed in *M. americanum* (Fig. 10d) and are present to a significantly lesser degree in the other taxa. Developmental progressions are best seen in *M. corchorifolium* (Fig. 10b-c) and *M. bicuspidatum*. In many respects, the bracts of *M. corchorifolium* are intermediate between the paired stipules in *M. coromandelianum* (Fig. 10a) and the bifid bracts of *M. americanum*.

Involucel

The involucel (epicalyx) of the individual flowers of *Malvastrum* is always composed of three distinct bracteoles. These are arranged in a more or less spiral manner either at the pedicel-calyx juncture or are adnate to the calyx at various levels. In exceptional cases one or more bracteoles may be slightly remote on the pedicel. The bracteoles vary in shape from the unusual deltate-cordiform structures seen only in *M. aurantiacum* (Fig. 11a), to the more frequent lanceolate bracteoles of *M. coromandelianum* (Fig. 11b), and finally to the linear or filiform shape seen in *M. tomentosum* (Fig. 11c) and

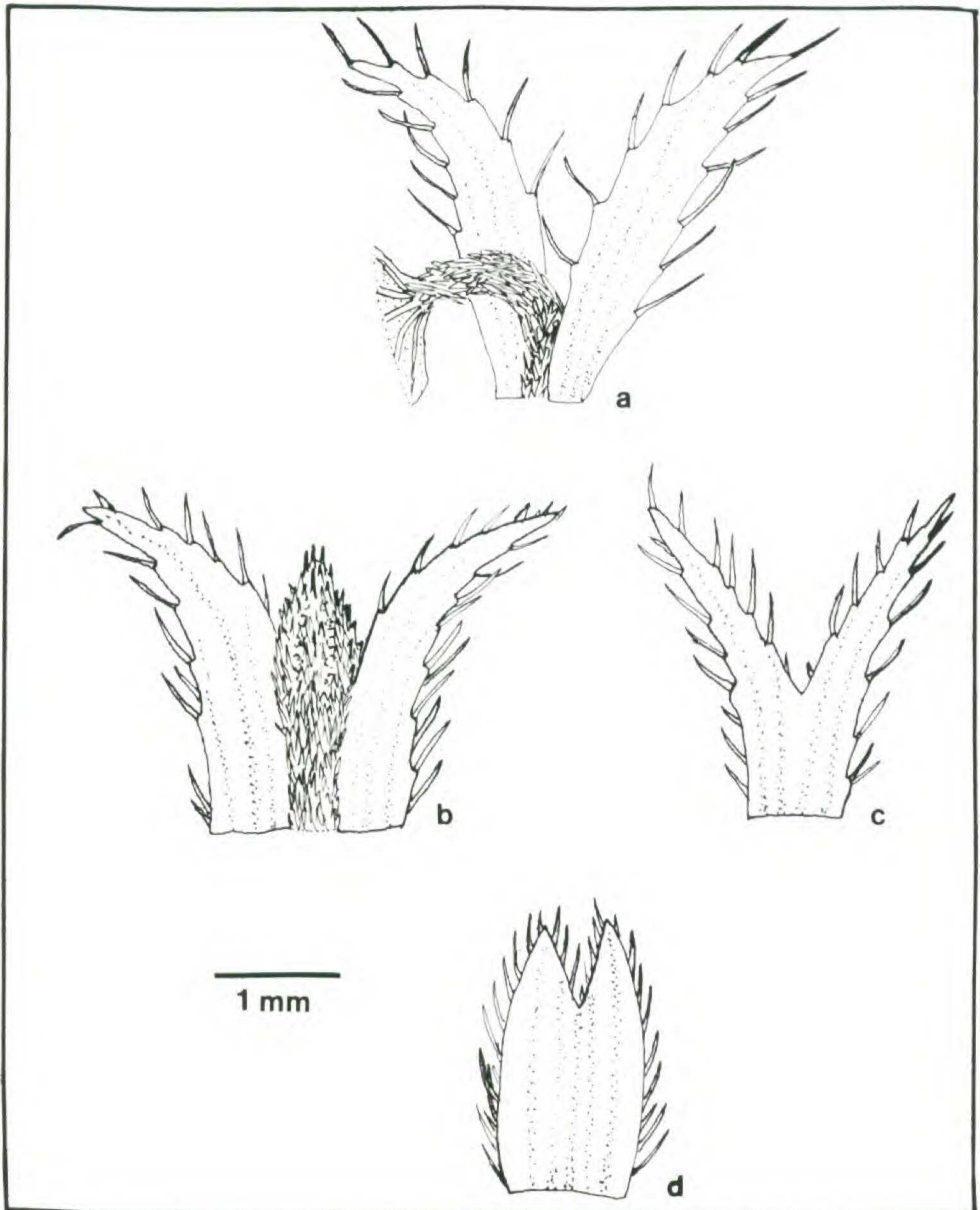


Figure 10. Evolution of the bifid floral bract in *Malvastrum*. a. Stipules of *M. coromandelianum* (Curtiss 6421). b. Leaf vestige (mature state) and adnate stipules *M. corchorifolium* (Correll & Evans 44026). c. Bifid bract *M. corchorifolium* (Molina 23070). d. Bifid bract, *M. americanum* (Ventura 2622). Adaxial surfaces.

others. On occasion the bracteoles are slightly falcate. The vesture, venation, and, to a lesser degree, the shape strongly resemble corresponding characters of the stipules and suggest a homology with those structures.

The bracteoles usually extend one-third to one-half the length of the calyx lobes in flower. Less frequently they extend to the lobe sinus (as in *Malvastrum aurantiacum*, *M. bicuspidatum* in part, and *M. hispidum*) or equal or exceed the calyx lobes (as in *M. americanum*, *M. corchorifolium*, *M. grandiflorum*, and *M. interruptum*). The bracteole length in relation to the calyx-lobes can be of value in distinguishing species, but is not particularly useful at the sectional level in *Malvastrum*. The length of the bracteoles varies from 2–3 mm in *M. spiciflorum* and some individuals of *M. hispidum* to a maximum of 18 mm in *M. grandiflorum*, averaging 4–8 mm. The width varies from 0.2–0.3 mm in *M. spiciflorum* and *M. tomentosum* to a maximum of 5 mm in *M. aurantiacum*, averaging 0.5–1.0 mm. While usually free or united to the calyx for less than 1 mm, the bracteoles are united to the calyx for as much as 2–3 mm in *M. aurantiacum*.

The bracteoles are erect and appressed in bud, are spread out as the calyx expands in fruit, but usually do not reflex. They possibly function along with the floral bract and vesture to protect the young flower buds from both water loss and predation.

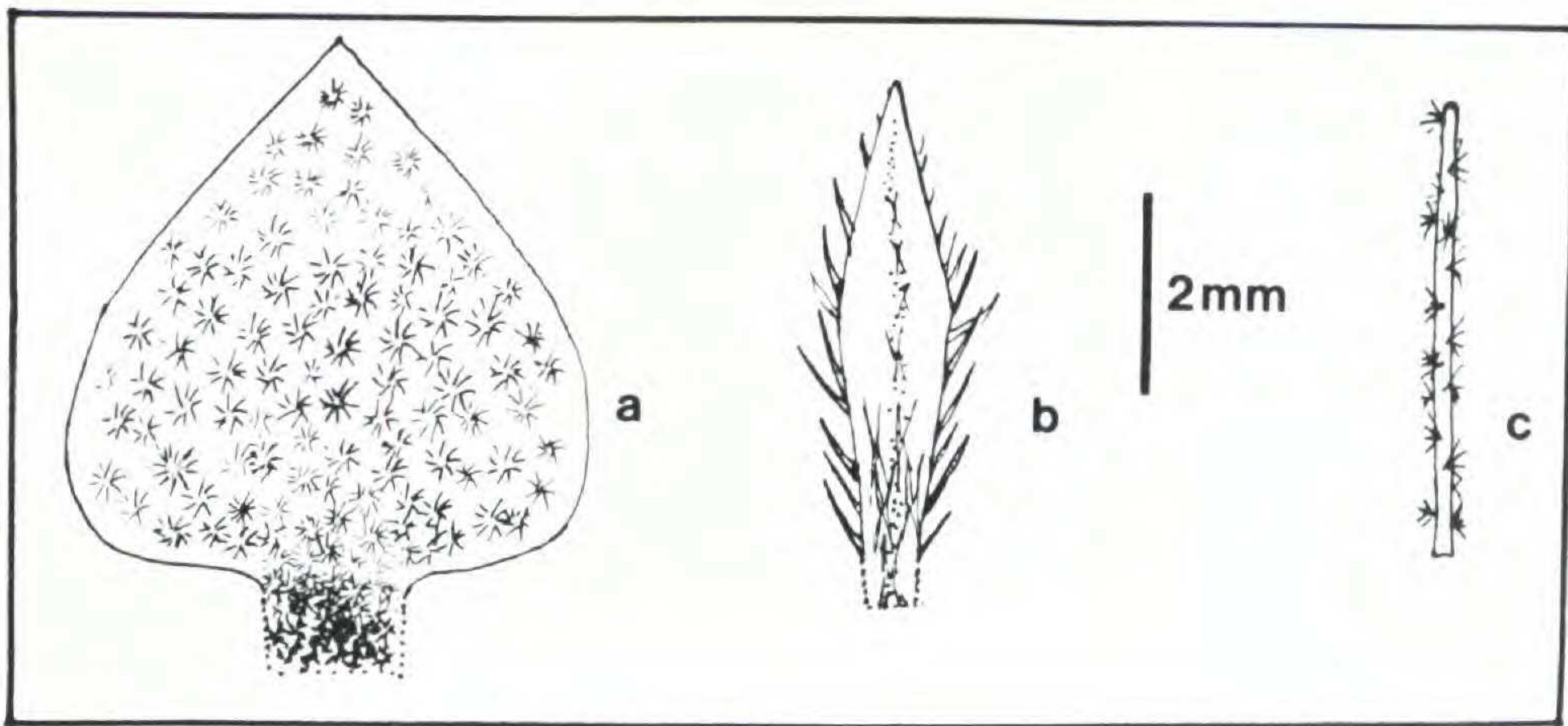


Figure 11. Involucellar bracteoles in *Malvastrum*. a. *M. aurantiacum* (Fryxell 1314). b. *M. coromandelianum* (Breedlove 20019). c. *M. tomentosum* (Stark 8973). Adnate portions stippled.

Calyx

The calyx in *Malvastrum* is composed of 5 sepals that are valvate in bud and united from 1/5 to 3/5 but usually 1/3 to half their length. The basal united portion is campanulate and glabrous within except for the basal nectaries. The lobes are deltate to narrowly triangular, acute acuminate to nearly cuspidate at the apex, and (1.5) 4–8 (15) mm long \times (1.5) 4–6.5 mm wide. The internal surface of the lobe is minutely pubescent marginally and in the upper half with arachnoid simple or stellate hairs. The external surface is pubescent, often densely so, with nearly the full range of hair types. Hairs of the calyx are of great diagnostic value since species-specific combinations are usually present.

The extent of lobing of the calyx and the length to width ratio of the lobes are too similar among the taxa to be of diagnostic value. The absolute length of the calyx from pedicel to lobe-apex is more useful, though also variable. The extremes at anthesis range from a minimum of 2.8 mm in *M. hispidum* to a maximum of 15 mm in *M. grandiflorum*. Since the calyx is usually somewhat accrescent by an additional 25%–75% in fruit it is important to indicate at what stage it is measured.

The venation of the calyx-lobes, while often obscure, is reticulate with usually 3–5 or up to 10 primary subparallel veins.

The orientation of the calyx-lobes in fruit is of great diagnostic value in some groups, such as in the subspecies of *Malvastrum bicuspidatum*, *M. coromandelianum*, and *M. tomentosum*. The orientation is, in most cases, correlated with the development of ornamentation of the fruit. Those taxa with rotate or spreading lobes often have mericarps with long distal-apical cusps and those with erect or incurved lobes often lack such ornamentation. Lobe-orientation, then, may also correlate with dispersal. Those fruits adapted for animal-transport are exposed for effective dispersal, and those not so modified are retained in the calyx cup for longer periods for gradual dispersal. Some taxa may have secondarily lost the rotate lobe orientation as a result of the disappearance of animal vectors within their ranges, as in several *M. bicuspidatum* subspecies, *M. coromandelianum* subsp. *capitato-spicatum* and subsp. *fryxellii*, *M. scoparioides*, and *M. tomentosum* subsp. *pautense*.

Corolla

The corolla of *Malvastrum* consists of 5 distinct petals united basally to the staminal column. The petals are strongly imbricate in bud. Aberrant flowers with 6 petals have been seen in cultivated specimens of *M. americanum* and *M. interruptum* but are of no diagnostic value. An 'ovary cup' is formed by the fusion of the petals and the lower staminal column. The petals have a short (0.5–2 mm) claw that lacks auricles at the base and which gradually widens into the main body of the petals. In shape, the petals are asymmetrically obovate and usually emarginate or unequally cleft as in many other genera of the Malvaceae, but those of *M. spiciflorum* are entire. The flowers are odorless.

The petals of *Malvastrum* are shades of yellow, varying from pale yellow to golden-yellow, yellow-orange, to pale orange. Those of the section *Tomentosum* in particular tend towards orange. The color, however, may vary slightly in intensity even within a taxon in different parts of its range, as in *M. coromandelianum* subsp. *coromandelianum*. In only one species, *M. grandiflorum*, the petal claws are red while the main body is golden-yellow, suggesting a greater attractiveness to insects.

The petals are elaborately vascularized with reticulate palmate veins that generally anastomose before reaching the margins. In this as well as shape they resemble to a remarkable degree the wings of certain insects.

In most taxa the petal claws are rather densely pubescent to ciliate-tufted along each margin with firm, simple or stellate hairs. These intermesh with those of adjacent petals obscuring the calyx below. This screen may serve to protect the delicate glandular nectary-hairs on the calyx in that region and to prevent the evaporation or thickening of the sparse nectar. In several cases the claw-hairs are very sparse and this may indicate a lack of dependence on nectar as an insect-attractant.

The size of the petals is occasionally of diagnostic value, but since they are fragile, mucilaginous, and usually last for only a few hours they are often not adequately preserved on dried specimens. They vary in length from a minimum of 2.0–3.0 mm in *Malvastrum hispidum* and *M. spiciflorum* to a maximum of 23 mm in *M. grandiflorum*. The width of the petals varies from a minimum of 1.5–2.0 mm in *M. hispidum* and *M. spiciflorum* to a maximum of 15

mm in *M. grandiflorum* and *M. aurantiacum*. Petal-size tends to correlate with the pollination mechanism. Autogamous species have the smallest petals occasionally subequal to the calyx and entomophilous species have the largest petals exceeding the calyx by as much as 8 mm. In several taxa, particularly in *M. bicuspidatum*, *M. corchorifolium*, and *M. coromandelianum* subsp. *capitato-spicatum* the petals are smaller on individuals approaching dormancy. This may also be the case in other members of the section *Tomentosum* as observed in herbarium specimens. This phenomenon is not conspicuous in the other taxa.

The orientation of the petals is variable and also seems to correlate with the pollination mechanism. Those species with rotate corollas are either known to be or suspected to be obligate or facultative outcrossers and those with campanulate corollas are suspected to be primarily autogamous (*M. amblyphyllum*, *M. chillagoense*, *M. corchorifolium* in part, *M. hispidum*, and *M. spiciflorum*). *Malvastrum corchorifolium* was seen to produce both rotate and campanulate corollas depending upon the time of year and position of the flower. *Malvastrum hispidum* is occasionally cleistogamous.

Androecium

The androecium of *Malvastrum* is composed of monadelphous stamens which usually arise (as seen in bud) from five groups of primordia (Van Heel, 1966). This five-ranked symmetry is retained at anthesis in *M. grandiflorum* and less frequently in *M. coromandelianum*, but for the most part is obscured by the densely packed nature of the anther cluster. The filaments are united into a slender column 1.0–7 mm in height and are free at their apex for an additional 0.5–2.0 mm. Each is terminated by a unilocular anther with a partially intrusive or incomplete septum. Two anthers occasionally terminate a filament, and bilocular or incompletely bilocular anthers are occasionally seen. The anthers are attached by the free portions of the filaments at various levels at the apex of the column, which is the same color as the corolla.

The filament-tube may be either glabrous or sparsely pubescent with minute 2–5-rayed stellate hairs similar to those of the petal claws. This character is diagnostic as variation rarely occurs within a taxon. For example, *M. aurantiacum*, *M. coromandelianum*, and

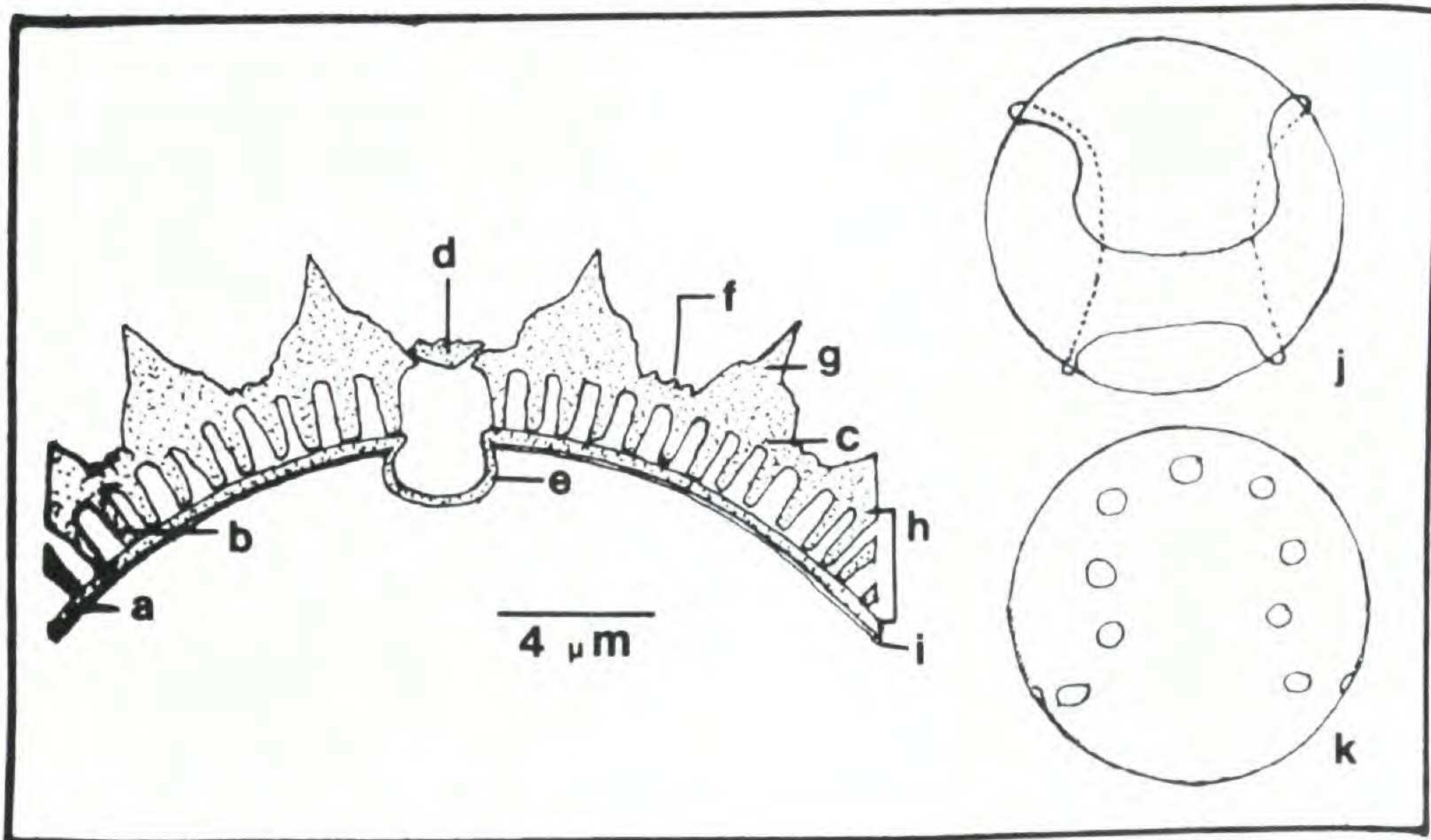


Figure 12. Pollen morphology in *Malvastrum*. a. Endexine. b. Ektexine columella. c. Tectum. d. Operculum. e. Apertural annulus. f. Verrucae. g. Spine (echina). h. Ektexine. i. Intine. j-k. Two views of most frequent aperture pattern—schematic (apertures not indicated in j; from Tressens, 1974).

M. hispidum all have glabrous staminal columns while those of the remaining taxa have at least a few hairs.

Anther number varies considerably both within and between taxa. The lowest number of anthers encountered is 5–6(7) in *M. spiciflorum*, followed by 8–13 (16) in *M. hispidum*. In each of these autogamous species the number is thought to be reduced from the usual number of 16–50 encountered in the majority (18) of the taxa. The highest number encountered is in the entomophilous *M. grandiflorum* with 108–111 stamens per flower. Stamen number tends to correlate with the type of pollination-system encountered, as do petal size and petal orientation.

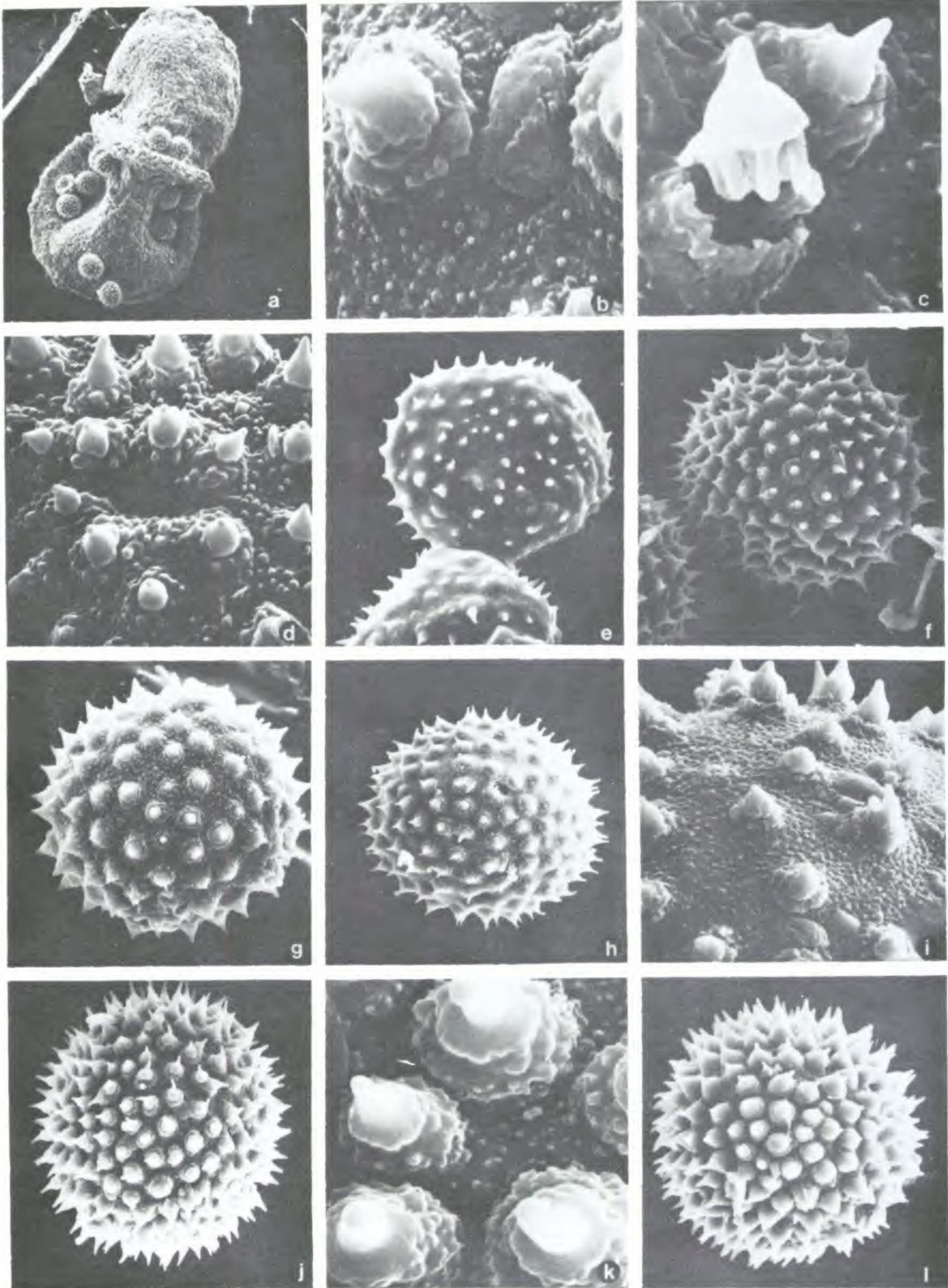
Pollen

The pollen produced by species of *Malvastrum* is spheroidal to slightly oblate, echinate, operculate, and panporate as in most other genera of the Malvaceae (Fig. 12–14). The grains vary in diameter from a minimum of 36 μm in *M. spiciflorum* to a maximum of 108 μm in *M. aurantiacum* (Fig. 13b, h & i), *M. coromandelianum* subsp. *coromandelianum* (Fig. 13j–k), and *M. grandiflorum*. The

average is 60–90 μm . The tectum is supported by a series of evenly-spaced columellae (Fig. 12b, Fig. 13c). The number of apertures varies from a minimum of 4–5 in *M. spiciflorum* to a maximum of about 35 in *M. grandiflorum*, with an average of 6–15 in the genus. The spines or echinae are rather short for the family, ranging from 2.3–3.8 μm in *M. spiciflorum* to a maximum of 10 μm in *M. aurantiacum*, averaging 4–7 μm in length. The apertures are usually arranged in a pattern resembling, in three dimensions, the seam of a tennis-ball or baseball and in two dimensions resembling a wide dumbbell (Fig. 12j–k, 14b). This pattern is most conspicuous in acetolyzed grains of *M. americanum*, *M. aurantiacum* (Fig. 13h), *M. coromandelianum*, and *M. hispidum* (Fig. 14b) but is obscure if the opercula are in place.

My measurements of pollen-diameter were consistently greater than those of Tressens (1974) who presented an excellent review of pollen in the genera *Malvastrum* and *Acaulimalva*. The difference was 4%–20% depending on the species. I feel that this was due to my preliminary KOH treatment which occasionally expands the grain. In addition, my measurements were taken from acetolyzed spores temporarily mounted in 70% alcohol, while Tressens recorded her diameters from specimens mounted in glycerine gelatin. However, other observations such as spine-length and aperture-number as well as relative size correspond well with Tressen's review, as well as measurements given by Hashmi (1970).

Figure 13. *Malvastrum* pollen I. a. Dehisced anther with several grains, *M. americanum* (Parks & Cory 20661). b. Operculate aperture and ornamentation, *M. aurantiacum* (Johnson 952). c. Spine structure showing columellae, *M. americanum* (Parks & Cory 20661). d. Open aperture and ornamentation, *M. interruptum* (Krapovickas et al. 18808). e. Immature surface ornamentation, *M. amblyphyllum* (Krapovickas et al. 19127). f. Mature grain, *M. amblyphyllum* (Krapovickas et al. 18558). g. Mature grain, *M. americanum* (Parks & Cory 2066). h. Mature grain, *M. aurantiacum* (Johnson 952). i. Ornamentation, *M. aurantiacum* (Johnson 952). j. Mature grain, *M. coromandelianum* subsp. *coromandelianum*. (Flores-Crespo 96). k. Ornamentation, *M. coromandelianum* subsp. *coromandelianum* (Cory 36085). l. Mature grain, *M. coromandelianum* subsp. *fryxellii* (Anderson et al. 9096). (a. 92 \times ; b, d. 3960 \times ; c. 5280 \times ; e, f, j, l. 660 \times ; g. 925 \times ; h. 460 \times ; i. 1320 \times ; k. 4950 \times ; magnifications calculated from instrument readings).



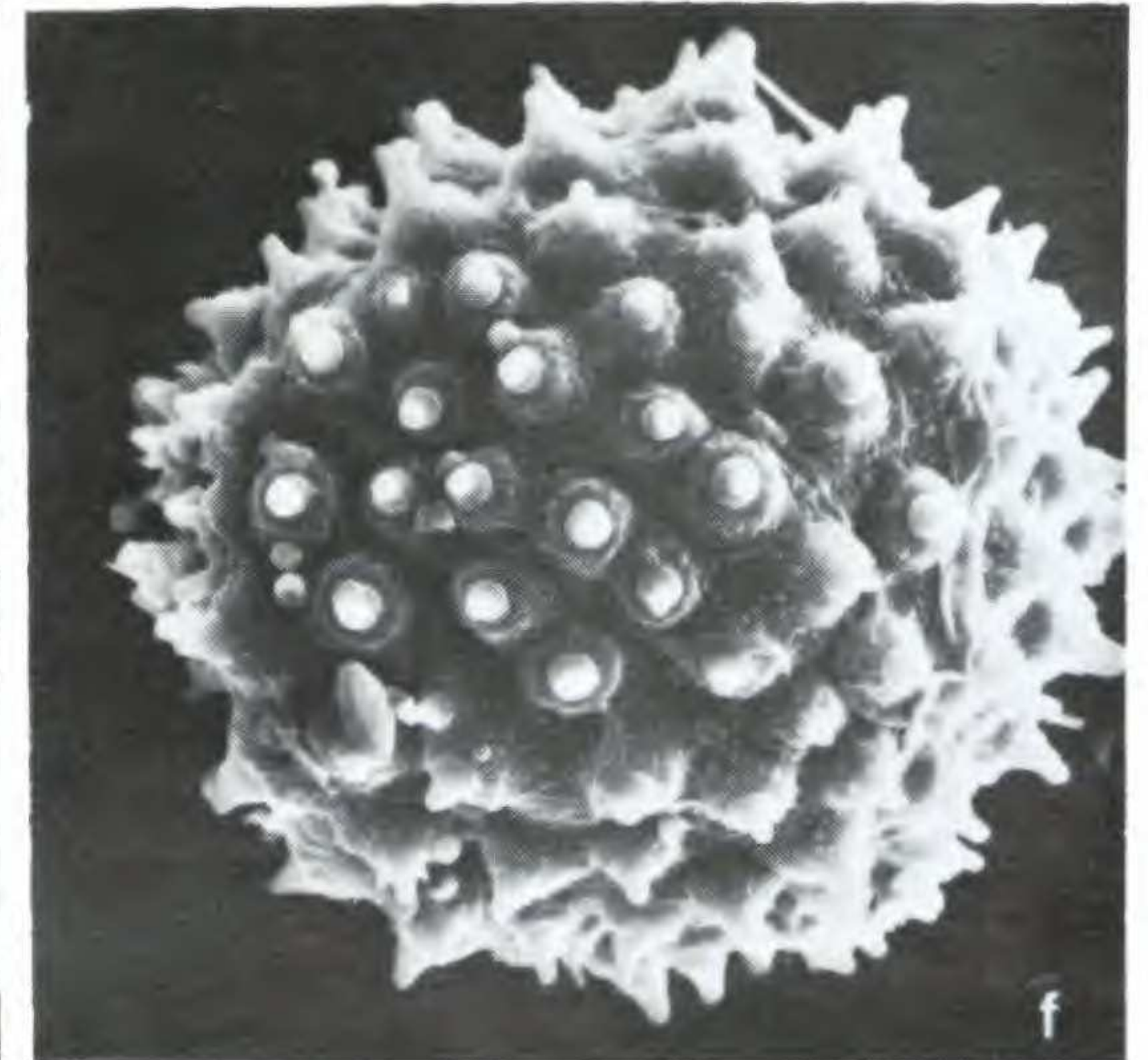
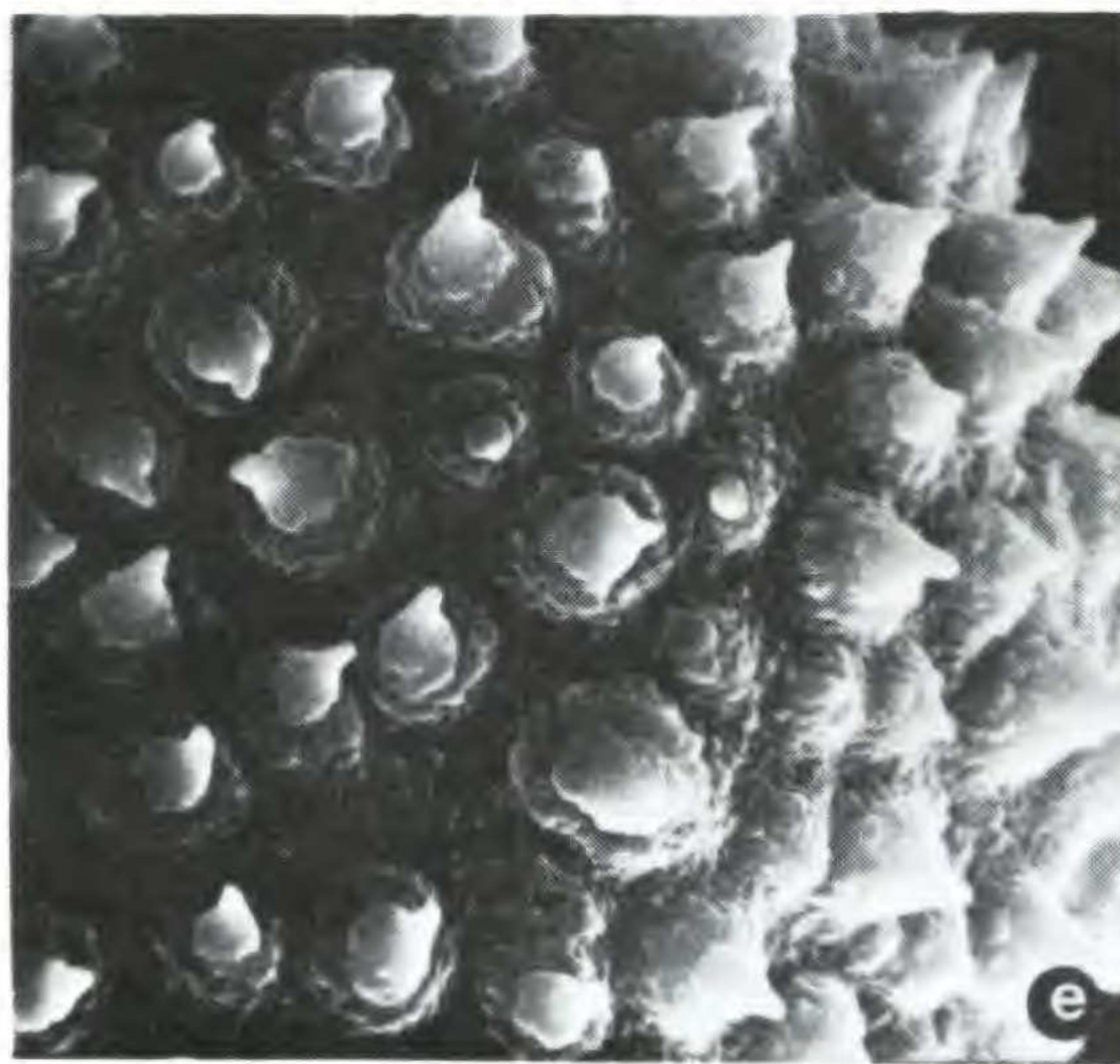
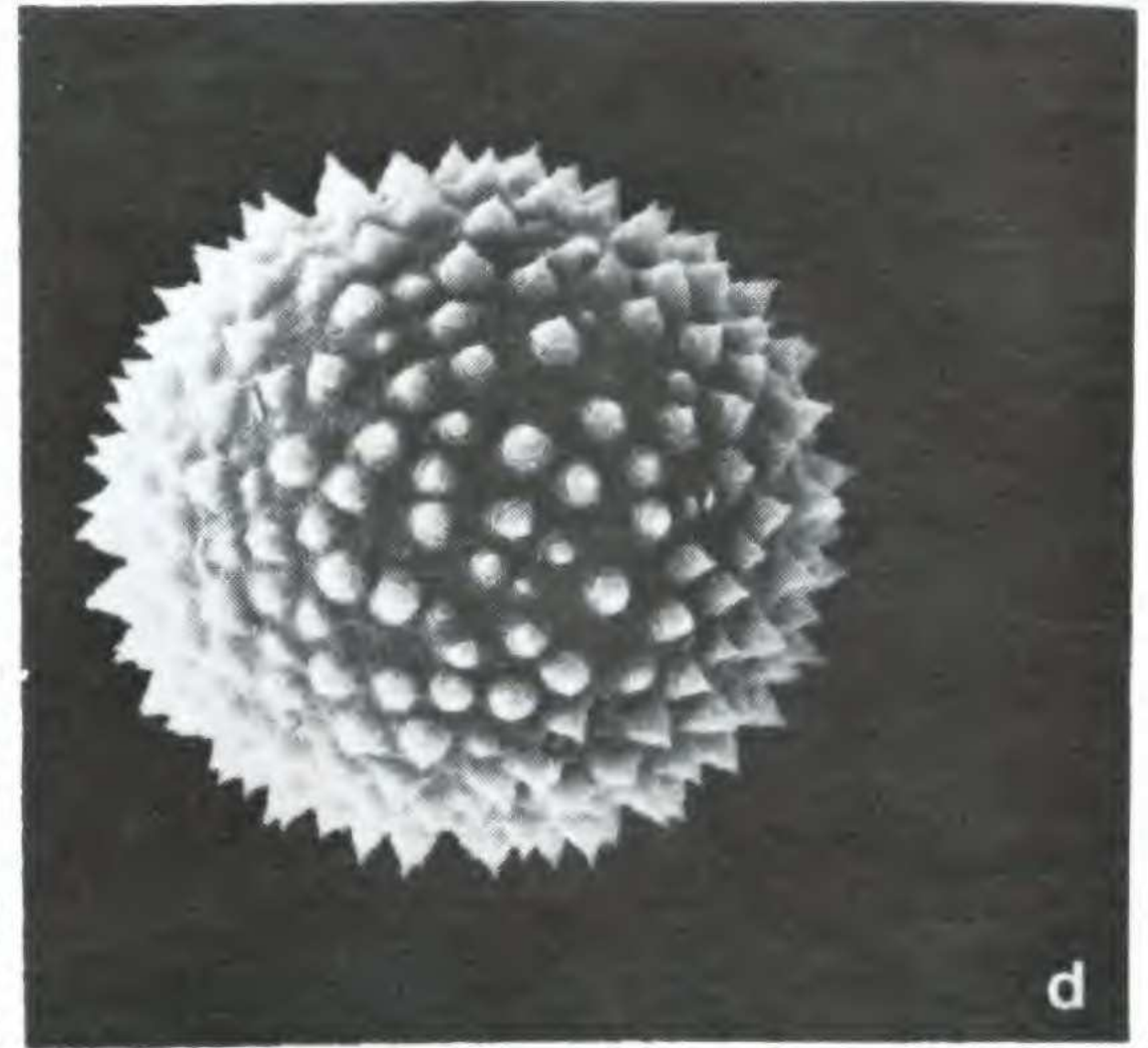
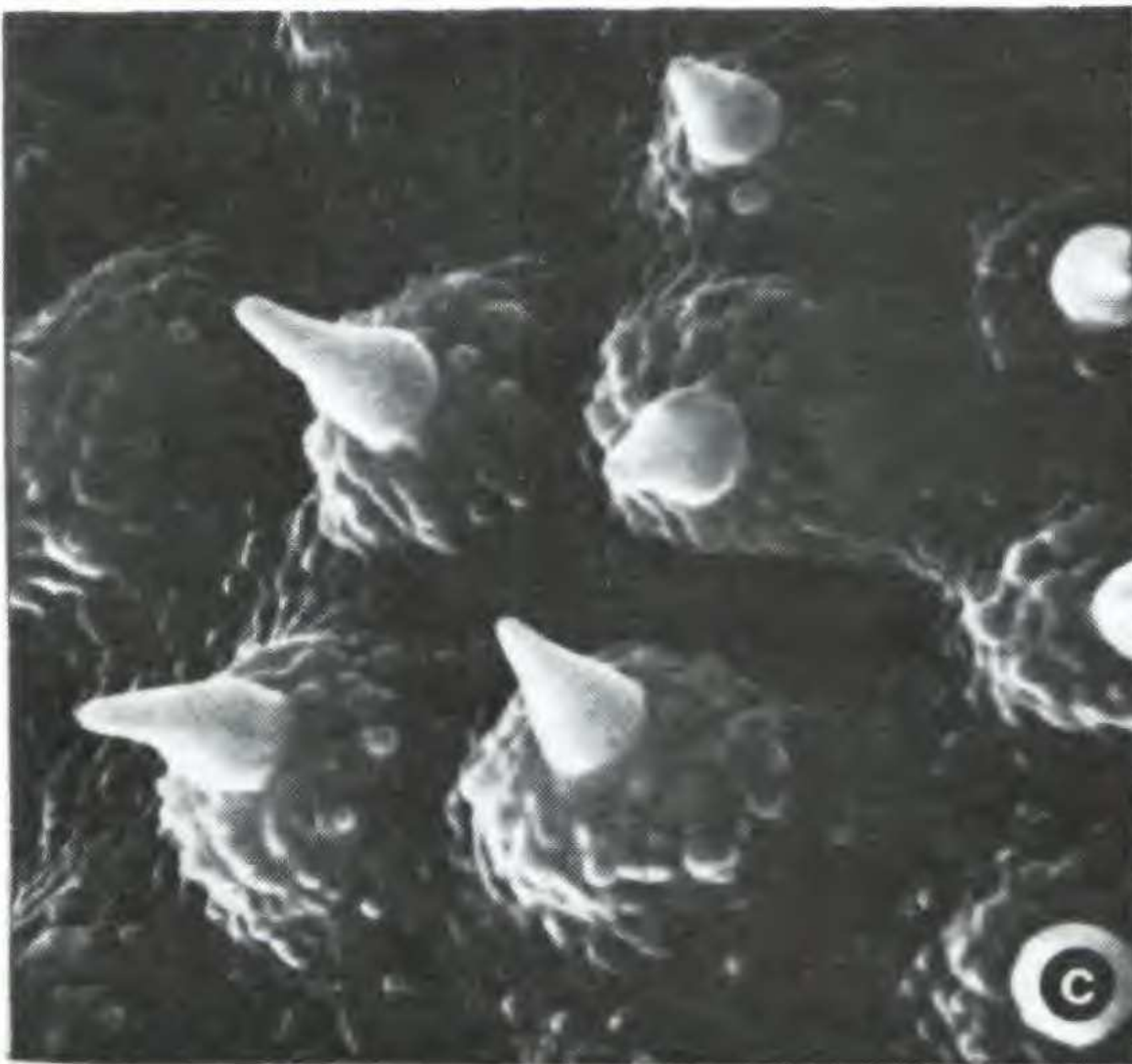
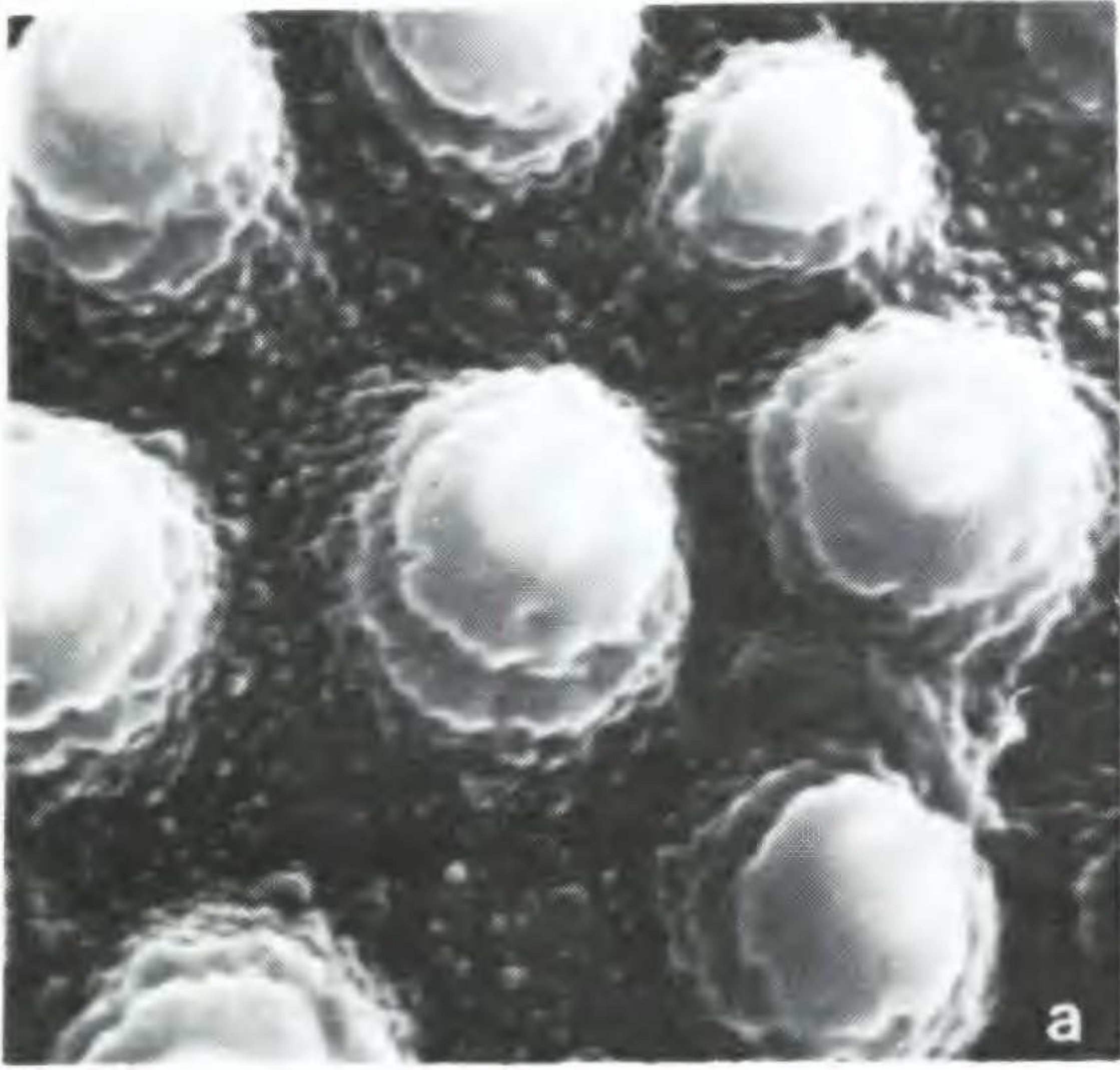
Gynoecium

The features of the gynoecium included in this review are the styles, stigmas, carpels, columella and carpocrater, and the ovules. Features of the gynoecium have been of great significance in delineating not only genera but also tribes in the Malvaceae.

In *Malvastrum* as in all other Malveae the single style branches above the ovary. In this genus the style is always glabrous. The branching in *Malvastrum* occurs at about 1/2 to 2/3 the distance above the apex of the columella and the number of branches equals the number of carpels. The style branches are erect or recurved. While in *M. grandiflorum* the branches remain erect even as the flower wilts, in most other taxa the branches recurve before, during, or after anthesis. This orientation, as discussed earlier, is very important to the breeding system as it can control outcrossing or self-pollination. The style or carpel number varies from a minimum of 5–6 in *M. hispidum* to a maximum of 18 in some individuals of *M. americanum* and *M. grandiflorum*. The unbranched portion of the style varies in length from 1.5–2.1 mm in *M. hispidum* and *M. spiciflorum* to a maximum of 12 mm in *M. grandiflorum*, and the branches vary in length from 0.5–0.8 mm in the former two to 7 mm in the latter. The styles may equal the stamens in height or exceed them by up to 5 mm.

While the capitate stigmas were among the first structures used to distinguish *Malvastrum* from other genera in the Malveae and from *Malva* in particular, when all of the taxa are examined not all of the stigmas are capitate (in the sense of being expanded at the terminus). In fact, in *M. chillagoense* the stigmas are smaller in diameter than the style branches. In *M. bicuspidatum* subsp. *campanulatum* the stigmas are subequal to the styles in diameter. Nevertheless, the stigmas are always terminal, never decurrent even slightly, and are mostly capitate with a subhemispherical to spherical shape and a

Figure 14. *Malvastrum* pollen II. a. Ornamentation, *M. coromandelianum* subsp. *fryxelli* (Anderson et al. 9096). b. Mature grain, some fungal damage, *M. hispidum* (Bates 2705). c. Ornamentation, *M. hispidum* (Bates 2705). d. Mature grain, *M. interruptum* (Krapovickas et al. 18808). e. Ornamentation, *M. interruptum* (Krapovickas et al. 18808). f. Mature grain, *M. scoparioides* (López & Sagastegui 7672); (a. 3300×; b-d. 660×; c. 3960×; e. 1980×; f. 725×; magnifications calculated from instrument readings).



papillose surface. The pollen-grain becomes rather firmly situated as its spines loosely interlock with the papillae. Usually only 1–4 grains can attach to a single stigma due to their size.

The carpels are loosely coherent or contiguous with one another but are adnate to the central columella, a structure that in position closely resembles the placental axis of capsular fruits in the Malvaceae. The number of carpels, 5–6 to 18, varies between and within species, but the range in variation can aid in species determination. As an example of intraspecies variation, the number may vary from 9 to 18 in *Malvastrum americanum*. Usually the number varies a great deal less than that. The carpel wall in *M. coromandelianum* has 4 layers of tissue (Fig. 15): an obscure epidermis, an exocarp of large irregular parenchyma cells, a mesocarp region of small sclerenchyma cells that is greatly thickened to form the cusps, and a single-celled endocarp of small firm cells that lines the locule. From the epidermis arise the translucent, firm, centrally (proximally) directed simple to multiradiate stellate hairs of the apical surface.

The columella is a generally persistent cylindrical, clavate, or peltate structure at the center of the calyx to which the carpels and style are attached. It is usually expanded above its base before fruit maturity and so produces a medial notch on the proximal margin of each mericarp corresponding to this expanded zone. It seems evident that its shape and dimensions can be of limited diagnostic use. For example, *M. bicuspidatum* subsp. *bicuspidatum* has a flared columella with a narrow base which contrasts with the turbinate columella of *M. bicuspidatum* subsp. *campanulatum*. This results in the very deep proximal notch in mericarps of the former and shallow notches in those of the latter. Variation in the columella does not seem to be of great diagnostic value above the species level in *Malvastrum* and varies to an extent within a single plant as it dries in fruit.

Associated with the columella and perhaps a basal outgrowth of it is a thin disc of tissue that is cartilaginous to chartaceous in the center and membranous or hyaline marginally. This is the carpocrater, a term proposed by Hochreutiner (1920) and applied by him to the structure as found in the genus *Cristaria*. The carpocrater in *Malvastrum* is far less developed than in *Cristaria*. It varies in diameter among the taxa but does not seem to be of great diagnostic value in *Malvastrum*. The carpels are completely free of the carpocrater but are subtended by it.

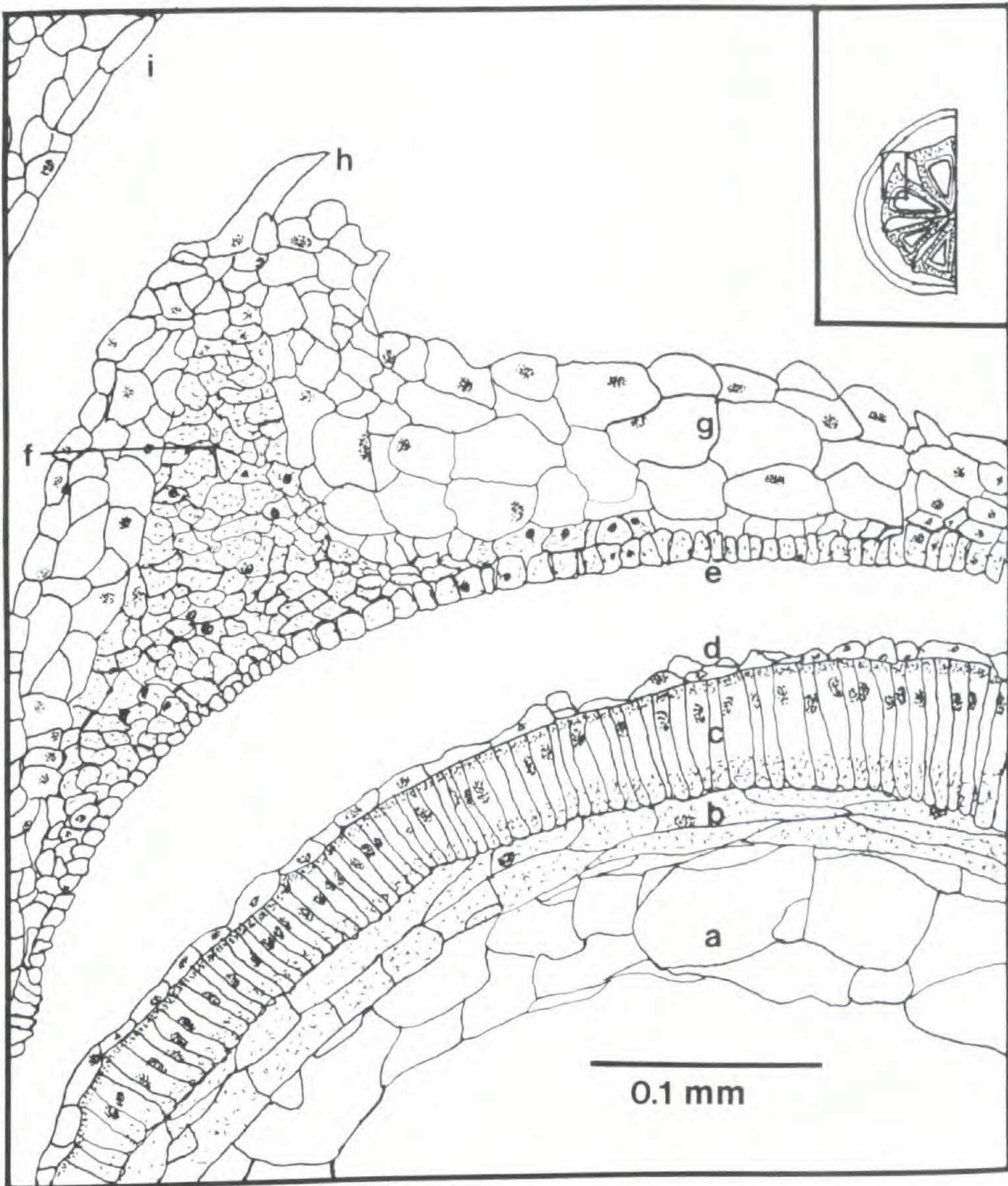


Figure 15. Seed and fruit tissues, *Malvastrum coromandelianum*. a. Endosperm. b. Inner integument. c. Outer integument. d. Epidermis of outer integument. e. Endocarp. f. Sclerenchymal support tissue for mericarp cusp (mesocarp) g. Exocarp. h. Trichome. i. Calyx. Inset: portion of fruit enlarged. Camera lucida, (Hill 5112).

The ovules in *Malvastrum* are always solitary and ascending in each carpel. Each is attached to the axile (proximal) placenta of the columella by a minute funiculus that is located immediately below the medial ovule-notch. The micropyle is present below the funiculus, and the young embryo begins its development in this lower region. As the embryo develops, the radicle is inferior. The endosperm is consumed by the embryo, but tissues are not well differentiated in the dormant seed.

Fruit

The mature ovary of *Malvastrum* is a complex oblate to discoid schizocarp. It consists of the mature carpels or mericarps associated with the central columella and carpocrater, and is enclosed by the accrescent persistent calyx. In most cases the dried corolla persists for a time, adhering to the withered style at the center of the fruit. The calyx itself may by means of its lobes enclose the fruit and prevent rapid dispersal or may expose the fruit allowing rapid dissemination. The pedicel, calyx, and columella normally do not abscise from the inflorescence axis.

The individual mericarps are either schizocarpic achenes or schizocarpic follicles depending on whether they are indehiscent or dehiscent, respectively. When the mericarps separate from the columella along the proximal surface, a small portion of the wall remains attached and a narrow opening in the region of the hilum results. In this sense, the seed is no longer attached to the pericarp. The opening is too small to allow the seed to escape.

The mericarp is the single most important structure used to determine taxa in *Malvastrum*. This is due to several facts: 1) the mericarps scarcely vary in morphology within a given taxon and so have been traditionally used to distinguish taxa in the tribe Malveae, 2) the mericarp often exhibits important specializations or structures suggesting the relationships of taxa, 3) the mericarps are usually present in both living individuals and herbarium specimens, and 4) the other structural features of the plant, both vegetative and reproductive, are often too variable to allow a definitive determination. For these reasons keys to the taxa are generally dependent upon characteristics of the mericarps. While often small, the important characters are visible with a hand lens. In shape the mericarp simulates a wedge cut from an oblate wheel of cheese. There are three surfaces: two lateral surfaces and a continuous apical-distal-basal surface. There is a single nearly straight proximal margin and two curved lateral margins. I feel that in the Malveae the terms proximal and distal referring to the relationship of the carpel and the columella are more precise and easily understood than the terms dorsal and ventral. The mericarps are conspicuously notched in direct relation to the amount of expansion in the upper portion of the columella. In mature fruits the columella has shrunk and drawn away from the notch, facilitating mericarp separation.

The size of the mericarp is of diagnostic value, but mostly in the case of the extremes. The height including ornamentation varies from a minimum of 1.0–1.5 mm in *Malvastrum spiciflorum* to a maximum of 6 mm in *M. aurantiacum*, the length varies from a minimum of 1.0–1.5 mm in *M. chillagoense* and *M. spiciflorum* to 5–6 mm in *M. aurantiacum*, and the width varies from 0.8 mm in *M. americanum* and *M. interruptum* to 2.0 mm in *M. amblyphyllum* and *M. grandiflorum*.

The pericarp is usually pubescent on the external apical surface, the apical and distal margins of the lateral surfaces, and, to a lesser degree, on the apical half of the distal surface. A few sparse hairs may occur in other regions. The hairs vary in type and density and are of diagnostic value. One taxon (*Malvastrum bicuspidatum* subsp. *tumidum* var. *glabrum*) has glabrous mericarps. The pericarp is usually green until it reaches maturity and dries to tan or brown. The mericarps of *M. aurantiacum*, *M. bicuspidatum*, and perhaps a few others not cultivated in this study become rose or raspberry-red and are very conspicuous in later immature stages, but at full maturity fade to tan or brown.

The pericarp is often ornamented with one or more mucros or cusps. This ornamentation is completely lacking on the mericarps of *Malvastrum chillagoense*, *M. hispidum*, and some populations of *M. americanum*. A minute single proximal apical mucro less than 0.1 mm in length is present on the mericarps of *M. interruptum*, *M. spiciflorum*, and the remaining populations of *M. americanum*. All of the other taxa have two or three conspicuous to obscure cusps or mucros. In the sections *Amblyphyllum* and *Tomentosum* there is a single proximal-apical mucro or small cusp 0.1–1.0 mm long and two distal-apical often conspicuous cusps 0.5–2.0 mm long on the pericarp. The cusp is often vertically dehiscent in the section *Tomentosum*. In the section *Malvastrum* the very conspicuous apical cusp, 1.0–2.3 mm long, is set nearly midway between the proximal and distal margins giving it a different aspect; the distal-apical cusps are also present but are generally smaller (0.2–1.1 mm long). In *M. aurantiacum* the distal cusps are flattened contiguous apparently non-functional vestigial structures. The cusps are often beset with conspicuous bristle-hairs up to 1.0 mm long that may aid in dispersal by increasing the tendency to become “hooked” on fur, feathers, or clothing.

In addition to the cusps, the mericarps of *M. amblyphyllum* and *M. grandiflorum* have prolonged, briefly winged distal-lateral margins that are thin and translucent between their supporting ribs. The wings are so short (up to 0.5 mm long) that their value as a dispersal aid is obscure.

The thickness of the pericarp and its texture can also be diagnostic. In *Malvastrum hispidum*, *M. interruptum*, and *M. spiciflorum* the lateral faces are thin and nearly translucent. In *M. bicuspidatum* subsp. *tumidum* and subsp. *oaxacatum* the pericarp is shiny and leathery or chitinous and of moderate thickness. The remaining taxa have firm dull soft-woody pericarps that often have radial lateral supportive ribs. Those taxa with the most conspicuous cusps also usually have the thickest pericarps and the best rib-development. This probably gives added strength to mericarps adapted to long-distance transport.

The degree of dehiscence of the pericarp is variable within the genus. While *Malvastrum* was formerly considered to have only indehiscent or slightly dehiscent mericarps (Kearney, 1955), one taxon with completely dehiscent mericarps (*M. hispidum*) is now included in the genus. The mericarps of *M. americanum* and *M. corchorifolium* tardily split along the medial suture of the basal region to release the seed. The mericarps of the remaining taxa do not split, but the mericarps of several taxa, including *M. americanum*, *M. corchorifolium*, *M. coromandelianum*, *M. scoparioides*, and *M. tomentosum*, are unsealed at the proximal apical margin above the notch at maturity. In nearly every taxon, including those with indehiscent pericarps, a medial line or suture is present along the apical-distal-basal surface suggesting a connection with ancestral forms with loculicidally dehiscent mericarps as in *M. hispidum*.

The presence or absence of an endoglossum is of diagnostic value at the specific and subspecific level in *Malvastrum* although this structure is often small. When present, the endoglossum is found slightly distal to the proximal-apical margin on the internal apical surface. It is a small intrusive tissue that incompletely divides the lustrous internal chamber into a large seed bearing chamber and a small empty proximal-apical 'chamber.' The proximal margin of this 'chamber' may or may not be sealed, as described above. Those taxa with an endoglossum or endoglossum remnant include *M. bicuspidatum* subsp. *oaxacatum*, *M. corchorifolium*, *M. scopari-*

oides, *M. tomentosum* (both subspecies), and most populations of *M. americanum*. The remaining taxa lack this structure.

Seeds

Malvastrum seeds are basically reniform and have a very firm, three-layered seed coat that is completely glabrous. The outer layer of the seed coat (Fig. 15d) consists of a fragile external tissue that may produce a thin wax layer giving the seed a glaucous appearance. This coat is often absent or worn away after the seed is shed. The second layer is composed of densely-packed, radially elongated, heavily sclerified cells that are reduced in size in the regions of the notch and hilum (Fig. 15c). The third layer is composed of thin, non-sclerified tissues (Fig. 15b). The thick seed coat contributes to the durability and longevity of the seed. The seed retains a soft proximal-basal flap of placental or hilum tissue, which is often lost in age through abrasion. The color of the seed coat varies from gray to chestnut-brown or black.

Seed shape is determined by the shape of the enclosing pericarp to which the seed conforms when it is immature. The seed shrinks slightly as the seed coat hardens (shrinkage is most pronounced in *M. aurantiacum*). In some taxa of the section *Tomentosum* the seed has a medial distal-apical sulcus that conforms to the firm indented pericarp and enlarged cusps in that region, as in *M. bicuspidatum* (subsp. *bicuspidatum*, subsp. *campanulatum*, and subsp. *tumidum*), *M. guatemalense*, and *M. tomentosum* subsp. *tomentosum*. The seed of *M. aurantiacum* bulges in this same region conforming with the chamber expansion in that cusp area. Seeds from unusual populations of *M. americanum* var. *americanum* from northern Queensland, Australia, with apically prolonged mericarps have correspondingly narrow elongated seeds. In nearly all of the species the reniform seed shape is modified by the pericarp so that the portion below the notch is narrower and attenuated compared to the broader apical half.

Seed size varies in radial length from a minimum of 1.0 mm in *M. spiciflorum* to a maximum 2.5 mm in length in *M. aurantiacum* and *M. hispidum*; the height varies from 1.0 mm in *M. spiciflorum* to 2.5–3.0 mm in *M. aurantiacum*; and the width varies from 0.6–0.7 mm in *M. spiciflorum* to 1.3–1.5 mm in *M. aurantiacum* and *M. hispidum*.

Chromosome numbers

Chromosome numbers for members of the genus *Malvastrum* are summarized in Table 3, including counts obtained during the course of this study. I found that mitotic counts could be most readily obtained from apical and root meristems of seedlings at the early cotyledon-stage as the tissues were more difficult to hydrolyze at later stages. The seedlings were first pretreated in a saturated aqueous solution of monobromonaphthalene for 4 hours and then were fixed in a 3:1 ethanol: glacial acetic acid solution overnight. Next the seedlings were hydrolyzed in 1 N HCl for 30 minutes at 60° C, and the shoot and root meristems were placed in Feulgen staining solution for another 30 minutes. The meristems were then isolated and squashed in a drop of aceto-carmine solution and examined. Flower buds for meiotic counts were also pretreated as above, but after being fixed, the anthers were macerated in a drop of aceto-carmine, heated briefly over an alcohol flame, squashed and examined. My results were consistent with those of previous investigators. Selected preparations are illustrated in Figs. 16 and 17.

The base number found in *Malvastrum* is $x = 6$. Of the 22 taxa of *Malvastrum*, counts are known for all but six (i.e., *M. americanum* var. *stellatum*, *M. chillagoense*, *M. guatemalense*, *M. bicuspidatum* subsp. *tumidum*, *M. bicuspidatum* subsp. *tumidum* var. *glabrum*, and *M. tomentosum* var. *pautense*). There is only a single known diploid, *M. spiciflorum*, $2n = 12$. Among the remaining 15 taxa whose chromosomes have been examined, 10 are tetraploids with counts of $n = 12$ or $2n = 24$, and three (*M. aurantiacum*, *M. hispidum*, and *M. interruptum*) are hexaploids with reported counts of $n = 18$ or $2n = 36$. *Malvastrum corchorifolium* is an octoploid with counts of $n = 24$ or $2n = 48$. *Malvastrum scoparioides* may also be an octoploid with the single tentative count $2n = \text{ca. } 48$. Aneuploids have not been recorded for the genus.

The chromosomes are mostly acrocentric but (as in *M. americanum*, *M. corchorifolium*, and *M. coromandelianum*) 1 or 2 pairs are metacentric. In addition, usually 1 to 3 pairs have satellites (Fig. 16 d-d' and 17 a-a'). An idiogram of *M. coromandelianum* (as *M. tricuspidatum*) has been prepared by Hazra and Sharma (1971).

Table 3. **Chromosome numbers in *Malvastrum*.** References are to previous counts, vouchers cited refer to new counts.

Taxon	Count	Reference or Voucher
<i>M. amblyphyllum</i>	$2n = 24$	Krapovickas, 1954b; <i>Krapovickas 18558</i> (cult.) ¹
<i>M. americanum</i>	$n = 12, 2n = 24$	Skovsted, 1935, 1941; Krapovickas, 1951, 1954b; Bates, 1976; <i>Hill 6051</i> ^{2,3} ; <i>Hill 7640</i> ³ ; <i>Hill 6054</i> ³ ; <i>Molina 27315</i> (cult.) ¹ ; <i>Percival s.n.</i> (cult.) ¹ ; <i>Seymour 2362</i> (cult.) ^{1,4} ; <i>Ventura 2622</i> (cult.) ¹ ; <i>Williams et al. 23805</i> (cult.) ^{1,4} ; <i>Croat 9705</i> (cult.) ²
<i>M. aurantiacum</i>	$n = 18, 2n = 36$	Bates & Blanchard, 1970; <i>Hill 6430</i> (cult.) ¹ ; <i>Hill 5878</i> ³
<i>M. bicuspidatum</i> subsp. <i>bicuspidatum</i>	$n = 12, 2n = 24$	Bates, 1976; <i>Bye 6940</i> (cult.) ³ ; <i>Gentry 14522</i> (cult.) ³ ; <i>Lehto et al. 19487</i> (cult.) ^{1,3,4}
<i>M. bicuspidatum</i> subsp. <i>campanulatum</i>	$n = 12, 2n = 24$	Krapovickas, 1969; Bates, 1976
<i>M. bicuspidatum</i> subsp. <i>oaxacanthum</i>	$2n = 24$	<i>Krapovickas 23596</i> (cult.) ¹
<i>M. corchorifolium</i>	$n = 24, 2n = 48$	Krapovickas, 1967; Newton & Kisseadoo, 1978; <i>Contreras 5588</i> (cult.) ³ ; <i>Correll 43854</i> (cult.) ¹ ; <i>Correll 45520</i> (cult.) ¹ ; <i>D'Arcy 394</i> (cult.) ¹ ; <i>Fryxell 2861</i> (in part, cult.) ⁴ ; <i>Lakela 27892</i> (cult.) ¹ ; <i>Molina 27248</i> (cult.) ¹ ; <i>Seymour 6129</i> (cult.) ¹ ; <i>Standley 25780</i> (cult.) ¹
<i>M. coromandelianum</i> subsp. <i>coromandelianum</i>	$n = 12, 2n = 24$	Skovsted, 1935, 1941; Krapovickas, 1951, 1954b; Roy & Sinha, 1961; Bates, 1967b; Hazra & Sharma, 1971; Bir & Sidhu, 1975; Newton & Kisseadoo, 1978; <i>Fryxell, s.n.</i> (cult.) ¹ ; <i>Hall s.n.</i> (cult.) ^{1,4} ; <i>Hill 4465</i> ¹ ; <i>Hill 4579</i> (cult.) ¹ ; <i>Hill 5806</i> ² ; <i>Hill 5889</i> ³ ; <i>Hill 6061</i> ³ ; <i>Morel 8095</i> (cult.) ⁴

Table 3. Chromosome numbers in *Malvastrum*. References are to previous counts,

Taxon	Count	Reference or Voucher
<i>M. coromandelianum</i> subsp. <i>capitato-spicatum</i>	$n = 12$, $2n = 24$	Krapovickas, 1949; Bates 1967b
<i>M. coromandelianum</i> subsp. <i>fryxellii</i>	$2n = 24$	Anderson et al. 9096 (cult.) ^{1,4}
<i>M. grandiflorum</i>	$n = 12$	Krapovickas, 1974b
<i>M. hispidum</i>	$n = 18$	Bates, 1967a
<i>M. interruptum</i>	$n = 18$, $2n = 36$	Krapovickas, 1954b; Gutiérrez 357 (cult.) ¹ ; Krapovickas 22103 (cult.) ^{2,3}
<i>M. scoparioides</i>	$2n = \text{ca. } 48$	López & Sagastegui 8020 (cult.) ¹
<i>M. spiciflorum</i>	$2n = 12$	Krapovickas, 1954b
<i>M. tomentosum</i>	$n = 12$, $2n = 24$	Skovsted, 1935; Krapovickas, 1967, 1969. Iltis 1591 (cult.) ^{1,2,3,4} ; Stork 8973 ^{2,3}

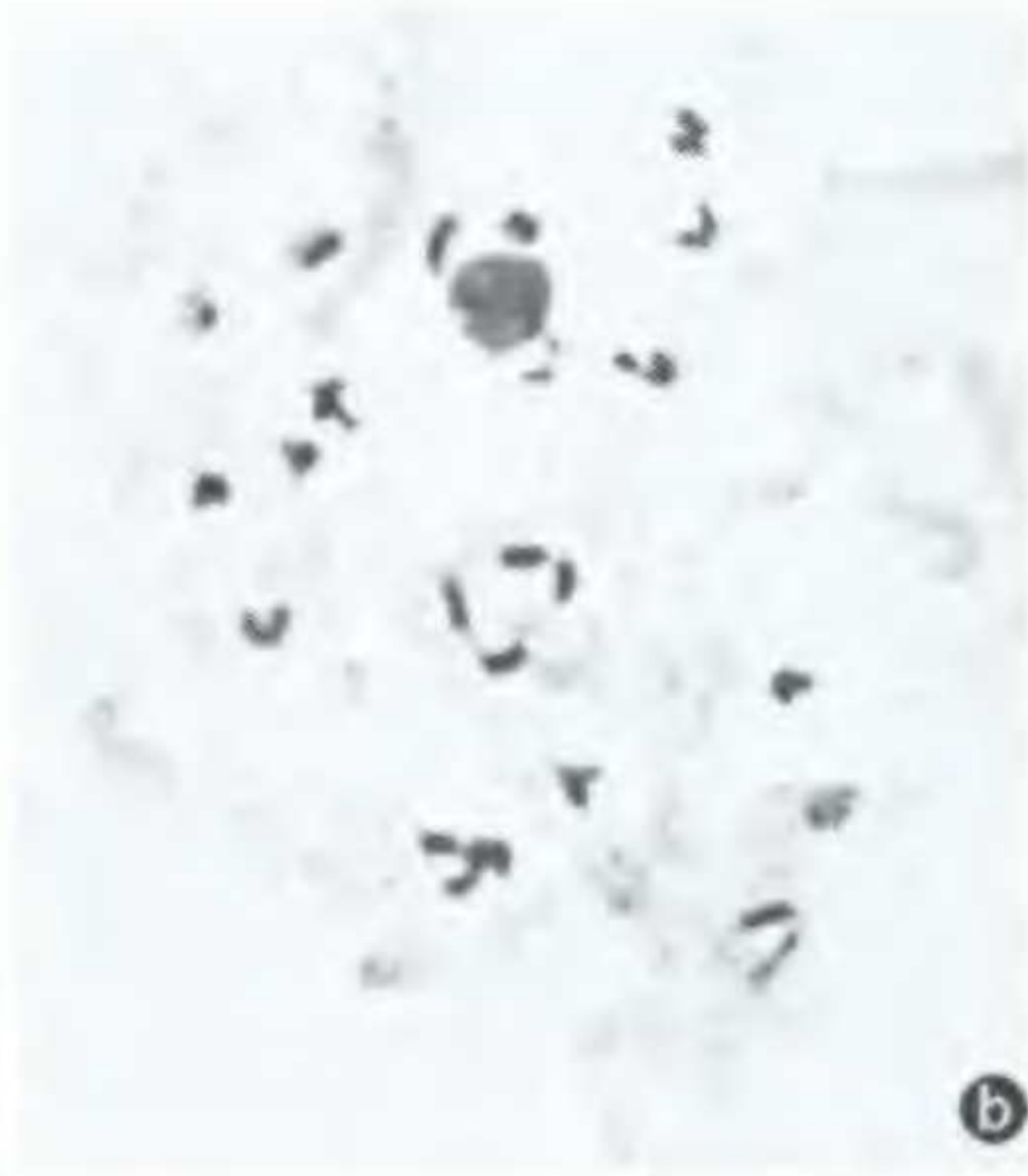
¹root tip²pmc³yng. pollen⁴shoot apex

PHYLOGENY

Infrageneric relationships

While the phyletic accuracy of all of the approaches to cladistics can be debated (see Funk & Stuessy, 1978), in order to demonstrate graphically one possible scheme of relationships within *Malvastrum* I have prepared a cladistic diagram (Fig. 18) using the Wagner Groundplan/Divergence method (Wagner, 1961). Phenotypic expressions for 60 characters were recorded for each of the taxa (see Appendix II) and divergence-values based on an hypothetical

Figure 16. *Malvastrum* chromosomes. I. a-a'. *M. americanum*, $2n = 24$, pollen mother cell, anaphase I (cult. Croat 9705). b-b'. *M. aurantiacum*, $n = 18$, immature pollen, prophase II (Hill 5878). c-c'. *M. bicuspidatum*, $2n = 24$, root tip, metaphase (cult. Lehto et al. 19487). d-d'. *M. bicuspidatum*, $n = 12$, immature pollen, telophase II (cult. Lehto et al. 19847). e-e'. *M. corchorifolium*, $2n = 48$, root tip, metaphase (cult. D'Arcy 394). f-f'. *M. corchorifolium*, $2n = 48$, root tip, metaphase (cult. Lakela 27892). All 696 \times .



ancestral state, designated as the origin, have been totaled for each taxon. Distances between the taxa have been determined by totaling the number of differences in their character states. These distance values, in combination with other characters such as geography and chromosome-number that are not included in the data matrix, have been used to determine the connections between taxa or with hypothetical taxonomic units (HTU's).

The scheme presented here is based upon *a priori* considerations concerning primitive and derived states within *Malvastrum* and the Malveae. In several cases the primitive character-state is considered to be not that which is most widespread in the genus but, instead, that from which other states are most probably derived. For example, even though only a single species, *M. hispidum*, has completely dehiscent mericarps (character 56) this is thought to be the ancestral state. While dehiscence could conceivably be a secondary development, it is not likely when all Malveae are considered. This follows from the fact that several rather unspecialized taxa have partially dehiscent mericarps and several related genera in the Malveae (e.g. *Tarasa*, *Malacothamnus*, and *Nototriche*) have completely dehiscent mericarps. In addition, dehiscence is characteristic of multi-seeded mericarps while indehiscence is characteristic of 1-seeded mericarps, which are derived.

The character-states for the flowers (characters 18-36) reflect the *a priori* assumption that the smaller, mostly autogamous flowers are derived from an earlier state involving moderate-sized entomophilous flowers. The flowers were probably reduced in size independently in the several taxa involved. A weakness in the distance matrix (Appendix II) results when all the small-flowered taxa are considered similar (such as *M. chillagoense* and *M. spiciflorum* which are actually considered to be only distantly related).

Several characters modified in one direction in the genus as a whole seem to have reversed in trend within individual sections of

Figure 17. *Malvastrum* chromosomes II. a-a'. *M. coromandelianum*, $2n = 24$, root tip, metaphase (Hall s.n., seeds only, Ghana). b-b'. *M. coromandelianum*, $2n = 24$, root tip, metaphase (cult. Hill 4465). c-c'. *M. coromandelianum*, $n = 12$, pollen mother cell, late prophase II (Hill 5806). d-d'. *M. interruptum*, $n = 18$, pollen mother cell, late prophase I (cult. Krapovickas et al. 22103). e-e'. *M. tomentosum*, $2n = 24$, root tip, metaphase (cult. Iltis & Iltis 1591). f-f'. *M. tomentosum*, $2n = 24$, pollen mother cell anaphase I (cult. Iltis & Iltis 1591). All 696X.



the genus or to have taken several directions. In at least one case the character reversal cannot be readily indicated (e.g. character 16, some taxa may have solitary axillary flowers as a result of a neotenus reversal from that of a more complex inflorescence). In another case an attempt has been made to indicate a character reversal (e.g. character 49, cusp length, where the shorter cusps of several taxa are considered to be derived from the larger ones). Characters that have probably developed in several directions are indicated by intermediate values (e.g. vestiture characters 3, 14, 15, 27 and 55, stamen number character 34, inflorescence character 16, and petal length character 28) with lower values assigned to the less specialized states. As a result of the problems inherent in this system the distance matrix must be considered together with independent trends in certain characters.

While the character states are useful to indicate relative specialization from an ancestral state, certain characters indicative of particular environmental situations are not considered to be especially useful in indicating true relationships. Characters such as duration (1), height (2), and leaf morphology (5–13) are not the best guides to relationships within *Malvastrum* and so have been given lesser importance in connecting taxa. Since these eleven characters are less than 20% of the total number they have affected the results to a lesser extent than have the majority of characters that seem to have phyletic value.

The data matrix presented in Appendix II allows the proposal of HTU's through which the extant taxa may be related. Characters that are primitive and shared within groups of taxa are used to propose a common connection at the shared level of divergence (the common ancestor). For example, all the members of the section *Tomentosum* share the same values for characters 1, 2, 4, 10, 11, 29, 30, 31, 33, 35, 36, 40, 47, 48, 56, and 58, the combination of which defines the HTU ancestor of the section.

One of the results of this numerical analysis has been the division of *Malvastrum* into seven sections. The first three sections (sect. *Sidopsis*, *Interruptum*, and *Americanum*) retain basically unornamented mericarps while the remaining four sections have ornamented mericarps.

The most divergent species, *M. hispidum*, is placed in the section *Sidopsis* (Fig. 18A). It was found to share a number of characters with members of section *Interruptum*, but differed from members of

tha section in nearly half of its characters. It seems to have been separated from the mainstream of *Malvastrum* evolution for a longer period than any other taxon based on its divergence value (differing from the ancestral state by 44 of the 60 characters) and its unusual disjunct occurrence in temperate North America. The completely dehiscent carpels, here viewed as the retention of a primitive character, have been used in the past to maintain the species as generically distinct from *Malvastrum*. The origin of *M. hispidum* remains obscure.

In contrast, section *Interruptum* (Fig. 18B) is one of the least divergent from the supposed ancestral state. The diploid *Malvastrum spiciflorum* retains a greater number (35) of presumed primitive characters than any other species with the exception of *M. americanum* (37) and would be placed even closer to the ancestral state were it not for its reduced flowers. *Malvastrum interruptum* has retained the larger flowers but is isolated from *M. spiciflorum* by its higher ploidy level. The two species share 37 characters of the 60 considered and also seem to have a similar ecology.

Members of the section *Americanum* (Fig. 18C), like those of section *Interruptum*, also retain many ancestral characters. This section poses an unresolved phytogeographic problem in that it is diverse not only in the New World but also in eastern Australia. *Malvastrum chillagoense*, thought to be derived from an early form of *M. americanum*, is seen to be more similar to other taxa according to the distance matrix (Appendix II) than to *M. americanum* but this probably reflects a simplification of characters during geographic isolation rather than any true relationship. Some populations of *M. americanum* var. *americanum* in northern Queensland, Australia show a trend of specializations similar to those of *M. chillagoense*. Vegetative and pollen characters further strengthen the affinity.

The section *Tomentosum*, composed of nine taxa in four species, shows the greatest coherence (Fig. 18D). Members of this section have been taxonomically and nomenclaturally confused for two centuries due to an incomplete understanding of their ranges, ecology, and morphology. The Central American members of the section seem to have differentiated in comparatively recent times since 60% of their examined characters are shared. As discussed previously, adaptive radiation may have occurred after an ancestral population was introduced into the region via the Central American

land-bridge. The populations then became discontinuous as climatic and geologic conditions changed. Because of a supposed early dependence on animal dispersal within the group, the taxa with long cusps and stronger pericarps are considered to be more primitive than those with smaller cusps and a leathery pericarp; this is the reversal of a trend found in the genus as a whole. Three taxa of the section remain in South America. Both *Malvastrum scoparioides* and *M. tomentosum* subsp. *pautense* seem to have lost the lowland species' mericarp elaborations which are probably of advantage for animal-dispersal and have become adapted to higher elevations. As a result there has been some convergence in characters in the two taxa, reflected in the numerical analysis.

Closest to section *Tomentosum* is section *Amblyphyllum* (Fig. 18E), composed of the two species *Malvastrum amblyphyllum* and *M. grandiflorum*. While sharing many characters with the last section, these two species differ particularly in their less specialized inflorescences and more specialized mericarps. The mericarps are narrowly winged on their distal margins and the flowers are among the few whose styles do not recurve when the petals wilt. The two species in this section share 44 (or 73%) of the 60 characters examined.

The section *Malvastrum* is composed of four taxa in two species (Fig. 18F). The numerical analysis has shown that *M. aurantiacum* and *M. coromandelianum* are related, though distantly. These are the only two species in which the apical cusp is remote from the proximal margin. The section probably had its origin in the lowland Paraná basin of South America. The most closely allied section to the section *Malvastrum* according to the numerical analysis is the section *Amblyphyllum*.

The seventh section is the section *Corchorifolium* composed of the single species *Malvastrum corchorifolium* (Fig. 18G). Morphological and chromosomal evidence summarized in Table 4 as well as observations of living plants from various areas of its range have convinced me that this species has resulted from allopolyploidy in a hybrid between *M. americanum* and *M. coromandelianum*. This connection has been indicated in Fig. 18 by a dotted line. The octoploid chromosome number ($2n = 48$) as well as its range, combined with the large number of intermediate characters present in *M. corchorifolium*, support this hypothesis. The species probably arose after chance hybridization occurred between the two pre-

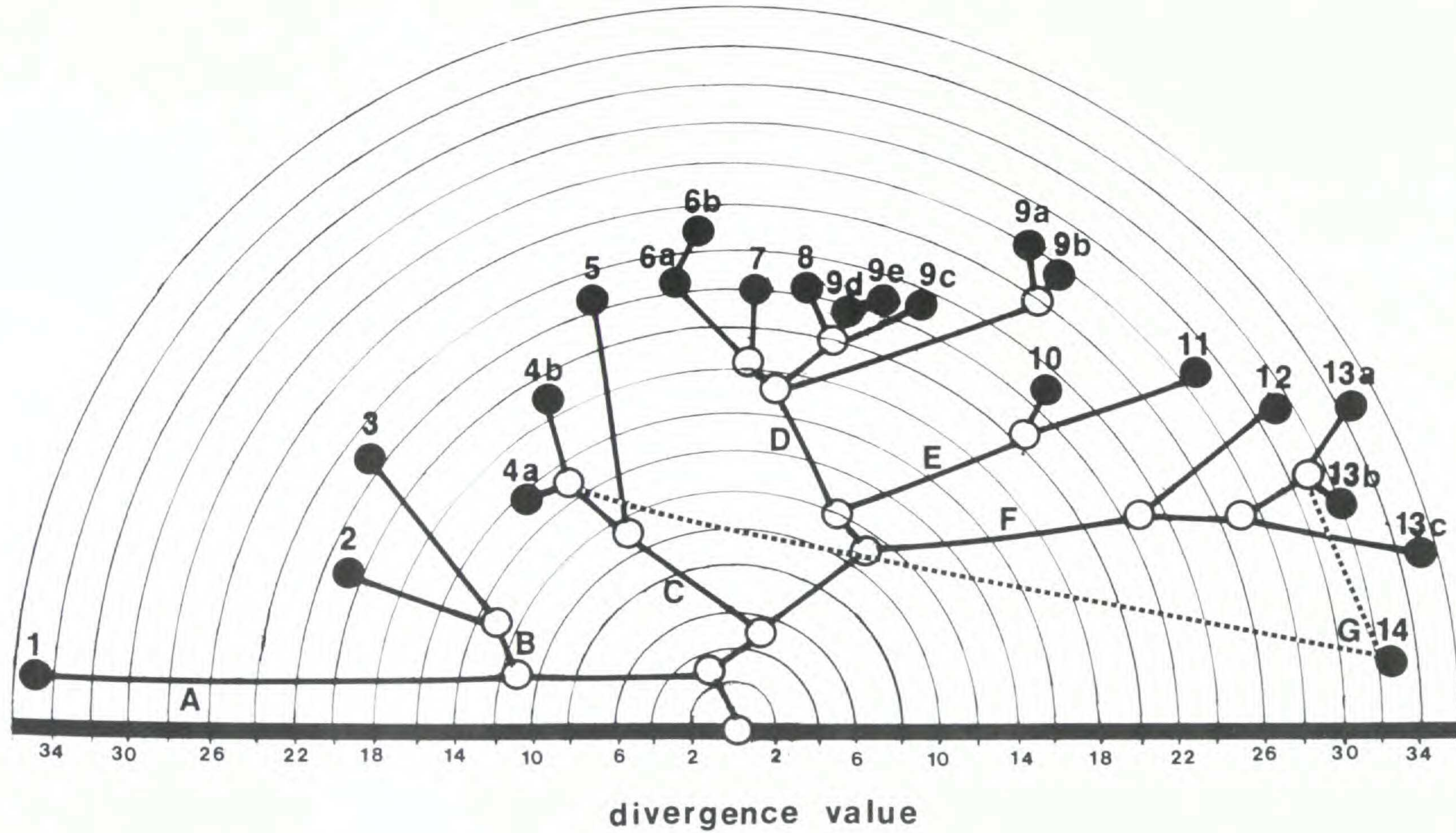


Figure 18. Wagner Tree for *Malvastrum*. A. Section *Sidopsis*. B. Section *Interruptum*. C. Section *Americanum*. D. Section *Tomentosum*. E. Section *Amblyphyllum*. F. Section *Malvastrum*. G. Section *Corchorifolium*. Open circles indicate hypothetical ancestors plotted at points of shared primitive characters. See appendix II for OTU code explanation.

Table 4. Evidence for allopolyploid origin of *M. corchorifolium*

Character	<i>M. americanum</i> var. <i>americanum</i>	<i>M. corchorifolium</i>	<i>M. coromandelianum</i> subsp. <i>coromandelianum</i>
chromosome number	$2n = 24$	$2n = 48$	$2n = 24$
filament column length	2.03 mm	2.02 mm	1.95 mm
column vesture	pubescent	1-3 hairs	glabrous
pollen size	49-60 μm	66-89 μm	70-91 μm
carpel number (mean)	13	12	11.5
mericarp height	1.8 mm	1.9 mm	3.0 mm
mericarp length	2.4 mm	2.8 mm	3.0 mm
endoglossum	present	present, but small	absent
calyx-lobe length	5.9 mm	5.5 mm	4.9 mm
calyx vesture (adaxial)	simple and 5-8-radiate, 2 sizes	simple and 4-8-radiate, 2 sizes	simple (margins only), 2-4- radiate, 1 size or gradational
bracteole length (mean)	6.6 mm	5.6 mm	5.1 mm
pedicel length at anthesis (mean)	0.1 mm	1.0 mm	1.9 mm
bifid floral bract	always present	often present	absent
first flowering	16-20 weeks	12 weeks	6 weeks
daily anthesis (local comparison)	5-6:30 pm	4-6 pm	4-5:30 pm
inflorescence type	dense terminal spike, lowest 1-3 flowers remote, sessile	terminal spike, lowest 4-6 flowers solitary-axillary, sessile	solitary-axillary, pedicellate
leaf vesture (adaxial)	5-6-radiate	4-5-radiate	simple
branching	single main stem, branching in upper 1/3 to 1/2	single main stem, branching in upper 1/2	several main stems (in age), branching near base

sumed parents in Central America where they had become sympatric after the emergence of the land bridge. Both *M. americanum* and *M. coromandelianum* have a gametic chromosome number $n = 12$, and while the hybrid is probably not fertile there are no barriers to gametic exchange. The three species occur together in the region of Nicaragua, Honduras, Guatemala, and Chiapas, Mexico, as well as in certain parts of the Caribbean. Being an autogamous species, *M. corchorifolium* has apparently persisted and even expanded its range as a result of a greater tolerance to semi-arid conditions and to areas of brackish and limestone soils than is shown by the other two species.

While hybridizations were attempted among the species raised in the greenhouse, the results were inconclusive for the most part. Often, flowering of a given taxon was not coincident with anthesis in other taxa. Nevertheless, the more significant difficulty was that of technique. Since anther dehiscence occurred before or as the flowers opened, emasculation in bud was necessary to prevent self-pollination. However, this was difficult to accomplish without damage to the flower, not only because of their often small size in bud, but also because the exposed flower-parts were too delicate to withstand drying after the calyx-lobes and petals had been removed. Crossing was most effectively accomplished in species whose flowers bore stigmas that were exerted from the anther-cluster. Sixty-two crosses were performed in 1978, and the resultant seeds were planted early in 1979. As indicated in Table 5, wherein the female parent is listed first, fruit set varied from 0–10% success to 80–100% success. Although the results are based on fruit set alone, a few tentative conclusions may be drawn. *Malvastrum corchorifolium*, *M. interruptum*, and *M. grandiflorum* seem to be the most isolated species—the former two as a result of high ploidy levels and the latter probably as a result of unknown incompatibility factors. I would speculate that the elongated style in *M. grandiflorum* may make the ovary inaccessible to pollen grains of other taxa with short pollen-tubes. Of the 886 seeds produced from successful crosses and planted, only 21 seeds (2%) germinated. Of these 21 individuals, six died soon after germination. The 15 survivors resulted only from the crosses showing 80–100% success listed in table 5. The successful crosses help support the phylogeny proposed (e.g., the apparent success of the *M. amblyphyllum* × *M. grandiflorum* cross presents

Table 5. Hybridization results based upon % fruit set

Parentage	Seed sources
0-10% Success	
<i>M. americanum</i> × <i>M. corchorifolium</i>	Hill 7640 × Lakela 27892; Silva-Santos 28017 × Steere 1010
<i>M. coromandelianum</i> × <i>M. corchorifolium</i>	Morel 8095 × Correll 43834; Hill 4579 × Seymour 5442
<i>M. interruptum</i> × <i>M. amblyphyllum</i>	Gutiérrez 357 × Krapovickas 18558
<i>M. interruptum</i> × <i>M. coromandelianum</i>	Gutiérrez 357 × Corral-Lorenzoni 13; Gutiérrez 357 × Board 1106a
<i>M. interruptum</i> × <i>M. corchorifolium</i>	Gutiérrez 357 × Proctor 18585
<i>M. interruptum</i> × <i>M. grandiflorum</i>	Gutiérrez 357 × Krapovickas 19300
<i>M. grandiflorum</i> × <i>M. americanum</i>	Krapovickas 19300 × Hill 7640
<i>M. grandiflorum</i> × <i>M. bicuspidatum</i>	Krapovickas 19300 × Bye 6940
<i>M. grandiflorum</i> × <i>M. coromandelianum</i>	Krapovickas 19300 × Hill 4579
30 - 50% Success	
<i>M. americanum</i> × <i>M. coromandelianum</i>	Hill 6054 × Fryxell 720a; Hill 6054 × Corral-Lorenzoni 13
<i>M. americanum</i> × <i>M. grandiflorum</i>	Hill 7640 × Krapovickas 19300
<i>M. bicuspidatum</i> × <i>M. coromandelianum</i>	Bye 6940 × Corral-Lorenzoni 13; Lehto 19487 × Hill 4579
<i>M. coromandelianum</i> × <i>M. grandiflorum</i>	Percival s.n. × Krapovickas 19300; Breedlove 20019 × Krapovickas 19300
80-100% Success	
<i>M. amblyphyllum</i> × <i>M. grandiflorum</i>	Krapovickas 18558 × Krapovickas 19300
<i>M. aurantiacum</i> × <i>M. coromandelianum</i>	Hill 6430 × Corral-Lorenzoni 13; Hill 6430 × Hill 4579
<i>M. coromandelianum</i> subsp. <i>coromandelianum</i> × <i>M. c.</i> subsp. <i>capitato-spicatum</i>	Board 1106 × Varela 52
<i>M. bicuspidatum</i> subsp. <i>bicuspidatum</i> × <i>M. b.</i> subsp. <i>campanulatum</i>	Bye 6940 × Waterfall 13918

further evidence supporting the close relationship of the two species). While infertility may explain the low percentage of seed germination, seed dormancy is another likely explanation.

My conclusion resulting from these hybridization attempts is that, while the subspecies are capable of interbreeding, the species of *Malvastrum* are effectively isolated from one another, a conclusion also supported by the lack of intermediate specimens in herbaria.

To summarize, speciation in *Malvastrum* has resulted from two processes in particular: 1) autopolyploidy or allopolyploidy, and 2) geographic isolation. Geographic isolation has resulted from 1) geologic and climatic changes and from 2) discontinuous dispersal of the fruits by means of animal transport. Several lineages or sections are now indicated by the data accumulated during the course of this study of *Malvastrum*.

Intergeneric relationships

During the early period of *Malvastrum* classification a very few morphological characters were used to show its alliance with other genera in the Malvaceae. Gray in Sprague & Gray (1849, p. 47) assigned *Malvastrum* to the tribe Malveae and placed the genus in the subtribe Sideae Presl. The stigmas of all of the members of this subtribe were said to be capitate. Alefeld (1862) proposed the tribe Malvastridae, typified by *Malvastrum*, and placed the tribe within the subfamily Sideae. Members of the new tribe had mericarps bearing solitary ascending ovules, and the subfamily Sideae was separated from the subfamily Malveae by its capitate rather than decurrent stigmas. The tribe Malvastridae included four genera: *Palaua* Cav., *Malvastrum* A. Gray, *Kitaibelia* Willd., and *Diplopenta* Alef. (= *Pavonia* Cav.). *Malvastrum* was assigned to the tribe Malveae by Bentham in Bentham & Hooker (1862), where it has remained. The genus was further placed in the subtribe Eumalveae (= *Malvinae*) together with *Althaea* L., *Lavatera* L., *Malva* L., *Callirhoe* Nutt., *Sidalcea* A. Gray, and *Napaea* L. and was distinguished from these by its capitate and not decurrent stigmas. The solitary ascending ovule and single series of carpels defined the subtribe. Schumann (1890) also concluded that the ascending ovule was a very important taxonomic character in the tribe Malveae and also placed *Malvastrum* in the subtribe Malvinae, also noting its exceptional capitate rather than decurrent stigmas. Kearney (1951b) also considered the importance of the capitate stigmas and ascending ovules in *Malvastrum* but, for the first time, realized that it and other uniovulate genera were closely allied to certain pluriovulate genera. As a result, *Malvastrum* and 17 other genera were assigned to the subtribe Abutilinae.

Classification within the tribe Malveae is currently in a state of flux. Bates (1968, 1969) and Bates & Blanchard (1970) have

proposed 16 "alliances" of genera that are thought to represent at least three major evolutionary lines. Until more information is accumulated, formal taxonomic status cannot be given to the alliances. Chromosome numbers have been used as a basis for the re-evaluation of previous classification systems. Bates & Blanchard (1970) have pointed out that the major evolutionary trends in morphology within the tribe have been reductional. This includes sequences such as those leading from a woody to a herbaceous habit and a general reduction in the size and complexity of floral organs. In contrast, specializations have occurred in a few organs, such as in the mericarps, leading to more effective seed dispersal. One of the greatest problems in determining phylogeny within the Malveae is the occurrence of similar reduction series in separate lineages. In particular, the similarity in mericarps in several unrelated genera have led to the taxonomic confusion in *Malvastrum*.

Bates & Blanchard (1970, p. 929) have proposed that a very significant event in the evolution of the Malveae was the early establishment of base chromosome numbers of $x = 7, 6,$ and 5 through aneuploid reduction from a probable base-number of $x = 8$. Again, a single line is not indicated and so species with a like base-number are not necessarily related. Elaboration of the base-number has occurred in several genera through euploidy and aneuploidy and still other changes are thought to have occurred by means of hybridization between species with different base-numbers.

Malvastrum is considered to be in a line separate from the other alliances, and has no close relatives. The basic chromosome-number $x = 6$ is shared only by members of the *Gaya* alliance (*Cristaria* Cav., *Gaya* Cav., and *Lecanophora* Spegazzini) and by *Mala-cothamnus chilensis* (Gay) Krap. whose generic placement is uncertain. The occurrence of $x = 6$ in the three otherwise divergent groups is most likely coincidental and does not indicate a common ancestry. Therefore, intergeneric relationships concerning *Malvastrum* cannot be based upon chromosomal evidence as yet.

Malvastrum, like the other uniovulate Malveae, probably has been derived from early pluriovulate members of the tribe with pseudocapsular loculicidally and septicidally dehiscent fruits. In this regard the mericarps of several species of *Malvastrum* retain a complete or incomplete loculicidal dehiscence, most frequently along the proximal-apical margin. The ancestral group also seems to have had two-chambered fruits partitioned by an endoglossum.

In time, all of the ovules with the exception of the single ascending basal ovule in the lower chamber were lost and the upper chamber with its associated endoglossum was likewise reduced or lost. A highly reduced upper chamber bounded beneath by a minute endoglossum remains in several species of *Malvastrum*. The ancestral entity from which *Malvastrum* was derived likely had yellow flowers and the calyx undoubtedly was subtended by a spirally arranged tribracteolate involucl, characters shared by all of the contemporary species. The base chromosome number $x = 6$ was probably derived by reduction from a higher number of $x = 7$ or 8 and, once established, was subsequently modified by euploidy in the genus.

No other contemporary genus has such a combination of characters. A similar but less extreme reduction series in the mericarp has occurred in *Sphaeralcea* but the different basic chromosome-number ($x = 5$), the frequent occurrence of more than one ovule in the mericarp, and the frequently mauve or salmon-orange corolla color as well as other characters suggest that the two genera have been separate for a long period. Nevertheless, when all of the Malveae are examined, there is a degree of morphological coherence between the *Sphaeralcea* and *Malvastrum* alliances, both of which seem to have originated in South America. The ancestry of the two alliances should probably be sought in the diverse, comparatively primitive *Abutilon* alliance whose members, while individually often specialized, frequently retain pluriovulate loculicidally and septicidally dehiscent schizocarpic or pseudocapsular fruits. Within the alliance, genera such as *Wissadula* Medicus, *Briquetia* Hochreutiner, *Dirhamphis* Krapovickas, *Batesimalva* Fryxell, *Bastardiastrum* Bates, and *Allowissadula* Bates possess a well-developed two-chambered mericarp, but the basal ovule is pendulous. Within *Anisodonteia* Presl, paired with *Lavatera* in its own alliance (Bates & Blanchard, 1970), both two-chambered pluriovulate and single-chambered uniovulate mericarps are found, demonstrating that the different reductional states can occur in a single genus. It is interesting to note that in the pluriovulate species of *Anisodonteia* the basal ovule is pendulous, while in the uniovulate species the ovule is ascending. I cannot now assess the probability that the ascending ovule in *Malvastrum* is a primitive condition or that the ovule changed its orientation as the mericarp was reduced.

To be continued in Vol. 84, Nos. 838 & 839 (April & July, 1982).