1973

An Anatomical and Morphological Study of Datiscaceae

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AN ANATOMICAL AND MORPHOLOGICAL
STUDY OF DATISCACEAE[1]

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INTRODUCTION

The Family Datiscaceae contains three genera and four species. *Octomeles* and *Tetrameles* are monotypic genera of tall trees in the Old World tropics. The former is common in riverine rain forests of Malesia; the latter grows in different types of monsoon forests from New Guinea to India. The genus *Datisca* has a Mediterranean-Californian disjunction, and the two species are herbaceous perennials 6–10 ft tall.

Datisca glomerata (Presl) Baill. ranges from the Sierra San Pedro Martir of Baja California to northern California and occurs at elevations from 200 to 6,500 ft, depending roughly on the latitude (Fig. 1). A typically riparian species, it can be found in sandy soil along waterways in a variety of *Quercus* woodlands and coniferous forests in the coast ranges and on the eastern and western sides of the Sierra Nevada Range. Genera commonly found with *D. glomerata* are *Alnus, Fraxinus, Rhus, Ribes,* and *Salix*.

Datisca cannabina L. occurs on the southern slopes of the western Himalayas in India, Kashmir, Pakistan, and Afghanistan and in the southern part of Tadzhik S. S. R. The most eastern collection sites in Iran are in the Elburz Mountains, and from this area the range extends westward through the Middle East, and Turkey to Crete (Fig. 2). The apparent disjunction in the range in eastern Iran may be the result of inadequate collections or bibliographic oversight. Because there was no opportunity to vist European herbaria during this study, the map is based mostly on published records. If no specimen has been collected there so far, the species may yet be found in this region, because the Turkmen-Khurasan ranges form an almost continuous chain from the eastern end of the Elburz Mountains to Afghanistan. *Datisca cannabina* occurs at elevations of 1,000–6,000 ft in a broad range of riparian habitats similar to those of *D. glomerata*. Associated plants in

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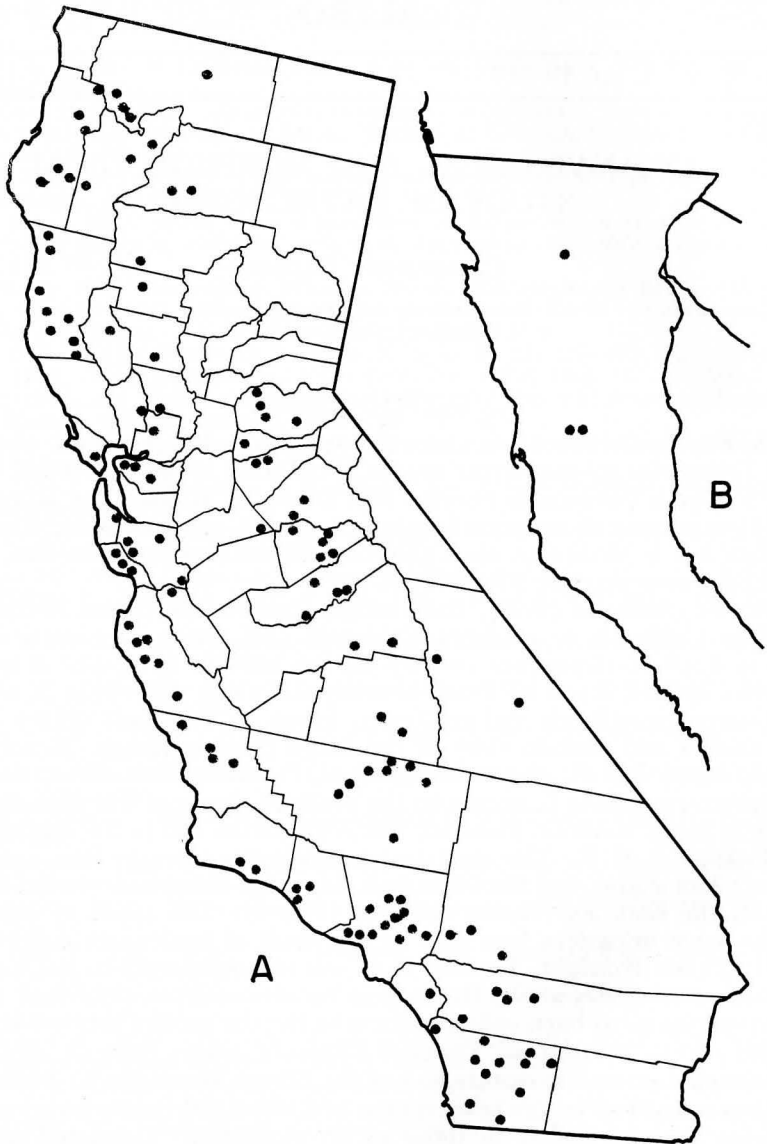
DATISCA GLOMERATA (PRESL) BAILL.

Fig. 1. Distribution of *Datisca glomerata.*—A. California.—B. Baja California. Scale slightly greater than in map A.—Dots represent specimens seen in the following herbaria: CAS, DAV, DS, JEPS, POM-RSA, UC.

Turkey include *Quercus coccifera* L. and *Fontanesia phillyreoides* Labill. (Davis, 1949); and in Afghanistan, *Quercus baloot* Griff. and *Cedrus deodara* (Roxb.) Loud. (Kitamura, 1960). Although *D. cannabina* has long been used in these areas as a source of yellow dye for wool and silk, its range is certainly natural and not the result of transportation by man.

Tetrameles nudiflora R. Br. is a common to infrequent component of monsoon forests from Australia, eastern Papua, and New Guinea through the Lesser and Greater Sunda Islands (except Borneo), southeast Asia, Assam and Bengal, the Western Ghats of India, and Ceylon (Fig. 3). The length of the dry season in these areas may vary from five months in Assam to one or two months in eastern Sumatra and western Java, where the tree is uncommon. Abundance increases northward on the Malay Peninsula into Thailand and Indo-China. Limestone soils are the preferred substrate throughout the range; for instance, on Peutjang Island of the west coast of Java, *Tetrameles* is on saturated, coral-derived soil left by the great tsunami of 1883. The high water table is not present all year long. A similar habitat is found on Timor and presumably on the rest of the Lesser Sundas (Drees, 1951; Kartawinata, 1965). In Viet Nam it is considered a limestone indicator (Ngan, personal communication, 1970). As a member of the *Tetrameles-Stereospermum-Cedrela* formation, it occurs in parts of the Assam Valley (Rowntree, 1954), and in other types of forest up to 2,000 ft in Bhutan and Sikkim.

Tetrameles and *Octomeles* grow within a few miles of one another in several places where strips of riverine rain forest cut through predominately evergreen or wet deciduous forest having a short dry period; for example, the Brown River area in Papua (Fig. 7). The dry period need only be long enough for *Tetrameles* to lose its leaves and set buds. The rainfall in this region is around 80 in. a year. The soil is described as neutral olive stratified, poorly drained, and probably alkaline.

Ordinarily *Octomeles sumatrana* Miq. tends to form gregarious stands along rivers and streams up to 2,000 or 3,000 ft, but it is never found in the mangrove zone (Fig. 4). Sometimes trees occur in ravines in primary and secondary dipterocarp forest in Borneo where they are not directly associated with a water course, however. It also commonly sprouts up in regrowth following agricultural clearing, along with pioneers like *Anthocephalis cadamba* (Roxb.) Miq., *Pterospermum*, and bambusoid grasses. When not gregarious, it is mixed with riverine Dipterocarpaceae (Browne, 1955, pp. 10, 82). In southern Papua (Fly River), where the narrow belts of riverine vegetation are bordered by monsoon forest, the associates are *Sonneratia caseolaris* (L.) Engl., *Terminalia, Livistona,* and *Nypa fruticans* Wurmb. (Royen, 1963).

Both trees attain great heights. *Octomeles* grows from 25 to 35 m in 4–10 years and reaches 60 m as a maximum (Fig. 5). The straight bole occupies 50–60% of the total height. A tree in the botanic garden at Bogor, Indonesia, outside the natural range, grew to 25 m with a dbh of 47 cm in four years (Koopman and Verhoef, 1938). On young trees the buttresses are only 2–3 m high, but on older ones they extend up to 6 m. *Tetrameles* has a sinuous

2   DATISCA CANNABINA L.

3   TETRAMELES NUDIFLORA R.BR.

4   OCTOMELES SUMATRANA MIQ.
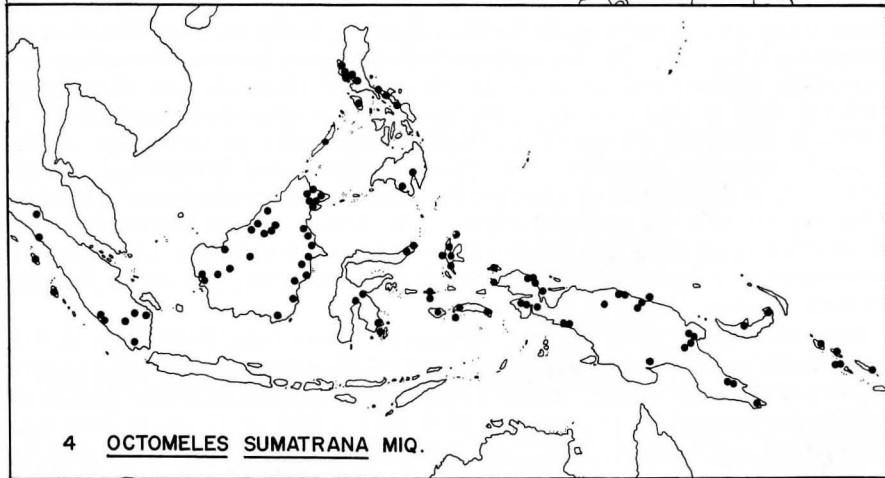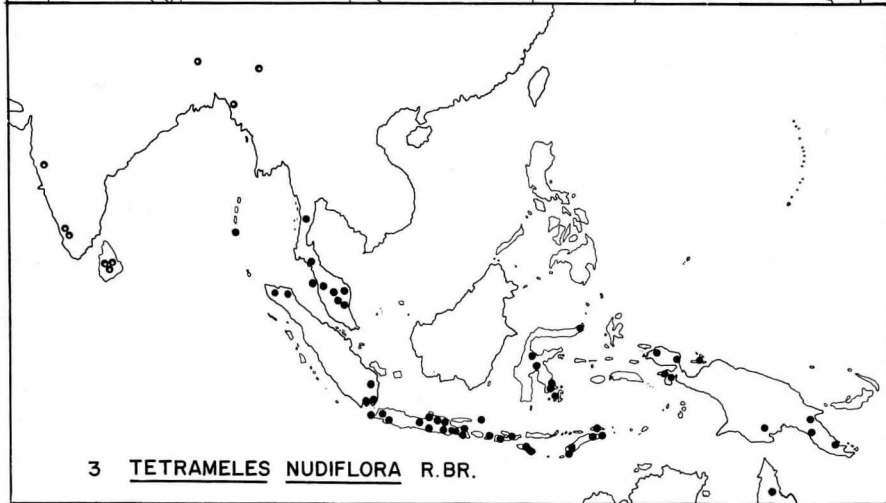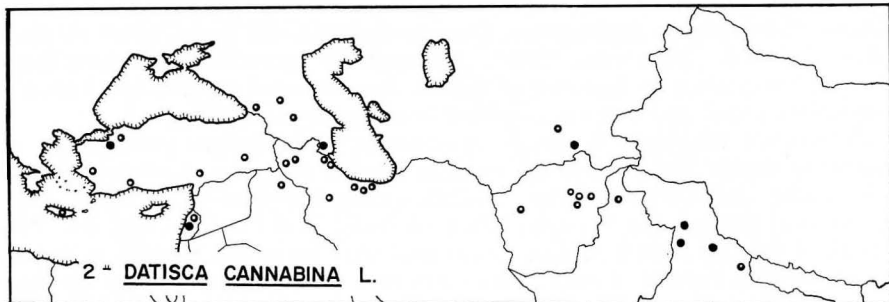
bole (Fig. 6, 7) and grows to 50 m. In wet areas individuals may be no taller than surrounding trees, but in dry areas they are widely spaced emergents, for instance in Assam and even in central Malaya (Pahang). In the Western Ghats the tallest trees of this species are about 30 m, and they often branch only 12 m above the ground (Santapau, 1953). The tree in Fig. 6 branched about 12 m above the 5 m buttresses and showed a clockwise branching spiral. Buttresses are frequently up to 6 m high (Fig. 8), but those on the 50-m tree in Fig. 7 were only 2.5 m.

Datisca was first discovered in Crete in the 1590's by a physician, Honorius Bellus, who sent plants to Italy for cultivation (Bauhinius and Cherlerus, 1651, pp. 466–467). In the following years it was described and illustrated by a swarm of herbalists, who were familiar with the unisexual flowers and the yellow dye in the roots; and Linnaeus himself (1760) commented on the possibility of parthenogenetic formation of its fruits.

According to Hasskarl (1866) the Palacca in Rumphius' *Herbarium Amboinense* (1743, vol. 3, p. 195, t. 125) is actually *Octomeles*. The illustration apparently represents the capsule valves on an old inflorescence axis, and mention of such an axis is made in the text. The rest of the description corresponds to *Octomeles*, although sometimes in a general way only, including a rank odor of leaves, domatia in the leaf-vein axils, and red veins on the leaf underside. Several discrepancies stand out, however: the bark of Palacca is fissured and the young petioles (?) are sticky. After the account of the fruit valves, which is accurate, Rumphius mentions some light yellow flowers in wide-spreading bunches and long fruits like those of "Canna fistulosa." There is just enough confusion here to prevent certainty, but *Octomeles* is probably what he had in mind. The tree was otherwise botanically unknown until 1861, when Miquel described it from Sumatra.

Even today very little is known about the family. Most of the work on these plants has been of very limited scope, and the systematic implications have been unclear. One of the objectives of this study has been to present an intrafamilial comparison of the three genera. They are, in fact, closely related, although there have been attempts to segregate the two trees as a separate family. A second objective has been to contribute to a better understanding of the relationships of the family within the Cistales of Thorne (1968) or Violales of Cronquist (1968). The latter may seem too ambitious because this study, though comparative, is certainly not comprehensive: several interesting and important subjects, such as embryology and root anatomy, are treated briefly or neglected. Nonetheless, from this vantage point, certain relationships seem clear. These will be discussed in the "Conclusions" section, along with a few comments on the distribution and taxonomic history of the family.

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Fig. 2–4.   Distribution of Datiscaceae, except *Datisca glomerata.*—2. *Datisca cannabina.* —3. *Tetrameles nudiflora.*—4. *Octomeles sumatrana.*—Dots represent specimens seen in the following herbaria: BO, CAS, DAV, DS, JEPS, KEP, LAE, PNH, POM-RSA, SAN, SING, UC. Circles represent records published in standard floras.
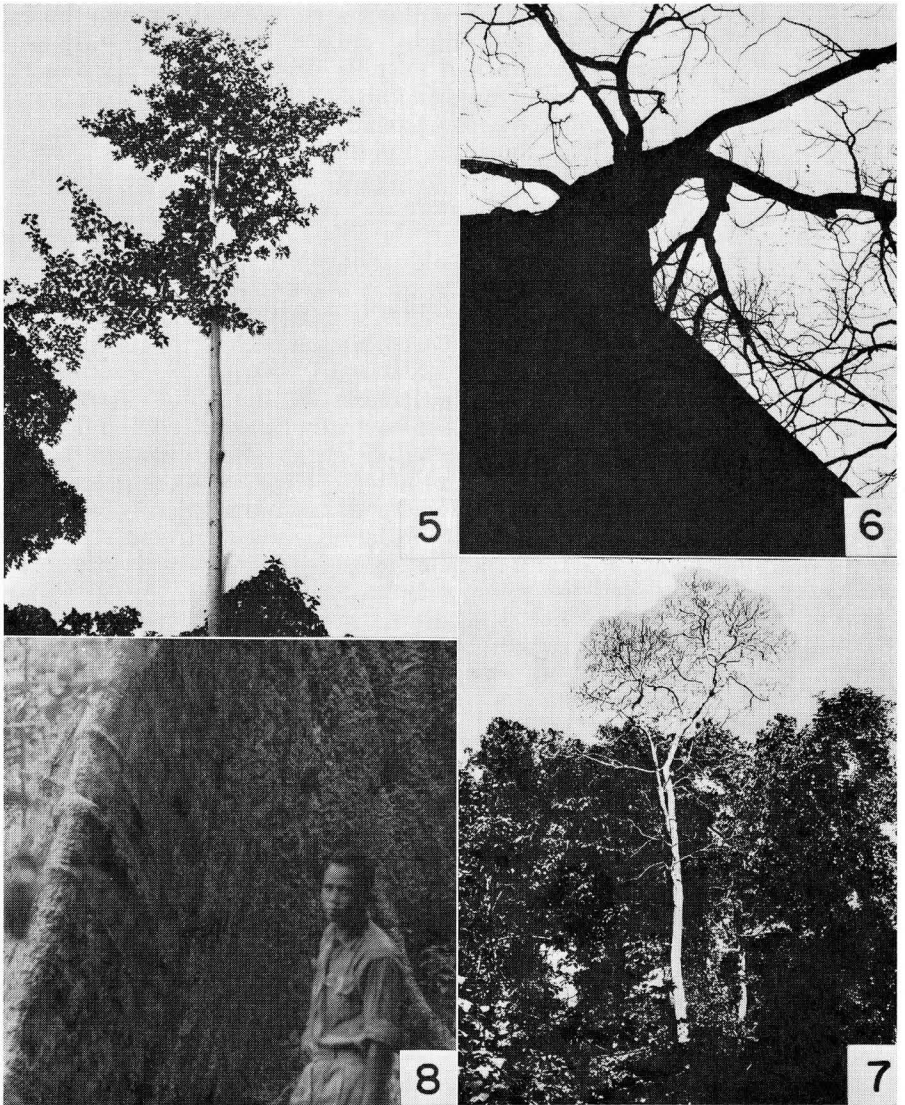
Fig. 5–8.—4. *Octomeles sumatrana.* Tree ca. 50 m, near Markham R., New Guinea.—
6–8. *Tetrameles nudiflora.*—6. Tree on Langkawi Is., W. Malaysia. Note clockwise
branching spiral.—7. Tree ca. 50 m, near Brown R., Papua.—8. Buttress on Langkawi
Is. tree shown in Fig. 6; ca. 6 m high.

MATERIALS, METHODS, AND ACKNOWLEDGMENTS

Materials of *Datisca glomerata* were collected in the wild in California except for seedlings, which were grown in the greenhouse at Rancho Santa Ana Botanic Garden, Claremont, California. The following collections are cited in the text or with the illustrations: *Davidson 1002*, Topanga Canyon, Los Angeles County; *Davidson 1557*, San Gabriel Mts., Los Angeles County; *Oettinger 933*, Forks of Salmon, Siskiyou County. *Datisca cannabina* was grown from seed obtained from the botanic gardens in Cambridge, England; the University of Graz, Austria; and the University of Warsaw, Poland.

Samples of *Octomeles* and *Tetrameles* were collected during a field trip to Malesia in 1970. Collection data for *Octomeles* is as follows: *Davidson 1124*, sapling, Gum Gum F. R., Sabah; *Davidson 1126*, *1127*, seedlings, Lungmanis, Sabah; *Davidson 1128*, tree, Lungmanis, Sabah; *Davidson 1482*, tree, New Guinea. Data for *Tetrameles*: *Davidson 1413a*, tree, Malaya; *Davidson 1413b*, sucker shoots on stump, Malaya; *Davidson 1469*, tree, Java; *Davidson 1493*, tree, Papua. Flowers, vegetative material, phloem, and cambium were preserved in alcohol. Male flowers of *Tetrameles* were not collected. Wood specimens were taken across the diameter of the bole at a level just above the buttresses, at mid-point 10–30 m above the ground, and at a level below the first branching. Samples from buttresses, limbs, and twigs were also included. Woods were kiln-dried and shipped to the U.S. with paraformaldehyde flake as a preservative. Male and female flowers of *Octomeles* (SAN 59701, SAN 59702, SAN 62084) supplied by Mr. P. F. Cockburn of the Forest Department, Sabah, have been used when necessary. The seedlings of *Octomeles* were grown at Lungmanis, Sabah, and were given to me by Mr. Bob Bragan of the U.S. Peace Corps. They were of two types. One was grown in the sun (*Davidson 1127*) and the other, in the shade (*Davidson 1126*). The shade-grown seedlings were much more robust than the ones given full sun. Voucher specimens for plants used in this study are deposited in the herbarium at Rancho Santa Ana Botanic Garden.

All material was prepared by standard microtechnical procedures. Woods of the two trees sectioned poorly on the sliding microtome and had to be embedded in parowax. Phloem was stained with safranin-fast green and with lacmoid, following the procedure of Cheadle et al. (1953). Observations on ergastic substances in *Octomeles* and *Tetrameles* were made on hand-sectioned, preserved material; but in *Datisca* fresh material was used. Phloroglucinol-HCl was used as an indicator of lignin. Pollen of *Datisca* was fresh; that of *Octomeles* was preserved.

Fiber measurements were taken from macerations, but vessels were too large to macerate well and had to be studied in tangential sections. All figures represent the average of 50 measurements. Pollen measurements were taken from photographs.

I am particularly indebted to my advisors, Dr. R. F. Thorne and Dr. Sherwin Carlquist, for their invaluable advice and assistance. Field work would have been impossible without the aid of the following people: Mr. P. F. Cockburn (Sabah); Mr. W. F. Null, Dr. E. Soepadmo, and Mr. Low

Fong Choong (W. Malaysia); Dr. A. J. G. H. Kostermans and Dr. M. A. Rifai (Indonesia); and Mr. J. S. Womersley (New Guinea). Mr. Leonard Hancock of the Chevron Oil Field Research Co. prepared the scanning EM photographs, and Dr. J. S. Henrickson arranged to have the transmission EM work done.

Finally, I am grateful to the trustees of the Rancho Santa Ana Botanic Garden for provision of laboratory facilities.

ANATOMICAL AND MORPHOLOGICAL OBSERVATIONS

FLORAL MORPHOLOGY

Octomeles.—Male and female flowers of *Octomeles* are sessile and linearly attached on long, axillary spikes (Fig. 9A). The spikes are pendant and unbranched; and they may reach a length of up to one-half meter, although axes bearing male flowers are often somewhat longer than those bearing females. Commonly a single axis may bear over 100 flowers. The female flower develops into an essentially tubular ovary that is surmounted by a "crown" composed of the inner nectary cup, the perianth tube, and the styles (Fig. 11). Petals are absent. Styles are opposite small calyx lobes and are terminated by capitate or peltate stigmas. The numerous ovules are borne on 6–8 placentae that are cuneiform in transection and alternate with the styles. In fruit the ovary enlarges from 3 or 4 mm to 6 or 8 mm in diam and reaches 12–13 mm in length (Fig. 10). Dehiscence is longitudinal.

The perianth tube of the male flower bears calyx teeth 2–3 mm long alternating with petals 3–4 mm long (Fig. 12). Both whorls are valvate in bud. The inner cup is lined with a large nectary, on the rim of which the stamens are borne. The 6–8 filaments are opposite the calyx teeth and carry basifixed anthers that are folded abaxially over the filament tip. At anthesis the stamens expand to a length of 15–16 mm.

Typical *O. sumatrana* Miq. occurs in Sumatra and Borneo (Fig. 11). It has flower parts in 6's and 7's and has obtuse to subcordate, ovate leaves. Warburg (1891) described *O. moluccana* from the Philippines, Celebes, and New Guinea and proposed that it differed from *O. sumatrana* Miq. primarily in having floral parts in 7's (occasionally in 6's), but never in 8's, and in having round-cordate rather than ovate-cordate leaves (Fig. 9, 10). Because flowers seen in this study from both Borneo and New Guinea were mostly hexamerous and heptamerous, only rarely octomerous, this distinction between the two cannot be upheld. It has not been accepted in the most recent treatment of the family for *Flora Malesiana* (Steenis, 1953).

Tetrameles.—Female flowers of *Tetrameles* are sessile on pendant, branched axes (Fig. 13). As in *Octomeles*, a tiny bract subtends one, two, or more floral primordia on a young inflorescence. The inflorescence axes are in the axils of finger-like bracts and are grouped at the tips of leafless branches from which they spring at the start of the rainy season. Branches in the flowering axes are also subtended each by a tiny bract. The tetramerous or occasionally pentamerous female flowers are 3–4 mm long and 2.5–3 mm
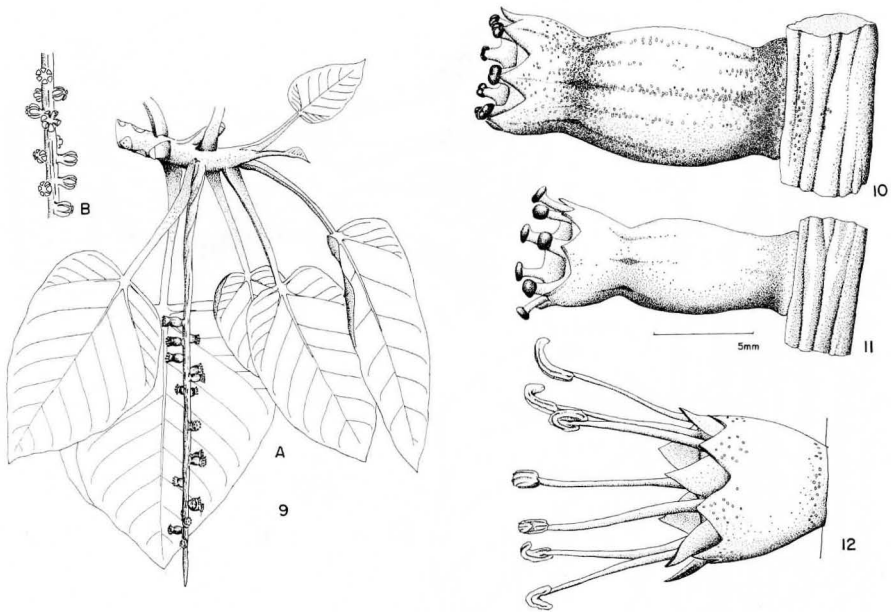
Fig. 9–12. *Octomeles sumatrana.*—9. *Davidson 1482.* A. Inflorescence with female flowers, ×¼. B. Capsules of an old inflorescence, ×⅜.—10. *Davidson 1482.* Fruit. Circles represent peltate trichomes.—11. *SAN 62084.* Female flower. Peltate trichomes not shown.—12. *SAN 59702.* Male flower (Fig. 10–12 drawn to same scale.)

in diam (Fig. 14). The crown is not as pronounced as it is in *Octomeles,* and there appears to be no nectary. Styles are opposite the sepals and bear grooved, spatulate stigmas. Petals are missing. Ovules develop on placental ridges that alternate with the styles, as in *Octomeles* and *Datisca.* In fruit the ovary becomes globose, with a diameter of 4–4.5 mm (Fig. 15). Dehiscence is by means of an apical pore formed when the four lobes separated by the prominent sutures at the top of the ovary dry and bend downward toward the locule. A similar process occurs in *Datisca.*

Axes bearing the male flowers of *Tetrameles* are shorter than those of the females and are somewhat more rigidly spreading at the branch ends. Steenis (1953) calls them panicles and says the male flowers are slightly fragrant. The male flowers have short calyx tubes and are tetramerous like female flowers. There are in some instances a few weakly developed lobes alternating with the sepals, but for the most part petals are absent. Stamens are on the rim of the inner cup opposite the sepals. The anther is basifixed and dehisces longitudinally (Fig. in Steenis, 1953, p. 386).

Datisca.—Inflorescences of *Datisca* are greatly shortened so that the flowers are axillary on the main axis or on lateral branches (Fig. 16). At the base of a lateral branch, flowers of *D. cannabina* may be pedicellate on very
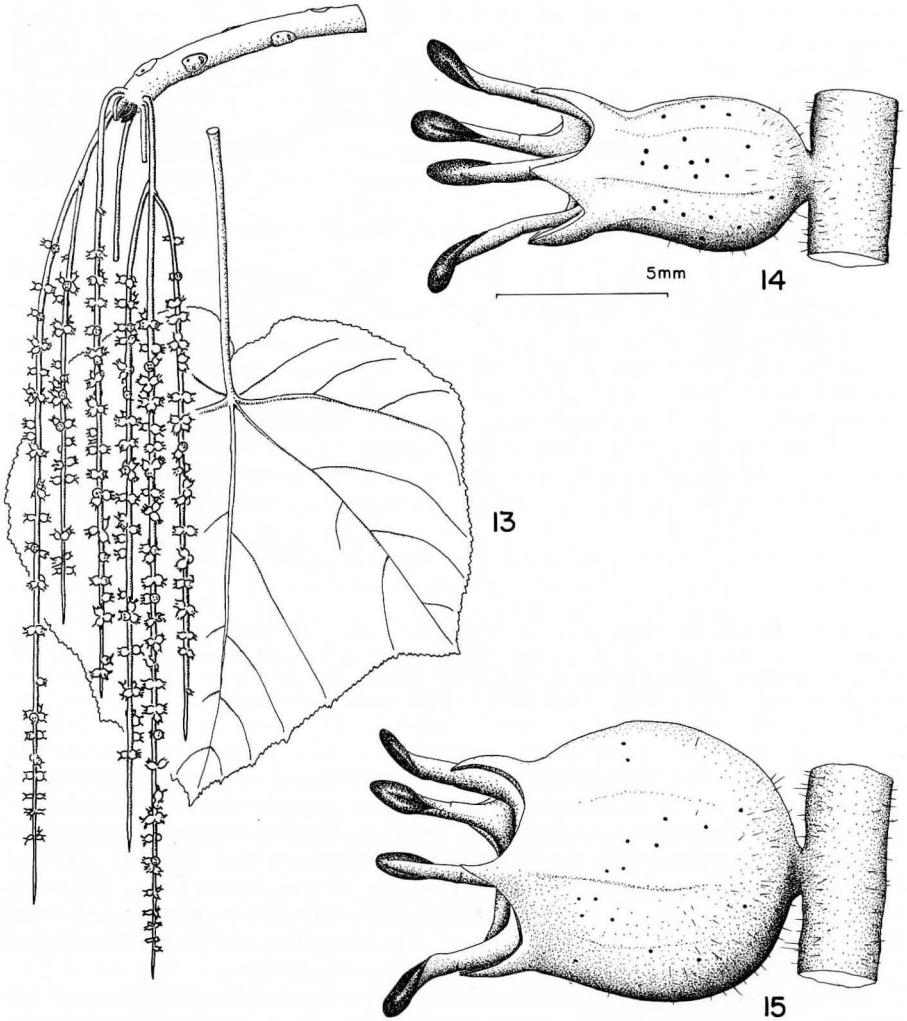
Fig. 13–15. *Tetrameles nudiflora*. Fruit and flowers drawn to the same scale.—
13. Inflorescence with female flowers and fruits, ×⅓. Inflorescence from *Davidson 1413a*; leaf from *Davidson 1413b*.—14. Female flower. Black dots represent stalked and sessile glands.—15. Fruit.

short inflorescence axes; but this is much less common in *D. glomerata*, in which there is only a swelling to which the glomerules of flowers are attached. Wydler (1878) interpreted the flower clusters of *D. cannabina* as dichasia. Inadequate flowering material prevents confirmation of this in the present study, but the axillary glomerules of *D. glomerata* are cer-

Fig. 16–18. *Datisca glomerata.*—16. *Davidson 1557.* Main axis and lateral branches with hermaphrodite flowers, ×⅓.—17. *Davidson 1002.* A. Hermaphrodite flowers. B. Fruit, transection.—18. *Davidson 1002.* Male flower. Note buds at the base of the pedicel.

tainly determinate. On large, robust plants of the latter species the flowers mature acropetally in the axils of leaves that are essentially the same as those on the main axis; i.e., they are pinnately compound, and the leaflet margins are denticulate. Leaves on the flowering branches of *D. cannabina* are short, lanceolate, and mostly entire or obscurely toothed.

The pedicel of the female flower bears a tiny bract (Fig. 17A). Typically this bract is on the lower half, but sometimes it is present at the conjunction of two pedicels. It is always single, never has a bud in its axil, and is gland-tipped. The flowers do not mature simultaneously, but instead there are several tiny buds at the pedicel base of the first flowers (shown for the male, Fig. 18). Each is subtended by its own bract, which is much smaller than the solitary one above it. In cases in which the inflorescence axis tends to grow out in *D. cannabina*, bearing ten or more flowers, buds still develop on the pedicels.

Datisca glomerata is androdioecious, i.e., the male and hermaphrodite flowers are on separate plants. The hermaphrodite flowers are protogynous

and 3- or 4-merous, although sometimes only one or two (or no) anthers are present on a given flower (Fig. 17A). The nearly sessile anthers are 4–5 mm long and alternate with the styles. In transections the overy is somewhat angular (Fig. 17B), a quality lost upon drying, and is 4–6 mm long from the base of the ovary to the base of the sinuses between the lobes. Calyx lobes are opposite the styles and are about 1–1.5 mm long. Petals are lacking. The style base is 3–4 mm long from its insertion on the crown to the cleft, and the branches extend about 10 mm beyond this. The crown is very shallow and apparently contains no nectary. *Datisca cannabina* is completely dioecious, and the female flowers have much shorter styles and stigmas than the hermaphrodite flowers of *D. glomerata*. The ovaries of the flowers of the two species are otherwise alike.

Male flowers of both species are axillary in the same sense as the females and hermaphrodites (Fig. 18). Associated with the perianth lobes there is usually a member on the pedicel slightly proximal from the others. This lobe may be homologous with the bracts on the lower part of the pedicels of female and hermaphrodite flowers, because a corresponding bract appears otherwise to be lacking. It is not usually associated directly with a stamen or a stamen trace; but the flower is small, and such evidence is weak. Pedicels of the male flowers often reach lengths of 2 cm or more. At the base of each are tiny buds, as in the female and hermaphrodite flowers, but there are no subtending bracts (Fig. 18). Calyx lobes number from 4 to 10; and anthers, from 6 to 20.

FLORAL ANATOMY

Octomeles.—The vascular cylinder in young inflorescence axes of *Octomeles* consists of about 40 collateral bundles connected by interfascicular cambium. In the mature axis a cambium produces vessels that are solitary, in pairs, or in radial files separated by multiseriate, homogeneous rays with erect cells only (Fig. 26–27). The mature intervascular pit pattern is alternate with transversely or diagonally elongate apertures and closely spaced chambers that appear polygonal in face view. Before initiation of cambial activity, bundle-cap fibers develop adjacent to the phloem of each bundle. At maturity the phloem zone is as wide as the xylem and is surrounded by a complete ring of sclerenchyma, including brachysclereids that differentiate next to the bundle-cap fibers toward the cortex. The sieve-tube elements have conspicuously nacreous lateral walls (Fig. 27), and sieve plates are simple and transverse or compound and oblique. Two to four companion cells in a single strand accompany each sieve-tube element.

The epidermal cells are tiny and cuboidal in paradermal section and are covered with a thin, smooth cuticle. Cells of the pith and cortex may contain either crystal sand, larger prismatic crystals, occasional druses, or starch grains. In older inflorescence axes many of the large, rounded pith cells have thin, lignified walls. Starch in the cortex is restricted to a zone two or three cells thick just outside the bundle-cap fibers. Both pith and cortex contain quantities of large, branched sclereids that develop very early in ontogeny of the axes (Fig. 22).
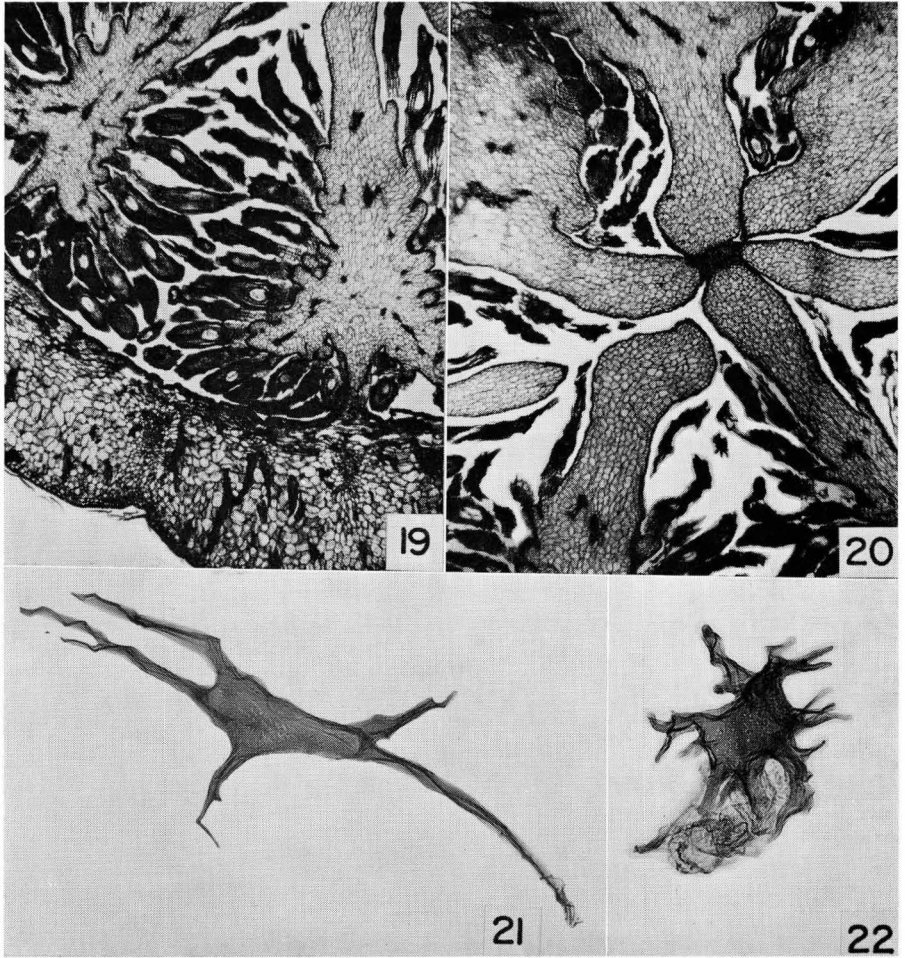
Fig. 19–22. *Octomeles sumatrana.*—19. *Davidson 1482*. Transection of ovary showing placentae with very narrow bases. Note very small cells opposite the groove in the wall. ×35.—20. *Davidson 1482*. Transection of placentae at the center of the ovary, ×35.—21. *SAN 59701*. Elongate branched sclereid from ovary wall (maceration), ×170. —22. *SAN 59702*. Branched sclereid from pith of inflorescence axis (maceration), ×170.

One to several floral primordia are subtended by a small, caducous bract. The nodes of bracts proximal on the axis are trilacunar, but distally they are unilacunar. Toward the base of the axis there is often a small, petiolate leaf. All parts of the young axis are densely covered with peltate scales that persist but are more widely scattered on mature parts.

The ovary wall of *Octomeles* is thick and basically parenchymatous (Fig.

19) with an epidermis of small, cuboidal, tannin-filled cells as seen in para-
dermal section. The locule is lined between the placentae with two or three
layers of flattened and tangentially elongate cells, just abaxial to which
there is a narrow zone of similarly oriented branched sclereids. In the outer
ovary wall the sclereids are almost entirely radially oriented and are
elongate (Fig. 21), except where they are parallel to the axis of large
bundles. The sclereids are also abundant in the crown and are parallel to
the long axis of the perianth tube and the styles, as seen in a median longi-
tudinal section of the flower. They are directed toward the apex of calyx
lobes. The interior of the crown is lined by small, dark-staining nectary
cells that extend upward toward the sinuses between the styles in attenuated
arms.

The placentae are large, and they usually meet at the center of the locule
(Fig. 20). The placentae are attached to the ovary wall on very narrow
ridges that frequently contain branched sclereids. Very rarely sclerenchyma
is present in the enlarged part of the placentae.

In the ovary and fruit wall, patches of small parenchyma cells extend
from the epidermis to the locule lining at the position of each stylar bundle.
Their appearance is like that of bundle-sheath extensions in leaves, except
that there are no sheath cells here, and they correspond to slight grooves
in the wall (Fig. 19). These grooves are the lines of rupture when the
outer parenchyma wall dries and falls away from the axis, revealing an
inner, sclerified layer that dehisces laterally (Fig. 9B). The lines of de-
hiscence correspond to the places where the sheets of flattened sclereids
that line the locule are interrupted by the narrow base of each placenta. A
layer of collenchyma that passes through the base of the flower is continuous
with the collenchyma of the outer cortex in the inflorescence axis and helps
to strengthen the attachment of the flower to the axis. Long after dehiscence
of the fruit and separation of the axes from the tree, the capsule valves
remain attached to the fallen axes and take on a conspicuous, asteriate ap-
pearance. The ellipsoidal seeds are about 1 mm long and the outer epidermal
cell walls are concave, giving the testa a minutely pitted appearance.

The abaxial epidermis of the perianth tube of the male flowers is similar
to that of the ovary. The lower half of the cup is lined by a thick nectary
with upwardly extending arms alternating with the stamens (Fig. 23). Ex-
cept at the very base of the nectary tissue, the boundary between the nectary
and the parenchyma of the outer perianth tube is clearly marked by the
difference in cell size and by the presence of vascular strands, which are
more abundant at the border here than in the crown of the female. Even

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Fig. 23–27. *Octomeles sumatrana.*—23–25. SAN 59702.—23. Longisection of floral
tube of male flower in bud showing thick nectary, ×35.—24. Transection of male flower
bud and an anther. Note greatly expanded epidermal cells. Dehisced appearance of
the anther is an artifact. ×35.—25. Detail of Fig. 24 showing multiseriate endothecium,
×175.—26–27. Inflorescence axis. *Davidson 1482.*—26. Transection. Secondary xylem
is present. ×50.—27. Transection. Nacreous walls in the sieve tube elements. Note
extraxylary fibers (F). ×250.
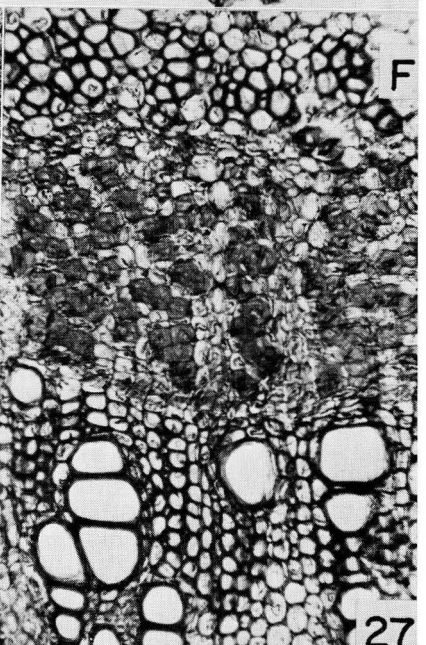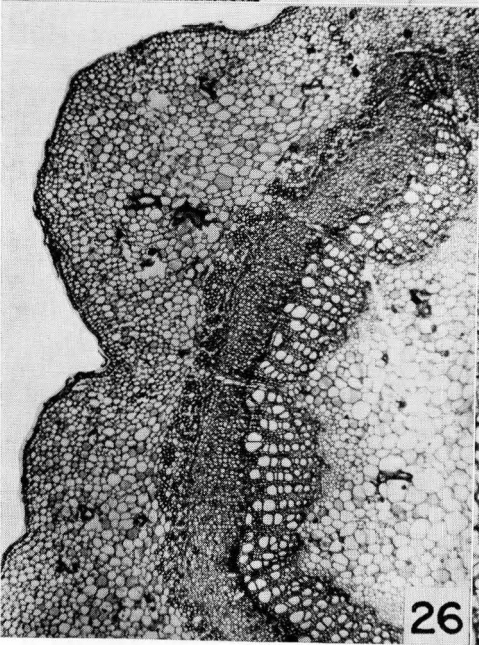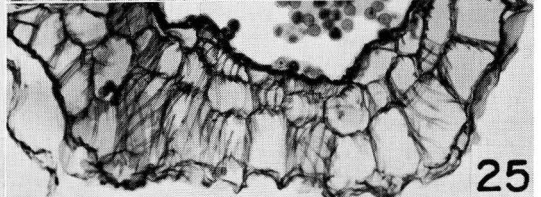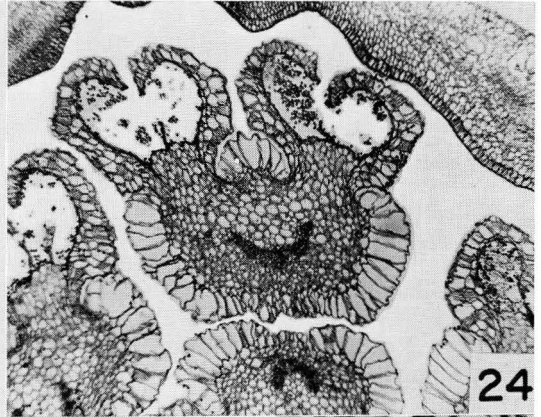
at the level of the nectary extensions, the alternating zones of smaller parenchyma cells between the actual nectary tissue can be distinguished from the outer tube. The abundant branched sclereids have only a vaguely radial orientation, and they are not found in the nectary. As in the female, there is a sheath of them around the large bundles.

The abaxial epidermis of the calyx lobes is the same as that of the crown, but the adaxial epidermis is papillate. Many of the papillae towards the margins are clavate and 2- or 3-celled. The position is reversed on the corolla lobes: papillae are abaxial; cuboidal, nontanniniferous cells are adaxial. The large papillae bear prominent ridges that correspond to the regular cell-wall and cuticular sculpturing on the abaxial side. In each case the ridges are formed by the primary cell wall, and not by the cuticle alone. The same sculpturing pattern is found in buds and in mature flowers and is not a dehydration artifact. Papillae at the tips of the corolla lobes have longer, more irregular ridges, often with a thin wing of cuticle extending some distance beyond the cell wall. Sculpturing is otherwise absent in male and female flowers. The tip cells appear glandular and sticky from the darkly-staining cell contents and the amount of debris that adheres to them. Stomata do not seem to be any more frequent on either calyx or corolla lobes than on the ovary wall, but they are often present in clusters in all three places. In bud the valvate lobes are held together by the interlocking papillae. There is no evidence of fusion below the sinuses.

Peltate trichomes occur on the outer surface of the calyx lobes, but not on the corolla. Frequently, files of cork cells, or "cork warts," occur on the calyx and ovary or fruit wall, but vascular traces near these warts are occluded by red-staining (with safranin) deposits that are perhaps indicative of origin through injury. The long axes of branched sclereids in the corolla are directed toward the tips of the lobes, but sclereids in the calyx show less tendency toward a constant orientation and are less numerous.

Epidermal cells of the filaments are anticlinally elongate. The anther is four-loculate, with each pair of locules attached to the large connective by a slender ridge (Fig. 24). All the subepidermal cells of the locule wall near the connective ridges develop endothecial thickenings, and the resulting multiseriate endothecium grades into biseriate toward the longitudinal dehiscence slit (Fig. 25). The thickenings are lignified single, double, and multiple helices with branches and are present on all walls. In small or oddly shaped cells the thickenings are so frequently branched and irregular that the helical nature is absent. Parallel to the locules run three broad zones of greatly expanded cells. Branched sclereids are lacking in the anther.

In the following discussion terms like connect, divide, and branch are used to describe the arrangement of the vascular bundles as they appear in serial transections from base to apex and cleared preparations of the ovary and crown of female flowers and of the floral tube of male flowers. The terms are not intended to have developmental implications. In addition the designations "stylar bundle" and "anther bundle" are used in place of the corresponding "dorsal bundle" employed in many studies because the former are considered to be morphologically more exact terms than the latter.
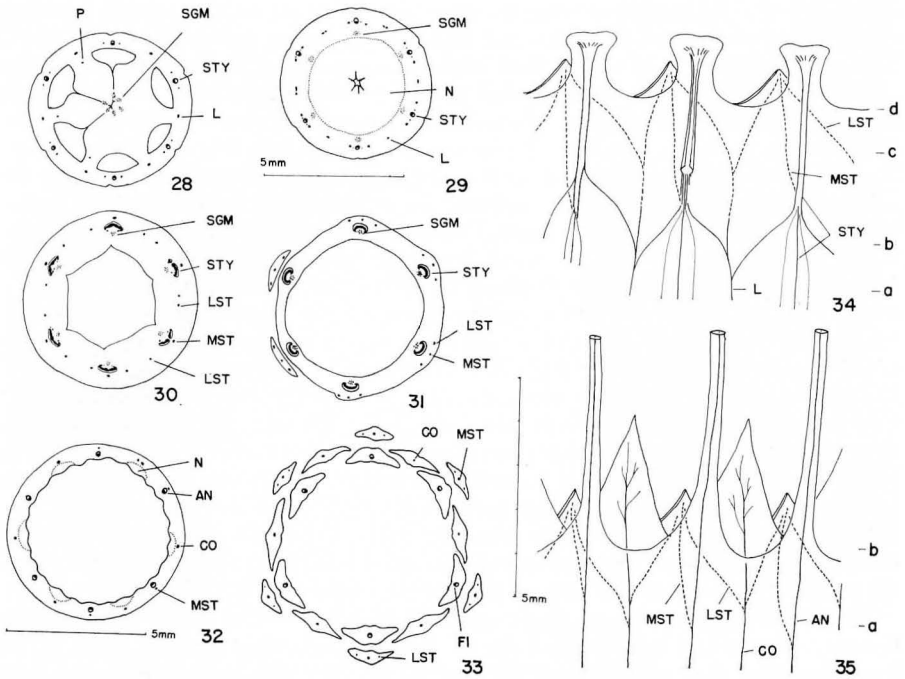
Fig. 28–35. *Octomeles sumatrana.* All figures drawn to same scale.—28–31. Transections of female flower.—28. Ovary at top of the locule.—29. Floral crown near the base of the nectary.—30. Nearly median.—31. Near lip of crown. Calyx lobes on left.—32–33. Transections of male flower.—32. Slightly above median, showing nectary extensions between the anther bundles.—33. Perianth parts. Inner whorl, filaments; middle whorl, corolla lobes; outer whorl, calyx lobes.—34–35. Bundle diagrams based on clearings.—34. Female flower crown. Lower case letters refer to corresponding transections: a, Fig. 28; b, Fig. 28; c, Fig. 30; d, Fig. 31.—35. Male flower; upper part of floral tube. Corresponding transections: a, Fig. 32; b, Fig. 33.—(*Key:* AN, anther bundle; CO, corolla bundle; FI, filament trace; L, lateral bundle; LST, lateral sepal trace; MST, median sepal trace; N, nectary; P, median placental bundle; SGM, stigmatoid tissue; STY, stylar bundle.)

Floral primordia of *Octomeles* contain 6–8 procambial strands, depending on how many anthers or styles will be present in the mature flower. Approximately one sixth to one seventh of the vascular cylinder of the inflorescence axis extends into the fully developed flower, but the number of initial traces may be obscured by branching. The ovary wall contains 6–8 stylar bundles, between which are one or two lateral bundles (Fig. 28). Clearings of the ovary wall reveal tiny horizontal traces connecting these 12–16 major bundles throughout the ovary length. Within the wall of the crown at a variable distance distally from the top of the locule, the lateral bundles bifurcate, and each half forms a lateral trace of a calyx lobe (Figs. 29, 30).

At a level slightly proximal from the points of bifurcation, the lateral bundles give rise to two traces that join the stylar bundles on either side (Fig. 34). The two or three tiny traces that often accompany a stylar bundle in the ovary wall fuse with it around this level. In the upper part of the crown the stylar bundle, which is semicircular in transection, gives off abaxially the median calyx trace (Fig. 31). Occasionally one or two traces lie parallel to it. Within the style and very near the stigma, the phloem and xylem may be intermixed or the xylem may appear in transections to be in two semi-circular bands with phloem abaxial to each. Stigmatoid tissue runs down-ward within the "trough" formed by the style bundle and then inward toward the center of the flower along the outer end of each suture (Fig. 28). Small cells that are distinctly unlike those of the placentae, but through which the tips of the placentae are connected, represent the intraovarian continuation of this tissue (Fig. 20). These cells, although extremely small in transection, are vertically elongate, and toward the top of the locule they may extend radially for a short distance along the margins of the placental tips. In ovaries in which the placentae do not meet at the center, only a small amount of this tissue is present at the tips. In several instances pollen tubes have been observed in the locule adjacent to this tissue.

The placentae contain three bundles each. The two wing bundles are extensively branched; but the central, adaxial bundle remains integral (Fig. 28). Their courses at the top of the locule could not be followed.

As in the female flower, there are 6–8 bundles at the base of the male flower. Somewhat below the base of the nectary, they branch into 12–16 large bundles and several smaller ones (Fig. 32). The nectary traces that branch from these consist mostly of phloem. At the level of the nectary arms, each of the 6–8 corolla bundles branches in three directions, and the median trace of the three forms the corolla lobe trace. Within the corolla lobe this trace ramifies freely into a number of traces that do not diminish in size. Possibly the lobes are hydathodes. The two lateral branches derived from the branching of the corolla bundle form the lateral sepal traces of adjacent calyx lobes. At a level slightly distal to the branching of the corolla bundles, the anther bundles branch radially into two traces, the abaxial of which is the median sepal trace and the adaxial of which is the filament trace. Thus, a filament contains a single nonbranching trace, a corolla lobe contains one trace that branches within the lobe, and a calyx lobe has a median and two lateral traces (Figs. 33, 35). A number of variations on this pattern can be found. Sometimes branching of a corolla bundle is asymmetrical, resulting in only one lateral trace. A lateral calyx trace may

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Fig. 36–40. *Tetrameles nudiflora. Davidson 1413a.*—36. Transection of inflorescence axis, ×190.—37. Nearly median transection of ovary wall. Note hypodermis and sclerenchyma of locule lining. ×190.—38. Longisection of sessile gland on ovary wall, ×190.—39. Transection of stalked gland on ovary wall, ×375.—40. Elongate scleren-chyma of ovary locule lining (maceration), ×190.
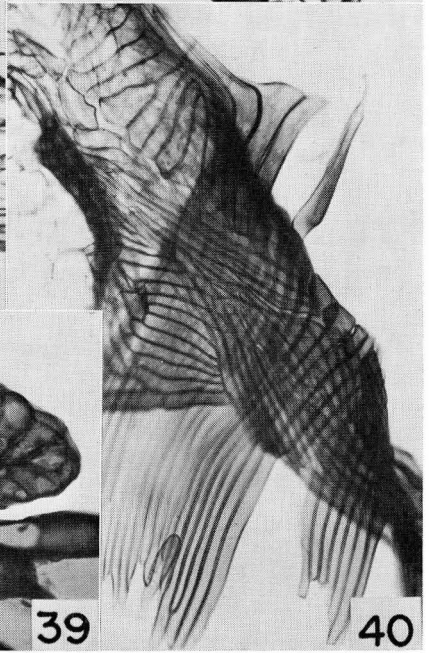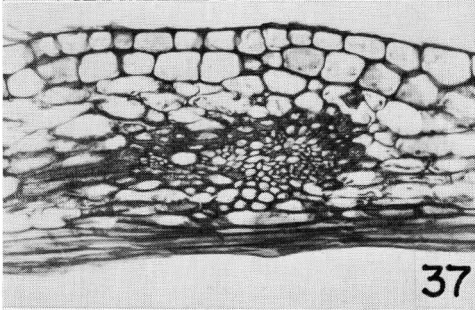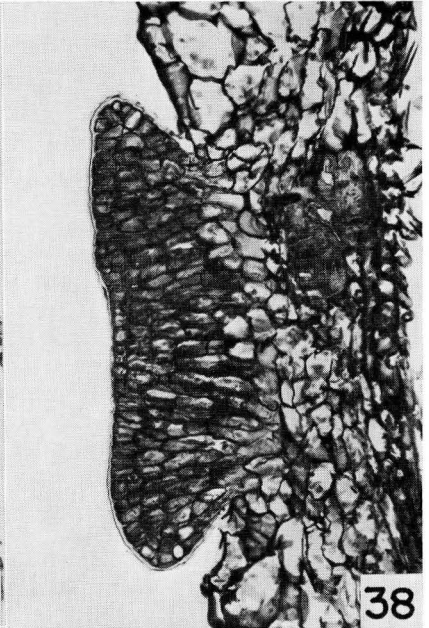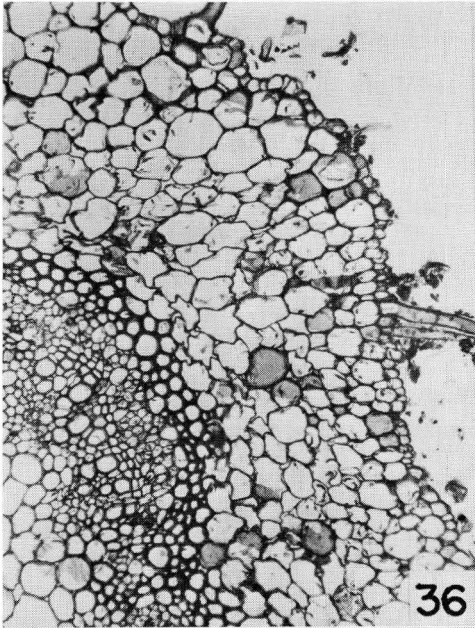
be composed of branches from both a corolla trace and a median calyx trace; or a median calyx trace may branch into two smaller laterals.

Tetrameles.—The anatomical structure of the inflorescence axis of *Tetrameles* is similar to that of *Octomeles* (Fig. 36). Cambium develops in the same way, but secondary growth is much more limited. A cylinder of extraxylary fibers and brachysclereids encloses the phloem, but no starch zone is present outside it, at least not in mature axes. The xylem and extraxylary fiber zones are approximately equal in width and are wider than the phloem. Druses, prismatic crystals, and spherites of calcium oxalate are found sporadically in pith and cortex. Spherites are more common in vegetative parts and are discussed in greater detail under that heading. Branched sclereids and sclereid nests are present only in the pith. At the points of branching of the axes the large pith cells sclerify slightly without filling in the intercellular spaces, and branched sclereids are slightly more common than elsewhere in the axis.

The axis is much more slender than that of *Octomeles*, and it is not grooved. In addition it is densely covered with three types of trichomes: septate, spicular hairs with thickened, often lignified walls; unicellular, 2-armed hairs that have similarly thickened walls and that are raised on podia; and multiseriate, stalked glands. Large, sessile glands are also common. The bracts subtending floral primordia are tipped by stalked glands that are considerably larger than those on the rest of the young inflorescence.

Between bundles the overy wall of *Tetrameles* is about eight cells thick. The epidermal cells are tangentially elongate and are larger than those of the overy in *Octomeles*. The hypodermal layer is frequently enlarged, but not always uniformly so (Fig. 37). Internal to this are five or six layers of flattened parenchyma and three layers of elongate cells lining the locule. The few branched sclereids are not oriented in any particular direction and have short arms. Abaxial epidermal cells of the calyx lobes are larger than the adaxial ones, but neither surface is papillate. The epidermis of the lobes and of the rest of the flower is covered by a thin, sculptured cuticle. The sculpturing pattern consists of ridges that are formed by the primary cell wall and that are mostly oriented parallel to the long axis of the cell. The inner area of the crown is lined by small cells that stain lightly and appear not to serve as a nectary, although nectary cells are frequently very difficult to detect in preserved material because they differ so slightly from surrounding parenchyma. In addition to septate hairs and stalked glands, there are also on the ovary large, sessile glands, especially on the lower half (Fig. 38). Both sessile and stalked glands (Fig. 39) are represented in Fig. 14–15 by black dots. In fruit the three layers of elongate, curved cells lining the locule develop thick, lignified walls, as do the parenchyma cells immediately peripheral to them (Fig. 40). These elongate cells are oriented similarly to those in *Octomeles* but do not have the same function. As the fruit dries, they prevent it from collapsing; and at the same time the four lobes formed by the sutures at the top of the ovary shrink and fold downward toward the locule, leaving a pore through which the seeds escape. The seeds are 1 mm

or less long and have a loosely-fitting seed coat that acts as a wing. There are a few druses in the fruit wall, the placentae, and even the seeds, but no starch grains.

Four bundles are present at the base of the female flower. Approximately at the level of the locule base, they divide into eight large and several small bundles in the wall and one in each placenta. Above the base of the locule each placental bundle branches into three traces. Of the eight major bundles, four are opposite the placentae and are laterals, and four alternate with them and are stylar bundles (Fig. 41). At the top of the locule there is a bifurcation of the lateral bundles, and the strands so formed branch into two more traces (Figs. 42–45). The major traces derived from the second branching join adjacent stylar bundles at a more distal level, and the minor ones form the lateral sepal traces (Fig. 43). Proximal from the first bifurcation of the lateral bundles, traces branching from the stylar bundles form the median sepal traces. Frequently two stylar bundles appear between a pair of placentae, both of which fuse in the crown. The placentae contain three distinct traces throughout their length; i.e., the wing traces are not obscured by extensive branching of ovule traces as they are in *Octomeles*. The central, adaxial placental trace fuses with a lateral or a lateral branch at the top of the locule, and at the same level the wing traces follow an oblique course to the adjacent stylar bundles. The stigmatoid tissue is visible as four pairs of strands at the top of the locule where the placentae meet (Fig. 42). The members of each pair follow the sutures and stylar grooves to adjacent stigmas (Fig. 44). The tissue is adaxial to the normally bicollateral style bundles. The stylar groove is papillate. The adaxial part of the phloem in the style bundle is derived topographically from the median placental trace. The placental traces consist mostly of phloem with only a few vessels abaxially, and no "inversion" of these traces occurs before fusion with the stylar bundles.

In the fruit wall, cells of the large bundles and some of the traces are heavily sclerified, even in the calyx lobes and styles; thus the vessels and sieve tubes are completely embedded in sclerenchyma. The sclerenchyma consists of extraxylary fibers with diagonal, slit-like pits and brachysclereids with simple, circular pits. Cells at the periphery of the bundles are sclerified on their inner and radial faces only. Sclerenchyma also accompanies the stigmatoid tissue.

Datisca.—The wall of the ovary and of the fruit of *Datisca* is very thin (Fig. 46). A hypodermis is present, as in *Tetrameles*, though it is never conspicuous because the epidermal cells are large and are the same size as the cells beneath the hypodermis. The outer wall of the epidermal cells is sculptured with wavy ridges parallel to the long axis of the cells and is covered with a thin cuticle. As in the other genera, the ridges are formed by the primary cell wall, but they are more prominent here than in *Tetrameles*. The locule lining is similar to that in the other genera also: the innermost cells are elongate and lignified; but the cells of the layer abaxial to this are shorter, although still lignified. There are no bundle-cap fibers or sclereids anywhere in the wall.
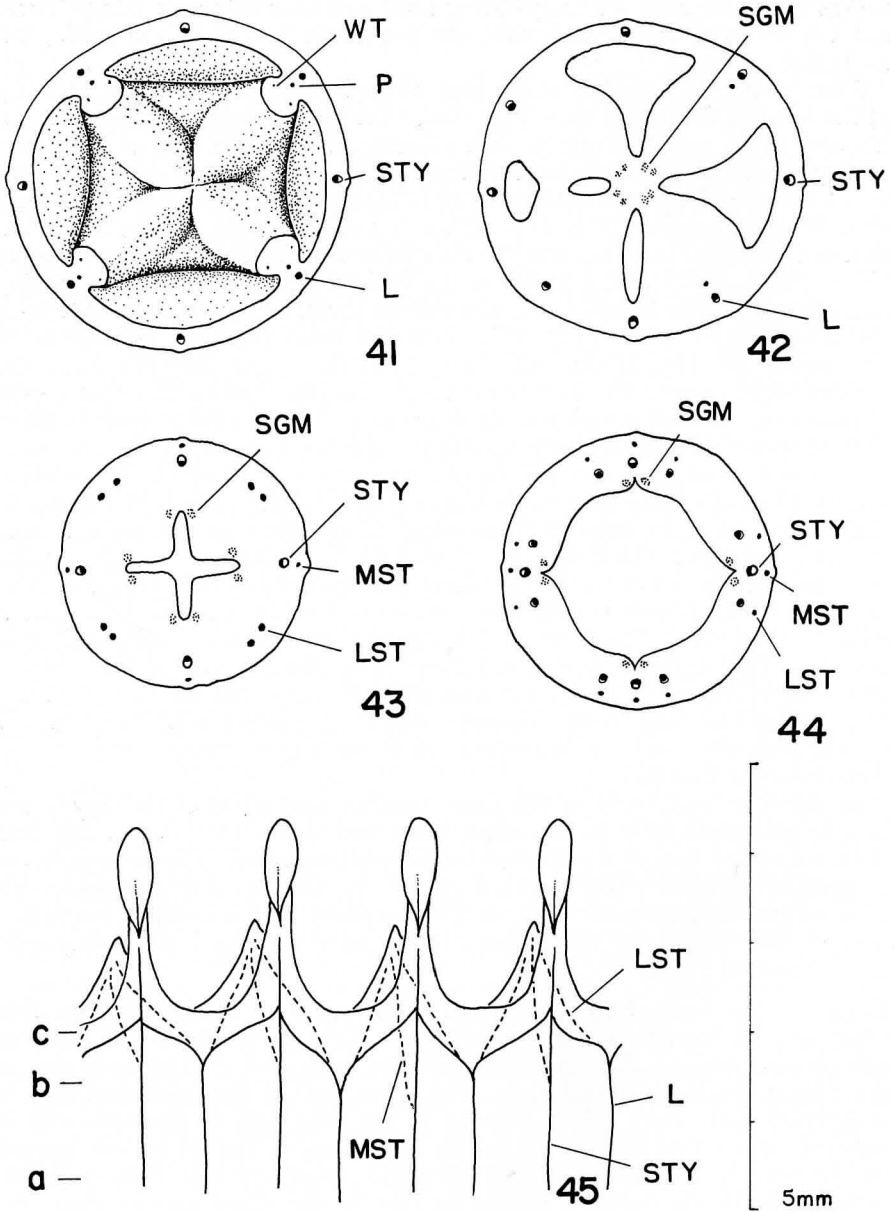
Fig. 41–45. *Tetrameles nudiflora. Davidson 1413a.* All figures drawn to same scale.—
41. Distal half of the ovary showing convergence of the placentae at the top of the
locule.—42. Transection of ovary at the top of the locule.—43. Transection of the ovary
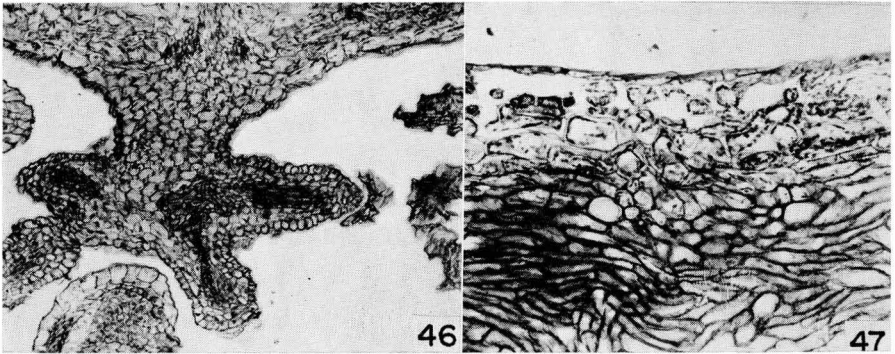
Fig. 46–47.—46. *Datisca glomerata*. *Oettinger 933*. Transection of ovary showing placenta, ×195.—47. *Datisca cannabina*. *CAS 220844*. Transection showing sclerenchyma between fruit wall and lobes of fruit at the top of the locule. Hypodermis is not visible in this fruit. ×195.

Cells lining the sutures at the top of the ovary are sculptured and covered with a thin cuticle, and many contain spherical inclusions of unknown composition. These inclusions are not the same as the spherites seen elsewhere. The crown is very shallow and without a nectary. In fruit the walls become dry and papery and are held rigid by the lining cells. The stigmas absciss. Dehiscence of the capsule is poricidal through gaps left by the drying valves at the top, as in *Tetrameles*. Elongate cells similar to those of the locule lining are present between the valves and the fruit wall at the top of the locule and are perhaps involved in the dehiscence mechanism in which the valves fold downward toward the locule (Fig. 47).

The bisexual flower of *D. glomerata* is a 6- to 8-bundle structure, depending on how many styles are present. Transections at the distal end of the pedicel show a complete vascular cylinder. At a slightly distal level the cylinder is no longer present, but instead there are three or four large stylar bundles, and alternating with them are the bundles supplying the anthers. The anther bundles correspond to the laterals in the female flowers of the other two genera. At the base of the locule the anther bundles each branch into two bundles, the adaxial of which is included in a placenta at a slightly distal level. Each placental bundle branches into two wing traces and a median trace that is adaxial to the wing traces. The course of a wing trace is difficult to recognize in transections because of the numerous connections with the median trace and the branches to the ovules. Most of the

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at the base of the floral crown.—44. Transection, nearly median, of crown.—45. Bundle diagram of female flower crown. Lower case letters correspond to the following sections: a, Fig. 42; b, Fig. 43; c, Fig. 44.—(*Key*: WT, wing trace of placenta; other abbreviations as in Fig. 28–35.)
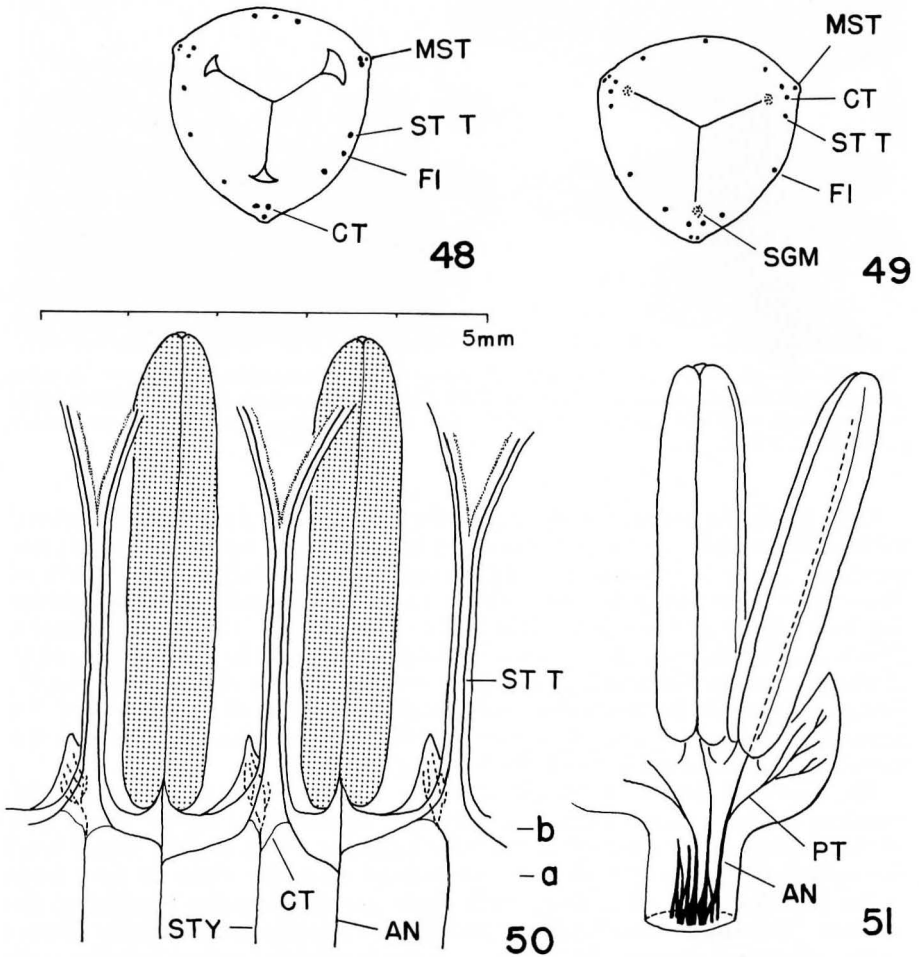
Fig. 48–51. *Datisca glomerata. Davidson 1002.*—48. Transection of the ovary at the top of the locule.—49. Transection near the base of the floral crown.—50. Bundle diagram of hermaphrodite flower. Anthers are stippled. Correspondence of transections: a, Fig. 48; b, Fig. 49.—51. Bundle diagram of male flower.—(*Key:* AN, anther bundle; CT, connecting trace between stylar bundle and lateral-derived style trace; FI, filament trace; MST, median sepal trace; PT, perianth trace; SGM, stigmatoid tissue; ST T, style trace; STY, stylar bundle.)

small traces with horizontal courses in the ovary wall appear to be derived topographically from the stylar bundles. Branching of the stylar and anther bundles takes place in a narrow zone in the crown. The anther bundle branches into three traces, the median of which forms the filament trace (Fig.

48). The two side branches form lateral style traces that are separate on either side of the stigmatoid tissue (Fig. 49). Stylar bundles, alternating with the placentae, each give off a large peripheral strand into a perianth lobe. Near the level of this divergence the stylar bundles are connected, as seen in clearings, to the lateral-derived style traces on either side by two very tiny traces (Fig. 50). Occasionally no such connection occurs, however. Branching of the anther bundle may occur proximally within the crown, but ordinarily it is near the crown lip, and the course of each trace is almost horizontal.

The perianth lobes each contain a median trace that branches into a number of smaller traces within the lobe (Fig. 50). Conspicuous, elongate air spaces in each lobe have their long axes directed toward the lobe apex. Numerous guard cells are present in the epidermis. Possibly the lobes function as hydathodes. The single tiny bract on each pedicel and the tiny buds also contain one trace apiece.

The anthers of the male flowers are identical to those of the hermaphrodite flowers. The endothecium of the 4-loculate anther is uniseriate, except near the connective, where the adjacent cells also have thickenings. Dehiscence is longitudinal, and in sectioned, mature anthers the pollen grains are present singly and in tetrads.

Vascular tissue in the pedicel of the male flower is in the form of a cylinder. At the distal end, however, discrete traces are present, each one being an anther trace. The anther traces all tend to form at approximately the same level (Fig. 51); or one or two branchings may occur at a lower level of the cylinder. Traces in any perianth lobes proximal from the rest are from this lower branching level, as are those of a few lobes in the main whorl when these lobes are very numerous (15 or more). The anther bundle extends to the end of the connective. The perianth lobes each contain a single median trace with many branches, and guard cells in the epidermis are abundant.

Basic anatomy of male and female flowers of *D. cannabina* is like that of *D. glomerata* (Montemartini, 1905; Himmelbauer, 1909a, 1909b). Only dried fruits and male flowers were available for direct examination, and they showed no anatomical differences from the California species. The details remain uninvestigated, however. The female flowers of *D. cannabina* have much shorter styles and stigma branches than the hermaphrodite flowers of *D. glomerata*.

POLLEN

Pollen grains of *Octomeles* are spheroidal and tricolporate (Figs. 52, 53). The diameter in polar view (based on 50 measurements) is 10–11 μ mounted in permount and 11–12 μ in lactophenol. Colpi are about 7–7.5 μ long, and the pores are 1 μ or less in diam (Fig. 54). The distance from pole to colpus is 2–2.2 μ.

The terminology used here is that of Faegri as illustrated by Larson, et al. (1962). The exine is about 1.5 μ thick and is composed of ektexine with an unornamented tectum, numerous small columellae, and a very thick foot
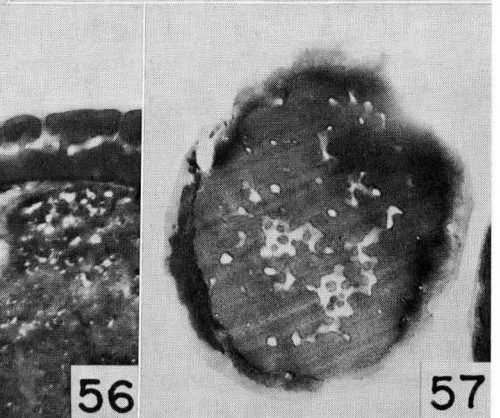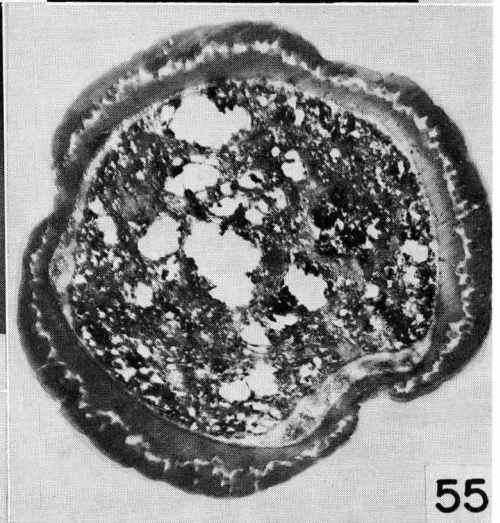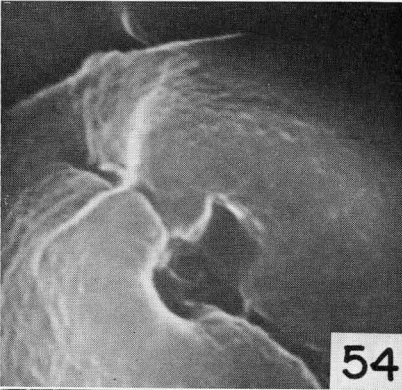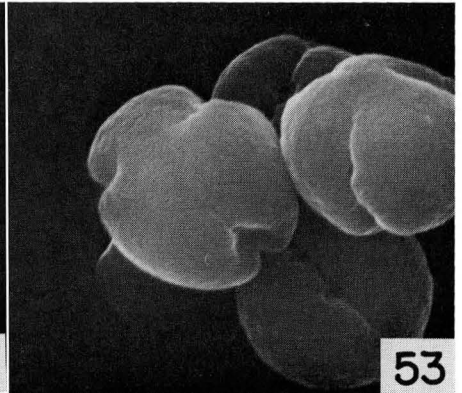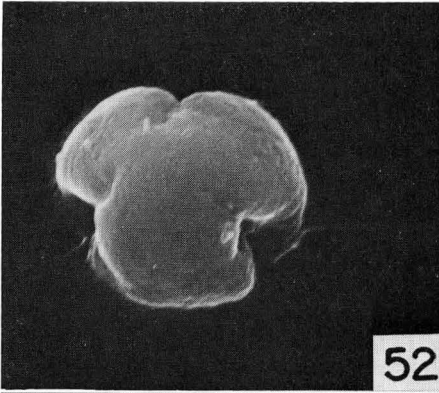
layer (Fig. 55). The zone interpreted here as the foot layer shows no dif-
ference in electron density from the tectum and columellae. A less electron-
dense layer, designated endexine in this terminology, is not recognizable.
Instead, beneath the foot layer is a very thin, dark layer, the structure of
which is not apparent in the photographs (Fig. 56). Toward the colpi the
exine tapers gently to 1 μ or less in thickness. Scanning EM photographs
show very slight pits in the tectum, many if not all of which correspond to
minute pores (Figs. 54, 57). The tectum and foot layer are of approxi-
mately equal thickness. Columellae are roughly hour-glass shaped and vary
one from another in thickness; they may be radially directed or somewhat
askew (Fig. 56). The cavernous zone in the ektexine is thus very uneven
in appearance. At the pores exinous material protrudes slightly. This part
of the exine appears to be continuous with the thin, dark zone beneath the
foot layer, and at the pores it has a lamellate structure. Across most of the
rest of the colpus it forms a concave membrane about 1 μ thick, and the
lamellate structure is not visible. Ektexinous elements are also included on
this part of the membrane (Fig. 56). When pollen was put through the
safranin-fast green staining series, the intine stained green only when the
grains had actually been sectioned and the exine cut. The intine is very
thin, except opposite the pores, where it is 1.5 μ; and opposite the colpi,
where it is 0.5 μ or so and gradually tapers in thickness toward the poles.

Pollen grains of *D. glomerata* and *D. cannabina* are identical in scanning
EM photographs (Figs. 58, 62). They are tricolporate, spheroidal, and fre-
quently in tetrads. Diameter in polar view varies from 13 to 16 μ in both
lactophenol and permount, but the most frequent diameter in a sample of
50 grains was 15 μ. Colpi are 10–12 μ long (Fig. 59), but the pores were not
measurable in the photographs. Distance from pole to colpus is about 3 μ
(Fig. 60).

The exine is slightly less than 1 μ thick. In scanning EM photographs the
tectum has a rougher appearance in *Datisca* pollen than it does in that of
Octomeles, and beneath it is a more even zone of columellae (Fig. 61). In
this case the endexine is definately distinguishable from the electron-dense
foot layer (Fig. 63, 64). Opposite the colpi the endexine is thickened, and
apparently the structure is nonhomogeneous, especially on either side of the
thickened regions (Fig. 63). The intine is very thin and is difficult to
recognize in the photographs. Measurements comparable to those given for
Octomeles could not be made.

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Fig. 52–57. *Octomeles sumatrana* pollen. SAN 59702.—52–54. Scanning electron micro-
graphs.—52. Polar view of a single grain, ×3,300.—53. Several grains, one polar, one
equatorial, ×2,800.—54. Nearly equatorial view of pore, somewhat distorted, ×10,000.—
55–57. Transmission electron micrographs.—55. Nonequatorial section, slightly oblique,
through the colpi. Note the very thick foot layer. ×8,000.—56. Equatorial (or nearly
so) sections; upper left: section through pore. Note dark layer beneath foot layer and
thick intine. ×15,000.—57. Tangential section through ektexine showing columellae
and pores, ×13,000.
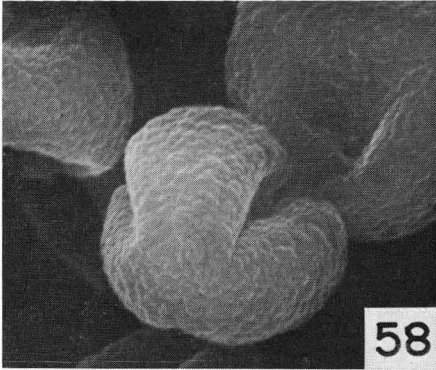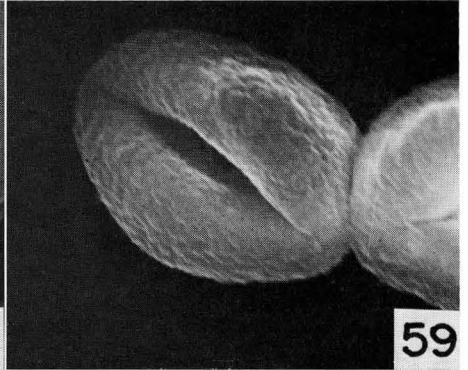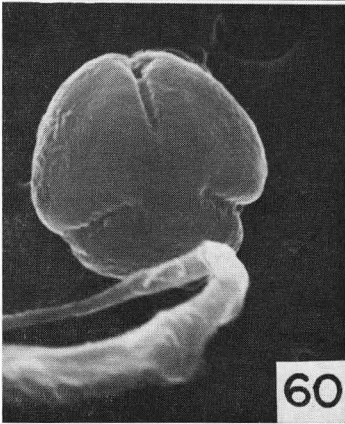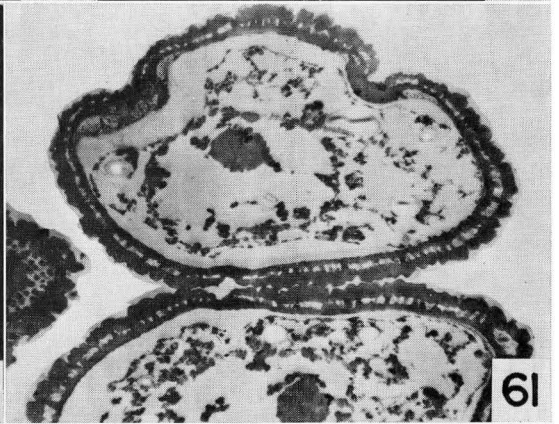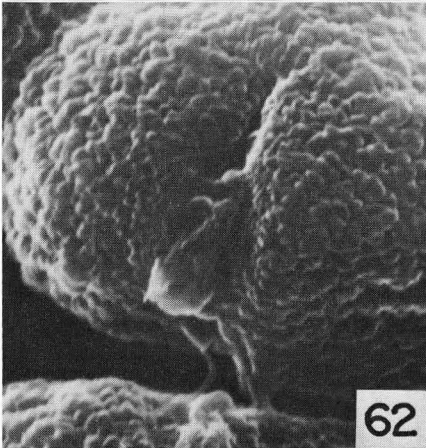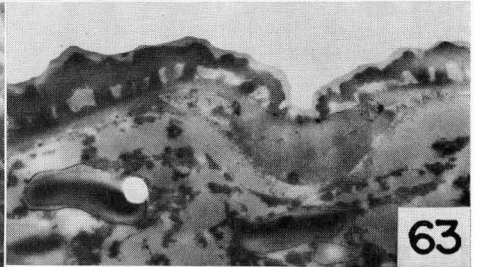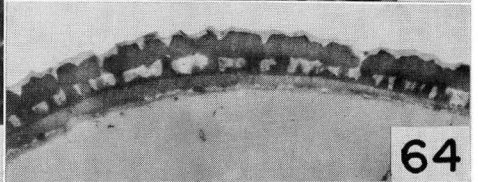
Grains are binucleate before dehiscence of the anther, and at germination the fusiform generative nucleus usually proceeds first into the pollen tube. Some pollen grains contain giant starch grains and very little cytoplasm, and these are presumably nonviable. Most pollen grains contain tiny starch grains, and the pollen tube may contain anistropic crystals. Observations were the same on pollen that had germinated on stigmas and on Synthetic Mucor nutrient agar (Hesseltine, 1954).

VEGETATIVE ANATOMY OF PRIMARY AXES, PETIOLES, AND LEAVES

Octomeles.—Stem and petioles of seedlings and saplings are winged, but young branches on trees are not. The epidermal cells of stems are small and rectangular in face view and are covered by a thin, smooth cuticle. The outer cortex, including the wings, is collenchymatous; the inner, parenchymatous. Both regions have narrow, schizogenous air spaces directed longitudinally. Vascular bundles are closely spaced and connected by interfascicular meristem only a few millimeters below the apex. Bundle-cap fibers appear before secondary development starts. The cortex of young stems contains numerous branched, forked, or unbranched sclereids. Around the periphery of the pith branched sclereids are horizontally oriented and abundant; however, they have no special orientation toward the center. As the stem grows and the pith enlarges, these sclereids become more widely scattered, although a very heavy concentration of branched sclereids remains in the nodal cortex opposite leaf gaps and at corresponding levels in the outer pith. The large parenchyma cells of the outer pith sclerify slightly without filling in the intercellular spaces around them, and similar sclerification occurs in the original interfascicular areas. Bundle parenchyma may remain unsclerified until rather long after secondary growth has begun.

After initiation of cambial divisions within the seedling axes, the bundle-cap fibers become septate. Both these and the libriform fibers in the xylem may be septate (in the sun-grown seedling only), mucilaginous (Fig. 65), and amyliferous at the same time. Parenchyma cells contiguous with the network of bundle-cap fibers sclerify on all faces as stem girth increases, and a complete cylinder of sclerenchyma is formed that persists in the boles of large trees; but this is a slow process compared to that in *Tetrameles*, and stems 25 mm in diam may still have only isolated fiber strands and brachysclereids outside the phloem.

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Fig. 58–64.—58–59. *Datisca cannabina* pollen. *CAS 220844* (*Walther, s.n.*). Scanning electron micrographs.—58. Polar view, ×2,900.—59. Nearly equatorial view, ×2,900.—60–64. *Datisca glomerata* pollen. *Davidson 1557.*—60. Polar view of grain in an early stage of exine development (scanning EM), ×2,900.—61. Oblique sections of two grains, presumably part of a tetrad, in an early stage of exine development (transmission EM), ×3,900.—62. View of colpus (scanning EM), ×6,900.—63. Section through a colpus. Note thick endexine and nonhomogeneous regions on either side of the thickening (transmission EM). ×10,000.—64. Transection of exine showing stratification of ektexine and endexine. Intine very thin (transmission EM). ×7,700.
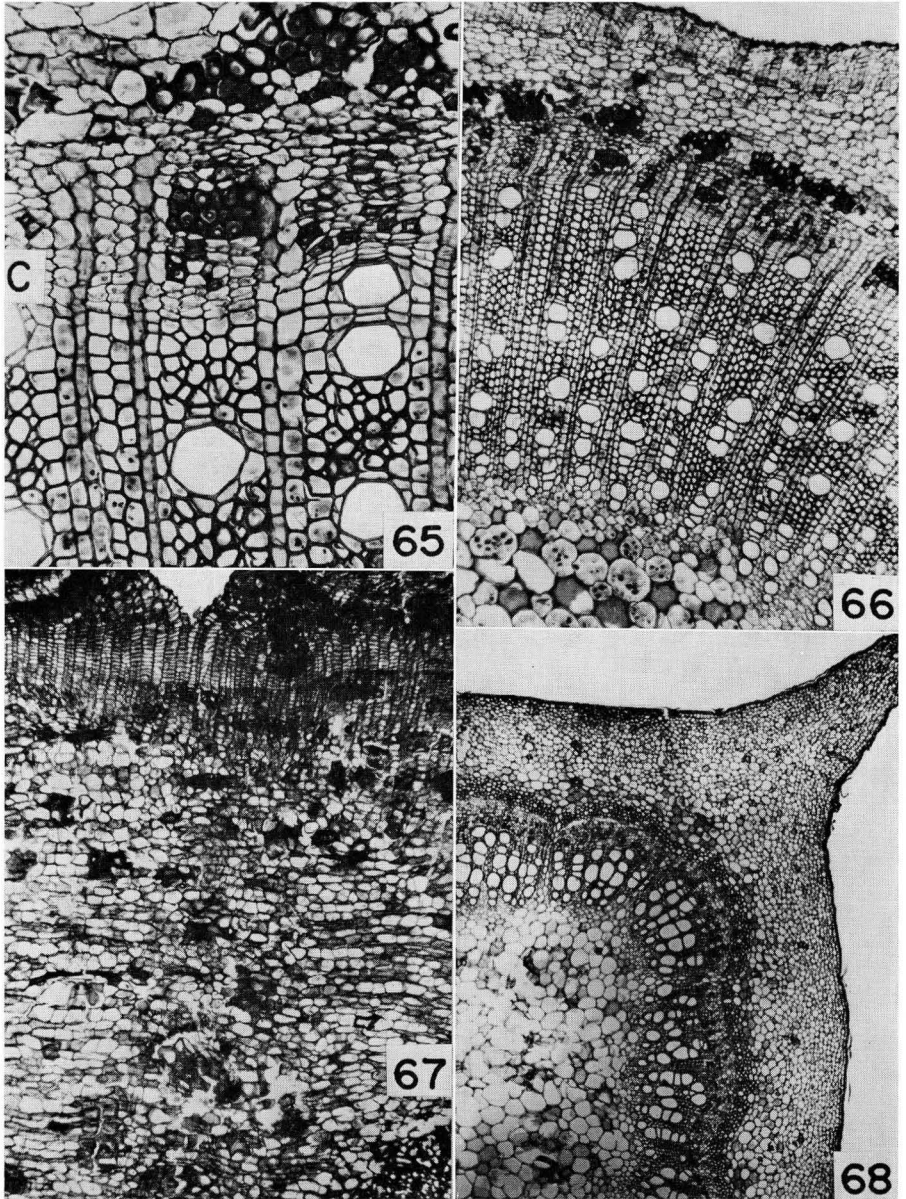
Fig. 65–68. *Octomeles sumatrana.*—65. *Davidson 1127*. Transection of 4-month-old seedling stem showing mucilaginous extraxylary and secondary phloem fibers. Note cambium (C). ×230.—66. *Davidson 1127*. Transection of seedling stem showing periderm and pith. Note large starch grains in pith. ×45.—67. *Davidson 1482*. Transec-

Periderm formation is superficial (Fig. 66). Phelloderm in young stems is two or three cells thick, but in the trunk of mature trees above the level of first branching, it is 5–10 cells thick; and in the base above the buttresses it is often over 20 (Fig. 66). This thick phelloderm layer is chlorophyllous and contains numerous branched sclereids and brachysclereid nests. Successive periderms develop in the outer cortex or perhaps in the phelloderm itself, but the interval between formations could not be determined. Rhytidome at the base of a tree has only two or three periderm layers present, with a few layers of phelloderm or cortical cells between them. The external face of the bark is usually smooth or slightly bumpy, with the chlorophyllous layers easily visible in cracks between the thin, exfoliating periderm. Herbarium labels occasionally mention deep fissures in the bark that are perhaps an indication of considerable age. No such trees were used in this study.

The original bundle-cap fibers are still identifiable at the base of a tree, although the strands are widely separated (Fig. 67). At the 10-m level and in the bole above it these fibers are united into a complete cylinder by tangential plates of brachysclereids, but the cylinder is incomplete at the base and around the buttresses. A cortex containing brachysclereids and branched sclereids, both solitary and clustered, extends half the distance from the outer phloem boundary to the phellogen; the phelloderm extends the other half. The cortex can be distinguished from the outer phloem parenchyma by its lack of extraxylary fibers and collapsed sieve tubes, but the boundary between cortex and phelloderm is not so easy to find. Between the large inner cortical cells and the radially aligned phelloderm cells lies a zone of comparatively small and actively dividing cells that appear to be derived from the phelloderm, although they have no radial alignment. If this is true, then what appears to be cortex is actually cortex and phelloderm; but a more detailed histogenetic study is needed to clarify the nature of the supposed "meristematic" region.

Starch grains and starchy chloroplasts stain black with IKI, and care was taken to distinguish between the two. Starch grains are present throughout the cortex of seedlings, but later in development they are restricted to a bi- or triseriate zone just outside the bundle-cap fibers and to a somewhat broader zone beneath the epidermis. In the subepidermal zone the starch disappears where periderm first arises, e.g., at lenticels and sites of injury; and later it disappears entirely as the periderm spreads. There are no starch grains in the phellogen or its derivatives. Single and multiple grains in the outer pith (Fig. 66) are much larger (10–20 μ in diam in alcohol) than those of the inner pith and cortex (5–10 μ in diam). The starch sheath outside the bundle-cap fibers and sclerenchyma cylinder follows the median and lateral petiolar bundles and all the smaller traces into the petiole, where

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tion of cortex and periderm from just above the buttresses. Original bundle-cap fibers in lower right. Note lenticel. ×33.—68. *SAN 62084.* Transection of petiole at midpoint between lamina and axil, ×33.

the sheath reforms. Rhombohedral crystals, single and clustered, are present in the inner cortex, absent in the outer, and abundant in the pith. A similar distribution of crystals is found in young and old petioles.

The following discussion is based on serial transections of mature nodes and petioles; and, as in the floral anatomy section, terms like "divide," "diverge," and "pass" are used to describe the arrangement of the bundles as they appear in the sections taken in sequence from the node toward the distal end of the petiole.

In each lateral gap two bundles are present, one of which (LT 2) remains closer to the gap than the other (LT 1) up to a level just below the axil (Figs. 69, 70). At this level the second bundle at each lateral gap passes diagonally into the petiole (Fig. 71). The laterals and median U-shaped bundle lose their fiber caps immediately after divergence from the cauline vascular cylinder. The median bundle branches into three broad bundles (Fig. 70: a, b, c); and about the same level traces d and e branch from the adaxial margins of bundles b and c, respectively (Fig. 71). In Fig. 72 traces h, i, and k, are branches of b and c also. There may be 2–4 traces in this central region. Traces f and g are branches of traces d and e, respectively. The courses of these last four traces are almost always shifted toward the adaxial side of the petiole, as is that of trace i (Fig. 73). In many petioles sectioned there are four traces in the center instead of the three, h, i, and j in Fig. 72; and of these four, the middle two almost always assume positions distally in the adaxial part of the completed ring. Traces h and k pass laterally or abaxially. A regular branching pattern is thus found only in bundles a through g. The adaxial part of the ring also includes 4–5 strands from each of the four lateral gap bundles (Fig. 74). All traces elongate tangentially and form a ring enclosed by extraxylary fibers about 5–10 mm above the axil (Fig. 68). Fibers appear first on the abaxial side of traces just before ring formation is complete. The entire transition from leaf gap (Fig. 69) to the final ring (Fig. 74) is from 10 to 15 mm long in petioles of the size indicated by the scale.

It should be noted that the same pattern of bundle branchings occurs in larger petioles, although the ultimate number of bundles involved in formation of the vascular ring is considerably greater. However, in petioles of a very young seedling 17 cm high, the pattern is completely different. A single bundle is present in each lateral gap. Branching of these lateral bundles takes place in the transition region near the level of the axil, and 2–3 traces result from each. The median bundle does not branch, and a complete cylinder of xylem is never formed.

Between the air spaces and the epidermis of the petiole is a zone of collenchyma the cells of which have less prominent thickenings than those of *Tetrameles*. The large parenchyma cells just inside the vascular cylinder sclerify slightly, as they do in the stem. Distribution and morphology of sclereids is the same as that in the stem. The cambium produces a small amount of secondary xylem in large petioles, and the extraxylary fiber strands are united by brachysclereids.

The closed vascular cylinder dissociates into bundles at the distal end of

the petiole, and the fibers are lost (Fig. 75). Adaxially, groups of bundles are in the form of two small rings that can be followed in transverse sections into the largest pair of leaf veins that branch from the base of the midrib (Fig. 76). In the midrib the traces unite to make broad, often folded bundles whose convoluted parts and their associated traces diverge into the large veins that branch from the midrib (Figs. 77, 78).

Secondary veins branching from the midrib are pinnate and are connected by tertiary veins that follow a nearly straight course. Toward the proximal end of the secondary veins the tertiary veins connect with the midrib. From the basal pair of secondary veins branch 5–7 large, unpaired tertiary veins (Fig. 9A). The most proximal of these tertiaries appears to branch directly from the midrib, although the bundles in it are derived from the few traces associated with the folded bundles after the latter have diverged from the vascular arc of the petiole. In fresh material the midrib and large veins are bright red, thus providing a conspicuous field characteristic.

Leaves of *Octomeles* are dorsiventral, and at least two adaxial tiers of long palisade mesophyll are clearly differentiated from the abaxial spongy tissue. Usually a third layer of short palisade cells is present between the two. Epidermal cells on both surfaces have sinuous, interlocking anticlinal walls, as seen in paradermal section, and are covered with a thin, smooth cuticle. Opposite the veins they are rectangular in paradermal sections and elongate along the vein axis. A conspicuous, nonchlorophyllous hypodermis is present. The hypodermal cells begin to enlarge very early in leaf ontogeny and are derived from the subsurface marginal meristem and not from the protoderm. Bundle-cap fibers are located on the ab- and adaxial sides of large bundles, on the abaxial side only of small bundles; and they are absent from the smallest traces. Sheath extensions accompany all but the smallest. Large, branched idioblastic sclereids are common throughout the lamina and are mostly oriented with their long axes perpendicular to the laminar plane. They may extend from one epidermis to the other and branch at both ends; or they may be shorter and more freely branched.

Bundle-cap fibers are septate, although transverse division may occur before sclerification, resulting in a series of 4–5 brachysclereids. Chambers formed by the septae are uninucleate.

The palisade and spongy tissue in leaves of sun and shade seedlings tend to intergrade. Where recognizable with certainty, the palisade layer is one cell thick in the sun seedling and one or two in the shade. No hypodermis is present in either, but instead the adaxial epidermal cells are enlarged. There are no sclereids in the leaves of the seedlings other than the extraxylary fibers. Anticlinal walls of the epidermal cells on both surfaces are slightly sinuous to interlocking as seen in paradermal section (Fig. 93).

Mesophyll anatomy of the small leaf on the inflorescence axis is similar to that of the cauline leaves: sheaths, sheath extensions, and bundle-cap fibers show the same distribution; but palisade and spongy tissue are not sharply differentiated from each other. A hypodermis is present, but in certain places, especially close to the veins and sheath extensions, it may be
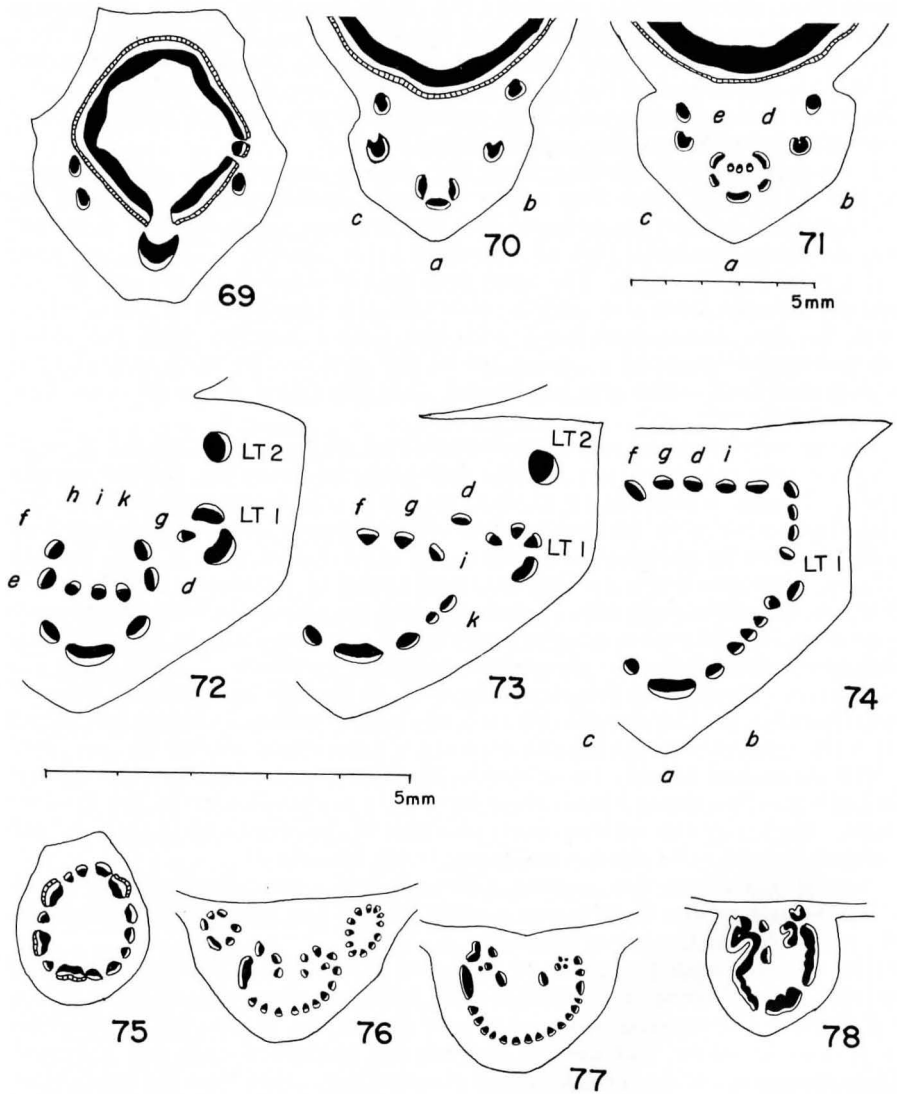
Fig. 69–78. *Octomeles sumatrana.*—69–75. Transections of petioles taken in sequence from the node toward the distal end. Hatching indicates extraxylary fibers.—69. The node.—70. Branching of the median petiolar bundle has occurred.—71. Branching of bundles *b* and *c* is slightly proximal from this level. Note positions of lateral bundles.— 72. Branching of bundles *d* and *e* has occurred. Branching of LT 1 is apparent.— 73. Bundles *f*, *g*, *d*, and *i* are adaxial.—74. The vascular cylinder is present.—75. Distal end of the petiole. The vascular cylinder is composed of discrete bundles. Extraxylary fibers are present opposite a few bundles.—76–78. Transections of the midrib taken

replaced by short palisade cells. Anticlinal walls of the epidermal cells on both surfaces are straight.

Anisotropic crystals are few in the epidermis. Crystal sand, and larger prismatic crystals are more abundant along the large veins, but they are also present in the rest of the mesophyll. Parenchyma cells of the cotyledons of very young seedlings contain a few small crystals. Crystals are uncommon in the leaves of sun and shade seedlings and are present only in the epidermis of the material examined. The chloroplasts contain multiple starch grains that give them the appearance of having cross-walls, even when unstained with IKI.

Stomata are confined almost entirely to the abaxial leaf surface and follow an anomocytic pattern of development. They are not sunken, and transections and clearings reveal that a narrow ledge projects beneath them from the surrounding epidermal cells. Guard cells are not heavily cuticularized, and a thin, cell-wall rim is present on the stoma side of each one.

Young flowers, inflorescence axes, and leaves are densely covered with peltate trichomes. Trichome primordia continue to develop on ab- and adaxial sides of leaves until the laminae are 7 or 8 cm long from base to apex. The first trichomes to mature have long stalks and overtop the rest. These do not persist on fully developed parts. Those that persist have short stalks and are located in pits the diameter of which is just slightly greater than that of the stalks and the depth of which is just equal to the stalk length. The uniseriate lamina of the trichomes has an entire margin, and the cells may or may not be radially elongate. Anisotropic crystals are present in the lamina and the stalk.

Ontogeny of the peltate trichomes was studied on floral primordia and bracts of inflorescence axes within 5 mm of the apex. Development follows the same pattern in each case. The terms anticlinal and periclinal are used here with reference to the plane of the leaf lamina. A single protodermal cell differentiates as a papilla. The orientation of the first anticlinal division of the papilla has no fixed relation to the long axis of the organ on which the papilla occurs (Fig. 79), but the second and third anticlinal divisions are always perpendicular to the first (Fig. 80). The 4-celled structure resulting from these divisions elongates to about 20–25 μ and enlarges distally. Each of the cells then divides periclinally once about the level of the outer epidermal cell wall (Fig. 81). The cells of the distal tier are divided by anticlinal or oblique walls that are often present in pairs in adjacent or diagonally opposite cells (Figs. 82, 83). No mitoses were seen, thus the question of synchronous division remains unanswered. The oblique walls almost always slope toward an adjacent or opposite cell of the same tier. They may be straight or curved, with the curvature parallel to the

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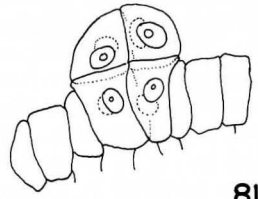in the same sequential direction.—76. Midrib at the proximal end of the lamina.—77. Midrib at a level a few mm distal to Fig. 76.—78. Median transection of midrib.—(*Key*: LT 1 and LT 2, lateral traces; see text for further explanation. Scale for Fig. 69–71 and 75–78 is given below Fig. 71; scale for Fig. 72–74 is given below Fig. 72.)
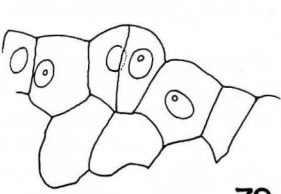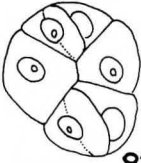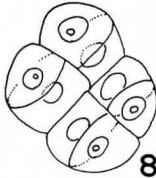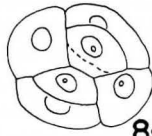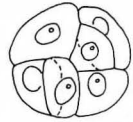
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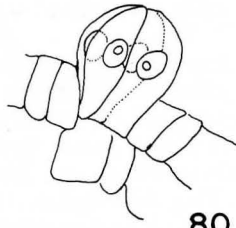
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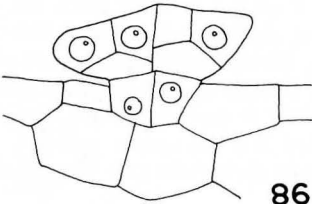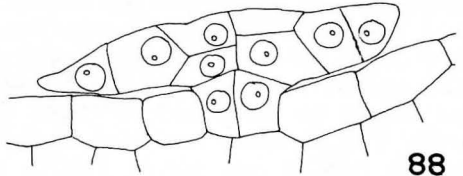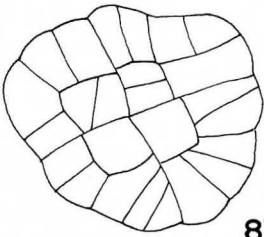
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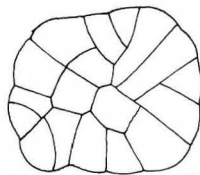
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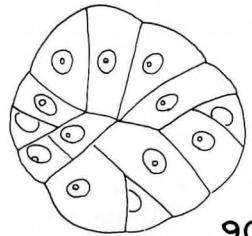
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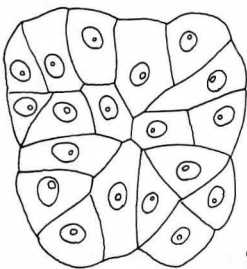
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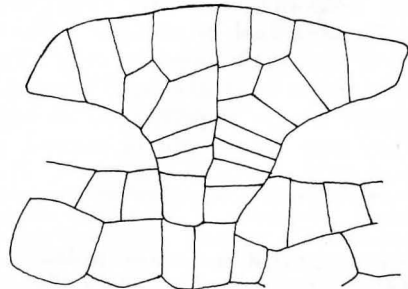
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outer wall of the original cell of the tetrad (Figs. 84, 85). If the oblique wall is curved, the inner of the two cells formed divides once periclinally (Figs. 86, 87). A second periclinal division often follows in either the distal or the proximal cell of two formed by the first division. Anticlinal walls in the peripheral cells tend to be directed outward at this stage, and the curvature of the first walls is still evident (Fig. 87). Further anticlinal divisions in the peripheral cells contribute to the formation of the trichome lamina (Fig. 88). In Fig. 89 two of the first divisions of the tetrad were curved and two were straight. If the first divisions are straight, the two derivatives divide anticlinally; and the planes of these second walls are perpendicular to the plane of the first or oblique (Fig. 90). The lamina preserves a 4-lobed outline reflecting the original four cells of the terminal tetrad until late in trichome development (Fig. 91).

Only two tiers of cells are present in the stalks of the tallest trichomes, those that are the first to arise on primordial organs; but the cells are elongate. The cells of the mesophyll directly beneath the trichome are often elongated in the same direction, and the trichome is thus on a podium. The stalks of the trichomes that develop on larger organs a few millimeters below the apex are shorter than those of the first ones; but after the lamina has begun to widen, the cells in the two stalk tiers may divide periclinally a number of times (Fig. 92). Occasionally the stalk of a mature trichome is multiseriate rather than quadriseriate.

Unusual peltate trichomes, studied by Melchior (1949), are present in broad pits on the abaxial leaf surface of *Octomeles* (Figs. 93, 94). The beginning ontogenetic stages of the stalk and lamina of these structures are similar to those of the ordinary trichomes, but more periclinal and oblique divisions occur in the stalk and in the lamina around the stalk (Figs. 97, 98). Viewed from the top (Fig. 99) the lamina presents no differences. A ring of protodermal cells around the base of the stalk continues to divide anticlinally and shows a slight buckling (Fig. 98). Ground meristem beneath the trichomes differentiates into a very compact mesophyll that is achlorophyllous (Fig. 94). Outside this area the mesophyll is lacunose, and the hypodermis is present. The protodermal cells divide and keep pace with the differential expansion of the mesophyll and are at first elongate

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Fig. 79–92. *Octomeles sumatrana. Davidson 1482.* Ontogeny of peltate trichomes. Derived from transections and paradermal sections of leaves. All figures drawn to same scale.—79. Stage following the first anticlinal division of the initial.—80. Four-celled stage.—81. Eight-celled stage.—82. Two straight walls in the distal tier.—83. Four straight walls in the distal tier.—84. Two curved walls in the distal tier.—85. One curved and one straight wall in the distal tier.—86. Longisection of trichome showing two periclinal walls in the developing trichome lamina.—87. Longisection. Anticlinal divisions have been initiated in the marginal cells of the lamina.—88. Face view of the lamina. Note that the curved walls formed in the distal tetrad are still evident.—89. Face view.—90. Face view.—91. Face view. Note that 4-lobed appearance of the original distal tetrad is preserved.—92. Longisection. Note intercalary divisions in the stalk. (For further explanation, see text.)
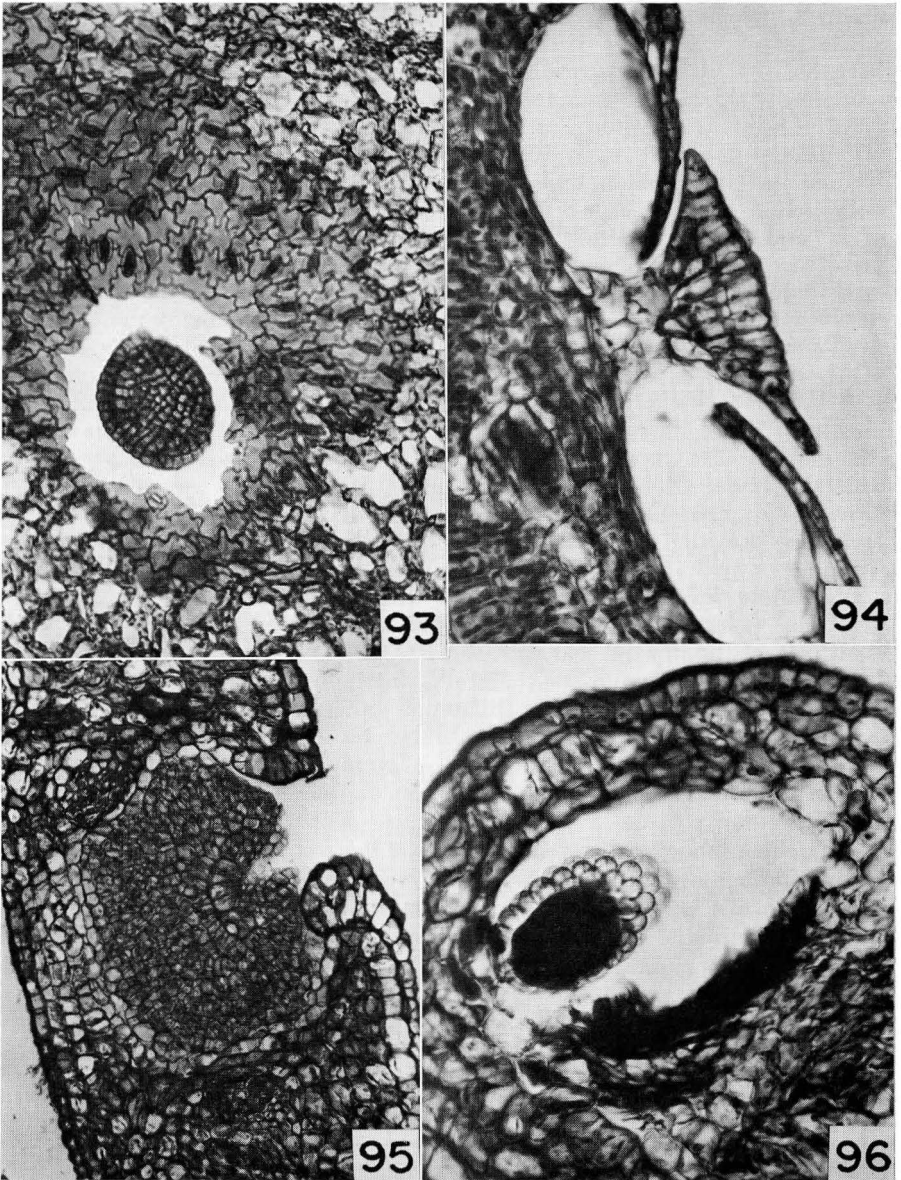
Fig. 93–96. *Octomeles sumatrana*. Leaf sections.—93. *Davidson 1127*. Paradermal section through a sunken peltate trichome. Note stomata. ×200.—94. *Davidson 1482*. Longisection through a sunken peltate trichome. Note compact mesophyll beneath the chamber. ×390.—95. *Davidson 1482*. Longisection through a domatium. Note indentation in the glandular cell mass. ×200.—96. *Davidson 1482*. Longisection through an
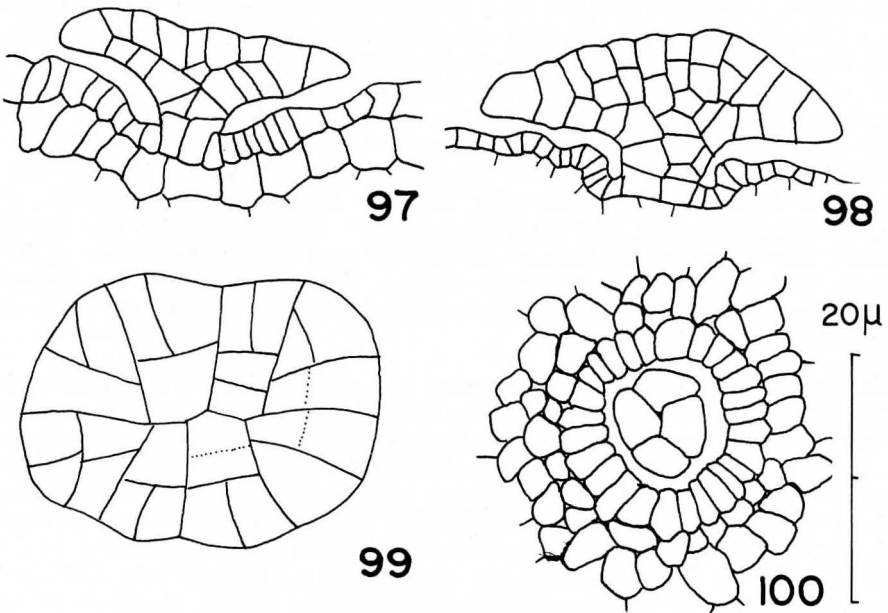
Fig. 97–100. *Octomeles sumatrana. Davidson 1127.* Ontogenetic stages of the sunken peltate trichomes. All figures drawn to the same scale.—97. Longisection.—98. Longisection. Note slight buckling of protoderm.—99. Face view of trichome lamina.—100. Paradermal section through the stalk and elongate cells of the protoderm.

(Fig. 100). Around the rim of the enlarging depression, divisions in the protodermal cells contribute to the formation of the uniseriate roof. At maturity the stalk is multiseriate, as is a broad zone of the lamina around it. A peripheral zone of the lamina 1–5 cells in width is uniseriate. Veins often, but not always, end free in the areoles beneath these structures, suggesting that they are hydathodes. Melchior (1949) speculates that they are absoptive hairs similar to those in Bromeliaceae.

Domatia are present on the abaxial surface of cauline leaves along the veins and in the vein axils. Only rarely do they open on the adaxial surface. Domatia on the small leaf on the inflorescence axis open on either the abaxial or the adaxial surface or on the lamina margin. Leaves of the seedlings are free of them. Residing inside are tiny mites, sometimes two or three to a chamber, that appear to feed there. Uninfected domatia have within the chamber a mound of small, deeply-staining cells beneath which

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occupied domation showing an egg case (?) and the darkened, compressed cell walls of the glandular cells on the floor. From a leaf on the inflorescence axis. ×390.

are several layers of callus-like cells that are later replaced by a meristematic zone (Fig. 95). The meristematic zone produces more callus cells toward the chamber. The mound of cells has a pit at the apex and appears to be glandular. In the course of infection the glandular cells are destroyed. Their compressed cell walls line the bottom of the chamber and remain black after safranin-fast green staining. Domatia at this stage sometimes contain peculiar objects that appear to be egg cases (Fig. 96). Some chambers contain only hypertrophied callus cells. Domatia here represent a special kind of extrafloral nectary, but their phylogenetic connection with the broad, sessile glands commonly present on petioles and inflorescence axes of this genus and *Tetrameles* is probably remote. They may instead be derived from nondomatial pits such as those normally formed in the vein axils on leaves of *Tetrameles* (Fig. 112).

Tetrameles.—Anatomy of the primary axis and petiole of *Tetrameles* is similar to that in *Octomeles*. Points in common are cortical air cavities, closely spaced vascular bundles connected by interfascicular meristem, septate and gelatinous bundle-cap fibers, and abundant sclereids. Stems and petioles are never winged, however, and the distribution and concentration of sclerenchyma is somewhat different. In the four specimens examined there was variability in the amount of sclerenchyma that seemed to be correlated with the flowering, leafy, or dormant state of the axis. Within a few millimeters of the apex of the leafy (Peutjang Island, *Davidson 1469*) and dormant (Papua, *Davidson 1493*) branches, transversely oriented sclereid plates are present in the pith and cortex, and individual brachysclereids and sclereid nests are present in the cortex (Fig. 101). The sclereid plates are circular in transection (Fig. 102), and in older stems sclerification unites several small groups of plates on the same transverse planes into compound plates 3 or 4 mm in diam. There are transitions in sclereids from short-armed astrosclereids that have obviously intruded some distance among the surrounding cells to brachysclereids that have simply filled in the intercellular spaces immediately adjacent to them. The arms of the astrosclereids in the axis do not equal the length of those in *Octomeles*. In the cortex a continuous strand of brachysclereids is present peripheral to each bundle, and the interfascicular areas are frequently sclerified.

Sclereid plates are present just below the apex of flowering branches and sucker shoots (Malaya, *Davidson 1413a, 1413b*), but cortical sclereids first appear in transections a few centimeters below the apex. The bundles are connected by interfascicular meristem. In immature axes still lacking bundle-cap fibers, the entire vascular cylinder is enclosed by a uniseriate starch sheath with conspicuous granular contents that stain red-brown with safranin. This is obviously a form of tannin, sometimes referred to as "granular tannin," although the configuration may be an artifact. In older axes with bundle-cap fibers, the granular material cannot be seen, and the starch sheath contains only single and multiple starch grains.

Bundle-cap fibers accompanied by brachysclereid strands are present a centimeter or so below the apex of dormant axes, but the brachysclereid

strands alone are present in transections taken a few millimeters below the apex. In flowering axes that are nondormant this relationship is reversed: the bundle-cap fibers are present much closer to the apex than are the brachysclereid strands. In several cases the strands almost completely enclose the fiber bundles. These extraxylary fibers nearly always have thick, gelatinous walls. They may become septate before (in dormant stems) or after (in flowering stems) secondary growth begins. Sclerenchyma forms in the gaps between the fiber bundles, and thus a cylinder similar to that in *Octomeles* encircles the phloem. Cells on the outer boundary of the sclerenchyma cylinder toward the cortex are sclerified on their inner and side faces only.

Periderm forms superficially (Fig. 102), and in dormant stem tips it is continuous with the periderm of the bud scales. Initially the phelloderm is three or four cells thick, and a few of the cells are sclerified; but at the base of the bole above the buttresses, it may be ten or more cells thick and heavily sclerified. Round lenticels are numerous and have protruding from the center a pad of phellem with the appearance of a piece of vermiculite. The same kind of lenticel was seen on several other trees growing in a similar habitat near *Tetrameles*: e.g., *Macaranga*. Phellem cells are thick-walled and often tanniniferous. The cylinder of sclerenchyma formed in connection with the bundle-cap fibers in young stems persists and can be found at the base of the bole above the buttresses (Fig. 103). At this level there are many individual, broad sclerenchyma plates in the outer-phloem parenchyma alligned parallel to the sclerenchyma cylinder. The lack of fibers and obliterated sieve tubes indicates that here, as in *Octomeles,* the cortical zone is persistent (whether it is derived from the original cortex or from the phelloderm) and that the phellogen continues to develop superficially. The bark is ordinarily smooth, but it is sometimes described as fissured. In the buttresses the sclerenchyma cylinder is broken by gaps, and the very broad region between the outermost gelatinous fibers and the periderm contains numerous tangential sclerenchyma plates.

Large single and multiple starch grains are present in the pith, xylem and phloem parenchyma, and cortex; and they have the same distribution within these areas as they do in *Octomeles*. Starch grains in the sieve tubes are tiny and occur in the slime plug only. The lumina of most of the brachyscleres are cuboidal because of the presence in them of large cuboidal, anisotropic crystals. The periderm in tangential section shows an abundance of druses that dissolve slowly in 10% HCl, and most of them are attached to cell walls. Druses also occur in the pith.

Spherical bodies called "sphaerocrystals" (Möbius, 1885) and "spherites" (Metcalfe and Chalk, 1950, p. 700) occur in the cortex, starch sheath, xylem and phloem parenchyma, and sclerenchyma of *Tetrameles*, but not in the pith. In paraffin-embedded material stained with safranin and fast green, these bodies are translucent with a central area that accumulates fast green; in unstained spherites the central area is bright like the hilum of a starch grain. In both cases radial striations in the structure are evident, and alternating light and pale spheroidal zones of approximately equal width
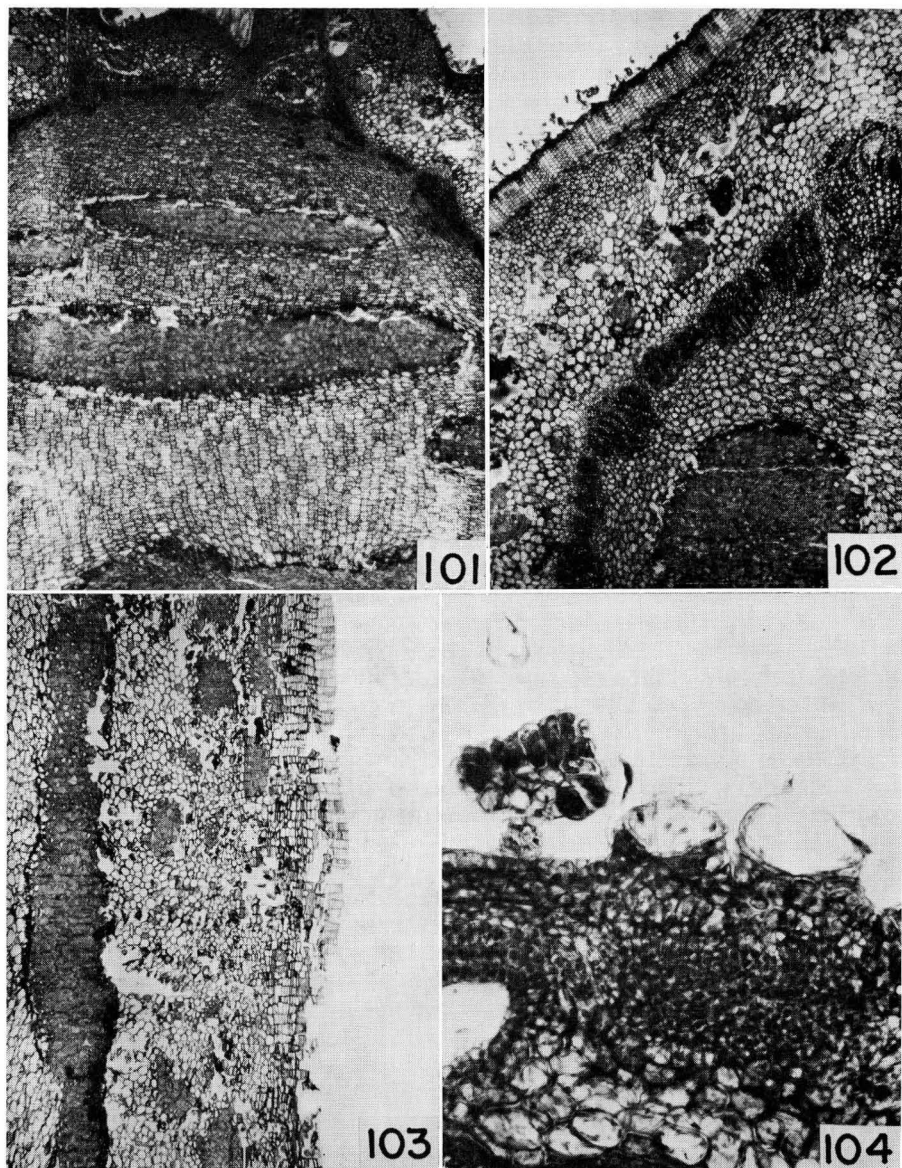
Fig. 101–104. *Tetrameles nudiflora.*—101. *Davidson 1469.* Nonmedian longisection of apex showing flat plates of sclerenchyma, ×38.—102. *Davidson 1469.* Transection ca. 5 mm below the apex. Note cortical air spaces. ×38.—103. *Davidson 1493.* Radial section showing part of sclerenchyma cylinder and sclereid nests in cortex, ×38.— 104. *Davidson 1413b.* Transection of young leaf showing stalked gland (cf. Fig. 39) and the bases of two septate hairs, all three on the adaxial surface. Leaf vein is below. ×370.

are visible in ordinary light. In polarized light a Maltese cross pattern is present. Möbius (1885) suggests that they are a special form of calcium oxalate. Chemical similarity or identity of the spherites and druses is possible, although both may occur within a single cell in the cortex, and druses only are seen in the pith. Spherites have been described in Cactaceae (Möbius, 1885; Bailey, 1961), Combretaceae, and Caryophyllaceae (Haberlandt, 1914) but not in Cucurbitaceae and Begoniaceae. No inclusions similar to the "resinocysts" in *Begonia* (Zalewski, 1897) are present in Datiscaceae.

Bundles of the bud scales are arranged in a ring in transection and are not connected by interfascicular cambium. Bundle-cap fibers and brachysclereid strands are absent. Transversely oriented sclerenchyma plates similar to those in the stem occur in the pith, and nonflattened sclereid nests are found in the pith and cortex. Periderm 15–20 cells thick is present abaxially; short-stalked or sessile glands (colleters) with columnar cap cells, differing considerably from those on the leaves, are present adaxially.

Nodes of *Tetrameles* are trilacunar, and the pattern of bundle arrangement in transection at the proximal end of the petiole is similar to that of *Octomeles*. The main difference is that only a single trace occurs in each lateral gap. The single median bundle branches above the level of the node but below the abscission layer into three smaller bundles (Fig. 105, *a, b, c*), and usually two small traces are present lateral to the middle one of the three bundles. Slightly distal to this level a dichotomous branching of bundles *b* and *c* occurs, and the resulting traces (Fig. 106, *d* and *e, f* and *g*, respectively) can be seen on the adaxial side of the petiole in transection. In the same section bundles *a, b,* and *c* are on the abaxial side. Subsequent branchings of strands labelled *a* through *g* in the figures is not regular; for example, trace *e* in Fig. 106 branches numerous times, and at more distal levels (Fig. 107, also *e*) it is represented by six traces that are present in the adaxial, lateral, and abaxial parts of the vascular ring. Traces corresponding to *h, i,* and *k* that were of fairly regular occurrence in *Octomeles* petioles are not present in *Tetrameles*. The lateral bundles branch several times, and the traces so derived occupy positions in the adaxial "shoulders" of the petiole (Fig. 108). Up to eight traces that result from these irregular branchings may not be included in the ring, but instead may become inverted medullary bundles. Bicollateral bundles at proximal levels and strands of included phloem at distal levels result from the fusion of these included traces with bundles that occupy positions in the completed vascular cylinder.

In the large petioles from sucker shoots (*Davidson 1413b*) a cambium unites the bundles, and a complete cylinder of xylem and phloem is formed distal to the zone of bundle arrangement above the node. Secondary growth is very limited. Extraxylary fibers are present in the same median region of the petiole as in *Octomeles*, but they never form as thick or as complete a zone. In mature petioles of the Peutjang Island trees individual bundles are in a ring in median transections and are not connected by even a hint of an interfascicular cambium. The bundle zone between the xylem and the phloem is sclerified, but bundle-cap fibers are lacking or are very weakly developed. The function of support is apparently transferred in
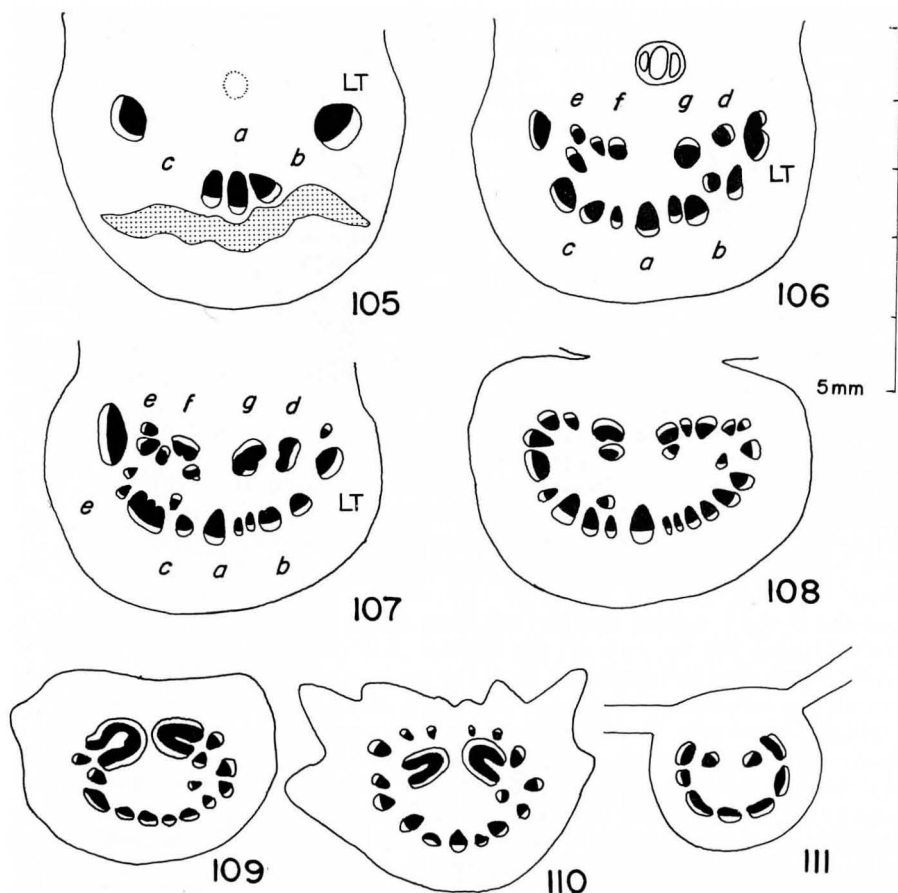
Fig. 105–111. *Tetrameles nudiflora. Davidson 1413b.*—105–108. Transections taken at ca. 1 mm intervals in sequence from the node toward the distal end of the petiole. All figures drawn to the same scale.—105. Distal to the node. Stippling denotes the abscission layer. Dotted circle indicates the procambium associated with the axillary bud.— 106. All major bundles are present. Note axillary bud.—107. Branching of one of the lateral bundles has occurred.—108. The complete vascular arc.—109. Transection at the distal end of the petiole.—110. Transection of leaf midrib at basal end of leaf.— 111. Transection of midrib midway between base and apex of leaf.

part to the well-developed region of angular collenchyma between the zone of longitudinal air spaces and the epidermis. The internal bundles and phloem strands may also be accompanied by extraxylary fibers.

Brachysclereid nests and branched sclereids are abundant in the parenchyma inside and outside the vascular cylinder. The brachysclereid plates in the central area are widely separated in mature petioles, and the paren-

chyma cells around them are stretched and distorted. Broad, sessile glands, identical to those on the female flowers and inflorescences are also common on the petiole.

At the distal end the vascular cylinder is again composed of discrete bundles on the abaxial side, but on the adaxial side they remain fused. In transverse section the adaxial part of the vascular supply appears conduplicately folded in many petioles (Fig. 109). Several very small traces supply the two lowermost pairs of leaf veins. At a level slightly distal to their divergence, the conduplicate or variously oriented adaxial bundles enter the largest of the basal, palmate veins; and they are frequently accompanied by three or four traces (Fig. 110). In the midrib the bundles are arranged in an arc in transection. The two bundles at the adaxial ends of the arc are internal to the others and are inverted, or almost so. The inverted bundles of the arc enter subsequent lateral leaf veins (Fig. 111).

At the base of each petiole and bud scale is an abscission zone, on the stem side of which is a layer of densely aggregated branched sclereids. Single and multiple starch grains are present in parenchyma internal and external to the vascular cylinder, but they are concentrated in the starch sheath. Spherites may occur in parenchyma internal or external to the vascular tissue, but they are often in the sclerenchyma as well. Rhombohedral, anisotropic crystals are present in some petioles and absent in others.

The dorsiventral leaves of *Tetrameles* have much thinner laminae than those of *Octomeles*. The 1- or 2-layered palisade zone and the spongy mesophyll are not as sharply differentiated from each other because the palisade cells are short and the spongy tissue is more compact, except around the stomates (Figs. 112, 113). Anticlinal walls of epidermal cells in paradermal section are sinuous but not interlocking on ab- and adaxial surfaces, and the outer wall is covered by a thick cuticle. The epidermis and uniseriate hypodermis lack chloroplasts. Stomata are confined to the abaxial surface, and their mature appearance is anomocytic, although developmental stages were not followed. Sclereids are absent from the lamina but are present interior to and outside the vascular arc of the midrib and large veins.

The venation pattern of the cordate leaves is pinnate; but, as in *Octomeles*, two or three pairs appear to branch directly from the midrib base. As a result the pattern appears to be a combination of palmate and pinnate (Fig. 13). Secondary veins branching from the midrib and the smaller tertiary veins connecting these protrude on the abaxial surface, and their connections with the lamina are constricted. The same is true of the midrib itself. Veins of a lower branching order may protrude slightly. Traces frequently, though not always, end freely in the areoles. In the axils of large veins are tiny chambers, but they do not contain mites and are probably not domatia (Fig. 112). Large bundles are often bicollateral and are surrounded by sclerenchyma that includes septate bundle-cap fibers opposite the phloem. Collateral bundles have bundle-cap fibers abaxially and may have brachysclereids adaxially (Fig. 112). Traces lack sclerenchyma. All bundles and
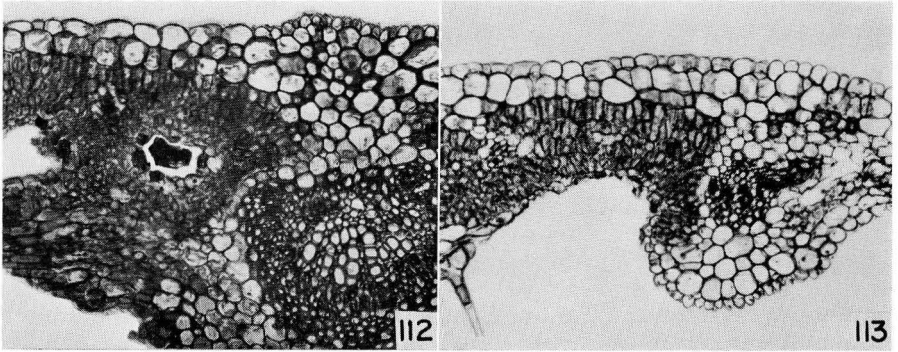
Fig. 112–113. *Tetrameles nudiflora. Davidson 1469.* Leaf transections.—112. Section through a large vein near its junction with a smaller one showing small chamber formed in the axil, ×190.—113. Section through a small bundle with a trace joining it on the right. Hypodermis, bundle sheath, and sheath extensions are evident. Note septate hair in lower left. ×190.

traces are enclosed by conspicuous sheath cells containing "granular tannin" (Fig. 112). The presence of sheath extensions of large, nonchlorophyllous cells is correlated with the presence of sclerenchyma adjacent to the bundles (Fig. 113). Air spaces are present outside the vascular arc in the midrib and the large lateral veins. Between the air spaces and the epidermis is a zone of angular collenchyma. A large amount of xylem, including numerous large and irregularly shaped elements, is present in each leaf tooth, and the abaxial surface and margin of these teeth bear slightly sunken stomata, the guard cells of which are larger than those on the rest of the lamina. The concentration of stomata on the teeth appears to be greater than elsewhere, although no measurements were taken, and the teeth show typical hydathode construction.

Spherites similar to those in the rest of the plant are present in the parenchyma of the leaf veins and in the sheaths of even the smallest traces, but they are missing in the mesophyll. Other types of anisotropic crystals are uncommon; and starch, other than the soluble form in the chloroplasts, is absent.

Young leaves and petioles of *Tetrameles* are densely pubescent. Components of the trichome complement are the same as those on the female flowers and inflorescences: uniseriate, septate hairs (Fig. 124); uniseriate, 2-armed hairs that are raised on podia (Fig. 128); and bi- or quadriseriate-stalked glands (Fig. 104). Broad, sessile glands similar to the one in Fig. 38 are present on the petiole only. Stalked glands are associated with the veins on both leaf surfaces, but on the abaxial side they are limited mostly to the constricted part of the veins toward the lamina and to the vein axils. On the petiole they tend to be more common proximally than distally. Mature leaves are sparsely pubescent adaxially but remain densely so abaxially.

Septate hairs are associated with veins and traces on all parts of the lamina; the 2-armed hairs occur only on the midrib and large lateral veins.

Developmental stages of the glands studied here are entirely from young leaves, as are the stages of the other types of trichomes discussed below. Stages seen on the few young inflorescences available appeared to parallel those on the leaves. Early ontogentic stages of the colleters and the broad, sessile glands were not encountered.

At the beginning of the ontogeny of a stalked gland, a single protodermal cell differentiates as a papilla (Fig. 114). The papilla elongates and divides anticlinally once (Fig. 115). Very rarely two anticlinal walls perpendicular to the first are then formed. Thus, the stalk is ordinarily biseriate. The two (or four) cells divide periclinally in a plane about the same level as the outer epidermal cell wall of the organ on which the gland is developing (Fig. 115). A second and third series of periclinal divisions usually occur in the distal and penultimate tiers of cap cells, respectively, and the two distal tiers alone take part in formation of the gland head (Figs. 116, 117). Divisions beyond this appear to follow no definite sequence. In biseriate forms the anticlinal divisions establishing the initially quadriseriate nature of the head may occur first in the distal (Fig. 115) or in the penultimate (Fig. 117) tier. Fig. 118 shows a commonly observed stage seen on leaves in which there appear to have been two series of oblique divisions in the distal tier, the divisions in the second series of which were perpendicular to those of the first (Fig. 119). A mature gland is shown in Fig. 104. The head is rotund and frequently hollow, and the cap cells are radially elongate. As in the peltate trichomes of *Octomeles*, intercalary divisions may occur in stalk cells late in gland ontogeny, and the mature stalk may thus be multiseriate. These cells may also elongate somewhat.

The initial stages in the development of the 2-armed hairs and the septate, spicular hairs are apparently the same. No organs are present that bear only one or the other, but on the very young leaves the developing 2-armed types are recognizable before definite preliminary stages of the septate types can be detected. The beginning stage of each is a single papilla, the base of which is surrounded by two or more distinct rings of protodermal cells. Ontogenetic divergence begins at this point. The base of the septate hair primordium enlarges, and a single ring of 7–15 basal cells is flattened tangentially (Fig. 120). These basal cells often undergo a few divisions parallel to the cell wall of the expanding base, and the hair is then slightly raised on a podium (Fig. 121). At maturity the basal cells are very flattened, and they enclose most of the bulbous base except the very central part which abuts on the hypodermis (Fig. 122). In macerations of leaf material the basal cells remain attached to the hair base. The papilla itself grows outward perpendicular to the epidermal plane and reaches a length from 0.13 to 0.35 mm at maturity (Fig. 123). During elongation the hair becomes multinucleate (Fig. 124), and after its thick, lignified walls appear, 3–6 septae form. Chambers resulting from the septation may be uni- or binucleate.

The 2-armed hairs are raised on podia that develop late in the ontogeny
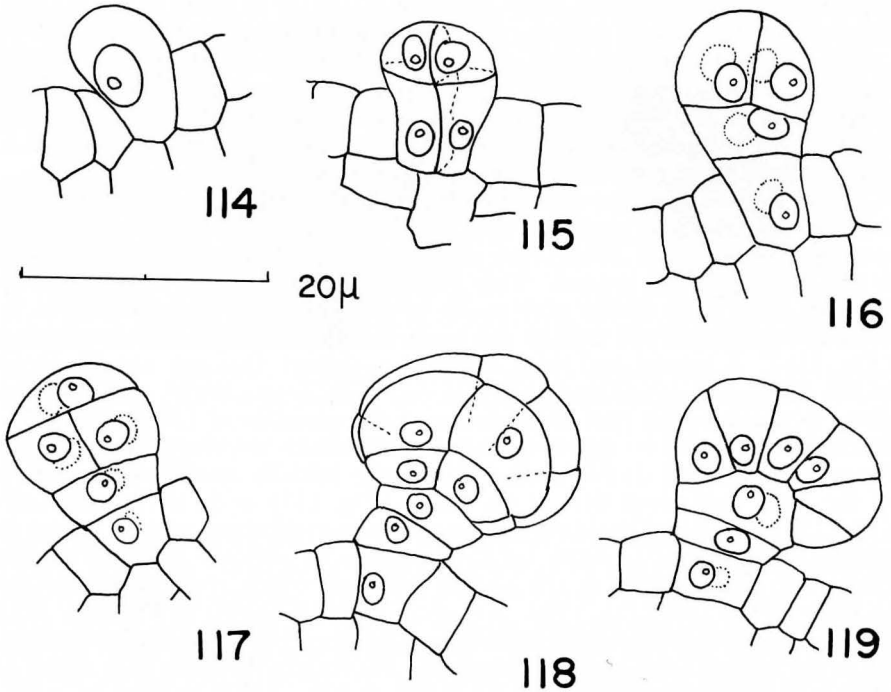
Fig. 114–119. *Tetrameles nudiflora. Davidson 1413b.* Ontogenetic stages of stalked glands. Drawn from young leaves with the aid of a camera lucida; all figures to the same scale.—114. Initial.—115. Four-celled stage.—116. Eight-celled stage.—117. First anticlinal division is in the penultimate tier.—118. Young gland.—119. Optical section of gland shown in Fig. 118.

of the expanded cells (Fig. 125). Occasionally the podia are very small or lacking. The papilla from which the expanded cell develops elongates in opposite directions parallel to the epidermis of the supporting organ. The podium arises through anticlinal divisions of the protodermal cells in a ring surrounding the base, or attachment of the hair (Fig. 126). In this case the attachment does not expand as it does in the septate hairs. Hypodermal cells beneath may also divide and be included in the center of the podium (Fig. 127). The cells surrounding the base, but not the entire podium, remain attached in macerations. In many cases a deep transverse cleft appears at midsection between the two arms and opposite the attachment. These hairs at maturity have thick, lignified walls and are multinucleate, but not septate (Fig. 128).

Datisca.—Anatomy of the primary axis of *Datisca* differs markedly from that of the other genera. Although there are no noticeable differences between the two species, the following observations are based on material of *D.*
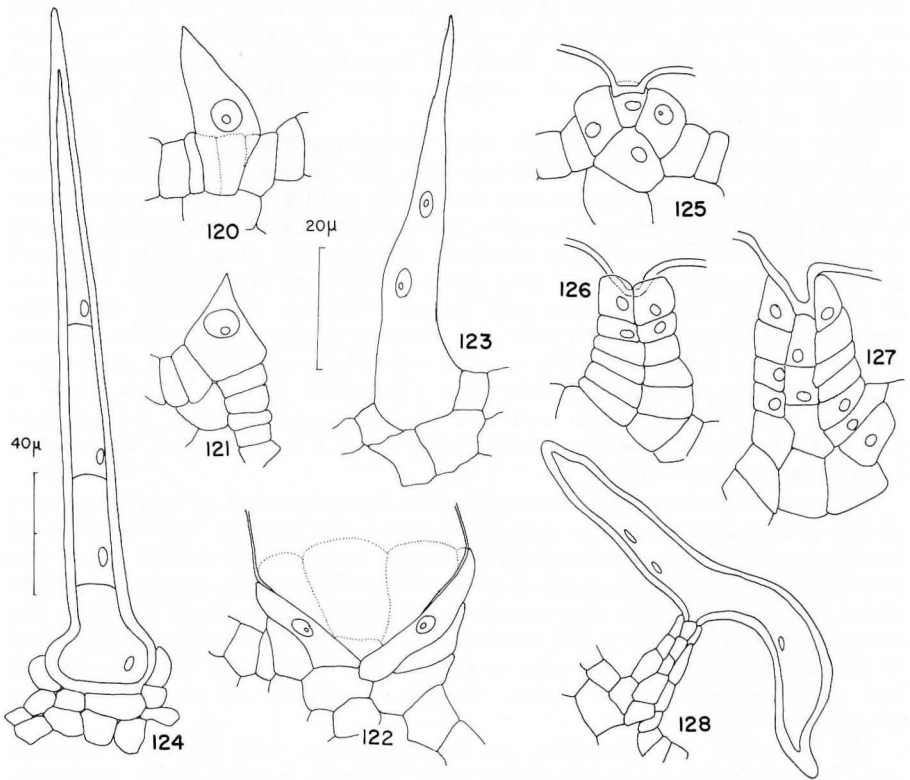
Fig. 120–128. *Tetrameles nudiflora. Davidson 1413b.* Ontogenetic stages of trichomes taken from transections of young leaves. Drawn with the aid of a camera lucida. Scale for Fig. 120–123 and 125–127 shown by Fig. 123; scale for Fig. 124 and 128 shown by Fig. 124.—120–124. Septate hairs.—120. Early stage. Base just beginning to enlarge.—121. Hair primordium raised on a short podium.—122. Base showing flattened cells around it.—123. Immature hair with two nuclei.—124. Mature hair showing thickened walls, septae, and expanded base.—125–128. Two-armed hairs.—125. Early stage in the development of the podium.—126. Immature podium with nonelongate cells.—127. Longisection of podium and attachment of the 2-armed hair showing hypodermal cells.—128. Mature 2-armed hair with three nuclei.

glomerata only. The outer cortex is collenchymatous, but cortical air spaces are absent. Bundle-cap fibers are nonseptate in most stems, but in large ones with a centimeter or more of wood, a few extraxylary fibers may develop septae. These fibers usually are in discrete strands, i.e., a complete cylinder of sclerenchyma does not develop, even in many thick, woody stems. Rarely, however, a full cylinder of sclerenchyma is present in young stems with only a small amount of secondary xylem. Medullary bundles are frequent and are also accompanied by bundle-cap fibers. Epidermal cells

are elongate in the direction of the long axis of the stem, and the ridges in the outer cell walls are minutely undulate and are parallel to the long axis of the cells, as in *Tetrameles*. Periderm formation is superficial, and very little phelloderm is produced, except as part of the vertically elongate lenticels on old stems.

Outer cells of the pith lignify after secondary growth begins, but the walls remain thin and do not intrude into the intercellular spaces. Parenchyma of the vascular bundles may not lignify until 4 or 5 mm of wood have been produced, and often it remains unlignified. Certain parenchyma cells of the bundles become radially elongate in a direction away from the vessel elements they surround. The pith hollow begins to form within 5–10 cm of the apex of the main axis and lateral branches and results from the stretching of the central pith cells and ultimate tearing of the walls. A zone of parenchyma 1–2 mm thick is present around the periphery of the hollow adjacent to the vascular cylinder, but the width of the hollow itself is variable. Near the root-stem transition the pith is not hollow. Anthocyanin pigments that are frequently visible at the base of the main axis are located in cells of the outer cortex.

Nodes are trilacunar and no complicated rearrangement of bundles occurs at the proximal end of the petiole. Instead the median and two lateral bundles are aggregated into a broad vascular arc, on each side of which is a tiny wing trace that is a branch of a lateral bundle or of the arc itself. At the distal end of the petiole the vascular arc branches into three bundles, the lateral two of which form the median traces of the two proximal leaf lobes or pinnae. Wing traces are also present in the midribs of the pinnae and leaf lobes and in the leaf rachis. Bundle-cap fibers are absent from the petiole.

The leaves of *D. cannabina* are imparipinnate, with opposite leaflets; and the margins of the leaflets are evenly toothed. Leaves of *D. glomerata* are deeply divided or are imparipinnate, usually with 3–5 leaflets that are very irregularly toothed. The epidermal cells contain numerous tannin sacs. The outer epidermal cell walls on the leaf are not ridged, and the cuticle is not sculptured; but in the center of each cell wall there is a tiny papilla, or projection. An expanded hypodermis is not present in seedling leaves, but instead the adaxial epidermal cells are enlarged, as is the case in the seedling leaves of *Octomeles*. Leaves of mature plants may have an enlarged hypodermis on ab- and adaxial sides, or the epidermis may be en-

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Fig. 129–139.   *Datisca glomerata*. Glandular trichomes. Scale for Fig. 130–139 shown between Fig. 130 and 131.—129. Mature trichome. Glandular head is stippled. Circles represent plastids other than chloroplasts.—130. Longisection through a trichome initial after the first oblique division.—131. Longisection, nonmedian, showing two oblique divisions.—132. Longisection, nearly median, showing initial stage in the formation of the trichome stalk.—133–138. Serial transections through a trichome stalk showing the positions of the cell walls from near the base (Fig. 133) to the apex (Fig. 138). Note pyramidal cell at the apex.—139. Immature trichome, before cell expansion. Note plastids.

130

131

20μ

133

134

132

135

136

137

138

139

40μ

129
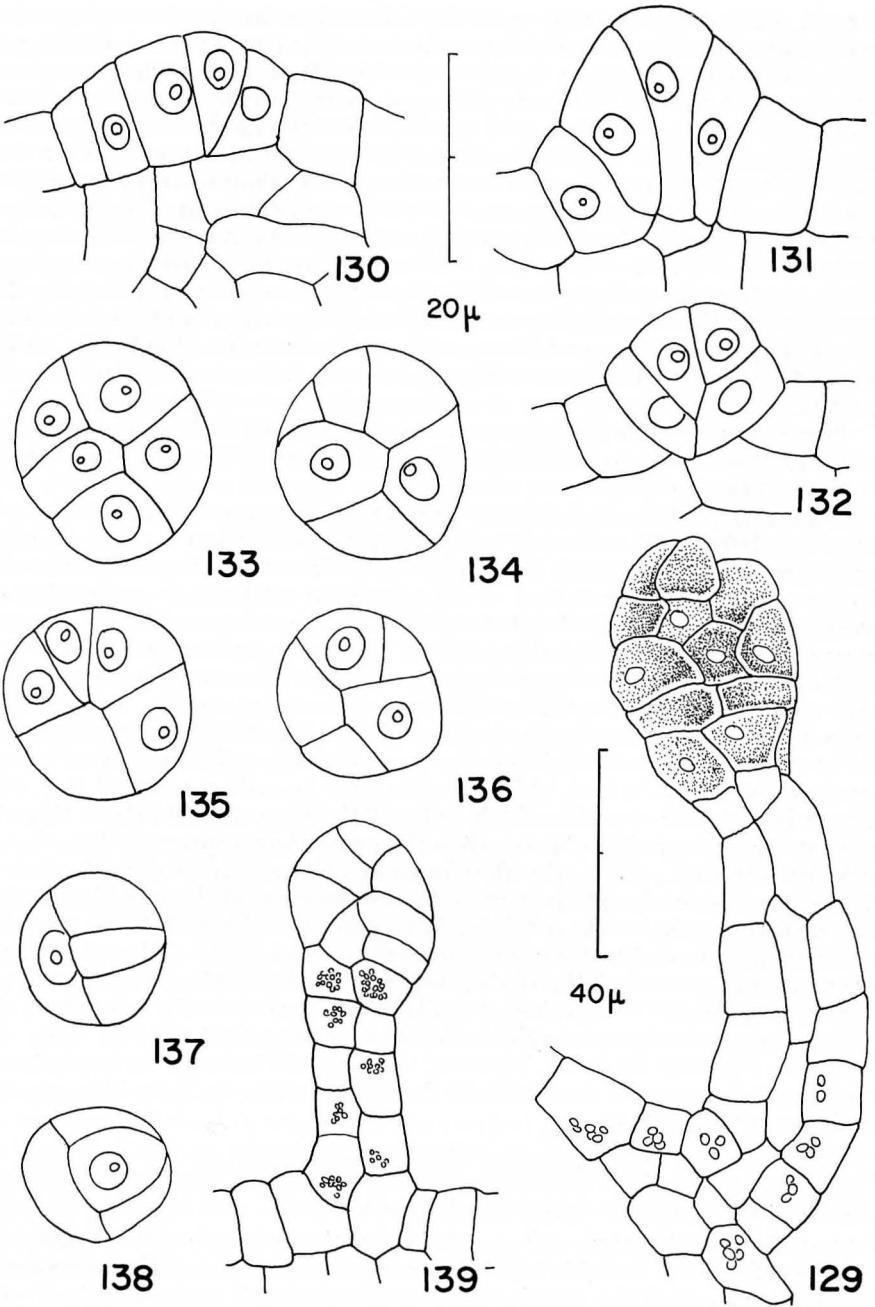
larged. Stomata are present on both surfaces but are much more common
on the abaxial. Those on the leaves have an anomocytic development pat-
tern, and their appearance at maturity is similar to that of the stomata on
the stem and petiole. The only difference is that in the last two cases the
epidermal cells are elongate, and on the leaves the epidermal cells, as seen
in paradermal section, have sinuous anticlinal walls. Leaf and leaflet mar-
gins are papillate, and the leaf teeth contain an abundance of transfusion
tracheids. The teeth are also covered with stomata, as in *Tetrameles* and
Octomeles, and the observed guttation at these teeth indicates that they are
hydathodes. Palisade cells of the dorsiventral lamina are frequently irregu-
lar in shape and the tissue is not at all compact, sometimes giving the im-
pression that the mesophyll is composed of spongy tissue only. Intercellular
tannin deposits often occur between the palisade cells. Bundle-sheath ex-
tensions and sclerenchyma are absent, and small traces end freely in the
areoles.

Anisotropic crystals are infrequent in alcohol-fixed and fresh material of
stems, petioles, and leaves of *Datisca*, but a starch sheath is present peripheral
to the bundle-cap fibers.

Multiseriate, stalked glands are present on all parts of young axes and
are from 100 to 200 μ long (Fig. 129). They persist but are more widely
scattered on mature parts. Tannin sacs are common in the stalk cells and
in the gland head. Ontogeny of the glandular trichomes was studied on
young leaves of both species, but no differences were seen. A single proto-
dermal cell enlarges and bulges slightly above the level of the other cells,
although it never becomes a conspicuous papilla. Occasionally a few proto-
dermal cells surrounding the initial appear to enlarge slightly, too, but they
take no part in the development of the gland. The initial divides obliquely
(Fig. 130), and the "distal" of the two resulting cells divides obliquely
again (Fig. 131). In fact, oblique walls form in each new distal cell until
the stalk is 4–6 or more tiers high (Fig. 132). Figs. 133–138 show that the
oblique walls may slope in any direction; and they apparently form in no
regular sequence. Thus, the development of the glandular trichomes of
Datisca is completely different from the development of those in *Tetrameles*:
the elongate stalk results not from intercalary periclinal divisions and cell
enlargement alone, but from oblique divisions in a distal cell and the sub-
sequent enlargement of the derivatives so that the originally oblique walls
appear periclinal. The periclinal walls in the mature stalk are not in the
same plane, but alternate with one another in longisection (Fig. 139). In-
tercalary divisions do occur, however. Oblique divisions in various orienta-
tions contribute to the formation of the gland head. Radially elongate cap
cells are not present.

DISCUSSION AND CONCLUSIONS

RELATIONSHIPS OF THE GENERA OF DATISCACEAE

A study of the anatomy and morphology of the three genera of Datiscaceae
supports the belief that this family is a natural one. Three of the four species
are dioecious, and the fourth, *Datisca glomerata*, is androdioecious with

protogynous hermaphrodite flowers. The ovary is inferior, petals are absent except in the male flowers of *Octomeles*, sepals are inconspicuous, and styles are separate and borne on the rim of the floral crown opposite the sepals. Placentae are parietal with numerous ovules, and in *Octomeles* they divide the locule into 6–8 chambers. The indeterminate inflorescences of *Octomeles* and *Tetrameles* appear to be homologous with the lateral branches of *Datisca*; the determinate, axillary flower clusters, or dichasia, of *Datisca* are then homologous with the 1–3 flowers grouped in the axil of each small, caducous bract on the pendant axes of *Octomeles* and *Tetrameles*. Floral vasculature of *Octomeles* and *Tetrameles* is present in an almost identical pattern at the top of the ovary, except that the number of perianth parts and styles is different in each case; but floral venation of *Datisca* is slightly different. In the last instance each style contains two traces that are derived topographically from adjacent lateral bundles in the ovary wall, whereas in *Octomeles* and *Tetrameles* the single style trace is a continuation of the large stylar bundle. This stylar bundle corresponds to the "dorsal bundle" referred to by most floral anatomists. Dehiscence of the capsule in *Octomeles* is by sclerified valves that split open opposite the placentae after the outer parenchyma of the ovary wall has dried and fallen away. Although the fruits of *Datisca* and *Tetrameles* have the same sort of sclerified locule lining that occurs in *Octomeles*, the dehiscence mechanism is entirely different. Lobes at the top of the locule fold downward forming a pore through which the seeds escape. The difference in floral venation between *Datisca* and *Tetrameles* is obviously not related to a difference in dehiscence mechanism, but must relate simply to the large, branched stigmas in the former genus. The significance of this difference should probably be minimized in comparisons of the two, and the similarity in dehiscence mechanisms, which presumably have persisted despite the difference in habit and habitat, should be emphasized.

Seeds of *Octomeles* and *Tetrameles* are 1 mm or less in length, and those of *Tetrameles* are winged, making wind the most probable dispersal agent in each case. However, the small seeds of *Datisca* are more likely distributed by stream and river currents; and long-distance dispersal in mud on bird's feet or in their feathers is also a possibility. The seeds possess no obvious adaptations to this latter type of dispersal, other than their small size, and they are not as well adapted for wind-dissemination as one might expect them to be if wind were involved here. Adaptations for wind-dispersal are very clear in some other plants in the same habitat as *Datisca*, e.g., *Salix* and *Alnus*.

The considerable specialization of male and female flowers of *Octomeles* can best be explained in relation to the method of pollination. The anthers are large and contain masses of small pollen grains, thecae are prominently displayed on the large connective, and the connective epidermis is composed of greatly enlarged cells. The flower is firmly attached to the inflorescence axis, and the floral parts other than the androecium contain numerous branched sclereids, suggesting a somewhat "destructive" pollinator; moreover, the flowers are borne on long axes away from the branches. The

whorls of separate stigmas and flaring stamens surrounding a large nectary and the large number of ovules also appear to be correlated with a specific pollinator. Not surprisingly, then, bats have been reported as visitors of these flowers in the evening (Meijer, 1968, pp. 60–61).

The features of *Tetrameles* indicate that several methods of pollination are possibly operative. Precocious flowering and long pendant or clustered inflorescences are frequently indicative of anemophily, and the emergent crown certainly provides ample exposure to the wind; but the small stigmas and numerous ovules (and perhaps nectaries) are not usually characteristics of wind-pollinated plants. Foresters often speak of *Tetrameles* as a "bee tree," indicating that it is frequently associated with some hymenopteran. Pollination is probably accomplished by both wind and insects.

Datisca is usually regarded as wind-pollinated, although the possibility of insect agency cannot be ruled out. Pollen grains of *Octomeles* and *Tetrameles* are very small and are never united in tetrads at maturity, but those of *Datisca* are often shed from the anther in tetrads and have a more conspicuously sculptured exine, suggesting that the plants may be to some extent entomophilous. Also the large numbers of ovules in the ovaries and viable seeds in the capsules are probably correlated with a more efficient pollination method, unless seed development follows apomixis. Self-incompatibility tests and more field work are needed before the reproductive biology of *Datisca glomerata* can be understood. If self-incompatible, this descriptively androdioecious species would be functionally dioecious.

Leaves of Datiscaceae are alternate and estipulate. The three genera differ one from another in foliar morphology and anatomy and especially in trichome complements. *Octomeles* and *Tetrameles* are similar in their petiolar anatomy, a situation possibly related to the emergent nature of the crowns and the consequent similar exposure of the leaves to the environment; but *Datisca* differs in having 3-trace, unilacunar nodes with a very simple pattern of bundle rearrangement at the proximal end of the petiole.

Differences in trichome ontogeny are also important in distinguishing *Datisca* from the other genera. The two kinds of peltate trichomes in *Octomeles*, those present in chambers and apparently hydathodal and those not in chambers, are probably phylogenetically related. The stalked glandular trichomes of *Tetrameles* can be interpreted as part of the same phylogenetic series because they have an ontogeny similar to that of the others, although the number of cells in transections of the stalks of each differs: the glands are biseriate and the peltate trichomes are quadri- or multiseriate. The septate, spicular hairs and the 2-armed hairs of *Tetrameles* are clearly related to each other evolutionarily and have no counterpart in either of the other two genera.

Ontogeny of the glandular trichomes of *Datisca* is completely different, and one can suppose that they are independently derived. Another possibility, however, is that both are evolutionarily derived from the same prototype and have diverged through change in the orientation of the first (and subsequent) planes of division in the initials. The occurrence of more than one basic type of trichome ontogeny in one family does not

seem unlikely, despite the conservative nature of this ontogenetic process (see Carlquist, 1958, 1959a, 1959b); but more surveys concentrated on the trichome complements of single families or closely related taxa are needed before a definite statement can be made.

Literature on domatia, or acarodomatia, deals mostly with their taxonomic usefulness or their mere presence in certain taxa, e.g., Dipterocarpaceae and Rubiaceae. Evidently almost no work has been done to assess the actual relationship of occupied domatia to their inhabitants. Mani (1964, p. 3) includes within the world of plant galls all those structures that "are actively produced by the plant as a result of abnormal growth activity [caused by animals]." Therefore, the domatia of *Octomeles* might be considered galls because of the small amount of hypertrophied tissue present in them. The matter of classification is more complicated, however: they are here interpreted as extra-floral nectaries that are evolutionarily related to the apparently nonnectariferous cavities in the vein axils of *Tetrameles* leaves. They are associated with two or fewer traces containing approximately equal amounts of xylem and phloem and are probably not hydathodes. An interesting study would be to determine the number of mite species involved and to see if the association is obligate or fortuitous.

Evidence from anatomy and morphology of fruits and flowers does not support the separation of *Octomeles* and *Tetrameles* into their own family, as was done by Airy Shaw (1964). Overlap of certain features, such as the similar dispersal mechanisms of *Tetrameles* and *Datisca*, indicate that an emphasis on size and woodiness is perhaps unjustified. Studies of wood anatomy (in press) and embryology (in progress) will also be brought to bear on this matter. The differences between Datisceae (*Datisca*) and Tetrameleae (*Octomeles* and *Tetrameles*) do not even necessitate subfamilial rank for the two groups; rather they are better treated as tribes, as was done by Warburg (1895) and by Gilg (1925b).

FLORAL BIOLOGY, POLLINATION, AND GEOGRAPHIC DISTRIBUTION

Dioecism is often mentioned as a common characteristic of wind-pollinated plants, and the consensus has been that adaptation to this method of pollination precedes the change in sexuality of the flowers. Kaplan and Mulcahy (1971) suggest that the reverse is true for *Thalictrum*, i.e., that dicliny is a response to selective factors favoring a greater degree of outcrossing and that anemophily may then follow this change. A similar argument can be applied to Datiscaceae, even though wind pollination may be of secondary importance in the family. Carlquist (1966; 1973) has reasoned that dicliny and dichogamy are important in maintaining high levels of heterozygosity in insular plant species and that this condition contributes to the long-range evolutionary survival of populations geographically isolated from their source areas. Similarly, dioecy promotes heterozygosity in the "insular" habitats of Datiscaceae.

Not inconceivably, limestone "islands" were available for colonization by *Tetrameles* during Tertiary times. The geological history of India and Assam has involved both uplift and sinking from at least the early Tertiary

onward, and even central India near Nagpur, the collection site of *Tetra-meleoxylon*, show some signs of having been characterized by marine conditions at this time (Lakhanpal, 1970). The geologically active nature of the Malesian region also leads one to believe that the limestone islands here have been varied in their size, abundance, and distribution. Possibly, then, *Tetrameles* arose in response to selection for an efficient outbreeding system in insular limestone areas in Indo-Malesia before the present-day boundaries of Southeast Asia and India had been established. Grant (1958) suggests that a very strong selective pressure is necessary for evolution of dioecy because of a presumed lowering of fertility; but any lowering of fertility can theoretically be offset by production of numerous ovules, especially if this compensatory mechanism is accompanied by an efficient pollination system. Ancestral plants characterized by the last two features might be considered "preadapted" for dioecy. One might not expect such strong selective pressure in extensive populations of a *Tetrameles* ancestor, such as those of *Tetrameles* itself that now occur in the edaphically and climatically similar regions of continental Indo-Malesia, because conditions would already be favorable for outcrossing. The ancestors of *Tetrameles* probably did have ovaries with numerous ovules (see the next section), but their method of pollination is obviously unknown.

The same reasoning is applicable to the evolution of *Octomeles* and *Datisca*, each of which occupies a riverine or riparian habitat that is or was at some earlier time essentially insular. The instability and uncertain duration of any particular part of a riverine habitat may also have been a factor in the evolution of these genera; and in the case of *Octomeles* this would be especially true in places where areas of deep alluvium are restricted in their extent so that the river affects the habitat directly. Even Rumphius (1743) noticed that individuals of *Octomeles* seldom reach great age because of flooding or undercutting of the banks. Among plants favored in such situations are those that produce strong root or rhizome systems, do well in saturated soils, reproduce asexually (e.g., bamboo), reach seed-bearing age quickly, and produce abundant, easily dispersable seeds. The last two qualities are parts of a system that may promote genetic recombination (Grant, 1958), and they are also features of *Octomeles*.

Interestingly, *Octomeles* is not always heavily buttressed. Trees of *Octomeles* seen in this study were often very tall but had small buttresses. Buttresses on *Tetrameles* are usually much larger, although those on the tree from the Brown River in Papua were small also. The size of buttresses in the family is probably related to age of the trees. These observations do not support the belief that buttresses help prop up trees or act like webbed feet to keep them from sinking into the mud. They may, instead, result from a kind of "hypotenuse" effect in which water and minerals follow the shortest course from the root to the crown. This would also act as a positive feedback system, something like that mentioned by Smith (1972), except that the amount of photosynthetic activity is probably unimportant in this process. Photosynthetic tissue is present throughout the broad flanks of the buttresses on both *Tetrameles* and *Octomeles* as well as on the margins.

The diversity in form and size of buttresses (cf. *Canarium* and *Tetrameles*)
on tropical trees indicates the improbability that any one explanation will
account for their development, but a connection between superficiality of
the root system and buttressing seems plausible.

The small wind-disseminated seeds, fast growth, and strong light tolerance
of *Octomeles* also enable it to occupy "pioneer" habitats in newly logged
places and in cleared agricultural areas.

The present-day distribution of Datiscaceae suggests that the family prob-
ably had its origin in Indo-Malesia. The two species of *Datisca*, then, repre-
sent temperate outliers of a tropical distribution. *Datisca glomerata* of
California is a component of the Tertiary flora that once extended from
eastern Asia across Beringia to North America.

Relationships of Datiscaceae to other families

The difference in morphology suggested by Airy Shaw (1964) as reasons
for removing *Tetrameles* and *Octomeles* [Tetramelaceae (Warb.) Airy
Shaw] from Datiscaceae (*Datisca* only) and allying *Datisca* with Halo-
ragaceae appear to be habitat- (or habit-)related, and their phylogenetic
significance is difficult to evaluate. He mentions the following character-
istics as differentiating Datisceae from Tetrameleae: willowy, herbaceous
habit, pinnate or pinnatifid leaves, stamens in indefinite numbers and with-
out fixed arrangement in relation to the sepals, long filaments, and long
anthers. If one wishes to emphasize differences, several much more interest-
ing ones are present, for instance, trichome ontogeny and petiolar anatomy;
but these do not require the postulation of an entirely separate phylogenetic
derivation for Tetrameleae on one hand and Datisceae on the other.

The possibility of relationship between Datiscaceae and Haloragaceae
deserves some consideration, however. The pinnate or pinnatifid leaves and
indefinite numbers of stamens of *Datisca* are scarcely strong arguments for
allying this genus (and thus *Octomeles* and *Tetrameles*) with Haloragaceae
because leaves of most members of the latter family are simple, except in the
completely aquatic *Myriophyllum*, and the stamens are arranged in a
definite relation to the perianth parts. Flowers of most Haloragaceae (ex-
cept *Gunnera*) are hermaphrodite, and the anemophilous species are pro-
tandrous (Schindler, 1904; Orchard, 1972), a characteristic often, but not
always, associated with anemophily. Species of *Myriophyllum* are monoe-
cious with unisexual flowers, the females of which mature before the
males. *Datisca glomerata* is androdioecious, and the hermaphrodite flowers
are protogynous. Although a tendency toward dicliny exists in Haloragaceae,
it appears more likely a result of convergence than an indication of relation-
ship; also, the method of dichogamy differ. The resemblances in the flowers
of the two families are suggestive despite the above-mentioned differences,
but the patterns of floral vasculature differ somewhat because of the differ-
ences in the number and arrangement of floral parts. Styles of Haloragaceae,
although separate as in Datiscaceae, are antipetalous, not antisepalous, and
the traces within them are derived topographically from antipetalous bundles
(equivalent to the lateral bundles in the hermaphrodite flowers of *D.*

glomerata) instead of from the antisepalous stylar bundles (Orchard, 1972). One would expect differences related to differential preservation of floral parts, and these should probably not be given great emphasis.

The nature of placentation in each group offers little help in approaching the question of relationship here. Placentae of Datiscaceae are obviously parietal and bear many antropous ovules; in addition, those of *Octomeles* form septa across the locule and thus approach an axile condition. Placentae of Haloragaceae are apical or lateral on septa, if septa are present, and ovules are few. Septa may be absent or incompletely developed at the top and bottom of the locule. This condition may be interpreted as derived from axile or as derived from parietal, depending on one's point of view and the importance attached to a central column of vascular tissue at the convergence of the septa.

Pollen of Haloragaceae is usually 4–5-colpate or 4-5-porate and is frequently aspidate, conditions never found in Datiscaceae. In addition the two families differ in details of the exine; for example, sculpturing, internal lamellation, and thickness around the apertures (Praglowski, 1970).

Glandular trichomes are present in *Haloragodendron*, a segregate of *Haloragis* proposed by Orchard (1972) but not yet validly published. Their ontogeny and hence their similarity to those of Datiscaceae are unknown. Other hairs of Haloragaceae are unicellular or uniseriate. Trichome complements of the two families appear to show little correspondence.

The relationship of Datiscaceae to Begoniaceae, first proposed by Lindley (1846) and maintained in the most recent phylogenetic arrangements (Cronquist, 1968; Takhtajan, 1959; Thorne, 1968), is difficult to verify. The specialized succulent-woody or herbaceous habit of members of Begoniaceae results in an almost total lack of anatomical correspondence to Datiscaceae. Vessel elements in the secondary xylem of two species of *Begonia* examined by the writer have simple perforation plates, although Metcalfe and Chalk (1950) mention also the presence of long scalariform plates. Possibly they saw lateral wall pitting, which in long vessel elements is easily mistaken for a perforation plate. Intervascular pitting is scalariform and bordered; vessel element-axial parenchyma pitting is scalariform and half-bordered. Libriform fibers are septate with simple pits. Rays are very tall and wide and are composed mostly of square and erect cells. An analysis of the wood of Begoniaceae has not yet been done and is very much needed.

Floral characteristics of Begoniaceae are varied, but inferior ovaries and unisexual flowers are common to both families. Stigmas of both are antisepalous, and in *Hillebrandia* they are widely separated as in Datiscaceae; however, in other Begoniaceae stigmas and styles are variously contorted and branched. The androecium is similarly varied and dehiscence of the anther may be lateral or poricidal (Irmscher, 1925). Floral venation of the two families shows a little correspondence (Gauthier, 1950) that reflects the similarity in arrangement of floral parts in the case of the female flowers; but perianth members of Begoniaceae are large and showy, and their venation differs accordingly. The axile placentation in members of Begoniaceae is usually interpreted as derived from parietal, and ovules are numerous on

the one or two placental ridges that extend into the locule. Some members of the section *Mezierea* of *Begonia* have, in fact, parietal placentae that do not meet at the center of the locule; and in *Hillebrandia* placentae are axile in the lower part of the ovary and parietal at the distal end (Gauthier, 1959). As mentioned before, placentae of Datiscaceae are uniformly parietal.

Species of *Begonia* are usually monoecious and the male flowers may mature first (Matzke, 1938). In some cases flowering intervals are spaced such that the male and female flowers are never observed together on the same plant (Smith and Schubert, 1946). A tendency toward dioecy is definitely present, then, even though actual dioecy is rare in the family.

Pollen of Begoniaceae has not been investigated except by Erdtman (1952). The pollen in the Rancho Santa Ana Botanic Garden pollen-slide collection conforms to Erdtman's description and is prolate and tricolporate with conspicuously lalongate ora. Sculpturing and bacculation could not be discerned. Pollen grains of Datiscaceae are also tricolporate with lalongate ora, but the pollen of each family thus far investigated is of a type so widespread in dicots that few characteristics of possible phylogenetic significance can be found.

The over-all impression is not one of close phylogenetic relationship of these two families. However, the possibility exists that both represent separate derivations from the same group ancestral to Flacourtiaceae. Within Flacourtiaceae (especially the tribes Flacourtieae and Homalieae) are all the same trends and characteristics present in Datiscaceae and Begoniaceae: tendency toward an inferior ovary, monoecy and dioecy, separate stigmas, capsular fruit, numerous anatropous ovules and seeds, inflorescences with many flowers, tendency toward anemophily, valvate sepals, and nectar glands between gynoecium and androecium. Parietal placentation is present in most members; but in some (e.g., *Flacourtia*) the locule is incompletely divided into a few chambers; and in *Eichlerodendron* placentation is essentially axile (Gilg, 1925a) because the placentae fuse in the center, as in *Octomeles*.

Pollen grains of Datiscaceae and Begoniaceae fall within the morphological range of those of Flacourtiaceae, especially the tribes Homalieae and Flacourtieae. Gains of these two tribes are fairly small, more or less spherical, and tricolporate. Also, the endoapertures are often elongate in an equatorial direction, as in Datiscaceae, and the tectum is smooth or finely reticulate (Schaeffer, 1972). Thus, the tendencies and features of these tribes, none of which is significant by itself or uncommon, appear to support inclusion of Datiscaceae within Cistales (sensu Thorne, 1968). This was pointed out also by Brown (1938). The isolated position usually granted to the family evidently results from a consideration of the following differences represented in Datiscaceae: inferior ovary, specialized wood, estipulate leaves, little endosperm, lack of broad, leafy cotyledons, valvate perianth parts, and differentiation of calyx and corolla lobes in male flowers of *Octomeles*.

Unfortunately, so little is known about Flacourtiaceae that conclusions such as these must be drawn with reservation. Comparison of tendencies in

wood anatomy and pollen are based on observations of a very limited number of species. The evidence accumulated so far, however, indicates only that Datiscaceae form a natural group within Cistales and that the family may be related to Begoniaceae through common ancestry with Flacourtiaceae.

SUMMARY

An anatomical and morphological study of the three genera of Datiscaceae has been undertaken to test the closeness of intrafamilial relationship and to determine, if possible, the systematic position of the family.

Octomeles and *Tetrameles* are monotypic trees up to 150–180 ft tall. They are strictly Old World genera, the former occupying riverine rain forest habitats in Malesia (Borneo to the Solomon Islands) and the latter growing in monsoon and wet-deciduous forests from New Guinea to Ceylon and India. *Datisca cannabina* L. has a Mediterranean distribution extending from Crete and Turkey to Kashmir. *Datisca glomerata* (Presl) Baill. is restricted to California and Baja California. Both species of *Datisca* occur in riparian habitats in Oak woodlands and coniferous forests in their respective ranges. The three genera are related by their similarities in floral morphology, but the difference in habit between the herbaceous datiscas and the two trees results in a nearly complete lack of anatomical correspondence. A conspicuous difference in ontogeny of glandular trichomes of *Datisca* and *Tetrameles* does not seem to be habit- or habitat-related, however.

A theory has been presented to explain the dioecy of three of the four species (and androdioecy of *D. glomerata*) as a response to selection for an effective outbreeding system in essentially insular situations.

On the basis of characteristics and tendencies present in Flacourtiaceae, Datiscaceae appear to be correctly placed within Cistales (Violales). Little anatomical correspondence is present between Datiscaceae and the possibly related Begoniaceae, again because of the great specialization of the members of the latter family, but both may be related through a common ancestry with Flacourtiaceae.

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