MORPHOLOGY OF THE ANDROECIUM IN MALVALES

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CONTENTS

INTRODUCTION

Two theories dominate the morphological interpretation of stamens. According to the classic theory stamens are sporophylls homologous with foliage leaves and they bear marginal sporangia. According to the telome theory, on the other hand, the stamens represent contracted branching systems of telomes with apical sporangia. Lam (1948) thought that both types may occur in the Angiosperms.

The present study was undertaken to decide which theory better accords with the facts in *Malvales*. At the outset it was limited to the vascular course in the *Malvaceae* and the issue was settled entirely in favour of the telome theory. But as I could not explain why the position of the fields of carpels in *Malope trifida* is exactly the reverse of that in *Kitaibelia vitifolia* I was led to investigate the early developmental stages. After this *Kokia rockii*, with vascular bundles linking the rows of stamens, came into the picture. As a result it proved necessary to broaden the study, and, later, *Bombacaceae*, *Sterculiaceae*, *Tiliaceae*, and *Elaeocarpaceae* were included. This broadening modified the initial ideas, I came fully to agree with Arber's conclusion (1933):

> 'It follows that the study of the external form, the vascular system, and the ontogeny, should not be pursued as three separate branches, but should be treated as one indissoluble whole.'

The techniques used are all customary. These are, first, the paraffine technique for making microscopic slides that are stained mainly by saffranin and fast green; second the clearing technique, generally by mixture of chlorallactophenol and hydrogenic oxide at raised temperatures; and third, the use of a powerful dissecting microscope. Because of the difficulties involved in a proper orientation of the irregular (contorted) floral primordia for microtomy, another method of approaching the ontogeny, study of histogenesis, was used only rarely. Only now and then have any results from this method been included in the text.

A descriptive, a comparative, and an interpretative chapter have been devoted to each family. After that a general interpretation covers the separate interpretative sections. This is followed by a discussion of the validity of the telome and classic theories. The descriptions have been limited to such features as appeared relevant to the present study. To convey a general impression of each species, a more or less descriptive floral formula has been added. For fuller information the reader is referred to classificatory works.

Hall (1956) was in favour of omitting all figurative language in describing the course of vascular bundles. My experience, however, is that descriptions of that kind are dull and laborious to read. Therefore although I have used figurative language I have endeavoured to keep it from becoming superfluous, lest it lead to faulty conclusions.

SOURCES OF THE MATERIAL USED FOR THIS STUDY

Abroma augusta, Botanic Garden (B.G.) Bogor. — Abutilon darwinii, B.G. Leyden (L.) — A. indicum, B.G.L. — A. megapotamicum, B.G.L. — Aceratium oppositifolium, unknown provenance. — Adansonia digitata, cult. St. Eustatius, B.G. Honolulu, cult. near Hyderabad. — Althaea officinalis, B.G.L. — A. rosea, B.G.L., B.G. Delhi. — Althoffia pleiostigma, Hoogland 5049, v. Royen and Sleumer 6171, Brass 25273. — Anoda lavateroides, B.G.L. — Apeiba echinata, Uittien 4149, 6749. — A. tibourdou, Pulle (1920) 217. — A. spec., Breteler 3867, 3910. — Argyrodendron actinophyllum, B.G. Adelaide. — Aristotelia macqui, B.G.L. — A. fruticosa, Allan sine num., Travers sine num. — Ayenia magna, Suringar sine num., Boldingh 7099, Smith 426. — A. montana, Pringle 8407. — Berrya cordifolia, B.G. Bogor. — B. javanica, B.G. Bogor. — Bombacopsis quinata, Breteler 3436. — Bombax buonopozense, cult. near Abidjan. — B. ceiba, B.G. Bogor, Delhi, Rehovot. — B. ellipticum, B.G. Berlin-Dahlem. — Brachychiton populneum, B.G. Coimbra. — Byttneria pilosa, B.G. Bogor. — Camptostemon philippinense, Delmaar 1973. Sulit, Phil. Nat. Herb. 12277. Miranda sine num. — C. schultzii, Brass 8517. — Carpodiptera cubensis, Howard

1447. — Ceiba mandoni, Herzog (1924). — C. pentandra, B.G. Bogor, Popta 551. — C. pubiflora, Hassler (1913) 11724. — Cephalohibiscus peekelii, Hoogland 5134. — Cheirostemon platanoides, Herb. d'Alleizette. — Chorisia crispiflora, Ule 9597. — Cistanthera papaverifera, Leeuwenberg 2530, 2890. — Clappertonia ficifolia, Zenker 1475, Lörzing 11968. — Coelostegia borneensis, SAN 37996. — C. griffithii, Kostermans 5262, cult. Java. — Cola nitida, B.G. Bogor, B.G. Singapore. — Colona auriculata, B.G. Bogor. — C. scabra, BW. West New Guinea 6728. — Commersonia bartramia, Wight 244, Lei 642, Bakhuizen van den Brink sine num. — Corchorus aestuans, B.G. Meerut, Delhi. — C.capsularis, Lei 98, 992. — C. hirsutus, de Wilde 159, Rugel 275. — C. olitorius, B.G. Meerut, Delhi. —C. tridens, B.G.Delhi. — Cullenia ceylanica, B.G. Bogor. — Diplodiscus paniculatus, Sulit, Philip. Nat. Herb. 14317, 22897. — Dombeya calantha, B.G. Delhi. — D. wallichii, B.G. Berlin-Dahlem. — Dubouzetia campanulata, McKee 5534, Schlechter 15145. — Durio acutifolius, SAN 34716. — D. grandiflorus, SAN A 4660. — D. graveolens, Samsudin A 180, Kadir A 2787. — D. lanceolatus, Kostermans 6441. — D. oxleyanus, Endert 45 E. 1. P. 463, 566. — D. testudinarum, Kadir A 2772. — Elaeocarpus spp., B.G. Bogor, Kew, and Edinburgh. — E. homalioides, Ledermann 12858. — E. monocera, Ramos B.S. 20564, Elmer 18204. — E. nouhuysii, N.G.F. 13655. — Entelea arborescens, G. Univ. Auckland. — E. palmata, B.G.L. — Erinocarpus nimmonii, B.G. Bombay. — Eriolaena quinquelocularis, Hohenacker 1533, Wight 235. — Firmiana colorata, B.G. Bogor. — Fremontia californica, Eichler 16193, B.G. Univ. Calif. — Glossostemon brugueri, Herb. d'Alleizette. — Glyphaea grewioides, Zenker 4337. — Goethea cauliflora, unknown provenance. — Gossypium hirsutum, B.G.L. — Grewia hirsuta, cult. Madras. — G. laevigata, Garrett 732, B.G. Bogor. — G. oligandra, Pierre 3822. — G. orientalis, B.G. Delhi. — G. tenax, B.G. Delhi. — Hampea integerrima, Hallier 881. — Helicteres angustifolia, B.G. Bogor. — H. lanata, B.G. Bogor. — Heliocarpus americanus, Pringle 879, Ule 9601. — Heritiera littoralis, Heinig 1093, Achmad 1341. — Hermannia abyssinica, Penne & Matteoda 1758. — H. candicans, B.G. Coimbra. — H. exappendiculata, Hildebrandt 1259. — Herrania albiflora, Surinam. — Hibiscus campylosiphon, Phillippine plants 446, Cuming 1063. — H. micranthus, B.G. Delhi. — H. pulvinulifer, Docters van Leeuwen 9280. — H. rosa-sinensis, B.G.L. — H. syriacus, B.G.L. — H. trionum, B.G.L. — Hibiscadelphus giffordianus, Hawaii. — Hoheria spp., B.G. Christchurch. — Kitaibelia vitifolia, B.G.L. — Kleinhovia hospita, B.G. Bogor. — Kokia rockii, Hawaii. — Kostermansia malayana, SFN 36998. — Kydia calycina, Garrett 249, Wight 173. — Lagunaria patersonii, B.G. Coimbra. — Lasiopetalum acutiflorum, Maiden sine num., Pritzel 701. — Lavatera spp., all B.G.L. — Leptonychia glabra, Kadim and Noor 143. — L. macrantha, Zenker 1726, 3761. — Luhea divaricata, Hassler 11533, Smith & Klein 11902, Reitz & Klein 8019. — L. ochrophylla, Martius 523. — Malope trifida, B.G.L. — M. crispa, B.G.L. — Malva alcea, M. moschata, M. sylvestris, various localities in the Netherlands. — M. verticillata, B.G.L. — Malvastrum capense, B.G.L. — Malvaviscus arboreus, B.G. Bogor, B.G.L. — Matisia ochrocalyx, Ule 6193. — Melhania incana, Wight 236, Backer 36318. — Melochia pyramidata, Suringar sine num., Backer 3876, Millar 15627. — M. umbellata, Korthals sine num., Bünnemeyer 8174. — Microcos argentata, Pleyte 620, Schram BW 5972. — M. cinnamonifolia, Haviland 2256. — M. florida, Junghuhn, Korthals sine num. — M. ledermannii, Hildebrand BW 7279, Brass 28149. — M. pentandra, Ledermann 8783. — M. schlechteri, Clemens 1069. — M. stylocarpa, Mendoza Philip. Nat. Herb. 41874. — Modiola caroliniana, B.G.L. — Mollia speciosa, Ule 5991. — M. spec., Ule 8418. — Muntingia calabura, Lam 7334, B.G. Bogor. — Napaea dioica, B.G.L. — Neesia altissima, Bakhuizen v. d. Brink 5884, 7621. — N. malayana, Ridley 3770. — Ochroma lagopus, cult. Abidjan. — Pachira aquatica, B.G. Palermo. — P. insignis, cult. near Abidjan. — P. macrocarpa, B.G.L. — Papuodendron hooglandianum, Womersley, N.G.F. 4160. — P. lepidotum Havel, N.G.F. 15401. Hoogland 5156. Henty, N.G.F. 10538. — Pavonia spp., B.G.L. — Pentace polyantha, Kostermans 19376. — P. triptera, Ridley 6363c, Maingay 243. — Pentapetes phoenicea, G. Calcutta, Korthals sine num. — Pityranthe verrucosa, B.G. Peradeniya. — Plagianthus betulinus, B.G. Christchurch. — P. divaricatus, G. Berkeley. — P. glomeratus, Eichler 12958. — P. pulchellus, Darbyshire 513, B.G. Singapore. — P. sidoides, unknown provenance. — Pterocymbium beccarii, Hoogland 4375, Pullen 1071. — Pterospermum javanicum, cult. Delhi. — Quararibea guianensis, Surinam. — Ruizia variabilis, B.G. Naples. — Rulingia corylifolia, unknown provenance. — R. pannosa, Hubbard 3409, Maiden sine num. — Scaphium javanicum, cult. Delhi. — Schoutenia glomerata, B.G. Bogor. — S. ovata, Jacobs 4887, Koorders 30069. — Sericolea spp., Brass 30691, Brass & Collins 31257, Eyma 5379, Hoogland 5548, Saunders 723, Womersley 5336. — Sida retusa, B.G. Bogor. — S. spp., all B.G.L. — Sidalcea candida, B.G.L. — S. malvaeflora, nat. loc. in Mendocino County and from Mt. Tamalpaio, California, U.S.A. — S. oregana, nat. loc. near Washington and Pullman, U.S.A. — Sloanea archboldiana, Brass & Versteegh 11174. — S. guianensis, Reitz & Klein 8952, Surinam. — S. javanica, Bakhuizen v. d. Brink sine num., B.G. Bogor. — S. lamii, unknown provenance. — S. lasiocoma, Hatschbach 7165. — S. myriandra, Clemens 1048. — S. sogerensis, Forbes 607, Havel N.G.F. 9135. — S. spec. Millar & van Royen N.G.F. 18747. — Sparmannia africana, B.G.L. — Sphaeralcea umbellata, B.G.L. — Sterculia alexandri, B. G. Kirstenbosch. — S. bidwilli, B. G. Palermo. — S. diversifolia, B. G. Bogor. — S. laevis, B. G. Bogor. — S. lurida, G. La Mortola. — S. nobilis, B.G. Kirstenbosch. — S. platanifolia, B.G. Palermo. — S. rubiginosa, B.G. Bogor. — S. rupestris, B.G. Palermo. — S. villosa, Dehra Dun. — Theobroma spec., Lindeman 5725.

— T. cacao, Surinam. — Thespesia populnea, Hoogland 4272, N.G.F. 8615, van Royen Bougainville I. 1963. — Thomasia macrocarpa, B.G. Adelaide. — T. pauciflora, B.G. Kew. — T. solanacea, B.G. Kew. — Tilia platyphyllos, B.G.L. — T. tomentosa, G. Leyden. — Trichospermum javanicum, de Voogd 541. — Tricuspidaria dependens, B.G.L. — Triumfetta althaeoides, Curtis 234. — T. annua, Bullock 606. — T. appendiculata, Specht 379, 701. — T. bartramia, B.G. Delhi, Garrett 253, Schiffner 2203. — T. neglecta, Cardoso sine num., Schimper 1460. — T. suffruticosa, Lörzing 12868. — Urena lobata, B.G. Bogor. — Vallea stipularis, B.G. Kew, Edinburgh. — Waltheria americana, unknown provenance.

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MEANING OF ABBREVIATIONS USED IN THE FIGURES

cort.b.	cortical bundle
g	gynoecium
gaph	gynandrophore
h	epicalyx part
n	nectariferous tissue
p	petal
pld	petaloid
pld. st.	vascular bundle supply of petaloid-stamen group
p. st.	petal-stamen trace
Rp	petal radius in the flower
Rs	sepal radius in the flower
S	sepal
Slat	lateral sepal bundle
Sm	median sepal bundle
Smg	marginal sepal bundle
st	stamen
std	staminode

MALVACEAE

A. DESCRIPTIVE PART

1) Malopeae: S(5)n-(P5-St∞)-C(∞)
Malope trifida Cav.
Kitaibelia vitifolia Willd.

Malope trifida

The sepals form a lobed calyx tube giving it by their v-form a pentagonal cross-section with angles in sepal radii. Each sepal is provided with a basal field of nectariferous trichomes on its inner side.

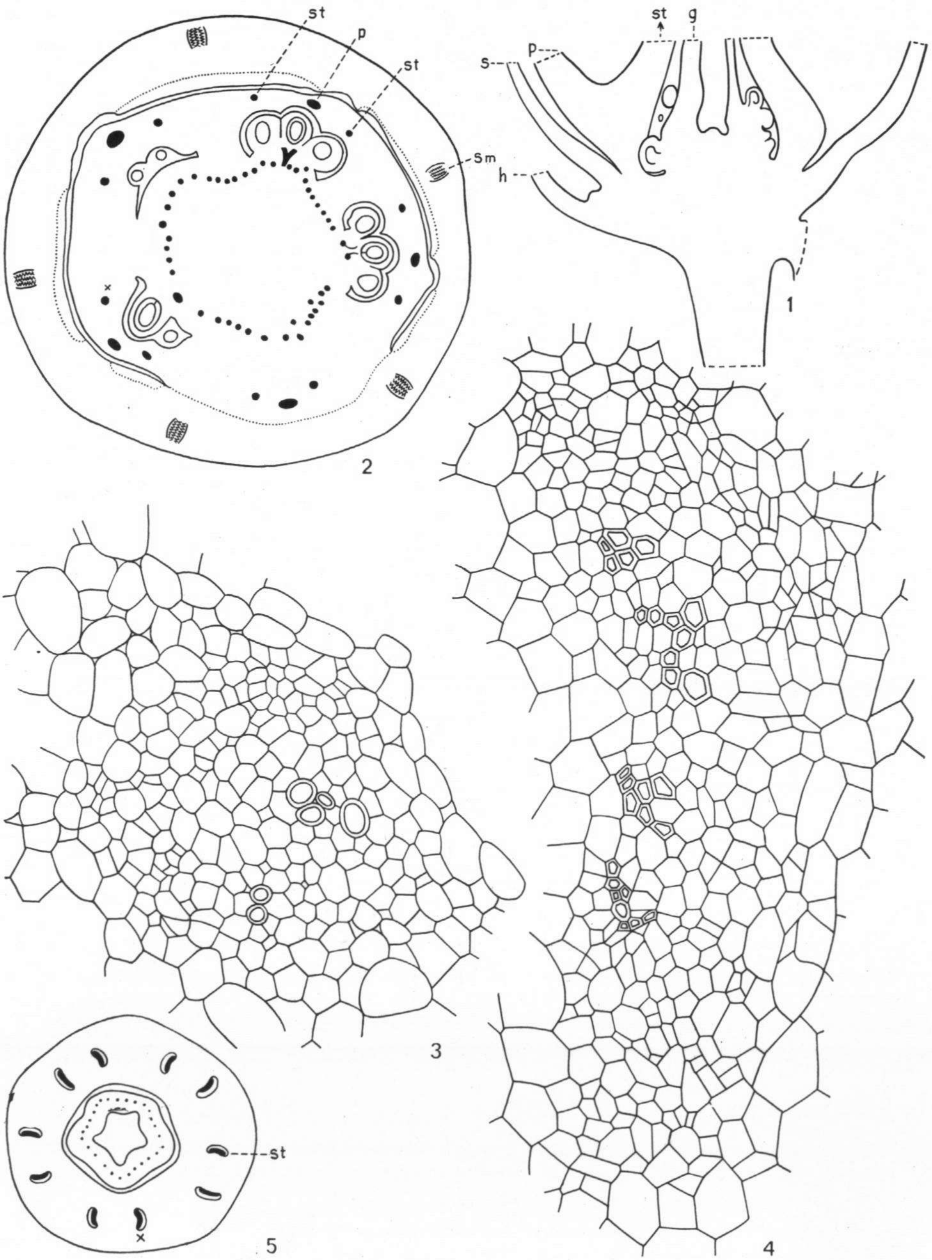
The contorted corolla is composed of five asymmetrically cuneate petals which are attached to the basal part of the stamen tube. Therefore this basal part may be distinguished as the petal-stamen tube (fig. 1).

The stamen tube bends around the ovaries and tapers into a cylindric tube surrounding the styles. The petal-stamen tube is somewhat pentagonal with the angles in petal radii. There it is also thinner than in sepal radii, in correspondence with the alternisepalous position of the lower ovaries (fig. 2). Above the level of divergence of the petals the tube is pentagonal with the angles in sepal radii (fig. 5), but distally, where the stamens become free, it is again pentagonal with the angles in petal radii. Apically the tube terminates into five antesepalous lobules, which are split up into filaments (fig. 7).

The stamens diverge from the tube in, at first sight, ten rows parallel to the flowering axis. However, below, the rows lie towards petal radii, above more between sepal and petal radii. When the points of attachment are projected on a plane perpendicular to the flowering axis five pairs of rows result which are not radial, but more or less at right angles to the petals. The stamens of the different rows do not form whorls.

The filaments are forked. The part below the fork may be long in the lower stamens, shorter in the higher, and absent in the apical stamens. Also upwards the way of forking changes from collateral to diagonal and finally to serial. The diagonal forking admits of two positions of the branches, one of which is only realized as all the branches of such forks on the side of the sepal radii are placed higher than the other branches (fig. 6). Each branch of a filament bears a reniform theca lying with its two parallel pollen sacs in the plane of the branches. In the distal part of the stamen tube, where the common part to a forked stamen becomes shorter and shorter and ultimately disappears, stamens occur which seem to bear only one theca with two pollen sacs. Conversely, in the proximal part of the staminal region, where the unforked parts of the stamens gradually become longer and the forked parts shorter, stamens may finally occur with two half-reniform thecae in line, forming an anther with four pollen sacs.

However, the general organisation is changed in variable degree, presumably in relation with the contorted character of the corolla and the androecium itself. To begin with, the attachment of the petals is slightly oblique and not strictly alternisepalous, as the overlapping side is inserted lower than the other side and farther from the alternisepalous radii. Here the v-form of the sepals probably plays a part as well. Secondly, the rows of stamens are not placed symmetrically to the petal radii, but more at right



Malope trifida. — Fig. 1. Full-grown flower, l.s. — Fig. 2. C.s. at calyx base (20 ×). — Fig. 3. Stamen fascicle trace indicated by × in fig. 2, c.s. — Fig. 4. Stamen fascicle trace indicated by × in fig. 5. — Fig. 5. Base of stamen tube, c.s. (15 ×).

angles to the obliquely inserted petals. As a consequence the rows in front of the overlapped petal halves lie more towards petal radii, the rows in front of the overlapping petal halves more towards sepal radii. Moreover, these latter rows count more stamens with fewer deviations which begin to be separated from the tube at a lower level than the stamens of the other rows.

The carpels are placed around the free apex of the receptacle also in ten longitudinal rows which are more or less situated between sepal and petal radii. They are placed transversally, the fusing styles pointing into antepetalous direction. Often the rows are linked by normally placed carpels, below in petal radii and above in sepal radii.

Developmental phases

After the development of a calyx the flowering apex becomes flat and five-angled in alternisepalous radii. Next the periphery of this apex is elevated as a wall, certain parts of which will give rise to the staminal buttresses. The first manifestation of this development is the occurrence of a rather wide radial groove on the inner slope of the wall in petal radii which intensifies the pentagonal character of the border between the wall and the rest of the apex. The groove extends over the wall, growing narrower in centrifugal direction. Only after the start of the development of the groove in petal radii a groove in sepal radii originates which is shallower, narrow on the inside slope and becoming wide toward the outside slope of the wall (fig. 11). In this stage five pairs of staminal buttresses result with elliptic outline, the long axis being directed from sepal radii inwards to petal radii outwards.

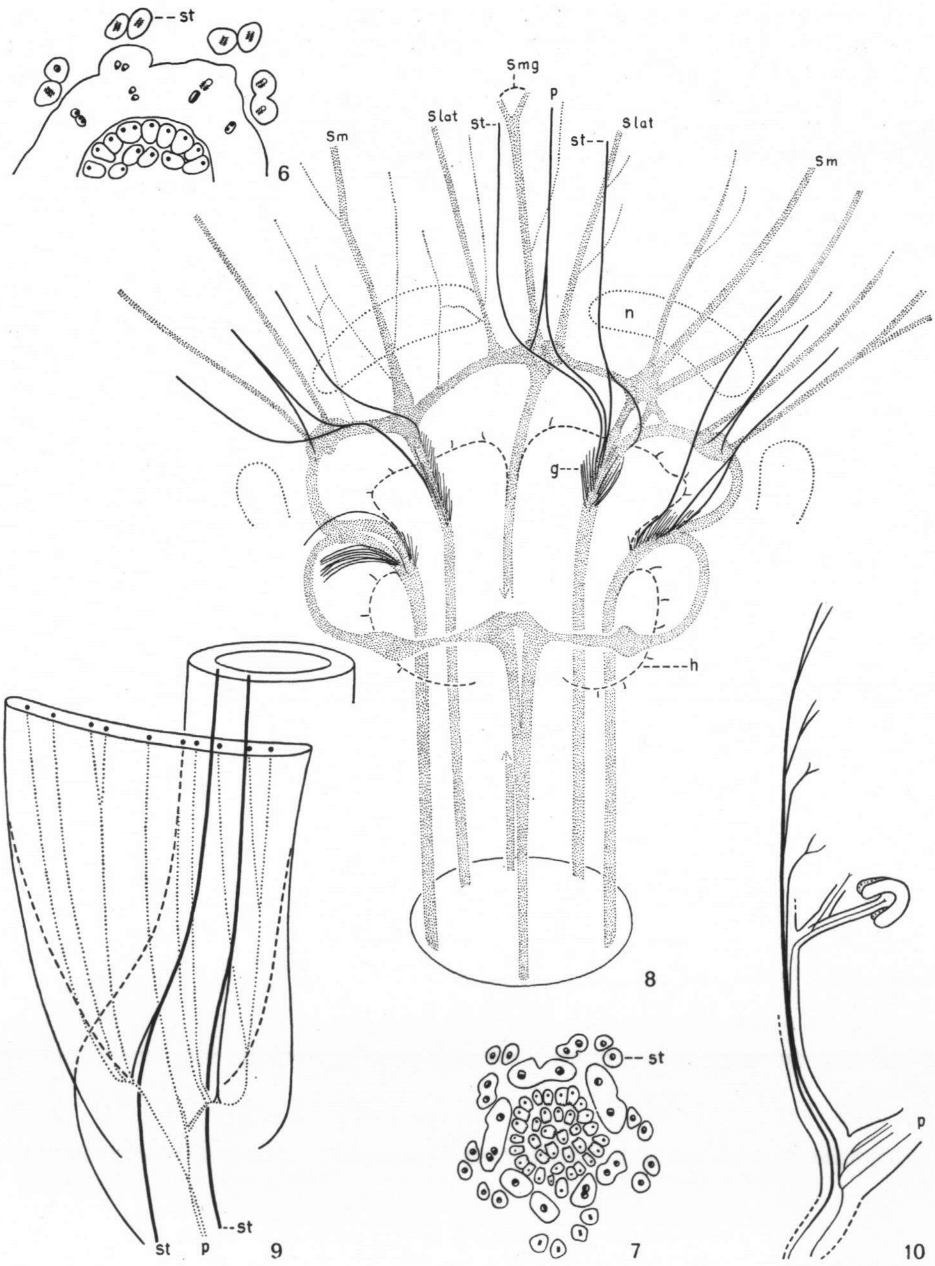
Accordingly the residual apex is widest in petal radii and the outward coils of the pistillary arrangement come to lie there. The first signs of the carpels only appear when the pollen sacs are formed.

During the subsequent development of the primordial tube especially the antepetalous parts of the wall grow in height and bulge inward somewhat over the apex. Moreover, on the buttresses a series of tangential grooves originates in centrifugal direction delimiting parts which grow upwards as stamen primordia (fig. 12). The primordia on two antepetalous buttresses are situated more or less exactly beside each other.

In the beginning the first formed stamen primordia are situated on the adaxial sides of the inward bulging butresses, but later extension growth may catch the central tube portions and place these stamens on top of the tube. Equally, the development of the first stamens may be arrested for some time, which, judged by the marked crowding, may be due to lack of space. Later by the intervention of the longitudinal growth the crowding is eased and the development of the primordia is resumed. Sometimes the inner parts of the wall in sepal radii may produce one or two juxtaposed stamen primordia, bridging two adjoining rows centrally. Mostly these primordia remain undeveloped.

The anther primordia from hemispheric become elliptic before they split into two half-anthers. The division is usually collateral, but in the first formed anthers frequently serial and diagonal. During the division the primordium becomes stalked by a filament, later the bases of half-anthers taper into the branches of the filament. After that the pollen sacs become visible. Finally growth elevates the young tube on a sterile proximal part.

Some features are probably related with the contorted character of the androecium. First the change that the staminal buttresses undergo during later development from their symmetrical arrangement to the position required by the external situation described earlier. Second the fact that the staminal buttress situated in front of the overlapping petal half is slightly advanced in development. Moreover, the later formed primordia in that row curve towards alternisepalous radii. The primordia of two antepetalous rows may not be juxtaposed but alternate.



Malope trifida. — Fig. 6. Stamen tube at the level of stamen divergence, c.s. — Fig. 7. Distal c.s. of stamen tube. (Figs. 6 and 7. 15 ×). — Fig. 8. Course of vascular bundles. — Fig. 9. Innervation of petal and two stamen groups in front. — Fig. 10. Branching stamen fascicle trace.

The petal primordia start as tiny, slightly oblique tangential ridges on the outer base of the buttresses that approach nearest the alternisepalous radii. They become visible at the same time as the fourth or fifth stamen primordium. Then, when the stamen primordia are beginning to divide, they may be seen to grow sidewards and slightly upwards under the buttress, forming the petal half that is being overlapped. Later they grow sidewards and slightly downwards under the other buttress giving the overlapping petal half.

The first signs of the ovaria appear simultaneously along the margin of the apex, which is star-shaped with lower more or less alternisepalous rays.

Vascular bundle supply (fig. 8)

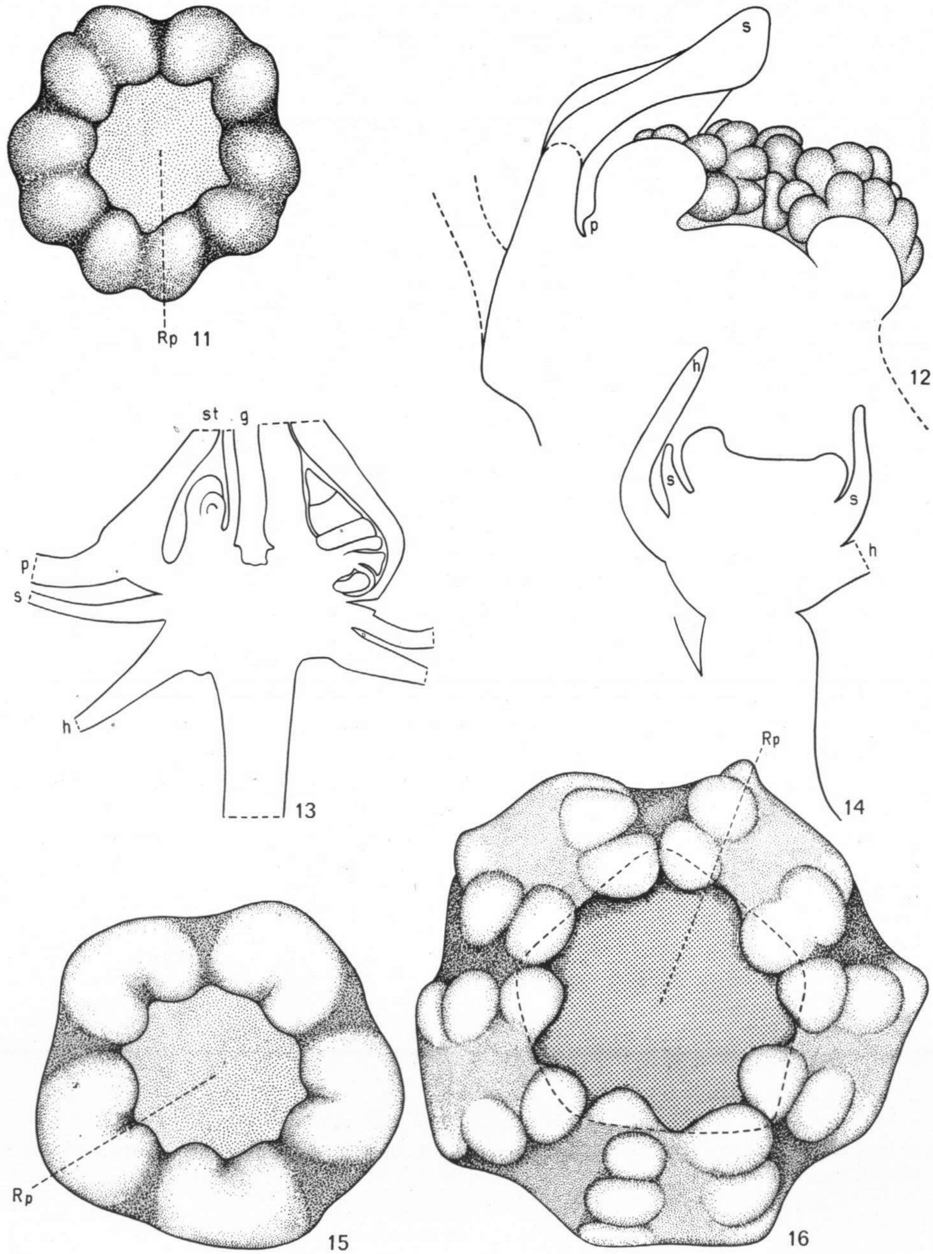
In the base of the flower six to eight main bundles leave the stele, five in sepal radii and some others in petal radii. They are c-shaped in cross-section. The outer parts of the bundles in sepal radii move outwards and trifurcate into a median sepal trace and two sepal basal lateral traces, the latter of which give off some sepal laterals. The sepal marginal bundles are also attached to the sepal basal laterals of adjoining sepals by the other part of double traces. In that way the phenomenon of cross-arcs linking the main bundles is brought about. However, in other flower sectors, these traces are connected to the stele by way of a sepal commissural marginal trace, which represents one of the main bundles leaving the stele in petal radii often combined with petal traces.

On applying a cross-section through the flower on the level of the calyx base (fig. 2, 3) we see a pentagonal stele and five triplets of bundles around it which are situated in the alternisepalous part of the petal-stamen tube. The median members of the triplets are the petal traces, the lateral members the stamen fascicle traces (fig. 9). They are collateral bundles, but the xylem of the stamen fascicle traces is neither directed towards the centre of the flower, nor does it face the petal radii. It is directed towards a position in between, more or less perpendicular to the line which may be made up by the projection of the points of stamen insertion on the cross-section concerned. It follows that the stamen fascicle traces may be considered to be paired not only by their non-equidistant position but also by their anatomy. However, the triplets are not necessarily placed symmetrically to the alternisepalous radii, they rather show the deviations in position corresponding to the external conditions which were described above in relation with the contorted character of the androecium.

Downwards the stamen fascicle traces are mostly attached to the flanks of a main bundle in sepal radii, a right trace to a right flank, a left trace to a left flank (the stamen fascicle traces considered as antepetalous pairs). So the traces show a bending course between sepal radii and the bases of the organs they serve. When we follow this course upwards, the bend is to the right if the petals overlap with their left margins and to the left if the petals overlap with the right margins, from which it may be deduced that the shortest stamen fascicle trace goes to the advanced half of an antepetalous stamen group.

The petal trace or part of it may, besides with the sepal commissural marginal trace, also link with the nearest flank of a main bundle in sepal radii. Frequently a stamen fascicle trace has a double origin too. Often the petal trace and the stamen fascicle trace which bends farthest out of sepal radii have a common basal trace. They sometimes proceed along a sepal basal lateral for some distance forming a concentric bundle with it.

By means of the clearing techniques some variations can easily be traced, as for instance 1) a petal trace coming from an adjacent main bundle, 2) all stamen fascicle traces coming from the same flank of the main bundle, 3) the trace of the advanced stamen group coming from the median sepal trace higher up, from the sepal commissural marginal trace, or from a sepal basal lateral bundle.



Malope trifida. — Fig. 11. Staminal buttresses (80 ×). — Fig. 12. Young androecium with stamen primordia (80 ×).

Kitaibelia vitifolia. — Fig. 13. Full-grown flower, l.s. — Fig. 14. Young phase in androecium development, l.s. (40 ×). — Fig. 15. About the same phase, s.v. (80 ×). — Fig. 16. Phase with stamen primordia, s.v. (80 ×).

The fan-shaped major innervation of the petals is formed by a basal trifurcation of the petal trace and the subdivision of the basal laterals. Moreover, some abaxial parts of the stamen fascicle traces are attached to the proximal parts of the basal laterals (fig. 9).

In the proximal part of the stamen tube the stamen fascicle traces appear in cross-section as slightly bean-shaped bundles which are placed more or less at right angles to the surface of the petals (fig. 5). Upwards they become stretched radially by an increase in the number of more or less tangentially orientated vascular bundles (fig. 4, 6). Distally these combinations differentiate into vascular bundles which are split off in abaxial direction (figs. 6, 7). The separate traces move outwards gradually and split into two halves in the cortex or in the common base of the filament, remaining collateral and with the xylem directed towards a position intermediate between the centre of the flower and the petal radii. The traces to the lowest stamens are given off as the most abaxial portions of the stamen fascicle traces. They can often be followed to extend downwards as groups of vessels in the stamen fascicle trace which become free again and are attached to the petal basal lateral bundles. Sometimes the most abaxial parts of the stamen fascicle traces end blindly instead of going into a filament.

Other authors *

Eichler (1875) noted that in *Malope* the epipetalous rows are shifted more towards the sepals. See under *Kitaibelia* for further opinions.

Kitaibelia vitifolia

Some significant differences from *Malope trifida* will be treated here.

A cross-section of the receptacle is circular to slightly pentagonal, on the level of the calyx with the angles in petal radii, on the level of the pistil with the angles in sepal radii.

The margins of the navicular sepals are inserted higher on the receptacle than the median parts. Likewise the antepetalous regions of the petal-stamen tube are inserted higher than the antesepalous regions, the latter of which are also broader (fig. 13).

The corolla and the androecium are slightly contorted. The petals are almost symmetrical organs, often with a hardly oblique insertion, the overlapping lower side in front of the median sepal sectors.

The stamen tube ends in five antesepalous portions which fall apart into stamens, but sometimes in addition into a tiny and irregularly placed tooth-like protuberance. The ten rows of stamens are not equidistant but are rather arranged in five pairs on either side of the petal radii. However, in the distal regions of the tube the distance between the rows may vary somewhat, a relatively wide space in antesepalous regions remaining a constant feature. In case the contorted character is not marked the rows sometimes have an equal number of stamens which may then be placed in whorls. Reduced stamens on the antesepalous margins of the tube seldom occur.

The carpels are transversally situated in ten rows, the fusing styles pointing into antesepalous direction. Often normally placed carpels link the rows in sepal radii below and above in petal radii, thus forming a wave-line. The outward bends of this wave-line being antesepalous and the inward bends antepetalous, the location is exactly the reverse of that in *Malope trifida.*

Developmental phases

Figs. 15 and 16 show that, contrary to the condition in *Malope trifida*, the antesepalous grooves in a primordial stamen tube develop in advance of the antepetalous grooves.

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* The data on Malvaceae provided by Saunders can be found in her publications of 1936 and 1937. On the other families she gives data only in 1937.

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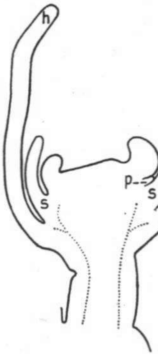

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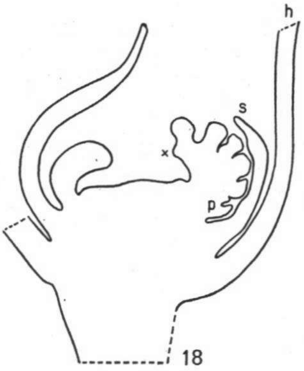

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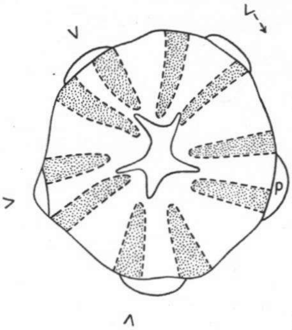

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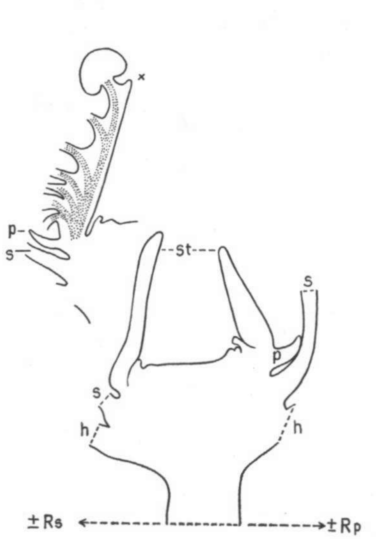

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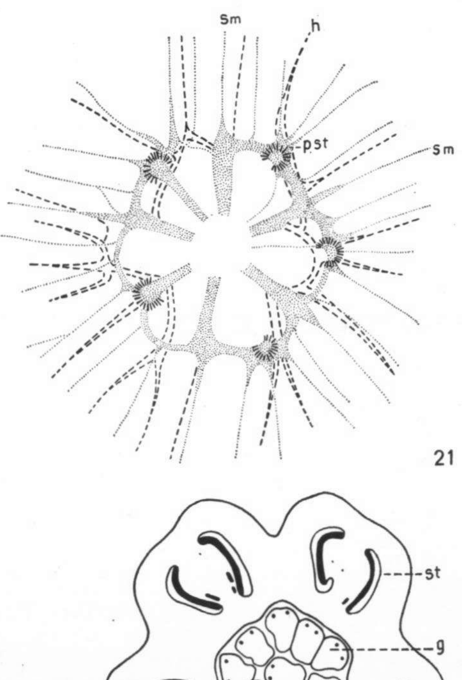

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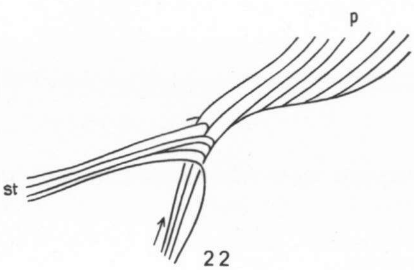

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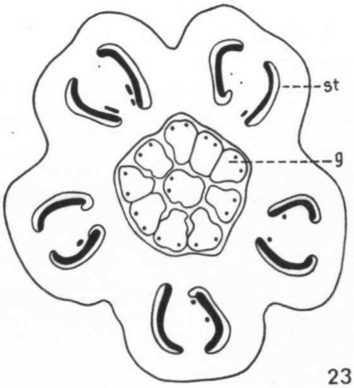

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Kitaibelia vitifolia. — Fig. 17. Phase in which the first stamen primordia start dividing, l.s. — Fig. 18. Older phase in which pollen sacs are formed, note sterile apex at ×. — Fig. 19. Same phase as in fig. 18, dotted regions show where stamens are placed, s.v. (Figs. 17, 18, 19. 20×). — Fig. 20. Young budding phase, sterile apex at ×, l.s. (10 ×). — Fig. 21. Course of vascular bundles. — Fig. 22. Connection of petal and stamen traces.

Abutilon darwinii. — Fig. 23. Base of the stamen tube, c.s. (25 ×).

Moreover, the antepetalous groove is not as wide and deep as in that species, the antesepalous groove on the other hand deeper and narrower. Later, when the stamen primordia originate, the antepetalous staminal buttresses are developed still stronger as compared to the antesepalous sterile regions (figs. 16 and 17). As a consequence the border between the primordial tube and the residual apex, given in fig. 16 by an interrupted line, is pentagonal with the angles in sepal radii. As it is in this phase that the very beginning of a gynoecial wall becomes evident along the margin of the apex, it follows that the outer carpel primordia will be situated in sepal radii.

Also in this phase, when the third stamen primordia appear in each row, the petals can be observed to arise under the wall in petal radii. They grow sidewards and outwards under the buttress which is situated more in front of the sepals. It should be added that observations on microtome slides seem to suggest that the petals are already initiated before any of the stamens. If this is true, the development of the petals lags behind from the start.

Whereas during early phases the buttresses develop rather strongly, later (fig. 18) the sterile parts between them grow markedly in height and width giving rise to the antesepalous, forward bulging, terminal portions of the tube (fig. 19). In adult flowers these sterile regions sink into insignificance beside the stamens (the beginning of this process is given in fig. 20).

Vascular bundle supply

Five main bundles leave the vascular cylinder of the flower base in sepal radii together with a variable number in petal radii. The sepal innervation is formed by trifurcation of the main traces in sepal radii and produces cross-arcs or sepal commissural marginal traces by the double traces of its marginal bundles (fig. 21).

The petal-stamen traces are normally orientated collateral bundles — c-shaped on cross-section — lying in petal radii, which are attached either to both flanks of the sepal commissural marginal traces or to the sepal basal laterals. They spread fan-like into the tube. On the level of petal separation the flank portions proceed into the stamen tube as two antepetalous stamen fascicle traces, whereas the bundles of the middle portion split serially into outward petal nerves and inward stamen traces. The lateral ones of these stamen traces join the stamen fascicle traces, the median ones, on the contrary, end blindly (fig. 22). So, as in *Malope*, the abaxial parts of the stamen fascicle traces are connected with the petal traces and the outermost parts do not serve stamens. The last feature is more clear in *Kitaibelia vitifolia.*

In the half-anthers the single vascular bundle often splits into two prominent, bending side branches. From the base of each side branch a tiny bundle may go upwards or a tiny bundle may arise from the point of splitting.

Other authors

Payer (1857) already observed that the apex on which the carpels will develop has five corners in petal radii in *Malope* but in sepal radii in *Kitaibelia.* However, he mixed up these observations in the text, as remarked by Dickson (1864). Also Duchartre (1845) was aware of the difference. Saunders (1936), on the ground of mature structure, saw the correlation between episepalous part of stamen tube thick and lower epipetalous ovaries in *Malope,* epipetalous part of stamen tube thick and lower episepalous ovaries in *Kitaibelia* respectively. It is this correlation which is here made understandable by ontogenetic observations. Saunders noted the petal-stamen trace in *Kitaibelia,* the flanks of which give the stamen fascicle traces.

Goethart (1890) presented an ample description of the ontogeny in *Kitaibelia,* which may be summarized here as follows. Within the calyx an obtuse pentagonal margin arises on the apex, the alternisepalous corners of which are more protruded than the intermediate regions. These '*Staminalpodien*' become 2-lobed and on either side of a radial groove two halves grow upwards and outwards. The stamen primordia arise on them in centrifugal direction, the apical parts remaining sterile. They come to lie in two rows which are slightly shifted out of petal radii. The base of the primordia is elliptic and orientated obliquely towards the median of the petals. They are split, except the basal ones that give an anther with two pollen sacs. The petals are initiated by periclinal walls before the stamen primordia, but their later growth is retarded.

2) MALVEAE: $S(5)n-(P5-St5/\infty)-C(2/\infty)$
  2a) ABUTILINAE
    Abutilon darwinii Hook. *f.*
    A. megapotamicum St. Hil. & Naud.
    A. indicum Sweet.
    Sphaeralcea umbellata G. Don
    Modiola caroliniana G. Don
    Kydia calycina Roxb.

  2b) MALVINAE
    Althaea rosea Cav.
    A. officinalis L.
    Lavatera trimestris L.
    L. olbia L.
    L. cretica L.
    Malva sylvestris L.
    M. neglecta Wallr.
    M. crispa L.
    M. alcea L.
    M. moschata L.
    Sidalcea malvaeflora A. Gray
    S. candida A. Gray
    Napaea dioica L.
    Malvastrum capense Garcke

  2c) SIDINAE
    Plagianthus betulinus A. Cunn.
    P. pulchellus A. Gray
    P. divaricatus Forst.
    P. glomeratus Benth.
    Sida elliotti Torr. & Gray
    S. triloba Cav.
    S. rhombifolia L.
    Anoda lavateroides Medic.
    Hoheria populnea A. Cunn.

Abutilon darwinii

The calyx tube is in cross-section slightly pentagonal with the angles in sepal radii. Its inner base is covered with an annular field of nectariferous trichomes.

The petal-stamen tube is circular at its base, epibasally its inner outline is pentagonal with the angles in sepal radii, whereas the form of the peripheral outline varies according to the oblique attachment of the contorted petals. This attachment is not symmetrical to the alternisepalous radii, it is high in petal radii and low towards a left or right adjoining sepal radius as the petals overlap by their left or right margins respectively.

Immediately below its stamens the tube is broad, to narrow again upwards as more stamens diverge. It is longitudinally grooved by five deep grooves and five alternating shallow grooves by which (fig. 23) ten rows of 15—20 stamens are separated. The rows are situated between sepal and petal radii, those in front of the overlapping petal halves slightly more towards sepal radii, those in front of the overlapped petal margins more towards the petal radii. The former count some more stamens than the latter and extend further downwards. The tube terminates into five free upper parts which are the prolongations of the antepetalous tube parts separated by the deep grooves (fig. 25). Except distally, the rows of stamens are not formed by single forked stamens, but by a series of two forked stamens side by side. The structure of the stamens is like that in *Malope*.

Eight to thirteen locules constitute the pistil; if there are ten they are placed between sepal and petal radii. The outline of the pistil conforms to the perianth on each level, and, where the pistil is free, is as many-angled as there are locules.

Developmental phases

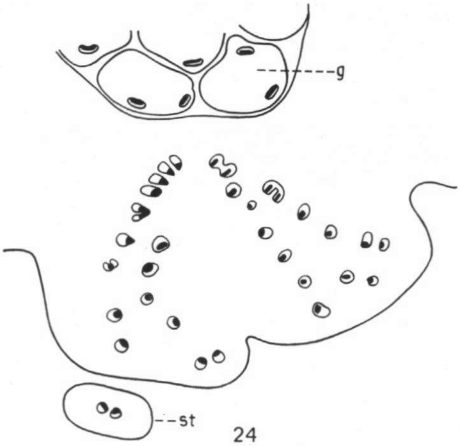
The hemispheric apex which appears within the young calyx becomes flat and slightly pentagonal with the angles in petal radii. A peripheral wall and a central depression arise on it. On the wall five alternisepalous parts begin to develop upwards as staminal buttresses, separated by five grooves in sepal radii, which are narrow centrally and wide peripherally. During further development very narrow and superficial grooves originate in petal radii, which divide the alternisepalous parts in two half-buttresses. Because of the prominent development of the buttresses, especially its bulging inwards, the inner side of the primordial tube becomes pentagonal with the angles in sepal radii.

On the half-buttresses the stamen primordia arise in centrifugal direction on either side of the median groove, the first four or so on the inwards inclining slope. From the summit towards the peripheral base, where the buttresses become increasingly broader, an additional lateral row of stamen primordia appears on either side of the median rows, which also develops in centrifugal direction (fig. 26). Possibly there are even some primordia of third rows appearing sometimes near the perianth. These lateral primordia do not originate by a division that is externally visible, but arise on the buttresses separately although mostly juxtaposed to the primordia of the median rows. On their summit where the buttresses begin to become broader, small lateral primordia may be present which do not grow further. During the division of these primordia, which is a process proceeding in centrifugal direction, 1) the innermost primordia split serially or may remain unsplit, giving anthers with three or four pollen sacs, 2) the innermost lateral primordia split later than the median ones, 3) the median primordia approaching the petals may be later in development than the lateral primordia. The plane and speed of the division itself would seem to depend on spatial conditions. All other lateral primordia develop later than the median ones, and accordingly in adult flowers the lateral stamens may be somewhat smaller.

In the very beginning the wall of primordial carpels is circular or very slightly pentagonal with the angles in sepal radii.

Vascular bundle supply

In the base of the receptacle five stelar parts bend outwards at almost right angles. The median parts of these main bundles are the sepal traces which, by trifurcation, form the sepal median bundle and two sepal basal lateral traces. The outside sepal lateral



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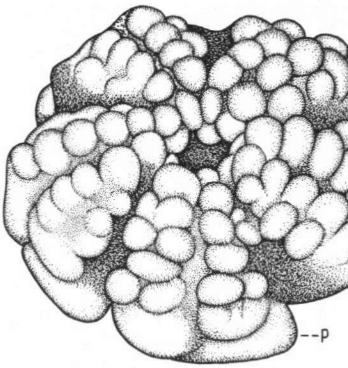

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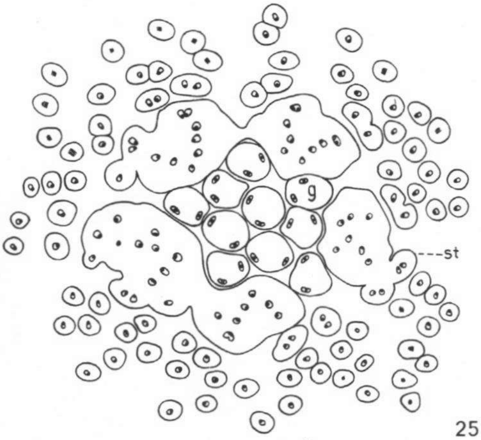

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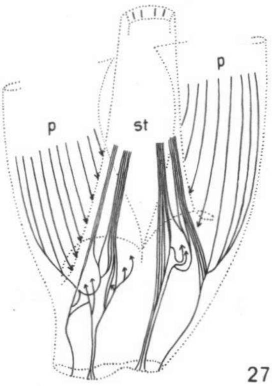

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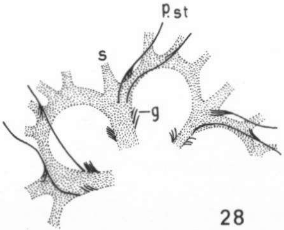

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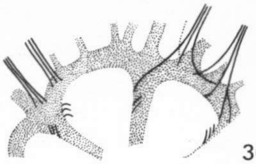

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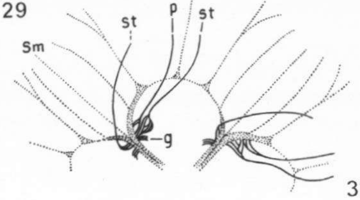

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Abutilon darwinii. — Fig. 24. Proximal stamen bearing region of the tube, c.s. (35 ×). — Fig. 25. Distal region of stamen tube, c.s. (20 ×). — Fig. 26. Development of stamen primordia. (80 ×). — Fig. 27. Ramification of petal stamen fascicle traces. — Figs. 28—30. Attachment of petal stamen to sepal supply.

Abutilon megapotamicum. — Fig. 31. Attachment of petal stamen traces to sepal supply. — Fig. 32. Attachment of petal traces. — Fig. 33. A stamen fascicle trace.

nerves form a cross-arcs system by means of their double attachment to the basal lateral traces of two adjoining sepals. The sepal laterals give off many side-nerves which supply the nectary field.

Proximal flank parts of the main bundles continue the vascular system upwards supplying the pistil.

More peripherally to the flanks of a main bundle two traces are attached which show a course bending from sepal towards petal radii, to the right if the petals overlap with their left margins and to the left if the petals do so with their right margins. One of these petal-stamen traces runs to a petal radius, the other does not fully arrive in this radius. Where they cross the sepal basal lateral traces small connections with these bundles may be present. In other cases the whole origin of the traces lies at the sepal basal laterals in a fasciculate manner (figs. 28—30). In the petal-stamen tube both petal-stamen traces split irregularly into the petal nerves and two stamen fascicle traces (fig. 27), the one situated close to the petal radius giving the bulk of the petal nerves. Some petal nerves join both traces by means of a double origin.

The stamen fascicle traces spread into the stamen tube forming (as viewed in cross-section) five pairs of bean-shaped vascular combinations, the xylem facing petal radii (fig. 23). However, towards the fertile region each combination changes through segregation and splitting of its constituting parts into two juxtaposed rows of vascular bundles. The xylem of both rows faces the petal radii. An exception should be made for the adaxial parts of the combinations which only separate into a single row of stamen traces (corresponding with the external situation explained above). Often the stamen traces of two juxtaposed rows lie in pairs. They move outwards immediately, at the same time splitting collaterally into two half-anther traces (the central ones serially, others diagonally) mostly while still in the tube (figs. 24, 25).

Abutilon megapotamicum

Six to nine stamens stand in single rows, no lateral rows being present. The pistil have five antesepalous cells.

Petal and stamen fascicle traces come from the sepal traces separately and by way of a fasciculate base (fig. 31). The petal trace gives only a few median petal nerves. The laterals are attached to the stamen fascicle traces, but first move downwards for a certain distance into the direction of the petal trace before bending towards the stamen-fascicle trace. The most median of these petal laterals even may have a 'reluctant' second trace towards the petal trace in the form of a bundle with interrupted xylem (fig. 32). Some middle and some basal stamen traces may join the stamen fascicle trace by common traces (fig. 33).

Abutilon indicum

A very short stamen tube consists of five diverging antepetalous groups of stamens. Each group is composed of two rows of two to five stamens, those near sepal radii having the higher number. Basal stamens often do not split, their anthers containing three or four pollen sacs.

Other authors on various Abutilon spp.

Saunders mentioned the presence in *A. avicennae* of five annular vascular cordons above the level of departure of sepal traces, which, higher up, separate into outward petal-stamen strands and various inward pistil traces.

Van Tieghem (1875) noted in *A. pictum* that by fusion of the flanks of adjoining sepal bundles five annular vascular systems originate in petal radii, which, higher up, divide into an outer arc and an inner residual stelar part. In the petal-stamen tube the outer arcs split into five pairs of alternisepalous bundles in one whorl. Each of these paired bundles gives off petal traces outwards. Accordingly the stamen tube shows five pairs of epipetalous bundles, from which successive stamen traces are detached serially, entering into ten rays of unilocular stamens arranged in pairs in front of the petals.

Sphaeralcea umbellata

The calyx is campanulate and five-sided, the edges are in petal radii where they are inserted somewhat lower than the sides. The stamen tube is pentagonal with the angles in petal radii on the outside and in sepal radii on the inside, or, in other words, the alternisepalous parts of the stamen tube are thickest and inserted lower. The pistil containing about 50 cells is almost circular.

Two longitudinal antepetalous rows of split stamens are placed along each edge of the distal parts of the long stamen tube. The tube tapers upwards and is slightly indented apically between two rows of stamens in line with the edges. There the lateral distance between two rows of adjoining antepetalous pairs is reduced (the filaments may even be fused superficially) by the fact that the higher stamens are inserted more and more towards sepal radii. On the other hand the lower stamens are successively placed farther towards petal radii, so that together the stamens occupy a wave-line.

A row is formed by 8—11 stamens, the basal ones of which are sometimes staminodial. In accordance with the contorted conditions the rows that are situated more in petal radii, in front of the overlapping part of the petal, count more stamens than the other rows.

Developmental phases

The peripheral region of the floral apex within the young calyx gives rise to a wall which forms ten staminal buttresses by means of the upward growth of parts situated more or less in alternisepalous angles followed by parts situated between sepal and petal radii to the left or to the right as petal margins overlap to the right or to the left. The position of the buttresses is diagonal, being directed inwards toward the sepal radii and outwards towards petal radii. They are separated by very deep alternisepalous radial grooves (fig. 34). However, they are also separated by antesepalous very shallow sterile regions of the tube which widen outwards. In fact, it seems appropriate to speak of antesepalous buttresses which are fertile along the margins and separated by deep radial grooves.

The places whereupon the stamen primordia develop centrifugally, are low on the inner and outer borders, and high in the middle parts. The stamen primordia first formed arise on the inner slopes and may be somewhat slow in developing further. The later stamen primordia of the rows that are initiated more between sepal and petal radii, develop into the direction of the petal radii by a bending course. As development proceeds the antepetalous regions outsize the sterile antesepalous ones, the difference in depth between the grooves diminishing (figs. 35, 36). The antepetalous indentation and the antesepalous lobing of the tube margin becomes evident.

If the stamen primordia begin with the formation of the thecae (the apical ones coming behind), the petal ridges arise tangentially below the last-formed stamen primordia. It follows from fig. 35 that the primordia become elliptic with the long axes at approximately right angles to those of the buttresses (the margins of the antesepalous trapezoid primordia). Later the direction becomes parallel to the sepal surface, as usual.

Supply of vascular bundles

Five main bundles bend outwards in the receptacle, the peripheral parts of which produce sepal median and basal lateral bundles by a proximal trifurcation. The basal laterals give off laterals, but the outside laterals form cross-arcs by their double origin at two adjoining basal laterals.

The flanks of the main bundles bend outwards less markedly and both reach antepetalous regions by an oblique course. If the petals overlap to the left, a left flank produces the left stamen fascicle trace, the right flank the right stamen fascicle trace and the petal trace. However, part of the petal trace and the right stamen fascicle trace may be connected with the top of the cross-arcs.

Upwards in the petal-stamen tube the traces form a number of bundles, spreading tangentially, the laterals of which form the stamen fascicle traces, the middle ones the petal nerves. However, on this level also a connection exists between part of the stamen fascicle trace and a petal trace.

In the base of the stamen tube two stamen fascicle traces meet laterally and form an antepetalous vascular combination which is semi-circular in cross-section, and faces the centre of the flower. Upwards, this combination falls apart, starting with the abaxial and finishing with the adaxial parts.

Modiola caroliniana

Upon the rim of a small tube some more than ten stamens are placed, one or two in front of the overlapping petal halves and one in front of the other petal half. The one in front of the overlapped petal half and the lower one of the other row are mostly developed badly, sometimes with two collateral pollen sacs, or they are absent. The upper stamen of the advanced row is often unsplit, showing four pollen sacs. Sometimes also stamens with three pollen sacs are present.

The developmental stages are very minute, very much contorted, and moreover irregular. The primordia are not placed terminally on the young tube but along the margins of antesepalous lobes.

The vascular bundle course in the receptacle is very much like that in *Malope trifida.*

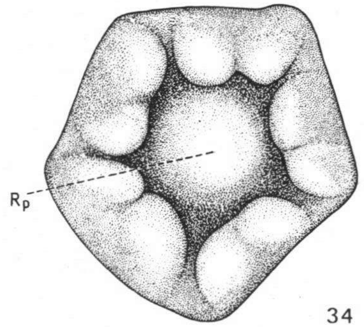
Kydia calycina

The aestivation of the corolla may be contorted, cochlear, or quincuncial. The stamen tube terminates in five free arms alternating with the petals. One to four almost sessile half-anthers are placed one above the other in two rows along the abaxial side of the margins near the apex of the arms.

Five alternisepalous petal-stamen traces are either attached to the epicalyx or calyx innervation or come from the stele directly. They spread tangentially into the petal-stamen tube, the flanks proceeding as the stamen fascicle traces, the middle parts as the petal nerves. Two stamen fascicle traces coming from two adjoining petal-stamen traces go into one alternipetalous arm, and, higher up, fall apart into furcating stamen traces.

Althaea rosea

The stamen tube is pentagonal with the angles in petal radii except inside at the base, where it is circular to slightly pentagonal with angles in sepal radii. Just above the petal level the tube is provided with an annular ridge. Along the edges of the upper half 9—20 stamens are inserted one above the other in two rows, though subapically they may be placed in pairs side by side (in one flower of *Abutilon indicum* two young stamens occurred side by side on the summit of the staminal buttress). About five lowermost stamens may be placed more or less between the rows and bear anthers in various in-



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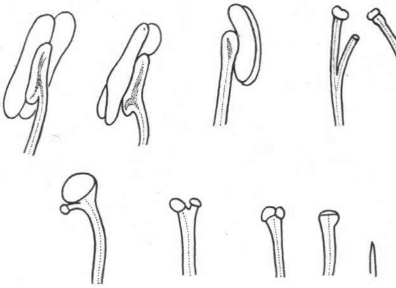

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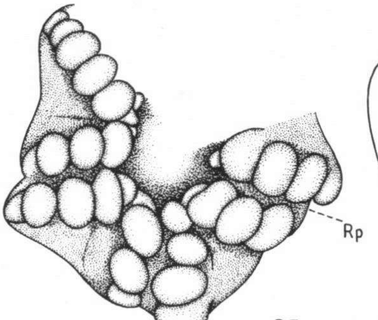

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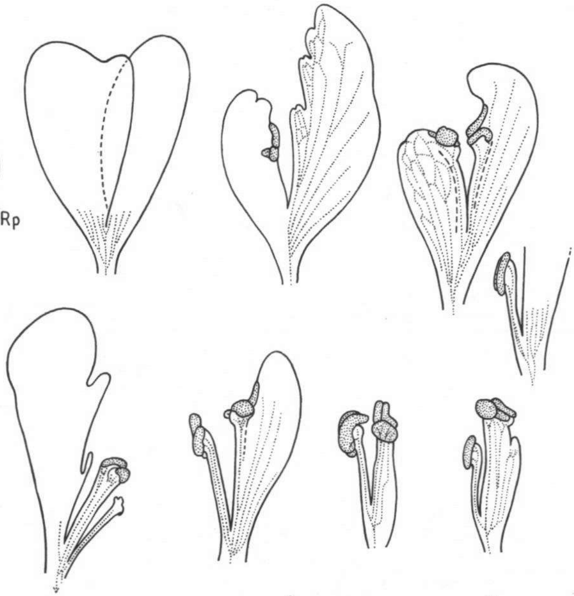

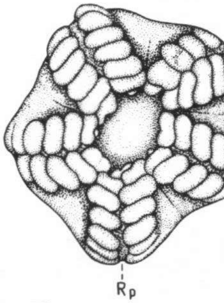

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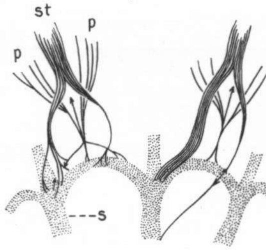

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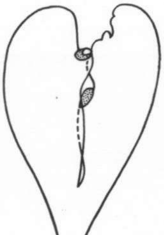

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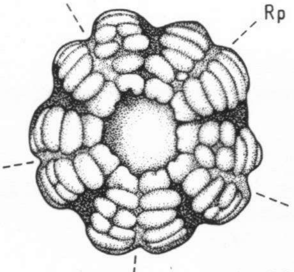

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Sphaeralcea umbellata. — Figs. 34—36. Successively older phases in androecium development. (Figs. 34, 35. 80 ×; fig. 36. 40 ×).

Althaea rosea. — Fig. 37. Stamens and staminodes. — Fig. 38. Attachment of petal and stamen fascicle traces at sepal supply. — Fig. 39. Young phase in androecium development, s.v. (40 ×).

Double Althaea rosea. — Fig. 40. Petaloid stamens.

completely developed stages (the androecium consists of five antepetalous vertically elongate horseshoe stamen combinations). The rim of the tube is slightly indented in petal radii. The petals and androecium show only slightly contorted characters.

The anthers are asymmetrically reniform (fig. 37); in the lowermost stamens they consist of small, often bilobed, sacs. If here the division fails to develop, the top of the filament may be somewhat swollen (fig. 37). Ultimately the basal stamens are represented by hairy subulate structures.

Developmental phases

On a peripheral wall, developing on the border between the young calyx and the floral apex, five staminal buttresses arise in the alternisepalous angles. The buttresses become separated by outwards widening grooves in sepal radii; they are narrow and low on the inside and outside, high and broader in their middle parts. The first of the centrifugally arising stamen primordia come to lie in two rows on the inner slope of the buttresses, the next subapical ones frequently in pairs on the broad summit (fig. 39 gives a very regular primordium). If paired primordia occur, the lateral ones arise later, as in *Abutilon*. As the primordia originate a radial small groove extends over the surface of the buttress in centrifugal direction, separating the two rows.

As the antesepalous parts of the primordial tube do not at first develop so strongly, the inner outline of the tube is pentagonal with angles in sepal radii and the pistil is shaped accordingly. However, later, the antesepalous sectors develop considerably in height, so that the young tube appears to be divided terminally into five antesepalous lobules (cf. *Kitaibelia*).

The petals become visible relatively late, at a time when the stamen primordia start forming the thecae. The pistil develops still later.

Vascular bundle supply

Five portions leave the stele in the flower base, the middle parts of which form the sepal innervation. The sepal lateral traces by their double bases form a cross-arcs system, to which the fasciculate base of the petal trace is attached. Both stamen fascicle traces which in the petal-stamen tube are situated on either side of each petal trace, are attached to the flanks of a main bundle in sepal radii by a fasciculate or attenuate base, and accordingly have an oblique proximal course (fig. 38). Especially those in front of the overlapping petal halves may have a marked fasciculate base. At the level of the petal insertion there is no further connection of parts of a stamen fascicle trace with petal traces.

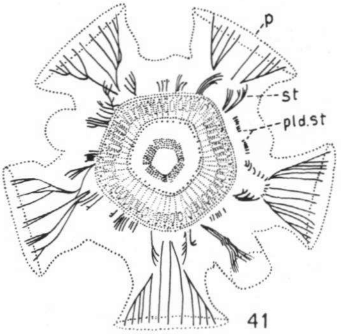
The stamen fascicle traces meet in petal radii by spreading outwards, to form in the base of the tube an in cross-section c-shaped collateral bundle with the xylem directed inwards. The middle parts of these vascular combinations give off bundles with interrupted xylem into the less developed lowermost stamens, whereas the flank parts gradually fall apart into stamen traces, which move outwards towards the successive higher stamens. In the connectives there is a distinct but irregular spreading of the vascular tissue.

The annular ridge described above does not receive any bundles.

Althaea officinalis

The flowers are smaller, the stamen tube and the pistil are both pentagonal with the angles in petal radii. Only two or three stamens are present in each row, more concentrated distally, often unsplit and then bearing 4 pollen sacs, or almost unsplit. The contorted characters are marked.

To a sepal trace often a strand is attached which runs upwards into the tube in sepal radii and ends blindly apically. Sometimes stamen traces are attached to the traces towards epicalyx members.



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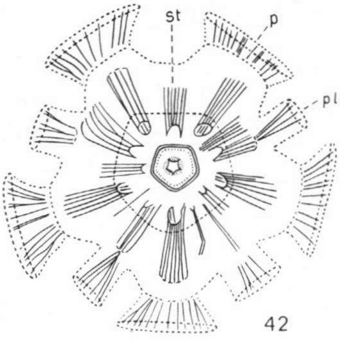

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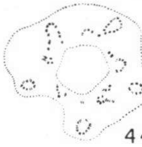

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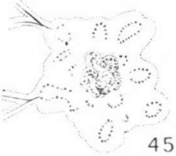

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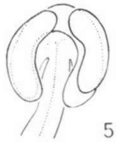

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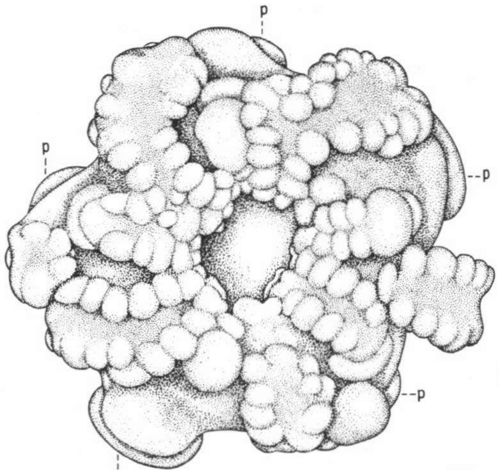

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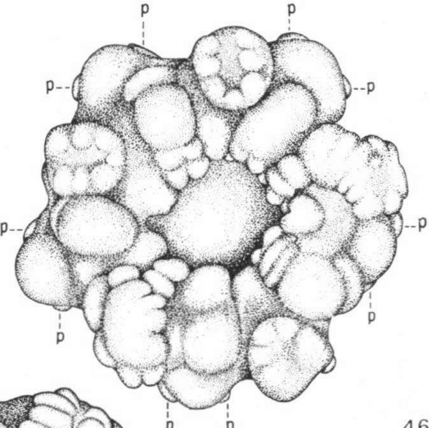

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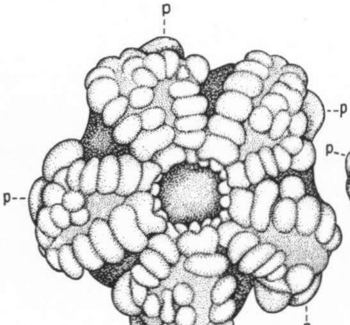

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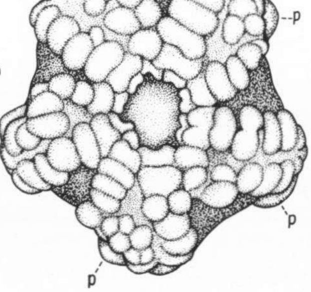

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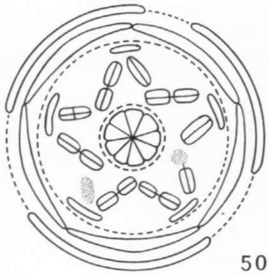

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Double Althaea rosea. — Figs. 41—42. Vascular bundle supply in two successive cleared c.s. of the same flower in which additional stamen groups take part in the tube formation. — Figs. 43—45. Tube of such flowers, c.s. — Figs. 46—49. Primordial phases of double flowers (40 ×).

Lavatera cretica. — Fig. 50. Flower diagram. — Fig. 51. Anther with three pollen sacs.

Other authors on, chiefly, Althaea rosea

According to Duchartre ten staminal primordia originate in five alternisepalous pairs, and many primordia develop later on. The lateral distance between the pairs is smallest inwards so that there the primordia are shifted irregularly by lack of space.

Sachs (1874) and Eichler (1875) also mentioned twelve more or less split stamens in two vertical collateral rows in front of each petal.

Goebel (1886) saw five epipetalous hemispheric primordia with a shallow median longitudinal groove. The first staminal primordia take only about one tenth of the entire size of a primordial half.

Goethart observed that a double splitting results in four juxtaposed two-celled anthers. In *A. cannabina* five sterile antesepalous big teeth are present in line with the major rows, sometimes flanked by small teeth terminating the minor rows of stamens. In *A. narbonnensis* the first stamens occur on triangular alternipetalous primordia, either on the summit or close to it on either side and then leaving a small antesepalous tooth which may not belong to the staminal buttresses.

Double Althaea rosea

In all double flowers epicalyx, calyx, and five petals are present as they are in single flowers.

Some stamens are petaloid

The petaloids are preferably situated along the outer margin of the middle parts of the antepetalous horseshoe combinations of stamens, which in that region may count two or three members next to one another in each row.

We meet all transitions between a normal stamen and an entirely sterile bipartite petaloid (fig. 40). The filament or one of its forks can be foliarized exclusively. It is remarkable that the inner margins of the bipartite petaloids may show a series of teeth, as if they represented a double row of stamens (fig. 40).

Each of the petaloids receives a vascular bundle as a side-branch of the stamen fascicle trace. As in a petal, this bundle ramifies fan-shaped by basal dichotomies and forms many anastomoses (not all given in fig. 40).

The primordia which arise laterally on the high middle portions of the alternisepalous staminal buttresses can be observed to grow further as petaloids.

Additional groups as parts of the stamen tube

Antesepalous groups of stamens may be present on top of the tube, higher and more inwards than the usual groups, each usually in the axil of their own smaller and higher placed petal. The innervation toward these groups is the same as that of the normal groups (figs. 41—45). It is noteworthy that the gynoecium which normally is pentagonal with the angles in sepal radii, now has its angles in petal radii.

Often these groups, or their halves, are not placed exactly alternipetalous, but more in front of the overlapped petal parts, where they may even be connected with the normal groups, also as regards the vascular supply.

When the groups lack a private petal, some petaloids may be present in the group abaxially or an abaxial median part becomes separate in the form of a small number of stamens, above which the vascular bundles of the flank parts unite. Other sterile or partly fertile petaloids may occur among the stamens of these groups.

Free additional stamen groups and absence of tube formation

There are flowers with more than five (for instance 14) large sterile petaloids above the level of the normal petals. These petaloids surround the bases of some (say eight) small groups of normal or petaloid stamens, which are placed on short elongate axes.

Moreover, a tube may be absent. It appears very difficult to unravel the mass of organs presented by these flowers and to detect any system in it, especially so because there are no two flowers exactly alike. However, it is possible to study the developmental stages near the apex of the inflorescences which bear these flower at the base. Then it immediately appears that small negligible protuberances present in the full-grown flowers are equivalent to whole stamen groups which do not grow out. Two of these phases are illustrated in figures 46 and 47.

Fig. 46 represents a case in which one can easily discern three or even four almost strictly alternating whorls of five stamen groups. The second whorl which is antesepalous, is developing in advance of the others, whereas the peripheral and inner groups develop slowly or may not develop any further. It seems that development within each group is centrifugal and stamen primordia are formed along the margin of more or less radially elongate buttresses. All groups, except two of the third whorl and those of the inner whorls, are provided with abaxial large petaloid primordia, the outermost groups with the normal petals.

Fig. 47, representing a somewhat later stage, illustrates striking contorted combinations of the groups distinguished above, as if they were arranged along parastichies. The petaloids of the composing groups may flank the combinations.

Floral primordia consisting of similar combinations which more and more resemble the normal conditions occur frequently. In figs. 48 and 49 two such phases are given. In the first figure the combined nature of one half of each row is still evident from the position of the stamens as well as from the constant presence of a lateral small petaloid. In the second figure these petaloids are absent or feebly developed and furthermore there are less supernumerary stamens. In fact these primordia may grow further into flowers which were described above to possess antesepalous groups approaching the antepetalous ones.

It should be noted that the size of the primordia increases with the degree of doubleness.

Other authors

Goebel said that the outside primordia of two epipetalous double rows of monothecous anthers may become petaloid, whereas the inner primordia may split further into small stamens, petaloids, or intermediate structures. Sometimes there may be later primordia between the two original rows. The stamen primordia may also change into petaloids without division.

Lavatera spp.

The calyx is campanulate, in cross-section pentagonal with the angles in petal radii. The corolla is contorted, the petals frequently inserted too much to the left or right of petal radii when overlapping by their right or left margins respectively. However, in *L. cretica* the aestivation of the corolla is variable.

The stamen tube may be more or less spirally twisted, the torsion lines going upwards to the left or to the right, as the petals overlap by their right or left margins respectively.

Along the upper half of the tube the stamens are inserted in ten rows, which are more or less equidistant halfway up, but above placed closer to sepal, below to petal radii. The rows in front of the overlapping petal halves have more stamens — for instance 4 instead of 3 — the lowermost of which may occur in a reduced form, unsplit with 2 pollen sacs. The three stamens of the minor rows are inserted at levels between the four stamens, and a formation of whorls may result especially among the middle stamens of different rows because they are situated on the same level. Either above the minor row only or above both rows the tube may extend upwards by a sterile part unlobed.

The exact position of the rows is not symmetrical to sepal and petal radii, but deviates somewhat according to the contort characters.

In *L. cretica* 10 or fewer stamens are placed apically or subapically on a short tube. In front of the overlapping petal half one or sometimes two more or less perfectly serially split stamens may be present, in front of the other petal half there may be either an unsplit stamen with 2, 3, or 4 pollen sacs or no stamen at all (figs. 50 and 51).

Developmental phases

A pentagonal peripheral wall with alternisepalous angles arises on the floral apex within the young calyx tube. On this wall 10 radial grooves appear, the first five in sepal radii widening outwards, the next five in petal radii remaining narrow. As a result ten staminal elliptic buttresses are elevated, which centrally are situated between sepal and petal radii, peripherally more towards petal radii, together constituting a wave-line. It is only by further growth that the situation of the buttresses becomes asymmetrical.

The wave-line position may also be demonstrated by the diagonal orientation of the young stamens in *L. cretica*. In this species the buttresses are very low when stamen formation starts upon them. However, when later the sterile tube parts are beginning to grow out, the stamen primordia appear to be placed in the middle of the young tube, not on its rim or appressed to the perianth.

The petal primordia become visible after the first stamen primordia, at first under the rows between sepal and petal radii and later also somewhat lower under the other rows in petal radii.

Vascular bundle supply

Middle parts of five main bundles in sepal radii form the sepal trace which trifurcates into a sepal median bundle and two sepal basal lateral traces. Two basal laterals of adjoining sepals may join in petal radii forming cross-arcs by the double bases of their laterals.

The flanks of the main bundles run more inwards forming the petal-stamen traces. Moreover, if the petals for instance overlap with their left margins, the flanks run to the right, the left flank giving off the left stamen fascicle trace, the right flank the right stamen fascicle trace and the petal trace. The right stamen fascicle trace may also be partly attached to the left side of an adjoining main bundle and the petal trace may be partly connected with the cross-arcs.

At the level of petal divergence some abaxial parts of the stamen fascicle traces may link up with the lateral petal traces. Conversely, some petal laterals may partly join the stamen fascicle traces. In addition, irregular nerves come from the proximal parts of other petal nerves to end blindly in the stamen tube.

In *L. cretica* some stamen traces end blindly up in the tube. It may happen that all petal laterals at one side are connected with the stamen fascicle trace.

Other authors

Payer pictured five epipetalous fields of centrifugally developing stamen primordia.

Duchartre described the ontogenesis for various *Lavatera* spp., as was given here under *Althaea*.

Malva spp.

The calyx tube is — in cross-section — circular to slightly pentagonal in the proximal regions with angles in the petal radii. The petals are usually contorted, sometimes imbricate, almost symmetric and inserted rather precisely in petal radii (if the petals overlap to the left, they may be inserted slightly to the right of petal radii and somewhat lower at the left side. The stamen tube is slightly pentagonal in petal radii and sometimes twisted.

The stamens are placed in ten more or less equidistant rows along the distal part of the tube, but in the proximal regions the rows are more antepetalous (in androecia with a higher number of stamens). There are two to five stamens in a row. The row in front of the overlapping petal half mostly has more stamens than the other row, and is inserted further downwards. The rows may reach equally high on the tube, but in flower buds it is evident that one of the rows may have a higher placed stamen whereas the other row may show a sterile prolongation instead. The apical and basal stamens are often unsplit and may have two, three, or four pollen sacs, which may be reduced (fig. 52). The stamens of two adjoining rows are not juxtaposed but are placed alternate like the links of a zipper. However, in a given row the stamens are on the same level as those in the rows next to the adjoining rows, with the result that all stamens taken together are placed in a number of alternating whorls of five stamens situated between sepal and petal radii. The number of whorls equals the total amount of stamens in two adjoining rows.

In *M. neglecta* two stamens are present in the rows, but in front of the overlapped petal half the basal stamen may be reduced or absent. In *M. crispa* ten or fewer stamens terminate the tube irregularly and bear mostly unsplit anthers with two, three, or four pollen sacs.

Developmental phases

Upon a peripheral wall, bordering the apex within the calyx primordium, alternisepalous elevations arise separated by antesepalous outwards widening sterile regions. While these elevations increase in size, stamen primordia become visible upon them in two rows at either side of a radial groove and in centrifugal direction. The first-formed primordia come to lie on the inner slope of the primordial wall, their further development is slower than that of the subapical primordia, which are placed on the summit of the young tube.

The petal primordia appear as tiny tangential ridges under the abaxial side of the staminal buttresses, when the upper stamen primordia start division by a radial groove and the outer primordia become visible. The petal ridges mostly show a slightly oblique orientation. Later they may extend somewhat more into the direction of their lower halves near petal radii. The pistil arises late.

Vascular bundle supply

Five or fewer unequal portions are given off by the vascular cylinder in the flower base more or less is sepal radii. The most lateral flank parts of these main bundles give the pistil vascular supply spreading inwards tangentially. The middle parts bend outwards as the sepal traces, which mostly trifurcate immediately into a sepal median and two sepal basal lateral bundles. The latter give off sepal laterals and produce cross-arcs or minor transverse connections. It should be stressed that the innervation towards the calyx is variable, especially in small flowers. As a consequence the attachment of the petal and stamen fascicle traces is equally variable.

The residual flank parts of the main bundles represent the bases of the petal and two lateral stamen fascicle traces (figs. 54, 55). The proximal part of the petal trace shows an oblique course and is attached by a multiple base to the flank of a main bundle and to one of the sepal basal laterals. A common bundle may be formed with this sepal basal lateral for some distance. This bundle has the xylem situated in a circle. One of the stamen fascicle traces may sometimes form part of this combination too. The other stamen fascicle traces which remain closer to the sepal radii, mostly have their origin on the other flank of the main bundle, or, by a multiple base, also on an adjoining main bundle.

If the main bundles happen to be situated more towards petal radii, the proximal course of the petal and stamen fascicle traces is hardly or not at all oblique.

Abaxial parts of the stamen fascicle traces link up with the petal basal laterals or they sometimes form partly lignified connections towards the petal innervation (fig. 53). Other traces, which are attached to more median petal laterals, end in the tube blindly. Sometimes the proximal parts of the petal basal laterals are reduced, the petal laterals then being all attached to the stamen fascicle traces. In *M. crispa* the petal trace and the stamen fascicle trace in front of the overlapped petal half run very close together or may form a common basal bundle. On the other hand, the second stamen fascicle trace may be independent (fig. 53).

In the normal half-anthers there may occur some irregular splitting of the single vascular bundles, in the basal and upper unsplit stamens the bundles in the anther may split unmistakably into two branches.

Other authors

Goebel investigated the development in *M. sylvestris* and *rotundifolia.* An apically depressed primordium forms five circular alternisepalous protuberances on its margin, separated by flat regions. Before the first stamen primordia arise it is possible to distinguish a minor and a major half of the protuberances by the appearance of an indistinct longitudinal groove. The major halves lie more toward the sepals. The first five stamen primordia arise on the major halves, the second five somewhat later and more outwards on the minor halves.

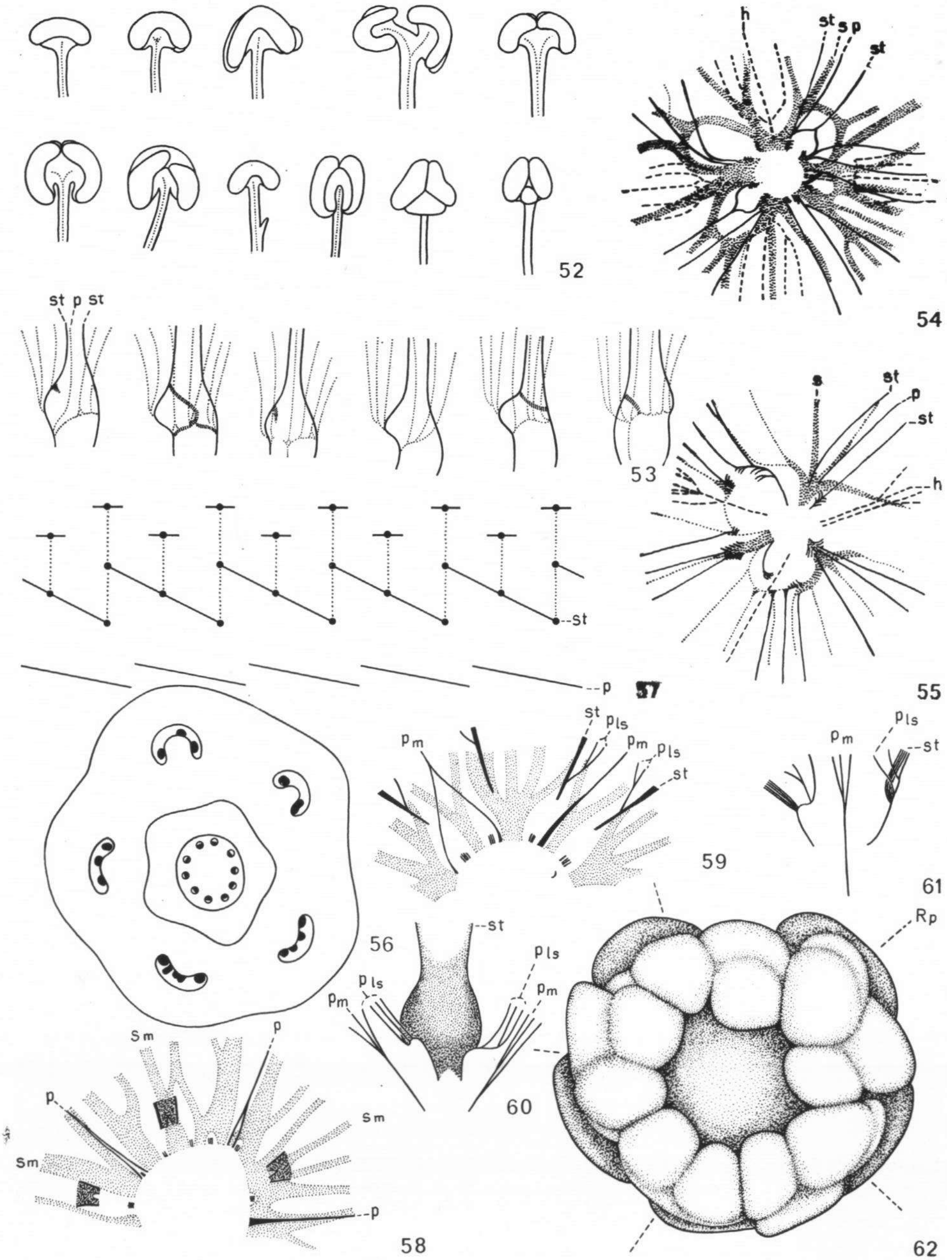
Both Frank (1876) and Goebel (1886) investigated flowers with 10 stamens of *M. crispa,* and neither of them succeeded to find epipetalous elevations which are divided by radial grooves. There are five pairs of primordia from the start and one member of each pair is earlier and bigger than the other. The second five may occur in a reduced state or be absent, a condition leading to that in *M. parviflora.* If flowers with five stamens are present, there are no protuberances which divide by radial grooves, but five primordia arise on a low annulus towards sepal radii. Goethart stated that varying culture conditions may change the number of stamens in *M. crispa* from five with anthers containing 2 pollen sacs to ten split anthers having 4 pollen sacs each.

Sidalcea spp.

The calyx is in cross-section pentagonal with the angles in sepal radii. The petal insertion does not deviate much from the petal radii. Proximal antepetalous parts of the tube are somewhat thicker than the alternate parts. Distally, where the stamens diverge, the tube is pentagonal in cross-section, below with the angles in line with the rows counting three stamens, above with the rows having two stamens. After dehiscence of the thecae the tube is twisted chiefly basally, the torsion lines going upwards for instance to the right, if the petals overlap to the left.

Along the distal part of the tube the stamens lie in ten equidistant rows, which are neither situated in sepal nor in petal radii. The rows in front of the overlapping petal halves consist of three, the alternate rows of two stamens. The total of 25 stamens is arranged in five alternating whorls of five stamens each, the basal, middle and upper whorls of which are formed by the rows with three stamens, the intermediate whorls by those with two stamens.

The forked filaments become shorter upwards, they are flattened and the forks are slightly fused laterally. In addition, in *S. candida* the filaments of the two basal antepetalous stamens are fused laterally. And in *S. malvaeflora* (fig. 57) the filaments of the middle stamens of the rows of three may join these proximal phalanges to the left or right of



Malva spec. div. — Fig. 52. Anther forms. *Malva crispa.* — Fig. 53. Connections between petal and stamen fascicle traces. *Malva alcea.* — Fig. 54. Diagram of vascular bundle supply. *Malva moschata.* — Fig. 55. ditto. *Sidalcea oregana.* — Fig. 56. Proximal region of stamen tube, c.s. (40 ×). — Fig. 57. Scheme of phalanges in the androecium.

Napaea dioica. — Figs. 58—59. Attachment of petal and stamen fascicle traces at sepal supply. — Figs. 60—61. Attachment of petal lateral traces at stamen fascicle traces. — Fig. 62. Primordial androecium (140 ×).

both basal antepetalous stamens as the petals overlap to the right or left respectively. As a result these broad proximal phalanges have the same contorted position as the petals.

Developmental phases

In very young phases ten elliptic primordial staminal buttresses arise on the border of the apex within the calyx. They are almost parallel and lie on either side of the petal radii, separated by outwards widening antesepalous grooves. However, five lie slightly more in petal radii, five more in sepal radii. Somewhat later the inside part of the buttresses near sepal radii extends more inwards and a first stamen primordium is developed (later the tube above has its edges more in petal radii). This primordium will give the upper stamen of a row with three stamens. These first formed stamen primordia remain somewhat smaller than those which originate next in centrifugal direction, among which are the stronger ones in the row near sepal radii (later the tube has its edges below nearer sepal radii).

The petal primordia are first visible under the minor rows, in petal radii, later under the major rows more in sepal radii and lower. The fusion between the filaments is formed late during ontogeny.

Vascular bundle supply

In the flower base the vascular cylinder falls apart into five portions near sepal radii. Their peripheral parts form the sepal traces, their central flank parts the pistil innervation, and their middle flank parts the petal-stamen supply, which accordingly needs an oblique proximal course to reach the proper radii (a course to the right, if the petals overlap to the left).

The sepal traces, by a trifurcation, each form a sepal median and two sepal basal lateral traces, the latter of which unite into a cross-arc system. From the top of the cross-arcs sepal commissural marginals diverge.

In the petal-stamen tube a petal trace comes to lie approximately in petal radii with two stamen fascicle traces on either side, one to the row with fewer stamens closer to the petal trace, the other more towards sepal radii.

The connection of these traces with the underlying vascular tissue is very variable. Generally the stamen fascicle traces of the larger rows are attached to the flanks of the nearest main bundles, but sometimes to the vascular cylinder deep in the receptacle or pedicel. The petal trace and the other stamen fascicle trace run along a sepal basal lateral towards the other flank of the main bundle, but they may have other multiple connections with the sepal basal lateral trace.

At the level of the petal insertion part of the lateral petal traces has a connection with the stamen fascicle traces, or may show a course into the direction of the petal median trace first but then suddenly, as if it were changing its mind, bends towards the stamen fascicle traces.

The stamen fascicle traces in the stamen tube above petal level spread tangentially and meet in petal radii in *S. candida* (fig. 56). Upwards they separate again before splitting into the stamen traces. Some of them which are situated more in petal radii end blindly.

There is not the least fusion of the vascular bundles of the filaments that compose the staminal phalanges.

Other authors

Eichler and Schoute (1936) both described the androecium as consisting of 1) five epipetalous lower contorted appendages which each bear four or more monothecous paired anthers, 2) a middle alternipetalous appendage of one pair of monothecous anthers, and 3) an upper epipetalous similar appendage. Both find the relation to the normal structure unclear.

Saunders said that the lower phalanges are mostly innervated only by both epipetalous stamen fascicle traces, whereas upper episepalous phalanges are formed by filaments of two rows of adjoining epipetalous groups.

According to Roush (1931), who made a monograph of *Sidalcea*, there would be 1) ten linear antesepalous diantheriferous phalanges, and 2) outer antepetalous phalanges which are either, in annuals, broad with about five anthers, or, in perennials, narrow bi- or trifid with two anthers. The species treated here are listed by her under perennials.

Napaea dioica

A. *Male flowers*

The cross-section of the calyx and the stamen tube is circular. The petals are asymmetrical, eared at the base, and inserted rather irregularly.

Ten rows of 1—3 stamens each are placed along the distal part of the stamen tube separated by variable distances, but often near the sepal radii. The rows in front of the overlapping petal halves count more stamens than the other rows. The basal stamens of the rows may be unsplit and bear two pollen sacs. The tube has no sterile prolongation The 6—11 cells of the pistil are very narrow.

Developmental phases

Along the periphery of the but slightly pentagonal apex, within the young calyx, a distinct circular wall arises, the upper rim of which becomes subdivided into ten staminal buttresses. These primordial elevations which are situated more or less between sepal and petal radii, sometimes appear to be paired because five more antesepalous, narrow, radial grooves separating the elevations are slightly deeper than the alternate ones (fig. 62). The buttresses, which, owing to the contorted characters, are placed more toward the sepal radii, produce more stamen primordia than the other rows and reach more inwards and outwards.

The successive petal primordia arise very early and grow out irregularly more or less in petal radii.

When the thecae are formed the young tube is provided with a distinct small sterile upper part with five antesepalous lobules. The pistil arises very late.

Vascular bundle supply

The vascular cylinder coming from the pedicel widens gradually into the receptacle and falls apart into an irregular number of branching sepal traces, among which a sepal median trace and a sepal commissural marginal trace may sometimes be distinguished, which give off sepal lateral bundles. Other traces give the pistil innervation, but often also petal median traces, though these traces may be connected by a double base to the side of sepal traces (figs. 58, 59).

The petal median traces only ramify into some petal middle bundles. The petal lateral traces of two adjoining petals, each together with a stamen fascicle trace, come downwards as far as halfway the petal-stamen tube and end there blindly (figs. 60, 61). Moreover during their proximal course they may be connected by non-lignified vascular tissue (fig. 60), the whole complex then showing a double base before it fades away.

B. *Female flowers*

The petals are much smaller and are not eared. The stamen tube is also small bearing a ring of reduced stamens on top. The cross-section of calyx and stamen tube is slightly pentagonal with the angles near petal radii. The pistil consists of broad cells.

Developmental phases

The apex within the young calyx is slightly pentagonal with the angles in petal radii.

A low wall arises along its periphery which is irregularly subdivided into stamen primordia. The development of the stamens does not pass beyond the stage of division in half-anthers.

Supply of vascular bundles

Sepal traces come from the stele in the flower base spreading into a sepal median and two sepal basal lateral traces. The sepal marginal bundles of two adjoining sepals have a common basal bundle, which links up with the top of a cross-arc. The cross-arcs are formed by the double bases of the sepal laterals and the commissural marginals which connect these bundles to the sepal basal laterals on either side. Both flanks of each main bundle spread inwards to give the pistil innervation, whereas one flank may give some tiny traces towards the petal-stamen system. These traces form a number of badly developed strands next to one another in the base of the petal-stamen tube, after having reached antepetalous regions by means of an oblique course. Ultimately a petal trace is separated with on either side a stamen fascicle trace, there being no further connection between these traces or their branches at the level of petal divergence. Sometimes only two traces are present in each flower sector, a stamen fascicle trace going to the major stamen group and a trace combining the petal trace and the stamen fascicle trace belonging to the row of stamens in front of the overlapped petal halves. This last stamen fascicle trace may be absent or end blindly upwards. On the other hand some reduced stamens may have bundles ending blindly downwards.

Malvastrum capense

Attention is drawn to some interesting features concerning the vascular supply of a petal and its two staminal rows in front.

Five main bundles enter the floral receptacle. The middle parts of them diverge outwards as the sepal traces. Two opposed flank portions proceed their course upwards and outwards, uniting into an inwards open u-shaped bundle and at the same time bending away from the sepal radii. The outer flank parts of this bending bundle spread inwards as the pistil innervation and the middle flank parts fall apart into the petal and stamen fascicle traces as usual. In this way the gap above the sepal trace is closed and a partial stele reconstituted.

At the level of petal divergence the stamen fascicle trace to the major staminal row, which lies more near sepal radii, may pass on without any connection with petal traces. However, some petal laterals may be attached to it now and then, as they are normally attached to the other stamen fascicle trace which is closer to the petal trace. The petal trace itself gives off petal laterals too (fig. 63).

Plagianthus spp.

Although the corolla is mostly contorted, it may be quincuncial in *P. betulinus*. The petals are inserted rather precisely in alternisepalous radii.

The number of stamens terminating the tube is small. In *P. pulchellus* each of the ten rows has two serially split stamens one above the other, the basals of which may bear only one half-anther. In *P. betulinus* ten serially split stamens are situated on the rim of the tube, some of which may have only two pollen sacs. Sometimes a stamen with two pollen sacs may occur below an upper one. In *P. divaricatus* a serially split stamen appears in front of the overlapping petal half, a stamen with two pollen sacs in front of the other half. *P. glomeratus* has five antepetalous split stamens, only now and then two side by side or one with two pollen sacs.

The number of pistil cells ranges from 1—5; if five in *P. glomeratus* they are antesepalous.

Vascular bundle supply

P. betulinus has ten main bundles in the base of the receptacle, which form the median sepal traces and the alternate sepal commissural marginal traces. However, fewer than ten main bundles often occur because 1) one of the main bundles branches proximally into a sepal median and a commissural marginal trace which by an oblique course reaches a petal radius, 2) the commissural marginal trace is by a double base attached to two adjoining sepal median traces. A third cause is at work in *P. sidoides* and *glomeratus* which both have only five main bundles. Here a main bundle may trifurcate into a sepal median and on either side two sepal commissural marginal traces. The various ways of vascular supply, including that of petals and stamens, are drawn in fig. 64.

The petal-stamen innervation is mostly attached to the underlying vascular structure by two basal traces, one of which divides into a petal trace and a staminal trace towards a minor row. The basal traces may be attached 1) to a main bundle in petal radii, 2) one to the main bundle in a sepal radius, the other to the sepal commissural marginal if such a trace is split off from the main bundle, 3) one to the main bundle in sepal radii, the other directly to the stele. In *P. sidoides* one basal trace may connect with a sepal commissural marginal in petal radii and trifurcate into a petal trace and two stamen traces on either side. In *P. glomeratus* (fig. 65), the species with five stamens, the stamen traces are attached to the proximal parts of the petal basal laterals. If two stamens are present in front of a petal they have a common bundle which by a double base is attached to both petal basal laterals. The petal trace has no lignified connection downwards, but ends blindly above the sepal commissural marginals in petal radii.

Other authors

Payer gave one figure without explanation.

Sida spp.

The stamens are placed in five pairs of antepetalous rows which consist each of one to three stamens. In *S. elliotti* mostly two stamens are present in each row, in *S. rhombifolia* one or two, in *S. triloba* one. The basal stamens of the advanced rows may be unsplit, retaining a double vascular bundle, or they are absent. These rows are situated more towards the sepal radii, in front of the overlapping petal halves. The tube may be indented terminally alternate to the petals.

The number of pistil cells in *S. elliotti* is about 10; if ten they are placed more or less in sepal and petal radii. In *S. rhombifolia* the number is five or more; if five they are about antesepalous.

Developmental phases

Above the calyx primordium a low wall arises along the border of the floral apex which is provided with five angles alternate with the sepals. On this wall sets of two elliptic staminal buttresses develop which are separated by antesepalous outwards widening grooves. One of the buttresses is higher than the other and placed more towards sepal radii. It is extended inwards where the first stamen primordia appear near sepal radii, almost meeting laterally. The following primordia arise in centrifugal direction.

The petals become visible under the staminal buttresses in a very early phase.

Vascular bundle supply

Five main bundles enter the receptacle and divide collaterally into a sepal median and a sepal commissural marginal trace, the latter of which runs obliquely towards the petal radii. However, often in *S. rhombifolia* and *S. triloba* and also now and then in *S. elliotti*, the sepal commissural marginals are formed by the union of two sepal basal laterals of adjoining sepals, giving cross-arcs.

From the proximal parts of the sepal commissural marginal traces sepal laterals are derived which form an anastomosing network of bundles. From this complex tiny bundles go towards the nectary tissue which almost entirely covers the inner calyx surface.

The flanks of the main bundles give the supply to the pistil and petal-stamen system, especially the flank on the side where the commissural marginals do not diverge. From this flank, and in *S. retusa* from the sepal basal lateral, a bundle is detached which, after having reached a petal radius, divides in a petal median trace and a second trace that ramifies into a stamen fascicle trace of a minor row and some petal lateral bundles. To the other flank or, by a multiple origin, to both flanks, another trace is attached which divides into the stamen fascicle trace of the major row and also into some petal laterals (not in *S. triloba*). This trace never fully reaches a petal radius.

Anoda lavateroides

In this species, as in the *Sida* spp., the mouth of the tube is indented alternate with five antepetalous pairs of stamen rows. The lateral distance between these pairs of rows is much larger than between the rows of one pair. The four or five stamens in each row are split collaterally or diagonally and are crowded on top of the tube.

Developmental phases

Above the calyx primordium the apex becomes flat and slightly pentagonal with the angles in petal radii. A central depression delimitates a peripheral wall, which is subdivided by deep radial outwards widening grooves occurring between sepal and petal radii into five protuberant parts. Subsequently, major halves of these protuberances near sepal radii become stretched radially inwards and outwards and a first stamen primordium arises on this half centrally, starting the major row of stamens. The second series of stamen primordia arises somewhat more outwards on the other half and starts the minor row of stamens close to the petal radii. By this alternating succession the development proceeds centrifugally, a shallow radial groove originating between the two rows (fig. 66).

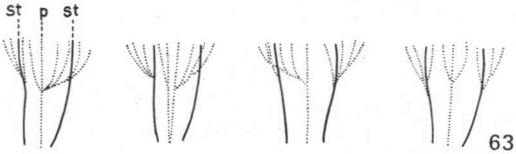
At the time the second stamen primordium appears, the very beginning of a petal becomes evident below the minor sides of the protuberances exactly in petal radii. If later the petal primordium grows sidewards it comes to lie obliquely and more to the outside below the major row, and inserted slightly to the right or left of petal radii if in a full-grown phase they overlap to the left or right respectively.

Supply of vascular bundles

The calyx innervation is formed by a trifurcation of the median outwards bending parts of five main receptacular bundles, giving a sepal median and two basal sepal lateral traces. From the sepal commissural marginal traces, formed by the meeting of two sepal basal lateral traces of adjoining sepals in petal radii, some bundles are detached proximally. They anastomose towards the sepal nectary fields.

The flanks of the main bundles and of one of the sepal basal laterals come together and form an adaxially open u-shaped bundle which bends into the direction of petal radii. Whereas the flanks of this bundle proceed towards the pistil, the middle parts form a petal trace and two stamen fascicle traces on either side, which all three go upwards into the petal-stamen tube. The petal trace and the stamen fascicle trace destined for the minor stamen row run close to each other near petal radii, the other fascicle trace is situated closer to the sepal radii on the side of the main bundles with which they are connected.

An abaxial part of the stamen fascicle traces may be attached to the petal basal lateral



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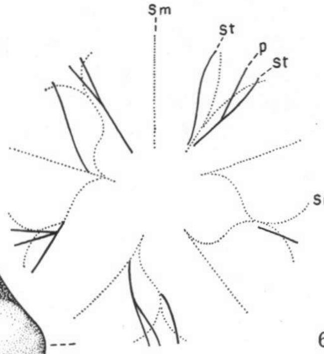

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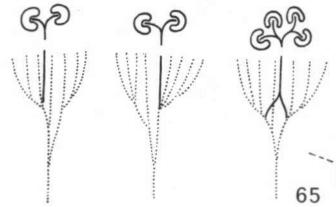

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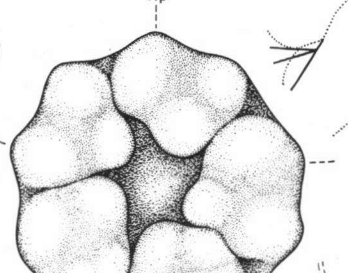

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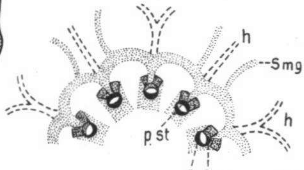

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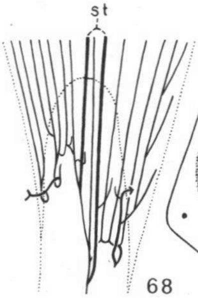

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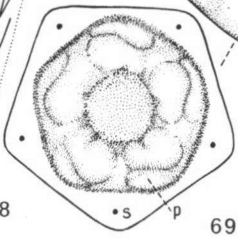

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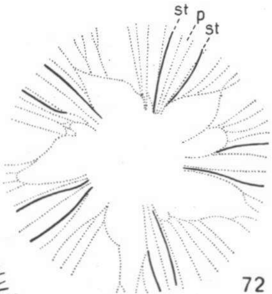

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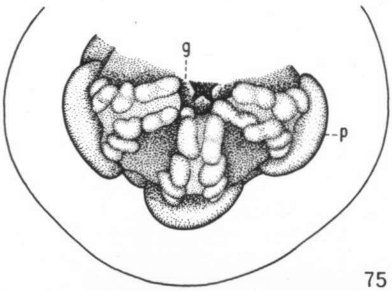

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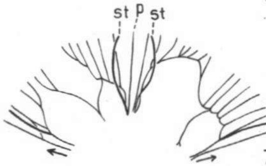

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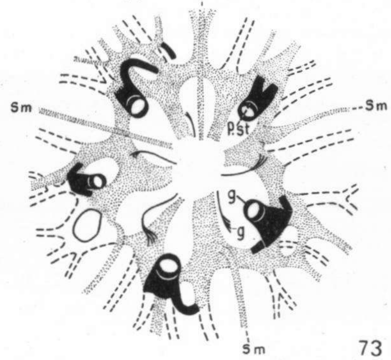

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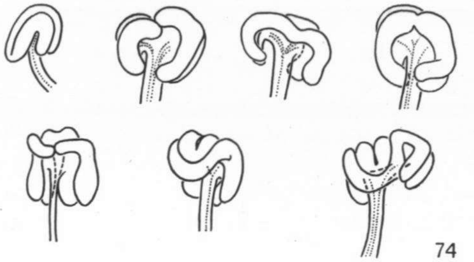


74

The explanation of these figures can be found at the bottom of the opposite page.

traces. The petal basal laterals of two adjoining petals may run into one another forming a ring which is moreover crossed by the stamen fascicle traces near sepal radii. Or stated otherwise, the outside petal laterals may be attached by double bases to the stamen fascicle traces of the major stamen groups and to the petal basal lateral traces.

Hoheria populnea

The antepetalous regions of the tube are thicker than the alternate regions above which the pistil cells are placed.

The short stamen tube is terminated by one stamen in front of the overlapped petal half and by one to three stamens above one another in front of the overlapping petal halves. The stamens are serially split, they are imbricate, and if the major rows count only two stamens, they are placed in three whorls of five stamens each.

Supply of vascular bundles

There are no important differences with the preceding species.

The petals have a fan-shaped dichotomous innervation with few submarginal anastomoses. Especially at the narrow overlapping margins the anastomoses are absent, the innervation there accordingly being open dichotomous.

At the level of petal insertion petal and stamen innervation are free from each other, though the abaxial parts of the stamen fascicle traces show a short downward course towards the petal basal lateral traces. However, a connection is not reached and the parts return to the rest of the trace.

3) URENEAE: S(5)n-(P5-St∞-Std)-C(10)
Urena lobata L.
Pavonia praemorsa Cav.
P. sepium A. St. Hil.
Goethea cauliflora Nees
Malvaviscus arboreus Cav.

Urena lobata

Below the calyx an epicalyx is present consisting of five alternisepalous parts which form a short basal tube. The calyx tube is also short, and as the sepals are somewhat triangular in cross-section, the tube is pentagonal, outside with the angles in sepal radii and inside with the angles in petal radii. It follows that the stamen tube which is very thin basally is on the whole pentagonal with angles in petal radii. So is the pistil with its five antepetalous cells.

The petals show an oblique implantation which is lower and closer to the petal radii on the overlapping side. Here also the petal is shorter and narrower.

The distal part of the stamen tube is sterile and in young phases terminating in five

Malvastrum capense. — Fig. 63. Attachment of petal laterals.

Plagianthus spp. — Fig. 64. Course of vascular bundles. — Fig. 65. Connections between petal and stamen traces.

Anoda lavateroides. — Fig. 66. Primordial phase in androecium development (80 ×).

Urena lobata. — Fig. 67. Course of vascular bundles. — Fig. 68. Connections between petal and stamen fascicle traces. — Figs. 69—70. Successive phases in androecium development (80 ×).

Pavonia praemorsa. — Fig. 71. Attachment of petal laterals.

Malvaviscus arboreus. — Fig. 72. ditto. — Fig. 73. Course of vascular bundles.

Lagunaria patersonii. — Fig. 74. Stamens up between the rows, near sepal radii. — Fig. 75. Developmental phase of the androecium showing change in stamen position (40 ×).

alternipetalous lobes, whereas in mature condition the mouth is irregularly stunted. The stamens are arranged is ten rows, five major rows of which are placed closer to the petal radii in front of the overlapping petal halves. They are represented by filaments with an anther of two pollen sacs. However, as they are mostly placed in pairs one above the other, it is evident that one pair is formed by a serially split stamen. There are one to three of these split stamens in a row, though sometimes unpaired stamens with two pollen sacs are present on top or base of the major row. Frequently, the stamens in the different rows overlap one another in bud. If their number is regular in all sectors of the flower they form whorls.

Developmental phases

Within the primordial calyx the floral apex becomes flat and pentagonal with the angles in petal radii. A slight central depression which is similar in outline delimitates a peripheral wall, upon which five lower radial regions originate in sepal radii whereas the corner parts are elevated. On either side of the petal radii these parts develop into radial elliptic staminal buttresses (fig. 69), which are unequal in size. Outwards of the minor buttresses the beginning of a petal primordium can be observed. Somewhat later some stamen primordia originate on these buttresses in centrifugal direction (fig. 70) as slightly diagonal elliptic protuberances. The petal primordia then extend below the major rows. In a later phase the stamen primordia split into two halves on either side of their short axes. As two diagonal directions are possible, it should be added that the upper half stamens of a pair are placed closer to sepal radii. The lobes on the tube develop late during ontogeny.

Supply of vascular bundles

Ten main receptacular bundles are formed in sepal and petal radii. Their middle parts bend outwards at right angles, trifurcating into median and commissural marginal epicalyx traces and into lateral parts which together form a ring. From this ring some lateral epicalyx traces and, on either side of petal radii, a sepal marginal trace are detached. From the proximal parts of sepal median and marginal bundles some special vascular bundles are given off which ramify towards the nectary field.

The flanks of each main bundle proceed their upward course and unite into concentric bundles which higher up split serially into the pistil traces inwards and the sepal median or the petal stamen traces outwards (fig. 67).

The petal-stamen bundle spreads tangentially and falls apart into two stamen fascicle traces and a number of ramifying petal traces, individualizing first the fascicle trace of the major stamen group. The more outside petal laterals on both sides do not necessarily have a basal connection with the middle laterals, but tend to form a common basal commissural marginal trace which, however, is not extended fully downwards (fig. 68). The fascicle traces split into stamen traces in the usual way. From the proximal parts of the petal bundles and from the stamen fascicle traces at the level of petal divergence some blindly ending bundles may go into the region of petal insertion.

Other authors

Payer gave one figure of *Urena lobata* in which two primordia are present in front of the petal, a large upper dividing one and another small and not dividing. From this figure Goebel (1886) concluded that the development is the same as in *Malva parviflora* There are alternipetalous teeth on the young tube's mouth.

Saunders saw that the petal-stamen cordons form large u-shaped bundles together with pistil traces and sepal commissural laterals which are attached to the stele.

Pavonia spp.

The species resemble *Urena lobata* very much. The formation of what we supposed to be in *Urena* petal commissural marginal traces is well marked, though here also the downward connection is lacking (fig. 71). Where the commissural petal traces branch into the petal laterals rather many tiny, or some stronger, blindly ending irregular bundles are given off into the region of attachment of the petal to the stamen tube. Some of the median petal nerves give off these tiny traces also, but not as much as the lateral nerves. These bundles are not given in the figure. In our material the mouth of the tube is irregularly five-lobed. If the lobing is regular, the lobes appear to be in line with the major rows. They develop late, when the stamens are already fully formed.

Other authors

Payer pictured a developmental series of *P. hastata*. The protuberances in front of the early appearing petals are longitudinally grooved from the beginning, showing a major and a minor side. Afterwards the major side is split into a larger upper portion and a smaller lower portion. Both portions and the minor side are split into two half-anthers. Goethart gave a similar description and adds that the development may be restricted to a first primordium on the major side. Moreover, the outer primordia may remain unsplit and give anthers with two pollen sacs. According to Saunders a large vascular cordon comes from the stele directly, the middle portion proceeding as a petal-stamen bundle (*P. multiflora*). Duchartre said that the stamens may alternate more or less (*P. cuneifolia*). Goethart and Saunders mentioned epipetalous teeth on the stamen tube, because, according to Goethart, the tips of the buttresses are not grooved radially. Payer described episepalous or epipetalous teeth, whereas one of his figures, a rather young phase, shows alternipetalous lobes. Duchartre already laid stress upon the existence of alternipetalous lobes in young stages.

Goethea cauliflora

The stamens have anthers with two pollen sacs. There are four or six of them one above the other in each of the ten rows which are situated along the distal end of the stamen tube.

Developmental phases

In the only floral primordium that could be studied, rows of three elliptic stamen primordia appeared, the outer ones placed more or less tangentially, the middle ones diagonally — the upper side directed towards sepal radii — and the inner ones radially. The pistil consists of ten cells, five of which in petal radii are in a reduced condition.

Vascular bundles

After giving off ten epicalyx traces, median and commissural marginal, and, on a higher level, ten similar calyx traces, the rest of the stele contracts into five almost concentric, but adaxially slightly open, vascular bundles in petal radii. Going upwards these bundles spread laterally and form the pistil supply inwards and the petal-stamen bundles outwards.

The petal-stamen bundle spreads into a semi-circular combination of small bundles which is open on the adaxial side. It falls apart into middle petal traces and two lateral stamen fascicle traces. At the same time it continues its upward course in an oblique manner, for instance to the left if the petals overlap to the right.

Malvaviscus arboreus

The contorted characters of the flower are the same as those in *Urena lobata*. The petals are provided with a small deltoid outgrowth of the proximal part of the margin on the overlapped side.

The stamens have anthers with two pollen sacs which are placed in ten rows along the upper half of the tube. The lateral distance between the rows is unequal, being less in front of the petals. The rows count two and three stamens one above the other in front of the overlapped and overlapping petal half respectively. Among the stamens five whorls may be distinguished, but sometimes all members of a row are situated too low or too high for their whorls. The predominance of the rows is also demonstrated by the fact that the whorls do not alternate because the rows are not equidistant. The basal stamens of the rows of three are often lacking, or their anthers are smaller and their filaments longer. Above the staminal region the tube has a sterile prolongation, especially in line of the minor rows, where this extension can be toothed.

The five pistil cells lie somewhat to the left or right of petal radii if the petals overlap to the right or left respectively.

Supply of vascular bundles (fig. 73)

As the perianth parts diverge on almost the same level, the innervation of these whorls is rather coherent. The vascular cylinder bends outwards into the receptacle and separates into three circles of bundles of decreasing divergence. An outer circle forms a ring from which the epicalyx bundles are detached, a middle circle consists of five sepal median traces and five alternate sepal lateral assemblages, an inner circle is formed by five small gynoecium traces. The middle and inner whorl of bundles may also run along the parts of the outer system first, then come free and return inwards.

In alternisepalous sectors five concentric — if not somewhat open adaxially — bundles are attached to the perianth, especially the lateral sepal innervation by a double collateral or multiple base. These complexes have a basal upward and inward course and split serially into the pistil innervation inwards and the petal-stamen system outwards.

From the collateral petal-stamen bundle, which spreads into the base of the stamen tube, two lateral parts proceed inwards as the stamen fascicle traces, whereas the other parts go into the petals. As in the preceding species outside petal laterals of adjoining petals may run downwards into a common commissural petal trace which here may be attached to the perianth innervation near sepal radii (fig. 72). Especially the petal laterals in the triangular proximal extension of the petals have this tendency. The normal connection with the middle laterals may equally be present or may be lacking. The bundles often show a partial downward course into median sepal direction, but then return to their normal attachment points.

Other authors

According to Payer the androecium starts with five alternisepalous, single, hemispheric protuberances along the periphery of the flowering apex. On their outside base they show tiny petal primordia. Also Duchartre, Frank, and Eichler pointed out the initial simple staminal buttresses, though it is not clear whether they refer to their own observations. The stamen primordia arise on it in two centrifugal rows and Payer noted that the upper stamens become situated closer to the sepal than to the petal radii. His reports on the sterile teeth which terminate the tube are conflicting. In his figures the teeth are epipetalous, and also Saunders said that they are epipetalous.

Saunders thought that the vascular structure in the flower base is indistinct (*M. mollis*). On the other hand, Rao (1952) saw the separate departure directly from the stele of epicalyx, five calyx and five alternating petal-stamen traces, the latter of which form petal traces in the middle and stamen traces on the flanks. The stamen traces are situated in epipetalous pairs, but, higher up, in whorls. Five of them innervate the sets of two stamens inclusive the sterile teeth.

4) HIBISCEAE: S(5)n-(P5/P5n-St∾-Std)-C(5)
Lagunaria patersonii G. Don
Gossypium hirsutum L.
Hibiscus trionum L.
H. rosa-sinensis L.
H. micranthus L. *f.*
H. syriacus L.
H. pulvinulifer Borss.: P5n
H. campylosiphon Turcz.
Hibiscadelphus giffordianus Rock
Papuodendron lepidotum C. T. White: P5n
P. hooglandianum (Kost.) Borss.: P5n
Cephalohibiscus peekelii Ulbr.
Thespesia populnea Soland. *ex* Corr.
Kokia rockii Lewton

Lagunaria patersonii

The stamens are arranged one above the other in ten rows along the upper part of the tube. The lateral distance between the rows is small in front of the petals, except in the distal regions where the rows become equidistant or even approach sepal radii. The vertical distance between the stamens decreases upwards and the tube terminates in an irregular sterile mouth.

The stamens have anthers with two pollen sacs, which may be regarded as half-anthers because they occur in pairs, in the upper part of the tube sometimes with a short common base.

The vertical distance between two members of a serially split stamen is always shorter than that between two members of successive pairs.

Deviating stamens (fig. 74) are often present in some sectors of the flower such as near the mouth of the tube alternate to the petals. For instance 1) a small anther with two pollen sacs which are connected at one end without the pollen mass being continuous; 2) stamens, the free branches of the filaments of which are very short, whereas the common parts are flat. The splitting of the vascular bundle lies more downwards; 3) stamens in which filament branches are altogether absent, the anthers being placed along a broad reniform connective. The filaments are provided with two vascular bundles; 4) the same, but with the pollen sacs of different half-anthers fused at one end in the middle of the stamen, the pollen mass being continuous or remaining separate. Anthers with three or four pollen sacs are the result; 5) the same, but the anther is more or less folded along a plane perpendicular to the connective; 6) complex combinations, which may be provided with a lateral short-stalked simple globular anther sac.

Developmental phases

The antepetalous parts of the young tube from the start develop in advance of the other parts. The stamens originate there in two rows perpendicular to the petal surface in centrifugal direction. From hemispheric the primordia soon become elliptic with the long axes perpendicular to the rows, but as the tube grows the long axis comes to be situated diagonally and ultimately radially (fig. 75). This means that the mature serial arrangement of half stamens is ontogenetically due to a collateral division.

During later development the rim of the young tube may form alternipetalous lobes inwards, which are usually sterile, but may often develop primordia submarginally and near sepal radii. These primordia develop into the deviating stamens described above, which link the normal stamens over the antesepalous upper portions of the tube. Still later the tube may show a sterile prolongation above the staminal rows.

The styles of the pistil originate alternate to the sepals.

Supply of vascular bundles

The vascular cylinder in the pedicel, which at the base provides traces to one or two basal bracteoles, is surrounded by cortical bundles the number and the lignification of which increases upwards. No downward connection of these small bundles to the stele is present.

Below the calyx three or four traces leave the stele successively going towards bracteoles which form a calyptra over the floral primordium. A number of the cortical bundles also enters into these appendages, and at the same time bundles come from the flanks of the epicalyx traces and ramify upwards into more cortical bundles.

At the calyx level five antesepalous loops of the widening vascular cylinder gradually move more outwards. Their median portions become free and trifurcate into a sepal median trace and two sepal basal lateral traces, which form sepal laterals and a cross-arc system. In this way, together with the cortical bundles a mass of bundles is produced in the rather thick calyx. We may express the situation in this way that many of the calyx bundles are attached by way of the cortex to the bracteole traces or proceed still further downwards, forming with the lateral bracteole traces an anastomosing and fading vascular supply down into the thick cortex of the pedicel. Moreover, it may be that in some sectors of the flower part of the calyx bundles unite into common bundles downwards, which may either be attached to the top of the cross-arcs or partly or wholly to the stele near the point of divergence of the median calyx trace.

Parts of the stele at the side of the sepal traces are detached and unite — closing the sepal gap — into collateral bundles which run upwards diagonally into the petal-stamen tube. Higher up these bundles split again into two parts, one of which is bigger because it represents the petal trace and the stamen fascicle trace toward the minor row in front of the overlapped petal half.

If the petal trace and the two stamen fascicle traces become free from one another and spread into the petal base and the stamen tube above, the fascicle traces meet outwards near the middle of the petal base forming a meristelic bundle (that closes the petal gap). From the middle portions of this bundle blindly ending stamen traces go into the tube, or they enter the petal base to form there, together with some branches from the bases of the petal nerves, another inner series of tiny nerves of variable orientation which equally end blindly not far upwards in the petal.

The traces of the alternipetalous stamens on top of the tube end blindly downwards in the base of or halfway down the tube.

Gossypium hirsutum

Five alternisepalous parts of the primordial stamen tube are developed much stronger than the alternate radial sterile regions. They give rise to sets of four or five stamens in ten parallel vertical rows, those in front of the overlapping petal halves counting one unsplit stamen with two pollen sacs more than the other row. The stamens below may be hardly split and show a bilobed connective, each lobe bearing two pollen sacs. The tube is provided with antepetalous teeth.

Supply of vascular bundles

Three median and three sets of four lateral epicalyx traces come from the stele and form a ring at the base of the epicalyx parts. To this ring and to the flanks of its traces many small bundles are attached, which together with the collaterally splitting bundles of the rest of the stele form a funnel-shaped mass of bundles.

This mass falls apart into three concentric layers, an inward giving pistil supply, another-outward-proceeding in the mass of calyx bundles from which higher up five sepal median and five commissurals emerge, and finally one in the middle which provides the pistil supply and a ring of bundles in the base of the stamen tube.

In this staminal ring five sectors may be distinguished separated by narrow antesepalous regions. Upwards the sectors fall apart into one or a few middle petal traces and two lateral groups, the latter of which split into petal lateral traces and stamen fascicle traces. The stamen fascicle traces are provided by fasciculate basal traces which adhere to the basal parts of many petal nerves and may form anastomoses.

In the connective the stamen vascular bundle undergoes a spatial spreading and dilatation upwards.

Other authors

According to Stephens (1963) the stamens are arranged in five double longitudinal rows. Within each row the stamens arise in pairs which in *G. tomentosum* are fused over half their length.

Hibiscus spp.

a) H. trionum

The stamens are placed in ten rows along the distal part of the tube, which above the upper stamens terminates into a sterile extension. In young buds the mouth of the tube is slightly lobed with alternipetalous lobes and is pentagonal with the edges in petal radii. In a mature stage on the other hand the mouth is irregularly toothed.

The rows count two or three stamens in front of the overlapped or overlapping petal half respectively, in accordance with the oblique insertion of the petal which is lower on the overlapping side. The two stamens are inserted on levels between the three.

The stamens are split serially. However, whereas those below have a long common filament and short forking branches, the upper stamens lack a common stalk, the halves being placed just one above the other, and the middle ones are intermediate. Sometimes small solitary half-stamens occur immediately below the stamens in the minor row or now and then subapically between the rows in petal radii. This last stamen may be provided with a private bundle.

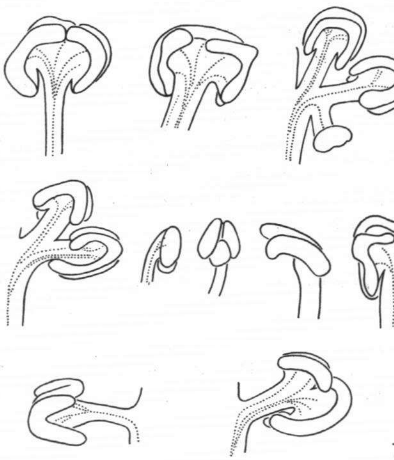
Single or paired or forked structures are present which are formed by a small multicellular stalk with a very big and long cell on top. These cells have a nucleus and granular cytoplasm and may show transverse septs (fig. 76). The total length of the structures is about one third of that of a normal stamen. They occur in line with the stamen rows downwards, on the rim of the tube, and, especially the forked ones, next to the stamens at the side of petal radii. The big cells may show irregularly shaped protuberances at the base.

Developmental phases

A peripheral wall arises along the border of the floral apex which is enclosed by the young calyx. It has rounded alternisepalous angles and broad radial grooves developing upon it by the elevation of staminal buttresses in the corners. The first differentiation on the buttresses is the forming of an oblique petal primordial ridge down on the abaxial side between sepal and petal radii. Next the buttresses grow bigger near petal radii and begin to form there the stamen primordia of the major rows in centrifugal direction. Also the primordia of the minor rows become visible, and the petal ridges extend under the major rows. The staminodial structures mentioned above appear later.

Supply of vascular bundles

A varying number of traces form a transverse ring from which many bundles separate going into the epicalyx, to each part mostly three.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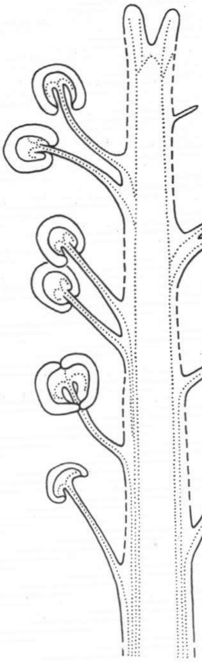
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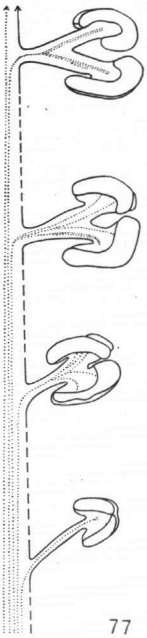
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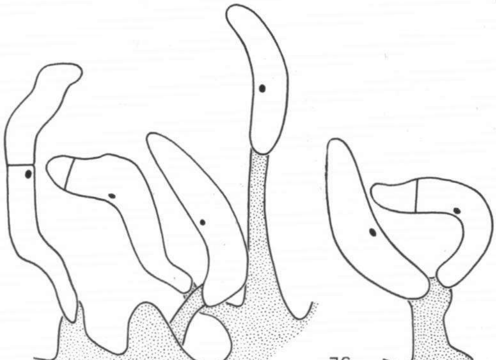
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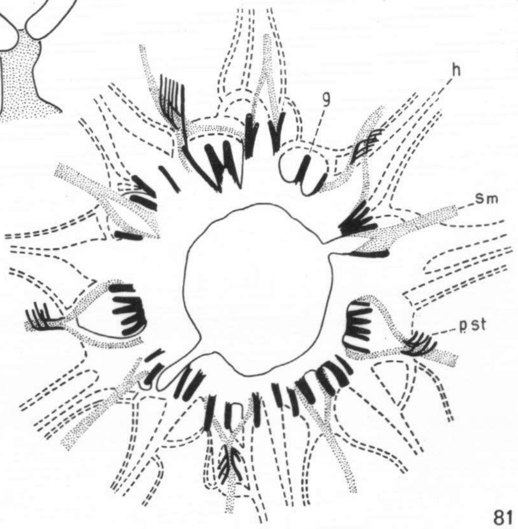

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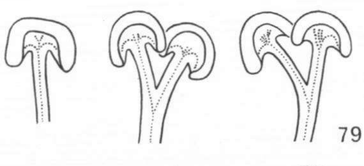
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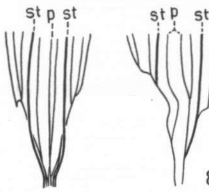

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Hibiscus trionum. — Fig. 76. Presumably glandular structures between the stamens.
Hilbiscus syriacus. — Fig. 77. Row of stames. — Fig. 78. Various stamens.
Hibiscus rosa-sinensis. — Fig. 78*a*. Var. *liliiflorus*. Two antepetalous rows of stamens. — Fig. 79. Some special stamens. — Fig. 80. Connections between petal and stamen fascicle traces. — Fig. 81. Course of vascular bundles.
Hibiscus campylosiphon. — Fig. 82. Lateral view on two thecae.

Five median traces with a single or collaterally double base and five commissural marginal traces represent the sepal traces. The latter usually have a fasciculate base, two parts of which are attached to the median traces on either side forming a cross-arc system, whereas a third part may belong to a main bundle running downwards in petal radii. The epicalyx and calyx traces join downwards into five main bundles in sepal radii and a varying number in petal radii by which they are connected with the vascular cylinder in the flower base. Sepal basal laterals and part of the epicalyx ring may together form concentric bundles for some distance.

Pistil traces are attached to the main bundles in sepal radii and to the petal-stamen traces. With the latter they form concentric bundles which run downwards and link up with the sepal commissural marginal trace. In this way a concentric bundle is formed again which has the fasciculate base mentioned above.

On its way up into the stamen tube the collateral petal-stamen trace spreads tangentially and falls apart into three collateral parts. The median part consists of one or a few bundles which by further division form the median petal vascular bundles. The lateral parts, higher up, separate into two collateral parts, the flanking parts of which give the main body of the stamen fascicle traces, whereas the central parts produce the petal basal lateral traces. The abaxial parts of the stamen fascicle traces or of their fasciculate bases are attached to the proximal parts of the petal basal laterals or sometimes of the petal medians. From the petal basal laterals petal lateral bundles depart, but in addition some tiny bundles move upwards into the direction of the stamen tube to end blindly before entering. Now and then one or a few similar tiny bundles move upwards from the petal median traces, end blindly or innervate a reduced stamen which may occur between the rows in petal radii.

The stamens each receive a single trace as part of the stamen fascicle trace. This trace splits serially whether the external division into half-stamens is evident or not. The staminodial structures are not innervated.

b) H. rosa-sinensis

The petal-stamen tube is in cross-section pentagonal with outside antepetalous and inside antesepalous angles, and the outlines of the calyx and pistil are conformable. The pistil has five cells which lie near sepal radii. The number of epicalyx parts is 5—8, if five the parts more or less alternate with the sepals.

The petals are asymmetrically obovate and have an oblique insertion, the overlapping margin being situated lower and more to the outside and for instance to the right of petal radii if they overlap to the left.

In its distal region the long stamen tube is loaded with stamens and sometimes strikingly twisted, the torsion lines going to the right upwards if the corolla margins overlap to the left.

The stamens all consist of a single filament terminating in a reniform connective along the margin of which are placed two parallel pollen sacs. They are arranged in ten vertical rows which approach each other near petal radii, but tend to be equidistant upwards. The distance between the stamens diminishes upwards. Moreover, the stamens in a row are placed in pairs, because the distance between two partners is smaller than between two members of adjoining pairs. Therefore the stamens may be considered as half-stamens.

There are 3—4 pairs of half-stamens in each row as these are placed in front of the overlapped or overlapping petal halves respectively. The pairs alternate, especially so in the middle staminal region, constituting seven whorls, the basal of which is formed by solitary half-stamens or by pairs of half-stamens with one of the halves in a reduced state. Often stamens are present with two half-anthers placed in line along a broad connective.

The tube is extended by a rather long sterile part which is toothed irregularly, although mostly the teeth stand in line with the minor rows of stamens. In fig. 78 a very clear case of a reduced upper stamen is given.

In var. *liliiflorus* there are fewer stamens which show a striking series of intermediate forms between the normal stamens and those with four pollen sacs along a broad connective (fig. 78). In the basal stamens anthers occur with two pollen sacs opposed to one pollen sac of double length, or with only two pollen sacs.

Developmental phases

Within the young calyx the apex forms five angles alternating with the sepals and is furthermore differentiated into a central depression and a peripheral wall. Upon this wall five parts are elevated extending somewhat to the left or to the right of petal radii. These elevations represent the staminal protuberances. They are divided by a shallow radial groove into a broad alternisepalous half and a narrow half more toward sepal radii.

During the upward growth of the staminal buttresses a small oblique ridge is cut off from the underside of their minor halves. Some time after this ridge is extended under the major halves, more downwards and towards the petal radii. In this way the petal with its overlapped and its overlapping half is developing.

After the appearance of the petals the stamen primordia begin to develop upon both halves of the buttresses in centrifugal direction. In the beginning the primordia of the adjoining halves lie practically side by side, but later, when the primordia increase in size, the alternation of the stamens becomes evident.

The primordia become ellipsoid and also grooved transversally, so that two thecae appear. While this happens, and the tube stretches, the primordia, first the upper ones, turn for 90 degrees, the lateral thecae reaching the upper position. Hereafter the growth of the lateral thecae is somewhat retarded.

The striking torsion in the distal tube part originates when the flower is about fully formed.

Supply of vascular bundles

In the base of the flower the vascular cylinder either falls apart into many bundles on the same level (fig. 81), or the cylinder may be reconstituted above the departure of a set of traces towards one or some perianth whorls.

First 5—8 median epicalyx traces are given off. The lateral epicalyx traces may relate to the cylinder directly, but are as a rule attached to the median traces by way of basal lateral traces.

If the stele is not reconstituted sepal median and commissural marginal traces are attached by a double base to the proximal flanks of the stelar parts that give rise to the epicalyx traces. The basal adaxial ring of nectariferous tissue on the calyx surface receives its vascular supply from amply ramifying and anastomosing bundles which come from the proximal parts of the sepal nerves.

Similarly, if above sepal level the stele is not reconstituted, either the petal-stamen trace is attached to the flanks of the sepal commissural marginal trace, or two collateral halves of the petal-stamen trace link up with the double base of the sepal commissural marginal trace. The residual stelar parts produce pistil traces.

The petal-stamen traces run upwards into the stamen tube, deviating from a radial course, for instance to the right if the petals overlap to the left. About halfway up their flanks turn to the inside to form the stamen fascicle traces, whereas the peripheral portions enter the petals with a bend for instance to the left if the petals overlap to the left.

The stamen fascicle traces, as seen in cross-section, spread into a series of bundles which is placed almost radially but is, in addition, more or less pointing towards petal radii with its flank parts. The traces towards the pairs of stamens are detached from the fascicled traces gradually and move outwards splitting towards the half-stamens. In the connectives the bundles dichotomize into two bundles which bend backwards, frequently leaving some tiny proximal branches to move upwards (fig. 78, 79). Lower down on the tube the intermediate stamens may show in each anther half only one bundle bending sidewards which from its base has tiny bundles fanning into the other direction. In the basal stamens the anthers with four pollen sacs show a similar fork of markedly anatropous bundles which have some tissue moving upwards.

The rest of the stamen fascicle traces are prolonged into the sterile end of the tube, especially into the teeth in line with the minor rows.

c) H. micranthus

The stamens are placed in three whorls of five, and above them the tube extends into a sterile irregular part. The upper stamens consist of two serial half-stamens on a very short common branch. The middle stamens are the only components in front of the overlapped petal halves. They also consist of two half-anthers which on the contrary are placed along the distal margins of a flat rhomboid connective terminating a single filament. This filament contains a double vascular bundle. The basal stamens and now and then the middle stamens bear on a single filament a single half-anther which may in addition be accompanied at one of its sides by a reduced structure in the form of a simple, stalked, globular pollen sac.

d) H. syriacus

The distal stamens are split serially, each filament branch bearing a reniform half-anther in a radial plane of the flower (fig. 77). Downwards the basal part and the two branches of a filament become shorter and flat, so that ultimately the half-anthers are placed in line along the margin of a semicircular flattened connective which terminates a single stalk (fig. 77). This structure often occurs in a more contracted form, the half-anthers together forming a broadly reniform anther with four pollen sacs. Down in the staminal region more reduced forms are found. In these anthers sometimes two pollen sacs in line are replaced by one of double length, the result being an anther with three pollen sacs (fig. 77, 78). The anthers with three or four pollen sacs may be folded along a median plane perpendicular to its surface to various degree (fig. 78). And at the same time a pair of anterior or posterior pollen sacs may be reduced and occur as one small sac (fig. 78). These sacs may also be present on solitary stalks in the basal staminal region, or as a proximal appendage of a forked distal stamen (fig. 78). Sometimes solitary filaments, topped by a half-stamen, are present in the basal staminal region.

Supply of vascular bundles

The vascular cylinder widens upwards into the receptacle and many traces are detached which gradually move outwards towards the epicalyx. The residual stele is not reconstituted but falls apart in five median sepal traces and circa ten other traces which divide collaterally in sepal laterals.

To the flanks of these sepal traces five more or less concentric bundles are attached by a fasciculate, often double, base. Higher up these bundles split into pistil traces inwards and petal-stamen traces outwards. More pistil traces come from other sepal traces directly.

The collateral petal-stamen traces stretch sidewards and lose their flank parts which are going to form the stamen fascicle traces. Almost directly from the base the fascicle traces are dissociated in as many stamen traces as there are stamens in one row (4—6).

The bundle in the branches of the filament of the upper stamens may be single, but is often double or multiple and then preludes to the grouping in the fan-shaped ramification of the bundles in the broad connectives of the lower anthers (fig. 77). The bundles in the filament branches are the forks of a common basal staminal trace which is connected with the stamen fascicle trace. The fan-shaped innervation becomes a single bundle in the basal reduced stamens.

In the folded anthers this vascularisation follows the folded nature. Sometimes in a filament a lateral isolated short bundle may be present.

e) H. pulvinulifer

Large fields of nectariferous trichomes are spread on the base of the stamen tube tapering towards the lowermost antepetalous stamens and extending on the inner bases of the petals. Long surrounding hairs hide these nectaries from view, which is probably the reason why they are not mentioned in works on classification. It should be noted that axillary to the calyx a very small ridge of nectariferous trichomes occurs.

The stamens do not differ from those in the preceding species.

Supply of vascular bundles

The vascular stele breaks up into a varying number of epicalyx traces outwards and five sepal median traces inwards, calyx and epicalyx traces having sometimes a common basal part. The epicalyx traces form an annular system beneath the epicalyx insertion from which all lateral epicalyx traces diverge (fig. 84).

However, five concentric bundles are also connected with this ring. Higher up they divide into sepal lateral traces outwards, pistil traces inwards, and into two middle flank parts which form the double base of the petal-stamen traces. The sepal laterals anastomose with laterals coming from the sepal median traces, thus giving a basal calyx ring.

The nectary fields are supplied by bundles attached to the proximal parts of the petal nerves. These bundles give a tree-shaped ramification with more or less isotomous main forkings and profuse tiny endings under the nectariferous surface (fig. 83).

f) H. campylosiphon

The flowers differ from those of the preceding spp. only in their pollen sacs, which are partitioned by means of transverse septs. The loculi of the two parallel pollen sacs of each theca do not show any tendency to be paired (fig. 82).

The supply of vascular bundles

Only a single flower could be studied which had six epicalyx leaves.

A whorl of prominent traces moves out of the floral stele, counting six epicalyx median and commissural lateral bundles. The twelve traces form twelve cross-arcs. All main sepal lateral traces are directly attached to the cross-arcs formed by the epicalyx traces. They form many anastomoses from which tiny bundles depart inwards perpendicular to the nectariferous surface. The five sepal median traces come from the stele directly or slightly conjoint with epicalyx traces in sepal radii.

The petal-stamen traces are represented by large semicircular bundles which have the xylem directed towards the floral centre. They are attached by a diffuse base at the proximal parts of sepal lateral traces. Upwards the trace separates into two rows of stamen traces which are placed perpendicular to the petal surface as seen in cross-section.

In the staminal region the traces diverge as usual, the lowermost near petal radii, the uppermost between sepal and petal radii.

The innervation of the thecae is formed by a bundle with two main anatropous branches in the plane of the theca, sometimes towards one side with two parallel bending branches. However, irregular tiny parallel branches accompany the main branches in all cases (fig. 82).

Other authors

Payer gave two figures, one of *Hibiscus illicifolius* and the other of *H. syriacus*, in which the stamen primordia are seen to arise centrifugally in two rows in front of each petal. Von Goebel concluded from these plates that the first primordia are so close together that the second five have to appear more downwards.

Saunders gave record of the conjoint petal-stamen and sepal commissural lateral traces. Rao said that the vascular system in *H. solandra* and *micranthus* is not different from that in *Malvaviscus*, except that in the last species the teeth are not vascularized.

Eichler stated that *Hibiscus* has five sterile teeth on the tube as have the *Ureneae*. Saunders stated more precisely that the teeth are epipetalous, because they lie in line with and are supplied by the prolongation of the vascular bundles of the stamen rows. According to Duchartre the teeth are alternipetalous, the more so in young phases.

Double flowers of Hibiscus rosa-sinensis

A part of this work, published in a previous paper (van Heel, 1962) is again presented here combined with new data in a more extensive form.

In an account on double *Hibiscus* flowers it is convenient to arrange the descriptions according to the increasing dissociation of the normal stamen tube into antepetalous parts and to follow the further development of these parts.

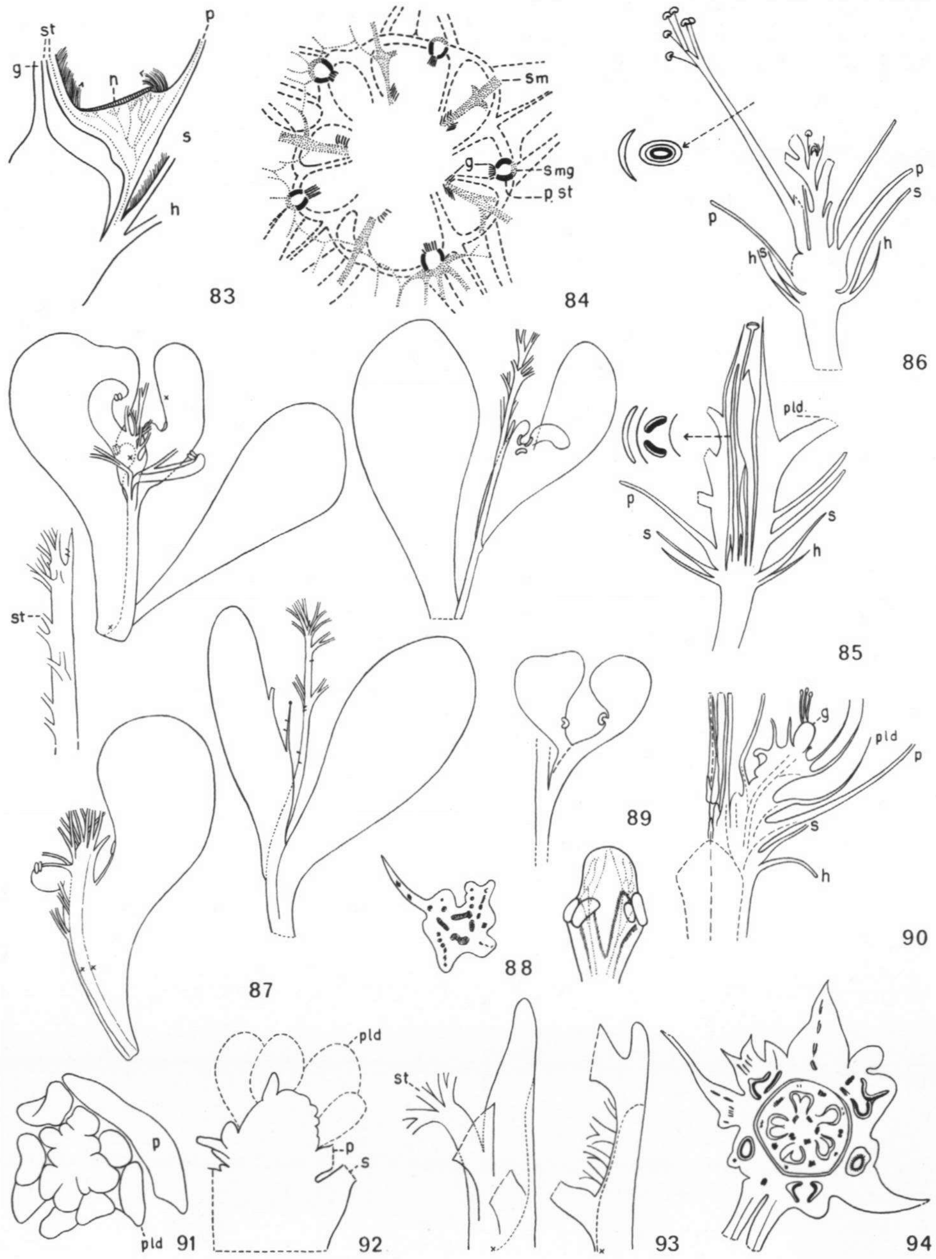
A) The flowers are normal except for five large sterile petaloids which are attached to the base of the tube in front of the overlapped petal halves. Above calyx level five collateral bundles occur in petal radii, which fall apart into a median petal trace and two lateral stamen fascicle traces. The fascicle traces together form an adaxially open meristele — closing the petal gap — from which traces are given off towards the petaloids and the stamens.

In a similar flower the distal stamens are inserted on almost the same level and two to four adaxial ones of each group form subulate appendages. They are fused laterally to form funnels which overtop the tube-parts. Corresponding with the aggregation of the stamens the stamen fascicle traces meet also adaxially forming five antepetalous cylindric combinations below the staminal region.

B) The flowers have normal tubes with ten rows of 3—5 bifurcated anthers. However, at the base two large sterile petaloids are present in front of each petal, a lower one in front of the overlapping half and a higher one in front of the overlapped petal side. The lower petaloid may be inserted so close to the petal margin that a partial lateral fusion may result. It may even be inserted alternating with the petals and bear an axillary tooth that can easily be severed from the tube base. Then it is innervated by traces connected directly with the underlying calyx supply, and the sterile axillary teeth receive branches from these traces.

In these flowers the gynoecium is replaced by a central prolification bearing big sterile petaloids in alternating whorls. The outer whorl is formed by a tube of alternipetalous members, which is about half as long as the stamen tube. Upwards the whorled arrangement becomes irregular.

C) A short tube is covered all over with sterile petaloids resembling small petals



Hibiscus pulvinulifer. — Fig. 83. Innervation of glandular tissue axillary to the petals. — Fig. 84. Course of vascular bundles.

Double Hibiscus rosa sinensis. — Fig. 85. Flower with tube left entire, l.s. — Fig. 86. Flower with free secondary axes, l.s. — Fig. 87. Several male free axes. — Fig. 88. Male free axis, c.s. — Fig. 89. Some special petaloid stamens. — Fig. 90. Free secondary axis surmounted by small pistil, l.s. — Fig. 91. The same, young phase, top view. — Fig. 92. The same, young phase, l.s. — Fig. 93. Incipient tertiary free male axes. — Fig. 94. Secondary tube, c.s.

and is prolonged into long teeth. The petaloids are inserted as the stamens usually are, three in front of the overlapping side and two in front of the overlapped side of the petal. The central prolification consists of oblong phylloids which bear a style projecting from between two apical lobes (fig. 85).

In some flowers of this type the tube seems to be terminated by five antesepalous petaloids. However, on closer observation these organs prove to belong to the central prolification and to adhere to the inside of the stamen tube by means of parenchymatic bridges. Also the vascular supply to these petaloids comes from a stele that is reconstituted above the level of divergence of the petal-stamen traces.

Other flowers of this simple type show a higher number of petaloids, the distal ones of which are inserted longitudinally more and more along the tube. Among the upper ones some may be divided like stamens and bear two subapical anthers of two pollen sacs along the median side of the lobes (fig. 89).

Sometimes a short tube is formed by five antepetalous groups of large sterile petaloids around a central prolification of similar petaloids. The groups become apparent through the presence of basal purple spots on the inside of the petaloids which all are directed towards a place in their middle. Sometimes in this place a tiny axis may occur ending into a few sterile small phyllomes. In addition, axillary to the petaloids tiny axes may occur, which may split into one or a few stamens or sterile teeth.

D) On a short tube one to five large sterile petaloids are arranged around the base of five more or less radially elongated antepetalous groups of stamens which are prolonged into long freely extending axes (fig. 86). One of the petaloids near petal radii may terminate the tube in a given sector of the flower and be a petaloid adaxial to the antepetalous axis, provided with xylem which is inverted in relation to the floral axis. In one flower these inverted petaloids were connate and formed a kind of paracorolla. Along the axis upwards the petaloid character of the appendages decreases (fig. 87). The intermediate organs are petaloids bearing pollen sacs, solitary or in thecae. The petaloids may be inserted along the axis longitudinally, owing to the extension of the middle portion of the axis during their primary development. When we compare the fertile petaloids with the bifurcated stamens we gain the impression that each petaloid is homologous with one such a stamen, but that the manner of foliarization may be different, one-sided or two-sided, comprising both forks or only one, and disrupting the anther to various extent (figs. 87, 89). The number of organs on each axis varies from 2 to 12, and is about the same in all sectors of a flower.

On the distal end of the axis the stamens are often all diverging outwards, the peripheral ones lowest, the central ones highest from the axis (fig. 87). Sometimes some central stamens are unexpectedly placed more downwards, and in that case they may be imperfectly developed, as are the peripheral lower stamens. Between the stamens a distal sterile subulate extension may be present which is often provided with a presumably nectariferous organ consisting of a multicellular conical lower part and a big apical ellipsoid cell. These structures may also occur on and between the filaments and may even terminate filaments forming imperfectly developed stamens.

The central prolification consists of alternating whorls of five large sterile petaloids which may sometimes bear small axillary axes with a few stamens. The outer whorl is composed of alternipetalous members which together form a tube. It may seem that the outer whorl is formed by antepetalous members, but in that case the real outer whorl is fused with the inside of the stamen tube, as has been mentioned under C.

The petal-stamen trace falls apart into a median petal trace and two lateral stamen fascicle traces which, higher up, meet in the petal radii to form a microholostele. From these steles traces are given off toward the petaloids, first to those inserted immediately above the petals, next to the second two, and then to the adaxial petaloid, if all these petaloids are present (fig. 95). Upwards this stele is prolonged into the free part of the axillary axis, and is flattened in correspondance with the external form. It finally falls apart into stamen traces more or less in two rows or in an elliptic combination, if viewed in cross-section.

Whereas the upper petaloids are each supplied by a single trace which comes from the axillary stele, the lower ones receive several traces. These traces may be attached to the stamen fascicle traces below the level on which the axillary steles are formed. The traces of the lowest petaloids may all be attached to the underlying sepal innervation, those of the next higher placed petaloids partly to the sepal supply, partly to the axillary steles (fig. 95).

Some small flowers of this type may show secondary axes without proximal large petaloids and ending in a few stamens only.

In some flowers there is hardly any extension of the axillary axes in their middle regions. Finally in some flowers the lateral fusion of the antepetalous sectors is not equally high.

E) Many flowers are provided with free antepetalous axes (fig. 90) which are terminated by a small pistil and bear 10—15 petaloids, the distal ones mostly provided with some pollen sacs. Some normal stamens may occur also below the pistil. These appendages decrease in size upwards, and the adaxial ones are bigger than the others. Above the basal petaloids the axillary axes may be without appendages for some distance or have only a few petaloids inserted there longitudinally.

The central proliferation consists of alternating pentamerous whorls of large petaloids, the outer whorl of which is formed by a tube of alternipetalous parts.

The basal petaloids of the free axes and also those of the central proliferation may bear tiny side-axes provided with some small petaloids and some teeth.

The axillary axes each have a stele which is composed by the junction of two flank parts of a petal-stamen trace. Petaloid traces are successively given off and the gaps are closed above them (fig. 88).

Some of these flowers have one or two subapical tertiary axes inserted on one or both adaxial lateral sides of each antepetalous free secondary axis (see photo in van Heel, 1962). Now and then one of these tertiary axes may again bear a small side-axis. All these axes bear petaloids and small pistils, but only the ultimate axes were observed to bear some pollen sacs on their upper petaloids. A part of the stele of the parent-axis enters into the lateral axes. However, no axillary connection with a petaloid could be ascertained.

In some other flowers the pistil terminating an axillary axis is formed by a whorl of proximally connate green lanceolate blades which attenuate into a style and enclose a bare residual apex. In other cases, the pistil may be still more open with many more or less fused non-whorled carpels, the lower ones of which may bear ovular structures or pollen sacs, as do the small upper cuneate petaloids. Within this more open pistil the apex consists of a complete primordial double flower for which the carpels serve as a perianth.

F) A few flowers of type E may have a tube of petaloids and stamens surrounding the secondary pistils (fig. 94). The pistils are formed rather normally, their styles protrude from the tube.

The tube is composed of five longitudinal parts that are separated from one another by thinner regions of tissue. It is terminated by an irregular number of teeth. Each part of the tube bears up to four proximal petaloids, some distal petaloids, and 2—6 bifurcate stamens, or, in less well developed cases, only a few petaloids. The proximal petaloids are inserted more or less transversally and form a common cluster with the distal petaloids on the free axis, as if together constituting an irregular perianth. This effect is caused by the extension of the middle part of the tube where the petaloids are inserted longitudinally.

The stamens of each group are surrounded by the distal petaloids, except upwards, where the tube ends in small teeth. The groups of stamens more or less constitute two longitudinal rows or an elliptic assemblage. It should be added that it also happens that the stamens and some petaloids below are elevated on a separate, small, free axis which projects from the tube part subapically, surrounded at its base by 2—5 of the distal petaloids (fig. 93).

Below the pistil the stele of the secondary axis falls apart into an inner ring which forms the pistil supply and five outer collateral bundles which represent the traces of the groups of the tube. Sometimes some minor groups, consisting of a petaloid and some stamens, occur between the five main bundles and are innervated separately. Each of the collateral bundles gives off a part toward the most proximal petaloid, above which two parts by further division innervate the rest of the appendages upwards in case the groups do not count many members. If, on the other hand, the tube parts are well formed, the collateral bundles join, above the basal petaloid adaxially as well as abaxially to give a complete tertiary stele (fig. 94). From this stele abaxial and adaxial parts diverge toward the lower and the higher organs of the groups respectively. If the stamens are elevated on another side-axis, the traces towards these stamens bend outwards into these axes.

Developmental phases

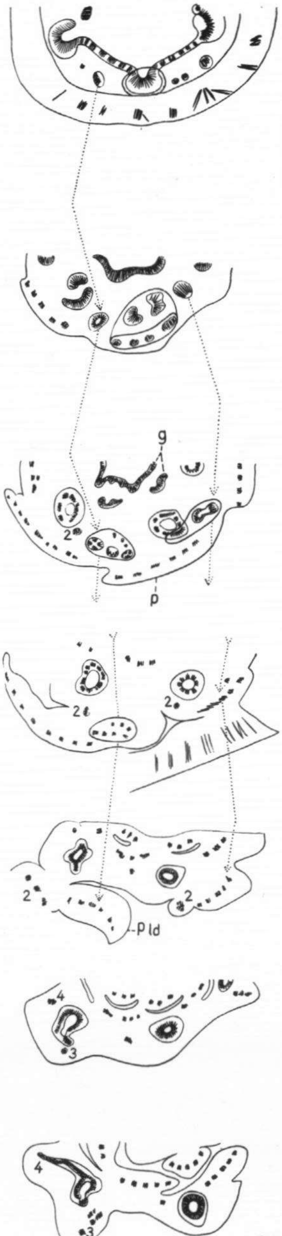
As usual, a central depression and a peripheral wall may be distinguished on the apex in an early phase. However, the development of alternisepalous contorted protuberances on this wall is more pronounced than it is normally, the sterile regions separating the protuberances failing to develop any further (fig. 96). The protuberances, after the separation of the petal primordia, represent the first phases of more or less free axillary axes. If a protuberance is large and remains hemispheric, petaloids arise around its base and upwards, a free axis being the result (figs. 91, 92). If, on the other hand, the protuberance, after the usual origin of a central tooth or petaloid and two peripheral lateral petaloids, remains more or less radially elongate, an axis will result which is proximally fused to its neighbours, and which furthermore may produce some more petaloids followed by stamens in two rows or in an elliptic field. This development takes place chiefly in outward but also in inward direction (fig. 100 for type D).

The lateral peripheral petaloid primordia arise in a definite sequence, namely first in front of the overlapped petal half. Often the petaloids in these phases seem together to form more or less alternating whorls, reminding the whorled groups of double flowers in *Althaea* (figs. 97, 99).

Independent antesepalous primordia were never found.

Other authors

For *Hibiscus* Masters (1869) and Penzig (1922) mentioned median and axillary prolification, petaloid stamens, and a polyphyllous corolla. According to Penzig the prolification axillary to the petals gives rise to imperfect flowers. Worsdell (1916) merely stated the dialysis affecting the androecium in *Malvaceae*. Von Goebel (1886) said that sometimes the radial half of an antepetalous protuberance forms one petaloid in *H. vesicarius*. According to Saunders in some cultivated *Hibiscus* two antepetalous staminal



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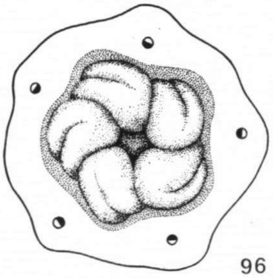

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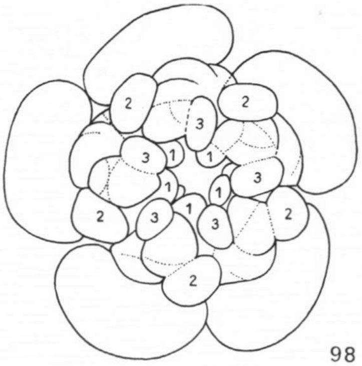

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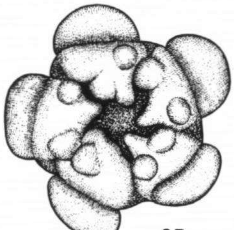

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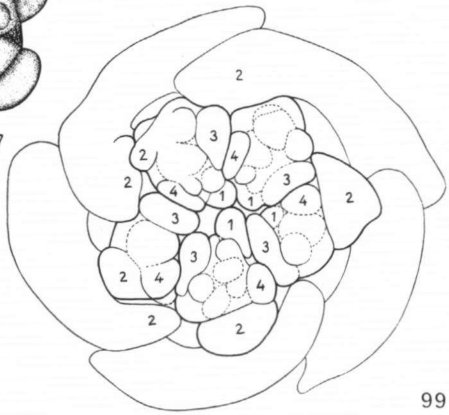

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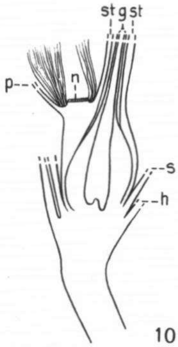

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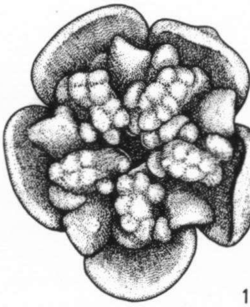

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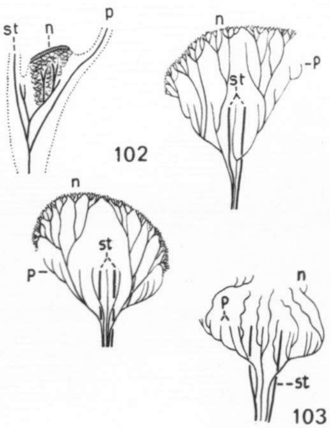

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103

Double Hibiscus rosa sinensis. — Fig. 95. Series of successively higher c.s. through receptacle of a flower with five free male secondary axes. — Figs. 96—100. Successively further developed primordia of double flowers. (Fig. 96. 80 ×. Other figs. 40 ×).

Papuodendron lepidotum. — Fig. 101. Flower showing gland between petal and stamen tube. — Fig. 102. Vascular supply of this gland.

Papuodendron hooglandianum. — Fig. 103. Vascular supply of gland.

vascular cordons meet distally and innervate the teeth, which may here be petaloid. For the facts given by Nozeran (1955) the reader is referred to my previous publication on this subject.

Hibiscadelphus giffordianus

The flowers are similar to those of *H. rosa-sinensis*, but are larger, have a fleshy calyx and more stamens.

Supply of vascular bundles

The epicalyx innervation is formed first by median traces and secondly by alternating commissural lateral traces or by basal laterals which are derived from the median traces. Above it the rest of the stele together with many parts from the flanks of the epicalyx traces form a cylindric bundle mass which upwards reconstitutes a stele. From this stele ten peripheral parts move outwards gradually as sepal median and commissural marginal traces. Moreover, many calyx bundles move directly downwards as cortical traces which connect with the epicalyx innervation.

Above the level of departure of the calyx traces the stele reorganizes and again ten parts move outwards gradually to form carpellary dorsal traces and alternating petal-stamen bundles.

The petal-stamen bundles in the base of the stamen tube form many bundles in a tangentially spread combination, the flanks of which will give the stamen fascicle traces. From their proximal parts these fascicle traces give off some blindly ending traces in the direction of the petal insertion.

Papuodendron spp.

The flowers resemble *Hibiscus* flowers. As a matter of fact, the genus is treated under *Hibiscus* by Kostermans (1960). The stamen tube is rather short and bears 1 or 2 serially split stamens in front of each petal half. In *P. hooglandianum* the tube terminates into a sterile extension with five about antepetalous teeth, whereas in *P. lepidotum* the tube terminates into filaments and is not extended into a sterile part.

The basal part of the stamen tube and the five regions where the petals are connected with the tube are covered with nectariferous trichomes as in *Hibiscus pulvinulifer* (fig. 101). Here also the nectariferous fields are enclosed by long hairs. The calyx has nectariferous hairs on its basal inner surface in *P. lepidotum*, but in *P. hooglandianum* such hairs are probably missing.

Supply of vascular bundles

As regards the vascularisation in the receptacle it may be mentioned that the petal-stamen traces together with sepal commissural marginal and pistil traces form concentric traces which link up downwards with the epicalyx innervation. Basally the stele breaks up into an irregular number of bundles which either represent sepal median and epicalyx median traces or divide collaterally into these two. Other pistil traces come from the flanks of these main bundles.

The innervation of the nectaries in *P. lepidotum* is given in fig. 102. The flanks of the collateral petal-stamen trace bend inwards to form the stamen (fascicle) traces. The median parts divide into median petal bundles and petal basal laterals. From these petal basal laterals, beside the petal laterals, one or a few bundles are given off on either side which produce a tree-shaped ramification system towards the nectary field. The proximal branchings may be clearly dichotomous, the many ultimate branchlets all bend in the direction of the petal, ending more or less perpendicular to the nectariferous surface. A nectary trace may sometimes be connected with a proximal part of a petal nerve.

In *P. hooglandianum* the nectary traces are shorter and rather poorly branched (fig. 103). They are attached to the proximal parts of the petal nerves as curling bundles.

Cephalohibiscus peekelii

The calyx is a thick cupule in which it is impossible to distinguish sepals. The corolla is contorted, its petals are spathulate and fleshy, with a thin lateral outgrowth near the distal end of the overlapped margin. The petals show an oblique insertion which on the overlapping side is lower than on the other side.

The stamen tube is rather long and wide, tapering upwards and terminating into five sterile, triangular, alternipetalous teeth which would, if they were larger, overlap one another in the way the petals do. The tube has five antepetalous rounded edges and its subapical part is loaded with stamens.

The stamens form ten rows which at first sight appear parallel to the floral axis. However, a second look reveals that whereas, below, the rows approach each other in front of the petals, they do so in alternate regions above. The rows consist of 10—11 sets of two stamens side by side, the filaments of which are free above, but downwards on the tube fused laterally more and more into longitudinally grooved flattened combinations (fig. 104).

The anthers are broadly reniform structures placed transversally. However, the usual pollen sacs are here replaced by three or four mostly unequal sacs in direct line. The stamens above and below have smaller anthers often with the normal two parallel pollen sacs. There is no difference in shape between left and right stamens on a given level of one row.

The five cells of the pistil, which contain median false septs, are placed more or less opposite the petals.

Supply of vascular bundles

Some traces are detached from the vascular cylinder in the pedicel, and, after splitting collaterally, enter three epicalyx segments. In addition they split into many small bundles which amply ramify into the periphery of the calyx cupule and strongly anastomose there towards the upper rim. In cross-section these bundles may be concentric for some distance.

The rest of the stele splits into a cylindric upwards widening mass of bundles, many of which may be concentric for some distance. This mass falls apart into three annular systems, namely 1) an inner ring of meristelic bundles that represents the pistil supply, 2) a middle ring as the petal-stamen vascular supply, 3) an outer main part which forms the calyx innervation. Whereas most traces of this calyx supply form the dispersed calyx vascular bundle system together with the traces that are attached to the epicalyx innervation, its adaxial traces already end beneath the surface of the proximal covering of nectariferous tissue.

The whorl of collateral bundles in the base of the stamen tube is either continuous or may be interrupted near sepal radii (fig. 105). During the upward course these bundles split collaterally, anastomosing sometimes, and many among them — not those in alternipetalous regions — bend outwards towards the petal bases. Here the bundles split collaterally and many of the marginal branches may invert for some distance, to revert again higher up where the petal margins become free (fig. 106).

The residual bundles maintain a continuous whorl which becomes pentagonal with approximately antepetalous edges. Higher in the tube the pentagon changes into a wave-line with antepetalous outward and antesepalous inward bends which, however, since the very tops of the bends seem to be cut, rather represent ten diagonal combinations of bundles (fig. 107). When considered as antepetalous pairs the combinations show xylem opposition. Each of these combinations supplies one of the stamen rows.

When proceeding upwards the combinations, by collateral division, spread into more bundles, part of these bundles inverting and becoming situated closer to petal radii (fig. 107). Thus for each row of stamens a double row of collateral vascular bundles with facing xylem is formed which is situated perpendicular to the petal surface. Pairs of bundles are separated from these double rows one after the other and gradually bend outwards into the pairs of juxtaposed of partly fused stamens of one row, to begin with the abaxial parts towards the lowest stamens. However, the curious thing is that before they enter each filament both members of a pair first divide collaterally into two parallel branches with facing xylem (fig. 104). At the bending point the xylem of all these traces is directed towards the flower centre, but the xylem opposition is regained in the filaments. Towards the lowest stamens the additional furcation of the filament traces often fails to develop or is present only in one of the pair members, in accordance with the multiple or single nature of the anthers. Upwards the two bundles together form a ramification system which spreads irregularly though mainly in the plane of the connective. Some vascular tissue may be present in the sterile teeth which surmount the tube.

Thespesia populnea

This species is very much like *Cephalohibiscus peekelii.* As a matter of fact it is the opinion of van Borssum Waalkes that *Cephalohibiscus* should be reduced to *Thespesia* (personal communication).

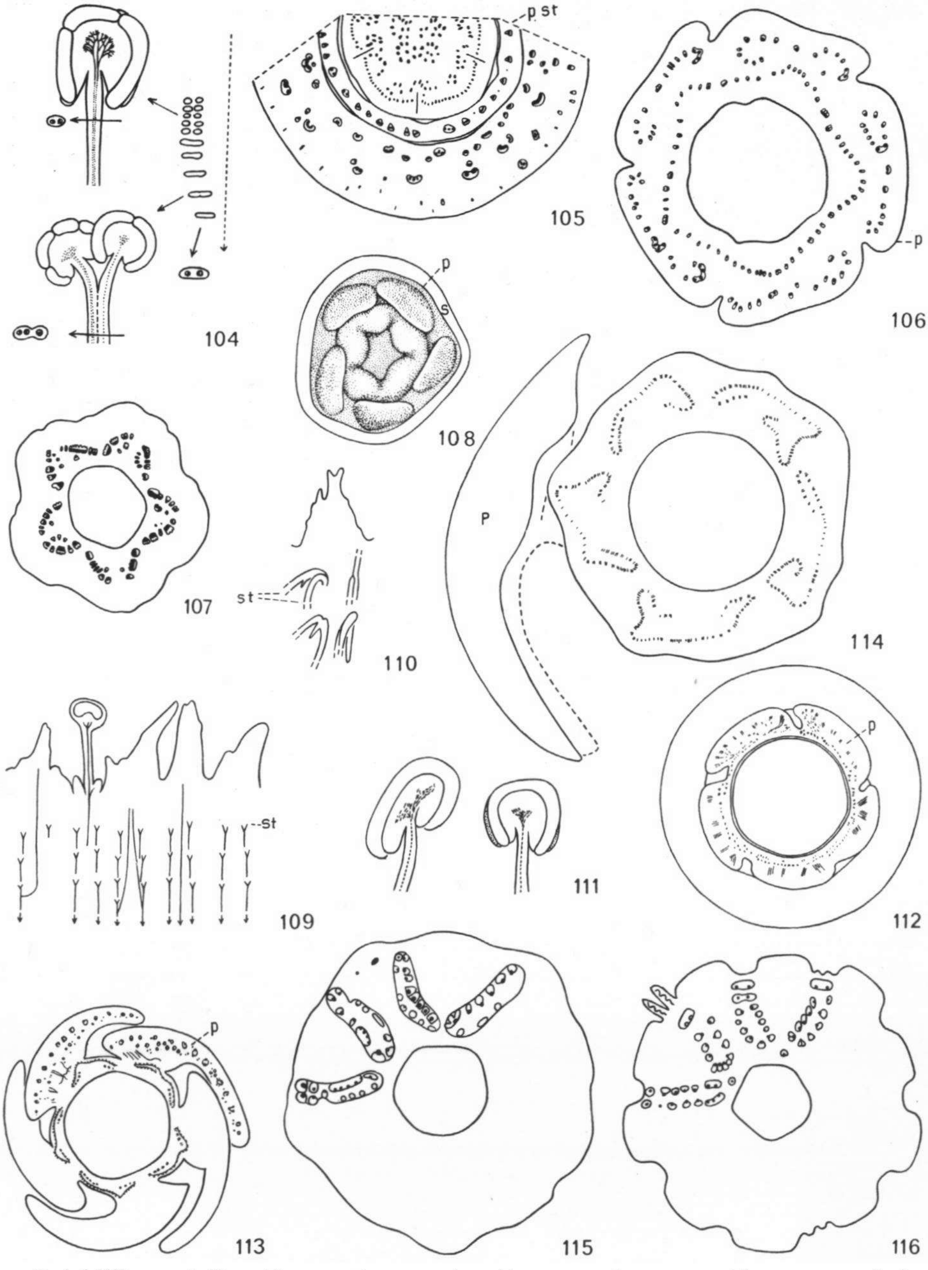
A few young floral phases were discovered in the bract axils of mature flowers. They show a very early stage of a stamen tube with five alternipetalous elevations (fig. 108). Accordingly the mature tube may end in five alternipetalous lobes. The tube may be twisted with the torsion lines for instance running upwards to the right if the petals overlap to the left.

Each row of stamens consists of stamens which are divided except for a common basal part. Each half bears a half-anther with two parallel reniform pollen sacs. The halves of a pair are not exactly equal, those towards petal radii being frequently larger than the outer halves. During ontogenesis the half-anthers are symmetrical.

Each half-stamen is provided with a single trace corresponding with the customary structure of the anthers. However, a double row of facing traces is supplied to each row of stamens as in *C. peekelii,* and two traces of each double row diverge into the split stamens one after the other. In other words, the point of splitting of the stamen bundles lies in the lower part of the tube instead of near the point where the stamens become free from the tube.

Kokia rockii

Along the distal part of a tube ten rows of 12—17 stamens are arranged, which may in floral buds be observed to approach sepal radii above and to bend towards petal radii below. Each stamen consists of a pair of half-stamens, the upper pairs of which may show a basal common part. The pairs develop through the postgenital collateral division of elliptic primordia, but later the two branches may come to lie diagonally or serially. The anthers are all, often asymmetrically, reniform and of about equal size. They are placed transversely and bear two pollen sacs. Downwards on the tube half-stamens occur either separately or one of the partners of a pair may be badly developed. The development of the stamens is centrifugal, but later the growth of the upper stamens



Cephalohibiscus peekelii. — Fig. 104. Representation of one row of stamens. — Figs. 105—107. Series of successively higher c.s. through base of petal stamen tube (5 ×).

Thespesia populnea. — Fig. 108. Initial androecium phase (40 ×).

Kokia rockii. — Fig. 109. Distal tube part, laid flat, with vascular bundle supply. — Fig. 110. Sterile appendages on the filaments. — Fig. 111. Some thecae. — Figs. 112—116. Series of successively higher c.s. through stamen tube. (Figs. 112, 113. 5 ×. Figs. 114—116. 10 ×).

is retarded. A special feature is formed by the subulate, mostly short, sterile branches attached to the inside of the proximal filament parts, belonging to the higher placed stamens (fig. 110). Between the rows one or a few stamens may appear below near petal radii, above near sepal radii. The latter may replace a lobe and be badly developed (fig. 109). The sterile extension of the tube has five bilobed lobes, the small lobes or teeth being situated in line with the rows of stamens. Later this lobing may become irregular with more tiny teeth along its margins.

Supply of vascular bundles

Above the level of departure of the epicalyx traces, the reconstituted stele falls apart into an outer continuous ring of calyx traces, five inner sectors towards the pistil, and a middle ring of bundles supplying the petals and stamens. The calyx traces enter the cupular calyx, branching into many parallel major bundles and many minor bundles which end beneath the basal adaxial nectariferous surface.

The petal-stamen ring is sometimes interrupted in sepal radii. From the very base upwards it is composed of a double whorl of concentric bundles except near the petal radii, where it is single. From this whorl many petal traces move outwards except perhaps near sepal radii. In the thick petals they form, besides the normal tangential series, many dispersed bundles inwards (fig. 113). Especially the bigger petal bundles have a concentric form.

Above the level of divergence of the petal traces the residual bundles ultimately separate into five antepetalous sectors of stamen traces. The flanks of the sectors are double with facing xylem, and the middle parts are single (fig. 112). Slightly upwards in the tube it appears that the innermost parts of the flanks more or less lose their facing position and for some distance form irregular inward loops as viewed in cross-section (fig. 113). In addition, higher up, the flanks change in position from parallel with to perpendicular to the petal surface. The middle parts of the sectors of stamen traces fade away upwards (fig. 114), though some bundles may persist and go to residual stamens near petal radii. Above this level ten double rows of bundles towards ten rows of stamens are formed, although the bundles of the inner parts are smaller and their lignification less marked, which perhaps means that the bundles tend to fade downwards. Higher up, at the level of stamen divergence, this difference is less marked. In cross-section, it is especially evident that the rows of traces approach one another adaxially in the sepal radii. In fact some linking bundles may be present there, going to persisting upper stamens near sepal radii (figs. 115, 116). These traces mostly end blindly downwards, but may also be connected with the row bundles.

Paired parts of the double rows move outwards into the paired half-stamens. The bundles have facing xylem, though at the bending point the xylem is directed towards the flower centre. In the filament the stamen bundle tends to the formation of a concentric combination of circa five xylem parts surrounded by continuous phloem. In the plane of the connective this bundle spreads in a broadly dichotomous way; in case the anthers are asymmetric one of the branching parts is longer.

B. COMPARATIVE PART

I. THE ARRANGEMENT OF THE STAMENS IN FULL-GROWN FLOWERS

The tube-formation

The androecium consists of stamens which form a tube by fusion of the filaments, except for the freely projecting distal parts. As the tube is very coherent it looks as if the free filament parts are complete stamens which are inserted on a tube. In the following we will use the notion of stamens being inserted on the tube, because it is convenient. As a matter of fact we are justified to do so, because both the ontogeny and the course of the vascular bundles indicate that the insertion of the distal filament parts on the tube reflects exactly the arrangement of the actual stamen bases on the receptacle. The petals are fused with the tube's base, markedly so in *Malopeae* and *Malveae*.

The rows of stamens

At first sight the stamens are inserted one above the other in ten longitudinal rows between sepal and petal radii. However, a more precise study reveals that the rows are not radial, because downwards they approach the petal radii, and upwards the sepal radii. If the insertion points are projected on a transverse plane of the flower ten rows result about perpendicular to the surface of the petals. Whereas in the middle or upper parts of the stamen-bearing region of the tube the rows are placed equidistantly or sometimes almost in sepal radii, they are placed more in front of the petals in the lower parts. There are also flowers in which the rows lie more near petal radii over their entire length. Similarly as the contorted petals are often inserted obliquely and not precisely alternate with the sepals, the stamen rows may also be shifted more towards sepal or petal radii. Moreover, the rows in front of the overlapping petal halves count more stamens than the other rows, because there is more room between the floral centre and the further outwards inserted overlapping petal halves. Therefore we may distinguish major and minor rows.

The wave-line formation

In some spp. a few stamens in imperfect stages may link the rows over the petal radii below, for instance in *Althaea rosea* and *Kokia rockii*. Moreover, in many spp. lower stamens are frequently not lying precisely in line, but are more towards the petal radii. Similarly the rows may be bent towards the sepal radii above, for instance in *Malope trifida* and *Sphaeralcea umbellata*. Finally, some imperfectly developed stamens may link the rows over the sepal radii above in *Kitaibelia vitifolia*, *Lagunaria patersonii*, and *Kokia rockii*. In *Napaea dioica* all stamens appear to be placed near the sepal radii. For these reasons we may state that the stamens are placed on a wave-line, the shanks of which show a full development, while the basal and upper bends are reduced.

The sterile parts terminating the tube

In many species of *Malvaceae* the staminal tube extends into a sterile part. In *Malopeae* and *Malveae* this character is not so outstanding. In *Kitaibelia* an occasional sterile tooth may occur on the rim of the tube near sepal radii. Small antesepalous lobes may also terminate the tube in *Sphaeralcea umbellata*. In *Kydia calycina* the tube is prolonged by five prominent antesepalous arms which bear the stamens. In most spp. the stamen tube is somewhat indented in petal radii, giving the tube a slightly lobed appearance with lobes near sepal radii, which are mostly split up into stamens, except for some uppermost sterile tissue of little importance in a few cases. In other species the tube is indented alternate with the petals and surmounted by slight antepetalous lobes which are consumed in the formation of stamens. We meet this condition in *Abutilon* and *Sida* spp., and in *Anoda lavateroides*.

In *Ureneae* and *Hibisceae* the tube is prolonged into a prominent sterile part which may be lobed or toothed. In *Urena lobata*, *Cephalohibiscus peekelii*, and *Thespesia populnea* this sterile apical extension is provided with distinct antesepalous lobes. In *Hibiscus* and *Pavonia* spp., *Malvaviscus arboreus*, *Gossypium hirsutum*, and *Papuodendron hooglandianum* antepetalous parts or lobes of the sterile tube extension are provided with teeth which are frequently in line with the minor rows.

A full understanding of the relations between these confusing data can only be reached by means of a study of the developmental phases. However, in advanced floral buds of *Hibiscus trionum*, the tube's mouth may prove to be lobed in antesepalous regions, and in buds of *Kokia rockii* it is evident that the tube is provided with antesepalous lobes which may themselves be lobed in line with the staminal rows or may bear less well developed stamens there, while more upwards small teeth are present along the tapering margins.

Summarizing we may state that the stamens occupy a wave-line, the inner and outer bends of which are absent, or may bear imperfectly developed stamens or staminodes. In contrast to the bends the shanks form the usual rows of stamens.

The double rows

Whereas the rows of stamens are as a rule formed by single forked stamens, in *Abutilon darwinii* they are formed by two forked stamens side by side, except in the distal region. Also in the subapical parts of the rows in *Althaea rosea* two forked stamens may be placed side by side. In *Cephalohibiscus peekelii*, on the other hand, we may speak of rows of two unforked stamens side by side, the filaments of which are towards the basal parts of the rows increasingly fused, forming longitudinally grooved bands.

The oligomerous androecia

The number of stamens present in a row may be limited to one, for instance in *Modiola caroliniana*, *Lavatera cretica*, *Malva crispa*, *Plagianthus glomeratus*, *Sida* spp. In that case the major row has mostly two stamens above each other. If these single stamens represent the minor rows, in front of the overlapped petal halves, they may moreover be badly developed or staminodial. Finally the single stamens in the minor rows may not develop at all, with the result that only five stamens remain forming the major rows in front of the overlapping petal halves (*Plaagianthus glomeratus*).

The whorls of stamens

The major and minor rows are frequently not placed simply side by side, the constituting stamens alternating like the links of a zipper. As a consequence, the stamens may be placed in alternating whorls of five when, in addition, chiefly in the middle stamen region, the rows are equidistant and the minor as well as the major rows are each on the same height in the different floral sectors. This effect is especially striking in *Lavatera*, *Malva*, *Sidalcea*, and *Hibiscus* spp., which have a medium number of stamens, viz. two or four in one row.

2. THE MATURE FORM OF THE STAMENS

The forked condition

The filaments are forked and each branch bears a reniform theca with two parallel pollen sacs. In *Hibiscus campylosiphon* the pollen sacs are partitioned by transverse septs. The thecae lie in the plane of the fork. Upwards in the staminal region the length of the common stalk decreases, so that ultimately the half-stamens are directly inserted on the tube. Upwards, the branching frequently changes from collateral to serial, passing through a diagonal stage in which the halves on the sides of the sepal radii are placed highest (in bud the halves of a stamen lie parallel to the sepal surface). In most *Ureneae* and *Hibisceae*, in *Plagianthus* spp. and in *Hoheria populnea*, only half-stamens seem to leave the tube. However, all these stamens are really the halves of serially split stamens, the branches of which are inserted on the tube directly. That this is so can be deduced from the arrangement of the half-stamens which is often distinctly in pairs. Moreover, in flowers of *Hibiscus trionum* and sometimes of *Lagunaria patersonii*, stalked serially split stamens may occur in the proximal region of the androecium, while upwards the length of the common stalks reduces to zero.

The unforked condition

Downwards in the staminal region the length of the stamens decreases, though also the distal stamens may be slightly shorter than the subdistal ones. Also the forked branches may become so short that ultimately the two thecae are placed in line upon a bilobed connective. If this trend is carried through, anthers with four pollen sacs result which down in the staminal region may furthermore pass into anthers with two pollen sacs passing through intermediate stages which show two anterior or posterior sacs in line and only one sac of double length on the opposite side. When we consider these anthers with two pollen sacs as the final products of this series of diminishing development, we may say that they do not represent ordinary half-stamens, but reduced forked bithecous stamens. Sometimes in this basal staminal region also single half-stamens may occur, judging the intermediate stages which have a very small sac on the side of a normal stamen half.

In the distal staminal region the structures described above occur seldom (*Malva* spp., *Lagunaria patersonii*), although single stamens with two pollen sacs are rather frequent (*Urena lobata*, *Napaea dioica*, *Plagianthus* and *Hibiscus* spp.). In *Abutilon darwinii* single forked stamens are present distally instead of two side by side.

Reduced stamens

In the phases of reduction described above the anthers still yield well-developed pollen, but there is a further reduction which finally leads to subulate sterile appendages replacing stamens. Intermediate stamens on mostly unsplit filaments bear slightly bilobed or spherical sacs, which replace the entire anthers or only their anterior or posterior halves (*Malva* spp., *Althaea rosea*). In *Hibiscus trionum* large nectariferous cells on unforked or forked stalks accompany the stamens either upwards and downwards in the rows or on the side of the stamens towards petal radii.

Special features

The unforked stamens of *Cephalohibiscus peekelii*, occur in double rows. Those in the middle of the staminal region have anthers with anterior as well as posterior up to four pollen sacs. Upwards and downwards the number decreases to one.

In the upper stamens of *Kokia rockii* one of the filament branches shows a sterile filamental secondary branch attached to the inside of its proximal part.

In *Sidalcea* spp. and also in *Sphaeralcea umbellata* superficial lateral fusions occur between stamens of different rows.

3. THE DEVELOPMENTAL STAGES OF THE ANDROECIUM

The origin of the rows of stamens

On the border of the floral apex which is enclosed by the young calyx a peripheral wall arises, leaving a lower part in the middle. First the wall which is on the whole pentagonal with alternisepalous angles, remains undifferentiated, but soon ten parts will develop upon it in advance of interjacent parts, forming ten staminal buttresses separated by sterile regions. The buttresses have a somewhat elliptic basal outline with the long axes not exactly radial. They represent the initial stages of the rows of stamens. The sterile antesepalous regions are rather broad and widening outwards, the sterile antepetalous regions narrower, at most somewhat wider centrally.

Sometimes the number of staminal buttresses seems to be limited to an initial five in alternisepalous regions, but it soon appears that they are divided superficially into two collateral parts by means of a shallow and radial groove at the time the stamen primordia arise upon them or only just before (*Abutilon* spp., *Althaea rosea*, *Anoda lavateroides*). In that case pairs of parallel buttresses are situated more in alternisepalous regions over their whole length. Also in *Kitaibelia vitifolia* antesepalous grooves originate in advance of the antepetalous grooves, as opposed to the condition in *Malope trifida.*

On the other hand staminal buttresses may be placed on a wave-line, the inward and outward bends of which are absent. In that case the buttresses approach one another near sepal radii with their central ends and near petal radii with their peripheral ends, and accordingly the alternisepalous groove is rather deep and also wide, especially in its central parts, while the antesepalous groove is rather shallow and wide especially in its peripheral parts. This is for instance the case in *Malope trifida*, on the staminal wall of which the alternisepalous grooves are earlier in appearance than the antesepalous grooves. For the same reason in *Sphaeralcea umbellata* and *Thespesia populnea* it seems appropriate to speak rather of trapezoid antesepalous staminal buttresses which are fertile along the margins and separated by deep radial alternisepalous grooves.

Intermediate conditions also occur, for instance in *Lavatera* spp., where the buttresses lie near petal radii outwards and between sepal and petal radii inwards.

The contorted condition

The ideal condition is sometimes almost reached in flowers which are hardly or not contorted. If contortion occurs the petals appear in an oblique way, namely more outwards and lower with their overlapping halves. As a result the staminal buttresses in front of these overlapping petal sides will develop more stamens towards of the periphery. Thus we are able to distinguish between major and minor rows of stamens. Moreover, the oblique petals are frequently inserted somewhat out of the petal radii. For instance, if they overlap to the left, the petals frequently deviate either to the right of petal radii so that the overlapping sides come to lie in alternisepalous regions, or to the left so that the overlapping halves come to lie in antesepalous regions. Correspondingly we see that the staminal buttresses deviate to the left or to the right, so that they approach sepal or petal radii instead of being placed in between these radii, especially so near the floral centre. Sometimes the major rows extend also more inwards (*Sidalcea* spp.).

The appearance of the petals

The primordial petals arise as oblique tangential ridges on the basal abaxial margin of the staminal wall, starting below the minor staminal buttresses and extending below the major buttresses. Generally in *Ureneae* and *Hibisceae* they would seem to arise before any stamen primordia, but in *Malopeae* and *Malveae* they arise rather when some stamen primordia are present. However, microscopic slides of *Kitaibelia vitifolia* suggest that the petals are initiated very early, but lay behind from the start.

The appearance of the stamens

On the buttresses the stamen primordia appear in rows in centrifugal direction. The later formed primordia may not merely prolong the rows in outward direction, but also along a line bending towards the middle of the petal, giving part of the outward bends of the wave-line described above.

Often the first stamen primordia arise on the inside slope of the wall (*Abutilon* and *Malva* spp.); they are followed by those reaching the summit and finally by those descending the outside slope. On the inside slope, quite close to the floral axis, the space available for the development of the initial stamen primordia is relatively limited. Accordingly the primordia may be rather crowded on the almost juxtaposed buttresses; they may even originate in a radially elliptic form. Their further development, chiefly the division into half-anthers or the stalking of the half-anthers, may be retarded, giving rise to stamens with four or two pollen sacs or to aborted forms. It may also happen that the development of the apical stamen primordia is temporarily arrested, and will only be regained after the very young tube has undergone some stretching (*Malope trifida*). On the outside slope the development decreases gradually, leading there to the same kind of reduced stamens.

The double rows

Seeing that upon the broad summits of the buttresses there is abundant space available and that the development is strong in that region, it is understandable that in *Abutilon darwinii* and in *Althaea rosea* an additional lateral row of stamen primordia arises there next to each median row on the side of sepal radii somewhat later. The additional row develops also in centrifugal direction, and its constituting stamens are situated rather precisely paired with the stamens of the median row. The predominant development of the middle staminal regions is also demonstrated by the fact that where, for instance in *Lavatera cretica*, fewer than ten stamens are present, these occur on the summits of the low buttresses and not on the apices.

The division of the stamens

Transverse parts of the buttresses develop into staminal protuberances, which are hemispheric first, but later become elliptic more or less perpendicular to the long axis of the buttresses. Then these elliptic protuberances become slightly tapering downwards and divided by a median division into two collateral halves, each representing a theca. Each theca forms an anterior and a posterior pollen sac and will become tapering downwards and finally stalked. In the elliptic stage the stamen primordia frequently turn for up to ninety degrees (*Lagunaria patersonii* and *Hibiscus rosa-sinensis*), except for the later formed primordia which stay in their original position. It is presumed that this turning has some bearing with a longitudinal development of the tube, which takes place especially in the antesepalous sterile parts. The middle primordia remain diagonal, with the highest halves placed towards the sepal radii. Sometimes the first primordia arise immediately in a turned position.

The tube formation

During the development of the stamen primordia the wall and the buttresses increase in size, representing the sterile and the congenitally fused fertile androecium parts.

Moreover, the buttresses are elevated upon a common sterile base, first chiefly with their central parts. This base later grows into the sterile proximal tube region.

In many spp. the buttresses develop considerably in advance of the sterile antesepalous regions (*Abutilon darwinii*) giving rise to a primordial tube which is thickest in alternisepalous regions, also inwards. The carpel primordia which arise late, will originate alternating with these inwards bulging young androecium parts, that is more or less opposite the sepals.

However, it appears that the fertile parts are advanced only in the beginning. Later the sterile parts of the primordial tube regain development vehemently, giving rise to a condition in which it appears that antesepalous trapezoid appendages which are fused proximally and somewhat bent inwards apically, bear stamen primordia along the fused and — in a reduced form — also along the free margins (*Kitaibelia vitifolia*). Later the inward bent parts stretch upwards in all cases.

In *Malope trifida, Sphaeralcea umbellata,* and *Lagunaria patersonii* the antesepalous tube parts are advanced from the start. Accordingly in *Malope trifida* the primordial alternisepalous carpels take the outward positions as opposed to the carpels in *Kitaibelia vitifolia.* Generally it may be stated that the carpel position depends on the time the carpel primordia arise on the receptacle correlated with the form of the inner base of the young stamen tube which may vary during its development as described above. For instance in *Urena lobata,* antepetalous carpels arise when the antesepalous part of the tube is enlarged. Moreover, the place of the carpels is influenced by the contorted characters.

The sterile parts terminating the tube

In the mature stage the original advanced condition of the antesepalous sterile tube parts — in the three spp. mentioned above — may persist as marked antesepalous lobes terminating the tube (also present in *Kokia rockii*). However, in most spp. in which the sterile tube parts originate somewhat late, these parts, when the flower reaches a mature stage, gradually become insignificant again through the final enormous enlargement of the fertile parts. Sometimes in *Malopeae* and *Malveae* hardly visible tiny teeth are present on the inside of the tube's mouth (*Kitaibelia vitifolia, Malva* spp.) which represent the apices of the sterile antesepalous tube parts.

In *Ureneae* and *Hibisceae* the tube is terminated by an obvious sterile extension which is formed by considerably stretched staminodial structures in line with the rows of normally built stamens. As in *Malveae* the original antesepalous lobes of the young tube become of unimportant size as compared to these staminodial regions during the later stages in development. Only in *Lagunaria patersonii* the antesepalous lobing may persist, but in an irregular form in my material. On the other hand in regular young buds of *Kokia rockii* the conditions are instructive. The tube is provided terminally with antesepalous tapering or rounded lobes, along the margins of which successively less well developed stamens may occur, first in line with the rows of stamens but ultimately bending towards sepal radii. Still higher large triangular to subulate appendages may arise. The most proximal of these appendages correspond with the teeth on the tube known from *Hibiscus* spp., the antesepalous apical lobe parts themselves correspond clearly with similar parts persisting in other spp. (*Lagunaria patersonii, Sphaeralcea umbellata* and *Malope trifida*). These apical parts are in most species outsized by the fertile parts, as stated above, and the original antesepalous lobing may then only be detected by the presence of a slight antepetalous indentation of the mouth of the tube present between the filaments.

4. THE VASCULAR BUNDLE SUPPLY TOWARDS THE ANDROECIUM

The stamen traces

Each stamen is supplied by a trace which divides into two traces near the place of external division into two half-stamens. The course of the traces corresponds exactly with the position of the stamens. Therefore it is evident that the stamen traces in the tube are arranged in ten rows more or less at right angles to the petal surface. The rows of vessels constituting the xylem of the stamen traces are not placed radially in the flower but perpendicular to the rows and on the side of the petal radii. Where the traces move out of the tube the xylem is directed slightly more towards the floral centre, and near the point of division of the traces the xylem of the branches may be slightly facing each other over a short distance. The traces move outwards successively, abaxial traces towards the lower placed adaxial traces towards the higher placed stamens. If in *Ureneae* and *Hibisceae* a close observation of the external features does not inform us on the paired condition of the half-stamens, this condition immediately follows from the division of the traces.

In *Abutilon darwinii* abaxial parts of the rows move outwards rather quickly, forming double rows over a short distance, and bifurcate into two stamen traces. The xylem of all unforked traces is directed towards the petal radii, that of forked traces more towards the floral centre.

The stamen fascicle traces

In the distal region of the tube where the stamens diverge the trace for each stamen is clearly dissernable. However, further downwards, in the sterile region of the tube, the stamen traces are more or less fused laterally, the abaxial traces linking up with the adaxial ones. This fusion may increase downwards and ultimately the combination of stamen traces may be represented by a bundle with only a few xylem groups and a cap of phloem which, in cross-section is more or less bean-shaped with the concave side directed towards a position intermediate between petal radii and the centre of the flower. This bundle is called the stamen fascicle trace.

When we follow the stamen fascicle trace in its upward course we may say that it divides into the successive stamen traces, or that the stamen traces separate from it successively. As stated above the trace may be more or less condensed. If there is hardly any condensation, the constituting stamen traces remain distinct and tend to be attached to the underlying vascular tissue separately (*Kitaibelia vitifolia*), a stage which is never fully reached. The fascicle traces may be considered as paired, first because of their xylem position, secondly because they are not placed equidistantly, but on the whole more towards petal radii, especially so in the proximal part of the tube.

The attachment of the stamen fascicle and petal traces

The attachment of the stamen fascicle traces usually takes place to the perianth — chiefly to the calyx — supply, and often by means of a double or multiple base in a rather variable fashion.

In *Malope trifida* and generally in the *Malveae*, in each flower sector two stamen fascicle traces and a petal trace are attached to the flanks of the sepal median traces, that is the stamen fascicle trace of a major stamen row to one of the sides, the minor stamen fascicle trace and the petal trace to another side. However, it is possible that the traces are (also) attached to the wrong side of the sepal median trace, or to the proximal parts of the sepal basal laterals, or to the cross-arcs (by a double or multiple basal course). This variable attachment is shown very well in *Althaea rosea* (fig. 38).

In correspondence with the contorted condition all these traces follow a basal, slightly oblique, upward course towards the petal radii. If the petals overlap to the left the deviation of the trace is towards the right, if they overlap to the right the deviation is to the left.

Frequently the petal and the minor stamen fascicle traces run very close together or have a common basal trace (*Malva, Sidalcea,* and *Plagianthus* spp.). The common basal trace, in its oblique upward course may sometimes lie very close along a sepal basal lateral trace and may even form a concentric bundle with that trace (*Malope trifida, Malva sylvestris*). In *Malvastrum capense, Anoda lavateroides,* and *Lagunaria patersonii* two stamen fascicle traces and a petal trace together form in the receptacle a basal, oblique, broad collateral bundle (which closes a sepal gap).

The petal trace may spread towards the petal base forming some middle bundles and two basal lateral bundles which are the common traces for the petal lateral nerves. Some abaxial parts of the stamen fascicle traces may be attached to the petal basal laterals, especially on the side of the overlapped petal half (*Malope trifida,* figs 9, 10). Other less abaxial parts of the fascicle may be attached to the other fascicle parts, but end blindly upwards instead of innervating stamens (*Lavatera olbia, Malope trifida*). Conversely, petal laterals may be attached to the stamen fascicle traces, mostly to the minor stamen fascicle traces (*Malvastrum capense, Sidalcea* and *Sida* spp.), so that the petal trace only produces a petal median or some petal middle bundles. Sometimes separate petal traces are no longer present in some or all flower sectors, all petal bundles being attached to the stamen fascicle traces (*Abutilon darwinii, Lavatera cretica, Malva* spp.). In *Anoda lavateroides* the petal laterals may show a double attachment at the petal basal lateral and the major stamen fascicle traces. Connections between the stamen fascicle traces and the petal innervation at the level of petal divergence are absent in *Althaea rosea* and in *Hoheria populnea.*

In the base of the tube above the level of petal divergence the stamen fascicle traces may unite in *Sphaeralcea umbellata, Althaea rosea, Lavatera olbia, Sidalcea* spp. and *Lagunaria patersonii.* Middle units of these combinations fall apart into small bundles which run upwards into the tube, soon to end there blindly, or — in *Althaea rosea* — to supply less well developed proximal stamens near petal radii.

In *Kitaibelia vitifolia,* and in the *Ureneae* and *Hibisceae* generally, the petal trace is spread tangentially, forming at the base broadly collateral bundles together with the stamen fascicle traces at their flanks. In this respect some species, such as *Hibiscus trionum* and *micrantha* are more or less intermediate between *Ureneae* and *Hibisceae* on the one hand, and *Malveae* on the other. Mostly, abaxial parts of the stamen fascicle traces join the lateral petal traces. In addition, in *Kitaibelia vitifolia, Urena lobata, Hibiscus trionum,* and *Kokia rockii* tiny bundles move upwards into the tube, coming from the middle petal nerves. These bundles soon end blindly or may innervate reduced proximal antepetalous stamens (*Hibiscus trionum, Kokia rockii*).

By means of double or multiple bases the collateral petal stamen traces are attached either to the sepal basal laterals near the summits of the cross-arcs or to the sepal commissural marginal traces (*Kitaibelia vitifolia, Urena lobata, Malvaviscus arboreus*). In *Papuodendron lepidotum* they may form together with pistil traces more or less perfect concentric bundles which are attached at the sepal commissurals.

In several *Ureneae* petal commissural marginal traces are present which end blindly downwards. Only in *Malvaviscus arboreus* they may be attached to the sepal supply.

Some special ways of attachment of the stamen traces

In *Gossypium hirsutum* and especially in *Cephalohibiscus peekelii* and *Kokia rockii* the collateral base of the petal-stamen supply is so much spread tangentially that in the base of the tube a pentagonal formation of bundles occurs, which may only be interrupted near sepal radii. In *Cephalohibiscus peekelii* from the entire pentagon petal traces separate outwards, leaving a similar formation of stamen traces inwards. This second pentagon changes into a wave-line upwards which in the stamen bearing region falls apart into ten diagonal double rows of stamen traces with facing xylem. Pairs of traces are given off towards the paired stamens. In *Thespesia populnea* also these double rows occur, which give off pairs of traces towards the paired half-stamens. In *Kokia rockii* the ring of petal-stamen traces and, above the level of departure of the petal traces, the broad sectors of stamen traces are double from the very base, except near petal radii. The stamen traces near petal radii end upwards blindly into the proximal part of the tube, or innervate rather badly developed stamens there. In this species, residual stamen traces or traces towards less well developed stamens or staminodes occur also in the distal tube part near sepal radii. They end blindly downwards. The flanks of the stamen trace sectors are double rows of stamen traces with facing xylem from the base. Upwards they form the shanks of a wave-line and give off pairs of stamen traces outwards which move into the halves of the stamens.

The division of the stamen bundles in the connective

The filament has a single collateral bundle. Only in *Kokia rockii* the bundle is concentric and spreads into the connective forming a coherent ramificating system which on the whole is dichotomous. In *Cephalohibiscus peekelii* each of the filament traces divides into two parallel bundles with facing xylem, which in the connective together produce an irregular but extensive ramification system.

In most species of *Malvaceae* there is some distinct short vascular bundle tissue at the end of the stamen bundle, which mostly is irregularly branching chiefly in the plane of the connective (*Malope trifida, Althaea rosea, Malva* spp.) but is sometimes slightly dichotomous (*Lavatera cretica*). However, in basal and upper unsplit stamens a prominent splitting of the vascular bundle takes place into two outward bending branches (*Malva* spp., *Hibiscus trionum*). In *Lagunaria patersonii* each of these branches consists rather of some branches one above the other. In *Kitaibelia vitifolia* and in *Hibiscus rosa-sinensis* also the half-anthers show two apotropous branches, each branch or only one showing a short tiny subsidiary branch which separates proximally and proceeds the upward course of the unforked bundle. Also in *Hibiscus campylosiphon* the two bending branches are irregular. In the connectives of the unforked stamens with four pollen sacs of *Hibiscus rosa-sinensis* var. *liliiflorus* the conditions are similar, the subsidiary branches being more prominent. Some stamens which are still forked, may have in each half-anther one outwards bending branch which gives off some subsidiary branches towards the median halves of the connectives (fig. 79). The situation in *Hibiscus syriacus* is similar to that in *Hibiscus rosa-sinensis*, with the difference that the division points lie more down in the filaments which, together with the connectives, tend to be flattened. The result is that the innervation seems to be fan-shaped, especially in the unforked lower stamens.

5. THE SEPALS, THE PETALS, AND THE GLANDULAR TISSUE

The sepals

The calyx is a lobed tube which in cross-section is slightly pentagonal in petal or sometimes in sepal radii, on the outside as well as mostly on the inside. In the material of *Malope trifida, Abutilon darwinii, Althaea rosea, Napaea dioica, Malvastrum capense, Sida* spp., and *Anoda lavateroides* the calyx is slightly pentagonal in sepal radii, at least in its epibasal parts. In *Lagunaria patersonii, Thespesia populnea, Cephalohibiscus peekelii, Hibiscadelphus giffordianus,* and *Kokia rockii* the calyx is somewhat thick and cupuliform.

The innervation towards the calyx takes place by a sepal median trace which divides into three bundles, a sepal median bundle and two sepal basal laterals on either side. The most lateral sepal bundles may form cross-arcs by their double or multiple bases, which link the systems of adjoining sepals over the petal radii. Especially in *Ureneae* and *Hibisceae,* they may likewise form sepal commissurals in some or all flower sectors which are connected with the stele in petal radii. In some *Hibiscus* spp. the lateral sepal traces are attached to the vascular bundle supply towards the epicalyx. In *Plagianthus betulinus* common traces occur which split into a sepal median trace and one or two oblique sepal commissural traces. In small-flowered species the calyx innervation tends to be most variable (*Malva* spp.). In thick calyces and corollas a ring-formed mass of dispersed bundles is found, many of which may become concentric in the proximal part, but collateral again higher up. The minor bundles of these thick calyces may move downwards through the cortex and link up with bracteole traces or end blindly, forming a sometimes conspicuous cortical system in the base of the receptacle and petiole.

The petals

The position and vascular bundle supply of the petals have been described extensively in the preceding paragraphs on the androecium. However, some details may be added here. The overlapping outer and lower parts of the petals are mostly inserted near petal radii, but in species in which the sepals are slightly pentagonal in sepal radii — as seen in an epibasal cross-section — they are situated nearer to sepal radii. If the petals overlap to the left the traces towards the petals and stamens always deviate towards the right and the young stamen rows have their torsion lines going towards the left (if followed from below upwards). In a mature stage an additional twisting may seize the stamen-bearing tube region, which is the reverse of that in a young stage, the torsion lines going towards the right in the above example (*Sidalcea* spp., *Thespesia populnea, Hibiscus rosa-sinensis*). The rows of stamens in front of the overlapping petal halves are always the major rows. In species with small flowers the aestivation of the corolla is sometimes variable or quincuncial, for instance in *Plagianthus betulinus, Lavatera cretica* (also in *Kydia calycina*). The petal primordia arise invariably first below the minor, later below the major rows of stamens and never exactly simultaneously. In *Ureneae* and *Hibisceae* they have the tendency to arise early in comparison with the stamens, though also in *Napaea dioica* and *Sida* spp. of the *Malveae* they may appear early. In the species with thick and cupular calyces the development is much in advance of the rest of the flower.

The glandular tissue

In almost all species of *Malvaceae* fields of nectariferous trichomes are present on the inside base of the sepals, in some even a continuous annular field is formed on the calyx base (*Abutilon darwinii, Hibiscus rosa-sinensis*). A number of side-nerves which ramify and anastomose abundantly under the nectariferous surface may be detached either from the proximal parts of the sepal nerves (*Urena lobata, Hibiscus rosa-sinensis* and *campylosiphon*), or from the lateral or commissural marginal sepal nerves only (*Abutilon darwinii, Anoda lavateroides*). In the thick calyces of *Cephalohibiscus peekelii* and *Kokia rockii* the adaxial members of the dispersed calyx bundles terminate their course under the nectariferous surface. In *Hibiscus pulvinulifer* and *Papuodendron* spp. the nectariferous tissue in the axil of the sepals is limited or absent. However, it is abundantly present in fields on the base of the petals and the stamen tube. In *Hibiscus pulvinulifer* some branches from the proximal parts of the petal nerves — and in *Papuodendron lepidotum* 1 or 2 branches from each petal basal lateral — give some basal forkings which end in profuse ramifications under the nectariferous surface. In *Papuodendron hooglandianum* only curling bundles coming from the petal nerves supply the nectaries.

6. VARIATION IN THE COURSE OF THE VASCULAR BUNDLES

The multiple attachment

Sepal lateral bundles, petal traces, stamen fascicle traces, and petal stamen fascicle traces are frequently attached to underlying vascular bundles by means of a double, multiple, or even fasciculate base. The variable connection of the sepal lateral bundles either leads to cross-arcs linking adjoining sepallary systems, or to sepal commissural traces in petal radii or to both in some or all flower sectors. In *Hibiscus rosa-sinensis* the sepal median and commissural traces and the petal stamen traces prove to be attached by double bases only if no reconstitution of the stele between bracteoles, calyx, and petals takes place (no growth in length of the floral apex intermittent to the forming of the different whorls). Otherwise, they are attached to the reconstituted stele directly. In *Abutilon darwinii* a stamen fascicle trace passing close over a cross-arc may show some tiny connections with this cross-arc. Not only sepal but also petal lateral traces may have double or multiple bases forming petal commissural lateral traces near sepal radii (*Urena lobata, Pavonia praemorsa, Malvaviscus arboreus*). In *Anoda lavateroides* outside petal laterals, mainly on the overlapped petal sides, may also be connected with the major stamen fascicle traces belonging to adjoining petals.

The attachment of peripheral traces to heterogeneous vascular bundles

In *Abutilon darwinii, Malva* spp., *Malvastrum capense* some or all petal laterals are attached to the stamen fascicle traces, especially to the minor ones. The minor stamen fascicle trace and the petal trace often run very close together or may have a common basal course. In *Malveae* the most abaxial parts of the stamen fascicle traces are usually connected with the petal basal laterals or even to the petal nerves basally. Some middle and lower stamen traces may join the fascicle traces by a common basal course in *Abutilon megapotamicum*.

Concentric bundles

Concentric or almost concentric bundles are of common occurrence in some species. They mostly have a distinct composed nature. In *Malva* they are composed of a sepal basal lateral, a petal trace, and a minor stamen fascicle trace; in *Urena lobata, Malvaviscus arboreus*, and *Hibiscus trionum* and *syriacus* of pistil traces and petal stamen traces; in *Hibiscus pulvinulifer* and *Papuodendron lepidotum* of pistil traces, sepal laterals, and petal stamen traces. Moreover, in *Hibiscus trionum* sepal basal laterals and part of the epicalyx supply may form concentric bundles. All these concentric bundles are attached to the underlying calyx or epicalyx supply in a double or multiple way.

Another kind of concentric combinations occur in the proximal parts of the fleshy calyces and petals or receptacles of some plants, such as *Cephalohibiscus peekelii* and *Kokia rockii*.

In the filaments of *Kokia rockii* the bundles are concentric.

'Hesitating' bundles

This phenomenon is related to the fact that many bundles have double or multiple traces. A bundle first deviates downwards towards a certain (heterogeneous) bundle, but ultimately rather suddenly returns towards another (more usual) attachment place, some diffuse vascular tissue possibly continuing the deviating course for some distance. This occurs in petal laterals which may be attached either to stamen fascicle traces or to the petal median traces in *Abutilon megapotamicum* and *Sidalcea* spp. In *Malvaviscus arboreus* the petal laterals may join commissural bundles or petal median traces. Furthermore abaxial parts of stamen fascicle traces may or finally may not proceed their course towards the petal basal laterals in *Malva* spp. and in *Hoheria populnea.*

Residual bundles

Some abaxial parts of stamen fascicle traces may end blindly upwards or innervate reduced antepetalous stamens in *Althaea rosea, Hibiscus trionum, Lagunaria patersonii,* and *Kokia rockii.* These abaxial parts are mostly connected with the bases of petal nerves. In *Althaea rosea* the traces may show interrupted lignification.

In the middle parts of the tube in *Kokia rockii* lignification is less in the stamen bundles belonging to the inner parts of the double rows.

In species with a tendency for petal commissural lateral formation these traces may fade downwards.

Up in the tube residual traces may occur in line with the stamen rows in *Lavatera cretica, Hibiscus rosa-sinensis,* and *Cephalohibiscus peekelii.* Traces to more or less reduced antesepalous upper stamens may fade downwards in *Lagunaria patersonii* and *Kokia rockii.*

In *Napaea dioica* minor stamen fascicle traces and stamen traces may end blindly downwards. Unlignified double based vascular tissue may link the stamen fascicle traces over the sepal radii.

C. INTERPRETATIVE PART

The staminal lobes

The stamens are arranged along the sides of more or less trapezoid alternipetalous lobes which are for the greater part fused congenitally forming a tube. Upon a low pentagonal wall (the proximal part of the primordial tube) the lobes originate in an inwards bent position which is largely corrected in a later phase of growth, the central parts being stretched in an upward direction more than the peripheral parts.

The apical and median regions of the lobes are at first mostly not very well developed, represented as they are by the more or less antesepalous wide and low regions of the primordial stamen tube. On the other hand the lateral parts of the lobes are advanced forming ten staminal buttresses which together are situated as it were along the antepetalous shanks of a wave-line with alternipetalous inward bends. Upon these buttresses the stamen primordia originate in centrifugal rows, no sterile tissue remaining between the stamens of adjoining lobes (figs 6, 24, 26, 36), except in *Kokia rockii,* where the stamens seem to be placed slightly submarginally. Also in the primordia of *Kitaibelia vitifolia* and *Lagunaria patersonii* the lower (outer) stamens are placed submarginally, the sides of the lobes being, in addition, placed more inwards. The lobes are thicker there (figs 16, 75, 116).

Most advanced are the lateral regions in, for example, *Althaea rosea, Abutilon darwinii,* and *Anoda lavateroides,* where commissural antepetalous buttresses are formed, which are only separated when the stamen primordia arise upon them. In cases like these there is a marked apical sterilization of the staminal lobes. Mostly these apical and median parts have a considerable growth later on.

In some other species the apical parts of the lobes may be rather well developed from the start, for instance in *Malope trifida*, *Sphaeralcea umbellata*, *Lagunaria patersonii* and *Thespesia populnea*. Here we note that on the whole the origin of the alternipetalous lobes, especially as regards the apical and median regions, is more sharply demarcated, the antepetalous buttresses not being so much advanced in contrast with the median parts of the lobes.

In some species, especially in those with initially well developed apical parts, the upward sterilization as it is demonstrated in the form of the stamens is gradual, leading to unsplit or monothecous or even less well formed stamens, and finally to completely sterile triangular and subulate appendages. In these central regions we may also notice a certain slowing down in the development of the primary formations, probably caused by lack of space, which is compensated after the beginning of the stretching of the staminal lobes. These gradually more undeveloped stamens or staminodes are placed more towards the alternipetalous regions in proportion to the height of their insertion on the staminal lobes. In several species such as *Kokia rockii* and *Lagunaria patersonii* they are still supplied by vascular bundles which may end blindly downwards.

The strength of the centrifugal development of the stamens gradually decreases outwards, giving rise to similar sterilized staminal structures. In some species these structures may originate more sidewards and seem to link the rows of stamens of adjoining lobes over the antepetalous regions (*Kokia rockii*, *Hibiscus trionum*, *Althaea rosea*). In *Kitaibelia vitifolia*, *Urena lobata*, *Lavatera olbia*, and *Malope trifida* there are only residual bundles in those regions.

The alternipetalous apical lobe parts and their staminodes may persist in some species, especially in those in which they are prominent from the start (*Lagunaria patersonii*, also in *Urena lobata*). But generally the apical lobes are later completely outsized by the ultimate stretching of the stamens, although sometimes a rest may remain in the form of a tiny subulate tooth. However, it should be added that in *Ureneae* and *Hibisceae* the subapical staminodes may be subject to this ultimate stretching, so that subulate appendages may surmount the sterile mouth of the tube in line with the staminal rows, somewhere between sepal and petal radii.

The contorted condition

The staminal lobes originate successively, although almost simultaneously, in an indefinite sequence. The same holds for the petals which frequently, especially in *Malveae*, arise rather late below the abaxial base of the buttresses and alternating with the staminal lobes. Irrespective of the sequence in their appearance the petals overlap one another in a contorted way and on their overlapping sides are inserted more outwards. Moreover, they are never placed in the alternisepalous radii in an exactly symmetrical way, but deviate towards the left or the right. This deviation is independent of the way in which the petal margins overlap and it may be of variable extent in flowers of the same plant. Generally the outward overlapping petal margins are inserted where most space is available. If fusion with the stamen tube is high the petals are placed more in front of the epibasal parts of the sepals which are there naviculate (frequent in *Malveae*). On the other hand, if the fusion is less prominent they are placed more in the corners between the insertion places of the sepals (frequent in *Ureneae* and *Hibisceae*).

The staminal lobes show the same deviation towards the left or the right as the petals, the margins, in addition, neither being placed radially in the flower, nor at right angles to the petal surface, but somewhat inclining towards this surface (figs 337, 338). The petals and lobes originate in an already contorted position, and the twisting continues during further growth. Correspondingly the position of the apical parts of the staminal lobes and their possible staminodial structures, which has been described above for an ideal flower, is shifted to a variable extent. This is precisely the reason why the place of sterile extensions of the mouth of the tube has been so much debated upon. Therefore also the position of the carpels is variable, alternating as they are with those parts of the staminal lobes which are most advanced when the carpel primordia arise, in agreement with the principle of the maximum available space.

The contorted condition is demonstrated by the oblique course of the (petal) stamen fascicle traces. Each staminal lobe receives two lateral (fascicle) traces. The direction of this oblique course is constant, namely either to the right if the petals overlap with their left margins, or conversely. It bears no relation to the deviation of the petals from the alternisepalous radii. In *Malveae* the petal insertion frequently deviates towards the side of that sepal at the median trace of which the petal and stamen fascicle traces are attached. On the other hand, in *Ureneae* and *Hibisceae* the petal insertion frequently deviates towards the far side of the alternisepalous radii. Still the direction of the oblique course of the petal-stamen fascicle trace remains the same, so that in the second case an attachment of the petal-stamen trace to the trace of the nearest sepal is not effectuated. It may be imagined that in the latter case the problem of avoiding the extreme long oblique way of the petal-stamen fascicle trace is solved by linking up the petal-stamen fascicle traces not with the sepal median trace, but rather with the sepal basal laterals near the alternisepalous radii on the side towards which the petals and staminal lobes deviate. This constant and independent oblique course shows that the same twisting affects the petals as well as the staminal lobes, which is a strong argument for considering the petals and the staminal lobes as intimately connected. It may account also for the peculiar inclination which is exhibited by the staminal lobes in relation to the petals, as described above. In *Malveae* the petal and minor stamen fascicle trace may often have common basal traces.

The contorted condition makes it possible that one of the margins of the staminal lobes — the one in front of the overlapping more outward situated petal margin — has the opportunity to develop more peripheral stamen primordia, because of the available space (major rows of stamens). The stamen primordia of a major and a minor row of adjacent staminal lobes may be arranged like the links of a zipper. In that case, and if the different floral sectors are of fairly equal size, several whorls of five stamens are formed.

The development of the rows may be limited to a single forked, unforked, or only monothecous stamen. Residual vascular traces show that these stamens represent the middle members of normally developing rows, not the most apical members. They originate from primordia which are placed on the summits of the staminal buttresses, the innermost and outermost primordia being reduced. It may also happen that only the major rows retain one stamen each, the minor rows being on the whole in a reduced form. The result is the occurrence of flowers with only five stamens which, owing to the contorted condition, may possibly be placed quite near the sepal or petal radii.

The structure and position of the stamens

The hemispherical stamen primordia become elliptic with the long axes placed perpendicular to the lateral sides of the staminal lobes. They fall apart into two collateral halves in line. An incipient longitudinal growth which takes place predominantly in the central parts and in the median plane of the initially retarded staminal lobes may move the elliptic primordia into a diagonal position, in the *Ureneae* and *Hibisceae* even into a position almost parallel with the lateral sides of the staminal lobes, so that the primordia seem to divide serially. The strongest longitudinal growth takes place in the uppermost lobe parts. This is conformable to the fact that especially the upper stamens are most clearly divided serially.

The traces of these stamens are divided — frequently while still being in the tissue of the lobes — into two collateral parts with a tendency toward xylem facing. The inner component of this division may go into the upper half of a serially arranged pair of half-stamens. Two half-stamens may diverge from the tube by means of a common base, but frequently each of the halves diverges from the tube directly, especially when they are arranged serially, suggesting the existance of individual monothecous stamens. In that case the arrangement in pairs follows from ontogeny as well as from the vascular course. In the free parts of the filaments the xylem is directed towards the centre of the flower.

The stamen traces are arranged as the shanks of the wave-line on which the stamen primordia are situated. They are not arranged tangentially, except at the very base of the tube in some species (*Cephalohibiscus peekelii, Kokia rockii*). This means that the staminal lobes have a certain thickness, especially in their proximal parts.

Downwards the stamen traces are fascicled into common traces, which remain collateral bundles with rows of vessels directed towards and placed perpendicular to the lateral sides of the staminal lobes (or the shanks of the wave-line on which the stamens are situated). In *Malveae* the stamen fascicle traces are connected with the flanks of the sepal traces or with the proximal parts of the sepal basal laterals in a multiple way. On the other hand in *Ureneae* and *Hibisceae* the fascicle traces are first attached to a petal trace basally together forming a petal stamen fascicle trace. This in turn is attached to the sepal basal lateral near the cross-arcs or to the sepal commissural lateral, also frequently by means of a multiple base. This difference in attachment may be correlated with the initiation of the petals, which in *Hibisceae* is on the whole rather early, so that later the incipient stamen fascicle traces may be connected with well-formed petal traces. In the *Malveae* the initiation of the petals is rather late. Therefore here the petal traces, especially the laterals, link up with already well-formed stamen fascicle traces. The difference in the time of petal initiation may be correlated with the extent of the fusion between petals and staminal tube. In *Kokia rockii, Cephalohibiscus peekelii,* and to a less degree in *Gossypium hirsutum* the stamen traces are not very fasciculated but remain spread tangentially and unite with the many petal traces forming common basal traces. These in turn are connected with the strongly spread calyx supply. This particular condition is thought to be related with the thickness of the calyces and the broad and flat flowering apices.

In *Abutilon darwinii* the members of the rows of stamen traces separate upwards moving directly into two rows of stamens which originate in pairs side by side, except in the upper (central) regions where the rows are single. Each of the stamens is divided into two half-stamens as usual. In *Thespesia populnea* there are double rows of stamen traces with facing xylem although the rows of the split stamens themselves are single, each of the traces going towards a half-stamen. Probably this feature may be explained by assuming that the longitudinal growth which seizes the staminal lobes takes place especially on the levels where the stamen traces *i.s.n.* are forked into two traces. In that case one may say that the forked parts of the filaments are also fused into the tube. However, this explanation will give difficulties in *Abutilon darwinii.* Moreover, the free parts of the filaments of the half stamens in *Thespesia populnea* mostly have a common base with which they adhere to the tube. It rather seems that our ideas are too rigid in considering the monothecous stamens as just ordinary half-stamens, and that this is the reason why the above explanation meets with some difficulties. Maybe we are not permitted to regard the ordinary bithecous stamen as the most stable construction in this group of plants.

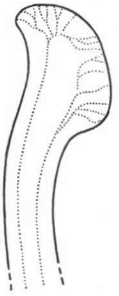
In *Kokia rockii* we also meet with the double rows of facing stamen traces in the tube, but here the uppermost split stamens bear reduced branches on the proximal parts of their filaments. Evidently this condition is intermediate between those of *Abutilon darwinii* and *Thespesia populnea.* At the same time it tells that the structures called half-stamens are not indivisible but may be divided again, not into monosporangiate products, but into the same reniform bisporangiate thecae. However, the first division is not externally visible in ontogeny; it must take place within the primordial lobe tissue. Maybe it can be demonstrated histogenetically in *Abutilon darwinii.*

Concurrently we note that in the peripheral regions as well as in the originally closely packed apical regions of the staminal lobes the more or less failing division may lead not only to bithecous anthers but ultimately to monothecous bisporangiate anthers, passing intermediate conditions with three pollen sacs, two in line and one of double length opposite.

All this means that the elliptic slightly stalked staminal meristem either may form a monothecous stamen or may form by an early division two equal and monothecous halves in line (if growing out above a certain maximum width). Moreover, the halves may repeat this process. However, it must be added that the division, if occurring in a later phase of development, may affect only the superficial or slightly deeper layers of the meristem giving rise to intermediate types of stamens with two bisporangiate thecae in line along a broad more or less bilobed connective. This view is properly illustrated in the series of stamens of *Cephalohibiscus peekelii* in which species fully developed members (secondary division) of the double rows (primary division) undergo a tertiary division in the pollen sac region, the less well developed members remaining in the form of thecae with two pollen sacs only. Here we also notice how we might interpret stamens with partitioned pollen sacs as in *Hibiscus campylosiphon,* namely as the result of a series of superficial divisions.

The thecae are innervated by single unbranched bundles. However, in most thecae of normal size the bundles are somewhat spread at the top in the plane of the filament. If the thecae are still broader we notice in this spreading vascular tissue a prominency into two lateral directions. If the sporangial tissue and also the peripheral parts of the connective are split, this leads to the occurrence of two sidewards bending branches with some residual tissue remaining in the middle. If the division has been carried on further, so that the two halves of a connective become stalked, the bending branches form the main bundles of the secondary thecae. These bundles may repeat this system of branching, as for instance in *Kitaibelia vitifolia* and in *Hibiscus rosa-sinensis* (and, not so distinctly, in *Kokia rockii*). In *Cephalohibiscus peekelii* each of the bending branches which are present as two opposed filament bundles, form a part of a complicated ramification system corresponding with the incipient tertiary division.


122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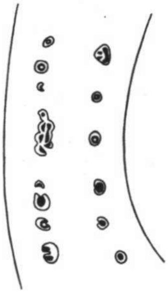
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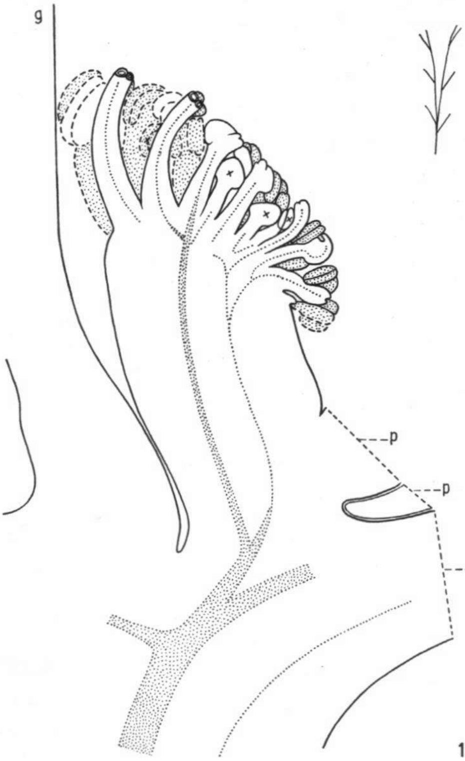

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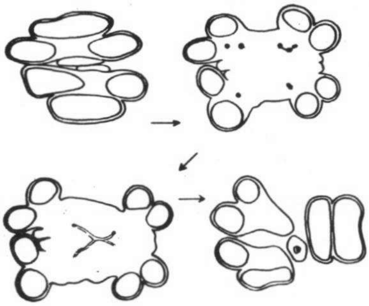
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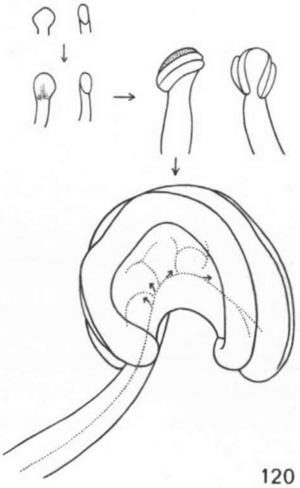
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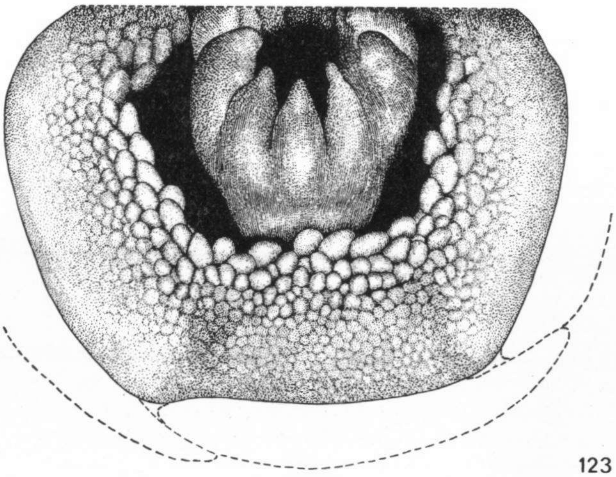
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Adansonia digitata. — Fig. 117. Tube, stamens not given, l.s., nat. size. — Fig. 118. Tube, c.s. — Fig. 119. Young stamen tube, l.s. — Fig. 120. Development of stamens (15 ×). — Fig. 121. Downward series of c.s. through anther. — Fig. 122. Vascular bundles in the anther. — Fig. 123. Developmental phase of androecium (30 ×).

BOMBACACEAE

A. DESCRIPTIVE PART

1) ADANSONIEAE

Adansonia digitata L.	S(5)n-(P5-St∞)-G(>10)
Pachira aquatica Aubl.	S(5)n-(P5-St∞)-G(5)p
P. macrocarpa Walp.	ditto
Bombacopsis quinata (Jacq.) Dugand	ditto
Bombax buonopozense Beauv.	ditto
B. ellipticum H.B.K.	ditto
B. ceiba L.	ditto
Ceiba pentandra (L.) Gaertn.	S5(P5-St5s)-G(5)p
C. mandoni Britt. & Bak.	ditto
C. pubiflora K. Sch.	ditto
Chorisia crispiflora H.B.K.	ditto

Adansonia digitata

The flowers are large, the perianth is fleshy and slightly perigynous.

The calyx is covered with glandular tissue on its inside base. The contorted petals may be almost entirely inserted in front of five apical parts, which may be observed in the calyx when the flower is in bud.

The stamen tube is relatively short and thick, in the staminal region still somewhat thicker outwards. The very numerous stamens are inserted all over the distal part of the tube, not only on the outside but also upon the rim and over a short distance on the inside (figs 117, 119).

The anthers seem to bear four pollen sacs, but a closer examination reveals that the pollen sacs are fused over the top, though occasionally the adaxial pollen sacs are divided in two parts by an apical median subdivision. The precise form of the anthers can be deduced from their ontogeny (fig. 120).

The pistil will be the subject of a future separate publication as it is as remarkable as the androecium. It may be summarized here that over a sterile syncarpous base the ovary is paracarpous (one-celled) with anatropous ovules on repeatedly forked funicles arranged along the sides of many inward projecting septs.

Developmental phases

The staminal protuberances which are first hemispheric later become tangentially elliptic. They are raised on a small downwards tapering stalk. Then the young stamens become spoon-shaped and an anterior and posterior pollen sac develop along the margin of the dilated upper part, giving rise to a reniform young anther. During the later phases of development the anthers are folded outwards along a median plane, the ultimate part of the filament and the connective at the same time slightly bending upwards. However, the stamens which are situated on the inside of the rim of the tube are folded inwards and bending outwards. Together with the folding the pollen sacs are somewhat shifted sidewards. The result is the impression of a more or less radially reniform curved anther with four pollen sacs which nevertheless are continuous over the top (fig. 120), though sometimes an apical subdivision occurs.

The stamen primordia grow on a big peripheral wall, as we find in Malvaceous flowers (fig. 123) but here the primordia occupy the entire wall, except on the inside. The wall represents the later upper part of the primordial tube, and is somewhat deformed in relation to the contorted position of the petals.

When we compare the staminal development in *Adansonia digitata* with that in other *Bombacaceae* and *Malvaceae*, it is surprising to find that the primordia do not divide into two halves, but immediately change into the folded anthers with two pollen sacs. Another important difference is that, following the centrifugal development of the main stamens, some new stamens may arise between and under the developing stamens. The later primordia appear on the surface of the wall, or now and then somewhat fused with the preceding stamens. This secondary development may proceed till late in flower development. The first smaller primordia can be seen to arise when the central stamen primordia become spoon-shaped (fig. 119).

Supply of vascular bundles

In a cross-section of the pedicel just below the calyx, we may first of all distinguish five major horseshoe vascular bundles near sepal radii, which are open towards the centre of the flower, secondly a large number of concentric cortical bundles among which five large ones alternating with the horseshoe bundles, and thirdly a stele or a number of medullary bundles which may probably be connected with the stele downwards in the floral stalk by means of several traces.

In the base of the calyx under the glandular surface, an inner sheath of bundles, which is formed by ramification of some flank parts of the horseshoe bundles, branches profusely. An outer sheath of calyx bundles is formed by the bulk of the borseshoe bundles and the cortical bundles. Downwards, part of the cortical bundles may be connected with bracteole traces.

The vascular supply towards each petal-stamen sector is formed by many branches coming from the inward bending flank parts of the horseshoe bundles as well as from the base of the outward calyx traces.

The supply towards the sepals and petal stamen tube is very irregular. It is represented by a tangentially arranged mass of profusely branching traces, each horseshoe major bundle giving the supply of one sepal (though marginal sepal traces may show a double origin) and most of the supply of an almost entirely antesepalous petal (fig. 124).

The petal stamen vascular supply in the very base of the tube forms a continuous pentagonal ring of bundles from which higher up many petal traces separate. The rest of the bundles is divided into two roughly pentagonal, continuous rings of numerous collateral stamen traces. The xylem of traces of different rings is facing each other. The inner ring supplies apical and subapical stamens, the outer ring only abaxial proximal stamens (fig. 118). Higher up, these traces together form the multiple bases of many concentric bundles or loose concentric combinations of collateral bundles (especially in the outer ring the traces may remain more or less separate) (fig. 118). Sometimes the bundles on those levels remain collateral, and then the xylem of the bundles of different rings is also facing each other, that of the outer ring being directed towards the flower centre.

In the distal tube part the concentric bundles split into intermediate collateral bundles in many directions, and each intermediate bundle ramifies into 2—8 stamen traces, among which those moving away from the surface diverge on a higher level and revert. The stamen traces are mostly collateral bundles with amply surrounding phloem. Sometimes the xylem may develop in several directions away from the centre of the trace and may be completely surrounded by phloem groups. Whereas the xylem of the collateral stamen traces of the inner ring remains directed towards the periphery of the flower, the xylem of the traces of the outer ring is directed towards the flower centre. Anastomoses frequently occur between intermediate bundles or between the proximal parts of stamen traces, especially in the outer ring. On the other hand, anastomoses are rare between traces belonging to different rings.

The course of the vascular bundles in the connective is variable. The bundles are collateral, they show a folded fan-shaped position (figs 120, 122) with or without a distinct median or a few concentrated middle branches and with the lateral branches towards both sides giving off minor nerves. In this branching pattern anastomoses may also be present (fig. 122). In the markedly curved anthers the main vascular bundles follow the curvature.

Other authors

According to Saunders (1937) numerous stamens arise in five groups. The vascular complements for the petals, antepetalous staminal groups, and sterile carpels are organized from the same vascular complex, hence these whorls are superposed, though owing to torsion of the corolla the loculi are not truly aligned with the petals. Each staminal vascular complement is, as in *Malvaceae*, organized in two portions. Hence each individual filament represents a half filament, bearing a monothecal anther.

Pachira spp.

The flowers are large and solitary. The receptacle narrows down gradually into a pedicel which is thick and stiff and bears 5—7 basal and 3 upper scale scars, so that the flower as a whole looks like a short shoot.

The perianth is somewhat perigynous. The calyx is cupular or campanulate with five very short and pointed lobes. On its inner base the calyx is lined by multicellular, presumably glandular hairs. In the region of calyx insertion five exterior, unequal, elliptic fields occur on sepal radii, which consist of numerous very slender anticlinic epidermal cells that excrete oily drops.

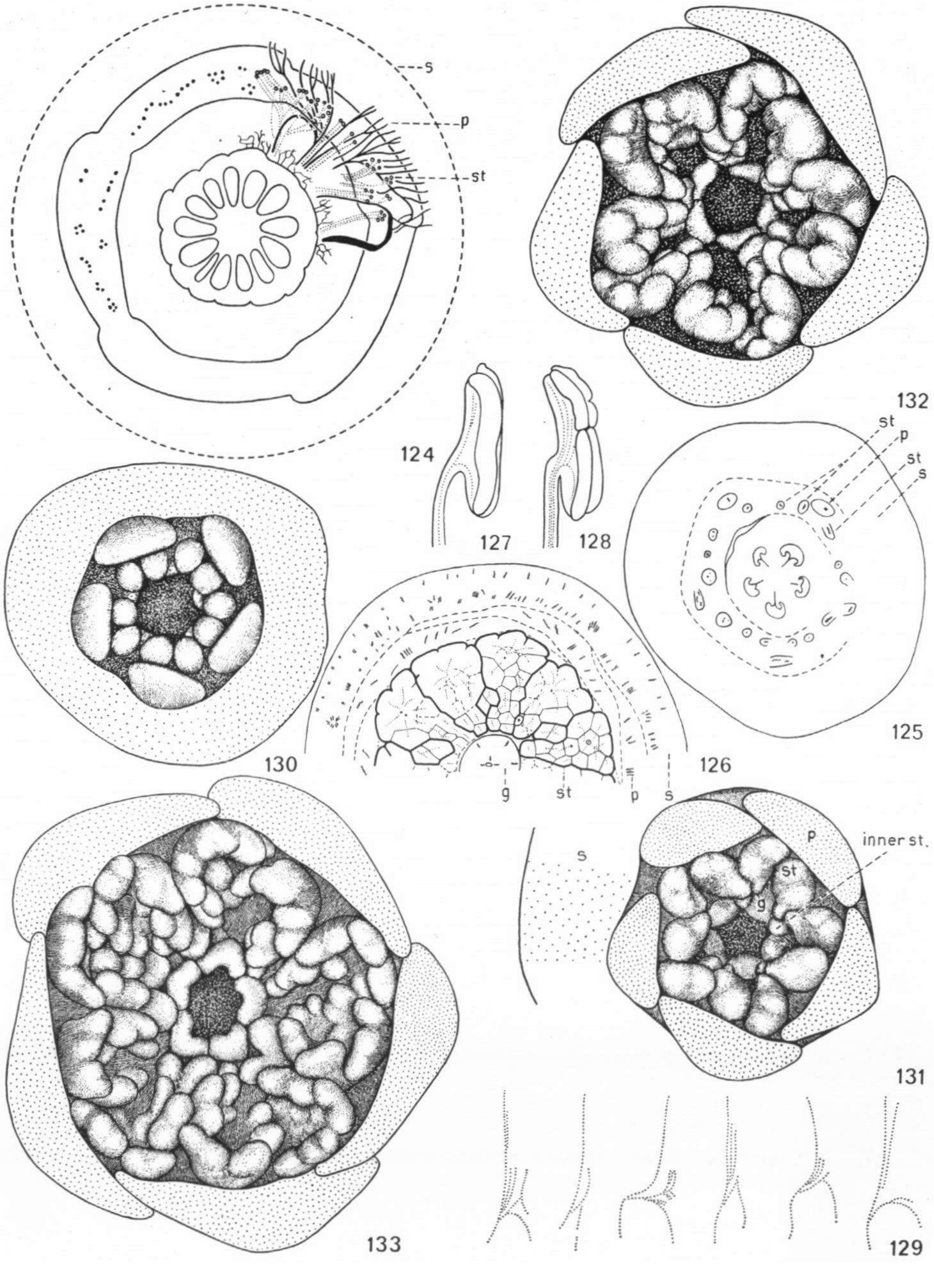
If the basal bracts on the pedicel are still present, some young floral primordia may be present in their axils. The three upper scars belong to phyllomes which keep the young flower bud covered for a considerable time before falling off. They may be compared with the epicalyx leaves in *Malvaceae.*

The contorted corolla is composed of long and narrow petals with a slightly oblique insertion which is for instance to the right of petal radii if the petals overlap to the left. In their lower regions the petals are thick in the middle parts, but thinner towards the margins, so that two halves result the overlapping one of which is somewhat broader.

The numerous radiating very long stamens are united basally into a tube on the outside of which ten parts can be distinguished by the presence of longitudinal grooves that correspond with the petal margins and median ridges. As a matter of fact, higher up, the tube falls apart into ten groups between sepal and petal radii below the level upon which the filaments become free (fig. 126). Moreover, adaxially between these groups five minor groups are present more or less on sepal radii, which may consist of one split stamen only, or probably now and then of some more. The adaxial stamens become free at a lower level than the peripheral ones. The stamens are all split into two monothecous, frequently asymmetrical, reniform twin halves which each contain two parallel pollen sacs (fig. 127, 134). Occasionally the pollen sacs are subdivided into two almost equal parts, or the connective is slightly two-lobed (fig. 128). The groups are formed by up to nine stamens, those in front of the overlapping petal halves counting some stamens more than the neighbouring groups.

Developmental phases

In the youngest phase available (fig. 130) we see a rather flat pentagonal apex lying within a massive cupular calyx, with the primordial petals in the corners. On their inside base the young petals are pressed against the sides of a low pentagonal wall. This wall, representing the primordial stamen tube, slopes gradually towards the periphery, but



Adansonia digitata. — Fig. 124. Connection of petal and stamen traces.

Pachira insignis. — Fig. 125. Base of petal stamen tube, c.s. (10 ×). — Fig. 126. Androecium, immediately above tube level, c.s. (10 ×). — Figs. 127—128. A normal and an abnormal theca. — Fig. 129. Vascular bundles in the connective. — Figs. 130—135. Successively older phases in androecium development, figs. 130—133 top view.

is rather well demarcated against the central residual apex. This demarcation is given by five inner, more or less alternipetalous, protruding wall parts — staminal lobes — which each bear a slight median primordium as well as ten large, lateral, elliptic, about radial, buttresses.

Whereas five of these ten large staminal buttresses extend slightly more outwards in front of the overlapping petal halves, the other five are placed in front of the overlapped petal halves.

In a later phase (fig. 131) in which five broad primordial pistil parts are present, a faint superficial lobing follows the change in shape of the outer staminal buttresses. The buttresses first extend in a direction that is not merely centrifugal but ultimately also bending towards petal radii, secondly broaden sidewards, towards the petal radii. Moreover, the outer parts of the staminal buttresses — and also the petals — become higher placed than the inner parts, in correspondence with the slightly perigynous character of the perianth. A faint lobing follows the change in shape of the buttresses, each lobe giving a rather flat protuberance with a circular base representing one stamen primordium. Later (fig. 132) the stamen primordia become elliptic with their long axes lying along the centrifugal and sideward line indicated above. The median alternipetalous protuberances on the staminal lobes become tangentially stretched and are the first to develop each into a single divided stamen. In a next phase (fig. 133), in which the stamen primordia are dividing along their long axes in two equal half-stamens, the sideward development of stamen primordia occupies the slopes of the staminal lobes which are facing petal radii. In a phase in which the first-formed stamens show the appearance of pollen sacs by a longitudinal groove over each theca, the sideward development may result into two additional rows of stamen primordia, the inner members of which seem to have been formed last.

In a few older buds the impression is that some young stamens are present below the alternipetalous primary stamens, which are also formed by the median protuberances on the staminal lobes. However, it is difficult to distinguish them from stamens formed later from the staminal buttresses.

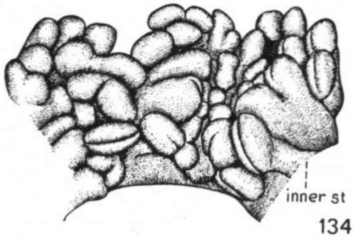
Supply of vascular bundles (figs 125, 126, 136)

In the base of the flower the closed vascular cylinder falls apart into five horseshoe-shaped bundles lying in sepal radii. On a lower level five small bundles either leave the vascular cylinder in alternate radii and ramify into the outer (cortical) calyx bundles, or these bundles depart from the proximal region of the horseshoe bundles.

The peripheral parts of the horseshoe bundles diverge to form in each sepal 3—5 main bundles which form many secondary nerves and anastomoses. The major nerves converge towards the rim of the calyx cupule, into the points which terminate the sepal parts. Many tiny bundles coming from the proximal anastomoses spread in a direction perpendicular to the glandular hairy surface of the calyx tube.

Above the level of divergence of the sepal parts, the flanks of the horseshoe bundles reconstitute a stele with five outward loops situated between sepal and petal radii. This is accomplished chiefly by the diagonal course of one of the flanks, for instance of the left flank going to the right in case the petals overlap with their right margins. This reconstituted stele falls apart into 1) five loops which form the collateral petal stamen strands, 2) five alternate stamen traces going to the inner primary stamens, 3) ten intermediate pistil traces.

During their further oblique upward course the petal stamen strands split into a median petal trace and two lateral stamen fascicle traces. The petal strand trifurcates at its base and forms by further division the concentric petal nerves.



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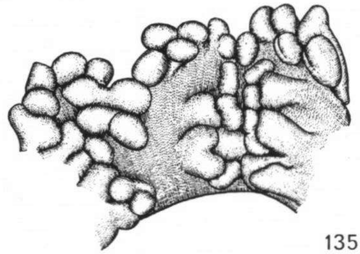

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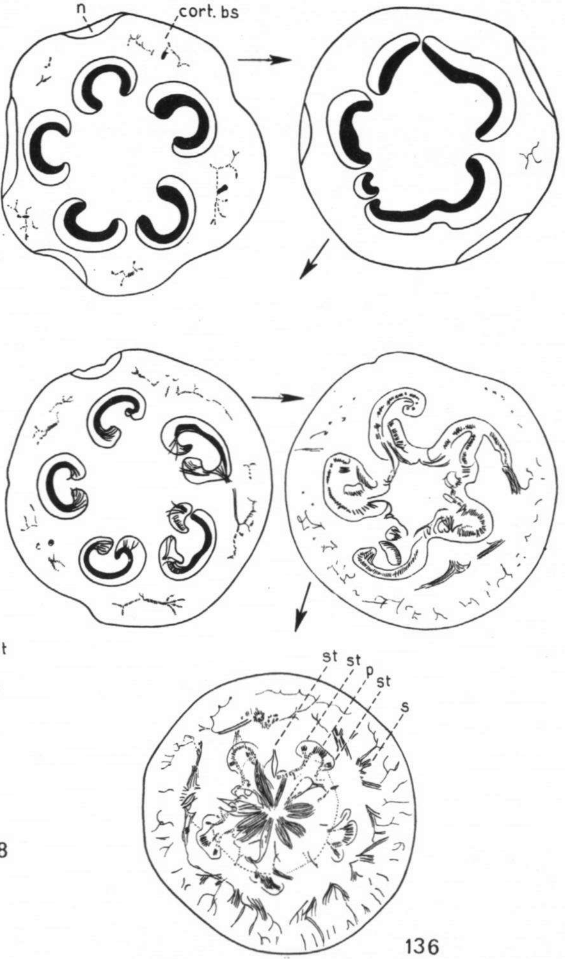

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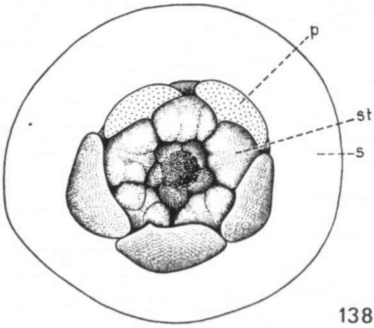

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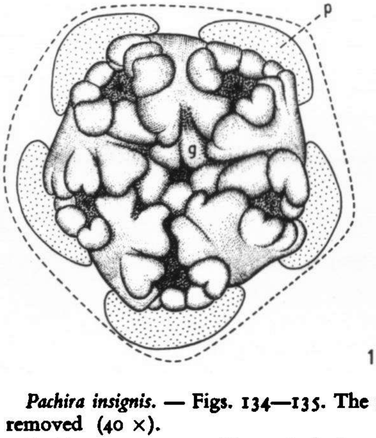

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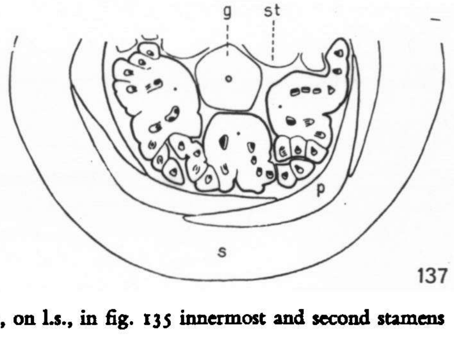


137

Pachira insignis. — Figs. 134—135. The same views, on l.s., in fig. 135 innermost and second stamens removed (40 ×).

Pachira macrocarpa. — Fig. 136. Series of upward c.s. through receptacle (10 ×).

Bombacopsis quinata. — Fig. 137. C.s. of flower at base of stamens (10 ×). — Figs. 138—139. Advancing development of the androecium (80 ×).

The ten stamen fascicle traces give by ramification the traces to all stamens which originate from the ten staminal buttresses. In the very base of the stamen tube the different bundles can be seen to be situated on a wave-line (fig. 125) which is formed by five outer petal traces, five inner stamen traces, and ten middle stamen fascicle traces. The notion of a wave-line is also convenient to make clear that the middle bundles are directed neither radially nor tangentially but in between these two, with the rows of vessels perpendicular to the wave-line and on the side of petal radii. In accordance with the contorted characters, the stamen fascicle traces in front of the overlapped petal halves lie closer to the petal traces.

Upwards in the staminal region the adaxial stamen traces separate from the fascicle traces first (fig. 126). All the stamen traces are directed with their xylem towards the centre of the groups. Higher up, the traces split into two half-stamen bundles, which are mostly composed of several radiate xylem groups, each with its own phloem cap, embedded in vascular parenchyma. In the plane of the thecae the stamen bundle splits into an upward continuing bundle which may have some smaller almost parallel subsidiary nerves, and into a shorter bundle bending downwards, that may be irregularly connected to the upwards going bundle (fig. 129).

Other authors

Robijns (1963) stated that five antepetalous paired groups form an outer whorl of stamens, an inner whorl being formed by five single alternating stamens.

Bombacopsis quinata

In the primordial phase given in fig. 138 it appears that the androecium is initiated as five alternipetalous buttresses placed upon a rather flat apex between the young petals and the five alternating primordial pistillary protuberances. On the inside the staminal buttresses are sharply differentiated from the residual apex by a somewhat lower median part and two well developed marginal parts. On the outside the buttresses slope gradually towards the periphery. Whereas along the margins stamen primordia originate in a centrifugal direction, the median parts of the buttresses stop development. Later (fig. 139), the buttresses lean over the central part of the apex, the middle parts remaining lower than the marginal regions, the latter growing upwards especially in the middle. On the whole the buttresses look like small thick leaves which have not yet straightened. The margins in front of the overlapping petal half is in advance of the other, and may even partly overlap the margin of an adjoining buttress.

As in *Pachira*, the development of stamen primordia, which first takes place along the growing margins centrifugally, suddenly proceeds along a sideward course towards petal radii. In this way the initiation of primordia is carried through sidewards along the peripheral bases of two neighbouring staminal buttresses till they meet near petal radii, giving rise to a wave-line arrangement. However, along the outward antepetalous bends the wave-line is not necessarily so very perfect, because at the place where the margins of the staminal lobes meet the primordia may be of unequal size, or a few ultimate primordia may be placed the more inwards. This contorted condition is also very evident in a cross-section of an advanced bud given in fig. 137.

Later the stamens become more clearly elevated on a tube upon which they are placed in a wave-line. It must be concluded that, though externally the flowers of this species resemble the *Pachira* flowers very closely, the differences in the androecium are significant.

The subsequent growth of the stamen primordia is similar to that of *Pachira* stamens, a remarkable fact being that the innermost thecae of the first formed stamens are retarded as compared with the outside thecae (cf. *Bombax ceiba*). They are more bent inwards and downwards, lying as they are next to the equally reduced median central parts of the buttresses. In older buds it may be observed that the tube ends in five small triangular lobes near sepal radii.

Supply of vascular bundles

In the base of the stamen tube fifteen equidistant bundles are present, among which five in sepal radii are less well developed and terminate upwards in small teeth which represent the tips of the staminal buttresses. The other ten bundles are situated slightly more outwards, they are collateral with their xylem not merely radially oriented but also directed towards the petal radii. Higher up, these stamen fascicle traces divide outwards fan-like into the stamens of the buttresses (fig. 137). From the position of the stamen vascular bundles and their xylem the way of sideward development of the stamens may be deduced.

One member of each pair of stamen fascicle traces is attached to the petal supply laterally, the combination in turn being attached to the sepal supply. The other stamen fascicle traces and the antesepalous traces are connected with the sepal supply directly.

Other authors

For *B. glabra* Robijns found the same arrangement of stamens as in *Pachira aquatica.* From some microscopic slides of floral primordia the author concluded that development is centripetal.

Bombax buonopozense

The filaments are divided at the base into two halves which each bear a reniform theca of two parallel pollen sacs. The stamens separate from a tube on a wave-line with outward antepetalous bends (fig. 140). The tube terminates into a rather prominent sterile collar which is slightly higher in alternipetalous and somewhat lower and thicker in antepetalous regions.

As to the manner of divergence the stamens fall apart into an inner whorl of five groups of three stamens each formed by the five alternipetalous inward bends of the wave-line, and five lower antepetalous groups formed by the outward wave-line bends. The stamens of the inner whorl have longer filaments and diverge more parallel to the floral axis.

Supply of vascular bundles

There are five portions of a reconstituted stele above calyx level which may be called petal stamen traces, because the petal innervation is formed by their middle parts and two stamen fascicle traces by their flanks. Higher up, the stamen fascicle traces are closed on the adaxial side, forming concentric bundles which scatter into individual traces towards the stamens belonging to the lateral halves of the outer groups and towards the lateral stamens of the inner groups. Accordingly, the lateral stamens of the inner groups belong to the outer groups as regards their innervation.

Alternating with the main petal stamen parts, from the reconstituted stele five other small parts separate which only form the forking traces towards the central stamens of the inner groups which are situated on the summits of the inward alternipetalous wave-line bends. Therefore, as regards the innervation only the upper stamens of the inner whorl really belong to this whorl. The sterile collar has no vascular bundles.

Other authors

Robijns stated that ten inner stamens are arranged in five alternipetalous pairs. Moreover, each of the antepetalous outer phalanges has four stamens with the filaments bending towards the inner whorl.

Bombax ellipticum

As only little material was available for study, some of the results are necessarily vague.

The pedicels bear 2—6 bracteoles some of which may have small axillary buds. Three more bracteoles are present immediately below the calyx.

The thick cupular calyx is surmounted by five small teeth which on that level alternate with the petals. Up to nine circular or elliptic differently sized fields of presumably glandular character encircle the calyx base. In addition a ring of glandular cells lines the inner base of the calyx cup.

The petals are mostly contorted elongate appendages. They deviate for instance to the right of their proper radii if they overlap to the left. As a matter of fact, sepal segments may be of unequal width and the petals imbricate, not contorted.

Numerous stamens are inserted on a short tube. They consist of twin halves, each half bearing a mostly asymmetrically reniform theca that may be slightly twisted. The tube is about circular in cross-section, but where the stamens diverge ten parts protrude in front of the petals. On the tube the stamens are placed in a whorl of five antepetalous W-formations, the lateral shanks of which are linked by central alternipetalous stamens. The position may be compared to a wave-line, the outward coils of which are again bent inwards. The tube is prolonged by a very low sterile ridge.

Development phases

The youngest primordial phase that could be studied is given in fig. 144. Though it is a bit irregular, it clearly shows on the left side the position of the stamen primordia on a wave-line upon a thick slightly pentagonal wall. Evidently the development proceeds in a centrifugal direction, even in the antepetalous inward coils. This last phenomenon may be observed still better in some older phases in which the median stamens of the antepetalous coils have thecae whereas the lateral stamens are still without. It should be noted that in these phases the stamens of the antepetalous coils are not as far developed as those which are situated in the shanks on the same level. The central summits of the wave-line are occupied by one or two juxtaposed stamens or they show irregular formations. The sterile prolongation of the tube is formed by the inward bending part of the wall.

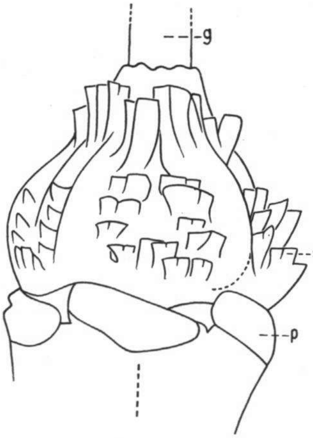
Supply of vascular bundles

Upwards the stele falls apart into a number of C-shaped inwards open, collateral main bundles, five of them large and in sepal radii, some others small, giving sepal supply only. The flanks of the large bundles curl inwards (fig. 141).

The inwards curled ends produce a vascular system ramifying under the basal glandular surface of the calyx cup. However, the distal part of this glandular surface is innervated by branches separating from the main calyx vascular system which itself is formed by the peripheral part of the large main bundles. This main system consists of parallel nerves, five of which go to the calyx teeth. They are linked by reticulate vascular systems.

The most central parts of the bending flanks of the main bundles continue as pistil supply. Two parts of the flanks of neighbouring main bundles together constitute broadly tangential concentric bundles. These bundles represent the common base of each petal-stamen vascular supply. These concentric bundles fall apart into many concentric to — upwards — collateral petal nerves, and ultimately into two lateral stamen fascicle traces. A separate trace with a mostly multiple base, linked to this system, goes to an upper alternipetalous stamen (figs 141, 142).

The stamen fascicle traces, of which there are accordingly two per petal, are also concentric. They tend to split into several secondary, concentric bundles upwards before they split into stamen traces.



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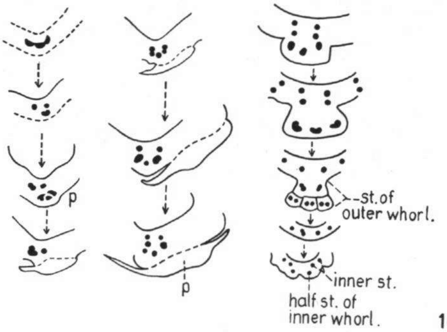

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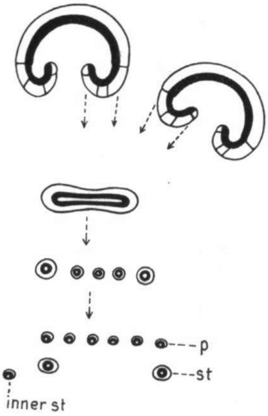

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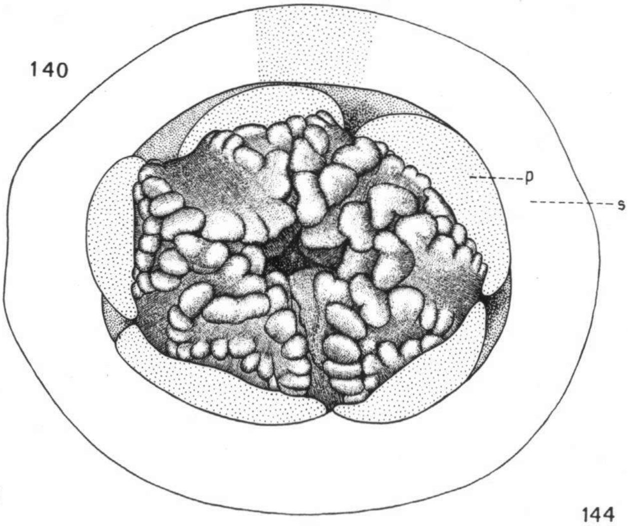

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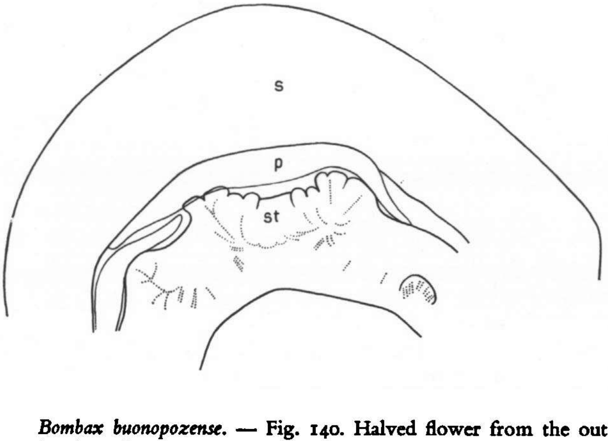

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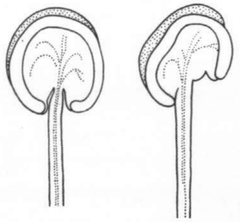


143

Bombax buonopozense. — Fig. 140. Halved flower from the outside.

Bombax ellipticum. — Fig. 141. Scheme of vascular supply toward petals and stamens. — Fig. 142. Base of stamen tube, cleared c.s. — Fig. 143. Thecae. — Fig. 144. Primordial androecium (40 ×).

Bombax ceiba. — Fig. 145. Supply of vascular bundles towards sector of stamens.

The stamen bundles may be double from the start; they split into the connective in a variable way (fig. 143) forming recurving branches.

Bombax ceiba

The flowers have thick pedicels on which are inserted some scattered bracteoles and three large bracteoles immediately below the calyx. The cupular calyx is provided with small apical teeth, at least in bud; later the cup splits irregularly. At the very base presumably glandular, elliptic fields occur on the outside, and a ring of glandular tissue is present on the inside. The petals are large obovate appendages, adnate to the base of the stamen tube. They are contorted and obliquely inserted, that is somewhat lower on the overlapping side.

There is a rather long conical stamen tube from which filaments separate on a wave-line. Moreover, the stamens are arranged in two whorls, the outer whorl consisting of the 4—6 stamens in each outward bend of the wave-line, situated in front of an overlapping petal half, the inner whorl comprising three stamens in each alternating inward bend of the wave-line. The inner whorl is effectuated by the greater length of the filaments which, in addition, diverge more parallel with the floral axis (cf. *B. buonopozense*).

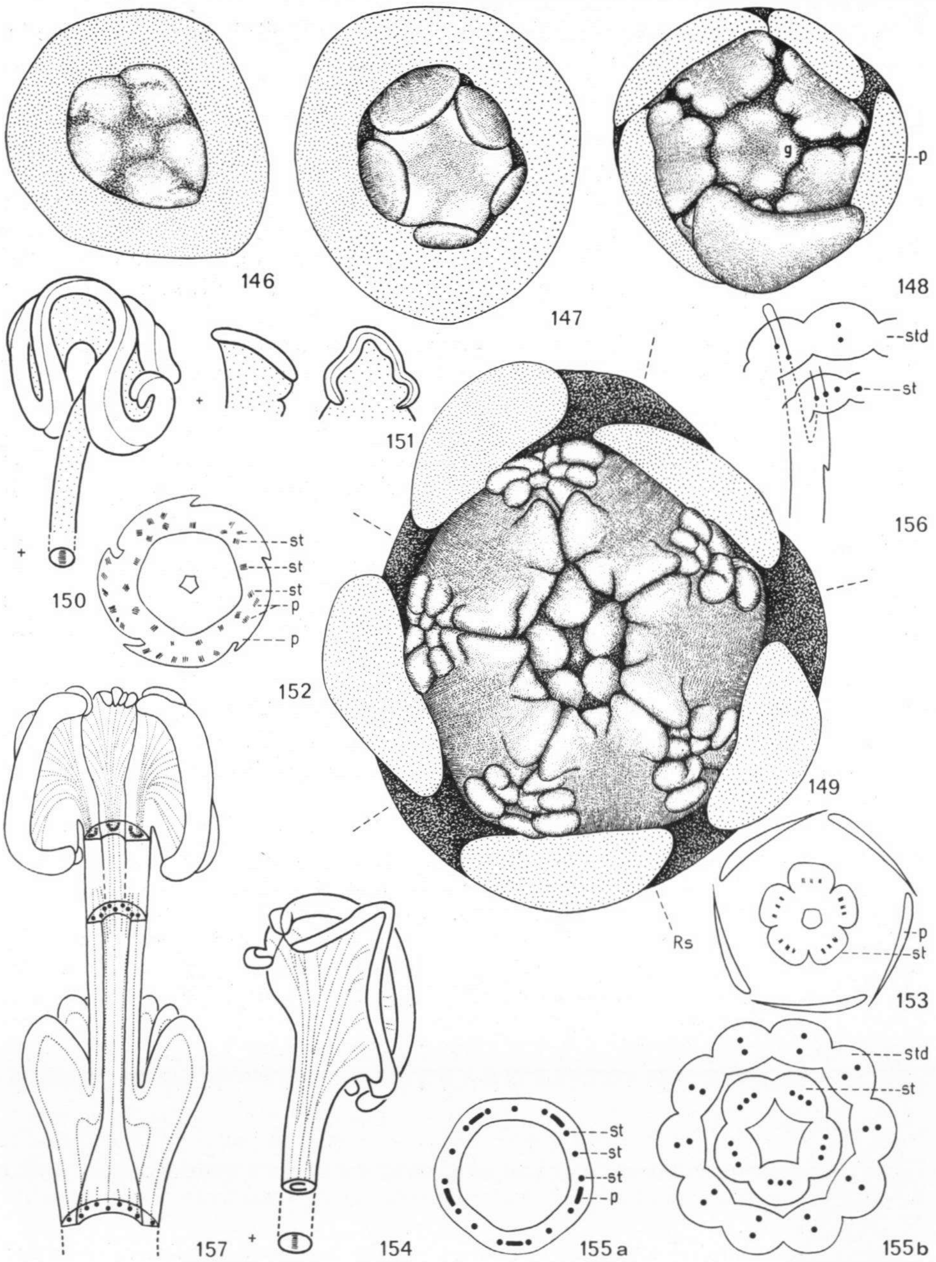
Whereas, as usual, all stamens of the outer whorl have proximally bifid filaments which each bear a half-anther, the inner whorl consists of five prominent central stamens flanked by two slightly lower placed half-stamens. The filament of such a large upper central stamen is longitudinally grooved and falls apart apically into two more or less adherent and concomittantly twisted connectives, each bearing a theca with two parallel pollen sacs. The thecae are often asymmetrically reniform and coiled laterally or curved medianly; especially the central ones are sometimes folded along a median plane. Thus the central stamens seem to be pairs of laterally fused half-stamens. Sometimes the lateral single half-stamens in front of the overlapped petal half is reduced to a subulate tooth or is altogether missing. Also now and then one of the peripheral stamens is present in the form of a half-stamen only.

The contorted characters are very marked in this species and the insertion of the petals is not at all alternisepalous. If, for instance, the petals overlap to the left the insertion deviates to the right, and although the staminal lobes are largely oppositisepalous they lie somewhat to the left of this position. Especially the later development of stamen primordia in the outward coils of the wave-line takes place more in front of the overlapping petal halves. As the pistil primordia alternate with the staminal lobes they are placed on the whole alternate to the sepals, though slightly deviating to the left.

Developmental phases

After the young calyx five more or less hemispheric protuberances arise on the apex (fig. 146). From these protuberances the petals are cut off laterally towards the periphery. The overlapping side of the petals is separated first and develops in advance of the other side. Later the residual parts of the protuberances (staminal lobes) assume the form of apple segments which lie on their sides with their backs facing inwards (fig. 148). Higher upon the apex they are followed by five alternating protuberances representing the stylar primordia.

While the summits of the staminal lobes remain free, stamen primordia develop along their margins in centrifugal direction. When on each margin the stamen primordia formed-first begin to divide into two thecae it becomes increasingly evident that their central thecae enlarge considerably whereas the peripheral thecae are retarded. Much later in ontogeny the central thecae of the central stamens on either margin of a staminal buttress are elevated on a common filament, forming the prominent alternipetalous



Bombax ceiba. — Figs. 146—149. Successively older phases in androecium development, top view (40 ×).
Ceiba pentandra. — Fig. 150. Mature stamen. — Fig. 151. Young stamen, lateral and outside view. — Figs. 152—153. Successively higher c.s. of petals and stamen tube.
Ceiba mandoni. — Fig. 154. Cleared anther. — Fig. 155 a and b. Stamen tube below and on the level of appendages. — Fig. 156. The same, on the level of appendages, detailed.
Chorisia crispiflora. — Fig. 157. Halved stamen tube, cleared. (5 ×).

fusion products of two heterogeneous half-stamens. The twin-thecae of these stamens are left alone and form the lateral half-stamens of the inner whorl. The fusion of the two half-stamens takes place while the sterile, often bilobed summit of the staminal lobes is left intact. However, in the mature flower the sterile summits are completely outsized by the immensely growing stamens, so that they can hardly or not be detected.

In the phase given in fig. 149 the staminal lobes are united basally by a common tube, and the stamen primordia developing along the margins meet in alternate radii. Some primordia even seem to link the margin bases over the rim of the tube, a more ample outward coil of the wave-line being the result.

Supply of vascular bundles

In the base of the receptacle five large parts diverge from the stele, together with a number of smaller parts which branch into the numerous nerves of the calyx cupule. Above the small parts the stele is mostly reconstituted, so that five stelar sectors remain, alternating with the large collateral sepal traces. These sectors move inwards to form the pistil supply, but basally they are frequently separated into two parts side by side through the outward departure of a middle trace which goes up into the stamen tube to end blindly under or in front of the insertion place of the fused pairs of half-stamens. Evidently such a trace represents a residual trace towards the apex of a staminal lobe.

The flanks of the large collateral sepal traces do not form sepal nerves, but proceed their course parallel with the floral axis and fall apart into a stamen fascicle trace and a trace splitting into a stamen fascicle trace and a petal trace. However, it may also happen that the flanks by lateral extension close the gaps above the peripheral parts of the large collateral bundles which go to the calyx. In that case petal-stamen traces are formed below the level on which they fall apart into a petal trace with a stamen fascicle trace on either side. If the petals overlap to the left, the right stamen fascicle traces are fused to the petal traces higher upwards than are the left ones.

The petal and stamen fascicle traces are all concentric bundles, except near the regions of splitting. By upward division the fascicle traces supply the lateral halves of each antepetalous U-formed formation of stamens which belongs to two neighbouring staminal lobes (fig. 145). All stamen traces bifurcate towards the bifid stamens, also the ten innermost traces which move towards the stamens of the inner whorl as the ends of the shanks of the U-formed arrangement. One fork of these traces supplies a single half-stamen, the other one the adjoining half of a central fused pair of half-stamens. Thus there is a double vascular supply for the central stamens, and it is proved by anatomy as well as by ontogeny that the single half stamens and the adjoining halves of the central stamens are twins because they originate by the division of a common primordium and receive the halves of a common trace. In the filaments the concentric vascular bundles become collateral upwards and spread in the connectives into a fan-shaped innervation. In the reniform thecae the middle branches of this supply are mostly not very well developed and in the asymmetrical thecae one of the lateral portions is developed stronger than the other. If the thecae are folded the vascular supply is also folded, and in that case middle parts are rather well developed.

Other authors

Rao (1952) recorded the division of petal stamen traces in a middle petal trace and two lateral stamen fascicle traces. Though his descriptions are rather vague, it is clear that he also observed ten basal stamen traces supplying the inner whorl of stamens. For that reason and for the double nerve in the filament of the central stamens he considered these stamens as double. Very probably Rao did not see the forking of the ten traces and therefore did not mention the pairing of the innermost half-stamens and the halves of the double stamens. Residual stamen traces in alternipetalous regions were apparently lacking in his material. Consequently he considered the flowers tetracyclic.

According to Robijns the androecium is formed by five pairs of fused half-stamens as an inner whorl and five antepetalous outer phalanges. However, ten half-stamens of the outer phalanges are bent inwards and are adjacent to and alternating with the inner stamens.

Davis and Mariamma (1965) recognized the inner stamens as being composed by more or less strong fusion of the halves of two adjoining stamens, the other halves of which remain free. This interpretation is in accordance with that given by the present author. Unfortunately Davis and Mariamma did not cite Rao.

Ceiba spp.

The petals are adnate to the base of a short stamen tube, they are contorted and rather precisely alternating with the very short lobes which terminate the cupular calyx. Epibasally they bear a transverse ridge in *C. mandoni* and *pubiflora.*

The stamen tube separates into five antesepalous large stamens, the anthers of which are more or less sagittate. The terminal part of the filament along which the connective is situated — also over the apex — may be bent inwards and downwards, for instance in *C. pentandra.* The connective and the two parallel pollen sacs are twisted, especially at the tails of the anther (fig. 150 gives a relatively little twisted anther). In *C. mandoni* the pollen sacs can be thinner at the anther top, a place where in *C. pubiflora* — a species with rather straight anthers — one or both pollen sacs may be sterile (fig. 154). Thus within *Ceiba* transitions exist between anthers with two and four pollen sacs. In buds of *C. pentandra* the anthers appear as free still largely untwisted structures without tails (fig. 151). The upper margin is V-shaped and open towards the periphery.

In *C. mandoni* and *pubiflora* the staminal tube not only falls apart into stamens but also bears ten short cylindric and rounded appendages which are placed between sepal and petal radii and are fused laterally at the base (fig. 156).

Supply of vascular bundles

The vascular supply of the thick calyx is formed by antesepalous sectors of the receptacular stele together with cortical bundles which fade out downwards in the pedicel where the bracteoles have fallen off.

In the base of the stamen tube one finds five more or less inner stamen traces in sepal radii and five alternating petal stamen traces. Higher up, the latter split into the petal supply in the middle and on either side a stamen trace between sepal and petal radii (figs 152, 153).

It follows that three traces enter each stamen, a median trace in sepal radii and two lateral traces belonging to adjoining petal stamen traces (fig. 153). In *C. mandoni* the lateral stamen traces loop into the median plane of the basal stamen tube appendages and pursue their course towards the anthers. Occasional diffuse vascular tissue may be seen to arise from these loops. It should be added that also the stamen traces in sepal radii show a short bend in the direction of the appendages (fig. 157 of *Chorisia crispiflora*).

Higher up in the filament the three traces form together a tangentially stretched or an outwards open C-shaped combination which splits into the fan-like innervation of the connective, the lateral parts for the tails, the median parts towards the top. All these bundles are collateral with the xylem directed towards the centre of the flower. The anther nerves may bifurcate and form twisting anastomoses under the surface of the pollen sacs.

A halved flower of Chorisia crispiflora is represented in fig. 157; it is evident that the relevant features are not different from those in *Ceiba*. According to Dawson (1944) the difference between *Ceiba* and *Chorisia* is formed by the absence or presence of the staminodial appendages respectively.

Other authors

Saunders thought that there are five antepetalous stamens which represent three united half filaments bearing three coiled half anthers. Superposition of petals, stamens, and sterile carpels is due to the same causes as in *Adansonia digitata*. Separation of each staminal vascular complement into two portions occurs in the same way as in *Malvaceae*. The further break-up of one of these portions leads to the formation of three staminal bundles on each petal radius. One triplet passes into each antepetalous filament.

2) MATISIEAE: S(5)n-(P5-St 15/10)-G(5/2)

Matisia ochrocalyx K. Sch.
Hampea integerrima Schlecht.
Quararibea guianensis Aubl.
Ochroma lagopus Sw.

Matisia ochrocalyx

A long stamen tube is subdivided into five long apical lobes which according to Bakhuizen van den Brink (1924) are antesepalous. On the outside of the lobes five elliptic sessile thecae are placed longitudinally in two rows, a row of two thecae, another row with a third lower unpaired theca (fig. 179). The thecae have two parallel pollen sacs and are dehiscent length-wise. The pollen are reticulate. The summit of the lobes is rounded and sterile.

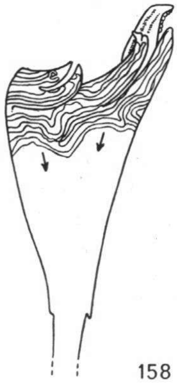
Three vascular bundles move upwards into the parts of the staminal tube, one median inner and two outer laterals. The median bundle slightly spreads tangentially, frequently in three portions, ending in the sterile apical part of the lobe. The laterals give off vertical series of small side nerves towards the thecae, the lower unpaired thecae being served by a distinctly separate branch.

Hampea integerrima

One badly preserved flower shows a stamen tube which bears distal thecae. In cross-section five alternipetalous bundles may be observed, which are outwards open c-shaped combinations of small traces. The pollen are echinate.

Quararibea guianensis

The slender flowers have very long staminal tubes to which the contorted petals are adnate at the base. The distal short part of the tube is sterile and ends into five small alternipetalous lobes which may be bilobed themselves. The flower has a distinct malvaceous appearance, the more so because half-anthers are inserted along the tube in three irregular superposed whorls which are separated by bare parts of the tube. The whorls each consist of five pairs of antepetalous thecae, except the basal whorl which has only the left or right members of the pairs in front of the overlapping petal halves. Frequently one partner of a pair is inserted somewhat higher than the other.The broadly reniform thecae are sessile on the tube, inserted longitudinally. The absence of filaments under the thecae constitutes the chief external difference with malvaceous flowers. The basal thecae tend to be inserted somewhat diagonally, with their lower ends directed towards the petals. The connectives are covered by small, obconical, multicellular,



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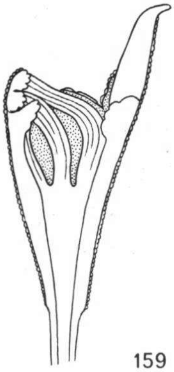

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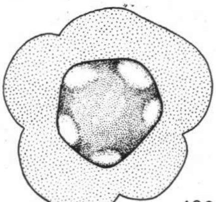

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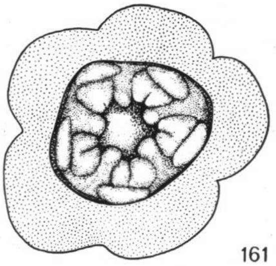

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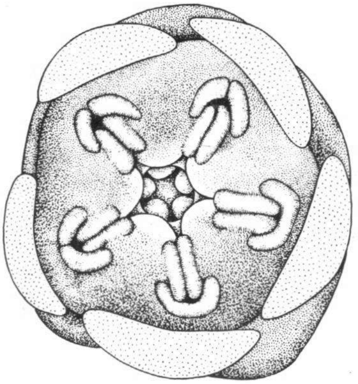

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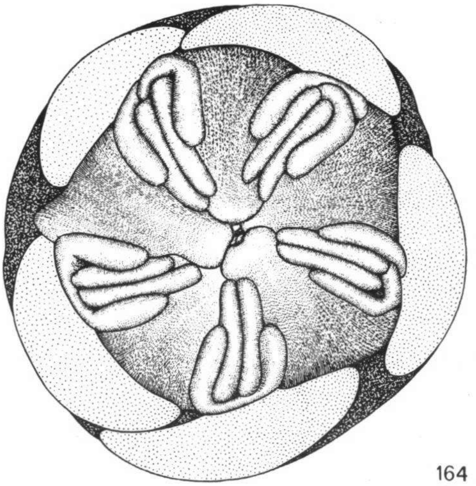

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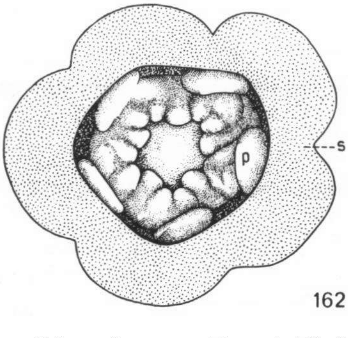

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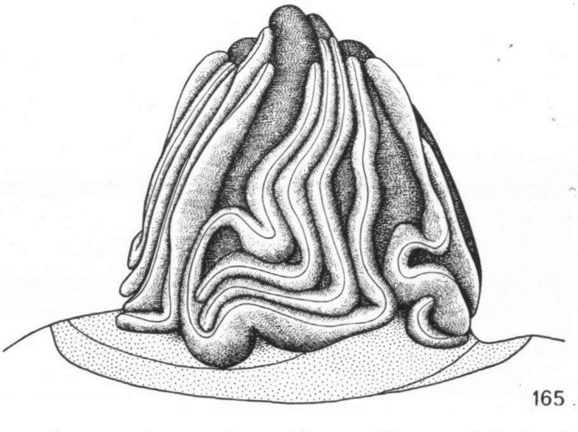


165

Ochroma lagopus. — Fig. 158. Distal part of stamen tube, nat. size. — Fig. 159. The same, halved and on the inside. — Figs. 160—165. Developmental series of the androecium. (Figs. 160—164 25 ×; fig. 165 12,5 ×).

glandular organs. However, these structures are limited to those sides of the connectives which are directed towards petal radii.

Developmental phases

On the floral apex surrounded by the young calyx a peripheral wall arises which is slightly pentagonal with the angles situated where the petals become separate. In the residual wall five alternipetalous trapezoid parts may be distinguished by the occurrence of five distinct antepetalous radial grooves and five alternipetalous, shallow, cuneate grooves. Along either margin of these buttresses a peripheral stamen primordium originates, the one in front of the overlapping petal half growing larger at first. The central low median regions of the buttresses develop only later on, bending over the residual apex, forming prominent alternipetalous lobes. Later still these parts become stretched and bilobed.

The staminal rudiments become elliptic with their long axes perpendicular to the place of petal insertion. Later the margin of the staminal buttress situated in front of the overlapping petal half develops farther in more outward direction, giving room for one more stamen primordium which later will belong to the lower whorl. This primordium, when growing elliptic, is somewhat bent towards the median petal parts.

When these peripheral primordia develop, the central primordia on the other margins outsize the originally bigger central primordia in front of the overlapping petal halves. They are the first to divide into two halves in line along the margin of the buttress, each half forming a theca with two parallel pollen sacs. The peripheral primordia in front of the overlapping petal halves do not divide but form solitary thecae.

The thecae remain sessile, but the tube is stretched between the halves of the central (now upper) stamens and the peripheral (now lower) half-stamens.

In some floral developmental phases, peripherally to the primordia in front of the overlapped petal halves, a tiny primordium may be observed to arise, which does not develop any further. These primordia would have formed the missing thecae of the lower whorl.

Supply of vascular bundles

Fifteen more or less equidistant bundles move up in the stamen tube, namely near sepal radii five which have the xylem directed inwards, and in front of the petals ten that have the xylem facing a position intermediate between the flower centre and the petal radii.

In the staminal region the antesepalous bundles form somewhat tangentially stretched bundles which may divide collaterally into the sterile bilobed lobes. The fertile bundles each divide into two parts, one towards a theca of the second whorl, the other towards the superposed theca of the upper whorl, thus proving anatomically that these thecae are twin halves. Moreover, the fertile bundle in front of the overlapping petal half gives off a branch at a lower level which forms the bundle towards the solitary theca in the lower whorl. This trace is not precisely radial, but slightly deviates in the direction of the median part of the petals. All stamen bundles are collateral.

In the thecae the bundles split into a poor fan-shaped innervation often with two prominent lateral nerves or into lateral nerves only, giving rise to a dichotomy.

Ochroma lagopus

The flowers are very large. The proximal parts of the quincuncial calyx are not all fused by their margins, but the margins of the outer sepals are adnate to the lateral outer surfaces of the inner sepals, with the effect that both margins of the inner sepals and one of the third sepal project freely inwards.

The very large stamen tube widens into an apical region which extends into five tapering and twisted arms. These arms are originally adjacent but later freely spreading (fig. 158, 159). The torsion lines of this twisting go upwards to the right if the petals overlap to the left, and conversely. The stamen tube shows in cross-section five thicker parts which are continuous with the five arms.

On the outside this apical region including its arms is entirely covered by an extreme convolution of an indistinct number of thecae each containing two parallel pollen canals. The lower part of this pollen mass is free from the tube though remaining so closely contiguous that it seems to be adnate. On the inside of the arms four parts may be distinguished by the presence of three longitudinal grooves.

Without a study of the developing phases it would have been impossible to understand the mature structure.

Developmental phases

Upon an irregularly five-angled flat apex the first signs of petals and of a peripheral androecium wall appear within the young calyx (fig. 160).

Somewhat later (fig. 160), with the petals situated along the outer slopes, the wall differentiates into 1) five low and narrow alternipetalous inward projecting radial parts, the central regions of which may be slightly thickened, 2) five broad and elevated antepetalous parts, which are not extending inwards very far. The elevated staminal parts become bilobed by the centrifugal development of a radial groove. The halves formed by the lobing show unequal growth, the members in front of the overlapping petal halves becoming larger. Here the petals are inserted more outwards, deviating for instance towards the sepal on the right side, if the petals overlap to the right. Correspondingly, in that case the alternipetalous parts of the stamen tube lie to the right of their proper places.

In a slightly later phase (fig. 162) the chief development appears to be formed by the occurrence of a tangential groove upon the larger lateral halves of the prominent antepetalous staminal elevations, subdividing the latter into an inner and an outer part, the outer of which is not directed radially but more towards the median region of the petals.

In a much later phase (fig. 163), the alternipetalous regions of the young stamen tube appear to have increased in such a way that the earlier antepetalous prominent staminal elevations now merely are portions of its margins. The alternipetalous regions form in this stage clearly five staminal buttresses which will later stretch into the arms of the tube. Except near the centrally situated summit both margins of each buttress are taken by two sessile thecae which are inserted longitudinally. Evidently the radial grooves which separated the alternipetalous buttresses in an earlier phase, have not entirely subdivided the staminal wall, as the lobes surmount a united tube part. In this respect it is also interesting to note that in some sectors of the flower the second thecae of adjoining buttresses may be fused at their ends, covering the margins of the sini between two buttresses. The summits of the buttresses remain sterile.

In a still later phase (fig. 164) the distinctly twisted growth of the thecae appears to be stronger than that of other regions of the buttresses. Some of the sterile summits of the buttresses are bilobed, and the lobes may be bilobed again.

In a young bud (fig. 165) the ileum-like formation of the thecae is started, especially at the basal part of the tube. Here the free ends of the buttresses already have the appearance of small distal arms.

Supply of vascular bundles

In the base of the receptacle a sinuous stele is present with five outward antesepalous bends; it is surrounded by a mass of concentric cortical bundles especially in alternisepalous regions (fig. 166).

Higher up, this stele falls apart into (fig. 167) 1) five antesepalous loops forming the calyx supply, 2) ten flank parts of these loops situated between sepal and petal radii, which represent stamen traces with facing xylem, 3) the sini between the loops which form the residual stele and the pistil supply, except for 4) the median parts of the sini which move upwards as the staminodial traces. The cortical bundles ramify abundantly on this level. Another more peripheral flank part of the outward stelar loops moves upwards as a petal trace along a very oblique course. However, the petal trace may also be attached to a sepal basal lateral higher up.

Both stamen traces prove to be the common bases of two stamen traces, which first adhere for some distance running upwards along an oblique course (fig. 169), closing, as it were, a sepal and petal gap. Still higher, the stamen traces, free again, are all concentric and move into the stamen tube, constituting the outward bends of a wave-line which they form together with the staminodial traces. The outward bends are situated in front of the overlapping petal halves. On this level the petal innervation is formed by tangentially stretched concentric bundles which split upwards into diffuse concentric or collateral petal nerves.

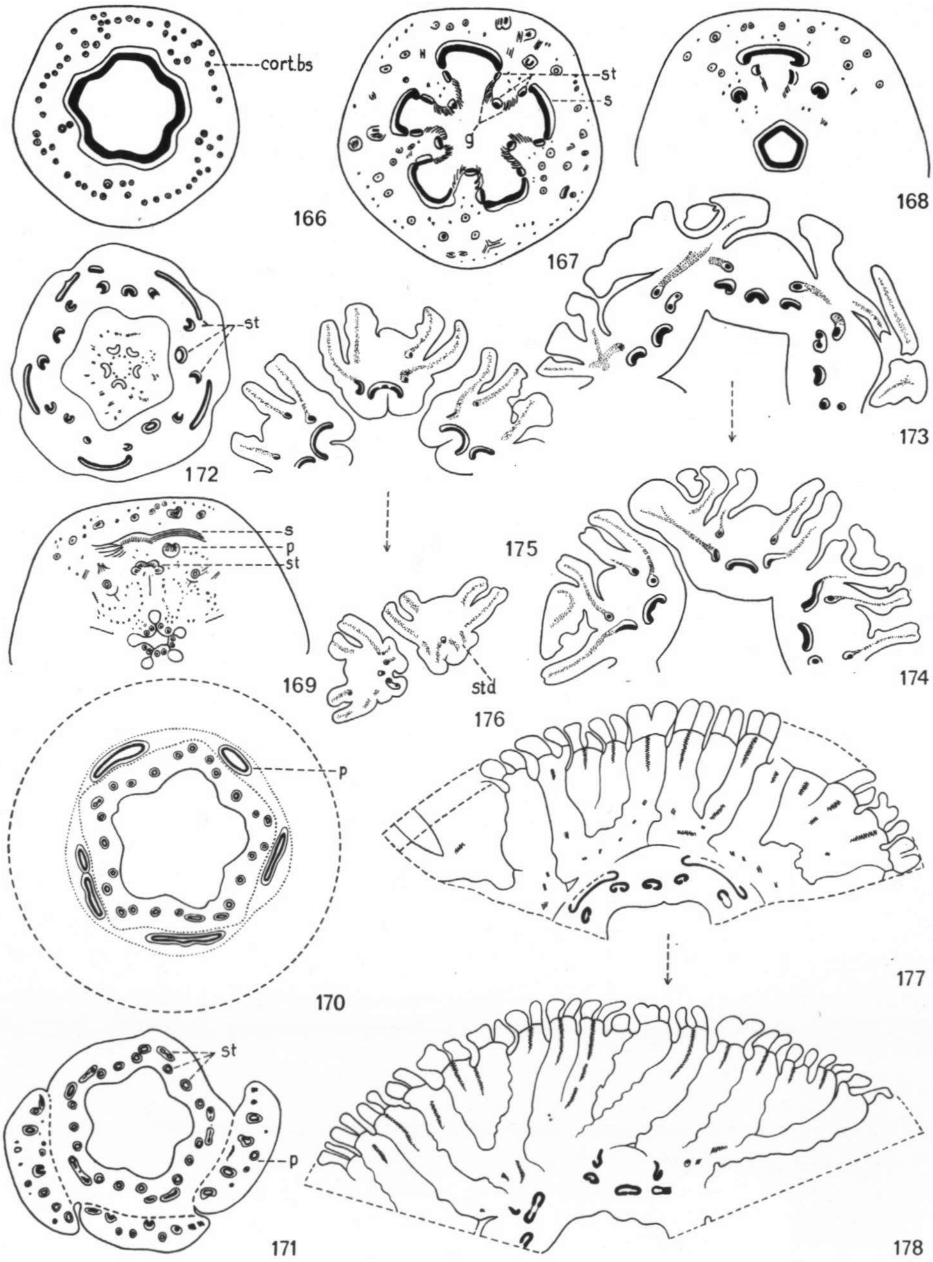
At the base of the staminal region part of the traces have again lost their concentric character, though the staminodial bundle may remain more or less concentric (fig. 171). The peripheral stamen traces fuse laterally to give off the innervation to the downward extension of the laterally fused peripheral thecae, thus completing the wave-line in front of the petals. Furthermore the staminal traces give off lateral parts outwards towards the thecae, the peripheral traces serving the peripheral, the inner traces the inner thecae (figs. 173—176 of a young flower). The traces are arranged perpendicular to the petal surface, with the xylem facing more or less the petal radii.

It is evident from this same series of cross-sections that the halves of the bilobed summits of the androecium parts are bilobed themselves, representing each an apical sterile furcated stamen along either margin of the staminal buttress. Here too the staminode trace can be observed to disappear for the greater part into these staminodial structures.

In figs. 177, 178, representing cross-sections of full-grown staminal regions, the original division into four thecae may still be recognized in the pollen sac mass by lines which run towards the tube surface. These lines prove to be formed by two epidermal layers pressed together.

C) DURIONEAE

Camptostemon philippinense (Vid.) Becc.	S(5)n-(P5-St10)-G(2)
C. schultzii Mast.	ditto
Durio acutifolius (Mast.) Kosterm.	S(5)n-P5-St(∞)-G(5)s
D. grandiflorus (Mast.) Kosterm.	ditto
D. oxleyanus Griff.	ditto
D. kutejensis Becc.	ditto
D. lanceolatus Mast.	ditto
D. graveolens Becc.	ditto
D. testudinarum Becc.	ditto
Neesia altissima Bl.	S(5)n-P5-St∞-G(5)p
N. malayana Bakh.	ditto
N. synandra Mast.	ditto



Ochroma lagopus. — Figs. 166—172. Upward series of c.s. through a full-grown flower base (5 ×). — Figs. 173—176. Upward series of c.s. through distal region of young stamen tube (15 ×). — Figs. 177—178. Distal region of mature stamen tube, c.s., the second on a higher level (7.5 ×).

Kostermansia malayana Soegeng	ditto
Coelostegia griffithii Benth.	S(5)n-P5-St∞-G(5)s
C. borneensis Becc.	S(5)n-P5-St∞-G(5)
Cullenia lepidota K. Sch.	S(5)n-St(∞)-G(5)s

Camptostemon spp.

In *Camptostemon philippinense* some flowers have anthers which are built normally but do not contain viable pollen. If pollen is present, it is echinate.

The calyx tube and the petals bear hairs at their inside base; in the calyx they are intermingled with glandular hairs.

The stamen tube ends in ten stamens which are not markedly arranged in antepetalous pairs. By their broad filaments and connectives they give the impression of having missed division. The two thecae in line are separated from each other by a variable distance. Often a short subulate protrusion of the connective appears between them (fig. 180).

Supply of vascular bundles

The epicalyx is supplied by six irregularly branching traces above which the floral stele is reconstituted. Higher up, the calyx is served by five trifurcating traces which show an oblique upward course, the residual stele constituting the pistil supply.

Five petal stamen traces are attached to the proximal parts of sepal basal laterals on one side, and run upwards obliquely, not fully reaching petal radii. They split into a middle petal trace and two lateral antepetalous facing stamen traces.

Each stamen trace moves up into a filament and divides serially in the connective if the anthers are provided with two thecae lying close together. Mostly, however, the dichotomy lies back in the broad filament, and both branches give a fan-like innervation towards the thecae, which are lying more apart. Sometimes even a secondary dichotomous arrangement may be present in each of these fan-shaped sets (fig. 180). Frequently, in intermediate stages, the basal dichotomy produces two prominent branches which bend sidewards towards the advanced sideward parts of the thecae, some other minor branches proceeding their course right ahead in the direction of the reduced parts of the thecae which touch in the median plane.

Portions of the pollen sacs may be tied off.

In *C. schultzii* five petal stamen traces originate each by two traces which are attached to both sepal basal lateral bundles and run upwards by an oblique course.

Ten rows of stamens are present below the mouth of the tube. They count two stamens each, one above the other.

Some stamens may be split into two half-stamens upon a common filamental stalk, others are distinctly provided with four pollen sacs and have a dichotomous bundle, most are intermediate. Two stamens of one row may have a short common stalk, or their filaments may be fused laterally.

Subdivision of the pollen sacs occurs frequently.

Durio spp.: D. acutifolius

This species belongs to the subgenus *Boschia* in which the structure of the pollen bearing organs is unusual. The filaments at the top either split into a whorl of 2—6 obconical 'thecae', or they are terminated by a single theca of the same shape. The number of thecae present on each filament decreases towards the periphery of the flower. The thecae (fig. 185) consist of a basal connective part and a globular upper part with a central columella above which the wall is slightly depressed. The actual pollen room lies like a ring around this columella and is lined by a tapetum. A slightly brown and reticulate epidermis followed by a hypodermis form the surface layers of the mature thecae. At dehiscence the columella desintegrates and the theca opens at the apical central depression. The hypodermis shows the usual wall thickenings, except over the columella. Reduced thecae are of rather frequent occurrence.

The filament is not prolonged beyond the thecae; it splits into the darkly coloured connectives or into connectives bearing two thecae side by side. Sometimes, especially in the median plane of the stamens, combinations of two thecae appear in the form of broadly obconical structures either with an oval or bean-shaped aperture and similar columella, or with two circular pores in line (fig. 184). If three thecae constitute a stamen, one of the thecae lies in the median plane.

The androecium consists of numerous stamens, the size of which diminishes outwards. There are 4—5 large inner alternisepalous stamens (the flower may be tetra- or pentamerous). They are followed by 4—5 pairs of alternating stamens (fig. 182), but the members of many a pair are fused as double stamens bearing two closely juxtaposed anthers, two neighbouring thecae of which may be more or less fused in the median plane (fig. 186). The stamens of the third whorl alternate more or less with those of the first and second whorl taken together. Towards the periphery the distribution of the stamens — which are there mostly bi- or monothecous — becomes irregular in mature flowers. The size differences suggest centrifugal development starting from five alternisepalous innermost stamens (fig. 184).

Near the perianth the monothecous stamens are staminodes, formed by slender apically thickened filaments. Some of these staminodes may be partly fused laterally, especially so in the antesepalous peripheral flower regions, giving rise to small petaloid organs. In alternisepalous regions the androecium is surrounded by five spathulate petals, each flanked by two, sometimes one, slightly more inner and smaller petaloids. Sometimes the distal parts of the staminodes which are situated between the petals, are slightly tangentially flattened, becoming cochleate around a subapical adaxial median furrow or cavity and there brownish and reticulate like a pollen sac (fig. 187). Sometimes the tangential flattening spreads over the entire length of the outer staminodes, so that slender petaloid structures arise between the petals, which have no characters left reminding of pollen sacs.

The glandular tissue is present on the inside base of the calyx.

Supply of vascular bundles

Five or six irregularly placed traces produce a large number of parallel bundles in the later bivalved epicalyx. Above these traces the stele is reconstituted and passes the rather long part of the pedicel which lies between epicalyx and calyx.

At calyx level five antesepalous main parts diverge from the stele, leaving gaps which are closed by tangential stretching of the alternisepalous parts immediately below the base of the pistil. Just below this level five single traces are given off for the five inner alternisepalous stamens. Also immediately below the pistil base a ring of small twisting bundles is connected to these stamen traces.

Moving outwards, the peripheral portions of the antesepalous main bundles divide into a median part splitting into three sepal traces, and into two flank parts which each run obliquely upwards in the direction of adjoining petal radii forming the well-developed petal stamen traces. Usually only one of the petal stamen traces continues as a petal trace, namely either the left or the right one of a pair attached to a main stelar part. However, sometimes two such petal stamen traces form a petal trace together. The petal traces divide into 3—5 petal main nerves (fig. 183).

During their upward oblique course 5—6 branches are given off from the petal stamen traces, the last of which go towards the petaloids next to the petals, dividing into 2—4 main nerves. The proximal branches form the supply of the more central, the distal branches of the more peripheral stamens. The lowermost branches go to the stamens in the second whorl. Two of them, which belong to the same antesepalous main stelar parts may come together in sepal radii and supply a double stamen. Some of these innermost staminal branches may give off a branchlet towards another stamen.

The residual (3—4) branches of the petal stamen trace undergo a proximal irregular subdivision each into 1—7 stamen bundles. Anastomoses between the stamen traces sometimes take place, infrequently so in petal radii. Thus the stamen and petal vascular supply is intimately linked, except for the trace of the antepetalous innermost stamen that is always separate.

The vascular bundles in the stamens are collateral. They always terminate as single bundles in the connective and do not enter the columella. Usually at the end of the filament the stamen bundle splits into three mostly spatially arranged secondary branches which on a higher level may each bifurcate towards two connectives. If fusion between two thecae is evident, a bifurcation may be present on a high level and with shorter branches. Stamens with only two or a single theca receive only one bifurcating or simple bundle. The double inner stamens, mentioned above, are supplied by two collateral traces which each behave as usual.

Durio grandiflorus

This is another species of the subgenus *Boschia* showing the same peculiar anther structure. However, as regards the arrangement of the stamens the androecium is as pictured for *Durio lanceolatus* in fig. 198. Five mutually free antepetalous phalanges or tangential series consist of about ten laterally fused filaments each. Each filament bears 3—8 thecae which are placed in a small capitule rather than in a whorl. No petaloids are present.

Durio oxleyanus

This species belongs to the subgenus *Durio* in which the anthers simply open by a slit. Still the anther structure in this particular species is rather remarkable. The petals are imbricate, not contorted.

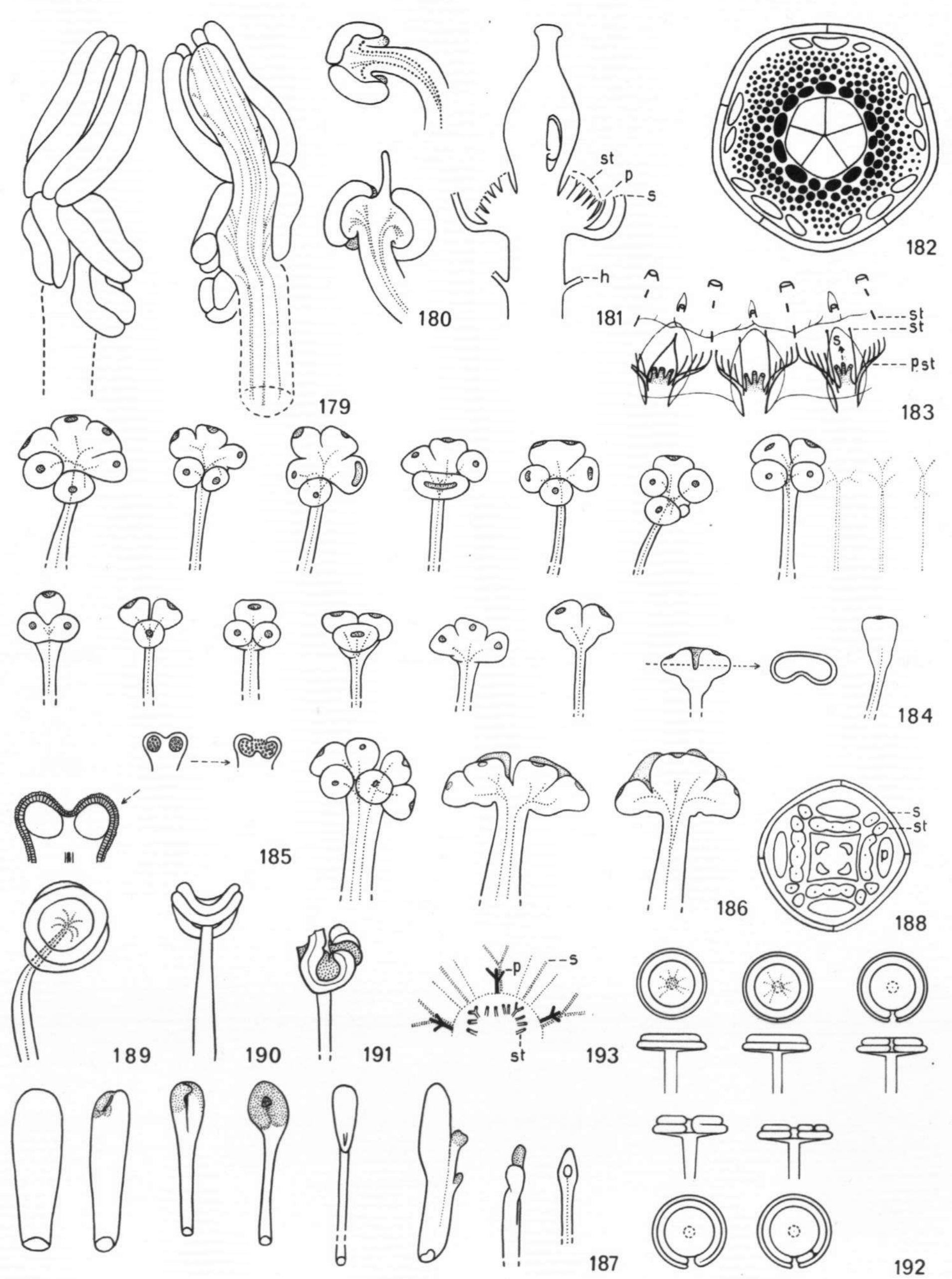
The stamens are arranged in five tangential series (phalanges). The series are somewhat bent inwards in front of the petals. Exactly in sepal radii stamens are lacking and there the phalanges are free from each other. On the other hand the filaments are the more fused laterally as they are situated nearer to petal radii. Some of the outside stamens near sepal radii may be free (fig. 188).

The anthers consist of a theca of two orbicular pollen sacs above each other. They are placed perpendicular to the end of the filaments, though in the lateral filaments they may be bent inwards. Moreover, in the more central stamens they may be slightly folded upwards on either side of a radial plane (figs. 189—191).

Deviations in the form of transverse septs or interruptions in the pollen sacs in the adaxial region of the anther rather frequently occur. Here also small pieces of the pollen sac may be separated (fig. 192). In that way a structure results resembling a reniform half-anther.

Supply of vascular bundles

Ten equidistant bundles leave the receptacular stele almost on the same level, giving trifurcating sepal median traces in sepal radii and combined sepal commissural petal traces in petal radii. Above this level the stele is reconstituted and gives off the traces



The explanation of these figures can be found at the bottom of the opposite page.

towards the stamens immediately, following a wave-line. Among them the highest traces move towards the innermost stamens near petal radii. The low outermost traces often have a common origin (fig. 193).

The filament trace is a collateral bundle which below the anther becomes almost concentric. It splits there digitately into a number of connective bundles, except in adaxial direction.

Durio kutejensis

An epicalyx is present consisting of two or three fused spreading parts. The calyx has five mostly unequal lobes and is glandular at its inner base.

The corolla is contorted, its petals deviate to the left or to the right of petal radii, if overlapping with their right or left margins respectively. The petals may even be practically opposed to the sepals. On the overlapping side they are inserted lower than on the other side. The unequal lobing of the calyx and the varying insertion of the petals interfere with the exact placing of the floral appendages.

The stamens cover a conical receptacle which is terminated by the pistil and bulges outwards roughly in front of the overlapping petal halves. There also, adjacent to the petal surface, the smallest stamens are inserted, the larger ones being placed more centrally. Five very large innermost stamens more or less alternate with these groups of stamens. Upwards they alternate with the five pistil cells (fig. 194).

The structure of the stamens is very peculiar, and reminds one of that in *Ricinus*. A dense capitulum of 10—30 thecae terminates each rather well developed straight filamental stalk (fig. 195). The flat reniform connectives bear two parallel pollen sacs along their upper margin. One may consider that two connectives are frequently fused laterally, giving rise to more or less markedly heart-shaped connectives with two separate sets of pollen sacs in line. Or the fusion products may be emarginate only and bear two parallel sinuous pollen sacs which may be regarded as two fused sets of pollen sacs. Intermediate stages are present in which the margin bears two pollen sacs in line on one side, and on the other side one continuous pollen sac of double length. Other thecae, which are not indented at their summit any more, but are unusually large, may represent the final products of this fusion series. These thecae are packed up in threes on a broad and short common filament.

When studying closer the main stalk of the composed stamens, we may notice that the upper part is longitudinally grooved, especially so in the inner stamens. These grooves foreshadow the upward separation into two or three secondary stalks which in their free parts are only very short. In their fused region they may even, in the large stamens, form together a narrow funnel.

Two or mostly three of these secondary parts occur, the median adaxial place being

Matisia ochrocalyx. — Fig. 179. Lobes of the stamen tube, left: on the outside, right: on the inside and cleared. Interrupted lines indicate lines of fusion with adjacent lobes (5 ×).

Camptostemon philippinense. — Fig. 180. Anthers, cleared.

Durio acutifolius. — Fig. 181. Flower on l.s. — Fig. 182. Floral diagram. — Fig. 183. Scheme of vascular bundle supply. — Fig. 184. Central and more peripheral stamens. — Fig. 185. Monothecate stamen, l.s. — Fig. 186. Double stamens, innermost in sepal radii. — Fig. 187. Structures on the periphery of the androecium.

Durio oxleyanus. — Fig. 188. Base of young flower, c.s. — Fig. 189. Abaxial view on lateral stamen. — Fig. 190. Abaxial view on stamen in petal radii. — Fig. 191. The same, dehisced. — Fig. 192. Schematic top and adaxial views on first a normal, and then slightly deviating anthers. Note the occurrence of partition walls and adaxial sterility. — Fig. 193. Vascular bundle course.

vacant. They split into three of the short filaments which are common to the thecae groups.

Thus the prominent staminal stalks bear a cluster of thecae which may be analysed as a sequence of three times a triple arrangement. In the outer stamens the successive subdivisions give only one or two parts. Assuming that a generally centrifugal development takes place in the androecium, it may be stated that the subdivision of the stamen primordia decreases outwards.

Especially in the inner stamens it is evident that the subdivision chiefly happens in median abaxial direction. There also the stamens are slightly bent outwards. Moreover, in the triplets of thecae groups the median abaxial parts are advanced (fig. 195).

In the capitulum of thecae subulate appendages are intermingled, the lower rather long and the upper ones short. Mostly these structures are inserted at the places of subdivision, but not necessarily as a continuation of the sinus tissue and not only above the distal subdivisions. They also occur just near, or lateral to, a fork in the vascular bundles. Once a forked appendage was found (fig. 196).

Supply of vascular bundles

As is immediately evident in fig. 194, the contorted characters are very marked. A succession of pentamerous whorls leaves the floral stele, namely five sepal and five petal traces, five outer staminal parts and five sets of three inner stamen traces. The whorls leave the stele on successively higher levels, mostly where the stele is still interrupted by the gaps caused by the lower whorl.

The petal traces leave the stele, not alternating with, but close to the sepal traces, moving to the left or right towards petal radii if the petals overlap to the right or left respectively.

Though the outer staminal parts alternate with the sets of inner stamen traces, the staminal traces as a whole neither alternate with the petal, nor with the sepal traces. The outer staminal parts as well as the sets of three inner stamen traces leave one gap in the stele. Frequently one of the inner stamen traces divides once, giving a total of four stamen bundles to reach each of the innermost staminal stalks (fig. 197). The outer staminal stelar parts are U-shaped and tangentially stretched; they are subdivided in many outward stamen traces which each divide in 1—3 stamen bundles on entering the stalks.

In the stalks the xylem of the bundles faces one another. The bundles split according to the external divisions described above. However, it should be noticed that splitting is mostly twice dichotomous and not trichotomous.

In the connectives the bundles mostly bifurcate once. In the laterally fused thecae intermediate cases occur showing one theca with an unbranched vascular bundle and the other with a forked bundle.

The larger among the sterile appendages may contain some central unconnected vascular tissue.

Durio lanceolatus and graveolens

The structure of the stamens is the same as that in *Durio kutejensis*, although subdivision is less profuse and sterile appendages are lacking. The chief difference lies in the arrangement of the stamens in five distinct antepetalous phalanges, like in *D. grandiflorus* and *testudinarum*. A few stamens may be situated next to the stamens of the phalanges in radial or diagonal direction, especially so in *D. graveolens*. The corolla is contorted.

Supply of vascular bundles (figs. 200, 201).

In the base of the receptacle the stele gives off five broad antesepalous portions, the major part of which trifurcates into three sepal traces. Moreover, from the same flank of each portion a petal trace separates which moves in alternisepalous direction by an oblique course. The stele is reconstituted above the gaps formed by the main portions.

The stamen traces each depart from the reconstituted stele directly, in antesepalous regions somewhat lower than in alternate regions, together following a wave-line. Sometimes in antesepalous regions a stamen trace shows a double origin. Each stamen trace may split into a few bundles going towards the staminal stalks.

In the rather similar species *D. graveolens* the attachment of stamen traces is more concentrated near sepal radii, though to varying degree. Together the traces are in a U-formation. However, the traces towards the inner stamens remain single and high in the petal radii, although together with the antesepalous traces they sometimes form almost a wave-line.

Durio testudinarum

Upwards, the staminal tube falls apart into five antepetalous phalanges, the median antepetalous members of which are placed more inwards and are fused higher than the lateral ones. Together the stamens are arranged on a wave-line, the lateral members of the phalanges not being placed so much to the outside as in the preceding species (fig. 202). The filaments bear a small irregular cluster of thecae which show the structure and fusions known from *D. kutejensis*. Sterile appendages are absent. The corolla is contorted.

A young bud

Apically the filamental stalks are slightly cup-shaped and bear the still small young thecae or anthers along the margin. Here the filament is broader than deep and more rounded on the outside than on the inside. In fact, the apex of the filament is hardly widened in the adaxial median part, especially not in the outer stamens. Moreover, there is no theca there. Consequently, the summit of the filament is of a dorsiventral structure (figs. 203—207). However, in the inner stamens, the anther seems to be composed rather of two (in one case three) of these dorsiventral structures which are directed towards the axis of the filament and fused in the middle. Accordingly, the outline of the top view is elliptic or dumb-bell shaped. The arrangement of these two components may be collateral as well as serial. Some of the outside stamens may have no theca or anther in their median abaxial part, so that they also look like being composed of two fused portions, although as a whole they are dorsiventral. (One mature stamen was found in petal radii which separated into two collateral free apical parts each bearing a small cluster of thecae).

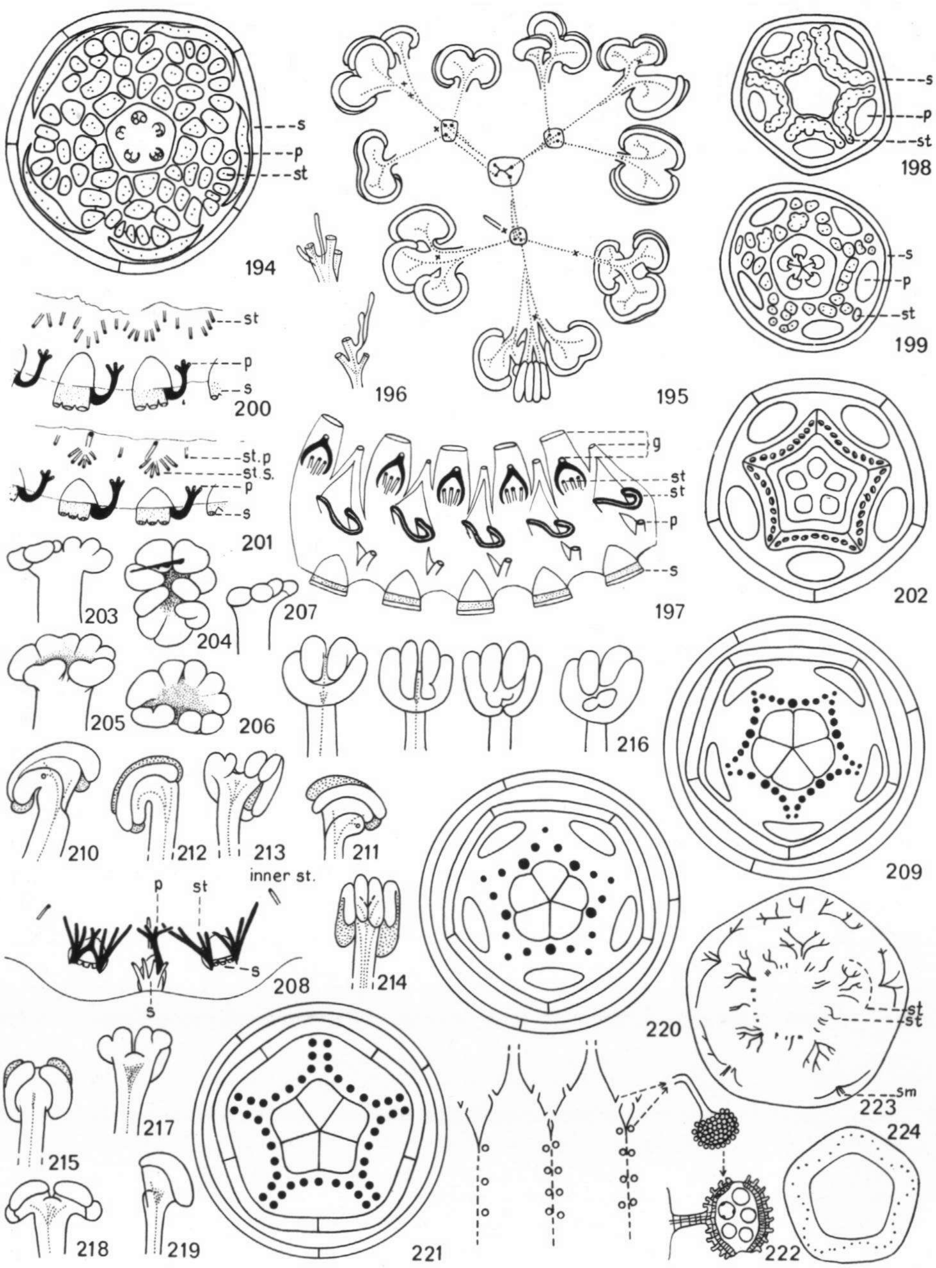
Supply of vascular bundles

In the base of the flower five antesepalous parts of the stele bulge outwards. Five other alternating parts leave the stele on different levels forming, besides lateral sepal supply, a petal trace. The petal trace becomes concentric before trifurcating upwards. Higher up, the antesepalous parts separate from the stele giving the middle sepal supply. However, the flanks of these antesepalous portions form two stamen fascicle traces which branch into the individual stamen traces. On the other hand, the traces for the innermost stamens in petal radii leave the stele directly and on a higher level. Together the stamen traces form a wave-line in the tube base (fig. 208).

The stamen traces are collateral bundles with the xylem more or less facing the centre of the flower. They may divide into two collateral branches in the distal part of the filament. Their ramification in the thecae is similar to that in *D. kutejensis*.

Other authors on Durio spp.

Kostermans (1958) described the stamens as grouped in five phalanges by means of



The explanation of these figures can be found at the bottom of the opposite page.

the slight adherence of the composing filaments at the base. Sometimes there are single stamens in between the five phalanges. In some species the phalanges are united into a tube. The filaments are said to bear many reniform cells which may represent half-anthers. In *Boschia* the staminal units are simply called anthers which open by a pore.

Saunders studied *D. zibethinus*. The stamens arise in five antepetalous phalanges which are more or less completely resolved into half filaments. If resolution is incomplete the anther is polythecal.

Neesia spp.

All the stamens are inserted directly on the receptacle along a wave-line the outer bends of which are more or less in front of the contorted petals (fig. 209). In a young bud five antesepalous arched elevations are present with young stamens developing along the margin in centrifugal direction. The first and innermost stamens lie more or less in sepal radii, alternating with the cells of the pistil. Basally the stamens are slightly adnate.

The distal part of the filament with its somewhat broader subapical region is bent outwards and even more or less backwards (figs. 210—214). Moreover, it is folded in adaxial direction so that a narrow or wide longitudinal groove results which by means of the resupination is situated apically. On either side of this groove a theca is inserted along the entire supinate part of the filament, each theca with two parallel pollen sacs. Whereas in well-developed stamens the thecae flare sidewards, in occasional simple specimens the resupination and folding is not very distinct (fig. 215). The anthers are directed with their apical grooves perpendicular to the wave-line.

Irregularities in the pollen sac formation are frequent at the resupinate tip of the connective. Here the outer pollen sacs of an anther may be continuous and the ultimate parts of the inner sacs may be isolated. Incidentally two pollen sacs of one theca can be linked at the end of the connective by a separate small sac.

Supply of vascular bundles

Following the floral stele upwards, we note the attachment of the sepal traces, and, higher up, on a level where the sepal gaps are not yet closed, the attachment of the alternating petal traces. Still higher, the stele is reconstituted and becomes pentagonal with the angles in petal radii.

Durio kutejensis. — Fig. 194. Flower base, c.s. Dots mean places of vascular bundles. Members of anatomically outer group united by means of small lines. — Fig. 195. Ramification scheme of a central stamen. At × places of elongate appendages. — Fig. 196. Details of appendages. — Fig. 197. Course of vascular bundles in the receptacle.

Durio lanceolatus. — Figs. 198—199. Flower base, c.s., second fig. on a higher level. — Fig. 200. Course of vascular bundles.

Durio graveolens. — Fig. 201. Course of vascular bundles.

Durio testudinarum. — Fig. 202. Floral base, diagrammatically. — Fig. 203. Lateral view on young stamen in petal radius, adaxial side on the right. — Fig. 204. The same, top view, adaxial side up. — Fig. 205. Adaxial view on young outer stamen. — Fig. 206. The same, top view. — Fig. 207. The same, lateral view, adaxial side on the left. (Figs. 203—207. 35 ×). — Fig. 208. Course of vascular bundles.

Neesia altissima. — Fig. 209. Flower diagram. — Figs. 210—211. Stamens, l.s. — Fig. 212. Stamen, lateral view. — Fig. 213—214. Stamens, adaxial view. — Fig. 215. Simple stamen.

Neesia malayana. — Fig. 216. Abaxial side of stamens with fusion and subdivision of pollen sacs.

Kostermansia malayana. — Fig. 217—218. Stamens, adaxial view. — Fig. 219. Stamen, laterally.

Coelostegia griffithii. — Fig. 220. Flower diagram.

Cullenia ceylanica. — Fig. 221. Flower diagram. — Fig. 222. Position of stamens on laid flat part of the tube, with details of a stamen and a pollen sac. — Fig. 223. Cleared floral receptacle. — Fig. 224. Cleared base of stamen tube.

From this reconstituted stele five traces are given off which divide into a U-formation of antepetalous stamen traces. Somewhat higher, another five traces depart which remain single and constitute the inner antesepalous stamen traces.

In the distal part of the filament a stamen bundle gives off two lateral branches which move upwards gradually into the thecae. Next the stamen bundle pursues its course into the resupinate part and simply ends there or forms a small isotomy, which is smaller the closer the thecae lie together near the apex of the connective. These small branches may not fully reach the thecae.

In *N. malayana* the stamen bundle is single with at best a rest of branching at the anther base. In this species the form of the anther is more condensed (fig. 216).

Some deviations may occur in the form of four, or five, fan-shaped branches which come from the stamen bundle almost at the same point on the level of the anther base. In one case the upper small branches have another small isotomy. Occasional simple anthers receive a single unbranched bundle.

Kostermansia malayana

In this species the flower parts appear to have the same arrangement as in *Neesia*. The anthers consist of two reniform thecae, each with two parallel pollen sacs which are placed extrorsily somewhat below the broadened apex of the filament. The innervation is fan-shaped (figs. 217—219).

Coelostegia griffithii

In young buds it is evident that the stamens are arranged on a wave-line the outward bends of which alternate more or less with the petals (fig. 220). Correspondingly the advanced inner stamens are situated in petal radii and alternate with the cells of the pistil. The stamens are small, the anthers are composed of four shortly elliptic or almost globular pollen sacs in square formation on top of the filaments. The abaxial side is somewhat larger than the adaxial. In the outer stamens on the adaxial side lateral fusion of the pollen sacs occurs, leading to the occasional presence of only one median sac. The thecae open by a slit.

Supply of vascular bundles

The vascular bundle supply is rather variable and may even vary in one and the same flower.

Five main portions may leave the stele and trifurcate into three sepal traces. From each flank one or two stamen traces are given off which by collateral division form three traces for the outer stamens. The petal trace is attached to one of the sepal laterals by an oblique course.

Above the main portions the gaps are not closed, and from the intermediate portions five single unbranched bundles are given off which represent the separate supply towards the inner stamens. The ten residual stelar portions go into the pistil.

Often, however, the three sepal traces are attached to the stele directly. Then petal and antesepalous stamen traces may be connected with the proximal parts of these traces, or directly with the stele quite near the sepal traces. If sepal traces are connected with the stele directly, they are so on an higher level than the main sepal portions mentioned above.

In another flower part sepal, petal, and all stamen traces are attached to the stele directly, except for the sets of three outer stamens which have a common basal trace in sepal radii.

Coelostegia borneensis

In this species the arrangement of the stamens appears to be like that in *C. griffithii*. However, the outward coils of the wave-line lie more in front of the overlapping halves of the mostly contorted petals. Consequently the inner stamens as well as the alternating pistil cells are situated somewhere between sepal and petal radii. If, in the future, more and younger non-dried developmental phases come available for study, it may prove that the staminal arrangement in *Coelostegia*, *Neesia*, and *Kostermansia* is in fact similar, but variable according to the contorted development.

Cullenia ceylanica

In cross-section the stamen tube has five angles in sepal radii. Its sides end in five linguiform alternisepalous lobes which are contiguous below but free above (fig. 222). Whereas along the margins of the lobes 7—9 stamens are placed, a separate stamen terminates each lobe.

The head of the stamens is irregularly spherical, in the upper stamen it is more rounded on the outside than on the inside and more gradually tapering into the filament. A most curious feature is that the heads carry numerous globules filled with only a few pollen grains and that the globules are each provided with a single, tiny, though multicellular stalk (fig. 222). Some of the cells of the epidermis of these pollen sacs, especially in the upper part, protrude outwards and possibly liberate their special cytoplasmic content by rupture of the walls. The layer of cells below the epidermis is provided with the characteristic local thickenings present in these layers in normal anthers. Another remarkable feature is formed by an annular transverse region half way up each sac in which the subepidermal layer with its thickenings is absent or lost (fig. 222). No doubt dehiscence of the sacs takes place by rupture of the wall along this annular region.

Supply of vascular bundles (figs. 223, 224)

Above the departure of the traces for the epicalyx the stele is reconstituted and remains five-angled in sepal radii. Five trifurcating sepal traces separate, the laterals of which join in alternisepalous radii. As there are no petals, the subsequent higher set of five traces given off is formed by the stamen fascicle traces. These traces divide by a more or less fan-like innervation, consisting of condensed dicho- or trichotomies, into the traces for the stamens, except for those at the top. Slightly higher up, five single traces move outwards into the upper stamens. In the base of the stamen tube the traces lie on a wave-line equidistantly, those for the upper stamens innermost (fig. 224).

In the spherical heads of the stamens the stamen bundles undergo a profuse ramification which starts with a collateral dichotomy, except in the upper stamen where it starts with a serial dichotomy. The next ramifications are frequently dicho- or trichotomies, but digitate and pinnate splitting also occurs. The upper branchlets are tiny and frequently fan-shaped.

Other authors

Kostermans (1956) stated that the upper part of the filament bears pedicellate, one-celled, glomerulate anthers.

B. COMPARATIVE PART

1. THE ARRANGEMENT OF THE STAMENS IN FULL-GROWN FLOWERS

A study of the external morphology presents a very diverse picture which can be made only partly coherent by applying developmental data.

In *Adansonia digitata* the numerous stamens are evenly distributed on the distal part of the tube, slightly extending also on the inside of the rim of the tube.

In *Pachira* spp. the tube falls apart into ten outer groups of stamens between sepal and petal radii and five single inner stamens in sepal radii.

In *Bombax* spp. the stamens are arranged on a wave-line and form a tube. The wave-line has outward lower antepetalous bends which in *B. ellipticum* are W-shaped.

In *Bombax buonopozense*, as well as in *B. ceiba*, three inner forked stamens in each inward curve of the wave-line form an inner separate whorl in consequence of a late change in growth, which is rather extensive and takes place parallel with the floral axis instead of at an angle. It should be remarked that in *B. ceiba* the triple formation is really formed by two lateral forked stamens, the most median parts of which fuse in the sepal radii giving the appearance of a third median stamen. In *B. buonopozense* the tube ends in a sterile part which may show five antesepalous lobes.

In *Ceiba* spp. the androecium is limited to only five antesepalous stamens.

Matisieae are fairly coherent as regards the androecium structure in that the staminal tubes end in five antesepalous lobes or arms which are apically sterile. In *Quararibea guianensis* the sterile apex is bilobed. In *Ochroma lagopus* the distal tube part and its arms are matted with a mass of twisted thecae. On the other hand *Quararibea guianensis* and *Matisia ochroleuca* look like *Hibisceae*, reniform thecae being placed in ten more or less antepetalous rows along the arms or on the tube longitudinally. Also the thecae are more or less whorled, and there is a major and a minor row corresponding with the contorted insertion of the petals. Only, the thecae are sessile (like in *Kydia calycina*, where they are also placed along antesepalous lobes of the tube).

In *Camptostemon* spp. there are one or two whorls of ten fused stamens which are probably paired.

In the *Durioneae* the stamens are generally placed in concave more or less antepetalous phalanges, that is to say they are fused more intimately as they are placed more inwards near petal radii and they may be almost free near the sepal radii. If the phalanges are very concave, the stamens give the impression of being arranged on a wave-line. In *Durio kutejensis* the flanks of the phalanges are probably prominently curled. In some *Durio* spp. a few additional stamens may sometimes be present more outwards. In *Durio testudinarum* the phalanges are raised upon a common tube. An exception to the rule is *D. acutifolius* in which species the stamens are free and are evenly distributed over the receptacle, the innermost in petal radii, the following alternating singly or in pairs until more outwards the pattern becomes indistinct. In *Neesia* spp. the stamens are inserted on the receptacle forming a wave-line with probably antepetalous outward bends and innermost antesepalous stamens.

The mature form of the stamens

The stamens are forked, each branch bearing a reniform theca with two longitudinal pollen sacs in the plane of the forking.

In *Bombax* and *Pachira* spp. the stamens are free on the level of bifurcation, in *Matisieae* the thecae are sessile on the tube one above the other. In *Camptostemon* spp. the stamens are mostly not or not entirely split, the connectives being often broad or even bilobed and bearing two thecae in line. In addition, the connective may protrude upwards from between the thecae. Occasionally in *Pachira* and *Bombax* spp. unsplit stamens occur, or one of the halves may be missing in peripheral stamens, or a subulate appendage replaces a half-stamen.

In *Adansonia digitata* and *Ceiba pentandra* stamens with two pollen sacs are present only which may be sterile at the apex. As a rule in *Ceiba pubiflora* and *Chorisia crispiflora*, four pollen sacs are present. In *Adansonia* the stamens are folded medianly away from the tube, suggesting to bear four pollen sacs.

In *Durio*, section *Boschia*, the filaments may bear up to six obconical often paired thecae which have a central columella and dehisce at the apex. More outer stamens may count fewer thecae, even only a single terminal theca. The most peripheral stamens are flattened and may be fused, forming a kind of narrow petaloids.

In *Durio*, section *Durio*, large stalks first divide into three secondary short parts which on their turn each split into three bases of groups of thecae. These groups consist of three or fewer often partly split members. Away from the most central stamen in petal radii the extent of development in the other stamens gradually decreases. Median adaxial places are not occupied by any splitting products. Worm-like appendages may frequently occur near the points of splitting. *Durio oxleyanus* has on its filaments orbicular thecae, which may be sterile adaxially in the median plane.

In *Neesia* spp. the distal parts of the filaments are resupinate and bear two longitudinal thecae latero-adaxially.

In *Cullenia ceylanica* the club-shaped connectives are covered with a mass of small, stalked, globular microsporangia which open by means of an annular transverse slit.

2. THE DEVELOPMENTAL STAGES OF THE ANDROECIUM

In the *Bombax* and *Pachira* spp. which are studied here, and in *Bombacopsis quinata* the ontogeny of the androecium proceeds in much the same way. The first primordial stages are lacking in my material (except in that of *Bombax ceiba*). In an early phase, near the border of the floral apex, a pentagonal wall is present with roughly alternisepalous angles and trapezoid antesepalous parts. These parts may be low (*Pachira* spp.) or may become somewhat elevated and bending inwards over the residual apex, forming antesepalous lobes of the wall. The carpel primordia will arise alternatingly with these advanced antesepalous regions of the wall.

In *Pachira* spp. median central regions of the trapezoid wall parts form protuberances which each give a single stamen primordium. However, the lateral regions form more or less radial elliptic buttresses on which stamen primordia may be observed to develop later, first in a centrifugal way and then in a latero-centripetal direction towards the side of the petal radii. In *Bombax* spp. and in *Bombacopsis quinata* the central median parts of the prominent lobes are usually somewhat retarded and sterile. Later they may form the free sterile, often bilobed, summits of antesepalous lobes, along the well developed margins of which the stamen primordia arise at first in a centrifugal and then sideward sequence. As a result of the sideward development the stamen primordia are arranged on a wave line. However, the sideward development is frequently somewhat curling, so that the stamens belonging to adjoining lobes do not link up over the petal regions so very smoothly. They may overlap each other in a contorted way which is the reverse of that of the petals. Much later the sterile apical parts of the lobes are completely outsized by the stretching fertile parts. The stamen primordia divide in the usual way giving two thecae parallel with the lobe margins. The central (*Bombacopsis quinata*) or the peripheral (*Bombax ceiba*) thecae of the innermost lateral stamens may be less well developed. The young anthers of *Ceiba pentandra* resemble alternipetalous trapezoid lobes which produce a continuous theca along the entire margin.

The development in *Quararibea guianensis* and *Ochroma lagopus* is quite similar to that of the preceding species. However, the median parts of the antesepalous lobes are at first retarded or lower, so that the development strongly resembles that in the *Malvaceae*. A low wall is subdivided in ten parts by deep, or in *Ochroma lagopus* by narrow, antepetalous grooves and shallow wide antesepalous grooves. Just as in *Malvaceae*, the median parts resume growth in a later phase, giving the sterile sometimes bilobed summits of the staminal lobes. As these parts may again be bilobed, they probably represent reduced stamens. Along each margin mostly two paired sessile thecae develop in line. In *Ochroma lagopus* the peripheral thecae may fuse over the petal radii, forming the outward bends of a wave-line configuration. The contorted conditions and the variable insertion of the petals have their influence on the relative positions of the organs described above. The margins of the lobes which are placed in front of the overlapping more outwards inserted petal halves, are slightly longer than the opposite margins. In *Quararibea guianensis* along the major margin an additional peripheral stamen may sometimes develop, which remains in the form of an unsplit theca.

Unfortunately I have not been successful in obtaining primordial floral stages of *Durioneae*.

In *Adansonia digitata* the stamen primordia appear all in centrifugal sequence over the outer surface of a large wall. Later some more primordia appear under the first-formed in an irregular fashion (cf. *Entelea arborescens*). In *Adansonia digitata* the stamen primordia can be followed to develop as usual from hemispheric to elliptic protuberances which become stalked and spoonshaped. Two parallel pollen sacs are formed along the entire upper margins. However, a curious fact is that here these structures do not divide into two equal halves, but are folded along a median plane.

3. THE COURSE OF THE VASCULAR BUNDLES IN THE ANDROECIUM

In *Adansonia digitata* in the very base of the tube a pentagonal ring of bundles gives off many petal nerves first, and then, above that level, falls apart into an inner and an outer ring of traces which innervate inner and outer stamens exclusively. The traces of these two systems have facing xylem. However, in the middle tube region the traces form concentric bundles or combinations which in the upper region divide into the final stamen traces by way of some intermediate bundles.

In all the other species of *Adansonieae* and *Matisieae* studied the supply is strikingly similar in spite off the diversity of the external features. In the base of the petal stamen tubes a number of bundles is arranged on a wave-line, with the petal traces in the outward bends, the antesepalous stamen or staminode traces in the inward bends, and ten stamen fascicle traces along the shanks. Downwards the stamen fascicle traces and the petal traces form the flanks and the middle parts of common collateral bundles, or only the minor stamen fascicle traces unite with the petal traces. This common trace is frequently attached to the flanks of main stelar parts going towards the sepals, or is connected with the stele which is reconstituted above these main sepal traces. All traces may have an oblique course in correspondence with the contorted character of the petals and the androecium.

A very constant feature is formed by the trace which leaves the (reconstituted) stele always as a single trace on a higher level, forming in *Pachira* spp. and probably in *Bombax ellipticum* an innermost antesepalous stamen trace, a blindly ending trace in all the other species.

The stamen fascicle traces have the xylem directed perpendicular to the wave-line and towards the side of petal radii. In *Adansonieae* they form by a fan-shaped splitting the different forking traces for those stamens which have their origin on the margins of the antesepalous staminal lobes. The inward curling of the sides of the lobes, which has been described above, can be excellently followed by the place of the stamen traces and their xylem. The xylem of the traces in the curling flanks faces the xylem of the other traces. In *Bombacopsis quinata* it is even evident that the staminal lobes overlap one another with inward bending flanks in a contorted fashion which is the reverse of that of the petals.

In *Ceiba* spp. and in *Chorisia crispiflora* three traces enter each stamen, viz. two stamen fascicle traces and the inner staminode trace the latter of which is situated in the middle and in a sepal radius. Upwards they form together an outward open C-shaped bundle with the xylem facing the floral centre, which in the connective divides into a fan-like mass of branches.

In the *Matisieae*, as in *Malvaceae* the fascicle traces forking once innervate the pairs of thecae present along each staminal lobe. A third lower unpaired theca of a major row may receive a separate branch of the fascicle trace. Upwards the median sterile trace is tangentially stretched and may either form some parallel laterals or go into the bilobed summits of the staminal lobes in a forking way.

In *Camptostemon* the petal stamen fascicle traces are connected with the proximal parts of the sepal basal laterals by means of an oblique course. Upwards the traces divide into a median petal trace and two facing lateral stamen fascicle traces; the latter supply each either one mostly unsplit stamen or two above each other. It is at once evident that, in the vascular supply, *Camptostemon* is unlike the other *Bombacaceae* studied here, especially as regards the absence of residual antesepalous vascular bundles. Maybe *Camptostemon* approaches the *Hibisceae*.

In *Durioneae*, except in *Durio acutifolius*, the stamen traces are generally placed on a wave-line. The most constant character is furnished by the innermost about antepetalous stamens, the traces of which are invariably connected directly with the reconstituted stele on a high level. The traces of the other stamens, which form the outer antesepalous bends, are attached to the underlying vascular supply in various ways. In *Durio kutejensis* they are separated from tangentially stretched vascular bundle combinations which diverge from the reconstituted stele above sepal level. In *Durio grandiflorus*, *graveolens*, *oxleyanus*, and *lanceolatus*, and in *Cullenia ceylanica* the traces come from the reconstituted stele directly, those of the antesepalous stamens sometimes aggregated near sepal radii. Finally in *Durio testudinarum* and *Coelostegia griffithii* the traces arise from two fascicle traces which link up with the flanks of the sepallary main traces. The petal traces are either connected with the sepal commissural traces or with the flanks of sepal median traces or come from the stele directly quite near those flanks. Stamen traces are not attached to them. In *Durio* the stamen traces are intermediate bundles which, on entering the filamental stalks, split into several bundles with facing xylem.

In *Durio acutifolius* traces come from the flanks of the main sepal traces. They have an oblique course towards the petal radii on either side and terminate there as the double bases of the petal traces. However, first a number of stamen traces and furthermore a petaloid trace are given off by these oblique traces. The stamen traces are here also intermediate traces which split into several secondary traces for the different filaments.

In *Neesia* the separate single traces of the innermost stamens lie more or less in sepal radii. Five stamen fascicle traces in petal radii come from the reconstituted stele giving the supply towards the outer antepetalous bends of stamens.

The division of the stamen bundles in the connectives

The vascular bundle course in the thecae is in principle fan-like, which is especially evident in *Bombax* spp. In *Camptostemon philippinense* undivided stamens have a vascular supply which in the connective or filament splits into two fan-like parts towards each theca. However, if the thecae are closely adjacent, there are two anatropous prominent branches with some smaller branches in between. In *Pachira* spp. the different thecae have an upward and a downward bending branch of the filament trace, and also some subsidiary branches in between the two. In *Neesia* spp. the bithecous anthers have a bending distal part of the filament bundle, which gives off two side branches towards the proximal parts of the thecae and finally forks once in the direction of the distal thecae parts.

In *Adansonia digitata*, *Ceiba* spp. and *Chorisia crispiflora* the fanning bundle system is more or less folded. Some middle branches may concentrate and may even form together a prominent bundle. In *Ceiba* many of the branches may fork outwards.

In *Durio* also a fan-like vascular bundle system occurs in the thecae, which is, however, frequently restricted to a pair of anatropous branches with little or no vascular tissue in between. In *Durio acutifolius* the simple filament bundle trifurcates and then, in the anthers with a higher number of thecae, the branches may bifurcate. In *Durio oxleyanus* the filament bundle becomes almost concentric and splits suddenly into a number of radiate branches into the orbicular connective, except in median adaxial direction. In *Durio kutejensis* a filament has up to three bundles, each of which may trifurcate several times. The xylem of the three bundles faces one another. Each trifurcation is really a condensed double bifurcation. In *Cullenia ceylanica* the peculiar connectives show an intricate ramification system which is caused by a bifurcation of the main branch perpendicular to the wave-line along which the stamens are placed.

4. THE SEPALS, THE PETALS, AND THE GLANDULAR TISSUE

The sepals

Towards the rather thick calyces, the middle traces are generally much spread tangentially, the portions of the stele which go to the sepal parts being broad. Sepal basal laterals are short, sepal commissural marginals are rare. In smaller flowers a trifurcation of the sepal median trace is more evident.

In each sepal part a small number of main nerves is present which are connected by a large number of smaller nerves and anastomoses. In the proximal parts of the sepals the bundles are often more or less dispersed. The outer nerves have cortical traces. Toward the glands the inner nerves form either direct side branches or a separate sheath of branches is formed from their proximal parts.

The petals

Generally, the bundles in the petals are more parallel than in *Malvaceae* and show less distinct forking of the branches, especially so in those petals which are more elongate instead of cuneate.

The glandular tissue

Glandular trichomes are invariably lining the inside proximal parts of the calyces. Moreover, in *Pachira* and *Bombax* spp. large antesepalous and smaller, dispersed, outside elliptic fields of glandular trichomes are present near the indistinct border separating receptacle and pedicel. These fields are not innervated.

5. VARIATION IN THE COURSE OF THE VASCULAR BUNDLES

The multiple attachment

In *Durio acutifolius* the petal traces may have double bases linking them with the flanks of two adjoining sepallary main bundles. In *Ochroma lagopus* the reduced stamen primordia near the summits of the staminal lobes may be supplied by traces which are attached to the median bundle of the lobe as well as to the traces of the more peripheral thecae.

Some special features

In the connective of *Pachira* spp. the middle bundles are somewhat reduced. They often show interrupted lignification and form commissurals. Commissural bundles are also formed by the sepal lateral bundles and outer staminal traces in some *Durio* spp.

In *Ceiba mandoni* and *Chorisia crispiflora* the lateral stamen traces make an outward loop below the surface of the lateral stamen appendages on the base of the tube.

Residual bundles

Some diffuse vascular bundles may depart from the loops described above in outward direction. Probably these appendages are formed about the time of development of the stamen bundles.

Other residual vascular bundles occur in the median planes of the staminal lobes in *Bombax*, *Pachira* and other genera, in the worm-like appendages of the theciferous structures in *Durio kutejensis* and in *Durio acutifolius* where they link the innermost stamen traces.

Cortical bundles

Cortical bundles are rather frequent in *Adansonieae* and in *Ochroma lagopus.* They may fade downwards near the level of bracteole insertion, or they may be connected with the stele below the calyx parts. They are often concentrated alternatingly with the main sepal median supply or they have their major bundles there.

Concentric bundles

Concentric bundles are of rather common occurrence, probably in correspondence with the thick flower parts in which they are situated, such as the petals in *Pachira* spp. *Bombax ellipticum* and *Ochroma lagopus.* Upwards these concentric bundles become collateral and may split into minor branches. The cortical bundles are also mostly concentric. Stamen fascicle traces may be concentric in their proximal course for instance in *Adansonia digitata, Bombax* spp., and in *Ochroma lagopus.* In *Pachira* spp. and in *Bombax ceiba* filament bundles are sometimes composed of several vascular groups. In the connectives they spread into collateral parts. In the filamental stalks in the subgenus *Durio* the different vascular bundles have facing xylem.

C. INTERPRETATIVE PART

The structure of the androecium

Among the *Bombacaceae* which have been studied *Adansonia digitata* stands apart and the *Durio* spp. also take a somewhat isolated position. On the other hand, the rest of the *Adansonieae* and the *Matisieae* have many features in common, and may easily be compared with the *Malvaceae.*

Adansonia digitata

Notwithstanding the fact that the stamen primordia do not divide in two, each forms a monothecous stamen, of which a multitude cover the terminal part of a big tube. An outer and an inner set may be distinguished among these stamens, judging the facing directions of the connectives and the separate rings of facing traces which innervate each set. Downwards the rings join and link up with the petal traces. It is at once evident that — like in *Malvaceae* — we are unable to regard the monothecous stamens as the division products of 'usual' bithecous stamens, the forked filaments of which would be united to form the tube tissue. Not even if the separation of the stamens and their traces in two facing sets is considered to give anatomical evidence of such a division. For the traces of several stamens — not of pairs of stamens — are gradually fasciculated into concentric bundles or combinations which run through the tube forming the two rings. The base of these concentric bundles may be somewhat spread, but never in as many traces as there are ultimate stamen traces. Therefore, if the anatomical features are advanced as arguments, the monothecous stamens must be considered as the final congenitally fused products of a multiple division which follows upon a proximal separation into two sets.

Other Adansonieae and the Matisieae

As in *Malvaceae*, the stamens are arranged along the sides of trapezoid more or less alternipetalous lobes which for the greater part are fused congenitally forming a tube. However, the apical parts of the lobes which terminate a slightly pentagonal incipient staminal wall, are generally more free than in *Malvaceae*, and not so markedly sloping downwards centrally. Their development is more extensive, also in the median region, except in *Pachira* spp. The carpels always arise alternating with these lobes.

Whereas in *Bombax* and allied genera the apical lobes are later completely outsized by the very large stamens, the lobes in *Matisieae* persist till in the mature phase, terminating the tube with five free arms. That is to say the lobes are initially more reduced in their central and median parts than in the *Adansonieae*, but, as in some *Malvaceae*, resume growth later on. *Quararibea guianensis* most resembles a malvaceous flower, the lobes being fused into a long tube.

Along the abaxial sides of the lateral lobe regions staminal buttresses (stamen fascicle primordia) arise — very distinct in the *Pachira* spp. — and develop into rows of dividing stamen primordia in a centrifugal way. The most apical parts of the lobes remain sterile, except in *Pachira* spp., where they are terminated by single furcated stamens which do not originate on the buttresses. In every other species of *Adansonieae* and *Matisieae* that has been studied this apical stamen is absent, although a residual bundle goes towards the place where it should have been. In this way the inward bends of a wave line are given on which we may imagine that the stamens are arranged. In *Bombax* spp. and in the *Matisieae* the sterile apical lobe parts are often bilobed, and sometimes the resulting parts may be bilobed again. It is clear that they bear stamen primordia, the development of which has been arrested early, so as to leave practically no trace in the mature stage, except for their vascular bundles.

The appearance of the stamen primordia immediately follows upon the development of the staminal buttresses along the sides of the staminal lobes. In *Pachira* spp. there is first a centrifugal row of primordia which then bends sidewards and finally also inwards. Primordia may even be produced which come to lie more inwards than the primary stamen primordia. In *Bombax buonopozense* this final development presumably produces a sterile collar surmounting the stamen tube. Residues of this sideward way of development occur in the more extensive growth of the proximal lateral parts of the staminal lobes in width and thickness, which we have described in some *Malvaceae*. The xylem of the vascular bundles of the lateral stamens in *Pachira* spp. is facing, so that we are justified to regard them as separate coherent groups of stamens. The xylem of the initial centrifugal rows is placed perpendicular to the sides of the lobes.

This additional sideward and at the same time centripetal development of stamen primordia may occur in gradually less advanced forms in several Bombac species and in *Bombacopsis quinata* (furthermore in Elaeocarpus and Dombeya spp. and probably also in Durio kutejensis). Ultimately a condition is reached in which only a limited sideward development takes place. The meeting of the stamens over the petal radii which in *Pachira* spp. is non-existent, in the intermediate cases becomes irregular and ultimately smooth. In that case the stamens of adjoining lobes link up over the petal radii, forming the so called outward antepetalous bends of the wave-line on which all stamens are thought to be placed. In Malvaceae these bends are reduced.

In *Matisieae* less advanced buttresses each develop two thecae in line on the free lobe margins, a second undivided monothecous stamen often following in *Matisia ochroleuca*. Like the *Matisieae Kydia calycina*, placed in *Malvaceae*, is provided with free antesepalous arms on the tube, lined with sessile thecae. In *Ochroma lagopus* the sideward development mentioned above may result in lateral fusion of the lower thecae of two adjoining lobes. The twisting of the connective tissue of the sessile thecae and the subsequent fusion with the lobe tissue give rise to the extreme mass of pollen sac tissue which covers the end of the large tube in that species.

In *Ceiba pentandra* each staminal lobe forms a single antesepalous monothecous stamen by producing a continuous theca along the margin. This is presumably also the case in some other *Ceiba* spp. and in *Chorisia crispiflora*, with the difference that the lobe apices remain sterile so that the resulting stamens are bithecous, and look like perfectly 'natural' stamens. Besides, the homology of these structures with the staminal lobes that produce rows of forked stamens, is proved by the innervation which is formed by a fan-like lot of branches each of which are forked; and finally by the identical three trace character of these innervations.

All traces of the stamens (paired or not) along the sides of a lobe are fasciculated, and the fascicle traces usually link up with the petal trace to form a common trace which is, by means of a slightly oblique course and an often double base, connected with the broad underlying sepal vascular supply or with the reconstituted stele immediately above. In this respect the situation is similar to that in *Malvaceae*. However, the traces of the more sideward developed stamens in *Bombax* and allied genera never link up with the petal traces directly, as do their sterile residual equivalents in some *Malvaceae*, but they are fasciculated with the traces of the first-formed stamens, as has been described above.

The chief difference between *Bombacaceae* and *Malvaceae* in this matter is formed by the constant occurrence in the *Bombacaceae* and the absence in the *Malvaceae* of a separate independent trace towards an innermost median stamen (in *Pachira* spp.) or towards the staminodial apex of the staminal lobe. (The results in *Bombax ellipticum* are left out of consideration here, because they are so variable and derived from only a few floral buds. Maybe there are five additional small outer staminal lobes.)

As a result each staminal lobe is served by a middle inner single trace and by two lateral outer fascicle traces, also in *Ceiba* spp. and in *Chorisia crispiflora*.

Durioneae

Studying the *Durioneae* we may ask to what extent the phalanges of stamens may be compared with the staminal lobes of the other *Bombacaceae* and *Malvaceae*. There is certainly a similarity in form, the phalanges being often somewhat concave and higher in their median regions. In *Durio kutejensis* the phalanges might be curled like the staminal lobes in *Bombacopsis quinata*, but this point has to be checked as soon as primordial material will be available. Furthermore in a number of *Durio* spp. and in *Cullenia ceylanica* the phalanges are raised upon a tube. The phalanges would seem to be staminal lobes of a more simple construction. The stamen traces are placed on a wave-line.

Another striking similarity is formed by the presence of single independent bundles towards the innermost central stamens which are presumably the primary stamens. The traces of the lateral stamens are attached to a reconstituted stele directly (more or less aggregated near sepal radii) or they are fasciculated into two common traces which are connected with the sepal median trace, as in the *Malveae*.

Some difficulties arise also when comparing the phalanges with the staminal lobes, first because primordial phases are absent, secondly because of the more or less precise antepetalous position of the phalanges (though some *Durio* spp. are strikingly contorted), and finally by the quite dissimilar staminal arrangement in *Durio acutifolius*. However, when considering the last-mentioned objection we may state that also the androecium of *Durio acutifolius* has five primary antepetalous stamens which have independent single vascular traces, the other traces being gradually fasciculated together with the petal traces into common traces attached to the sepal median supply. Also the presence of the same unique kind of stamens in *Durio acutifolius* as in *D. grandiflorus* which has phalanges, makes it plausible that the dispersed staminal arrangement in *Durio acutifolius* may be not far removed morphologically from the phalangial arrangement.

Therefore, taken all the evidence together, the phalanges may, in my opinion, be very well homologous with the staminal lobes.

The contorted condition

As far as could be deduced from what little evidence available the petals as well as the staminal lobes do not originate simultaneously, but in a sequence which may be influenced by the outline of the floral primordia. The overlapping is often contorted, or may sometimes be quincuncial. However that may be, the petals originate rather early and, if mature, are mostly contorted and obliquely inserted as in *Malvaceae*. Their deviation from the petal radii is very variable and often rather extreme, even to the extent of sometimes being placed entirely in front of the sepals, for instance in *Adansonia digitata*. In *Ochroma lagopus* the deviation seems to be the same as in most *Malveae*.

As a rule the staminal lobes alternate with the petals less precisely than in *Malvaceae*, and they are not so much inclining towards the petal surface (fig. 339). In *Bombax* and *Pachira* spp., and in *Ochroma lagopus* the lobes are placed more in front of the overlapped sides of the petals. In *Adansonia digitata* the trapezoid tube parts are clearly placed in front of the petals. In some *Durio* spp. the phalanges may be placed in front of the petals rather perfectly, the oblique course of the traces at the same time being less evident. However, in other *Durio* spp. the contorted condition is very marked (*D. kutejensis*) and the putative phalanges are placed less precisely in front of the petals.

As a result it may be stated that the position of the lobes and its stamens and of the alternating carpels is extremely variable owing to the differing extent of the contorted condition. The more the lobes are placed in front of the petals, the less evident is the contortion, and the less oblique are the traces. On the whole the contorted condition is less extreme than in *Malvaceae*.

In *Bombacaceae* also, the contorted condition leads to the existence of major and minor rows of stamens along the different sides of the staminal lobes. The major sides may even overlap the minor sides of adjoining lobes in a contorted way which is the reverse of that of the petals. In *Matisia ochrocalyx* and in *Quararibea guianensis* the major row counts an additional monothecous stamen which is innervated by a separate branch of the stamen fascicle trace.

As in *Malvaceae*, the direction of the oblique course of the (petal) stamen fascicle traces bears a constant relation to the way in which the petals overlap, not to the manner of deviation of the petals from the petal radii. The minor stamen fascicle trace is often united basally with the petal trace close by.

The structure of the stamens

The development and the forking of the stamen primordia is similar to that described for *Malvaceae*, with the difference that in *Pachira* spp. and in *Bombacopsis quinata* the division takes place parallel with the sides of the lobes. Also in *Matisieae* the thecae are situated one above the other in line with the sides of the lobes. Their paired condition can only be deduced from a study of the early ontogeny and the course of the vascular bundles, in the same way as in *Ureneae* and *Hibisceae*.

The innervation in the connective is more or less fan-like with a prominency of two anatropous lateral branches and a reduced state of the middle branches. In *Pachira* and *Bombax* spp. we meet this innervation in each theca, just as in *Hibiscus rosa-sinensis* and in *Kitaibelia vitifolia*. When in *Camptostemon* spp. the division of the stamens remains imperfect the fan-like system in each half is restricted to a sideward prominent branch and some minor branches in the middle. In this way intermediate stages are produced resembling those in *Hibiscus* spp. and again it is found that the situation in *Camptostemon* is much like that in *Hibiscus*. In *Ceiba* and *Chorisia* spp. the fanning vascular system is much more prominent, with forking branches, indicating that the stamens in these species are homologous to entire groups in *Pachira* and the other genera, as elucidated above. In *Neesia* spp. the vascular system in the stamens is more like that in Sterculiaceous stamens which are to be described later. In *Adansonia digitata* by folding and occasional apical sterility the monothecous stamens simulate bithecous stamens.

Monothecous undivided stamens, resulting from decreasing development, rarely occur in *Bombax* and allies, but are frequent in the major rows of the staminal lobes in *Matisieae*.

In the species of subgenus *Durio* the structure of the stamens is a manifestation of what in our opinion the stamens in *Malvaceae* are, viz. a several times isotomously, more or less profoundly divided, monothecous, reniform structure. Whereas in *Malvaceae* the members of this system are arranged in one plane, they are arranged spatially in subgenus *Durio*. In both, the members of each division have facing xylem. In the connective of the ultimate thecae the vascular supply is somewhat different from that in other *Bombacaceae* because the two anatropous lateral branches are developed rather strongly in contrast with the scarce middle branches.

The orbicular thecae of *Durio oxleyanus* may be related to normal monothecous stamens by a median adaxial sterilization, which as a matter of fact is often actually formed.

In the stamens of the *Durio* species of subgenus *Boschia* we may only meet ordinary characteristics in the pairing of the peculiar thecae and in the absence of these thecae in median adaxial places. For the rest we can only make connections with the ordinary structures by means of very wild speculation, so that it seems wiser to await intermediate stages, if there are any. The same thoughts may apply to *Cullenia ceylanica* in which only the position of the stamens in phalanges and the basally dichotomous innervation of the connectives would seem to offer comparable features.

STERCULIACEAE

A. DESCRIPTIVE PART

1) ERIOLAENEAE

Eriolaena quinquelocularis Wight S5n-P5-St∞-C(5)s

Each sepal bears two lateral fields of glandular trichomes on the base of the adaxial surface.

The stamens are probably arranged in one to three whorls, one stamen in sepal radii, three near petal radii. The anthers are four-sporangiate and introrse, their connectives are tapering and slightly mucronate prolongations of the filaments.

When five carpels are present they are probably antesepalous.

Vascular bundle supply

In the flower base five main bundles separate from the stele, the rest of which innervates the pistil. Each main bundle trifurcates into a sepal median and two sepal basal lateral bundles, the latter of which give off many sepal laterals. The distal parts of the sepal basal laterals of adjacent sepals together with their sepal laterals form an anastomosing complex of bundles. To this network many small anastomosing bundles are attached which belong to the episepalous glands. The proximal parts of both basal sepal laterals of two sepals and of one basal sepal lateral of a third sepal are more massive than the corresponding parts of the other sepal basal laterals. This is presumably due to the fact that the petal traces form portion of these proximal sepal basal lateral parts before they eventually separate, spreading fan-like into the petal nerves.

The stamen traces in our material are not lignified towards their bases, they could nevertheless be observed to point into the direction of the proximal perianth innervation.

Other authors

According to Gazet du Chatelier (1940) 1) five petal-stamen traces leave the stele superposed to and proximally conjoined with the five sepal traces, 2) another alternating set of five bundles leaves the stele ramifying towards an inner whorl of stamen groups.

2) FREMONTIEAE

Cheirostemon platanoides Humb. & Bonpl. and **Fremontia californica** Torr.
S(5)n-(Stdo/5s-St5p)-C(5)s

The free outer surfaces of the quincuncial calyx lobes are hairy, whereas the covered parts are glabrous.

The androecium of *Cheirostemon platanoides* consists of a sterile tube that spreads palmately into five long twisted fertile parts. These parts bear each two separate bisporangiate thecae laterally along their abaxial surface, the subulate apical region remaining sterile. As five thicker portions of the tube are prolonged straight into the five fertile free parts, also anatomically, we are justified to consider the androecium built up of five stamens with the filaments fused laterally.

The androecium of *Fremontia californica* is a short tube surmounted by five big stamens with twisted anthers (fig. 228). The important differences with *Cheirostemon platanoides* concern 1) the tiny sterile antesepalous teeth peripherally upon the rim of the tube which occurred in part of the material and 2) the transverse subdivision of the pollen sacs by means of many partition walls lined with tapetum, a feature not even mentioned by Harvey who monographed the genus. Frequently the partitions of two pollen sacs of one theca are situated next to one another. When pollen are being shed the thecae wall gets loose from both the longitudinal and transverse partition walls.

Developmental phases

A few young stages of *Fremontia* flowers (fig. 230) proved that the androecium originates from five laterally fusing, alternisepalous, trapezoid primordia which are each provided with a theca upon either margin and with free often bilobed apical parts. A second theca may develop below the first and lateral fusion may occur between first or second thecae ends. However, adult stages forming the outcome of these primordial deviations have not been found.

Vascular bundle supply

In both species the stamens possess an innermost median bundle which is concentric or collateral with the xylem facing the centre of the flower and two outermost lateral collateral bundles with the xylem facing a similar bundle belonging to an adjacent stamen (fig. 227). Towards the sterile end of the stamens the median concentric bundles fall apart into a tangentially stretched combination of small collateral parts, a minority of which is inverted (fig. 226). In the anther a lateral stamen bundle terminates into a number of abaxial branches which are gradually and succeedingly given off. The branches proceed in apical direction and bend towards the thecae spreading into some veinlets often dichotomously. This pattern closely resembles the vascularization of a stamen fascicle in *Malvaceae* (fig. 225 and 228). Five antesepalous bundles go upwards peripherally into the base of the staminal tube, then fade out very soon in *Cheirostemon platanoides*, but innervate the sterile teeth in *Fremontia californica*.

In *Fremontia* the connection of the staminal bundles with the underlying vascular tissue could be followed (fig. 229). Five antesepalous portions leave the stele of the flower base, the central parts spreading into the sepals. On the other hand, the flanks proceed upwards as the lateral staminal bundles of adjacent stamens, maintaining the opposition of their xylem parts. Sometimes parts of these flank bundles may unite in the sepal radii and form the vascular supply to the sterile teeth mentioned above. One may as well state that this supply has a double origin or that it closes a sepal gap in the stele. On a level slightly above the bases of the five main bundles an alternating set separates from the stele forming the median stamen bundles.

Other authors

Saunders pictured the attachment of the three stamen bundles to the receptacular traces exactly as described above.

3) DOMBEYEAE

Dombeya wallichii Benth. & Hook.	S(5)n-P5-(St5 × 1/7-Std5)-C(5)
D. calantha K. Sch.	S(5)n-P5-(St5 × 3-Std5)-C(5)
Pentapetes phoenicea L.	ditto
Melhania incana Heyne	S(5)n-P5-(St5-Std5)-C(5)
Ruizia variabilis Jacq.	S(5)n-P5-(St5 × 5/6-St5)-C(10)

Whereas the proximal parts of the stamens and staminodes together form a tube, the distal parts are free and imbricate. The staminodes are placed centrally, whereas those stamens that alternate with the staminodes are placed peripherally. The fusion is facial as well as lateral, a fact which is particularly evident when the number of stamens is high and the outer stamens separate from the tube instead of being its prolongation.

The place of the stamens and staminodes can be demonstrated by a cross-section of the tube base and its vascular bundles in *Dombeya wallichii* (fig. 231). The angles of the pentagonal tube occupy a position opposite the overlapping halves of the petals which are inserted more outwards than the halves that are being overlapped. Moreover, as the petals are inserted in alternisepalous radii, the angles of the tube are between sepal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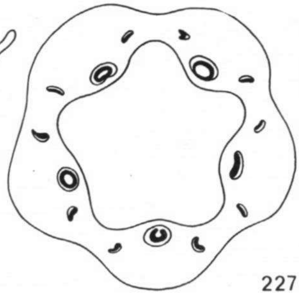
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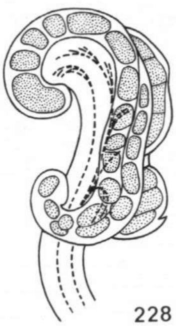
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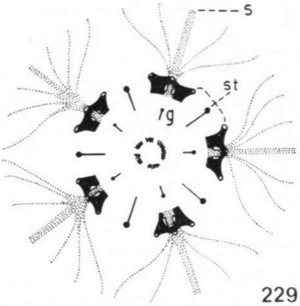

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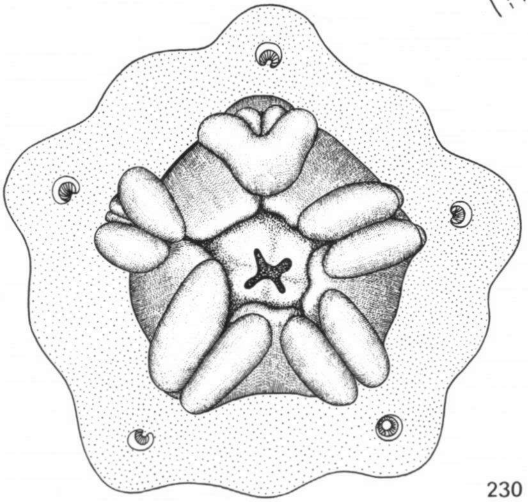
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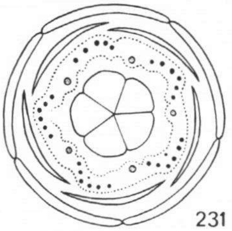
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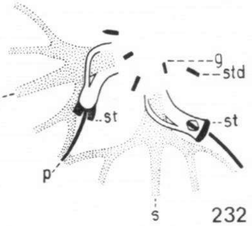

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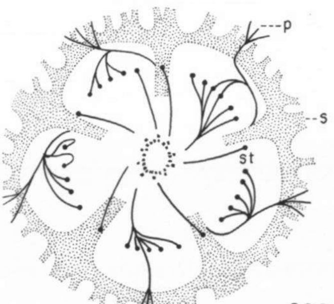

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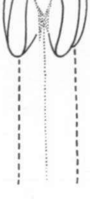
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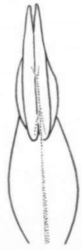
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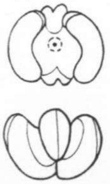
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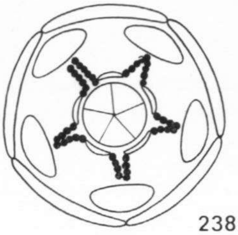
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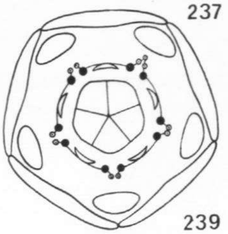

239

The explanation of these figures can be found at the bottom of the opposite page

and petal radii. The vascular bundles of the filaments are situated at the angles of the tube, whereas the staminode bundles lie in the middle of its sides. Together they form a faint wave-line corresponding to the imbricateness mentioned above. The lateral distances between the androecium members are dissimilar, the stamens being grouped together more closely in the outward bends of the wave-line. This feature together with the innervation give reason for speaking of five outer staminal groups and five inner staminodes (or stamens in *Ruizia variabilis*). Even the stamens within an outer group are frequently not equidistant, for, if the petals overlap to the left, the left stamens tend to be packed more closely. In addition, as the carpels alternate with the staminodes, the position of all floral parts above petal level may said to be adapted to the contorted character of the petals.

The anthers consist of two bisporangiate thecae placed along the tapering ends of the filaments laterally or laterally-extrorsily. The staminodes are lanceolate or spathulate blades.

Developmental phases

In young flowers of *Ruizia variabilis*, still without a tube, the anthers are situated more or less in three whorls. In young stages of *Melhania incana* the stamens and staminodes form two alternating whorls of neither exactly antesepalous nor fully antepetalous members.

Vascular bundle supply

Five parts leave the stele in the base of the flower, a median or a lateral part of each of which forms a trifurcating sepal trace. The sepal basal laterals belonging to adjoint sepals give a commissural system in *Pentapetes phoenicea*. In every species that was studied the traces of petals and outer stamen groups are connected basally with the flank or both flanks of the sepal trace or with the sepal basal laterals. On the other hand the traces to staminodes or inner five stamens (*Ruizia variabilis*) are connected with the reconstituted stele individually on a higher level somewhere in between sepal and petal radii. However, it is necessary to add some remarks on each species separately.

Dombeya wallichii

Traces coming from one or both sides of the sepal trace and from one of the sepal basal laterals together form a large collateral bundle on a higher level. This bundle represents the petal stamen trace which is characterized by its antesepalous fasciculate base and its direction towards a petal radius (fig. 232). If the petals overlap to the right, the petal stamen traces deviate to the left towards the petal radii. The bundle trifurcates into a middle petal trace and two side traces which reunite constituting the double base of a main staminal bundle (a petal gap in the collateral petal stamen bundle being closed). The main staminal bundle branches in as many stamen traces as there are stamens on a higher level.

Cheirostemon platanoides. — Fig. 225. Anther, c.s. — Fig. 226. Anther tip, c.s. — Fig. 227. Stamen tube, c.s.
Fremontia californica. — Fig. 228. Stamen cleared, back lateral vascular course omitted (5 ×). — Fig. 229. Supply of vascular bundles in the receptacle. — Fig. 230. Developmental phase of the androecium (50 ×).
Dombeya wallichii. — Fig. 231. Flower diagram, dots represent vascular bundles of stamens. — Fig. 232. Vascular bundle supply in receptacle.
Ruizia variabilis. — Fig. 233. Scheme of vascular bundle supply towards androecium.
Melochia umbellata. — Fig. 234. Stamen.
Hermannia candicans. — Fig. 235. Stamen. — Fig. 236. Anther just below attachment level, c.s.
Ayenia magna.— Fig. 237. above: Anther from the inside. below: *Ayenia montana*. Anther from the outside.
Glossostemon bruguieri. — Fig. 238. Flower diagram.
Leptonychia glabra. — Fig. 239. Ibidem.

Dombeya calantha

In this species the side traces do not fuse but remain apart as two bean-shaped bundles, their xylem facing one another (a petal gap is not closed), and give rise to stamen traces immediately or by branching once. The branching produces a trace to a middle stamen and another trace to the lateral stamen that is situated in front of the overlapping petal half.

In both species of *Dombeya* studied the sepal gap may not be closed by the bundles connected with the sides of the sepal trace, in which case a petal stamen trace is not formed like the one described above.

Pentapetes phoenicea

The petal trace is situated between petal radii and one of the sepal basal lateral bundles proximally. The three stamen bundles in each sector of the flower are connected with the underlying vascular tissue in a different way, the trace of the middle stamen with a sepal basal lateral, the trace of one of the lateral stamens with the sepal trace, and the trace of the other lateral stamen with the petal trace. It is thus evident that each of the stamen traces lies simply along the shortest possible way between the organ bases and underlying vascular tissue, if a common slightly diagonal course is taken into account.

Melhania incana

Following the vascular course upwards in the receptacle, a common bundle is observed first to accompany a sepal trace and one of its sepal basal laterals for a certain distance, then to become free somewhere between sepal and petal radii and finally to trifurcate into a middle petal trace and two lateral traces, one proceeding towards a staminode, another towards a stamen.

Ruizia variabilis

Five petal stamen traces show a bending course between antepetalous regions and the sides of sepal traces. Somewhere between sepal and petal radii a number of stamen traces are attached to the petal stamen trace at about the same point. Fig. 233 shows some variations to this theme, for instance 1) a petal stamen trace unconnected with sepal traces and attached to the stele independently, 2) a stamen trace belonging to an outer group coming from the stele independently, 3) a common staminal bundle, resulting in a number of stamen traces, connected with the stele independently. However, a few of these stamen traces have a double origin, one from the common bundle, another from the petal trace, 4) sometimes the base of a stamen trace points downwards in the direction of a sepal trace for a short distance before returning towards the petal trace.

Vascular bundles in the stamens and staminodes

The stamens have simple median bundles over their length. In addition, in the *Dombeya* spp. two lateral bundles are present in stamens and staminodes, which fade out upwards. In the peripheral stamens these lateral bundles are less clearly developed (suggesting centrifugal development). In *Melhania incana* the staminodes have these three bundles also. Moreover, the median bundle is here provided with a number of dispersed lateral branches distally.

A curious phenomenon to be reported here is the occasional presence of residual stamen bundles in the tube of *Dombeya wallichii*, which are situated in the median line of the outward bends of stamens, slightly to the inside of the normal stamens.

Other authors

In *Dombeyeae* Eichler recognised five outer antepetalous groups of stamens and an alternating inner whorl of five staminodes. Saunders and Rao are of the same opinion on anatomical grounds, but nevertheless Saunders gave a diplostemonous formula. Rao did not see the deviation of the petal stamen traces, though his figures show that the relative positions of the floral parts are by no means simple. Only Gazet du Chatelier described the petals and consecutive whorls as being placed between sepal and alternating radii.

4) HERMANNIEAE

Melochia pyramidata L.	S(5)-(P5-St5p-Std5s)-C(5)p
M. umbellata (Houtt.) Stapf	S(5)-(P5-St5p-Stdo)-C(5)s
Hermannia candicans Ait.	S(5)n-P5-St5p-Stdo-C(5)s
Waltheria americana L.	S(5)-(P5-St5p)-Stdo-C1

Melochia spp.

An anthophore may be present between calyx and corolla covered entirely with glandular trichomes.

The anthers are composed of two bisporangiate thecae; they are sessile on a tube, extrorse and slightly sagittiform. Small alternating staminodial lobes are also placed on the tube in *M. pyramidata*. In adult flowers of *M. umbellata* such structures are tiny or absent.

Developmental phases

In young flowers the staminodes are relatively big lobes in proportion to the anthers and are situated more inwards. Evidently the growth of the staminodes is arrested at an early stage, especially so in *M. umbellata*.

Vascular bundle supply

The petal stamen traces are attached to the sides of the sepal traces and have an oblique course. The stamen bundles are either adaxially open collateral or concentric. They bend backwards and then downwards into the connective of the lower anther half and may ultimately be divided into two juxtaposed branches. At the turning point two lateral parts of the stamen bundles proceed the upward course into the upper half of the anther (fig. 234). This bundle formation suggests that the anthers are resupinate.

Hermannia candicans

The contorted petals may be inserted slightly out of alternisepalous radii, their outer and overlapping margins being situated in the corner between two sepals.

The stamens with their winged filaments are placed exactly alternisepalously. In the section *Mahernia* the filaments are broad only in the middle. The anthers are attached to the filaments with their middle parts, hanging outwards. They are four-sporangiate and extrorse, the ends of the thecae projecting freely (fig. 232). A cross-section immediately below the point of attachment reveals a short, non-winged, downward extension of the filament adaxially on the lower half of the anther, thus suggesting strongly a resupination of the anther through an outward and downward bending of the apical filament part.

Vascular bundle supply

From the stele in the flower base five parts separate which are of unequal size and irregularly spaced. They ramify into a median sepal bundle and one or two sepal laterals or commissural laterals. There are five petal stamen traces, one or two of which may be connected with one sepal trace or may be attached to the stele independently. These traces become more or less perfect concentric bundles with an oblique course. A median abaxial portion of such a bundle gives the petal trace, whereas two lateral adaxial parts revert and recombine forming the stamen trace (the stamen trace is double, or a petal gap in the concentric bundle is closed).

In the anther the median stamen bundle is divided into two pairs of branches, one pair proceeding upwards, another, which is more strongly developed, proceeding downwards. Each pair consists of two bundles next to one another, or of two facing xylem groups enclosed in a circle of phloem strands. In the base of the filament a tangentially stretched collateral bundle is present which has a tendency to show three protoxylem points adaxially. However, later xylem and phloem may occur on the flanks or on the adaxial side of this stamen bundle (may surround the protoxylem).

Waltheria americana

A petal stamen trace is present, glandular tissue absent.

Other authors

Obdiplostemony in *Hermannieae* is generally recognised, except by Saunders. But for Gazet du Chatelier nobody noted the deviation of the petal stamen traces.

5) BYTTNERIEAE-BYTTNERINAE

Rulingia corylifolia R. Grah.	S(5)n-P5-(St5p-Std5s)-C(5)p
R. pannosa R. Br.	ditto
Commersonia bartramia (L.) Merr.	ditto
Byttneria pilosa Roxb., *B.* spp.	ditto
Ayenia magna L.	S(5)-P5-(St5p-Std5sn?)-C(5)p
A. montana Rose	ditto

Description of the species, Ayenia excluded

The androecium tube is short and pentagonal. Its sides are prolonged into triangular staminodial lobes, its protruding edges represent the proximal parts of stamens which turn outwards from between the sini of the staminodes.

The filaments broaden into rather sagittate connectives which are bent slightly backwards. The two bisporangiate thecae are widely separated by the connective; however, they converge apically in *Commersonia bartramia.*

Developmental phases

In young flowers of *Byttneria pilosa* in which a tube has not yet developed, the staminodes form an inner whorl alternate with the stamens.

Vascular bundle supply

In the flower base stelar parts may form sepal median traces, sepal commissural marginal traces or traces that combine the two last-mentioned traces for a short proximal distance. Five petal stamen traces may be connected with the proximal part of any trace mentioned. On a higher level the five staminode traces are attached to the stele independently. Stamens and staminodes have simple single bundles.

Ayenia

The form of the androecium tube is similar to that of the preceding species. An intricate construction is formed by the petals and staminodes enclosing the stamens, which may have some bearing to pollination.

The structure of the anther is unique, a median bisporangiate theca being situated between two lateral ones. In *Ayenia magna* the three thecae are parallel, in *A. montana* on the other hand the two lateral thecae converge apically. Accordingly the median theca is shorter and tapering apically (figs. 236, 237). In some flowers the filaments prove to persist, after the thecae are gone by some means or other. There is a tiny ridge around the filament below the anther where perhaps a fracture is preformed. It is interesting to note that, where in the flower no fields of glandular trichomes can be detected, the staminodes appear to be partly fleshy. Therefore, it would be worth while to have the opportunity to study these flowers profoundly morphologically as well as biologically.

Vascular bundle supply

Two alternating sets of five traces are connected with the stele as sepal and petal traces. The androgynophore contains a reconstituted stele, five angles of which are situated in the petal radii. Near the top of the androgynophore five stamen and five staminode traces are attached to the reconstituted stele. The stamen bundles are unbranched and end in the connective.

Other authors

The obdiplostemonous character of the flowers in *Byttnerieae* is generally admitted. According to Gazet du Chatelier five sepal median bundles leave the stele in the flower base, followed by five alternating petal traces, which trifurcate into a petal trace and two sepal laterals of adjacent sepals. The stamen and staminode traces were connected to these ten traces proximally. On the other hand, Rao mentioned independent petal stamen traces and staminodial traces. Evidently, the course of the vascular bundles is still more variable than that given above.

6) BYTTNERIEAE-THEOBROMINEAE

Glossostemon bruguieri Desf.	S(5)n-P5-(St5 × 7/11p-Std5s)-C(5)p
Leptonychia glabra Turcz.	S5n-P5-(St5 × 2/5p-Std5s)-C(5)p
L. macrantha K. Sch.	ditto
Herrania albiflora Goudot	S(5)n-P5-(St5 × 3p-Std5s)-C(5)p
Abroma augusta L.	S(5)-P5-(St5 × 3p-Std5s)-C(5)p
Theobroma spp.	S(5)n-P5-(St5 × 3p-Std5s)-C(5)p
Theobroma cacao L.	S(5)-P5-(St5 × 2p-Std5s)-C(5)p

Glossostemon bruguieri and Leptonychia spp.

Glandular trichomes cover the inner surface of the sepals, in *Leptonychia* only basally, in *Glossostemon* everywhere except basally.

The insertion points of stamens and staminodes lie along a wave line, the outer bends of which are antepetalous. The proximal parts of the antepetalous stamens and antesepalous foliar staminodes are fused laterally, but in *Leptonychia glabra* the foliar staminode is sometimes partly fused facially with the nearest stamens. In *Leptonychia* also the two or three outer antepetalous members of the androecium are staminodes, only two fertile stamens remaining in front of each petal. The staminodes are slender filaments without anthers. In *Glossostemon* the length over which the filaments are fused increases as the stamens are placed nearer the foliar staminodes and is shortest in the petal radii. Consequently the androecium appears to consist of five alternisepalous blades which bear the stamens along their proximal margins as lateral extensions.

The anthers of *Glossostemon* are composed of two parallel bisporangiate thecae situated adaxially along the backward bending distal end of the filament. In *Leptonychia* the anthers are more reniform.

Vascular bundle supply

Single unbranched bundles run towards the apex in the stamens of both species and in the outer staminodes of *Leptonychia.* The foliar staminodes in *Leptonychia* are narrow organs without vascular bundles. However, in *Glossostemon* they possess a trifurcate bundle which is probably connected with the stele independently. Petal stamen traces were seen in *Glossostemon*, combining a petal trace and a main stamen bundle which, on a higher level, spreads into the stamen traces. These common stamen bundles are more or less perfect concentric combinations of small bundles.

Other authors

Eichler mentioned five antepetalous stamen groups and five alternating staminodes in *Leptonychia.*

Herrania albiflora

The calyx is irregularly divided into lobes. Its base is provided with a rim of trichomes which are formed by a stalk of small cells and a big oval glandular cell on top. Similar trichomes cover the upward directed lobes of the staminodes.

The places of insertion of the stamens and staminodes lie along a wave line, the outer antepetalous bends of which are occupied by the stamens. The staminodes are large and foliar and occupy the antesepalous regions of the wave line. The proximal parts of stamens and staminodes are fused laterally and facially. The stamen groups are formed by two components side by side, one consisting of a single stamen, the other of two stamens which are fused chiefly facially (fig. 240 and 241). These different sets of stamens are placed invariably on the same side of a staminode in every sector of the flower. This curious position may be related to a contorted nature of petals or androecium, which unfortunately cannot be ascertained in the adult flower. Occasionally the paired stamina are replaced by a single stamen, or the outer member of a pair is situated peripherally more between the other stamens, so that an antepetalous triplet of stamens results (cf. *Theobroma*).

The filament is slightly bent backwards and broadened at its distal end. Here, along the apical margin and mostly a little adaxially, two bisporangiate thecae are situated that may touch in the median line.

Vascular bundle supply

In the base of the flower the stele falls apart into five antesepalous portions for the perianth and androecium, and into residual parts for the pistil. The five main bundles trifurcate basally into a median sepal trace and two lateral traces, one a petal stamen trace, the other a staminode trace. The petal stamen traces or the staminode traces are either the left or the right parts of the main bundles in every flower sector. This constancy as well as the direction of the deviation from a radial course taken by the petal stamen traces are no doubt related to the contorted nature of the petals and androecium, as was mentioned above for the stamen position. If the petal stamen traces are attached to the right flanks of the main bundles and deviate to the right, the sets of two stamens form the left components and the single stamens the right components of the antepetalous stamen groups.

The petal stamen traces are combinations of a median petal trace and two lateral stamen traces, one of which, on a higher level, appears to represent the double innervation to the sets of two stamens.

The lateral sepal bundles form a system of cross-arcs, occasionally interrupted by combined sepal commissural laterals and petal stamen bundles (fig. 242).

The staminodial bundles in some flowers appear to link up with the stele independently. There is in a staminode a median bundle which sometimes is joined by two lateral ones. The median bundle bears two succeeding sets of opposite lateral nerves each forming an anastomosing system of small bundles.

The stamen bundles are concentric in the filament; however, the traces and the bundles in the connective are collateral. The latter scatter into two side branches and some residual tissue in the middle. The side branches are scarcely lignified bundles with phloem all around.

Abroma augusta

The flower structure is very much like that in the preceding species.

The sepals have no glandular tissue, instead there is a deep receptacular disc on the inside of the petal base.

As the distal broadening of the filaments is flat and well developed, and the marginal thecae lie close together apically, the anther is reniform.

The correlation in the position of the stamens described in *Herrania albiflora* can here be seen in relation to the contorted petals. If petals overlap to the left 1) the insertion of the left petal side is more peripheral, 2) the left parts of the stamen groups consist of two stamens, 3) the petal stamen trace deviates to the right.

Theobroma spp.

The three species which were studied resemble the preceding ones very much. However, instead of the antepetalous stamen groups being composed of two different components, we find symmetrical triplets as were reported to occur now and then in *Herrania albiflora*. In *Theobroma* the filaments are fused more intimately (fig. 243).

The free distal filament parts are broadened, even bilobed, and, in addition, bent backwards. Two bisporangiate ellipsoid thecae are situated along the apical margins often somewhat adaxially, they are free from one another in the median line.

Vascular bundle supply

Three stamen traces are combined with the petal trace into a concentric petal stamen trace. The stamen bundle terminates in the connective unbranched.

Developmental phases

In a small floral bud (fig. 244) five petals occupy the corners of a flat five-angled receptacle. Inside of the petals a five-angled ring of stamen primordia may be observed, the angles of which lie in the petal radii. The pentagonal ring shows five large and high antepetalous primordia and five more flat antesepalous ones. Upon the larger primordia division lines develop producing one outer median and two lateral central stamen primordia.

Theobroma cacao

Glandular hairs are distributed over the pedicels and the pistil.

There are only two stamens between the staminodes. Evidently an outer middle one is missing. The stamens are orientated more radially. Petal stamen traces as well as independent staminode traces are present.

Other authors

The obdiplostemonous character of the flowers and the antepetalous position of the pistil cells was admitted by Eichler, and also by Gazet du Chatelier and Rao on the ground of the independence of petal stamen and staminode traces. Gazet du Chatelier pictured the petal stamen traces as connected with the stele independently and the staminode traces as attached to the sepal traces basally. According to him the antesepalous stamen bundles become collaterally double in *T. cacao*. On the other hand, Saunders interpreted the ten stamens of this last species as five antesepalous and five antepetalous ones. Cuatrecasas said that in *Theobroma* the androecium is formed of an outer whorl of five petaloid staminodes and an inner whorl of five antepetalous bifurcate or trifurcate stamens. On the ground of the forking of five single vascular traces, it is his opinion that the furcated stamens are the result of splitting, not of coalescence. The anthers are two-celled and each cell is unilocular.

7) LASIOPETALEAE

Thomasia pauciflora Lindl.	(S5-Po-St5p-Std5s)-C(3)
T. solanacea J. Gay	ditto
T. macrocarpa Hueg	ditto
Lasiopetalum acutiflorum Turcz.	S5-P5-St5p-Stdo-C(3)

Glandular trichomes are absent.

The sepals, stamens, and the small subulate staminodes form together a small cup around the base of the pistil.

The distal part of the filament is sharply bent outwards and bears a marked upward and a short downward extension, along which the bisporangiate thecae are attached a little extrorsily. The anthers of *Lasiopetalum acutiflorum* dehisce with a terminal pore.

Vascular bundle supply

In *Thomasia* spp. the stamen trace is connected with the sepal commissural trace. In *Lasiopetalum acutiflorum* the clearing method revealed that a petal stamen trace is attached to the sepal commissural trace, though incidentally the stamen trace is directly connected with the stele in petal radii. Sometimes the stamens are placed slightly out of petal radii and their traces are provided with a proximal bending course.

In the connective the collateral vascular bundle is spread into two parts side by side, each of which spreads slightly upwards and downwards. This branching tendency could not be detected in *Lasiopetalum acutiflorum.*

Developmental phases in Thomasia

The development of the petals — which probably originate independently from the stamens — is arrested very early, so that petals appear to be lacking in the full-grown flowers.

The anther development proves that the downward directed parts are morphologically the apical, slightly sagittate, anther regions and that accordingly the upward directed parts are morphologically the basal, strikingly prolonged anther regions. The anther is partly resupinate from the start. It originates as a hemispheric primordium, the lateral central regions of which begin to grow inwards first as the first signs of thecae, rendering the primordium a horseshoe-shaped appearance. This structure becomes elevated on a stalk. Secondly, peripheral lateral parts start to grow in outward direction, the median parts being arrested again, producing the other ends of the thecae. Afterwards the resupination is intensified.

Other authors

Eichler's opinion agrees with the flower formulas given above.

8) HELICTEREAE

Kleinhovia hospita L.	S5n-P5-(St5 × 3p-Std5s)-C(5)p
Pterospermum javanicum Jungh.	S(5)n-P5-(St5 × 3p-Std5s)-C(5)p
Helicteres angustifolia L.	S5n-P5-(St5 × 2p-Std5s)-C(5)p
H. lanata Kurz	ditto

Kleinhovia hospita

Five small inner staminodes and five alternating outer lobules together form the terminations of an androecium tube. Each of the outer lobules terminates into a median outer and two lateral central stamens. Together stamens and staminodes are placed on top of the tube following a wave line. The stamens are not equidistant and the petals are inserted somewhat obliquely. The anthers consist of two bisporangiate thecae placed transversally on top of the filament.

An irregularly split erect rim like a collar is present on the androgynophore proximally.

Developmental phases

In a young flower the rim has five or ten lobes in sepal and petal radii. At first the structure is axillary to the perianth, only late in ontogeny the androgynophore develops below this rim. The rim may be called a disc.

Vascular bundle supply

Petal stamen traces are connected with the bases of the sepal traces and run obliquely towards antepetalous positions. They separate into a petal trace and a main staminal trace. The latter divides in two branches, one of which divides again, giving a total of three stamen traces. The stamen bundles fade out in the connectives. The main stamen bundles traverse an androgynophore around its reconstituted stele. Below the level where they divide into stamen traces small bundles are given off to the pistil wall.

Neither in the disc, nor in the staminodes any vascular bundles could be detected.

Other authors

Rao mentioned the obdiplostemony and the connection of pistil bundles with the main stamen bundles. According to him the petal stamen traces are independent. Moreover he saw independent staminode traces, to which also pistil traces are attached.

Pterospermum javanicum

Tangential folds of parenchymatous tissue occur axillary to the petals, chiefly to their overlapping parts (fig. 246).

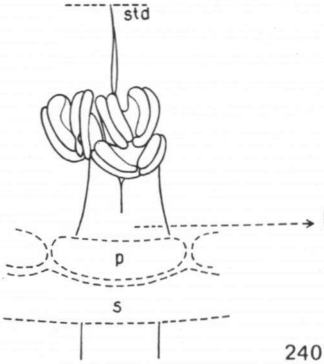
The stamens and staminodes are placed peripherally upon the androgynophore in a wave line, the outer bends of which are occupied by the antepetalous stamens, the inner bends by the staminodes. These antepetalous groups consist of two lateral inner stamens and one median outer stamen. However, it must be first conceded that one of the lateral stamens that is placed in front of the overlapping petal half, is situated more centrally than the other. Secondly that the outer stamen is not exactly median, but nearer to the lateral in front of the overlapping petal half (see bundles in fig. 250).

The stamens are linear and tangentially flattened, the connectives being simple prolongations of the filaments with slender bisporangiate thecae along the margins latero-introrsely. The apical part of the connective remains sterile, the inner pollen sacs tapering gradually towards the apex, sometimes forming septs. The staminodes are equally elongate structures. Whereas in cross-section their proximal parts are C-shaped and open towards the centre of the flower, their distal parts are polygonal.

The outline of the androgynophore is pentagonal with the angles in sepal radii.

Vascular bundle supply

A whorl of five sepal traces comes from the stele in the flower base, each of which gives off a petal stamen trace from the same side proximally (fig. 251). After the division of the petal stamen trace into a petal trace and a common stamen bundle, the latter goes upwards as a concentric bundle as in the petal radii of the androgynophore around a reconstituted stele (fig. 247). However, the xylem body of the main staminal bundles is frequently subdivided into two facing, bean-shaped, lateral portions or into more portions. Correspondingly, on a higher level the bundles separate into two lateral parts, and subsequently, into three parts by means of serial splitting of one of the lateral parts (figs. 248, 249). Moreover, the inner portions of these bundles contribute to the inner-



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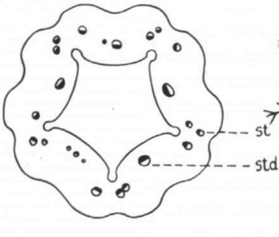

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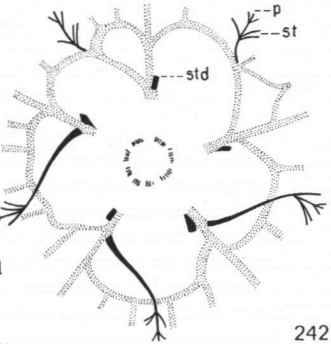

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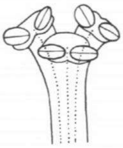

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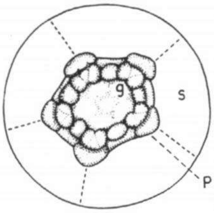

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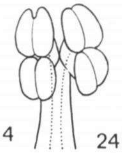

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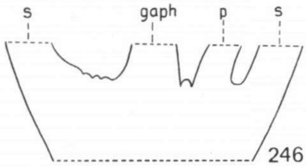

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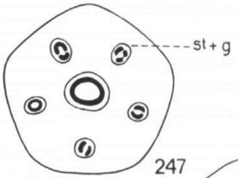

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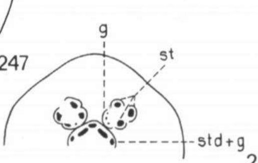

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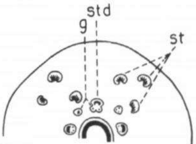

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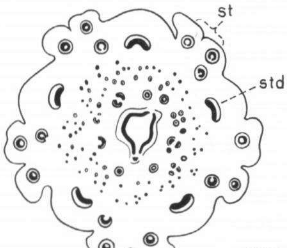

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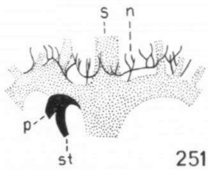

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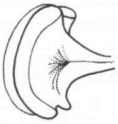

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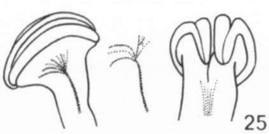

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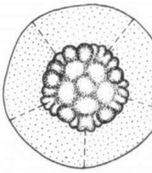

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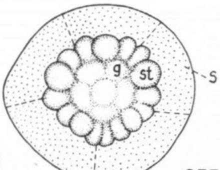

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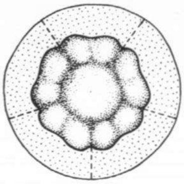

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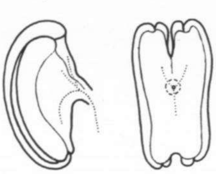

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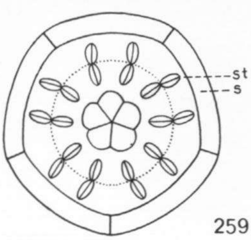


259

The explanation of these figures can be found at the bottom of the opposite page

vation of the pistil which as regards the central parts is served by the reconstituted stele. In this way the stamen traces originate as collateral traces, then become more or less concentric, but ultimately regain the collateral character in the filament and run upwards into the apex of the stamens unbranched.

Distally in the androgynophore five parts leave the reconstituted stele in sepal radii and become concentric. Pistil traces pass off from them adaxially, and the remaining abaxial parts form broad collateral traces towards the staminodes. Proximally in the staminodes these traces separate into three parallel parts which recombine distally.

Many anastomosing small bundles connect the inner basal glandular fields on the sepals with the bases of the sepal lateral bundles.

Other authors

According to Gazet du Chatelier the stamen groups are antesepalous. Rao also mentioned the position of the stamen traces in the gynandrophore, the independent origin of the staminode traces and the combination of both traces with pistil traces. In this species the petal stamen traces are said to be attached to the stele quite near the sepal traces.

Helicteres spp.

The contorted petals are obliquely inserted, with their overlapping sides in alternisepalous radii. The two antepetalous stamens are unequal, the one in front of the overlapping petal half being larger. The stamens are orientated rather radially, a position intensified by a slight twisting of the end of the filament. The connective is about half-reniform through the exclusive outward growth of the outer connective part. The staminodes are small foliar organs.

Vascular bundle supply

Petal stamen traces deviate from the bases of sepal traces.

The main staminal bundles are combined with pistil traces. They split collaterally into two stamen traces with almost facing xylem. This xylem opposition is in accordance with the radial orientation of the stamens. The stamen bundles do not extend into the connectives.

The staminodes do not show vascular bundles.

In *H. lanata* the petals are provided with small foliar appendages along the proximal margin or on the inner surface. The appendages are innervated by side-branches of the marginal petal nerves.

Other authors

Herrania albiflora. — Fig. 240. A flower sector with triplets of stamens on the base between two foliar staminodes. — Fig. 241. Stamen tube at level indicated in preceding figure, c.s. — Fig. 242. Course of vascular bundles.

Theobroma spec. — Fig. 243. Triplets of stamens. — Fig. 244. Young phase of androecium development.

Theobroma cacao. — Fig. 245. Pairs of stamens.

Pterospermum javanicum. — Fig. 246. Flower base, l.s. — Figs. 247—250. Upward series of c.s. through androgynophore and (fig. 250) androecium base. — Fig. 251. Attachment of petal, stamen, and gland supply at sepal innervation.

Sterculia bidwilli. — Fig. 252. Anther from the side.

Sterculia lurida. — Fig. 253. Stamens. — Fig. 254. Developing androecium (40 ×).

Sterculia platanoides. — Fig. 255. Ditto (40 ×).

Sterculia alexandri. — Fig. 256. Ditto (80 ×).

Pterocymbium beccari. — Fig. 257. Anther, laterally and adaxially.

Argyrodendron actinophyllum. — Fig. 258. Stamen from the side.

Cola nitida. — Fig. 259. Floral diagram.

Rao assumed that in *H. isora* L. the staminodes do not represent an inner whorl, but rather sterile inner median members of the outer antepetalous triple groups of stamens, the inner whorl of staminodes being suppressed. In my opinion this interpretation is very unlikely because the median members of staminal triplets should be the outer members, not the inner. Maybe Rao went wrong owing to the extreme contortion of the flower.

9) STERCULIEAE

Sterculia bidwilli Hook. *ex* Benth.	S(5)n-St(5×2/4p+5×1s)-C(5)p
S. lurida F. Muell. *ex* Benth.	ditto
S. platanifolia L.	ditto
S. rupestris Benth.	ditto
S. villosa Roxb.	ditto
S. diversifolia G. Don	S(5)n-St(5×2/3p+5×1s)-C(5)p
S. laevis Wall.	S(5)n-St(5×2p)-C(5)p
S. rubiginosa Vent.	ditto
S. alexandri Harv.	S(5)n-St(5×2)pn-C(3/5)p
S. nobilis Sm.	S(5)n-St(5×2)p-C(3)
Firmiana colorata (Roxb.) R. Br.	S(5)n-St(5×2/4)p+5×1s)-C(5)p
Argyrodendron actinophyllum (C. Moore) Edlin	ditto
Brachychiton populneum R. Br.	S(5)n-St(5×3)p+5×1s)-C(5)p
Pterocymbium beccarii K. Sch.	ditto
Scaphium javanicum (R. Br.) Kosterm.	S(5)n-St(5×2p)-C(5)p
Cola nitida A. Chev.	S(5)-St(5×2p)-C(5)s
Heritiera littoralis Dryand in Ait.	S(5)n-St5×1p?-C(5)s

Sterculia spp.

Glandular trichomes are not only situated on the inner bases of the sepals, they may extend to the receptacle between calyx and androgynophore and to the basis of the gynandrophore (*S. bidwilli* and *lurida*); they may cover the entire inner surface of the calyx, the androgynophore basis, and the outer parts of the filaments (*S. alexandri*), they may be present scattered over both sepal surfaces (*S. nobilis*), or may form a fringe along the calyx lobes (*S. laevis*).

In adult flowers of species with ten stamens two whorls of equidistant, basally fused stamens seem to be present on top of the androgynophore peripherally, one whorl of five long erect stamens, the other of five short divergent stamens. However, the points of attachment for all these stamens are placed on almost the same level and between sepal and petal radii.

In other species fifteen or more stamens follow a wave line upon the androgynophore around the five alternisepalous bulging cells of the pistil. Five antesepalous stamens are innermost, situated in the sini between the pistil cells. Two to four stamens occupy each alternisepalous bend of the wave line. The filaments are fused laterally along most of their length, and since the stamens which are situated more towards the sepal radii are progressively longer, the impression is gained of five antesepalous phalanges or blades extending into stamens and together constituting the androecium. If more than fifteen stamens occur, one of the sides of each phalange may bear one stamen more than the other, the phalanges showing an asymmetrical form. The anthers may be arranged in whorls of five members, as in some *Malveae*. If fifteen stamens are present the same phenomenon may give rise to three whorls.

Apically the filaments widen and are divided into two juxtaposed, ellipsoid, bisporangiate thecae with longitudinal pollen sacs. The thecae are lateraliter-introrse and fused apically more intimately than basally. However, by means of a marked resupination of the distal filament parts, the thecae appear lateraliter-extrorse. The resupination is largely obscured and only comes to light if attention is paid to a small median knob or tooth which points downwards from between the thecae. Evidently this tooth represents the sterile tip of the connective (figs. 252, 253, 257, 258). Lateral fusions may occur between outer as well as inner pollen sacs of one or both thecae mostly at the morphological base of the anther.

Developmental phases

In very young stages a roughly pentagonal wall may be observed on the periphery of the floral apex within the primordial calyx. The wall has antesepalous sides, on which ten stamen primordia may be delimited by five shallow grooves in sepal radii and five deep grooves in petal radii. Thus it is possible to consider the ten stamens as five antesepalous or alternisepalous pairs, which together occupy a wave line. Anyway it is clear that the adult St5+5 condition cannot be understood as five alternisepalous and five antesepalous stamens. In species with fifteen or more stamens (figs. 254, 255) centrifugal development of stamen primordia takes place on the pentagonal wall, the stamens in sepal radii originating first, and succeeding lateral primordia occurring more peripherally and downwards. The median planes of the anthers come to lie parallel with the wave line.

Vascular bundle supply

In the base of the flower five sepal traces separate from the stele. In some flowers the sepal traces trifurcate into a sepal median bundle and two sepal basal lateral bundles which form cross-arcs. In other flowers sepal commissural laterals come from the bases of the sepal traces and follow an oblique course towards the alternisepalous radii. These commissural laterals are combined with androecium-pistil traces. On a higher level the androecium-pistil traces are situated in the androgynophore along the reconstituted stele, on which they are proximally attached in some flowers. Basally they are collateral, upwards concentric bundles. Just below the summit of the androgynophore the androecium-pistil traces are divided into an adaxial pistillary part and an abaxial part, forming a main staminal bundle. This strand, on a higher level, is irregularly separated into two to four stamen traces. If in species with ten stamens the androecium-pistillary traces coming from sepal traces deviate to the left, the right partners of alternisepalous stamen pairs are the larger ones. In species with more than ten stamens the five inner antesepalous stamens are supplied by vascular traces separating independently from the reconstituted stele in the androgynophore distally.

The vascular bundle supply to the anther is exactly in accordance with the anther structure elucidated above, since the collateral bundle of the filament turns down into the tip of the connective below the thecae. From the distal part of this bundle a number of small side-branches spread towards both thecae, together producing a fan-like innervation that appears adaxially folded along a median line (figs. 252, 253). Now and then a few side branches may recombine and in that way form the supply to the filament tip. Sometimes also a middle bundle may be present isolated from the two sets of lateral branches.

Other authors

Eichler regarded the androecium as an irregular capitulum of stamens. So did Schumann, but he excepted species with a distinct ring of stamens. Gazet du Chatelier considered the androecium as being composed of five trifurcated antesepalous groups, the median members of which lie in sepal radii. Only Saunders and Rao recognized two obdiplostemonous whorls, the inner whorl of which comprises five antesepalous stamens.

Brachychiton populneum

Similar to *Sterculia* spp.

Between the antesepalous groups of three stamen primordia the apex may remain baren, but often a still lower stamen primordium may be formed in alternisepalous radii. The margins of the young sepals proximally bend over these stamen primordia and are only distally appressed to the apex.

In the anther two side branches simultaneously separate from the turning point in the median bundle, each supplying a theca (fig. 257).

Firmiana colorata

Similar to *Sterculia* spp.

Pterocymbium beccarii

Similar to *Sterculia* spp.

The lower ends of the alternisepalous combined stamen-pistil bundles, which surround the stele of the androgynophore, are connected fasciculately to the sepal traces basally as well as to the base of the stele in the androgynophore.

The vascular bundles in the anther are like those in *Brachychiton.*

Argyrodendron actinophyllum

Similar to *Sterculia* spp.

From the highest point of the curving anther bundle some irregular vascular tissue goes up to the upper thecae halves (fig. 258).

Scaphium javanicum

Similar to *Sterculia* spp.

A receptacular disc lies between the inner base of the sepal cup and the androgynophore like a thick, innervated, parenchymatous cushion covered with a dense mat of glandular trichomes.

From the floral stele five main bundles separate basally, the middle portions of which divide collaterally into sepal traces and sepal commissural marginal traces. Androecium-pistil bundles are attached as usually to the bases of the sepal commissural marginals in a fasciculate manner. The flanks of each main bundle fall apart into an irregular number of small bundles which upwards branch profusely beneath the trichome layer of the disc.

The filament seems to be attached to the anther subapically, giving the anthers a pendulous character. However, as the stamen structure is resupinate like that in *Sterculia* spp., the anthers are really attached epibasally not subapically.

Cola nitida

Probably there is a receptacular disc between the calyx base and the androgynophore.

The short laterally fused filaments of ten stamens are inserted on the androgynophore equidistantly and between sepal and alternating radii. The reniform anthers which consist of two bisporangiate thecae in one line, are situated in an almost radial plane of the flower. A slight deviation from this radial arrangement occurs because the outer and lower anther parts are situated more towards sepal radii (fig. 245).

Developmental phases

In young stages the lateral distance between the oval anther primordia is largest peripherally on alternisepalous radii, where the bases of the calyx margins touch the floral apex. Together the oval primordia occupy a wave line. The division of an anther primordium into two thecae above each other is late in ontogeny, when the anther primordium from oval has become reniform. The same spatial interrelation between anther primordia occurs in *Sterculia alexandri* in a somewhat more developed stage than the one given in fig. 259.

Vascular bundle supply

Either sepal traces and sepal commissural lateral traces or traces collaterally dividing into these separate from the stele in the flower base. Alternisepalous main staminal bundles are connected with the reconstituted stele in the androgynophore. These bundles are divided collaterally into two stamen traces below the level of stamen insertion. The stamen traces split serially and end towards the thecae fan-like.

Teratology

In an abnormal flower two alternisepalous pairs of anthers are replaced by one anther. One of the deviating anthers has two thecae above each other, the other two thecae side by side.

Other authors

According to Bodard (1960) the splitting of the anther in two thecae is accomplished by a very early '*sillon equatoriale*'. We agree with Bodard that the position of the carpellodes is antesepalous, and that there are twenty thecae or forty pollen sacs arranged in two whorls. Saunders as well as Gazet du Chatelier described five alternitepalous stamens.

Heritiera littoralis

A dense floor of glandular trichomes covers the receptacle between the base of the sepal cup and the androgynophore.

The number of stamens and carpels varies from three to five. If the whorls are isomerous, its members alternate, those of the staminal whorl being most probably alternisepalous. The anthers are like those in *Sterculia* but are more pendent.

B. COMPARATIVE PART

1. THE POSITION OF THE STAMENS IN THE FULL-GROWN FLOWERS

Apart from the *Fremontieae*, the arrangement of the stamens is similar in all groups of the *Sterculiaceae*. The stamens are placed on a wave line, the inner antesepalous bends of which are represented by foliar staminodes, the outer antepetalous bends by the stamens. The carpels alternate with the staminodes. Mostly the stamens form a tube by partly facial fusion of their proximal parts.

In *Sterculieae* the place of the inner staminodes is occupied by a stamen, or there is neither a staminode nor a stamen (the carpels being nevertheless situated in antepetalous regions). Also in *Ruizia variabilis* (*Dombeyeae*) there is a stamen instead of a staminode. In *Melochia umbellata* and *Hermannia candicans*, both of *Hermannieae*, the staminodes are tiny or absent and correspondingly the carpels are situated in front of the sepals, as opposed to the condition in *Melochia pyramidata* and in *Sterculieae* with ten stamens. However, in *Cola nitida*, of the *Sterculieae*, a species without innermost stamens, the carpels are placed in front of the sepals.

The number of stamens constituting the outer bends ranges from more than ten in some species to mostly three in *Theobrominae* and *Helictereae* or to two in many *Sterculieae*. The triplets are formed by two lateral stamens and one middle outermost stamen. In *Melhania incana*, *Hermannieae*, *Byttnerinae*, and *Lasiopetaleae* the outer places are taken by single stamens, giving rise to obdiplostemony. In *Leptonychia glabra* three of each five outermost antepetalous members are filiform staminodes. If the stamens and staminodes are increasingly fused towards the sepal radii, they give the impression of being situated in five antesepalous phalanges or lobes, as for instance in *Sterculieae* with fifteen stamens. In this manner in *Glossostemon bruguieri* the stamens seem to be inserted along the proximal parts of the margins of large foliar antesepalous staminodes. The stamens are not placed equidistant, but mostly they are aggregated versus the petal radii more and more. However, in *Sterculieae* with ten stamens they may be placed equidistant between sepal and and alternating radii.

The contorted condition may be observed also in the androecium. In *Dombeyeae* the outward bends are placed more in front of the overlapping halves of the petals. If in *Helictereae* and *Theobrominae* the outward bends are formed by triplets of stamens, one of the laterals and the middle member close to it may be placed more outwards in front of the overlapping petal halves. If the triplets are reduced to pairs, one of the members may be situated more outwards in front of the overlapping petal halves. In *Sterculieae* the stamens of a pair, or the lateral stamens of a phalange may be of unequal size.

In the *Fremontieae* a tube is formed by five alternisepalous elongate stamens, which along the free parts bear two lateral elongate thecae, the summits of the filaments remaining sterile. In *Fremontia californica* the pollen sacs are partitioned by transverse septs. Moreover, on the outside of the rim of the tube small teeth may occur alternating with the stamens.

2. THE SHAPE OF THE MATURE STAMENS

The stamens may have anthers which are straight and slender, with two long thecae placed along simple slightly tapering prolongations of the filaments, for example in *Dombeyeae* and in *Pterospermum javanicum*.

In *Byttnerieae* and *Sterculieae* the apical filament part is somewhat broadened and, in addition, slightly bent backwards. Along it the prominent, chiefly lateral, broadly reniform thecae may be approaching each other apically or remain more apart.

In *Sterculieae* the connective is not as broad as in *Byttnerieae*, and the thecae are relatively large, more introrse and more adjacent apically. Therefore the resupination is obscured though remaining often visible by means of the small sterile filamental apex which projects from between the thecae in outward direction.

In *Hermannieae* and *Lasiopetaleae* the resupination is extreme. In addition, in *Lasiopetalum acutiflorum* the upward extended anther tails dehisce by apical pores like the equally resupinate anthers in *Ericaceae*.

In *Ayenia* spp. the single antepetalous stamens have a small additional theca between the two 'usual' ones.

3. THE DEVELOPMENT OF THE ANDROECIUM

Few developmental phases have been studied, chiefly because the really primordial phases are so very tiny that they are either destroyed in dried herbarium specimens or are overlooked by those who collect material in liquid.

In young buds the anthers and the staminodes are relatively large, the mostly united basal part of the androecium developing fully only later on. Also the androgynophore is a late development.

In *Melochia* spp. the staminodes are relatively large in primordial phases, but soon their growth is arrested, especially so in *M. umbellata*. In that case the normal antepetalous carpel position has changed into a position in antesepalous regions.

In *Theobroma* spec. a five-angled low staminal wall produces five low elevations in sepal radii and five high and broad elevations in petal radii, the latter of which are superficially subdivided into triplets of stamen primordia in a centrifugal way.

In *Sterculia* spp. with ten stamens a pentagonal primordial staminal wall forms ten stamen primordia separated by five deep alternisepalous and five shallow antesepalous radial grooves.

The stamens are placed along the shanks of a wave-line with their long axes, the thecae lying both parallel with the wave-line and side by side. If more than ten stamen primordia are present, they arise on a slight pentagonal wall with five leading stamens in sepal radii and are followed by the others in a latero-centrifugal way. In a given phase there is reason to speak of antesepalous parts of the staminal wall, although no central median stamen primordia will develop upon them in the species with ten stamens. The carpels still arise alternating with these parts. The interrelations between place and time of carpellary origin and the form of the primordial androecium could only be followed very fragmentarily. However, the few facts available do not contradict the conclusions reached in *Malvaceae*.

Also in *Cola nitida* the oval stamen primordia are arranged on the shanks of a waveline. But here a late transverse division gives rise to two thecae in line.

In *Fremontia californica* two thecae arise along the margins of the five alternisepalous trapezoid primordia, the often bilobed summits of which remain sterile.

In *Thomasia* spp. the petals originate as usual, but their further growth is arrested early, so that in full-grown flowers they are very small or seem to be absent.On the hemispherical stamen primordia first the central-lateral parts develop, then they become stalked, and finally the peripheral-lateral parts arise. The latter prove to form the slightly sagittate apex of the anther. Thus the anther arises partly resupinate from the start, and the resupination increases later. The same applies to *Sterculieae*.

4. THE SUPPLY OF VASCULAR BUNDLES TOWARDS THE ANDROECIUM

The occurrence of a petal stamen (fascicle) trace is a constant character in all species with petals. The trace is attached to one of the flanks of a sepal trace or to the base of one of the sepal basal lateral traces. In *Dombeya wallichii* this attachment takes place by a multiple base. Accordingly the trace moves upwards and outwards in the direction of the petal radii by an oblique proximal course. One or two opposed flank parts proceed as stamen fascicle traces of as a number of stamen traces above the departure of the petal trace. Generally, if more stamens occur, first a fascicle trace is formed, sometimes by union of two flank parts of the petal stamen fascicle trace (*Dombeya wallichii*). In *Hermannia candicans* the supply towards a single stamen is formed that way. In *Lasiopetaleae*, on the other hand, the (petal) stamen trace is attached to the sepal commissural trace.

In *Pentapetes phoenicea* all traces are directly attached to the underlying vascular tissue in an oblique manner. In *Ayenia* spp. the traces are directly connected with the reconstituted stele in the androgynophore, and in *Pterocymbium beccarii* the combined stamen fascicle-pistillary traces have a fasciculate base connecting them witb the basal sepal traces as well as with the proximal parts of the reconstituted stele in the androgynophore.

In *Hermannia candicans*, *Glossostemon bruguieri*, *Leptonychia glabra*, and *Theobroma* spp. the petal stamen (fascicle) traces are more or less concentric bundles. In *Helictereae* the adaxial parts of the more or less concentric combined stamen fascicle traces represent traces of the wall of the pistil. In *Sterculieae* with more stamens the fascicle traces may also be concentric bundles from which the different stamen traces spread outwards. Apart from these pistillary traces the concentric traces chiefly contain two lateral bean-shaped facing xylem groups. Higher up, the stamen traces are directed with their xylem in a direction intermediate between the floral centre and alternisepalous radii. This is also the case in *Theobrominae* and in *Sterculieae.*

A most constant character is given by the inner whorl of independent traces going towards the staminodes or innermost stamens.

In *Fremontieae* there are also an inner whorl of independent traces and furthermore five pairs of outer facing traces which are attached to the base of the sepal traces. They supply the sterile summits and the thecae of the stamens respectively. These traces do not deviate by an oblique course, the innermost traces leaving the stele in alternisepalous radii.

As to the contorted condition it appears that if the petals overlap to the right, petal stamen fascicle traces deviate invariably towards the left and conversely. In that case, if antepetalous triplets are present, the right flank of the petal stamen fascicle trace may form a trace giving two stamens, the other flank producing only a single stamen.

The vascular bundles in the stamens

The stamen bundles are frequently single unbranched collateral bundles. In *Dombeya wallichii* especially the inner stamens show two parallel lateral nerves, as do the staminodes in most species. In addition, the middle staminode nerves may have some more side nerves. In *Hermannia candicans, Theobroma* spp. *Helictereae,* and in some *Sterculia* spp. the filament bundle may become concentric for some distance.

In the connective in *Hermannieae* the bundles are sharply resupinate and branch into two upward and two downward parts. In *Herrania albiflora* there are two side branches, one towards each theca, with some residual vascular tissue in the middle. In *Thomasia pauciflora* and in *Cola nitida* two parts of the stamen bundle proceed into each theca first in a collateral and then in a serial way, and in the end both branches spread somewhat fan-like. Moreover, in *Thomasia pauciflora* the bundle is resupinate. In *Sterculieae* a folded fan-like innervation may have some concentrated, even isolated, middle branches at the adaxial end. In *Brachychiton populneum* and *Pterocymbium beccarii* two upward branches come from a resupinate middle stamen bundle.

5. THE SEPALS, THE PETALS, AND THE GLANDULAR TISSUE

The sepals

The innervation of the sepals is formed by trifurcation of a sepallary trace into a sepal median and two basal common lateral traces, the latter of which give off the majority of sepal lateral bundles. Frequently the sepal basal laterals of adjoining sepals are linked over the petal radii, forming crossarcs. This character is constituted by the double bases of the outermost lateral bundles which are attached to adjoining basal lateral traces. Sometimes these lateral bundles form a commissural marginal trace which is connected with the stele directly in alternisepalous radii. Sometimes parts of the receptacular stele diverge which divide immediately into two portions side by side, one forming a sepal median, the other a sepal commissural marginal trace. The latter moves outwards by an oblique course towards the petal radii. This may for instance be the case in *Byttnerinae,* *Sterculieae*, and in *Hermannia candicans*. Sometimes in *Hermannia candicans* two sepal commissural traces may be combined basally with one of the sepal median traces.

In *Fremontia californica* the innervation of the coloured quincuncial sepals is more or less fan-like with a definite median nerve, main forks, and distal anastomoses in the lateral nerves.

In *Eriolaena quinquelocularis* the sepal laterals form an anastomosing bundle complex in alternisepalous radii.

The petals

In *Eriolaena quinquelocularis* the petal traces are attached to the sepal traces in a way similar to that described for *Tilia* spp. Mostly they are combined with two basal laterals of two sepals and with one of a third sepal.

Generally the petals are of slightly asymmetrical outline. They are contorted and inserted mostly not precisely in alternisepalous radii. The innervation is based by a trifurcation of a petal trace and proceeds fan-like with major forks and distal anastomoses. In the petals of smaller size the number of forks decreases while anastomoses are more frequent. Especially in *Byttnerieae* the petals have very peculiar shapes which are described fully by Leinfellner (1960). In *Helicteres lanata* the petals may have proximal marginal or facial appendages which are supplied by branches of the marginal petal nerves.

The glandular tissue

Usually fields of glandular trichomes occur on the inside base of the sepals, in *Eriolaena quinquelocularis* in the form of two lateral parts. In the same species and also in *Pterospermum javanicum* special tiny anastomosing branches from the sepal lateral bundles supply the glandular tissue.

In *Abroma javanica* and *Scaphium javanicum* glandular fields on the sepals are absent. Instead there is a deep receptacular disc on the inside of the petal or sepal base respectively. In *Scaphium javanicum* this disc is profusely innervated by strongly branching and distally anastomosing flank parts of the bases of the sepal traces. All these multicellular trichomes have a shortly cylindrical form.

Another kind of glandular trichomes occurs in the form of long slender threads of small cells with a big oval terminal cell. These structures may occur scattered over both surfaces or along the margin of the sepals, on the staminodes, the pedicel, or on the base of the androgynophore or the filaments. They are to be found especially in *Sterculieae* and *Theobrominae*.

6. VARIATION IN THE COURSE OF THE VASCULAR BUNDLES

The multiple attachment

Sepal lateral bundles may be attached by double bases to basal lateral traces of adjoining sepals, or to a sepal commissural marginal trace as well as a sepal basal lateral trace, forming cross-arcs in both cases.

The petal stamen fascicle trace in *Dombeya wallichii* may have a double or multiple basal attachment to the sepal supply. In *Pterocymbium beccarii* the stamen-pistil traces are attached in a fasciculate way to the petal trace as well as to the stele in the androgynophore.

In *Cheirostemon platanoides* and in *Fremontia californica* a trace occurs in the outer antetepalous regions of the staminal tube, which has a double base to the flanks of adjoining lateral staminal traces.

In *Ruizia variabilis* stamen traces may be connected by means of double bases with a petal trace and with an independent stamen fascicle trace.

Concerning the androgynophore

In *Ayenia* spp. and in *Pterocymbium beccarii* the stamen traces or part of them may be attached to the stele which is reconstituted in the androgynophore.

On different points of attachment for the same kind of traces

In *Eriolaena quinquelocularis* the five petal traces are attached to two basal lateral traces of two sepals and one basal lateral of a third sepal.

In some species, especially in *Sterculieae*, one or even two sepal commissural marginal traces may be attached to the sepal median trace basally.

'Hesitating' bundles

Some middle stamen traces in *Ruizia variabilis* may first be directed towards the sepal trace, but more downwards return towards the petal trace.

Concentric bundles

Concentric bundles commonly occur in *Sterculiaceae*. However, they are mostly incompletely concentric, the adaxial part in the median plane being less well developed or missing. The composed character of the concentric bundle is frequently evident, for instance in the combined pistil-stamen fascicle traces running through the androgynophore in *Helictereae*.

In *Hermannia candicans* the concentric aspect is achieved by an extension of the later-formed xylem towards the adaxial side.

Frequently the filament and the staminode bundles may be concentric for some distance, but are collateral at the base and in the distal parts. In *Fremontieae* the median sterile staminal bundles are more or less concentric.

Residual bundles

An outer antetepalous trace in *Fremontieae*, which has a double base, may innervate a sterile tooth on the outside of the rim of the tube in *Fremontia californica*, but fades away upwards in the tube of *Cheirostemon platanoides*.

In the anthers of *Brachychiton populneum* and *Pterocymbium beccarii* there is some residual vascular bundle tissue in the middle.

The stamen traces in *Eriolaena quinquelocularis* and the lateral stamen traces of the more peripheral stamens in *Dombeya wallichii* are not lignified towards their base, and probably fade away.

C. INTERPRETATIVE PART

The structure of the androecium

In the few primordia available the existence of staminal lobes as parts of a pentagonal wall has not been demonstrated, except in *Fremontia californica*. The wall itself may be extremely low or absent. The really young primordia are of very small size. The development of the anthers and foliar staminodes is always much in advance of that of the fused filamental parts.

Nevertheless the androecium structure must be similar to that in the preceding groups because there are quite a number of common features. Therefore we may assume that the formation of more or less antesepalous staminal lobes is reduced in *Sterculiaceae*. In the mature flowers the lobe formation may be illustrated most clearly by the phalanges of the *Sterculieae* and probably still more by those of *Glossostemon bruguieri* where the stamens are actually placed along the margins of lobes which terminate as foliar staminodes. Unfortunately, primordia of this particular species could not be obtained.

The common features may be listed shortly as follows:

1) The stamens are placed along the shanks of a wave line, representing the sides of the putative lobes, and are innervated by a pair of (petal) stamen (fascicle) traces.
2) The apical parts of the wave line may either be occupied by a single stamen (in some *Sterculieae* and in *Ruizia variabilis*), or by a staminode (in the majority of species). Some species have only tiny staminodes, in others staminodes are lacking. Apical stamens or the median parts of the staminodes receive a separate trace, so that the putative lobes are supplied by a three-trace system.
3) The latero-centrifugal sequence in the staminal development.
4) The contortion.

There are no objections to extend to the *Sterculiaceae* the conclusion drawn for *Malvaceae* and *Bombacaceae*, that the carpel position entirely depends on the stage the androecium has reached at the time of appearance of the carpel primordia. They always alternate with the advanced parts of the primordial androecium, the contorted condition of the latter taken into account. If apical stamens or staminodes are present on the putative staminal lobes the alternating carpels are situated more or less between the sepal radii (most *Sterculieae*, *Melochia pyramidata*). If staminodes are absent, the carpels alternate with the proximal lobe parts and are placed more or less in front of the sepals (*Melochia umbellata* and *Cola nitida*). If the staminodes are absent in a mature phase, but are visible in ontogeny, be it only in the form of a slightly inward outline of the low primordial staminal wall (*Sterculia alexandri*), the carpels will all the same alternate with the staminal lobes (also in *Scaphium javanicum*).

The number of stamens along the side of a staminal lobe may decrease form more than five to zero. Frequently there is one on each side, either forming pairs if apical structures are absent (*Cola nitida*, *Scaphium javanicum*) or triplets together with the innermost stamens (many *Sterculieae*) and staminodes (*Theobroma cacao*, *Helicteres* spp., other *Sterculieae*). In *Leptonychia glabra* the peripheral stamens are reduced to filiform staminodes.

As indicated above, the stamens are innervated by two single or fascicled traces, which are mostly attached to the side of petal traces. The xylem parts of the traces of adjacent putative lobes are facing each other and placed perpendicular to the shanks of a wave line. In some species, as in *Dombeya wallichii* and *Glossostemon bruguieri*, the traces are more aggregated in the outward bends, a feature which probably means that the apical sterilization of the lobes is rather extensive. There is also the usual independent whorl of single traces towards the innermost stamens or staminodes. Summarizing we may state that the staminal lobes receive a three-trace system.

Also in *Fremontia california* the five stamens which alternate with the tepals, receive three traces, a middle inner trace going towards the apex chiefly unbranching and two outer lateral traces giving off a series of more or less forking branches reaching the pollen sacs of the two thecae. Thus the similarity in the supply and also the xylem position of the vascular bundles of these stamens as compared with those of staminal lobes is very striking. Moreover, the primordial stages actually show that the stamens originate in the form of trapezoid lobes bearing a theca along each side. Therefore the homology between this stamen and the groups of structures which may be formed by a staminal lobe in most other species cannot be denied. The same lateral lobe parts which usually form a number of, frequently dividing, primordia, here form a continuous theca. It may be highly significant for this character of potential subdivision of the staminal lobes that the pollen sacs are partitioned by transverse septs. *Fremontia* can be fully compared in this respect with the *Ceiba* spp. and with *Chorisia crispiflora* in *Bombacaceae*. What is said about *Fremontia californica* is also valid for *Cheirostemon platanoides*, except for the fact that in the latter the pollen sacs are not subdivided. In the general form of its tube and the theciferous arms, and as regards the aestivation of the sepals, *Cheirostemon platanoides* may also be compared with *Ochroma lagopus*. The two stamen (fascicle) traces in *Fremontia californica* are attached to the sepal median trace without any oblique course, in accordance with the fact that the staminal lobes are not contorted.

There is a difference, however, in that the stamens in *Fremontieae* alternate with the tepals. However, we had better not stress too much this difference which may be due to, admittedly remarkable, changes in the general floral structure. Evidence of this is given by the singular form and colour of what we here call tepals, and secondly by residual traces and appendages that are present on the outside of the rim of the tube, where we usually find petals or connecting thecae.

The contorted condition

The petals, if present, are contorted; they are inserted obliquely and mostly not precisely in the petal radii. Also the putative staminal lobes are contorted, as shown by the asymmetrical phalanges in *Sterculieae*. And accordingly there are major and minor rows of stamens, the latter being situated in front of the overlapping petal halves. As in *Malveae*, the anthers of the different rows may be imbricate and form pentamerous pseudo-whorls for instance in *Sterculieae*. In *Dombeya* spp. it is especially evident that, as in many *Bombacaceae*, the putative staminal lobes are not alternating with the petals, but are present more in front of the overlapped petal sides. Moreover, the additional more inner stamen which may occur in the outward bend of the wave line, may give evidence for the reduced existence of the staminal lobes, because these stamens can be compared with the slightly inward bending margins of the lobes as found in some *Bombacaceae*.

The contorted condition gives rise to a kind of triplets of stamens which is unlike that mentioned above for the *Sterculieae*, since the median members are not formed by the innermost stamens. Mostly we are dealing here with asymmetrical more or less intimately fused triplets of stamens in the *Theobrominae* and *Helictereae*, which are constituted by two stamens along the major side of a staminal lobe and a single stamen of the minor side of an adjoining lobe. As a consequence the median member of a more or less alternisepalous triplet is placed outermost and represented by the second stamen of the major row. The two members of the major row may be placed closer together, the third member more apart but on a level between the others, corresponding to the tendency for pseudo-whorl formation. Additional evidence for this view is given by the existence of two facing stamen traces, one of which divides into two stamen traces towards the major row. In *Ayenia* spp. one of the rows may be considered to produce a single monothecous stamen only (conformable to the reduction forms found peripherally in the rows of stamens in many *Malvaceae* and some *Bombacaceae*). The other, major, row produces a stamen with one ordinary and one more peripheral small theca. These thecae are fused so intimately as to look like one stamen with, strangely enough, a triplet of thecae.

If there are only ten stamens, one on each lobe side, the primary stages may show clearly that the stamen primordia are placed between sepal and petal radii. Later one of them may be bigger (many *Sterculieae*) and placed more in front of the overlapping petal halves, if there are petals. Moreover, if there is a slight contortion, a fake obdiplostemony will result.

If only one of the sides of a staminal lobe gives rise to a single stamen primordium, the other side remaining sterile, another pseudo-obdiplostemonous situation may result in relation with the staminodes which represent the apical parts of the asymmetrical staminal lobes. It is evident that it is the major side of a staminal lobe which will produce the only lasting stamen, which accordingly is placed more in front of the overlapping petal half (*Melhania incana*). If the contorted character and the petal deviation are less markedly developed, the single stamens are seen to be placed almost precisely in front of the petals in mature flowers of *Byttnerinae* and *Thomasia* spp. and still more so in *Hermannieae* and in *Lasiopetalum* spp. which have no staminodes left. We may compare these conditions with quite similar conditions in *Malvaceae*, for instance in *Plagianthus* spp.

Also in the *Sterculiaceae* the (petal) stamen (fascicle) traces show an oblique proximal course, the direction of which bears a constant and reverse relation to the way the petal margins overlap. The oblique course may be thought to proceed from near the sepal median trace in the direction of the petal radii, and is especially evident in *Theobrominae* and *Helictereae*, and also in *Sterculieae*. Incidentally the traces are attached to the reconstituted stele. Sometimes the traces link up with the sepal commissural trace in *Byttnerinae*, *Sterculieae*, *Herrania albiflora* and *Scaphium javanicum*, the common trace being often attached to the sepal median trace basally by way of an oblique course. The oblique course of the (petal) stamen traces may also persist in the oligomerous androecia described above, proving that it is the contortion which may ultimately produce false obdiplostemony in those cases. In *Melhania incana* for instance the stamens and staminodes are still placed somewhere between sepal and petal radii. But in *Hermannia candicans* the stamens are placed in petal radii. The *Byttnerinae* are rather variable in this respect. Only in the *Lasiopetaleae*, where the petal development is arrested at an early stage the stamen traces are not oblique but directly attached to the sepal commissural trace.

The structure of the stamens

The stamens have two thecae, each with two parallel pollen sacs. Both thecae are situated along a connective that may be either long, in the form of a simple filament prolongation, or somewhat broader or reniform. The anthers appear to be somewhat 'folded' congenitally, the thecae growing on the margins in a slightly introrse manner. However, later formed peripheral anthers may be flatter in some flowers, resembling the bithecous anthers in *Malvaceae* and *Bombacaceae*.

A prominent character is formed by the congenital resupination which may in extreme cases lead to anthers which open upwards by means of pores in their tails (*Lasiopetaleae*, resembling *Ericaceae*). The resupination is accompanied by a bending of the vascular tissue. The bundles are usually collateral, sometimes concentric in part of the filament, or composed in the connective.

It is difficult to bring the innervation into a coherent picture. In *Cola nitida* and in the *Thomasia* spp., but chiefly in some *Sterculia* spp., the thecae receive a fan-like supply, in the *Sterculia* spp. touching in the median line. In other *Sterculia* spp. there are resupinate branches concentrated in the middle and furthermore some irregular lateral branches, in still others the supply is more simple. In *Brachychiton populneum* and *Pterocymbium beccarii* a single middle bundle with two bending laterals remain. This is also the case in *Hermannia candicans*, the middle bundle being moreover split apically into the tailed apex of the anther. In *Herrania albiflora* only two laterals are present, the middle tissue being in a reduced form.

In large staminodes the independent trace may give a middle branch and two minor parallel side branches. This configuration may also occur in inner stamens of *Dombeya wallichii*, though the laterals tend to fade away. The middle staminode bundle may have some side branches.

TILIACEAE

A. DESCRIPTIVE PART

1) BROWNLOWIEAE

Carpodiptera cubensis Griseb.	St±15
Berrya cordifolia Burr.	S(5)n-P5-St∞-G(2-5)
B. javanica Burr.	ditto
Brownlowia argentata Kurz	S(5)n-P5-St∞-Std5-G(5)
B. elata Roxb.	ditto
Pentace polyantha Hassk.	S(5)n-P5-St5 × (4/7)-Std5-G(3-5)
P. triptera Mast.	ditto
Diplodiscus paniculatus Turcz.	S(5)n-P5-St∞-Std5-G(5)
Pityranthe verrucosa Thw.	S(5)n-P5-St15-Std5-G(5)

Glandular trichomes cover the basal inner part of the calyx cups forming either a ring or five fields in sepal radii.

A small receptacular extension may occur between calyx and petals in *Pityranthe*.

The asymmetric petals are contorted, sometimes imbricate, they alternate more or less precisely with the sepals. An androgynophore may be short or absent.

Among the stamens groups cannot easily be distinguished, except in *Pentace*, where they seem to be more or less alternipetalous. In *Brownlowia* the stamens slightly adhere basally in five groups, and in *Diplodiscus* antepetalous regions count more stamens than the antesepalous ones.

If groups of stamens and staminodes are both present, they alternate. The narrow foliar staminodes forming an inner whorl of the androecium alternate with the cells of the pistil in case there are five cells. In *Berrya*, where staminodes are absent, pistil cells alternate with the anatomical stamen groups. However, the position of the stamen groups as related to the petals is variable, which is presumably due to the contorted character of the petals and androecium. Moreover, the exact position is difficult to define if primordial phases are lacking and as in buds the calyces are not yet lobed.

The anthers consist of two bisporangiate thecae along the apical margins of small reniform distal ends of the filaments. In *Pentace* two pollen sacs belonging to different thecae were observed to be replaced by one sac of double length, an anther of three sacs being the result.

Developmental phases

Young petals lie obliquely below the lateral parts of the five tangentially stretched common staminal protuberances on which stamen primordia develop centrifugally. The exact position related to the sepals cannot be ascertained, because the sepal lobes are not early developed. These phases were seen in *Brownlowia argentata* and *Pentace polyantha*. In *Diplodiscus paniculatus* the stamens develop centrifugally in five more or less antepetalous groups, those developing first alternating with the staminodes.

Vascular bundle supply

Five petal stamen traces which are attached to the bases of the sepal traces, split proximally into petal and stamen group traces. The petal traces deviate markedly towards alternisepalous radii. On the other hand, the almost concentric stamen group traces stay more in antesepalous regions. They spread into a variable number of separate stamen traces, supplying five anatomical stamen groups, no anastomoses occurring between the most lateral stamen traces of adjoining groups. In *Pentace polyantha* the anatomical groups coincide with the external groups. In *Pityranthe verrucosa* the anatomical groups consist of three more or less antesepalous stamens.

The staminodes receive single independent traces from the stele.

In *Berrya cordifolia* the sepal and petal traces come from the floral stele close together. In *Brownlowia argentata* lateral stamen traces give off traces to still farther lateral stamens. In *Diplodiscus paniculatus* petal stamen traces combined with sepal commissural lateral traces are attached to the proximal parts of the sepal median traces or to the stele independently somewhere between two sepal radii.

Other authors

Eichler mentioned for *Brownlowia* five alternipetalous fertile groups of free stamens and five epipetalous staminodes.

2) Apeibeae

Apeiba echinata Gaertn.	S5-P5-St(∞)-G(10)
A. tibourdou Aubl.	S5-P5-St(∞)-G(20)
A. spec.	S5-P5-St(∞)-G(15-20)
Glyphaea grewioides Hook.	S4-P4-St(∞)-G(8)

Apeiba spp., mainly A. echinata

The sepals are cucullate. The petals are imbricate. The stamens are inserted upon a rather flat receptacle surrounding the pistil which arises in the centre with an attenuate base or on a short gynophore.

The filaments are comparatively short. The form of the introrse anthers ranges from short and foliar in the peripheral, to more cylindric and longer in the central stamens. Anthers in *Apeiba tibourdou* are less foliar than in *Apeiba echinata.* All anthers have sterile and foliar flaring distal parts which in bud cover one another imbricately.

In each anther there are four pollen sacs forming two thecae which dehisce longitudinally. The outer pollen sacs reach upwards beyond the inner and continue as sterile sugmarginal ridges along the distal parts of the anther (fig. 262).

The sterilisation in the anthers increases towards the periphery of the flower. The anthers become shorter and more foliar and the pollen sacs are replaced by sterile ridges which eventually disappear. The peripheral staminodes are slightly connate.

It should be added that the above descriptions have been made from badly dried material, so that some details may have escaped attention.

In a sample of an unnamed species, fixed in F.A.A., it was disclosed that the slender anthers have pollen sacs with sterile distal parts, which nevertheless take part in the dehiscence. Only in the bilobed topmost region of the anther the pollen sacs are absent. In the outer stamens the sterile region is somewhat larger, and finally the outermost stamens are sterile spathulate organs (fig. 264). Probably among others some glandular hairs are present on the pistil wall.

Developmental phases

A flattened hemispheric apex entirely enclosed by the young calyx produces ten hemispheric stamen primordia on a low circular subapical wall. Probably before the first anther primordia the petal primordia arise in the rather flat corners of the apex between the young sepals. Together with the centrifugal development of more anther primordia the floral apex broadens considerably. In the centre a cavity is formed in which ten stylar primordia appear after the first anther primordia. In *A. echinata* the anthers grow in six to seven alternating whorls of ten members each, giving rise to twenty orthostichies (to a polystemonous androecium) (fig. 260).

In *A. tibourdou* the number of stamens is much higher and orthostichies are absent.

In the fixed material, mentioned above, we see that the hemispheric stamen primordia, which develop centrifugally on a low androecial wall surrounding the primordial pistil, first are flattened on the adaxial side and then become stalked and spoon-shaped. The pollen sacs arise along the sides of the primordial anther. Much later in ontogeny the top of the anther becomes bilobed and the distal parts of the pollen sacs are retarded in their further development. Thus the sterilisation of the upper anther region takes place during ontogeny. Some flower primordia have 15 or 20 carpel primordia in a single whorl with which the innermost whorl of stamen primordia alternates, fitting between the sini of the horseshoe-shaped carpel primordia. As the second whorl of stamens alternates with the first, and as this alternation is repeated during the centrifugal development, a total of 30 or 40 orthostichies of stamens result. However, many flower primordia have between 15 and 20 carpel primordia, or if they do have 15 or 20 carpel primordia some of these are slightly smaller or bigger than the rest. It is evident that also the innermost stamen whorl is irregular, some of the primordia being somewhat smaller or larger, and placed more inwards or outwards. Consequently, the orthostichies are absent.

Supply of vascular bundles

The sepals have many dispersed parallel bundles, the lateral ones of which converge inwards into the cucullate top.

The main bundles leave the stele of the flower base in sepal and petal radii forming sepal median and sepal commissural lateral traces. The sepal median traces trifurcate into a sepal midrib and two sepal basal laterals which give off the median half of the number of sepal lateral nerves. The outer halves of the sepal laterals of adjoining sepals come from the collateral division of the main bundles on the petal radii. Most of the middle sepal laterals have a double origin, one towards the sepal median trace, the other towards the sepal commissural marginal trace, thus giving the appearance of cross-arcs. The petal traces are attached to one or both sides of the distal parts of the main bundles on petal radii. In *Apeiba tibourdou* the petal trace is a broad collateral bundle spreading by means of a more or less distinct trifurcation into the petal nerves. However, in *Apeiba echinata* the petal trace is almost concentric and from the proximal part of each petal basal lateral a tiny bundle is given off which soon ends blindly in adaxial direction.

In *Apeiba echinata* the stele tends to be reconstituted above the petal level. Then it separates into a vascular supply towards the pistil inwards and an outward whorl of twenty main staminal bundles which have a radial course towards the stamen bases. From either flank each main staminal bundle gives off an orthostichous series of stamen traces with a collaterally double origin (fig. 261), forming a chain of traces. The stamen bundles are collateral bundles with the xylem opposed to the flower centre; they move upwards into the anther unbranched.

On the other hand in *A. tibourdou* staminal fascicle traces are connected with the perianth bundles. One fascicle trace may be attached to the proximal part of the sepal commissural lateral bundle or a petal stamen trace may be attached to it. As a matter of fact the main bundles leaving the stele in petal radii are concentric or almost so, except at the base. One, two, or three stamen fascicle traces may link up with the main bundles in sepal radii basally, or may leave the stele next to these sepal traces independently. Other stamen fascicle traces may leave the stele independently in about petal radii. In this way a total of fascicle traces is reached that more or less equals the number of pistil cells (*circa* twenty). It may happen that a fascicle trace coming from the petal stamen trace is joined by a bundle coming from the stele independently, or, stated otherwise, that the traces of antepetalous stamens partly adhere to the petal trace, partly to the stele. As opposed to those in *Apeiba echinata*, the stamen fascicle traces tend to become concentric. They ramify in a tree shaped manner into stamen traces, which may anastomose with one another proximally.

Most stamen fascicle traces in both species give off some tiny bundles from their proximal regions, which contribute to the innervation of the pistil wall.

In the unnamed *Apeiba* species, mentioned above, three sets of five traces leave the stele on successively higher level, namely five commissural sepal traces, five median sepal traces and five petal traces. The proximal flanks of the median sepal and petal traces separate and move in upward direction spreading into stamen traces outwards and pistil traces inwards.

Glyphaea grewioides

When comparing this species with the *Apeiba* species it may be noted that the innervation towards the androecium is slightly different. Two petal stamen traces are linked up with opposing flanks of the proximal part of the sepal commissural laterals. Some bundles separate from both traces proximally to form traces to one petal. The rest of the petal stamen traces runs upwards and sidewards towards the stamen bases by a tree-shaped ramification. Radially orientated short or long chains of staminal traces stand out among these ramifications, the bulk of the stamen traces departing from these chains in various directions.

3) TILIEAE

Entelea palmata Lindl.	S4-P4-St4 × ∞s-G(4)p
E. arborescens R. Br.	ditto
Corchorus olitorius L.	S5-P5-St∞-G(3-5p)
C. aestuans L.	S5-P5-St∞-G(3)
C. tridens L.	ditto
C. capsularis L.	S5-P5-St∞-G(5)s
C. hirsutus L.	S5-P5-St∞-G(3)
Sparmannia africana L.	S4-P4-St4 × ∞s-G(5-6)
Clappertonia ficifolia (Willd.) Decne.	S4-P4-St8+8sp-Std∞-G(8)
Cistanthera papaverifera A. Chev.	S(5)-P5-St5 × 3p-Std5-G(5)
Luhea divaricata Mart.	S(5)-P5n-St(5 × ∞)s-G(5)p
L. ochrophylla Mart.	S(5)-P5n-St5 × (∞)s-G(5)p
Mollia speciosa Mart.	S5-P5-St5 × (∞)s+5 × (∞)p-G(2)
M. spec.	ditto
Trichospermum javanicum Bl.	S5-P5-St10 × ∞-G(2)
Schoutenia glomerata King	S(5)-P0-St5 × 6/7p+5s-G(5)p
S. ovata Korth.	S(5)-P5-St5 × 6/7p+5s-G(3)
Tilia platyphyllos Scop.	S5-P5-St5 × 6/7s+5p-G(5)s
T. tomentosa Moench	S5-P5-St5 × 10/11s+Std5p-G(5)s

Entelea spp.

In *Entelea palmata* the antesepalous groups of stamens can easily be distinguished, although they almost meet in the petal radii. However, in *Entelea arborescens* these groups may only be delimited by the fact that the stamens in the petal radii may be smaller and fewer in number, though in a late stage of flowering the difference in dimension is no longer obvious. The anthers bear two pairs of pollen sacs arranged in two thecae; they are slightly sagittate and curved outwards towards a position about perpendicular to the filament axis. Some peripheral stamens may be sterile.

Developmental phases in Entelea arborescens

Along the margins of a rather flat elliptic flowering apex surrounded by the young sepals and the petal primordia four antesepalous staminal protuberances arise which are tangentially stretched. Upon these protuberances the hemispheric stamen primordia originate in centrifugal and lateral direction, starting with an innermost primordium in sepal radii or with two primordia, one on either side of sepal radii. Immediately after the first stamen primordia a subapical wall becomes visible on the apex which later differentiates into horseshoe-shaped carpel primordia. When the third row of stamen primordia appears on the apex the staminal groups meet in the petal radii (fig. 265). From this moment on the stamen primordia are initiated all around the apex towards its periphery.

In *Entelea palmata* the petals seem to be somewhat later in appearance than in *Entelea arborescens*, maybe even after the occurrence of the first stamens. Anyhow in both species the growth of the petals is arrested early in the ontogeny of the flower, and is only resumed later on.

The margins of the cucullate apices of the sepals touch the flowering apex in the antepetalous regions between the primordial stamen groups. In a later phase and more peripherally the protruding sepal margins may seem to delay the growth of the young stamens, as was stated above.

In late phases some new stamen primordia may often be observed between the older ones.

Supply of vascular bundles

In the base of the flower two consecutive sets of eight main bundles leave the stele, the rest of which forms the pistillary vascular supply.

The first set represents sepal median and commissural sepal lateral traces, which divide into middle and lateral sepal bundles respectively. Moreover, in *Entelea arborescens* either the sepal commissurals are combined with the petal traces near their bases, or the petal traces originate from the stele independently but again quite near the bases of the sepal commissural laterals.

The second set of eight bundles supplies the androecium. It consists of four large stamen fascicle traces in the petal radii, which give a number of stamen traces to the lateral parts of adjoining stamen groups, and furthermore of four small stamen fascicle traces which each give traces to the median parts of the stamen groups. Often, especially so in *Entelea arborescens*, instead of one of these stamen fascicle traces two are present side by side, in accordance with the two-topped condition of many antesepalous groups.

The tree-shaped ramification of the stamen fascicle traces produces some digitate chains from which traces move off in all directions.

Corchorus spp.

The flowers are rather small, the sepals are valvate, the petals imbricate. Above the perianth the receptacle contracts into a short androgynophore which upwards broadens again into a kind of collar below the stamens. The antepetalous proximal regions of the androgynophore are covered with glandular trichomes. The distal collar region may be somewhat broader and higher in sepal than in alternating radii.

Two or three rows of stamens are distributed irregularly over the raised receptacle in the middle of which the pistil arises (fig. 266). The anthers are adnate, but the bisporangiate thecae are prolonged sagittately downwards remaining contiguous. In addition, the anthers of the central stamens may be slightly resupinate, giving the impression of a peltate stamen. The number of stamens ranges from 8—17 in *Corchorus aestuans* to 30—35 in *Corchorus olitorius*.

Developmental phases

Although the sepals originate successively, they reach equal size very quickly. The apex bordered by these young sepals becomes a flattened hemisphere and a low wall is developed along its margin. This wall is pentagonal with rounded antepetalous angles. Upon it the central stamen primordia emerge in an irregular whorl, and as the wall gets broader more stamen primordia become visible in centrifugal direction.

When the first stamen primordia become visible, a pistillary wall develops on the margin of the upward growing apex and petal primordia successively appear below the staminal wall. The further development of the petals is postponed till the time of anthesis. The development of the androgynophore and its glandular fields and of the collar-like extension below the androecium are also late in ontogeny.

Supply of vascular bundles

Corchorus olitorius: Five segments separate from the vascular cylinder of the flower base more or less in sepal radii. Usually these segments divide proximally into a sepal median trace and one sepal commissural lateral trace on the same side, occasionally they divide into a sepal median trace and one commissural marginal trace on either side. All these bundles may follow a course deviating from a radial one in order to reach the bases of the organs they serve (fig. 267).

Three petal traces are connected with a sepal commissural lateral, where this trace divides collaterally. Vascular bundles towards the nectary could not be observed.

Five to ten single or common stamen traces are attached to one or both flanks of the sepal commissural marginals, either in the proximal region or near the division point. The stamen bundles are single collateral bundles with the xylem directed towards the centre of the flower.

In *Corchorus aestuans* either sepal commissural marginals may come from the stele directly in petal radii or two sepal basal laterals belonging to two adjoining sepals come together in petal radii for a short distance. One or two traces to the androecium — single or branching — may be connected to the proximal part of a sepal median or sepal commissural trace. Moreover they may sometimes be connected with the stele independently on the level of the collar.

In some material of *Corchorus tridens* sepal median traces and sepal commissural marginal traces are directly attached to the stele in their proper radii. The sepal median bundles trifurcate as usual, but the sepal laterals form a system of cross-arcs to which the sepal commissural marginals are not connected. The system of cross-arcs is composed by the double bases of the sepal laterals. The petal trace or traces are attached to the sepal vascular supply in the petal radii in many ways, even in one flower. The stamen traces originate through splitting of five segments that separate from the stele independently in the petal radii.

In other material bifurcating sepal commissurals are mostly attached to the base of the single sepal median traces, though one of them may be connected with the stele in a petal radius. Near this attachment point also the petal and stamen traces are inserted and they proceed upwards by means of a proximal oblique course. Obviously the course of the bundles is very variable in this species.

Other authors

Payer advanced that the stamens develop on five antesepalous buttresses and Eichler agreed by stating that in *Corchorus olitorius* the androecium starts with five alternipetalous stamen primordia. In addition Eichler mentioned *Corchorus siliquosus* which has 10 stamens in obdiplostemonous arrangement. According to Saunders in *Corchorus olitorius* 5 main bundles come from the stele which combine 3, 2, 2, 2, and 1 bundle(s) that shortly diverge singly and take up their position on their proper radii. Those in the petal radii give, among others, rise to stamen fascicle traces. As a result no antesepalous stamens are present and the antepetalous ones spread out laterally occupying both sets of radii. Rao recognized five antepetalous groups because he found five petal stamen traces, the staminal components of which undergo a primary splitting into three bundles each. But instead of entering directly the filaments of stamens as in *Sterculiaceae*, they undergo secondary splitting and give rise to 25—35 staminal bundles. The inner staminal whorls are suppressed.

Sparmannia africana

The stamens are placed upon an annular wall which is high and broad in antesepalous regions and low and narrow in petal radii. They may be subdivided into antesepalous groups notwithstanding the fact that in a later stage the groups meet in the petal radii, because no stamens are inserted exactly in these petal radii (fig. 268). The peripheral androecium members are nectariferous staminodes. The form of the anthers, their ontogeny and vascularization are as in *Entelea*. The petals are imbricate.

Developmental phases

The stamens appear on four antesepalous hemispheric protuberances which are situated on the margin of the growing apex. These staminal buttresses increase in size while more stamen primordia develop upon them. During the appearance of the first stamen primordia 1) a wall connecting the staminal buttresses in alternisepalous regions becomes visible, 2) the triangular petal primordia develop between and lower than the staminal buttresses and soon are arrested in further growth, 3) a pistillary wall arises.

The stamen primordia arise on the protuberances centrifugally as well as away from the median line of the protuberances. A median upper stamen primordium forms the starting point. Two stamen primordia arise next, somewhat lower than and on either side of the starting primordium. The third 'row' of stamen primordia may likewise consist of two pairs peripheral to and on either side of the primordia in the second row. However, there may also occur three stamen primordia alternating with those in the second row. The next primordia invariably originate alternating with and below the preceding ones. Towards the periphery of the flower the development of stamen primordia in lateral direction diminishes gradually.

Often both stamen groups belonging to opposed sepals are two-topped, or a single stamen group is two-topped. This character is formed by the presence of two starting stamens, or by the secondary stamen primordia being situated more centrally than the starting stamen. It is not related to the number of pistil cells.

Supply of vascular bundles (fig. 269)

Four sepal median traces are the lowest traces to leave the stele at the flower base. They trifurcate into a sepal median bundle and two basal sepal laterals. Several sepal laterals belonging to adjoining sepals form a cross-arc system by their double or multiple bases. Furthermore, in the same way, they are connected with the stele in petal radii by a sepal commissural marginal bundle. The origin of the petal trace is fasciculate, the traces in most cases coming from the proximal flanks and from near the division point of the sepal commissural marginal traces. Before entering the petals the petal traces trifurcate into branches which produce a fan-like innervation.

The vascular supply towards the stamen groups finds its origin in two sets of traces above each other. A lower set of four traces in petal radii is connected with the proximal parts either of the petal traces or of the sepal commissural marginals or is sometimes separated from the stele directly. These traces divide collaterally into two branches which go to different stamen groups on either side of the petal radii. The middle set consists of four traces which spread towards the stamens quite near their point of attachment to the stele in sepal radii. An additional upper set may be composed of some traces leaving the stele independently near petal radii; they divide into two collateral stamen traces. The fascicle traces ramify into stamen traces, the lower ones rather amply, the upper ones rather poorly. Together the stamen traces form an anastomosing network at their bases.

Other authors

According to Payer the stamens develop on hemispheric protuberances which are opposed to the sepals. They begin near the centre of the flower and proceed with much regularity, covering the whole surface of the protuberance. Eichler mentioned the existence of hardly separated alternipetalous stamen groups, the outer members of which are staminodes. Van Tieghem said that bending outwards from the stele four antesepalous stamen bundles split into radial branches which at the same time split in tangential subbranches. Saunders mentioned a breaking up of a portion of a main bundle in petal radii into antepetalous stamen strands, which fall apart in two half groups. Higher up, a bundle in sepal radii serves an antesepalous group of stamens. The half antepetalous groups are conjoined with the adjacent antesepalous groups on either side into five antesepalous phalanges. Four-celled pistils proved to have their cells antepetalous. Sporne (1948) also recorded four antesepalous groups innervated by four epipetalous and four episepalous trunk bundles.

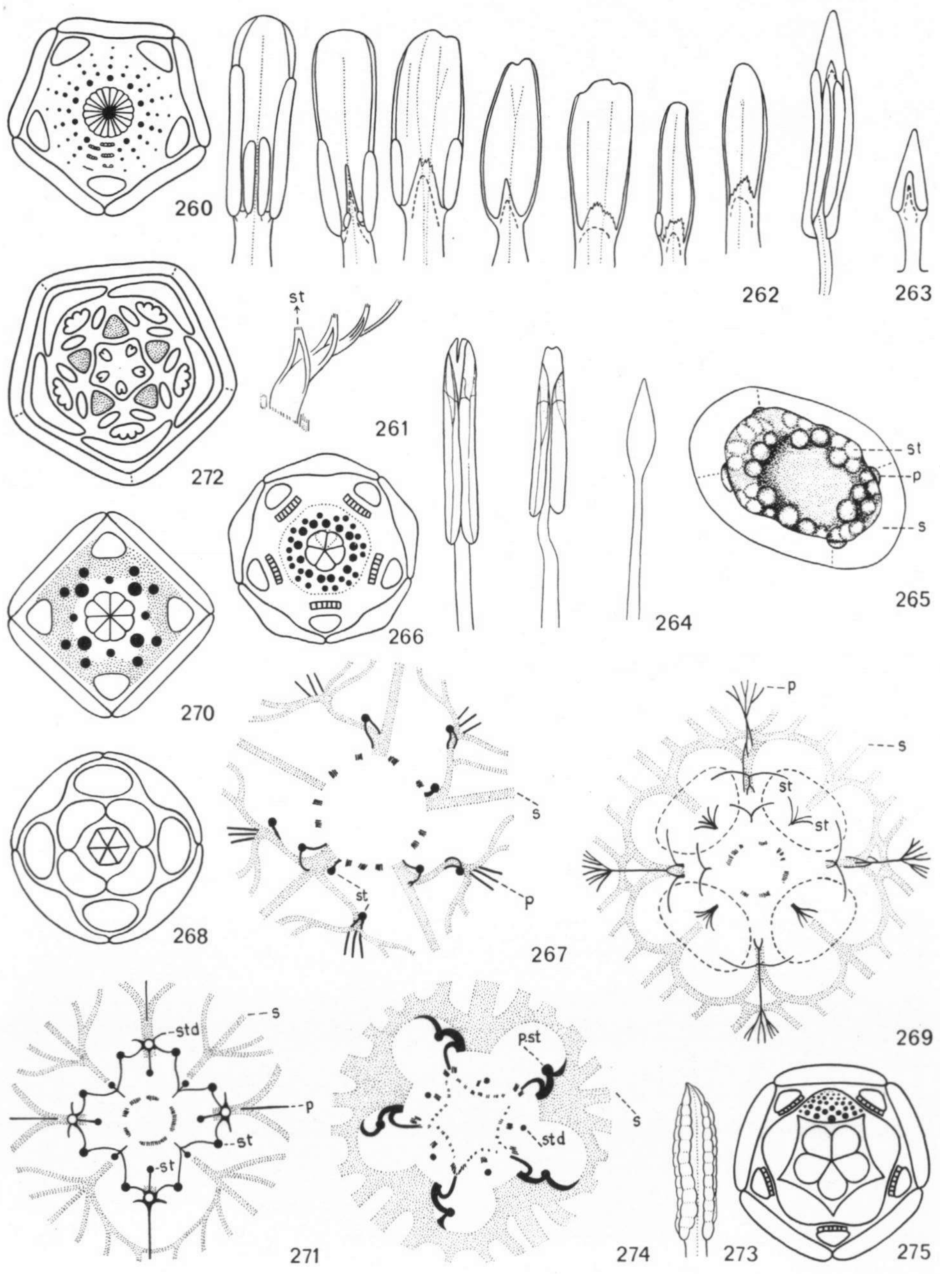
Clappertonia ficifolia

In a full-grown flower two whorls of eight stamens appear to be present, an inner whorl in sepal and petal radii and an outer whorl between these radii. Eight cells of the pistil alternate with the stamens of the inner whorl. From between the stamens towards the sepals and petals the receptacle is crowded with a multitude of staminodes (fig. 270). The filaments of the outer stamens are broad and short, those of the inner stamens, on the other hand, narrow and long, especially in the sepal radii. The anthers are sagittate at the base as well as on the apex and they dehisce latero-introrsely. The anthers of the outer stamens dehisce first. The staminodes are subulate and slightly thickened at their top, reason to consider the possibility that they are glandular.

Developmental phases

The few phases available make sure that, considering the ontogeny, the stamens are not whorled (fig. 270).

A very early stage showed four vaults on the apex in front of the sepal primordia. In another phase the antepetalous primordia are situated slightly more peripheral than the inner antesepalous primordia, but closer to the flower centre than the other stamens. Later stages show hemispheric stamen primordia in antesepalous triplets separated by lower regions which each bear a young petal with one stamen primordium in front. The median central primordium of the triplets is as large as the lateral peripheral ones or may be slightly larger. The triplet members are all advanced in development as compared with the antepetalous stamen primordium in this stage. So the stamen primordia in the future outer whorl are not equidistant, but in antesepalous pairs, and those in the future inner whorl are very unequal in size. The pistil primordium is present as a low wall. Evidently, the staminodes arise much later in ontogeny.



The explanation of these figures can be found at the bottom of the opposite page

Supply of vascular bundles (fig. 271)

Eight main bundles are separated from the vascular cylinder in the flower base, four upper ones of which in sepal radii ramify into sepal nerves. The four bundles in petal radii are concentric near their base. They are the basal bundles for 1) a peripheral portion which either forms a petal trace directly, or may split serially into a petal trace to the inside and a sepal commissural marginal to the outside (if a sepal commissural marginal is absent, the sepal marginal bundles form a cross-arc system), 2) two lateral peripheral portions which ramify very amply into staminode traces on either side of the petal radii without forming anastomoses, 3) two lateral central portions, 4) a central portion which supplies the antepetalous stamen of the inner whorl.

Above the separation of the main bundles the vascular cylinder is reconstituted. Then four traces are attached in sepal radii, which trifurcate into a trace towards the antesepalous stamen of the inner whorl and into two lateral traces. These lateral traces join the central lateral traces given off by the main bundles in petal radii. Together these traces form the double bases of the bundles of the stamens in the outer whorl, which in this way are indirectly connected with the stele. The vascular bundles in the stamens are collateral with in the inner stamens the xylem directed towards the centre of the flower and in the outer stamens directed towards a position intermediate between the centre of the flower and the petal radii. In the anther the bundles broaden and sometimes two branches are visible running downwards.

Cistanthera papaverifera

The androecium consists of three whorls, an outer one of five stamens, an inner one of five alternating staminodes, and a middle one of ten stamens situated in radii between the members of the outer and the inner whorl. Together the androecium members are arranged along a wave line on a conical receptacle.

The insertion of the contorted petals is often oblique and deviating slightly from alternisepalous radii (to the left if the petals overlap with their right margins). Accordingly the androecium members are often not placed exactly in either sepal or petal radii or in between these, although the outer members tend to be alternisepalous in front of the overlapping halves of the petals. Fig. 272 gives a diagram of a flower with almost ideal position of the petals.

Along the distal part of the filament the anthers have two longitudinal thecae which dehisce lateraliter-extrorsely by a slit. The two pollen sacs per theca are sometimes confluent at the base, they are attenuate and become sterile along the tapering apical end of

Apeiba echinata. — Fig. 260. Floral diagram. — Fig. 261. Vascular bundle supply towards orthostichy of stamens. — Fig. 262. Series of stamens from the flower centre towards the periphery.

Apeiba tibourdou. — Fig. 263. Stamen and peripheral staminode.

Apeiba spec. — Fig. 264. Ditto.

Entelea arborescens. — Fig. 265. Development of androecium (65 ×).

Corchorus olitorius.— Fig. 266. Floral diagram, places of stamens represented by dots. Alternating carpellary position occurs in *C. capsularis.* — Fig. 267. Course of vascular bundles in receptacle.

Sparmannia africana. — Fig. 268. Floral diagram with outline of stamen groups. — Fig. 269. Course of vascular bundles. Interrupted lines indicate outlines of stamen groups.

Clappertonia ficifolia. — Fig. 270. Floral diagram, dots representing filiform staminodes. — Fig. 271. Course of vascular bundles in the receptacle.

Cistanthera papaverifera. — Fig. 272. Floral diagram, dotted triangles represent staminodes. — Fig. 273. Partitioned anther. — Fig. 274. Course of vascular bundles in receptacle.

Luhea divaricata. — Fig. 275. Floral diagram.

the connective. By transverse partition walls they are chambered into cells which may or may not be juxtaposed (fig. 273).

The staminodes are lanceolate, at the base triangular in cross-section. It may be noticed that the stamens of the middle whorl are not orientated radially, but diagonally, pressed as they are between the stamens of the outer whorl and the sides of the staminodes.

Supply of vascular bundles

Five broad portions of the vascular cylinder in the flower base spread outwards and fall apart into sepal nerves the laterals of which form a cross-arc system. However, one of the flanks of these main bundles (the same in every flower sector) does not pass on into the sepals, but divides into two parts, the most lateral of which curves upwards into dorsal carpellary regions. The second part together with another trace which is attached to one of the sepal basal laterals, forms a petal stamen trace. This trace proceeds towards alternisepalous radii and splits into three antepetalous stamen traces and a petal trace. (Stated otherwise the petal stamen trace has a double origin.) (Fig. 274).

Above the bases of these main bundles the stele is reconstituted, and on almost the same level traces are separated which form the rest of the median carpellary vascular supply and, alternatingly, staminode and placental bundles.

Other authors

The arrangement of the floral parts given above corresponds to that given by Burret (1927), who on account of this arrangement would like to place *Cistanthera* rather near *Dombeya.* Schumann (1895) on the other hand placed the genus in *Tiliaceae.*

Luhea spp.

The petals are provided with a basal adaxial field of glandular trichomes; they are imbricate.

The stamens and the peripheral filiform staminodes are arranged in five antesepalous groups (fig. 275). Their proximal parts are fused, especially those of the inner stamens and the staminodes. In addition, the adaxial stamens of different adjoining groups are fused laterally in *Luhea divaricata.* The anthers consist of two bisporangiate thecae attached along the distal resupinate part of the filament, which are slightly prolonged inwards remaining contiguous. The apical point of the filament may project from between the thecae abaxially.

Developmental phases

On a rather flat apex subsequent to the sepals, a pentagonal wall arises the development of the alternisepalous parts of which lags behind. Upon the progressively growing antesepalous parts stamen primordia develop in outward and sideward directions away from a starting stamen that is situated adaxially in the sepal radii. Either a given primordium may be followed by a pair of younger stamen primordia or some new primordia may appear alternate to preceding ones. Later the production of primordia in lateral direction decreases gradually. The lateral stamen primordia of adjoining groups may come close together. A similar course of development is described for *Sparmannia.*

Supply of vascular bundles

Five c-shaped parts gradually separate from the stele of the receptacle, the rest of the stele supplying the pistil. The five loops fall apart into 1) a median peripheral sepal trace which trifurcates into a sepal median bundle and two sepal basal laterals forming a cross-arcs system, 2) one or two opposed flank portions destined for one or two petals. These traces bend in the direction of petal radii entirely independent from the sepal basal laterals.

The traces of each stamen group are connected with the basal parts of these sepal and petal traces in various ways or form minor parts of the loops themselves. Anyhow the stamen groups have more than one trace, each with a single or double base. The bundles in the filaments are single collateral bundles with the xylem opposite the flowering axis.

Tiny bundles come from the proximal parts of the petal traces and move in adaxial direction forming the vascular supply for the glandular fields.

Other authors

Eichler distinguished five hardly separated alternipetalous groups of stamens, each group provided with basal fringed scales. The cells of the pistil alternate with these groups.

Mollia speciosa

The androecium consists of ten distinct but contiguous and proximally fused diplostemonous groups of stamens. Within each group the stamens are fused by their proximal parts. The antepetalous groups fall apart into two collateral subgroups below the level on which the stamens become free. Moreover, the stamens in the antepetalous semigroups adhere in twos or sometimes threes before separating.

The anthers are long basifixed structures with two bisporangiate thecae which are feebly sagittate at their upper and lower ends.

The antesepalous groups comprise about eleven introrse stamens in a in cross-section triangular arrangement; the central stamens are longer than the peripheral ones. In the antepetalous groups which are trapezoid in cross-section, about forty stamens are present of which the central and lateral ones are larger and more fused than the peripheral ones. The antepetalous anthers are also introrse, not directed towards the centre of the flower, but towards a subperipheral point in the median line of the groups. So some anthers are present abaxially which are introrse in the usual sense.

The pistil is surrounded by quite a number of long hyaline hairs.

Developmental phases

In a very young phase we find a somewhat elevated pentagonal apex, in the angles of which the petal primordia are present. On the middle of the sides triplets of hemispheric stamen primordia are present in a dichasial configuration. In the centre the pistil appears as two horseshoe-shaped elevations. In this phase the development of the antepetalous groups begins as a still hardly observable tangential ridge whereupon later the first central stamen primordia will become visible. So the first antesepalous stamens arise earlier than the antepetalous ones in accordance with the diplostemonous relation between the stamen groups.

The stamen primordia within each group develop centrifugally, but it is remarkable that the lateral peripheral primordia are earlier than the median peripheral ones, as opposed to the condition in for instance *Sparmannia* (fig. 276). Among the stamens of the antepetalous groups the above sequence in development is still more evident, the direction being oriented towards median peripheral regions of the primordial group. Sometimes the development seems to start from two stamens, one on either side of the radii.

Supply of vascular bundles

Only a few dried flowers have been studied.

Five portions of the vascular cylinder in the base of the flower form the sepal traces in sepal radii.They trifurcate into a sepal median bundle and two sepal basal lateral bundles. The latter seem to be prolonged into a petal stamen trace beyond the point of attachment of the sepal marginal bundle. In other cases the petal stamen traces can be observed to run alongside the sepal basal laterals, mostly along both sepal basal laterals of two sepals and along one of a third sepal, although it sometimes happens that petal stamen traces have a double basis along two basal sepal laterals of adjoining sepals. The petal stamen traces split serially into petal nerves and an antepetalous stamen fascicle trace. One or two antesepalous stamen fascicle traces are connected with one or both flanks of the sepal trace basally. Consequently the points where the antesepalous stamen fascicle traces become free from the perianth innervation are more centrally situated than the corresponding points for the antepetalous stamen fascicle traces, as opposed to the external position of the stamen groups.

The splitting of the stamen fascicle traces during the upward course is chiefly in tangential direction below and more in radial direction higher up. The splitting is fan-like, but sometimes starts with a basal trifurcation or sequence of two dichotomies. The antepetalous stamen fascicle traces ramify into traces that supply the median parts of the antepetalous groups exclusively, the lateral parts of these groups being supplied by ramification of the antesepalous staminal fascicle traces! At the base of all the stamen traces a ring of many anastomoses is formed.

The bundles in the stamens are single and collateral, the xylem in the proximal parts of the filaments of the antesepalous stamens is directed towards the centre of the flower (fig. 277). The xylem in the antepetalous groups, on the contrary, is orientated towards a point medianly and subperipherally in the groups, conformable with some external characters explained above.

Other authors

Eichler said that ten simple stamens are here replaced by ten groups with many stamens. The inner epipetalous ones are deeply two-fid.

Trichospermum javanicum

The petals bear a field of glandular trichomes on their basal adaxial surface which is bordered by a hairy rim except on the basal side. Above the petals the receptacle is narrowed into an androgynophore which diverges again into a fringed rim below the stamens. The androgynophore is pentagonal in cross-section with the angles in sepal radii. The numerous stamens are not dispersed in groups, their form is like those of *Sparmannia* (fig. 278).

Developmental phases

The young sepals develop successively but reach same size very quickly. They enclose a slightly elevated pentagonal apex which becomes differentiated into a central depression and a low and broad peripheral wall. Upon this wall the stamens arise centrifugally after the corners are taken by the petal primordia. Later the wall with its stamen and petal primordia is indented in relation with the margins of the young sepals. However, in full-grown flowers no effect of this indentation is left.

Supply of vascular bundles (fig. 279)

Sepal median and adjoint sepal lateral bundles are connected with the receptacular stele by means of a trifurcating sepal trace in sepal radii. On the other hand marginal sepal nerves of adjoining sepals are attached to the stele through a commissural trace in petal radii. In addition some middle sepal traces have a double origin by which they are connected with both main traces, thus giving rise to a system of cross-arcs.

The basal flanks of a main bundle in petal radii each form a stamen fascicle trace which moves upwards towards the androecium, after giving off one petal trace or two uniting petal traces. The fascicle traces produce a tree-shaped ramification system which ends in stamen traces. Sometimes anastomoses occur between two ramification systems. In the androgynophore the stamen fascicle traces are either about equidistant collateral to concentric bundles with the xylem directed towards the flowering axis, or the traces lie more in antepetalous pairs with the xylem slightly opposed. In the stamens the bundles remain single and are resupinate.

Schoutenia spp.

The sepals are covered with glandular trichomes at the inside base.

Non-imbricate petals are present in the material of *Schoutenia ovata*, absent in that of *Schoutenia glomerata*. They are attached by means of a very narrow base.

The androecium is formed by five inner antesepalous stamens alternate with the bulging cells of the pistil, and five double more or less radial alternisepalous rows of three stamens each. Moreover, the alternisepalous groups often have an additional unpaired stamen which lies peripherally and in alternisepalous radii. If so, it may be remarked that the stamens follow a wave-line (fig. 280). Frequently the bends of the wave-line are slightly deviating from the proper radii.

The anthers consist of two long bisporangiate thecae along the slightly widened distal filament part; they are extrorse in *Schoutenia glomerata* and feebly introrse in *Schoutenia ovata*. The anthers in the two rows are not juxtaposed but imbricate. All anthers are placed parallel with the surface of the sepals. This feature is especially evident in floral buds. In *Schoutenia ovata* the petals are inserted very close to the alternisepalous stamens.

Developmental phases

The development of the stamen primordia is strictly centrifugal. First the primordia of the five central stamens arise on the middle of the sides of the pentagonal apex which is enclosed by the young sepals. After that the apex changes into an apically flattened hemisphere, the slopes of which bulge forward chiefly in the alternisepalous regions. On these staminal buttresses the primordia appear in centrifugal direction. Together with the first stamen primordia the first signs of the pistil and of the petals (in *Schoutenia ovata*) become evident.

Supply of vascular bundles in Schoutenia glomerata (fig. 281)

Sepal traces separate from the stele in sepal radii and trifurcate to form each a sepal median bundle and two sepal basal lateral bundles, the latter of which split into the sepal laterals.

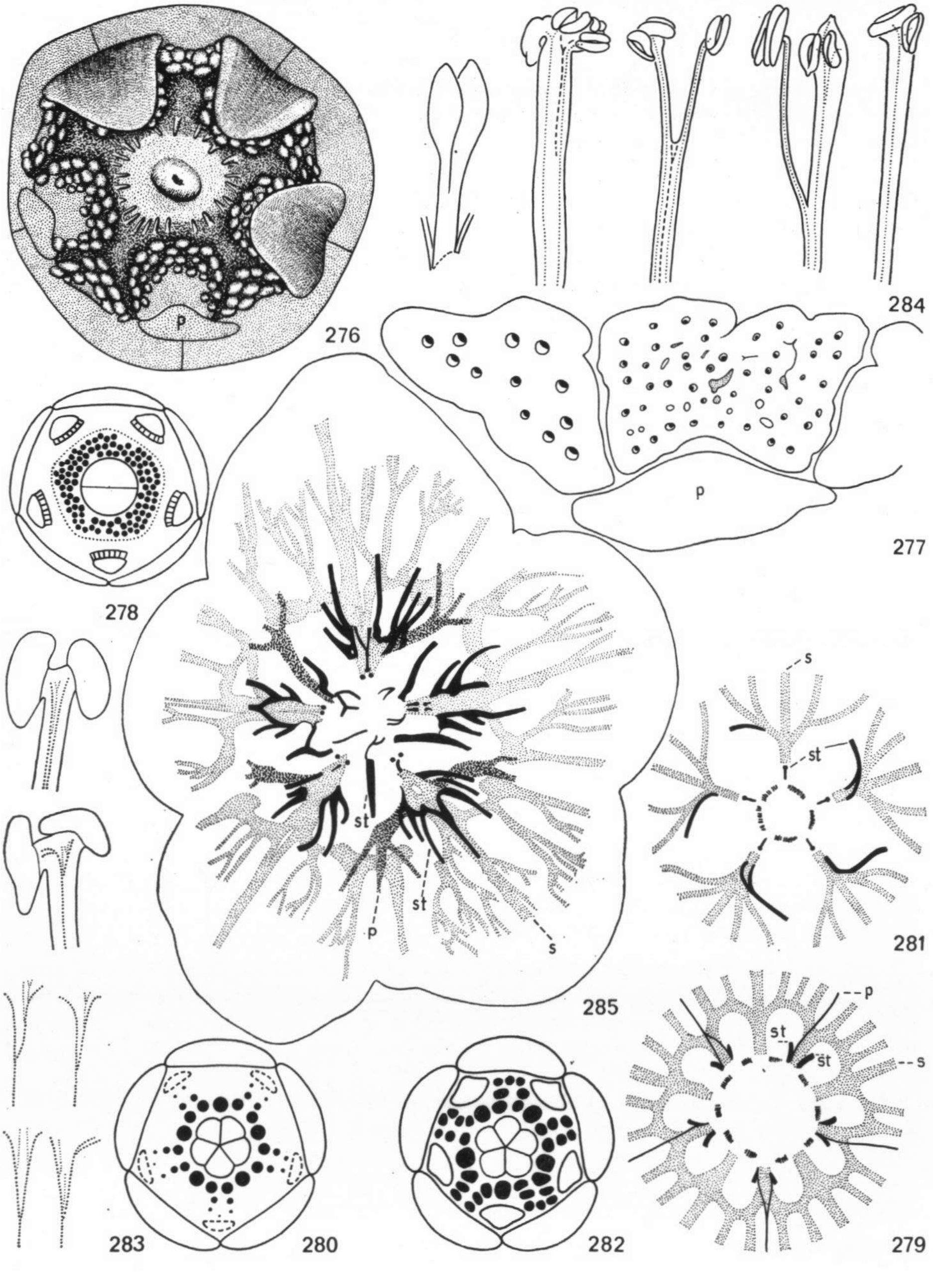
The stamen fascicle traces ramifying into the alternisepalous stamen groups have a course bending between petal and sepal radii, because they are connected with the basal part of the sepal traces. This connection may take place with one flank of the sepal trace or with both flanks by means of a double origin. Sometimes oblique stamen traces come from the sepal basal laterals directly. Above the level of the departure of the sepal traces the vascular cylinder is reconstituted. It is to this stele that the traces are attached which belong to the five inner antesepalous stamens. If the groups of stamens are placed for instance to the left of the petal radii, the oblique stamen (fascicle) traces reach sidewards less far, and the traces for the innermost stamens leave the stele also to the left of the sepal radii.

The bundles run to the apex of the stamens unbranched. They are collateral with the xylem of the central stamens directed towards the flower centre, that of the alternisepalous stamens moreover towards the petal radii, in correspondence with the non-tangential position of the anthers described above.

Tilia spp.

The sepals are covered with glandular trichomes at the inside base. The petals are imbricate, sometimes even quinquncial.

As the insertion places of calyx and pistil are pentagonal, with the angles in petal and



The explanation of these figures can be found at the bottom of the opposite page

sepal radii respectively, and as the corners between the sepals are taken by separate rhomboid insertion places of the petals, it follows that the places that are left for the stamens are arranged in a wave-line (fig. 282). Only one stamen (*Tilia platyphyllos*) or staminode (*Tilia tomentosa*) is situated in the petal radii, whereas the outer bends of the wave-line are formed by two radial rows of each three to four stamens (*Tilia platyphyllos*) or by an adaxially open sometimes asymmetrical u-formation of some more stamens (*Tilia tomentosa*).

The bisporangiate thecae are either sessile and placed lateral-abaxially along the more or less broadened end of the filament, or they are more or less stalked forming a fork which terminates the filament. Intermediate formations frequently occur, in which the connectives are more or less bilobed. In the antesepalous regions the anthers in buds are not orientated tangentially, but more parallel with the surface of the petals.

In both species — and in others too — the place in front of the petal may be taken by structures intermediate between foliar staminodes and stamens. In that case the normal single members are mostly replaced by some partly fused intermediate structures (fig. 284).

Developmental phases

The sepals as well as the petals arise successively.

On the elevated apex bordered by the young sepals and the petal primordia the stamen primordia appear strictly centrifugally, a stellate wall preceding this development hardly being evident.

The carpels become visible after the first stamen primordia.

When the anthers have developed from a hemispheric protuberance into a thick cuneate form, the sporangiate tissue becomes visible externally as light-coloured patches submarginally (introrse) on either side of the apex. In this phase the primordia are situated along a wave-line meeting laterally, so that the young thecae of the stamens of the radial rows face one another. It is only later that the thecae become slightly extrorse and still much later in ontogeny they may become stalked.

Supply of vascular bundles (fig. 285)

The nectary fields are supplied by small bundles coming from the sepal nerves. Trifurcating sepal traces are formed by the peripheral part of the rays of a stellate stele in the flower base. The sepal basal lateral bundles sometimes give rise to cross-arcs.

The basal flanks of the sepal traces do not bend outwards, but extend upwards and together may form a more or less complete concentric bundle. These bundles fall apart immediately into 1) median central parts towards the pistil wall, 2) one or two opposed flank parts forming the petal traces, if present in the flower sector, 3) flank parts towards the stamens, joined or not by median peripheral parts, (fig. 285). Mostly, four of the five petal traces are attached to either side of two sepal traces — probably of the lower sepals — and one is attached to the flank of a third sepal trace — probably of the middle sepal. The possibility of one petal trace being attached to one flank of each sepal is never found

Mollia speciosa. — Fig. 276. Developmental phase of androecium (40 ×). — Fig. 277. Basal c.s. of petal and antepetalous and antesepalous stamen groups (25 ×).

Trichospermum javanicum. — Fig. 278. Floral diagram, petals with glandular surface. — Fig. 279. Course of vascular bundles.

Schoutenia glomerata. — Fig. 280. Floral diagram, petals indicated by interrupted lines present in *S. ovata*.— Fig. 281. Course of vascular bundles in receptacle.

Tilia platyphyllos. — Fig. 282. Floral diagram. — Fig. 283. Precise innervation in forked stamens. — Fig. 284. Structures substituting the antepetalous foliar staminodes. — Fig. 285. Course of vascular bundles in receptacle, not diagrammatically.

realized. The petal traces show an oblique course between sepal and petal radii which is free or running partly along the sepal basal laterals. Sometimes they are connected with the stele directly in about alternisepalous radii.

The traces of the central antepetalous stamens or staminodes are connected either with the vascular cylinder directly, or, occasionally, with a petal trace if such a petal trace has an independent origin in a petal radius. In the filaments of the central and the most peripheral antesepalous stamens — if present — the collateral bundles have their xylem directed towards the centre of the flower, whereas in the other antesepalous stamens the xylem is moreover directed towards the sepal radii. In the forked stamens the vascular bundles are forked too, but always some tiny bundles come from the inside of the bending branches and continue an upward course or bend also towards the thecae (fig. 283).

The staminodes have a median bundle and a few minor parallel nerves proximally. The median bundles may have some side-nerves distally.

Other authors

Payer described the centrifugal development of the staminal primordia along the margins of five antepetalous protuberances like peltate scales. The first members may be staminodial. Later alternipetalous groups of stamens result from the union of adjoining halves of antepetalous phalanges. According to van Tieghem five staminal traces leave the stele in petal radii and divide radially and tangentially. Eichler conformed his views to those of Payer and recognized five antepetalous groups and five antesepalous pistil cells. According to Saunders the antepetalous groups are composed of a single antepetalous member in the centre flanked by half the antesepalous group on each side, because the separate traces to these components respectively come from the stele directly and from the base of the sepal trace dividing into halves.

4) GREWIEAE

Grewia tenax (Forsk.) Fiori	S5-P5n-St∞-G(2)
G. orientalis L.	ditto
G. laevigata Vahl	ditto
G. hirsuta Vahl	ditto
G. oligandra Pierre	ditto
Microcos cinnamomifolia Burr.	S5-P5n-St5 × 1/7s-G(1—3)
M. florida Burr.	ditto
M. stylocarpa Burr.	ditto
M. argentata Burr.	ditto
M. ledermannii Burr.	ditto
M. schlechteri Burr.	ditto
M. pentandra Burr.	ditto
Colona auriculata (Desf.) Craib	S5-P5n-St5 × 3p + 5 × 7/9s-G(5)p
C. scabra (Sm.) Burr.	S5-P5n-St5 × 5/8p + 5 × 7/9s-G(5)p
Erinocarpus nimmonii J. Grah.	S5-P5-St5 × ∞p-G(3)
Triumfetta appendiculata F. Muell.	S5-P5-St∞-G(2)
T. suffruticosa Bl.	ditto
T. althaeoides Lam.	ditto
T. annua L.	S5-P5-St0/5p-St5s-G(2)
T. bartramia L.	ditto
T. neglecta Wight & Arn.	S5-P5-St5s-G(2)
Heliocarpus americanus L.	S5-P5-A20-G(2)
Althoffia pleiostigma Warb. *ex.* K. Sch. & Laut.	S5-P5-A∞-G(3—5p)

Grewia spp.

The flowers possess an androgynophore, the cross-section of which is pentagonal with its angles in sepal radii. It is separated from the androecium by a small divergent rim or a hairy zone which are also pentagonal with the angles in sepal radii. The androecium part of the flower tapers, and its cross-section at the base pentagonal with the angles in sepal radii becomes about circular near the pistil.

A thick hairy rim crosses over the adaxial surface of the petals and descends along either margin towards the base. The proximal petal part bearing the rim is thicker than the distal part, especially so because a dense field of glandular trichomes covers the adaxial side. There are species, for instance *Grewia laevigata*, in which the distal part of the petals is much shorter than the proximal part, so that this part looks like a short subapical extension of the lamina.

About 15—60 stamens are inserted around the pistil in a ring consisting of some indistinct whorls. They are bithecate, tetrasporangiate, and pseudopeltate. Their real nature is most distinctly revealed in *Grewia orientalis* where the thecae lie introrsily along the distal resupinate part of the filament and are moreover somewhat sagittate at the base. The most distal short point of the bending filament projects freely (fig. 289). In the other species this resupination is very strongly developed, so that the pollen sacs are almost circular. In that case the point of the filament cannot be detected so readily.

Developmental phases in Grewia hirsuta and orientalis

The petal primordia take position in small triangular corner regions of the pentagonal apex which is enclosed by the young sepals. The proximal rimmed parts of the petals develop only late in ontogeny.

A low peripheral wall arises on the apex, upon which the stamens will develop beginning with five central ones in sepal radii and proceeding centrifugally. At first radial antepetalous strips of the wall remain lower than antesepalous regions, but later stamen primordia start to grow there too, be it more peripherally. The second row comprises ten primordia below and between the first five. They may be arranged equidistantly, in which case all the possible next rows are alternating, the third row being the first to produce stamens in petal radii. However, primordia in the second row may also be arranged in alternisepalous pairs. In this case the third and fourth row alternate with the two first rows as if these formed one unit, and the fourth row is the first to give primordia in petal radii. It should be stressed that this arrangement, given as a scheme, is really rather irregular owing to the inequality of the sectors of the flower in width and in height. The more regularly alternating arrangements occur in the productive androecia (figs. 286—288).

It is a striking feature in *Grewia hirsuta* that the most peripheral parts of the androecium wall develop unicellular hairs not only in the place of stamen primordia but also in the right time sequence. These hairs may occur in antesepalous parts, but also in antepetalous parts when the number of stamens is very small. If occurring in antepetalous regions they may link up with the hairs which in male flowers replace the pistil, separating the stamens into antesepalous groups.

Supply of vascular bundles

The petal innervation belongs to the distal part of the petal, the proximal thick margins being without any vascular tissue, also where they cross over the adaxial surface. By a basal trifurcation the petal trace branches into a median and some lateral bundles from which tiny bundles are separated towards the glandular field.

Five main bundles leave the receptacular stele in sepal radii. Their peripheral parts form the sepal traces which trifurcate outwards into a sepal median trace and two sepal basal lateral traces. The latter give off sepal lateral bundles part of which form cross-arcs through a double origin, the other trace being attached to the adjoining basal sepal lateral trace. The floral stele is reconstituted above sepal level and partly supplies the pistil.

Around this reconstituted stele in the androgynophore ten usually almost concentric bundles — they may be open adaxially — are situated in obdiplostemonous arrangement. They have a double or a multiple attachment by means of collateral strands to the proximal flanks of the sepal traces or to the cross-arcs. The strands of the antepetalous bundles — together with the petal traces — may run from the cross-arcs along the basal sepal laterals of adjoining sepals in the direction of the sepal traces (figs. 291—292).

Below the top of the androgynophore the adaxial parts of these concentric bundles are separated and pass on upwards to give a part of the vascular supply of the pistil wall. The abaxial parts form stamen fascicle traces which bend outwards dividing into stamen traces (fig. 290). This splitting is fan-like but often starts with a basal trifurcation, the single median branch being either the trace of a central stamen in sepal radii or of an outer antepetalous stamen, the lateral branches ramifying further. Whereas the stamen fascicle traces in petal radii supply more peripheral stamens, those in sepal radii supply more central stamens, the result being an anatomical obdiplostemony.

The stamen traces are collateral, their xylem being orientated towards the centre of the flower. The bundles are resupinate, even when the external resupination is not very evident.

The only flower of *Grewia oligandra* that could be studied proved to have only five stamen fascicle traces, of which one in a petal radius and four in sepal radii.

Microcos spp.

1. **Microcos ledermannii.** The sepals are navicular and cucullate, the petals ovate and bilobed. The latter are, in addition, provided with a basal adaxial field of glandular trichomes surrounded by hairs except at the base.

Above petal level the receptacle is elongated into an androgynophore which is pentagonal in cross-section with the angles in sepal radii. The androgynophore broadens upwards and passes into a free border above which upon an annular elevation the stamens are placed. However, regions in petal radii, covered with hairs, separate the stamens into five antesepalous groups. These groups consist of one median central stamen and two outer lateral ones and now and then a fourth peripheral stamen. The outer stamens of all groups are mostly not placed equidistantly, they rather approach one another in antesepalous regions (fig. 293).

Supply of vascular bundles (fig. 294)

In the base of the flower five sepal traces leave the stele and trifurcate each into a sepal median and two sepal basal laterals, the latter of which usually form a cross-arc system.

The attachment of the petal traces is very diverse. It may be directly to the stele, or to the top of the cross-arcs, or to the sepal basal laterals through an oblique course along these bundles. Sometimes a petal trace directly attached to the stele hardly misses the top of a cross-arc, with the result that some of the tissue of the traces makes a short cut towards the cross-arc. In other cases it seems that the cross-arcs are formed by double bases of the petal traces rather than by double bases of sepal laterals. The petal traces split into the petal bundles and tiny bundles below the glandular field.

The stamen traces are independently connected with the reconstituted stele in the upper half of the androgynophore, those of the central stamens on a higher level than those of the lateral stamens. It appears that the traces of two lateral stamens of adjoining antesepalous groups often join the stele close to each other. This is a reason to speak of alternisepalous pairs of outer stamens instead of the external antesepalous pairs. In that case the staminal arrangement would be obdiplostemonous. Sometimes a trace to a lateral stamen has a side-trace towards a fourth stamen.

2) **Microcos argentata** and **schlechteri** also have five groups of three (sometimes four) antesepalous stamens. They resemble *Microcos ledermannii* also in the direct attachment of the stamen traces to the stele, the lateral stamen traces being spaced irregularly or placed more in antesepalous or antepetalous pairs.

3) **Microcos spec.** The twenty stamen traces are placed on the stele in a wave line about equidistantly, the antesepalous ones on the higher level.

4) In **Microcos cinnamomifolia, florida,** and **stylocarpa** mostly five stamen fascicle traces are attached to the stele independently on a low level in the flower base (*M. florida*) or half way up the androgynophore (*M. cinnamomifolia*) or attached to the sepal traces. They split irregularly into a small number of branches, up to a total of 35 stamen traces in *M. cinnamomifolia.*

5) **Microcos pentandra** (figs. 295—296). The trifurcating sepal traces do not form cross-arcs. The petal traces are attached to the sepal basal laterals by means of an oblique course. Five traces of the five antesepalous stamens join the reconstituted stele high up in the androgynophore.

As the number of flowers per species that could be studied is low, it seems wise to assume that for each species the variability will be greater and will correspond to the data given for other species which have about the same total of stamens.

Colona spp.

The sepals are ovate and non-cucullate, the petals are spathulate and provided with a basal adaxial field of glandular trichomes.

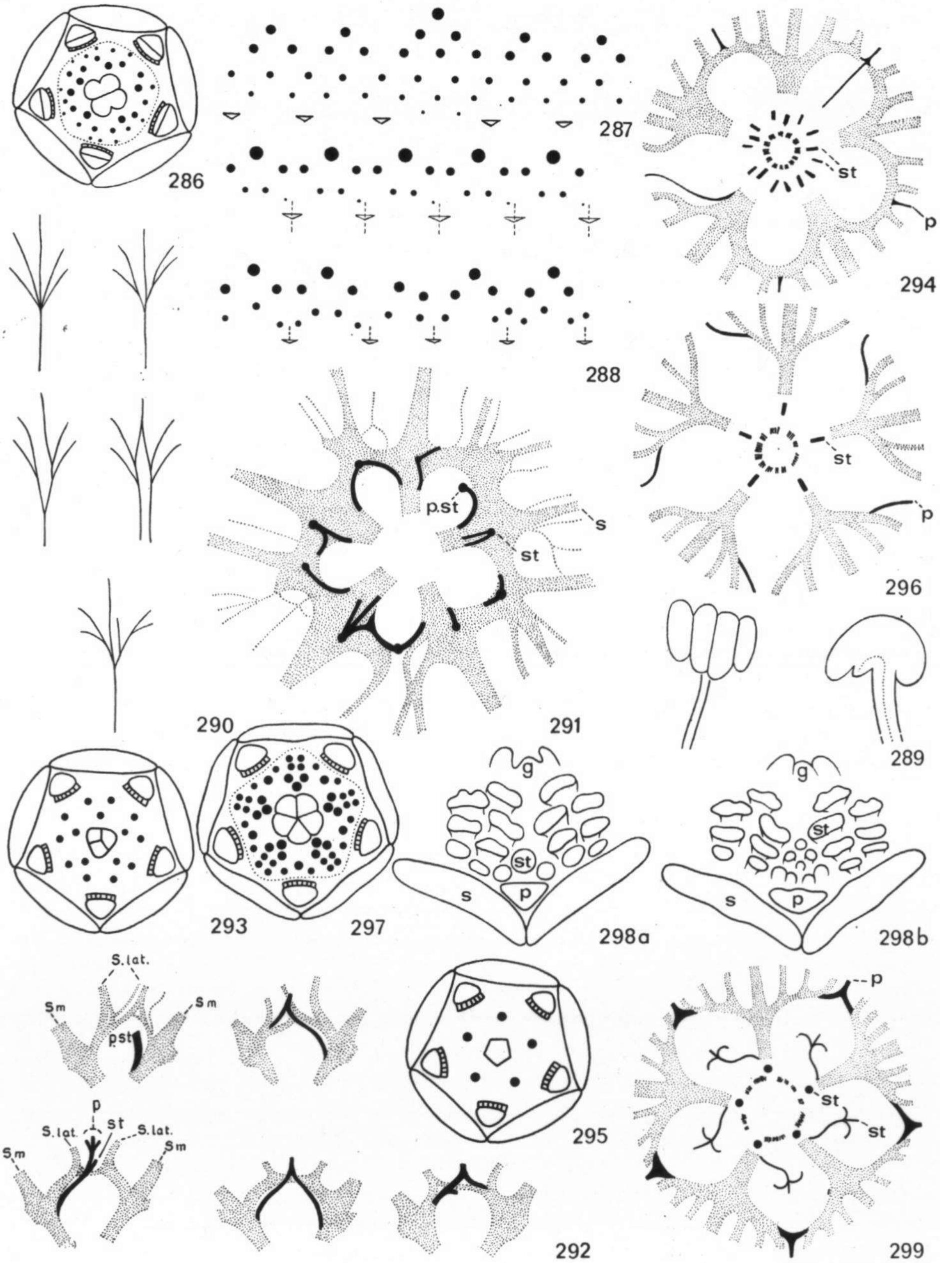
The receptacle and the androgynophore are both pentagonal in cross-section with the angles in petal and sepal radii respectively. The androgynophore terminates into a collar-like rim which is formed by five larger divergent and five smaller erect parts. The former are the antesepalous and lower, the latter the higher and antepetalous segments of the rim. As the stamens are inserted on a tapering receptacle immediately above the collar the basal antesepalous stamens are situated lower and more peripheral than the antepetalous stamens. However, higher up, the cross-section of the receptacle changes into a stellate form with antepetalous rays, so that on that level the antepetalous stamens are more to the outside than the antesepalous ones. The antepetalous stamens all lie on about the same level as the middle antesepalous stamens (fig. 297). The upper parts of the androecium between the upper antesepalous stamens are without antepetalous stamens. The stellate form changes gradually into the pentagonal form of the cross-section of the pistil base.

In *Colona auriculata* an upper median and two lower lateral antepetalous stamens are present, but in *C. scabra* some more antepetalous stamens are present, or the petal radii are unoccupied. The antesepalous groups consist of two radial rows of three or four juxtaposed or imbricate stamens each and of a single first stamen situated above and between these rows. This apical antesepalous stamen fits in between two bulging pistil cells.

Whereas in *Colona auriculata* the filaments of the antepetalous stamens are thinner and wither sooner than those in the antesepalous groups, in *C. scabra* such a difference is not evident. All anthers are bilocular and tetrasporangiate, introrse and resupinate. The thecae are shortly free at the base but remain in touch.

Developmental phases

The sepals, petals, and also the first antesepalous stamens do not arise simultaneously. Within the young calyx the hemispheric apex is flattened and on its margin five



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antesepalous staminal buttresses bulge forward which are kept separate by broad radial grooves in the alternisepalous radii. At the same time the petal primordia become visible under the margin.

A median radial furrow originates on the staminal buttresses, formed by the stamen primordia developing along it in centrifugal direction. Initially the central stamen primordium is on top of one of the two rows, but later, when the pistil wall becomes evident, it comes to lie more between the rows. Sometimes its further development is retarded.

A considerable lapse of time exists between the development of antesepalous and antepetalous stamens, the protuberances of the latter only occurring when the antesepalous stamens already show the formation of pollen sacs (fig. 298*a*). The antepetalous stamen primordia also develop centrifugally, in *Colona auriculata* three to five of them in a v-formation which is open to the outside. In this stage the antepetalous stamen primordia are situated on the same level as the basal antesepalous stamens. Evidently a progressive growth of the antesepalous sectors of the androecium takes place late during ontogeny. In *Colona scabra* the first three antepetalous stamen primordia are followed outwards by three more primordia and finally by some sublateral ones. The marginal primordia of the groups develop strongly. The median primordia may reduce or may not arise at all, even the starting primordium of the group may be absent.

Supply of vascular bundles (fig. 299)

Five sepal traces leave the vascular cylinder at the flower base in sepal radii and trifurcate into a sepal median and two sepal basal lateral traces, the latter of which produce the sepal laterals and a cross-arc system. The petal traces join the sepal basal laterals of adjoining sepals by means of a double origin. It may well be that the system of cross-arcs is chiefly formed by the attachment of the petal traces. In the very base of the petal the petal trace becomes concentric and the adaxial parts will split upwards abundantly into tiny unlignified bundles under the glandular surface.

With a basal flank of the sepal traces a stamen fascicle trace is connected which ramifies into stamen traces under antepetalous regions of the androecium. As a consequence it shows an oblique course running through the androgynophore. The splitting takes place in all directions by means of a sequence of dichotomies that may be variably comprimated into trifurcations. A basal trifurcation which is especially evident produces 1) a median branch serving the top antepetalous stamen or, by division, the whole antepetalous group, 2) two lateral branches which, by division, supply the halves of the antesepalous groups of stamens and the lateral antepetalous stamens in case these are not supplied by the median branch. However, the top antesepalous stamen is innervated by an independent antesepalous trace connected with the stele distally in the androgynophore. One of the upper stamens of the same row in every flower sector may receive a trace branching from the trace towards the first antesepalous stamen.

Some adaxial components of the ramifications towards the central stamens proceed upwards to the pistil wall.

Grewia hirsuta. — Fig. 286. Floral diagram, dots represent stamens. — Fig. 287. (*G. orientalis*). — Fig. 288. Arrangement of stamens. — Fig. 289. Resupinate stamens, abaxial view on the left, l.s. on the right. — Fig. 290. Schematic antesepalous stamen fascicle traces. — Fig. 291. Course of vascular bundles in receptacle. — Fig. 292. Attachment of petal stamen fascicle traces at sepal supply, lower three of *G. orientalis.*

Microcos ledermanni. — Fig. 293. Floral diagram. — Fig. 294. Scheme of vascular bundle course in receptacle.

Microcos pentandra. — Fig. 295. Floral diagram. — Fig. 296. Vascular bundle course in receptacle.

Colona auriculata. — Fig. 297. Floral diagram. — Fig. 298a. Sketch of stamen position in a very young flower. — Fig. 298b. Same in *C. scabra.* — Fig. 299. Vascular bundle course in receptacle.

Unconnected radial bundles are often present in the big antesepalous lobes of the collar-like rim peripheral to the stamens.

The bundles in the filaments are collateral, their xylem directed towards the centre of the flower.

Erinocarpus nimmonii

The sepals are broadly linear and cucullate, the cap is markedly mucronate. The petals are obovate and attenuate, the marginal basal parts covered with hairs which partly cross over the inner surface epibasally, reminding of the petals in *Grewia* which bear glandular fields. However, here neither sepals nor petals bear glandular tissue.

The androgynophore becomes broader in upward direction and, without a rim being formed, gradually passes into an almost flat receptacle packed with stamens and bearing the pistil in its centre. As the receptacle is broadest in its antesepalous parts, most stamens are placed antesepalously. In the flower bud the antepetalous stamens are pressed down by the sepal margins. Reniform fields of glandular trichomes cover the proximal halves of the androgynophore axillary to the petals.

The stamens consist of two introrse bisporangiate thecae fused along their long sides and attached to the filament dorsally in the middle. In the upper half of the anther the thecae are fused more intimately than in the lower half.

Supply of vascular bundles (fig. 301)

Five sepal traces leave the receptacular stele in sepal radii and trifurcate into a sepal median trace and two sepal basal lateral traces, the latter of which first give off sepal lateral traces and then form cross-arcs with the adjoining sepal basal lateral traces. The top of the cross-arc may point inwards, as if a connection of the sepal laterals with the stele in petal radii failed to develop. As a matter of fact these connections are often present in the form of collaterally dividing main bundles (sepal commissural marginal traces) attached to the stele in the petal radii.

Alternating with the sepal traces petal stamen traces are connected with the stele independently or they join by a double base the proximal flanks of the main bundles in petal radii. Not only the stamen fascicle traces are linked up with the proximal flanks of these petal stamen traces but also main gland traces (fig. 300). The most proximal is the stamen fascicle trace, attached by means of a double base; or there may sometimes be two stamen fascicle traces side by side. The two main gland traces are connected more outwards, each by a single or double base, or there may sometimes be two traces side by side. The point of separation of the main gland traces may be so much peripheral that it looks either as if they are attached to the petal lateral traces or as if the petal lateral traces are attached to the main gland traces. In their upward course into the cortex of the androgynophore the main gland traces at first almost pass on beyond the glands, but in the end they curve outwards and downwards. Meanwhile they fork collaterally and then also serially several times and form branches which progressively split up into small bundles anastomosing under the glandular tissue. During their upward and then outward bending course the stamen fascicle traces bifurcate more or less regularly several times to terminate into quite a number of radial arrangements which resemble what I called in other species chains of stamen traces, since each trace is attached to a more central one in the same radius (fig. 300). Some of the stamen traces are anastomosing and the traces of the most central stamens may link up with the branches of the stamen fascicle traces centrally to the radial arrangements. Either adaxial portions of the stamen fascicle traces or their primary branches form part of the peripheral pistil innervation.

In the stamen the simple vascular bundle for some distance bends away from the filament in the upper half of the anther.

Triumfetta spp.

The apex of the sepals is hooded inwards and prolonged into a long point outwards. However, in *Triumfetta appendiculata*, the apex is prolonged into a cuneate more or less biparted appendage.

The proximal part of the short cylindrical androgynophore bears five antepetalous fields of glandular trichomes, which are sometimes bilobed and, moreover, in *Triumfetta appendiculata* pass into each other in the sepal radii.

The androecium is separated from the androgynophore by a collar-like rim which in species with a small number of stamens is restricted to five antesepalous lobules or altogether absent.

The anthers contain four pollen sacs in two longitudinally fused thecae and are dorsifixed in their middle parts. The thecae are fused more intimately in the upper half of the anther than in the lower half, where they may be slightly sagittate.

The stamens are inserted in one to five whorls or, in *Triumfetta appendiculata*, are very numerous (up to 90) and indistinctly arranged. *Triumfetta neglecta* has only five stamens in sepal radii. *T. annua* and *bartramia* have ten stamens in an obdiplostemonous arrangement, although often some of the antepetalous stamens are missing. The obdiplostemony can be corroborated by the fact that 1) the larger stamens are the antesepalous ones, the anthers of which are enclosed in the hooded apices of the sepals when the flowers are in bud, 2) in the open flower the antesepalous anthers lie more inwards, 3) in *Triumfetta bartramia* the antepetalous stamens are inserted lower than the antesepalous ones (in *Triumfetta annua* they are placed on about the same level), 4) the antesepalous stamens develop first. *Triumfetta althaeoides* has a third whorl of ten stamens which alternate with the inner stamens taken as one whorl; sometimes they are placed in antepetalous pairs. In a fourth whorl moreover five or fewer stamens may be present. In *Triumfetta suffruticosa* a fourth and a fifth alternating whorl of ten stamens are present. However, the antesepalous members of the fourth whorl and the complete fifth whorl may be lacking. As in *Triumfetta althaeoides* the stamens of the last whorl may be arranged in antepetalous pairs. For convenience one may imagine that a sequence of alternating whorls of ten stamens forms the androecium, the first whorl of which forms mostly an obdiplostemonous arrangement (fig. 302).

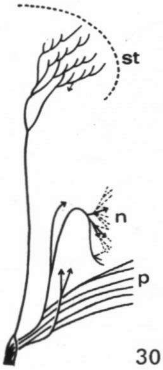
Developmental phases

The members of each whorl never arise exactly simultaneously.

The petals develop before the first stamens, but remain small till late in ontogeny.

The pentagonal apex enclosed by the young sepals becomes elevated and on the middle of its sides in sepal radii the first stamen primordia appear. These grow into rather large hemispheric protuberances which almost meet laterally. Then the apex resumes growth in every direction giving place to five new stamen primordia to arise on its angles on the same level as the first stamens (*Triumfetta annua*) or slightly lower (*Triumfetta bartramia* and *suffruticosa*). Meanwhile a subapical ring is formed representing the wall of the pistil. Together with the further growth of the apex new alternating whorls of ten stamens become evident. In *Triumfetta suffruticosa* and *althaeoides* the growth of the first antepetalous stamens is arrested for some time, but ultimately there is no difference in size among the stamens.

A few young stages of *Triumfetta appendiculata* were observed with about sixty stamen primordia already present, the innermost ones of which still without thecae. In these stages a first whorl of ten equally spaced stamens in sepal and petal radii occurs, not two succeeding whorls of five stamens. The next whorls are alternate.



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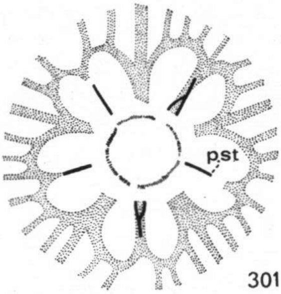

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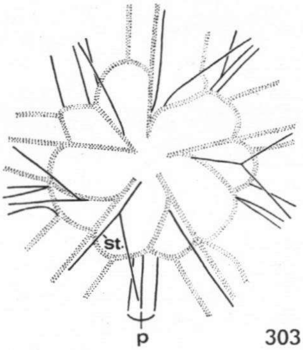

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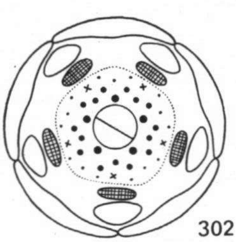

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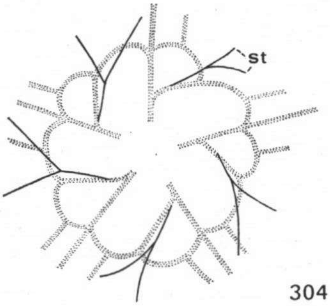

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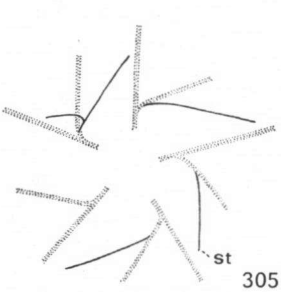

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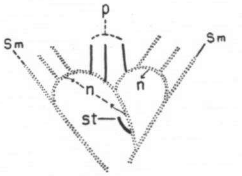

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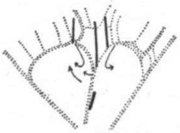

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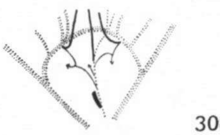

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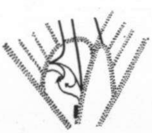

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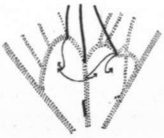

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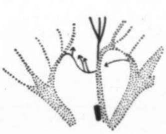

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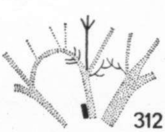

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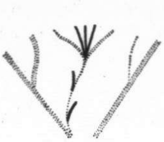

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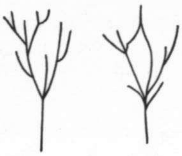

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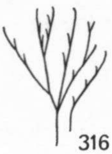


316

The explanation of these figures can be found at the bottom of the opposite page

Supply of vascular bundles

The median bundles of the sepals pursue their course into the apical prolongation, whereas the lateral bundles bend inwards and meet in the hood. In *Triumfetta appendiculata* the sepal bundles double into inner portions which deviate towards the cap, and outer portions which spread into the appendage, the median ones dividing palmately. The sepal bundles are connected with the stele by five traces more or less in sepal radii. A proximal splitting of these bundles produces a sepal median trace and, on the same side of every bundle, a sepal commissural marginal trace, the latter of which deviates from a radial course to reach its proper radius. Sometimes two sepal commissural marginals are attached to one sepal median trace whereas another sepal median trace remains single. Both a sepal median trace and a sepal commissural marginal trace give off sepal lateral bundles, the former starting with a trifurcation, the latter with a collateral division. Some middle sepal lateral bundles may produce cross-arcs by their double bases, one part of which is connected with the sepal median system, the other with the sepal commissural marginal system (fig. 304). However, in *Triumfetta annua* and frequently in *Triumfetta althaeoides* cross-arcs are absent.

The attachment of three petal traces to the cross-arcs is very variable (figs. 306—314), sometimes a petal median trace prolongs the sepal commissural marginal and then trifurcates into three subtraces. In *Triumfetta suffruticosa* the petal trace is attached to the sepal commissural marginal trace proximally to the collateral division.

In species with ten stamens, some outer ones of which may be missing, the innervation of the floral parts is extremely variable.

Triumfetta appendiculata may have flowers (fig. 313) in which the vascular supplies of the different sepals are separate. Moreover the supply to the petals is not in contact with the sepal innervation except for the attachment of the trace at the base of the sepal trace. Here the stamen fascicle traces are connected with the petal trace basally and two succeeding pairs of gland traces come from the petal trace more peripherally. However, in other flowers of the same species, things are complicated by the occurrence of semi-cross-arcs formed by traces in petal radii common to some sepal laterals of one or two sepals and the petal trace (figs. 311—312).

The innervation of the gland is often constituted by three traces, the median one of which is attached to the sepal commissural marginal trace, the lateral ones to the sepal basal laterals of adjoining sepals. Often the traces show some proximal dichotomous divisions but distally the ramification is very profuse and anastomosing, giving rise to tiny bundles beneath the glandular surface. In species with a reduced number of stamens the lateral gland traces are absent and the median one may fork collaterally once.

Erinocarpus nimmonii. — Fig. 300. Vascular bundles in part of flower towards a petal, gland, and a number of stamens. — Fig. 301. Course of vascular bundles in receptacle.

Triumfetta spp. — Fig. 302. General floral diagram. Dots represent stamens. Five innermost dots in *T. neglecta*. Ten to five inner dots in *T. annua* and *T. bartramia*. In *T. althaeoides* minor dots absent, crosses sometimes absent. Minor dots in *T. suffruticosa* sometimes absent.

Triumfetta bartramia. — Fig. 303—304. Vascular bundle supply in receptacle. In fig. 304 petal supply omitted.

T. neglecta. — Fig. 305. Attachment of stamen traces. Petal supply and sepal details omitted.

T. grandiflora. — Fig. 306. Attachment of petal, stamen, and gland vascular traces to sepal supply.

T. suffruticosa. — Figs. 307—310. The same.

T. appendiculata. — Figs. 311—313. The same.

T. althaeoides. — Fig. 314. The same.

T. suffruticosa. — Fig. 315. Stamen fascicle traces.

T. appendiculata. — Fig. 316. Ditto.

Stamen fascicle traces or stamen traces are connected by a single or double base mostly with the proximal part of a sepal commissural lateral, sometimes with a sepal median trace or with the basal trace which these two may have in common. Like the sepal commissural lateral traces the stamen fascicle traces deviate from a radial course to reach petal radii. Then in these radii they run upwards through the cortex around the reconstituted stele of the androgynophore to split into stamen traces beneath the androecium. On this level traces of the pistil wall join the dividing stamen fascicle traces.

The splitting results in stamen traces directly if the stamen number is low. However, when there are more stamens, a spatially digitate splitting which on closer observation proves to consist of contracted tri- and dichotomous divisions, first produces a number of, what we called earlier, chains of staminal traces. These proceed under the androecium in outward direction and give off stamen traces successively, sometimes first splitting into a few minor chains. Anastomoses between the central stamen traces may occur and the way of the splitting and the number of resulting stamen traces is always slightly different in the sectors of one flower. Some stamen traces may be attached to the stamen fascicle traces where these divide into the chains.

In *Triumfetta althaeoides* each stamen fascicle trace gives four to six stamen traces through either one or two dichotomously split short chains, whereas in *Triumfetta suffruticosa* (fig. 315), a species with more stamens, the number of stamen traces is larger and linked by two to three chains. In *Triumfetta appendiculata* with very numerous stamens the stamen fascicle traces bend outwards abruptly splitting digitately into three to five long chains which sometimes split again and give off a lot of stamen traces. The situation is as in *Erinocarpus nimmonii*, with the difference that the chains do not run radially since near the point of bending outwards they are aggregated near petal radii (fig. 316). It is remarkable that in *Triumfetta appendiculata*, and now and then in *Triumfetta suffruticosa*, stamen fascicle traces in the form and character of chains may be attached directly to the reconstituted stele distally in the androgynophore and in sepal radii. In some sectors of some flowers of *Triumfetta appendiculata* about three peripheral stamens may be innervated by a trace which is attached to a sepal basal lateral trace proximally, whereas in the other sectors these stamens are supplied in the normal way. In *Triumfetta neglecta* the traces of the antesepalous stamens join by a very oblique way the bases of sepal commissural laterals where these are combined with the bases of sepal median traces in the adjoining sepal radii. One of the stamen traces may be double, in which case no stamen trace is connected with an adjoining sepal commissural marginal trace (fig. 305). A similar feature is shown by the flowers with ten stamens, in which to the bases of the sepal commissural marginal traces, where these join the sepal median traces basally, traces are attached which run towards the petal radii dividing collaterally into an antepetalous stamen trace and an antesepalous stamen trace beyond the petal radii (figs. 303, 304). Irregularities are frequent in these species.

Other authors

According to Eichler there are five fertile hardly separable alternipetalous groups of stamens. Rao recognized five pairs of antepetalous stamens in the androecium of *Triumfetta rhomboidea*, because the staminal part of a petal stamen trace divides collaterally. The gland trace, separating serially from the petal trace also divides collaterally into two fading branches. In *Triumfetta rotundifolia*, a species with twenty stamens, the two staminal branches undergo secondary chorisis.

Heliocarpus americanus

This species resembles much the preceding ones.

The sepals are cucullate and mucronate and, like the petals, without glandular trichomes. These do occur on the androgynophore in five antepetalous fields which meet in sepal radii.

The *circa* twenty stamens are inserted in one or two irregular whorls. The anthers are like those in *Erinocarpus nimmonii*, but they are sagittate at the base as well as at the apex.

Supply of vascular bundles

Ten main bundles leave the stele in the flower base. Five in sepal radii form the sepal median bundles only. The other five in petal radii trifurcate into a median petal trace and two lateral parts which represent the common bases of the sepal lateral bundles. To the basal flanks of an antepetalous main bundle a stamen fascicle trace is attached, which higher up splits into one to five stamen traces.

More central parts of the flanks of these main bundles form the two major gland traces which give off many anastomosing tiny bundles during their upward course under the fields of glandular trichomes.

Althoffia spp.

An androgynophore is present which is pentagonal in cross-section with the angles in sepal radii. It widens upwards into a free fringed border by which it is separated from the androecium. The receptacular wall upon which the stamens are placed is slightly elevated, the lower part pentagonal in cross-section with the angles in sepal radii, the upper part with a circular to slightly pentagonal outline with the angles in petal radii. The anthers consist of two bisporangiate thecae fused along their long sides and dorsally in the middle attached to the filament. They are somewhat resupinate. The petals are covered with basal adaxial fields of glandular trichomes which are surrounded by hairs except basally. They are imbricate.

Developmental phases

The corners of the rather flat apex within the young calyx are taken by the primordial petals, the further growth of which is postponed. On the apex around a central depression, a ring-formed wall is elevated, upon which the stamen primordia develop. The first ten stamens to develop are placed in sepal and petal radii, the later ones arising in centrifugal direction. Stamen primordia also appear between the petal primordia, giving the androecium a pentagonal appearance. Ultimately, the most peripheral parts of the staminal wall develop as the free border mentioned above. First the primordial stamens in petal radii are pressed down by the projecting sepal margins, so that the antesepalous sectors appear slightly advanced. This effect is neutralized later.

Supply of vascular bundles

Near the sepal radii the sepal lateral bundles are connected with the sepal median trace, the more lateral ones of adjoining sepals on the other hand have a sepal commissural marginal trace in common which links them up with the stele. In addition, some of the middle sepal lateral bundles are connected with the stele by a double base along both ways, giving rise to a cross-arc system.

The petal trace joins one or both flanks of the sepal commissural marginal trace below the collateral division. Many tiny bundles come from the petal nerves to supply the glands. Sometimes, in a sector of the flower sepal commissural marginals are absent. In that case two sepal basal laterals of adjoining sepals join in petal radii and from this cross-arc the petal and stamen fascicle traces are separated. Sometimes a portion leaves the stele more or less in sepal radii; this part divides into a sepal median trace and one or two sepal commissural lateral traces.

The five stamen fascicle traces are attached to one or both proximal flanks of the sepal commissural marginals. Under the androecium, in antepetalous regions, they split collaterally several times into main secondary branches that ramify irregularly (sometimes more or less pinnately) into stamen traces, which may anastomose. Sometimes two fascicle traces come from the flanks of the sepal commissural traces. The androecium resembles that of *Trichospermum javanicum*.

Each stamen is provided with a simple bundle.

B. COMPARATIVE PART

1. THE ARRANGEMENT OF THE STAMENS IN FULL-GROWN FLOWERS

The stamens are mostly arranged in a continuous ring on a sloping receptacle, for instance in *Apeiba* spp., *Clappertonia ficifolia*, *Triumfetta* and *Corchorus* spp., *Trichospermum javanicum*, *Erinocarpus nimmonii*, *Heliocarpus americanus*, and *Althoffia pleiostigma*. In *Grewia* and *Colona* spp., and in *Entelea arborescens*, in antesepalous regions the stamens are placed more centrally. Another arrangement is formed by the antesepalous groups of stamens in *Entelea palmata*, *Sparmannia africana*, *Luhea divaricata*, and *Microcos* spp. The ring condition may be linked up with the arrangement in antesepalous groups by series as present in *Grewia* spp., in which either less well developed specimens or species with fewer stamens show the groups. Finally the stamens may be placed on a wave line with inner fertile or staminodial and outer fertile bends in *Cistanthera papaverifera*, *Schoutenia* and *Tilia* spp. In *Cistanthera papaverifera* and *Schoutenia* spp. the outward bends lie more or less opposite the petals, in *Tilia* spp. opposite the sepals. If no stamens develop in the middle of the outward bends it is possible to speak of antesepalous, or, in *Tilia*, antepetalous groups or phalanges which may meet in alternate radii. In this way in *Microcos* a state with antesepalous triplets of stamens is reached.

Only *Mollia speciosa*, with its ten groups in front of the perianth parts, does not fit in the picture. The antepetalous groups are collaterally double and are formed by stamens with thinner filaments. Also in *Colona auriculata* the antepetalous stamens have more slender filaments.

In *Brownlowieae* groups of stamens are not distinct, or difficult to locate. Where in *Tiliaceae* more or less perfectly separated groups of stamens occur they alternate with the pistil cells.

Concluding the above descriptions we may construct series leading from a continuous ring of stamens to antesepalous grouping or groups, and to a wave-line configuration.

2. THE MATURE FORM OF THE STAMENS

All anthers have two thecae which each consist of an anterior and a posterior pollen sac. In *Cistanthera papaverifera* the pollen sacs are partitioned by transverse septs. The thecae are situated along the margin of the distal part of the filament on either side of the apex mostly somewhat introrsely.

The distal filament part is usually slender, in *Schoutenia* spp. slightly broader, in *Brownlowieae* reniform. In *Tilia* spp. it is also broad, even two-lobed or forked, the thecae correspondingly being sessile or stalked. The distal part may be straight and slender in *Apeibeae*, *Mollia speciosa*, *Clappertonia ficifolia*, and *Cistanthera papaverifera*. However, in all the other plants studied here it is slender and resupinate, and at the same time the thecae are slightly prolonged at the basal end in adaxial direction, the tails remaining contiguous. The result is that the anthers are seemingly peltate, especially so, if resupination is extreme (*Grewia* spp.). However, in *Grewia* spp. and in *Luhea divaricata* the real character is clearly revealed by the apex of the filament which projects as a free point in abaxial direction downwards near the ends of the resupinate thecae. In *Erinocarpus* *nimmonii* and in *Triumfetta* spp. it appears that the thecae are fused more intimately at the morphological apex of the anther. The simple vascular bundles are also either straight or resupinate and run toward the apex. In *Heliocarpus americanus* the resupinate anthers are slightly prolonged also apically. In *Mollia speciosa* and still more so in *Clappertonia ficifolia* the straight anthers are tailed at the base and the apex, the tails in *Clappertonia ficifolia* not remaining in touch. Here a tiny branch from the median bundle runs into each tail.

Staminodes

Apical sterility occurs in *Cistanthera papaverifera* and is especially evident in *Apeiba* spp. The *Apeibeae* resemble the *Elaeocarpaceae* in the form of their stamens. The apical sterility increases gradually in the peripheral stamens, the anthers becoming broader and the pollen sacs and filaments shorter. Ultimately the outermost members of the androecium may be completely foliar staminodes which are sometimes connate (cf. *Sloanea myriandra*), a feature suggestive of the formation of petaloids.

In *Sparmannia africana*, *Luhea divaricata*, and *Clappertonia ficifolia* the outer androecium members are also staminodial but remain filiform and are glandular. In *Brownlowieae* and in taxa, where the members of the androecium are placed in a wave-line — *Cistanthera papaverifera* and a number of *Tilia* spp. — innermost foliar staminodes are present. In other *Tilia* spp. and in *Schoutenia* spp. no such staminodes are present. In *Tilia* spp. the inward bend of the androecium may be occupied by some structures intermediate between stamens and foliar staminodes.

3. THE DEVELOPMENTAL STAGES OF THE ANDROECIUM

The centrifugal development

The stamen primordia appear upon the receptacle in a centrifugal sequence.

In *Apeiba* and *Triumfetta* spp. the primordia are produced in alternating whorls more or less regularly. In *Apeiba* the number of stamens in one whorl is equal to the number of carpel primordia. As a consequence in *Apeiba* spp., and also in *Clappertonia ficifolia*, some *Triumfetta* and *Althoffia* spp., the ring of stamens appears to consist of alternating whorls of 10 (8), 15, or 20 stamens, or of two obdiplostemonous whorls of five stamens. In the androecia with many stamens this gives rise to double the number of orthostichies. In *Entelea arborescens*, *Grewia* spp., and in a way also in obdiplostemonous *Triumfetta* spp. the development, starting by a leading innermost stamen situated in sepal radii, proceeds in a latero-centrifugal sequence, and continues by alternating whorls after the petal radii have been reached. In *Grewia* the development sometimes proceeds by pairs of stamens. However, in *Sparmannia africana*, *Luhea divaricata*, and *Entelea palmata* after the petal radii have been reached, no further primordia will appear, so that the development seems restricted to antesepalous groups. Also in *Schoutenia* and *Tilia* spp. the development takes place in a latero-centrifugal direction, but is limited to a single row, no stamens originating peripheral to the first-formed stamens.

Colona scabra and *auriculata*, *Mollia speciosa* and in a way also *Clappertonia ficifolia* do not fit in this scheme. In these species ten developing groups of stamens may be distinguished, as can be expected from the mature condition in *Mollia speciosa* and *Colona auriculata*. In all three species centrifugal antesepalous groups are advanced and the first to develop. In the *Colona* spp. the development of 3—8 stamens in the antepetalous groups is latero-centrifugal. In *Clappertonia ficifolia* the antepetalous groups are formed by a single stamen and two fields of staminodes. As a whole the antepetalous groups are not placed more peripherally or more centrally than the antesepalous groups. In *Mollia* the centrifugal development also proceeds towards a median peripheral position in the antepetalous groups. Moreover, the development sometimes seems to start from two leading innermost stamens some distance on either side of the radii of these groups.

The appearance of the stamen primordia

Mostly a low staminal wall precedes the hemispherical stamen primordia which appear upon it. Only in *Mollia speciosa* and in *Triumfetta* spp. this phenomenon is less evident. The wall may be circular (*Apeiba* spp.) or pentagonal with antepetalous angles. In species with the stamens in groups, antesepalous staminal group protuberances originate which spread in latero-centrifugal direction just prior to the appearance of the stamen primordia upon them. In *Sparmannia africana* and *Luhea divaricata* the group primordia even spread over the alternisepalous regions in the peripheral flower parts, although there stamen primordia will not develop on them any more. In *Tilia* spp. and also in *Schoutenia* spp. a stellate wall appears on the receptacle in accordance with and immediately prior to the centrifugal origin of the stamen primordia. Thus the innermost parts of the walls become evident first, and are followed only afterwards by the outermost parts. Also in *Grewia* the antepetalous regions of the low pentagonal wall are initially lower.

Another interesting developmental phenomenon is the temporary inhibition of the growth of the stamen primordia near petal radii. Very probably this inhibition corresponds with the more or less cucullate character of the sepals as for example in *Entelea* spp., *Trichospermum javanicum*, *Grewia* spp., *Erinocarpus nimmonii*, *Triumfetta suffruticosa* and *althaeoides* and *Althoffia pleiostigma*. Maybe the projecting margins of the young sepals prevent the growing out of the young stamens for a certain time. Later there is no difference in size among the stamens. This is not an obligate relation, since in *Apeiba* spp. sepals are cucullate and staminal growth similar in all sectors of the flower.

In *Entelea* spp. some new stamen primordia sometimes appear under the older ones (cf. *Adansonia digitata*).

The androgynophore

The androgynophore of *Corchorus*, *Grewia* and *Triumfetta* spp., of *Colona auriculata* and *Althoffia pleiostigma* is formed by a late development of a narrow receptacular zone immediately above the petals. It is therefore understandable that its cross-section is pentagonal with the angles in sepal radii. The receptacle immediately above the androgynophore is bordered by a sterile rim, which may be more or less flaring. In *Althoffia pleiostigma* the most peripheral part of the androecial wall has actually been observed to develop into that rim. In *Colona auriculata* the rim exhibits unconnected radial vascular bundles of presumably staminodial nature. In *Grewia hirsuta* the rim is limited to a hairy zone which in few-numbered androecia and also in *Microcos ledermannii* may link up with hairy regions separating the antesepalous stamen groups. Here the hairs upon the rim are seen to originate following upon the last stamens. Thus it is clear that the rim is of staminodial nature.

The development of the stamen primordia

The stamen primordia arise on the receptacle as hemispheric primordia which later become dorsiventrally flattened, especially on the adaxial side. At the same time they are stalked, becoming more or less spoon-shaped, and two sets of two parallel pollen sacs develop in the marginal tissue on either side of the apex. The growth in length or width affecting the distal end of this structure defines the final form of the anther, whether it is elongate or reniform. The sagittate extension of the thecae, mostly on the side of the filament, as well as the resupination may occur in a much later phase. In *Pentace polyantha* a stamen on one of its sides has one pollen sac of double length instead of two in line. This may be comprehended as a one-sided fertilization of the margin of the young anther at the apex.

The inner surface of a dorsiventrally flattened stamen primordium is usually directed towards the flower centre. In *Schoutenia* and *Tillia* spp. dorsiventral surfaces lie parallel with the wave line on which the primordia are situated. And in the antepetalous groups of *Mollia speciosa* the stamen primordia are directed toward median subperipheral regions of the groups.

4. THE SUPPLY OF VASCULAR BUNDLES TOWARDS THE ANDROECIUM

The chains of stamen traces

In *Apeiba echinata* to the reconstituted stele twenty radial chains of stamen traces are attached, which move in outward direction under the places of insertion of the stamens. From each chain a succession of opposed flank portions is separated upwards which represent the double bases of an orthostichous series of stamen traces. In *Apeiba tibourdou* and in a third *Apeiba* spec., in which orthostichies are absent, about twenty stamen fascicle traces are attached to the flanks of sepal, petal, or sepal commissural traces (or at the stele immediately above these traces). They give a tree-shaped ramification system of traces towards the stamen bases. In *Glyphaea grewioides* ten petal stamen fascicle traces are attached to the flanks of the sepal commissural traces. The staminal parts give a tree-shaped ramification leading to radial chains from which the stamen traces depart in various upward directions. It must be concluded that whereas in *Glyphaea grewioides* radial chains of stamen traces occur which are fascicled, in *Apeiba* spp. the chains are attached to the stele or perianth traces directly. In *Trichospermum javanicum* ten petal-stamen fascicle traces are attached to the flanks of the sepal commissural traces, in *Althoffia pleiostigma* five, of which one may be double. They produce a tree-shaped ramification system each which either ends in stamen traces immediately, or — in *Althoffia pleiostigma* — first bifurcates. Also in *Erinocarpus nimmonii* five petal stamen fascicle traces are attached by a double base to the sepal commissural traces or to the stele directly. These traces ramify by means of some proximal irregular bifurcations into more or less radial chains of stamen traces. Chains of stamen traces are also present in *Triumfetta* spp. with many stamens and in *Althoffia pleiostigma.*

The stamen fascicle traces

Chains are absent in *Heliocarpus americanus* and *Triumfetta* spp. if the number of stamens is lower. In *Triumfetta* spp. and in part of the *Corchorus* material five (petal) stamen fascicle traces are attached to the base of the sepal commissural traces. As the sepal commissural traces are attached to the base of the sepal median traces, the commissural traces as well as the petal stamen fascicle traces have a basal oblique upward course toward, the petal radii.

In *Grewia* spp., part of the *Corchorus* material and in *Mollia speciosa* five petal stamen fascicle traces and five stamen fascicle traces are connected with the perianth traces in an obdiplostemonous way. Only in *Mollia speciosa* these ten traces might correspond to ten external stamen groups. In *Grewia* spp., where sepal commissural traces are absent, the petal stamen fascicle traces are either attached to the cross-arcs formed by the sepal laterals, or are attached — often by a multiple base — to the sepal median trace, running obliquely downwards along sepal basal laterals. The stamen fascicle traces in petal radii split into the minority of stamens, often by a basal trifurcation. In *Microcos* spp. five stamen fascicle traces are attached to the sepal median trace or to the stele immediately above. In *Microcos* spp. with fewer stamens five antesepalous triplets of stamen traces are inserted on the stele directly, the outer pairs of which may also be placed together close to petal radii. In part of the *Corchorus* material stamen (fascicle) traces are connected with the sepal commissural trace in its proximal and in its distal part. As the sepal commissural is attached to the sepal median trace by a basal oblique course the insertion points of the stamen (fascicle) traces are placed in an obdiplostemonous manner. In *Mollia speciosa* the petal stamen fascicle traces are attached either to the ends of the sepal basal laterals or to the proximal parts of these basal laterals by means of an oblique course. In this species sepal commissural traces may be absent. The other five stamen fascicle traces are attached to the base of the sepal median traces and split into the stamen traces of the antesepalous groups as well as into the traces of the lateral members of the antepetalous groups. As a consequence we might distinguish in *Mollia speciosa* on anatomical grounds an obdiplostemonous arrangement of inner triple antesepalous groups and outer simple antepetalous groups. Externally, however, we observe a slightly diplostemonous arrangement of ten separate groups.

Frequently the androecium is supplied by ten traces in obdiplostemonous arrangement, of which five outer (petal) stamen fascicle traces are attached to perianth traces, and five inner single stamen or staminode traces to the stele independently. This is the case for instance in *Colona auriculata, Clappertonia ficifolia, Brownlowieae, Schoutenia* spp., *Cistanthera papaverifera* and in a way also in *Tilia* spp. In *Clappertonia ficifolia* to each sepal commissural trace a concentric bundle is attached, which falls apart into a petal trace, two staminode fascicle traces, and an antepetalous stamen trace. The outer stamens between sepal and petal radii each have a double base connecting them with the antesepalous stamen trace as well as with the concentric bundles. On anatomical grounds we may distinguish in *Colona auriculata* a single inner stamen in sepal radii and alternate outer triple groups consisting of the median antepetalous groups and the two lateral rows of the antesepalous groups. The trifurcating traces towards these combinations are attached to the sepal median traces by an oblique basal course. Here, as well as in *Mollia speciosa*, the anatomical situation seems entirely in disaccord with the external condition, and in both species in much the same way, namely by the presence of inner single and outer triple groups. However, whereas in *Mollia speciosa* triple groups are antesepalous, they are antepetalous in *Colona auriculata*.

In *Brownlowieae, Cistanthera papaverifera* and in *Schoutenia* spp. we always observe five distinct petal stamen fascicle traces, which are connected mostly near sepal radii with the sepal supply by means of an oblique proximal course with a frequently double base. On the other hand inner single stamen or staminode traces come from the stele directly on a higher level. *Tilia* falls into this category too, but the inner single stamen or staminode traces are placed in petal radii and the outer stamen traces are immediately attached to the sepal median traces.

In *Entelea* spp. and in *Sparmannia africana* the course of vascular traces is not in accordance with the external antesepalous stamen groups. Eight stamen fascicle traces are attached independently to the stele, or those in petal radii are attached to the sepal commissural traces by a double base. The fascicle traces in petal radii undergo a basal bifurcation and innervate the lateral parts of adjacent stamen groups, the fascicle traces in sepal radii innervating fewer stamens in the central part of the stamen groups. This condition resembles that of the triple groups in *Colona auriculata* and *Mollia speciosa.* In *Sparmannia africana* in some flower sectors a trace may come from the stele near petal radii on a higher level, which bifurcates into two stamen traces. Sporne did not record these additional traces from his cleared material. In *Entelea* spp. the branching of the fascicle traces gives rise to short more or less radial chains of stamen traces. In *Luhea divaricata* more than ten stamen fascicle traces are attached to the perianth near sepal radii and innervate the antesepalous groups.

The vascular bundles in the stamens

In the filaments and connectives single and unbranched collateral bundles are present. Only in the anthers of *Clappertonia ficifolia* which are prominently tailed, a tiny branch of the median bundle goes into each tail. In the forked or bilobed connectives of *Tilia* spp. the bundles are forked, though some inside tiny bundles accompany the secondary branches or continue the course right ahead. The xylem is oriented towards the flower centre, except in *Schoutenia* and *Tilia* spp. where it is directed perpendicular to the waveline on which the stamens are situated. Consequently the direction of the vascular bundles is fully in accordance with the dorsiventral character of the stamens. In *Clappertonia ficifolia* the xylem of the outer stamens is directed toward a position which is intermediate between the petal radius and the flower centre. In *Mollia speciosa* the xylem of the stamens in the antepetalous groups is directed towards a point which is situated median subperipherally in the groups, in accordance with the position of the introrse anthers.

In *Trichospermum javanicum* the stamen fascicle traces exhibit slightly opposed xylem in in case they are placed in five antepetalous pairs rather than equidistantly.

5. THE SEPALS, THE PETALS, AND THE GLANDULAR TISSUE

The appearance of the petals

In *Trichospermum javanicum*, *Tilia*, *Grewia*, and *Triumfetta* spp., in *Colona auriculata* and *Althoffia pleiostigma*, and perhaps also in *Apeiba* spp. the petal primordia can be distinguished very clearly before any of the stamen primordia. In *Corchorus* and *Schoutenia* spp. and in *Sparmannia africana* petal primordia become only visible at the same time as the first stamen primordia, and independently of the androecial wall. In all cases the pistillary wall arises after the first stamen primordia. The sepals, petals, and the first stamens in sepal radii are recorded to appear successively in a number of species, for instance in *Tilia* and *Colona* spp.

In most *Grewieae* studied, the petals, if not reduced, do not overlap at all. In the *Apeibeae* and in most *Tilieae* (also in *Althoffia pleiostigma*) the petals are imbricate, in *Tilia* spp. sometimes quincuncially.On the other hand, in *Brownlowieae* and in *Cistanthera papaverifera* the petals are contorted.

The calyx supply and the attachment of the petal (stamen) traces

In *Mollia speciosa*, *Schoutenia glomerata*, and *Microcos pentandra* the calyx supply is formed by five sepal traces which by a basal trifurcation produce a middle sepal nerve and two basal lateral nerves on either side. From the basal laterals the sepal laterals diverge. The petal stamen fascicle or the single stamen traces in these species show a proximal oblique course by which they are connected with the distal or proximal parts of the sepal basal laterals or with the sepal median trace below its trifurcation.

In *Cistanthera papaverifera*, *Luhea divaricata*, *Tilia*, *Grewia*, and *Microcos* spp. some outside sepal lateral bundles have double bases connecting them with adjoining sepal basal laterals. In this way cross-arcs are formed linking two sepal supplies over the petal radii in some or all sectors of the flower. The base of the petal traces remains attached to the sepal basal laterals by an oblique course. However, if in sectors of flowers of *Microcos* spp. or *Althoffia pleiostigma* cross-arcs are present, the petal traces may be connected with them directly in petal radii. In *Grewia* spp. petal traces may be attached by double bases to the sepal basal laterals or sepal median traces of adjoining sepals. A comparable situation occurs in *Colona auriculata* and in *Microcos* spp., where the cross-arcs seem to be formed rather by the double bases of petal traces which are attached to the ends of adjacent sepal basal laterals. Sometimes in *Mollia speciosa* cross-arcs seem to be formed by the petal stamen fascicle traces in the same way.

Frequently the outside sepal laterals are not at all connected with their sepal median traces, but those of adjoining sepals come together downwards into a commissural sepal trace which leaves the stele in petal radii and shows a proximal collateral bifurcation. In the case of the presence of sepal commissural traces some middle sepal laterals may have double bases connecting them with the sepal basal lateral as well as with the sepal commissural trace. In this way a total of ten small cross-connections may be formed. This situation occurs in *Apeibeae, Trichospermum javanicum, Entelea* spp., *Sparmannia africana, Erinocarpus nimmonii*, and *Althoffia pleiostigma.* Also in *Heliocarpus americanus* and sometimes in *Triumfetta* and *Corchorus* spp. there are ten sepal traces, but cross-arcs are not formed. Sometimes the sepal median trace may give only the sepal median nerve, for example in *Corchorus* spp. In *Corchorus* spp. the course of the vascular bundles appears to be very variable in these respects. In part of the *Corchorus tridens* material cross-arcs are formed by sepal basal laterals only, the sepal commissural traces passing close over their summits. The petal trace is attached mostly by a double base (or fasciculate base in *Sparmannia africana*) to the basal flanks of the sepal commissural traces. However, in *Erinocarpus nimmonii* and in *Entelea* spp. the petal (stamen fascicle) traces may also come from the stele immediately above these traces. If in some sectors of a flower sepal commissural traces are absent, the cross-arcs may be formed by the sepal basal laterals. The petal traces are then attached to the cross-arcs (*Althoffia pleiostigma*). In *Corchorus* and *Triumfetta* spp. the sepal commissural traces are mostly attached to the sepal median trace by a basal oblique course. A number of three petal traces are connected with the sepal supply near petal radii.

It is evident that there is a correlation between the absence of sepal commissural traces and the occurrence of a distinct basal oblique course connecting the petal (stamen) traces with the base of sepal median or basal lateral traces.

The glandular tissues

Glandular trichomes occur in fields on the inner base of the sepals in *Brownlowieae, Schoutenia* and *Tilia* spp. On the other hand glandular fields occur on the inner base of the petals in *Luhea divaricata, Trichospermum javanicum, Grewia* and *Microcos* spp., *Colona* spp., and in *Althoffia pleiostigma.* In *Corchorus* spp., *Erinocarpus nimmonii, Triumfetta* spp., and *Heliocarpus americanus* the fields cover the proximal part of the androgynophore above the petals. However, in *Triumfetta appendiculata*, a species with numerous stamens, the glandular trichomes occur in a continuous ring upon the proximal part of the androgynophore. In *Sparmannia africana* and *Clappertonia ficifolia* the staminodes are glandular. In *Apeiba* spp. and in *Mollia speciosa* glandular tissue has not been found.

The fields may be supplied by tiny upward nerves attached to the proximal petal and sepal nerves. In *Colona auriculata* the adaxial parts of concentric petal traces ramify into numerous tiny unlignified bundles under the nectariferous surface. In *Erinocarpus nimmonii* to the petal basal laterals two gland traces are attached which bifurcate both, moving upwards and then downwards again in the androgynophore, and split into numerous tiny bundles. In *Triumfetta* spp. three gland traces are attached to the sepal commissural traces and the sepal basal laterals where also the three petal traces are attached.

6. VARIATION IN THE COURSE OF THE VASCULAR BUNDLES

The multiple attachment

Very often the sepal lateral bundles have double traces connecting them either with the sepal basal laterals of adjoining sepals or with a sepal basal lateral as well as a sepal commissural trace. In this way cross-arcs are formed.

Also the bases of petal(stamen) traces are often linked up with the sepal supply in a double or even multiple way. In *Microcos ledermannii* a petal trace coming from the stele and passing close over a cross-arc, may show some tiny connections with this cross-arc (fig. 294). In *Apeiba echinata* a radial chain of stamen traces may have a double origin, one to the base of the petal trace, the other to the stele. In *Triumfetta* spp. gland laterals show a double-or multiple- trace attachment to the sepal supply. In *Erinocarpus nimmonii* and *Althoffia pleiostigma* either two stamen fascicle traces are attached to the underlying supply or only one with a collaterally double base.

Concerning the androgynophore

A number of comparable features are related with the presence of an androgynophore. In *Corchorus aestuans* some stamen (fascicle) traces may be connected with the stele directly upwards in the androgynophore. In *Triumfetta appendiculata* and sometimes in *Triumfetta suffruticosa* the radial chains of stamen traces in sepal radii are directly connected with the stele. In *Colona auriculata* only the top central stamens in sepal radii have their traces attached directly to the stele. Also in flowers without an androgynophore the traces of the innermost stamens (or staminodes) are often the only which are connected with the stele independently (*Schoutenia, Tilia* spp.). If in *Microcos* spp. the number of stamens is high, stamen fascicle traces are attached to the sepal median traces or to the stele on a low level. However, if the stamen number is low, the stamen traces are attached to the stele separately high up in the androgynophore. In *Colona auriculata* and in *Triumfetta* spp. the stamen (fascicle) traces which are attached to the perianth traces in sepal radii run upwards through the androgynophore by an oblique course to reach the petal radii. Evidently the formation of an androgynophore, which appears to be late during the ontogeny, does not interfere at all with the formation of the vascular bundles. Possibly the young vascular bundle tissue with its pathway already established merely undergoes longitudinal growth during the development of the androgynophore.

On different points of attachment for the same kind of traces

Another interesting feature is shown by the petal stamen fascicle traces in *Mollia speciosa* and the petal traces in *Tilia* spp. and *Luhea divaricata*. By an oblique basal course they are connected with the mostly proximal regions of the sepal basal laterals. Frequently four of them are attached to four sepal basal laterals which belong to only two sepals, and a fifth to the basal lateral of a third sepal. Sometimes two traces are connected with both basal laterals of one sepal and the other three traces with one of the basal laterals of three other sepals. Never is one of the traces connected with one of the basal laterals of each sepal. This condition can possibly be explained by assuming a variable influence on the initiation of the vascular bundles in consequence of the variable distance between the higher placed primordia and the mostly quincuncially placed underlying young sepals.

Sometimes in *Tilia* spp. a petal trace comes from the stele directly and in that case the antepetalous staminode trace is attached to it basally. In part of the flowers in *Corchorus* and *Triumfetta* spp. the sepal commissural traces are attached to the sepal median traces basally. Incidentally two sepal commissural traces are linked up with one sepal median trace.

All these deviations seem due to the fact that these vascular connections occur along the physiologically most simple pathways. However, in obdiplostemonous *Triumfetta* spp. an antesepalous and an adjoining antepetalous stamen trace are attached by a basally oblique common trace to the base of a sepal commissural trace where this links up with the sepal median trace of an adjoining sepal. Here pathways seem certainly not the most simple.

The attachment of peripheral traces to heterogeneous vascular bundles

In *Triumfetta appendiculata* among the numerous stamens a few outermost may have their traces attached directly to the underlying sepal supply, instead of joining the fascicle traces. From each petal basal lateral in *Apeiba echinata* a presumably residual stamen trace moves upwards, the normal stamens on the other hand all being supplied by traces connected with the stele.

In *Colona auriculata* the traces of the lateral stamens of the antepetalous groups may either be connected with the median or with the lateral parts of the trifurcating fascicle trace which supplies the antepetalous groups as well as the lateral stamens of the antesepalous groups. However, one of the top lateral antesepalous stamens may also receive a trace branching from the trace of the top central antesepalous stamen, which is always directly connected with the stele.

Tiny bundles from the pistil wall link up downwards with the inner stamen (fascicle) traces in *Apeiba*, *Grewia* and *Triumfetta* spp., in *Colona auriculata*, and in *Erinocarpus nimmonii*.

In *Triumfetta* spp. a trifurcating petal trace may be attached to a sepal median or commissural trace, but, if a well-developed cross-arc is present, three petal traces are attached to the cross-arc side by side. In *Erinocarpus nimmonii* the two gland traces which are attached to petal basal laterals and bifurcate upwards, may be replaced each by two successive traces that are attached more peripherally to the petal marginals and do not bifurcate. Evidently whereas centrally situated gland traces have a common basal trace, peripherally placed traces are attached directly.

Residual bundles

Residual stamen traces occur in the androecium of *Apeiba echinata* and in the rim of *Colona auriculata* (see above).

Concentric bundles

Concentric or almost concentric — that is on the adaxial side only slightly open — bundles may occur for instance in *Tilia* spp. Here they are assembled by the bases of sepal, antesepalous stamen, pistil (and petal) traces. In *Clappertonia ficifolia* they are formed by the bases of petal, stamen, and staminode fascicle traces. The concentric bundles have collateral bases by which they are connected with the underlying vascular tissue (stele in *Tilia*, sepal commissural in *Clappertonia ficifolia*). Almost perfectly concentric stamen fascicle traces occur in *Grewia* spp. where they pass through the androgynophore. However, it is possible that these bundles also comprise pistillary wall traces. In *Apeiba echinata* petal traces may be almost concentric if some residual stamen traces are attached to the petal basal laterals. In *Mollia speciosa* the median sepal traces take a long sloping course through the cortex; they are almost or perfectly concentric bundles there.

C. INTERPRETATIVE PART

The structure of the androecium

a) *Evidence from the external observation*

The chief puzzle presented by *Tiliaceae* is how to compare the flowers with stamens entirely covering the receptacle between perianth and pistil with those in which the stamens are distinctly arranged in groups. Can we trace any intermediate conditions?

Beforehand we may assume that the ringed condition can be analyzed because the stamens are not arranged just haphazardly. There is a tendency to form orthostichies if the number of stamens increases. Moreover the centrifugal development has been observed to start by means of ten (eight) leading primordia in sepal and petal radii in *Apeiba echinata, Althoffia pleiostigma, Triumfetta appendiculata,* and *Clappertonia ficifolia.*

Signs of a slight grouping may be found in other *Triumfetta* spp., when the antesepalous stamens among the first ten anticipate those in petal radii. In *Grewia* spp. the grouping may be more extensive, if, alternating with and lower than the leading five stamen primordia in sepal radii, two stamen primordia arise in stead of one. If this be continued, stamen primordia will reach the petal radii increasingly later in ontogeny and more towards the periphery of the flower, and the inward bulging parts of the annular mass of stamens may be considered as the apical parts of staminal groups. These apical parts of the groups (or of the phalanges in *Tilia etc.*) may be compared with those of the staminal lobes in *Malvaceae* and *Bombacaceae*, especially so since during the ontogeny of both the appearance of stamen primordia is invariably preceded by a succession of low staminal elevations. The antesepalous groups of *Mollia speciosa* and the antepetalous groups in *Colona scabra* show how groups may change in phalanges by reduction of all their stamens except the marginal ones. The leading stamens arise on these meristematic parts almost, but never exactly, at the same time. If in *Grewia* spp., and also in *Microcos* spp., the number of stamens is low, the petal radii are not reached at all and five antesepalous groups are the result.

It is evident that wherever a ringed arrangement occurs the congenital concrescence of the stamens is more strongly developed. The meristematic wall grows to a large extent before any primordia arise upon it. On the other hand in flowers with fewer stamens there is a more gradual enlargement of the meristematic parts just before the appearance of the primordia.

In the *Entelea* spp., in *Sparmannia africana,* and in *Luhea divaricata* the grouped character is more pronounced, and the buttresses begin distinctly to bulge forward before the first stamen primordia arise upon them. Whereas in *Entelea arborescens* the petal radii are reached by the latero-centrifugal development of stamen primordia, in *Entelea palmata* these radii are not occupied. In *Sparmannia africana* and *Luhea divaricata* the meristematic wall begins to link the groups in the peripheral androecium parts over the petal radii, but no more primordia arise upon them.

As a conclusion it may be said that all kinds of transitions exist between the grouped and annular stamen position, resulting from differences in the extent of androecial development within a species, between different species of a genus, and also between different genera of the family. Here we have to call attention to *Mollia speciosa* in which species the grouped condition is at once evident, the antepetalous groups being moreover collaterally double.

In addition, in a study of the ontogeny, the existence of ten groups becomes clear in *Colona scabra* and *auriculata* and in *Clappertonia ficifolia.* Towards the full-grown stage this primary condition becomes largely or entirely obscured by postgenital receptacular growth, giving rise to a ringed arrangement with central grouping as in *Grewia* spp. Moreover, in *Colona scabra* an additional reduction in the median plane of the antepetalous groups may give rise to a breaking up of the mature androecium in distinct antesepalous groups. Of course it is tempting to transfer this influence into the congenital period, so that an originally grouped or more strongly grouped condition is concealed from the start.

The ringed arrangement may be assumed to be composed of groups of stamens which are congenitally fused to a varying extent by means of an initial broadening of the meristems in advance of the individualization of the stamen primordia. This must be as reasonable a possibility as that according to which a ringed condition may be deformed postgenitally into a grouped one, under the influence of perianth parts. Indeed the temporary inhibition of the growth of the stamens corresponding with the inwards projecting sepal margins is a remarkable and rather frequently occurring feature. We may consider also this influence at work during the congenital phases of androecium development, so that stamen primordia do not develop any more in antepetalous regions.

b) *Evidence from the course of the vascular bundles*

In this family the interpretation of the facts given by the course of the vascular bundles raises many problems. It seems hardly possible to reconcile all facts, because it is not easy to disentangle possibly constitutional and adaptive, plastic characters. Still also here the pattern is not without a certain constancy, so that we are forced to look for at least some explanation. What is more, if certain features are taken as significant we can find more arguments indicating that the ringed staminal arrangement is composed of groups.

For in *Grewia* spp. the stamen traces are fasciculated into ten obdiplostemonous groups, the prominently double based antepetalous fascicle traces supplying a minority of outer stamens. This is also the case in *Corchorus* spp., although the antepetalous fascicle traces are not always five in number. Even in subnormal *Grewia* flowers in which a rather small number of stamens is arranged in groupes because no stamens have developed in the petal radii, the resulting five groups may be supplied by traces branching from obdiplostemonous common traces.

The above condition is conformable with that in *Sparmannia africana* and *Entelea palmata,* in which the antesepalous groups of stamens are also, judging the vascular anatomy, composed of three subdivisions, namely an inner in sepal radii and two outer laterals between petal and sepal radii. The peripheral groups are innervated by the branching of proximally forking outer antepetalous fascicle traces.

So we may come to the conclusion that the externally homogeneous antesepalous groups are on certain histological grounds triple arrangements, the combination of which is produced fully congenitally. The parts of antepetalous groups may be incorporated in antesepalous groups. We may at least state that these groups receive a three-trace vascular system, the laterals of which are basally commissural.

This conception being somewhat unusual, we are fortunate to have an example of externally visible triple groups in *Mollia speciosa.* In this species, moreover, the orientation of the anthers and vascular bundles together with the sometimes double origin of the antepetalous groups underline the double and basally commissural nature of the antepetalous groups. In the direction of the vascular bundles we find back something of the orientation of the stamen fascicle traces in *Malvaceae* and *Bombacaceae,* namely as if the half-antepetalous groups belonged to the antesepalous groups, because they are not precisely directed towards the centre of the flower. In this context we must remind the curious arrangement of the stamens in *Muntingia calabura*. In *Colona auriculata* the antepetalous groups which are ontogenetically visible, are reduced and more commissural, taking the form of small phalanges. In *Clappertonia ficifolia* the ultimate phase is given by a single remnant stamen primordium in petal radii, flanked by two fields of staminodes. In *Microcos* spp. we may find antesepalous fascicle traces exclusively.

On the other hand it is not impossible that the antesepalous parts may be more or less reduced as compared with the antepetalous components of the groups, as is the common case in *Malvaceae, Bombacaceae* and *Sterculiaceae*. Here we think of *Cistanthera papaverifera* and *Schoutenia* spp., which in the stamens being placed on a wave-line and in the orientation of the stamen bundles resemble very much the androecia in the families mentioned above. But also in species with an annular arrangement of stamens the fasciculated nature of the stamen traces possibly shows that the fascicles may be compared with ten lateral group parts between sepal and petal radii. *Glyphaea grewioides, Erinocarpus nimmonii, Trichospermum javanicum*, and *Althoffia pleiostigma* are to be mentioned in this respect. In the petal radii they often have five double fascicle traces or double-based fascicle traces with a proximal bifurcation. Nevertheless we ought to be very careful with our conclusions here since residues of the antesepalous group portions are absent. Exactly these species are among those which de not show stamens in sepal radii which start the development.

What we have done in the foregoing is attributing a hidden composed character to ringed formations or coherent groups of stamens on analyzing first the ontogeny and then the structure and course of the vascular bundles. In so doing it is of great help that, as elucidated above, in other species of the same family, which show the most complicated of the possible forms, some of the putative combinations seem to be effectuated with the units free and striking the eye. Consequently, we ought not to be surprised when finding that the vascular system of these forms betrays a hidden still more complicated condition, which unfortunately will not be present within the family in an uncovered state. Then we have to extend our study to other families, in the case of *Mollia speciosa* probably to the *Flacourtiaceae*, where some genera seem to show still more intricate free groups. Therefore it is understandable that we are a bit uncertain about the interpretation of the vascular course in *Mollia speciosa, Colona scabra* and *auriculata*, and *Clappertonia ficifolia*, the course obviously being not entirely conformable to the external characters. However, there is one major resemblance with the state of affairs in *Sparmannia africana, Grewia* spp., and so on, in the fact that the ten groups of stamens in these plants either have a three-trace vascular system, the middle traces of which are the least branched or even single, or receive a trifurcating trace. If in the *Colona* spp. the antesepalous groups are supposed to receive three traces, the variable adherence of the supply of the antepetalous groups to the lateral traces of the antesepalous groups is conformable to the ontogenetic features of these flowers that have been described above, viz. the incorporation of the antepetalous into the antesepalous groups during ontogeny.

The contorted condition

In the above argumentation we have deliberately neglected the facts concerning the places of attachment of (petal) stamen (fascicle) traces, because they are so very difficult to interpret. We may distinguish three cases.

Firstly we are dealing with the oblique basal course of the sepal commissural traces towards the basal flanks of the sepal median traces, as frequently occurring in *Triumfetta* and *Corchorus* spp. (see also the *Sterculiaceae*). The most curious thing may not be the oblique course itself, considering that the big sepallary main trace may be an apt starting point for a new lateral bundle. The chief problem is presented by the fact that within a flower the direction of the oblique deviation is mostly the same in every sector. In fact we can hardly escape the suggestion that this phenomenon may be related with a certain contorted condition. Only now and then may one sepal trace give off two sepal commissural traces, or may two sepal traces each give off two commissural marginals.

In *Triumfetta* spp. the stamen fascicle traces are always attached to the oblique base of the commissurals, nearer sepal radii. The stamens the traces of which are fasciculated in this way are broadly situated in antepetalous fields. This is not in accordance with the fact that the innermost five stamen primordia in sepal radii are the first to develop. Only sometimes antesepalous upper fascicle traces are also present in *Triumfetta appendiculata* and *suffruticosa*. It is unfortunate that for the present we must leave this matter unsolved.

Secondly the petal traces in *Luhea divaricata* and *Tilia* spp., and in a variable way in *Microcos* spp., show an oblique course, whereas the sepallary and staminal traces are not oblique at all. The condition is especially frequent in *Luhea divaricata* and *Tilia platyphyllos*, in which to the basal laterals of two sepals four petal traces are attached, the fifth petal trace being connected with a basal lateral of a third sepal. We are tempted to think here of a relation with the frequent quincuncial origin of the sepals. In *Microcos* spp. the attachment is more variable and it may even seem to be contorted in *Microcos pentandra*. In my opinion, we will not gain insight in these problems before we know more about the phyllotaxis in the flower as related with the overlapping of the floral parts and the contorted features.

Finally we meet with the same peculiarities in the course of the (petal) stamen fascicle traces in *Mollia speciosa* and *Colona auriculata* on the one hand, and in *Cistanthera papaverifera* and the *Schoutenia* spp. on the other. In *Mollia speciosa* the petal stamen fascicle traces are attached to the sepal basal laterals in the same way as are the petal traces in *Tilia* spp. and *Luhea divaricata*. Only now and then a fascicle trace by a double base is connected with adjoining sepal basal laterals, giving the impression of sideward traces for lateral portions of antesepalous staminal triple groups (cf. the double-based antepetalous traces in *Grewia* spp.). We may draw a parallel with the meeting of two sepal basal laterals in petal radii, their subsequent common outward course, and then again their separation. As a matter of fact there is a remarkable similarity in the course of the sepal commissural traces and the (petal) stamen fascicle traces. Both may also be directly connected with the stele in petal radii, or may be attached to the main underlying vascular supply by an oblique basal course frequently with a constant direction of deviation. This is a strong argument for considering — as we have done above — the stamen fascicle traces in petal radii as the basally commissural marginal traces of adjoining, antesepalous, hidden or manifest, triple staminal groups.

The relation with the suggested contorted characters is most clearly shown in cases with a striking constant deviation of the (common) stamen traces in, for example, *Triumfetta bartramia* and *neglecta*, as described above. Here the influence of a twisting seems beyond doubt.

With this in mind it is very interesting to make an attempt to explain the position of the stamens in *Cistanthera papaverifera* and *Schoutenia* spp., and to make a comparison with that in *Tilia* spp. Then we note that phalanges of stamens with a three-trace vascular system, the laterals of which are commissural, are situated in two apparently stable positions linked by intermediate positions. Antesepalous (*Schoutenia*) or antepetalous (*Tilia*) phalanges are thought to be placed in stable positions, while intermediate phalanges which are especially evident in many *Schoutenia glomerata* flowers, occupy places between petal and sepal radii. The variable oblique course of the commissural stamen fascicle traces in *Schoutenia* spp. and in *Cistanthera papaverifera*, and the absence of it in *Tilia* spp., may indicate that these variable positions may be due to twisting and an oblique growth of the phalanges of stamens. In fact, the position of the vascular course and its three traces in *Cistanthera papaverifera* (fig. 274) presents an intermediate state which is here accompanied by slightly contorted petals. Also in *Tilia* spp. slight indications of an asymmetrical growth may be shown by the peripheral bends of stamens if these are rather well developed, reminding one of the curled sides of the staminal lobes found in *Bombacaceae*. The suggested features are of much importance in *Malvaceae*, *Bombacaceae*, and *Sterculiaceae*.

The structure of the stamens

The anthers are of the usual type, bithecous with four slightly introrse pollen sacs, and provided with simple bundles. During their (latero-)centrifugal development they grow from hemispheric primordia into flattened and then tapering spoon-shaped structures, which on either side of the apex show initial pollen-sacs occurring along the adaxial and abaxial side of the margin. The interrelation between the lateral and longitudinal growth in the apical parts of these structures defines the ultimate anther form. As in *Elaeocarpaceae*, this form is usually elongate, except in *Brownlowieae* and in *Tilia* spp. In *Tilia* spp. the connective is bilobed, even forked, and also the vascular bundle is forked with some tissue remaining in the middle. Consequently *Tilia* flowers resemble the flowers of *Malvaceae* and *Bombacaceae* not only in the arrangement but also in the form of the stamens. Moreover, they may be compared with some *Durio* spp. as regards the position of the stamens.

As in *Sterculiaceae* — but in a less extreme form and often later in ontogeny — the anthers are resupinate in many species. This is proved by the mostly short projecting filament points, by the ontogeny, and by the course of the vascular bundles. If the curvature is markedly developed, the anthers are seemingly peltate. Mostly the thecae are parallel, but, as in many *Sterculiaceae*, they may be slightly contiguous apically (*Erinocarpus nimmonii*, *Triumfetta* spp.).

Foliar staminodes may occur as apical parts of the phalanges of stamens (inward bends of the wave-line) in *Tilia* spp. and in *Cistanthera papaverifera*, once more indicating the affinity of these plants, inclusive *Schoutenia*, with *Malvaceae*, *Bombacaceae*, and *Sterculiaceae*. Most staminodes appearing as reduced forms in the late centrifugal development are filiform, some appear as rims or petaloids.

ELAEOCARPACEAE

A. DESCRIPTIVE PART

1) ELAEOCARPEAE

Elaeocarpus spp. A, B, and C	S5-P5-St5 × 3/5p + 5s-G(2/3)
E. nouhuysii Koord.	S5-P5-St5 × ∞p + 5s-G(2/3)
E. monocera Cav.	ditto
E. homalioides Schltr.	S5-P5-St5p + 5s-G(3)
Aceratium oppositifolium DC.	S5-P5-St5 × 2p + 5s-G(3)
Dubouzetia campanulata Planch. *ex* Brongn. & Gris	S5-P5-St5 × 7p + 5s-G(5)p
Tricuspidaria dependens Ruiz & Pav.	S(5)-P5-St5 × 2p + 5s-G(5)p
Sloanea sogerensis E.G. Baker	S4-P4-St∞-G(4)s
S. javanica (Miq.) Szysz. *ex* K. Sch.	S(4)-P4-St∞-G(4)p
S. lasiocoma K. Sch.	S4-P0-St∞-G(4)s
S. guianensis (Aubl.) Benth.	ditto
S. myriandra A. C. Smith	S(4)-P(4)-St∞-G(4)s
S. lamii A. C. Smith	S4/5-P4/5-St∞-G(3/4)
S. archboldiana A. C. Smith	S5-P(5)-St∞-G(4)

Elaeocarpus spp.

Sepals as well as petals are valvate and provided with a proximal median ridge on the ventral surface. Moreover, the margins of the sepals are thick and more or less induplicate. All these inward directed ridges of the perianth parts fit in between lobes of the fleshy annular staminal disc. This lobing consists of five pairs of large antepetalous lobes and where the petal margins are projecting inwards, of five pairs of small antesepalous lobes. Around the pistil the disc is unlobed and bears the stamens in a ring.

In all species studied exactly in the sepal radii five innermost stamens are present. The location of the other stamens is different and variable.

In *Elaeocarpus nouhuysii*, a species with many stamens (fig. 323), the petal margins do not correspond to small lobes of the staminal disc, the result being that the disc has ten lobes separated by deep furrows in petal radii and less deep furrows in sepal radii, corresponding with the median ridges on the perianth parts only. The stamens, except for the five innermost in sepal radii, are spread over the upper parts of the glandular lobes irregularly. Frequently, however, one of the stamens occurs more or less precisely in petal radii some distance away from the pistil. It is remarkable that the stamens often give the impression of being arranged in more or less radial rows, together forming an irregular W-formation between two antesepalous primary stamens.

In some floral buds of *Elaeocarpus monocera*, the insertion places of the numerous stamens link the antesepalous stamens through a marked W-formation.

We may recognize this W-formation also in *Elaeocarpus spec. A* (fig. 319) in which it is formed by only five stamens. Frequently the median antepetalous stamen may be inserted more outwards than the flank stamens, in which case the stamens together form a wave-line. In *Elaeocarpus spec. B* the stamens in petal radii are absent (fig. 320).

In *Elaeocarpus spec. C* (fig. 321) the W-formation is restricted to three stamens. The median one is mostly situated exactly in sepal radii, mostly forming one whorl with the inner stamens in petal radii. The flank stamens constitute a second alternating whorl. In addition, in some sectors of some flowers four antepetalous stamens occur which may either be placed irregularly or with the fourth stamen in petal radii.

Finally in *Elaeocarpus homalioides* ten stamens form an obdiplostemonous arrangement, although frequently also they are placed in one whorl. In this species the disc is not indented in relation to the petal margins (fig. 324).

In the material of *Elaeocarpus spec. B* the inner antepetalous parts of the disc are developed rather strongly and correspondingly the cross-section of the pistil base is pentagonal with the angles in sepal radii. This is contrary to the normal condition as found in *Elaeocarpus spec. A.*

The anthers consist of four long pollen sacs placed in two lateral thecae along the distal part of the filament in an equifacial or slightly introrse manner. The apical part is sterile and prolonged into an abaxial awn. At dehiscence the wall between two pollen sacs of a theca disappears and the apical anther part is divided into an ad- and abaxial part reaching the top of the pollen sacs (fig. 317).

Developmental phases

Only one early stage belonging to *Elaeocarpus spec. A* was available for study (fig. 318). The stamen primordia develop along the border of an apex with five alternisepalous rays. The leading primordia are those of the innermost stamens in sepal radii, the others arise in centrifugal direction. The pistil appears late.

Vascular bundle supply

In the base of the flower five sepal traces leave the stele and trifurcate into a sepal median trace and two sepal basal lateral traces. The basal lateral traces first give off some sepal lateral bundles and then frequently a petal lateral trace. The sepal basal laterals of adjoining sepals may form cross-arcs because some of the sepal lateral traces are connected by a double base with basal sepal laterals on either side. In the same way in *Elaeocarpus spec. B* sepal commissural marginal traces are formed which join the stele in petal radii.

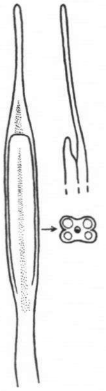
The petal traces are separated from the stele directly and pass outwards close over the sepal innervation. They may give off two lateral traces which each divide collaterally producing a total of five major petal nerves. However, often one of the petal laterals or both move sharply downwards at the base and are attached to the sepal basal lateral traces. Sometimes a petal lateral bundle is attached by a double base to the petal trace as well as to the sepal basal lateral trace (fig. 322).

All flowers have a common feature in the direct supply from the stele of a single trace towards each innermost stamen in sepal radii, whereas all other stamens are supplied by five ramifying traces or portions which leave the stele in petal radii on a lower level. For that reason the other stamens may be designated as the antepetalous stamens. In *Elaeocarpus spec. A* the stamen fascicle traces give by a fan-like ramification five stamen traces.

In *Elaeocarpus spec. C* two traces may be present side by side instead of one stamen fascicle trace. If one fascicle trace is present, it may trifurcate into three stamen traces, one of which sometimes gives off another branch towards a fourth stamen. If two stamen fascicle traces are present lying side by side, a division of one or both gives three or four stamen traces. If both fascicle traces divide, the median branches may unite again to form the trace of the middle one of three stamens. Sometimes, viz. in *Elaeocarpus spec. C*, a small portion leaves the stele gradually and falls apart into a median petal trace and two lateral stamen fascicle traces.

In *Elaeocarpus homalioides* each stamen receives a trace from the stele directly, but the trace of an antepetalous stamen may be attached to the proximal part of the petal trace in case this stamen is situated more peripherally.

In *Elaeocarpus nouhuysii* the stamen fascicle traces split into a fan-like arrangement of antepetalous stamen traces. They are connected with the petal trace into a petal stamen fascicle trace which separates from the stele in petal radii.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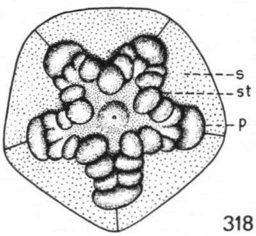

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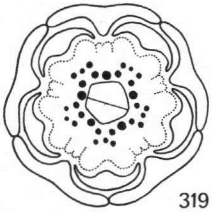
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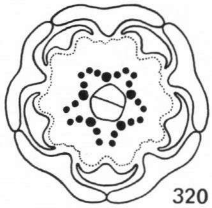
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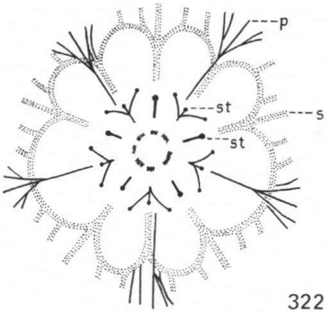

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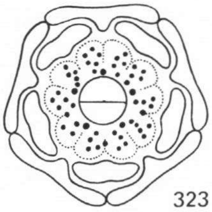
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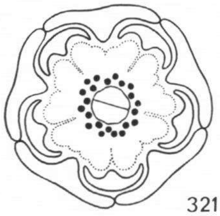
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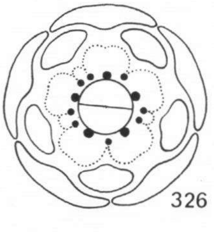
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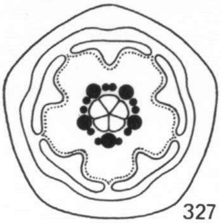
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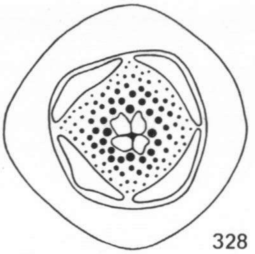
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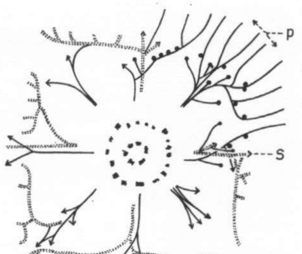


329

The explanation of these figures can be found at the bottom of the opposite page.

In all species tiny bundles come from the proximal parts of the stamen traces and anastomose under the surface of the peripheral part of the glandular disc. The antesepalous stamens contribute little to this system. On the other hand a pair of these tiny bundles towards the disc may come as two opposed flank parts from the proximal part of the petal trace.

The stamens are each provided with a simple collateral bundle with inwards directed xylem, which goes up into the distal filament part to the ends of the pollen sacs.

Other authors

Rao described the petal stamen traces in *Elaeocarpus robustus* and *ganitrus*. They split into a petal median trace and two flank parts. The latter parts give a number of antepetalous stamen traces directly or by means of a basal ramification into two or three branches. The upper five antesepalous stamens are innervated by separate single traces which come from the stele directly.

Aceratium oppositifolium

The flower structure is very much like that of *Elaeocarpus*. The disc is hemispherical and indented only peripherally in relation with the median ridges on the perianth parts. The anthers are not awned. There are five triplets of stamens (fig. 325) consisting of an inner member in sepal radii and two peripheral lateral members. During development the median stamens are in advance of the lateral ones.

Vascular bundle supply

Five sepal traces leave the stele and give off some sepal lateral traces. Five alternating bundles leave the stele on a higher level and divide into a set of collaterally dividing sepal laterals, a pair of petal laterals and a pair of bundles which unite in the middle to form the petal median trace. Some of the middle sepal laterals are attached by double bases to the sepal trace as well as to the commissural system and accordingly form cross-arcs. Sometimes the petal median trace comes from the stele directly.

Upwards a collaterally dividing staminal trace, or two stamen traces side by side leave the stele directly in petal radii. Still higher the supply towards the innermost stamens comes from the stele in sepal radii. The disc innervation is as in *Elaeocarpus*.

Dubouzetia campanulata

The floral structure is very much like that in *Elaeocarpus*. The chief difference lies in the pistil which has five antepetalous cells. Below five uppermost antesepalous stamens which alternate with the pistil cells, about seven stamens are inserted in front of each petal.

Above the level of departure of the sepal median and sepal commissural marginal traces, first five antepetalous portions, and second five upper single traces are separated from the reconstituted stele. The antepetalous portions immediately fall apart into petal traces and traces for the stamens in front of the petals, whereas the single traces represent the traces of the uppermost stamens in sepal radii.

Elaeocarpus spec. (A). —Fig. 317. Stamen, ventral side left, lateral view on the right, and a c.s. — Fig. 318. Developmental phase of the androecium (60 ×). — Fig. 319. Floral diagram.

Elaeocarpus spec. (B). — Fig. 320. Floral diagram.

Elaeocarpus spec. (C). — Fig. 321. Floral diagram. — Fig. 322. Course of vascular bundles in receptacle.

Elaeocarpus nouhuysii. — Fig. 323. Floral diagram.

Elaeocarpus homalioides. — Fig. 324. Floral diagram.

Aceratium oppositifolium. — Fig. 325. Floral diagram.

Sericolea spec. — Fig. 326. Floral diagram.

Tricuspidaria dependens. — Fig. 327. Floral diagram.

Sloanea javanica. — Fig. 328. Flower base, diagrammatically. — Fig. 329. Course of vascular bundles in cleared flower base, dots representing places of attachment of stamen traces.

Tricuspidaria dependens

The floral structure resembles that of *Elaeocarpus*. The sepals are partly fused. The glandular disc is lobed in relation with the adaxial surface of the petals. On the upper part of the disc fifteen equidistant stamens are inserted in a whorl or in antesepalous triplets. Sometimes the lateral members of the triplets are inserted more to the outside (fig. 327). The pistil has five antepetalous cells, as in *Dubouzetia*.

Developmental phases

The sepals and petals arise successively, but very soon the primordia of each whorl reach about equal size. On the apex within the petal primordia a low peripheral wall arises which is slightly pentagonal with antesepalous angles. On this wall five stamen primordia arise — not simultaneously — in sepal radii, followed by two primordia on either side. In the petal radii no primordia arise; the lateral stamen primordia may meet in the petal radii. The disc develops only fully after the formation of the stamens.

Vascular bundle supply

Five sepal traces separate from the stele in the flower base and trifurcate into sepal median and sepal basal lateral traces, the latter of which form sepal lateral bundles and cross-arcs. Five alternating petal traces leave the stele, which form only the median petal bundles. The lateral petal traces are attached to the cross-arcs. Again five traces come from the stele in petal radii (not exactly on the same level), which divide each collaterally into the traces for the lateral stamens. For this reason the stamens may be called antepetalous. Often in some sectors of a flower the petal traces are united basally with the traces for the antepetalous stamens. Ultimately five single traces leave the stele for the primary stamens in sepal radii.

Tiny bundles come from the petal trace and from the antepetalous stamen traces, which ramify into an anastomosing network of bundles lying under the glandular surface of the disc.

Sloanea spp.

The flowers are mostly tetramerous, the petals may be sepaloid or absent. Between the places of attachment of the stamens the conical receptacle has a fleshy glandular surface. In *Sloanea lasiocoma* the disc shows a free annular region between an inner and a peripheral ring of stamens.

The often numerous stamens bear four pollen sacs which are arranged in two thecae along the distal part of the filament. The anthers and their pollen sacs taper upwards and end into a sterile mucro. A latero-introrse dehiscence takes place by a slit that is chiefly open at its apex. In *Sloanea myriandra* the outer stamens are small and without thecae, they may cohere laterally. The stamens develop in centrifugal direction.

The position of the pistil cells, if four, is antesepalous, except in *Sloanea javanica* in which it is antepetalous. In all floral buds (fig. 328) the innermost stamens which during development are in advance of the others alternate with the pistil cells. Slightly more outwards one or two stamens alternate with the first stamens. However, still more outwards the pattern is irregular (in mature herbarium material).

Vascular bundle supply

In all species studied the stamen bundles are single and run unbranched into the mucro.

Sloanea sogerensis (fig. 330). Four sepal median traces separate from the stele in the flower base, followed by four alternating sepal commissural lateral traces. Both produce sepal lateral bundles, the former by the side-branches of a proximal trifurcation, the latter by the side-branches of a proximal collateral division. Some of the middle sepal lateral traces form cross-arcs by their double or multiple basal traces, which are partly attached to the sepal median partly to the sepal commissural lateral traces.

The petal nerves come together in two petal basal lateral traces by which they are attached to both proximal flanks of a sepal commissural lateral trace. Some of the outside petal laterals may either be attached by their own common trace to the proximal part of the sepal median or commissural lateral trace, or they may be attached directly to the sepal basal laterals. Frequently petal lateral or middle bundles have double bases connecting them with two of the common traces mentioned above, or with the sepal basal laterals.

The majority of stamen traces is attached to the petal traces directly contributing to the mass of vascular tissue present in alternisepalous regions. However, some stamen traces are either linked up with the basal parts of the sepal median and commissural lateral traces, or directly to the stele above the point of divergence of these traces.

The carpel dorsal traces leave the stele in sepal radii.

Sloanea javanica (fig. 329). Four alternating sets of four traces each leave the vascular cylinder on successively higher levels of the flower base. The lowest are the sepal traces which trifurcate into a sepal median and two basal sepal lateral traces. They are immediately followed by the spreading petal stamen traces in petal radii to which many stamen traces are attached. Next are the petal stamen traces of sepal radii which by a collateral division produce two branches that split into some marginal petal traces and a number of stamen traces. Lastly the carpel dorsal traces leave the stele in petal radii.

Thus the organization of an additional (commissural) petal stamen trace in sepal radii is the prominent difference with *Sloanea sogerensis*, exactly in correspondence with the second important difference formed by the alternate location of the pistil cells.

Now and then some sepal laterals may be attached to the petal stamen traces in petal radii either fully or by means of the other part of a double base. Sometimes a few marginal petal traces may be connected with the sepal innervation. Some stamen traces may come from the stele directly just above the place of divergence of the petal stamen traces in sepal radii.

Sloanea myriandra. The vascular bundle supply of only one flower could be studied. In the flower base eleven portions of the stele separate gradually, forming loops if viewed in cross-section. When the stele suddenly widens funnel-shaped the outer parts of the separating portions bend outwards and strongly ramify into a plexus underlying the sepals and petals, from which the numerous nerves to these organs are given off.

The flanks of the separating portions proceed upwards, closing the gap above the perianth traces or almost so, and give a tree-shaped ramification ending in numerous stamen traces. Other parts of the stele bend inwards almost perpendicular to the flowering axis to reconstitute the vascular cylinder in the centre of the flower.

Sloanea lamii. The sepal nerves join the vascular cylinder by menas of sepal median and commissural marginal traces and form cross-arcs by the double bases of their middle laterals.

The petal traces are attached to the proximal flanks of the sepal commissural marginal traces.

Stamen fascicle traces leave the stele directly in sepal and petal radii or are sometimes attached to the proximal parts of the perianth bundles. In addition, stamen fascicle traces leave the stele between sepal and petal radii and frequently give rise to radial series of stamen traces.

In a flower of **S. archboldiana** many small twisting bundles come from the stamen traces and innervate the disc.

In **S. lasiocoma,** a species without petals and with fewer stamens, two sets of sepal traces are separated from the stele, the first giving a sepal median and some sepal lateral traces, the second, after a collateral division giving only some sepal laterals. Some sepal laterals have a double trace so that they are attached to both main traces producing cross-arcs. Moreover, on almost the same level some traces leave the stele supplying stamens which are situated between sepal and petal radii. The bulk of the stamen traces is connected with the proximal parts of the main sepal traces, chiefly with the commissurals. In some flowers they are not at all connected with the sepal median traces. Some of them may divide into a few stamen traces.

In material of **S. guianensis,** which in anatomy resembles *S. lasiocoma* very much, stamen traces are never connected with the median sepal traces.

Other authors

According to Eichler *Sloanea* is provided with five alternipetalous groups of stamens, which are hardly separate.

2) ARISTOTELIEAE

Aristotelia macqui L'Hérit.	S5-P5-St5×2p+5s-G(3)
A. fruticosa Hook. *f.*	S4-P4-St4s-G0
Sericolea spp.	S5-P5-St5×2/1p+5s-G(2)
Vallea stipularis Linn. *f.*	S5-P5-St5×2s+5×3p+5s-G(5)p
Muntingia calabura L.	S5-P5-St∞-G(5)p

Aristotelia macqui

Between calyx and pistil the receptacle is formed by a glandular disc, except at the insertion places of petals and stamens. Petals and stamens are placed in a wave-line, meeting laterally (fig. 331), and leave open the entire upper part and five lower alternipetalous parts of the disc. The outer bends of the wave-line are formed by the petals, the inner bends by triplets of stamens consisting of a median upper stamen in sepal radii and two lateral lower stamens. Mostly a lateral stamen is placed closer to the other lateral stamen in the same triplet than to a lateral stamen of an adjoining triplet. Frequently one or both lateral stamens are lacking or they are present as small, subulate, sterile organs. If they are absent, the disc is developed instead, and its upper part linked with its alternipetalous lower parts.

The anthers have four pollen sacs arranged in two thecae which are attached latero-introrsily on either side of the distal part of the filament. During budding stages the central stamens are larger than the lateral stamens.

Vascular bundle supply (fig. 332)

Five sepal traces are the lowest traces to leave the vascular cylinder in the flower base. They trifurcate into a sepal median and two sepal lateral bundles. By a double base the trace of the central stamens in sepal radii is attached to their proximal flanks.

Five alternating main traces leave the stele on a slightly higher level, and during their outward course give off three pairs of bundles by means of opposed flank parts. The first pair is formed by the traces of two lateral stamens of adjoining triplets, which for that reason may be considered antepetalous stamens. The second pair is formed by traces towards the same sepal laterals as are served by way of the sepal median traces, and which accordingly show a double origin. The third pair is formed by petal lateral traces.

In the upper part of the disc some unconnected and irregularly distributed vascular tissue is present.

Aristotelia fruticosa.

The tetramerous flowers are provided with four stamens in sepal radii only. The disc has four antesepalous lobes in the middle of which the stamens are placed. The course of vascular bundles is similar to that in *Aristotelia macqui*. A trace is present in one sector of a flower which runs towards the place where in *Aristotelia macqui* a lateral stamen is situated.

Sericolea spp.

On the strength of arguments put forward by van Balgooy *Sericolea* is treated here under *Aristotelieae*.

The floral structure resembles that of *Elaeocarpus* in many characters. For instance the disc, though smaller, is indented in correspondence with the ridges on the perianth parts. However, another kind of small sometimes bilobed lobes may occur on the disc in front of the petals in some or all sectors of most flowers. This variable occurrence is related to the stamen position.

In all flowers there are five innermost stamens in the sepal radii. They alternate with sets of one or two outer stamens. If two outer stamens occur, the antepetalous lobe is present, if one stamen occurs the antepetalous lobe is absent. The two stamens are placed exactly between sepal and petal radii, or closer to sepal radii. The single stamen is placed in a petal radius, sometimes in the same whorl as the inner stamens, but mostly more outwards. As a consequence some flowers may have ten stamens in obdiplostemonous arrangement and no special lobing of the disc, others may have fifteen stamens and five additional antepetalous lobules. Actually most flowers have two antepetalous stamens in three sectors and one antepetalous stamen in the two other sectors (fig. 326). One young flower was observed with a third stamen outwards of the two antepetalous stamens and placed in petal radii. Unfortunately in that flower the disc had not yet developed. Mostly the outer stamens are a little bit shorter than the inner ones. The anthers are like those in *Elaeocarpus*, but not awned.

Vascular bundle supply

Mostly four alternating whorls of traces leave the stele of the flower base, namely sepal and petal traces and two sets of stamen traces. The stamen traces of the upper set are those for the antesepalous stamen. The traces of the lower set may divide collaterally into two antepetalous stamen traces. Two stamen traces may leave the stele directly side by side. Sometimes the staminal trace is connected with the petal trace basally.

Vallea stipularis

The sepals are valvate, the petals imbricate. Between perianth and pistil the receptacle forms a well-developed disc which by a whorl of laterally meeting stamens is divided into an inner wall and five small outer parts in front of the petals.

The androecium consists of five central stamens in sepal radii, followed outwards by a whorl of ten stamens situated between sepal and petal radii. A third whorl is formed by five stamens in petal radii, and the last and most peripheral whorl has five pairs of stamens on either side of the sepal radii. The differences in level of insertion are only small. Members of the last two whorls may be absent in certain or all flower sectors.

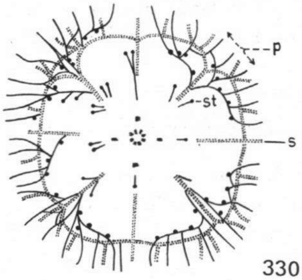
The anthers contain four pollen sacs distributed over two thecae which are attached along the distal part of the filament and may be slightly sagittate.

Developmental phases

The development of the stamens takes place strictly centrifugally in the sequence given above (fig. 333). The petals arise earlier than the first stamens, the pistil is later. The full development of the disc takes place late in the ontogeny.

Vascular bundle supply

Sepal median and sepal commissural lateral traces form two whorls which are succes-



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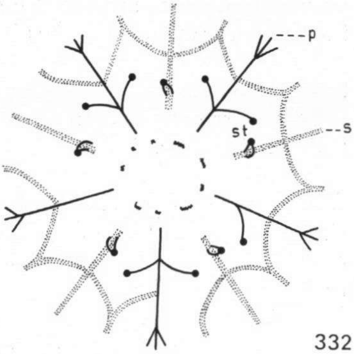

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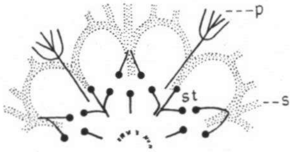

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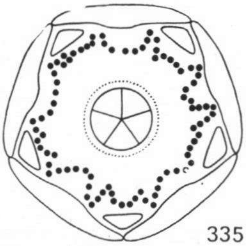

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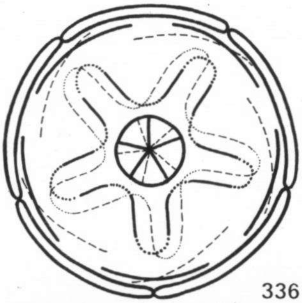

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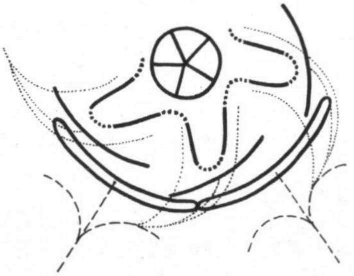

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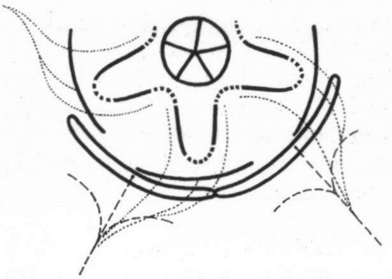

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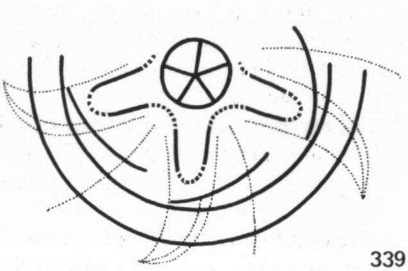

339

The explanation of these figures can be found at the bottom of the opposite page.

sively separated from the vascular cylinder in the flower base. Both give off sepal lateral traces, partly to the same lateral nerves which accordingly by their double origin produce the effect of cross-arcs.

One collaterally dividing bundle or two bundles side by side are attached to the proximal part of the sepal median trace. They represent the traces of the outer antesepalous pairs of stamens.

On a higher level two sets of five traces leave the stele in petal radii, one immediately above the other. The first set produces the petal traces which split into the complete petal innervation, the second set the stamen fascicle traces. The latter traces give by two successive divisions three traces each, going to two stamens in the second whorl and a third one in a petal radius. Sometimes two traces leave the stele side by side, one of which gives off a third trace. Anatomically these three stamens are antepetalous. Ultimately five traces towards the central stamens come from the stele directly.

Sometimes two pairs of opposed flank bundles are separated from the base of the sepal commissural lateral trace, a central pair forming the two traces of the antepetalous stamens, a peripheral pair forming two traces which unite as the petal trace. Here the traces are attached to the perianth traces, but it may also occur that a loop-formed portion separates from the stele gradually and falls apart in the five required traces side by side (fig. 334).

Many tiny bundles spread irregularly into the upper part of the disc, coming from the bases of the stamen traces of the inner two whorls.

Muntingia calabura

Between stamens and pistil the receptacle is developed as a high, annular, glandular disc which is provided with long hairs on the outside, just as are the parts of the receptacle outwards of the antesepalous stamens. However, immediately around the insertion of the pistil the receptacle is not housed disciform. The situation is like in *Mollia* which in young phases shows within the stamens a very flat receptacle free of appendages but covered with a hairy ring at some distance around the pistil.

Meeting laterally the numerous stamens are arranged in a single whorl, leaving free part of the receptacle towards the perianth, especially in front of the sepals. The whorl of the stamens has a sinuous form caused by 1) two prominent outward coils laterally in front of the petals, 2) shallow outward coils in petal radii, 3) the fact that the antesepalous parts are situated more centrally than the antepetalous parts (fig. 335).

The stamens consist of two reniform bisporangiate thecae attached latero-introrsily along the distal filament part, resembling those in *Tilia*. The thecae are prolonged chiefly downwards and remain free from each other.

Developmental phases

In the only young bud which could be studied the stamens seem to develop strictly centrifugally. The disc develops afterwards.

Sloanea sogerensis. — Fig. 330. Same as fig. 229.

Aristotelia macqui. — Fig. 331. Floral diagram. — Fig. 332. Course of vascular bundles in flower base.

Vallea stipularis. — Fig. 333. Floral diagram. — Fig. 334. Vascular bundle supply in flower base.

Muntingia calabura. — Fig. 335. Floral diagram.

Malvaceae. — Fig. 336. General diagram. Wave line represents places of stamen insertion. Dotted: more or less reduced regions. Interrupted line: contorted condition. Full line: ideal condition. — Fig. 337. General diagram for *Hibisceae*. Interrupted line: vascular supply of sepals. Dotted: vascular supply of petals and staminal lobes. — Fig. 338. Same for *Malveae*.

Bombacaceae. — Fig. 339. General diagram. Wave line represents places of stamen insertion. Dotted: vascular supply of petals and staminal lobes.

Supply of vascular bundles

The vascular cylinder widens suddenly in the base of the flower and gives off five sepal median and five alternating sepal commissural lateral traces which bend outwards on almost the same level. Whereas the median traces form the sepal median bundles only, the commissural lateral traces form all the sepal lateral bundles of adjoining sepal halves by means of a ramification system with a main collateral division. Occasionally, one of the sepal lateral nerves is connected with the median as well as the commissural lateral trace by a double base.

The rest of the stele continues its course for some distance as ten portions. On a higher level these portions each give off two tiny traces which first bend inwards almost perpendicular to the flowering axis and then curve upwards to supply the dorsal carpellary wall and the centre of the pistil.

The rest of the ten portions each fall apart into two stamen fascicle traces. The twenty stamen fascicle traces may be joined by some others coming from the flanks of the main sepal traces. All stamen fascicle traces ramify irregularly into an annular anastomosing vascular system from which the stamen traces arise. In one flower the ten portions, mentioned above, immediately pass in the anastomosing system.

In each stamen a single bundle runs unbranched towards the top of the filament.

Other authors

Eichler stated that, according to Bocquillon, *Muntingia* has five alternipetalous groups of fertile free stamens and five groups of sterile antepetalous stamens. Rao recognized only fertile stamens. He further described the vascular ring under the androecium, but for the rest his data are very conflicting.

B. COMPARATIVE PART

1. The structure of the androecium

In the *Elaeocarpaceae* the receptacle near the stamens consists of a glandular disc. The anthers are straight and slender and have two thecae with two pollen sacs each; some are apically sterile. They are provided with simple vascular bundles. In sepal radii five innermost stamens are present which alternate with the antepetalous pistil cells if there are five. Also in *Sloanea javanica* — by Schumann placed in a separate section — four innermost antesepalous stamens alternate with four antepetalous pistil cells. However, in the other *Sloanea* spp. studied here, innermost antepetalous stamens alternate with antesepalous pistil cells.

The innermost stamens develop first and are followed by the later stamens in a centrifugal sequence. Except in the *Sloanea* spp. — which have numerous stamens equally spread all over the receptacle — the later stamens do not only develop outwards, but also sidewards, starting from the places of the innermost stamens in two directions towards petal radii. We are dealing with a latero-centrifugal way of development.

In this way, in *Elaeocarpus nouhuysii* even coiled rows of stamens are formed which are implanted in disc tissue as are the stamens in *Sloanea* spp. This arrangement may be considered the starting one in a series of decreasing development leading to a state in which only the innermost stamens in sepal radii remain. Intermediate phases are frequent in *Elaeocarpus* spp. with minor rows of stamens. In *Tricuspidaria dependens, Dubouzetia campanulata*, and *Aceratium oppositifolium* the flowers have fifteen stamens, in each flower sector two on either side of the innermost stamens. In *Aristotelia macqui* one of the lateral stamens may be missing or shaped as a subulate appendage. In *Sericolea* spp. the sets of two stamens between the innermost ones may be replaced by one stamen in petal radii in some sectors of the flower. In *Elaeocarpus homalioides* the flowers show ten stamens in one whorl or in an obdiplostemonous position. And finally in *Aristotelia fruticosa* we have a species with only four stamens left in sepal radii.

The places exactly in petal radii may be occupied or not. If they are not occupied the impression is that the stamens are arranged in antesepalous groups, for instance in *Aceratium oppositifolium*. In *Sericolea* spp. we note that, while in some flower sectors two stamens are present between the innermost antesepalous stamens, in other sectors only a single stamen occurs, which is placed exactly in the petal radius. If there are two stamens an additional lobe forms part of the disc in that region, but in the case of only one stamen there is no further lobing. Evidently the question of either two stamens near petal radii or a single one precisely in petal radii is settled by the available space. There may be a slight inequality of the floral sectors due to quincuncial development. As a matter of fact sepals and petals arise successively in primordia of *Tricuspidaria dependens*.

In *Vallea stipularis* and in *Elaeocarpus spec. B* the formation of rows is not very evident. In *Vallea stipularis* the latero-centrifugal development is complicated by a further formation of some peripheral stamens alternating with the three first formed stamens. As regards *Elaeocarpus spec. B* it seems appropriate to wait till primordial phases are available for study before drawing conclusions. The same holds for *Sloanea*.

There are some features indicating that the disc represents sterile androecial tissue. Traces towards the disc tissue are attached to the proximal parts of stamen traces, though hardly or not at all to those of the innermost stamen traces. Finally, in *Sericolea* spp. the more advanced development of the disc corresponds to the presence of more stamens in certain sectors of the flower.

2. THE SUPPLY OF VASCULAR BUNDLES

The scheme of the staminal arrangement offered above is seemingly contradicted by the course of the vascular bundles. With the exception of *Sloanea* the stamens are invariably supplied by five inner single traces towards the innermost antesepalous stamens and five outer fascicle traces in petal radii. The inner traces are almost exclusively attached to the stele, the outer traces may be connected with the petal supply. Therefore, judged from anatomy the androecium would be composed of an obdiplostemonous arrangement of five inner antesepalous single stamens and five outer antepetalous stamen groups. Moreover, as in *Elaeocarpus spec. B*, *Aceratium oppositifolium*, and *Vallea stipularis* the presumed antepetalous groups are frequently supplied by two traces side by side, the antepetalous groups may be considered as double. The conclusion reached above that in *Vallea stipularis* the stamens in the petal radii are not to be taken as separate groups is corroborated by the fact that these stamens are not supplied by a separate trace coming from the stele, but receive a trace branching from one of the other antepetalous stamen traces.

In *Sloanea* many single or branching stamen traces are connected with perianth bundles, chiefly with petal bundles in alternisepalous regions. The petal traces are mostly attached to the sepal commissural traces. However, a number of stamen (fascicle) traces, either upper or inner ones, may come from the stele directly between sepal and petal radii or above the divergence of the main perianth traces. Here the course of the vascular bundles is rather variable. Applying the origin of the traces as a criterion the androecium seems to consist of quite a number of stamen groups, the upper ones of which are free while the lower ones are connected with the perianth. In *Sloanea javanica*, above and alternating with the usual stamen traces which are attached to the petal innervation, an additional whorl of petal stamen traces is attached to the stele on a higher level in sepal radii. These branch into lateral petal nerves of adjoining petals and nerves of the stamens in front. The next higher whorl consists of the carpel dorsal traces in petal radii, alternating with the additional whorl of petal stamen traces. As a consequence this additional whorl is in the same position as the whorl of single traces for the innermost stamens in *Elaeocarpus* and other genera.

The sepal innervation mostly orginates by the branching of two successive and alternating sets of traces, median and commissural sepal traces in sepal and petal radii respectively. In sectors of the flowers in *Elaeocarpus* spp., in *Tricuspidaria dependens*, and *Sloanea javanica* nearly all sepal laterals may be attached to the sepal median traces. Generally the petal traces depart from the stele independently.

3. VARIATION IN THE COURSE OF THE VASCULAR BUNDLES

The clearing technique gives us the opportunity to study the variability in the course of the vascular bundles, especially in the different parts of a single flower. In so doing we meet with several interesting correlations. For instance, the connection of certain traces with perianth traces instead of either with the stele or their own kind of traces, may be correlated with the presence of reduced organs. In *Vallea stipularis* outer antesepalous stamens are frequently lacking. If they are present their traces are connected with the median sepal supply. Incidentally in this species the petal trace and the antepetalous stamen trace(s) are connected with the sepal commissural trace in its proximal part. Correspondingly the outermost stamen in the petal radius may be missing. In *Aristotelia macqui* the trace towards the innermost antesepalous stamen is connected with the proximal sepal median trace by means of a double base. Moreover, the antepetalous stamen supply and the petal trace are connected with the sepal commissural trace. Correspondingly in this species the lateral outer stamens may be reduced.

It appears from these correlations that among the stamens especially the peripheral ones may be less well or not at all developed, in accordance with the conclusion of the centrifugal development. So in *Tricuspidaria dependens* the lateral stamens may be situated more outwards than the inner stamens. In that case the traces supplying these stamens are attached to the petal innervation. In other flower sectors, where all stamens are in one whorl, the traces come from the stele directly. Much the same are the conditions in *Elaeocarpus homalioides*, in which the trace serving an antepetalous stamen is connected with the petal trace only if that stamen is situated slightly more outwards than the inner stamens in sepal radii. Finally in *Tricuspidaria dependens* peripheral disc traces come from the perianth, more central traces from the stamen traces.

It would seem that the traces towards these peripheral, later formed, stamens come rather from heterochtonous vascular tissue at hand using a more direct way. We may observe similar ways in perianth traces. In *Sloanea sogerensis* outer petal laterals may link up with the sepal median or commissural traces. In *Tricuspidaria dependens* the petal laterals are connected with the sepallary cross-arcs. In *Elaeocarpus* spp. some petal laterals, especially submarginal ones, may be connected with the sepal system, others, mainly submedian ones, with the median petal trace. In that case petal laterals in between may have double bases relating them to both origins. Also this ambivalent condition produces the phenomenon of the cross-arcs. Here either some middle sepal laterals are connected with the median as well as with the commissural sepal traces by means of double basal traces, or, in case there is no sepal commissural trace, some marginal sepal bundles have double bases relating them with the sepal basal laterals of adjacent sepals.

C. INTERPRETATIVE PART

The most interesting genus is probably *Sloanea*, because of the androecium as well as of perianth characteristics. However, much more material, properly fixed, in developmental series, has to come in before a morphologist can reveal the structure. In the species without petals, such as *Sloanea lasiocoma*, alternisepalous groups of stamens may be distinguished on account of the position of the innermost stamens which alternate with the sepals. Furthermore these groups may be considered to have a more compound nature, in view of the diverse vascular bundles by which they are served. Most remarkable in this respect are the traces coming from the stele directly between sepal and petal radii, which we also noticed in *Muntingia calabura*. They may suggest a triple nature, representing the lateral partners. An important feature may be observed if comparing *Sloanea sogerensis* with *Sloanea javanica*, the only visible difference between these species being formed by the position of the carpels. For it appears that the antepetalous place of the carpels in *Sloanea javanica*, which is unusual for *Sloanea*, corresponds with the presence of an additional whorl of antesepalous petal stamen fascicle traces. Thus, anatomically, the location of the carpels is in accordance with the principle of the alternation of successive whorls of primordia. In this way the existence of an additional whorl, which is hidden from direct view (also during ontogeny?), is betrayed by the vascular system. At the same time these supplies give a hint to the possibly complicated (triple) character of the androecium also in *Sloanea*.

Muntingia calabura resembles *Mollia speciosa* (*Tiliaceae*) not only in receptacular characters and in the presence of an anastomosing ring of bundles under the staminal region, but also in the arrangement (not in the shape) of the stamens. We note a centrifugal development of fifteen what we have called earlier phalanges of stamens, namely five in sepal radii and ten smaller ones between sepal and petal radii. Consequently we may think of triple antesepalous arrangements of stamen groups, more reduced than in *Mollia speciosa*, but still with many-membered middle portions. As a matter of fact the reduction of the groups to mere phalanges of stamens can be observed in the antesepalous groups in *Mollia* and the antepetalous groups in *Colona*. In *Muntingia calabura* the lateral parts of the triple arrangements are supplied by separate fascicle traces derived from the stele between petal and sepal radii (cf. *Sloanea lasiocoma*). In *Mollia* they are more commissural.

The supposed limitation of the staminal development to a marginal growth as phalanges, is also shown in *Vallea stipularis*. Here two additional stamen primordia on the outside of and alternating with the first three antesepalous primordia are frequently omitted in some flower sectors. The traces of these stamens, as opposed to the other stamen traces, are attached to the perianth traces, once more showing their tendency towards reduction.

In *Vallea stipularis* also the single peripheral stamen which is present in the petal radii may be absent in some floral sectors, so that antesepalous groups are formed by the phalanges. The same change may be observed in *Elaeocarpus* spp., in which we may construct a reduction series starting from the rather extensive and coiled (cf. *Pachira*, *Bombax etc.*) phalanges in *Elaeocarpus nouhuysii*. It is especially evident in *Aceratium oppositifolium* and in *Aristotelia macqui* that the antepetalous places are left open together with a further limitation in the development of the phalanges to sets of three stamens.

In *Sericolea* spp. in some flower sectors only one stamen originates between the leading stamens instead of two in other sectors. We are inclined to think that this depends on the available space, in correlation with a quincuncial character of the sepals (cf. *Tilia*). *Elaeocarpus homalioides* shows a still further reduction to a more or less obdiplostemonous arrangement of ten stamens, and finally in *Aristotelia fruticosa* we may find the antesepalous leading stamens only.

As regards the vascular bundle supply all species, except *Sloanea*, have one feature in common, namely the independent supply of single traces towards the four or five leading innermost stamens in sepal radii. In *Muntingia calabura* this trace branches into the traces of a number of stamens. All the other stamens are supplied by the branching of stamen fascicle traces which are often not linked up with the petal traces. In the place of each of these fascicle traces two (fascicle) traces often occur side by side in some *Elaeocarpus* spp., and very obviously so in those cases, mentioned above, in which the antepetalous receptacular places are not occupied by stamens (cf. a similar case in *Muntingia calabura* as compared with *Mollia speciosa*). If outermost stamens are present in the petal radii, they are innervated by branches of (one of) these stamen fascicle traces, showing that they do not represent separate outermost antepetalous groups.

The double character of the antepetalous supply again marks the possible triple nature of the antesepalous phalanges of stamens, even when the phalanges are formed by only a few stamens. It may at least be concluded that these groups receive three traces, the laterals of which may be commissural.

The few available ontogenetic data all indicate a grouped character by the successive origin of leading innermost stamen primordia. Only in *Tricuspidaria dependens* the occurrence of a wall in advance of the stamen primordia has been demonstrated.

DISCUSSION AND GENERAL INTERPRETATION

The value of the vascular bundle course

During this study attention has been paid to the variation in the course of the vascular bundles in different flowers of the same species and in different sectors of the same flower. This was accomplished by the use of clearing techniques, by which the vascular bundles can be readily observed, be it only through their lignified parts. When she introduced the chloral-lactophenol method in floral morphology, Vautier (1949) failed to take this limitation into account, stating that the stamen traces in *Polygonaceae* have no connection with the underlying vascular bundle supply.

In the field of interpretative floral morphology the present study leads to the following general considerations, some of which may provide a motive for experimental research.

The lateral sepal bundles have double or multiple bases by which they may be connected with laterals of their own sepals, with laterals of adjoining sepals, with petal traces, and with the stele in alternipetalous radii. In the last two cases the calyx innervation is formed by ten traces. Nevertheless, since the five alternating traces are considered to represent commissural traces, no one will be misled into concluding that there are ten sepals. Where the same occurs in the androecium, however, authors regard the stamens as being arranged in ten obdiplostemonous groups (Saunders, 1937; Gazet du Chatelier, 1940; Rao, 1952). To me it seems more logical to assume the presence of five three-trace groups that may be fused laterally at the base, the more so since, with a few relevant exceptions in *Tiliaceae*, alternating group primordia and separate alternate stamen primordia are never found. In the following this view forms the keystone of our interpretation.

Whereas some traces seem to diverge simply as parts of the stele, the direct attachment of other traces to traces of underlying floral parts is frequently double, multiple, or brush-shaped. If longitudinal growth of the floral apices is intermittent with the successive formation of floral whorls, the traces to a new whorl will reconstitute a stele. On the other hand, if the flowers are broad, the traces are attached directly to the traces of the underlying floral parts. This differerence can easily be studied in various flowers of *Hibiscus rosa-sinensis*. In *Malva* species the supply towards the calyx is even entirely linked up with the epicalyx supply.

The multiple bases suggest that an incipient primordium provides a stimulus for new trace formation within a certain diffuse range. The reaction may be started from anywhere within this range where vascular tissue happens to be present already. In this way some new traces may originate from the flanks of one or several nearby traces.

Evidently this formation tends to establish itself over the shortest possible distance. The tendency may even interfere with the natural alliance of the traces, for instance when a trace that passes close over another, lower trace, shows some cross-connections or, in other floral sectors, is attached to the lower trace entirely. The influence of distance may also be shown if petal primordia follow upon a markedly quincuncial calyx (e.g., in *Tilia*), four out of five petal traces generally attaching obliquely to the traces of two, supposedly the upper, calyx members. Since marginal traces, that are formed as the last traces of a floral part or of a group of floral parts, come to lie close to the traces of other floral parts it is conceivable that they are often connected with the traces of other parts rather than with those of their own kind. For instance, lateral petal traces are more likely to be connected with the commissural sepal supply if it is present in a given floral sector, and the lateral stamen traces of a group of stamens with the perianth supply. As these last-formed parts are under the influence of reduction there is a correlation between reduction and a heterogeneous attachment of traces. This heterogeneous attachment leads to the occurrence of peripheral organs or peripheral parts of groups with a separate vascular supply; because of this they are easily mistaken for separate entities. Consequently, since it must take variability into account, study of the attachment places is arduous and the results must be used very judiciously. As far as possible in this study, therefore, use of the attachment places of vascular traces as arguments has been avoided. Sometimes the development of a trace may even be overrun by intervening meristematic growth, so that a sudden deviation may take place in the course of the trace (as, for instance, in the appendages on the stamen tube of *Chorisia*).

If it is true that a trace can be formed from a more or less diffuse starting region we may also assume that an oblique basal course of the trace may result if underlying vascular bundle tissue is present on only one side of the region. This may be the case, for example, if the site of a primordium of a new floral part is not exactly between and above two preceding parts. This concurs with Hagemann (1963), who maintained that the primary morphogenesis rules the course of the vascular bundles. If this deviation in the course of a trace is constant for a whorl of organs we might suppose that an additional spiral growth in the apex had affected the place and form of the primordia. This growth could be quite extreme, judging from its independent character in the material of *Triumfetta* spp.

Since the time of Van Tieghem (1884), the concentric (amphiphloic) nature of a vascular bundle has been advanced as an argument for the axiality of its organ. However, since concentric bundles in the receptacle prove to fall apart into traces for a number of very different flower organs or parts of organs, during this study we have come to doubt whether this relation is inevitable. Cortical bundles in the thick cortices of bulky flowers as well as the bundles in the stout filaments of *Bombax* spp. and *Kokia rockii* and the bundles in thick petals are concentric. Therefore we think that a vascular bundle has a tendency to become concentric if it is embedded in a large amount of tissue. Bonnemain (1962) described the appearance of concentric cortical bundles in the fruitstalks of *Solanum melongena.*

The supposedly conservative character of vascular bundles, that is the persistence of bundles after their floral parts have been reduced, has led to much discussion in works on floral morphology. Residual bundles can be valuable tools in comparative morphology. According to Arber (1933), it was Henslow who in 1888 for the first time formulated the conservatism of vascular bundles. Arber (1933) and Saunders (1934) had a violent dispute over the question, Saunders advocating, Arber rejecting conservatism. In my opinion many specious arguments have been advanced by authors who have not taken pains to look for ontogenetic facts (Saunders, 1934, and Puri, who reviewed the subject in 1951). That is to say, may instances affirming conservatism have been presented by those who, because they studied only the mature stages of the flower, failed to see any residue of the organ itself. And on the other hand those who observed cases in which the organs and the traces were lost simultaneously did not try to find out whether the organ had arisen at all. And residual organs without (lignified) traces are taken as proof of the contrary. In this study it has frequently been observed that 'lost' organs occurred ontogenetically. Stamen primordia, sometimes extremely slight ones, are formed close to the apex or base of staminal lobes and provided with vascular traces. These primordia cease to develop so early that later they are completely outsized by the surrounding tissues. Consequently in a mature stage they either are no longer visible, or else are easily overlooked especially when clearing techniques are employed. Hall (1956) suggested that this might be the reason why vascular bundles are said to be conservative.

In conclusion it may be remarked that when a mature flower is being examined, the presence of a loose bundle may reveal the location of a reducing organ, but considering that the initial development of an organ always precedes the differentiation of the vascular bundle tissues, the vascular bundle is never more conservative than the organ itself. The interrupted lignification of these residual traces often furnishes evidence of the reduction. In such cases the traces lose their function. On the other hand, in the instances of the congenital fusion of organs into axial or foliar structures, traces are incorporated and do not cease to function. The same is true of postgenital fusion. Here individuality is lost without a direct reduction. Saunders (1934) also noticed that each of these two ways of reduction has a different bearing on the problem.

The nature of the stamen groups

In the families under consideration the androecia are formed by five — or, in some *Tiliaceae*, ten — groups of stamens that have a three-trace supply of vascular bundles and that may be free or, to a variable extent, fused laterally.

During early floral development the existence of these groups is manifested on the apex by the successive appearance of rounded or angular trapeziform protuberances which, during their further latero-centrifugal development, may meet laterally and then even proceed together as an annular whole (*Tiliaceae*; also, according to Ihlenfeld, 1960, *Mesembryanthemum*). These protuberances, on which the stamen primordia arise latero-centrifugally, may, since they apparently show a certain phyllotaxis, have a certain morphological value instead of merely representing the result of the fusion of stamens. Recently this criterion was also applied by Leins (1964) and Hiepko (1964). Moreover, especially in *Bombacaceae* and *Malvaceae*, the protuberances tend to be phyllomic in form. In a number of *Tiliaceae* the development of the stamen primordia does not start in groups but immediately begins annularly upon very regularly formed apices or annular meristems. The primordia here tend to be arranged in orthostichies (cf. Waterkeyn on *Gnetum africanum*, 1959). Chiefly because of the extremely regular development in the different floral sectors, this annular arrangement may be considered a secondary development. This is contrary to the opinions of Edlin (1935), Corner (1946), and Parkin (1951) who regarded the annularity as original and the grouped androecia as derived. Hiepko (1964) showed this opinion to be untenable in *Paeonia*.

The groups may bear anthers all over (in *Tiliaceae*) or along the central marginal parts only. This marginality is caused by a limitation of the development of primordia in the peripheral regions of the groups. This limitation is manifested ontogenetically by transitory stages in the antesepalous stamen groups in *Mollia speciosa* and *Vallea stipularis* as well as in the antepetalous groups of *Colona scabra*. In the cases where the development of the stamen groups is limited in this way we are dealing with the staminal lobes in *Malvaceae* and many *Bombacaceae* or with less well-developed lobes, called phalanges, in most *Elaeocarpaceae* and *Sterculiaceae*. Since their apical parts are not incorporated in the floral apex but are like more or less free appendages, especially in *Bombax* and allied genera, during their primary development these three-trace lobes have the form of small thick bracts in a pre-aestivation position. For this reason also the lobes can easily be seen to originate partly free, succeeding one another.

At the same time, however, the apical part of the lobes is under the influence of reduction, bearing reducing stamen primordia. Whereas the median lobe traces are absent in *Malvaceae* and residual in *Bombax*, in *Sterculiaceae* they supply foliar staminodial lobe parts. In other plants, like, e.g., many *Elaeocarpaceae*, a number of *Sterculia* and *Tilia* spp., *Schoutenia* and *Pachira* spp., the apical parts of the lobes are occupied by a single stamen that is supplied by the median vascular trace only. The location of the invariably alternating position of the carpels depends on the measure of development of the apical parts of the staminal lobes. This is illustrated in *Malvaceae*, where, for instance, *Malope trifida*, *Sphaeralcea umbellata*, *Thespesia populnea*, and *Lagunaria patersonii* still have relatively well-developed apical regions, so that the (fields of) carpels alternate with the staminal lobes. On the other hand, in most other Malvaceae, in which the apical lobe parts are weakly developed, the carpels alternate with the proximal commissural parts of adjoining staminal lobes. The same correlation was also observed by Gazet du Chatelier (1940) and myself in Hermannieae.

In *Pachira* spp. large lateral protuberances appear on the small-sized staminal lobes on either side of the leading apical stamen. Upon these protuberances a fairly large number of stamens appear, changing in direction from latero-centrifugal to latero-centripetal. It is interesting to note that Leins (1964, 2) also seems to have observed a certain change in the direction of the development, to wit, in some *Rosaceae*. These stamens are innervated by traces with facing xylem that result from the branching of the lateral (stamen fascicle) traces of the staminal lobes.

In the *Malvaceae* and in flowers with less well-developed staminal lobes, as a rule the stamen primordia originate in only two small rows along the lobe margins latero-centrifugally. Between this and the development in *Pachira* spp. we may observe a number of intermediate stages, as, for instance, in *Bombacopsis quinata*, *Bombax buonopozense*, *Elaeocarpus nouhuysii*, perhaps also in *Durio kutejensis* and to a slight extent in *Dombeya wallichii*. In these species a further peripheral lateral and even somewhat inward development of stamen primordia may occur in the lower lobe regions. Even in some *Malvaceae* (*Kitaibelia vitifolia*, *Kokia rockii*, and *Lagunaria patersonii*) the last stamens along the lobe side do not originate exactly along the margins; thus some place at the side is left unoccupied, the lobes being thicker there and provided with rudimental vascular bundles. In still more *Malvaceae* we find rudimental bundles in that place. While the staminal lobes and the phalanges of stamens give the impression of small leaf blades terminating in stamens, the phyllomic appearance is increased if the lobes are well-developed, as described above. In that case they seem to have rather flaring and curling lateral parts that may even overlap one another contortedly. When the development is less extreme the lobes may also overlap in a later phase, for instance imbricately, as in *Ochroma lagopus*.

In the series of decreasing development of the stamen primordia on the staminal lobes, the size of the lateral protuberances arising on the lobes prior to the individualization of the stamens upon them also decreases. Just as with the entire staminal lobes, we may regard these protuberances, here called staminal buttresses, as units of a somewhat individual nature, which compose the staminal lobes. We see a certain tendency towards the arrangement of three spatially disposed subgroups viz. one inner median that is single or, in Tiliaceae, often multiple and two outer lateral ones into somewhat phyllomic structures. This is especially evident when a medium degree of sterility and flattening of the upper composing parts is present, as in *Bombacaceae* and *Malvaceae*. Such structures are neither purely caulomic nor phyllomic (see also below). Therefore we may call them cladosporophylls; this term was used by Lam (1948) for the female structures in *Coniferae*, with their well-known phylogenetic derivation according to Florin. Studying the figures in Florin (1951), it is interesting to discover in this respect that the basal vascular supply of the ovuliferous scales in Conifers often seems to be triple. We may also refer in part to the interpretation of the structure of the macrosporophylls of *Cycas revoluta* as accepted by Meeuse (1963). In most *Tiliaceae*, however, the spatially arranged triple staminal groups are incorporated into the receptacle as such.

These triple combinations have a vascular bundle system that is supplied by the branching of three traces, each trace corresponding with one of the three parts distinguished above. Whereas the two lateral (fascicle) traces are attached to the sepal supply of two adjoining sepals, either directly or else combined with the petal supply of two adjoining petals, the middle trace is always attached directly to the sepal supply or to the stele.

Likewise, when judging the three-trace supply, there are three subdivisions to be distinguished in the stamen groups of the *Tiliaceae*, both in the separate groups and in the groups that are congenitally more or less fused into an annular arrangement. The lateral traces may be commissural to variable extent, generally near the base only. The median trace usually supplies more than one stamen. Perhaps in *Mollia speciosa* a free triple stage is retained, although with basally commissural antepetalous groups. This is probably also the case in *Muntingia calabura*, though in a slightly more condensed form.

Besides *Mollia speciosa*, some other species in *Tiliaceae* also have ten groups of stamens. In *Clappertonia ficifolia* and *Colona* spp. the existence of the — visible only ontogenetically — single-trace antepetalous groups is largely obscured during the further growth of the flower. Moreover, since in *Colona scabra* the median members of the antepetalous groups may become reduced during ontogeny, and in other floral sectors are absent from the start, the antepetalous groups are assimilated by the adjoining antesepalous groups as two collateral halves. In the closely similar *Grewia* spp. this assimilation might occur congenitally. In *Colona* we are dealing with stamen groups whose existance is hidden during ontogeny.

Here I should like to call attention to a paper by Hiepko (1964) in which he revealed the remarkable fact that the vast receptacle smoothly covered with numerous stamens in *Paeonia* is the result of additional growth processes starting from a number of stamen groups that are ontogenetically clearly distinct and that follow in the phyllotaxis of the floral phyllomes. I have been able to confirm these results from my own observations.

If this process of concealment is thought to be accelerated and to take place in a congenital phase, it follows that the more or less spatially arranged triple groups of stamens may be supposed to have had a freer existence before being incorporated into the receptacle, to a certain extent fusing laterally, to form an annular androecium in the *Tiliaceae*. This individuality is still partly revealed by the more flattened staminal lobes in *Bombacaceae* and *Malvaceae*. Likewise it follows that the median and lateral partners of the triple groups may be considered to have had a separate individuality; this is still shown to a limited extent in such cases as *Pachira*. The lateral partners may have been parts of a former five antepetalous stamen groups.

In *Sloanea* spp. perhaps ten groups of stamens are present, though hidden, changing into five alternisepalous groups.

The location of the stamen groups in the flower

Regarding the position the androecium units distinguished above occupy in the flower, it will be evident that the triple groups in *Tiliaceae* and *Elaeocarpaceae* are nearly all situated in front of the sepals. On the face of it, the triple groups or staminal lobes in most *Bombacaceae*, *Malvaceae*, and *Sterculiaceae* are also located in front of the sepals, although we often observe that the groups find themselves somewhere in between the antesepalous and antepetalous positions. In *Malvaceae*, Goethart (1890) observed a shifting of staminal buttresses and its correspondence with the oblique insertion of the petals. Especially in *Bombax* and allied genera the staminal lobes seem to be located more in front of the overlapped sides of the petals. Furthermore, in some cases the groups are doubtless antepetalous, as in *Tilia*, some *Durio* and *Sloanea* spp., and, after a fashion, also in *Adansonia digitata*.

For many reasons, discussed in the preceding chapters, we are inclined to believe first, that there may be two stable positions for a group of stamens, viz., the antepetalous and alternipetalous, and second, that in *Bombacaceae*, *Malvaceae*, and *Sterculiaceae* the difference between these two positions may be caused by a variable spiral growth, a twist, that takes place in the floral apex at a very early stage of its development. Without it the staminal lobes would originate in an antepetalous position. Spiral growth would also be the cause of the asymmetrical growth and insertion, the contortion of the staminal lobes and the petals. The contortion of the androecium in *Sidalcea* was observed by Schoute (1936). In double flowers of *Althaea rosea* (fig. 47) a spiral arrangement of additional petal-stamen groups is shown very clearly. The twisting is revealed in the independent and constant oblique basal course of all the vascular traces towards the staminal lobes in a flower. The direction of this oblique course discloses the direction in which the twisting works; it has been shown to bear a constant relation to the contortion of the petals.

Chadefaud (1951, 1) and Reboulet (1957) found a relation between the position of the stamens and the contortion in *Carica papaya*. Reviews by Eichler (1875) and Goethart (1890) provide excellent proof of the differences of opinion about the location of the stamens, and especially the sterile teeth on the tube in malvaceous flowers. In my opinion this discrepancy is caused by the variability in the twisting and the contortion.

In many species of *Malvaceae* and *Sterculiaceae*, in which the staminal lobes are more precisely alternipetalous, the basal course of the traces is fairly oblique (fig. 337 and 338). On the other hand, in *Bombax* and allied taxa the alternation with the petals reaches only halfway, the basal course of the traces being, accordingly, not particularly oblique (fig. 339). In the plants with antepetalous staminal lobes or groups the traces are not oblique at all.

Consequently we are forced to conclude that *Tilia* is unlike other *Tiliaceae*, not only in the splitting of its stamens and the form of the stamen groups, which is more like that of staminal lobes, but also in the position that these groups occupy in the flower. In *Schoutenia* spp. alone do flowers with similar stamen groups occur; these, however, are located variably between antesepalous and antepetalous regions, the group traces being, accordingly, more or less oblique.

Study of the correlations described above is hampered by the variable, not always exactly alternisepalous, position of the petals and correspondingly of the stamen groups in their relation to the petals. In *Malvaceae* the position of the petals seems to be largely determined by the maximum available space which, because of the variable height of fusion of petals and staminal lobe primordia and the variability of the time at which the petal primordia appear, does not always prove to be the same. In *Bombax* and its allies the place of the petals is extremely variable, even to the extent of being mainly antesepalous (decidedly so in the material of *Adansonia digitata*).

In the *Sterculiaceae*, Gazet du Chatelier (1940) distinguished between the diplostemonous *Sterculieae*, *Byttnerieae*, and *Lasiopetaleae*, and the obdiplostemonous *Dombeyeae*, *Helictereae*, and *Hermannieae*. The obdiplostemony he regarded as deriving from the torsion of the stamen fascicle trace. As far as I know, he is the only author who was aware of the oblique course of these traces prior to the present publication. Whereas in the obdiplostemonous groups what seem like petals must in reality be pseudopetals, being 'branches' belonging to the antesepalous stamen fascicles, the petals in the diplostemonous groups must be real petals. I am unable to agree with the theoretical diplostemony Gazet du Chatelier attributed to the *Sterculiaceae*. As a matter of fact, he himself conceded that he could not interpret the frequent occurrence of the antepetalous position of the carpels in his study; furthermore, he found that he must distinguish five antepetalous stamen groups in the *Sterculieae*. In my opinion there are five, and not ten, groups in all *Sterculiaceae*.

On the other hand, from the present study no serious difficulties would arise when applying and extending the idea of Gazet du Chatelier that the petals are a kind of bracts to stamen groups in *Malvaceae*, *Bombacaceae*, and *Sterculiaceae*, all the more so because the intimately related petals and stamen groups as a whole are located with great variability in relation to the sepals. This would, of course, lead us close to the gonophylls and gonoclads of Neumayer (1924), the protective units of Lam (1961), and the gonophyll theory of Melville (1962, 1963). However, I cannot find any difference in structure between pseudopetals and real petals in the *Malvales* (nor does Gazet du Chatelier mention anything of the kind in *Sterculiaceae*). The features in the double flowers of *Althaea rosea* and *Hibiscus rosa-sinensis* strongly indicate the close connection between (additional) petals and axillary stamen groups. Here, however, the groups that in *Hibiscus rosa-sinensis* are like an axis are commissural formations, the antepetalous regions of the staminal lobes being advanced (see Van Heel, 1962). In normal flowers of some species of *Malvaceae* advanced commissural development of the staminal buttresses has also been found. These problems certainly offer a field for study; hereby the value of the nectaries occurring on the petals, chiefly in *Tiliaceae*, must also be taken into account.

Rao (1952) distinguished between obdiplostemonous *Sterculiaceae* and the other haplostemonous families that retain the antepetalous stamen groups only. Nevertheless, in my opinion Rao was seriously mistaken in regarding the outer triplets of stamens, that occur in many *Sterculiaceae*, as separate antepetalous triple groups. Except in a few *Tiliaceae* there are no primordia corresponding with such groups. According to Rao, the median stamens of the outer triplets must be located innermost, as though, in our terminology, forming the leading stamens of the putative antepetalous groups. Actually, in the flower the median stamens of the outer triplets are located outermost and represent the most marginal and peripheral members of the major side of one of the five antesepalous stamen groups. The position of the *Bombacaceae* was established by Rao by the study of *Bombax ceiba* only, and in this species Rao failed to observe that median vestigial bundles of the staminal lobes exist. Finally, in his representation of evolutionary lines, sepals and petals have been confused.

The nature of stamens

Whatever its ultimate form, the stamen starts as a hemispheric primordium that in theory could continue development in any direction required by the general organization. The development immediately following is a certain flattening, the primordium becoming more or less elliptic in outline. (This phase of flattening also occurs in the early development of stamens, e.g., in many *Tiliaceae*, that later become completely stalk-like in appearance through excessive longitudinal growth, beside which the lateral dimensions become insignificant). In this slightly flattened structure the main form of the anther develops at once and at the same time it is elevated on a slightly tapering stalk, becoming club- or spoon-shaped. Additional local or over all longitudinal or lateral growth may take place later on. Moreover, the development of the entire apical region of the stamens of *Elaeocarpaceae*, *Apeiba* spp., *Pterospermum javanicum* and others may be arrested. In many *Sterculiaceae* the anther has been shown to originate in a resupinate position, inverted as in most *Ericaceae* (Mathews & Knox, 1926), but the other way round. In some *Tiliaceae* this resupination is present to a minor degree, developing late.

In *Bombacaceae* and *Malvaceae* the primordial structure mentioned above has been shown to develop into a stamen with a monothecous reniform anther. A division usually occurs, however, resulting in two equal monothecous stamens in line. Saunders (1936) believed that in *Malvaceae* the half-stamens are caused by halving of the petal stamen vascular supply by the divergence of the petal trace. In *Sterculiaceae* she found that the fascicle trace coming from the petal stamen trunk cord remains whole and that the stamens are therefore bithecous. Even if accepting this reasoning that admits vascular bundles to determine external shape, I cannot understand why halving of the groups implies halving of the stamens.

The results of the division may be located on different stalks generally with a short common base, sometimes entirely separated. They may, however, also be located on a single stalk, representing a normal bithecous stamen. These two extremes are linked by a gradual series of intermediates formed by stamens with bilobed 2—4-sporangiate anthers. This series is caused by gradated differences in the time at which the division processes start on the stamen primordia, a very late process giving rise only to a median break in the sporangial tissue of a monothecous stamen primordium.

The other extreme, namely the entire separation of two monothecous stamens, is the result of a division that takes place so early that it can never be observed on the stamen primordia themselves. In that case the separate primordia initiate in the underlying tissue viz. the staminal lobe margins. Perhaps in these places a division might be demonstrated on the cellular level, for example in *Abutilon darwinii*, where stamen primordia arise upon the lobe margins distinctly paired (each of which will presently divide once more). In *Adansonia digitata* also we may consider that the results of successive divisions arise immediately upon the large annular meristem. It is this process of accelerated division that is referred to when we say that a ramification is hidden congenitally in the receptacle or in any basal tissue. In *Hibisceae* we can observe that in a later phase of development the halves of a stamen primordium, that are originally provided with a common base, may be disrupted by a marked longitudinal growth of the staminal lobes, so that the halves appear to be completely separated. Only now and then, when the longitudinal growth of the staminal lobes happens to be somewhat advanced, do the halves initiate separately. In this way branching may be concealed by postgenital processes.

In the preceding paragraphs we have seen this process of congenital and postgenital concealment at work on groups of stamens. The same process is generally recognised on the level of inflorescences (see, e.g., the interpretation of the inflorescences of *Sparmannia* by Troll, 1957, based on the ontogenetic sequence of the flowers aggregated on a common stalk; further, the interpretation of *Platanus* inflorescences given by Boothroyd, 1930, and quoted by Eames, 1961, on the evidence of the vascular bundles). In these cases flowers sink into a receptacle. Why not extend this idea to organs? Finally, it is clear that Zimmermann was applying this same principle when he traced the original components of axes and leaves in their main vascular bundles.

The isotomous division takes place more than once in the stamen primordia in some species of *Bombacaceae* and *Malvaceae*, thus repeating the production of more or less individualized monothecous stamens. The monothecous stamen itself remains intact and in these families forms an entity that cannot be analyzed without indulging in pure speculation. This successive division occurs in *Abutilon darwinii*, *Althaea rosea*, *Kokia rockii*, and *Cephalohibiscus peekelii*, giving rise to double rows of stamens divided once or twice along the staminal lobe margins, and further in the subgenus *Durio* and in *Adansonia digitata*. A double division in *Althaea rosea* was mentioned by Goethart (1890).

Whereas in the malvaceous cases the dichotomous divisions, up to the third degree, all take place in one plane, in the two bombacaceous cases they take place spatially and to a higher degree. The traces resulting from division have facing xylem, at least in their proximal part. In *Adansonia digitata* all the forkings, including the fundamental forkings in the base, are hidden in the tube tissue. In *Durio* the ramifications are the freest. The isotomous splitting of the vascular bundles in the externally undivided ultimate monothecous stamens of *Durio* spp., *Kitaibelia vitifolia*, and *Hibiscus* spp. indicate a potential further division. In the ramifications of the *Durio* stamens we also meet with a frequent triple arrangement that on closer observation proves to consist of two forkings, a phenomenon that can often be found in the branching of vascular traces, to wit, of petal traces and staminal fascicle traces. In the weaker development of the stamen primordia resulting from successive division and occurring towards the median regions of the staminal lobes we may again find something of the limitation in the development of stamens to the marginal parts of the groups, where groups change into staminal lobes, as described above.

The vermiform appendages in the much divided stamens of *Durio kutejensis* occur not only in an angular position near the ultimate thecae, or as a protrusion between them, but also angular to the subdistal ramification of the vascular bundles and now and then just laterally to a mesome. A forked appendage was found once. In my opinion, therefore, these appendages are equivalent to products of divisions in the meristem that have failed to become fertile, or, in other words, to sterile axes. The frequent presence of less well-developed thecae in the stamens of *Durio kutejensis* also point towards this interpretation. Moreover, in *Kokia rockii* one of the forked branches may have a similar sterile structure right at the base. We may also compare these structures with aborted filiform stamens in the proximal staminal region of several species.

The general structure of the stamens and the appendages are strongly reminiscent of *Ricinus communis*. The appendages in *Ricinus* are, however, always immediate prolongations of the common stalk of two terminal thecae. Therefore Van der Pijl (1952) considers that the thecae are placed laterally; according to him, this indicates phyllospory. Regarding this structure Zimmermann (1959) agrees that there is a feeble expression of a flattening development. About *Hillebrandia sandwicensis* (*Begoniaceae*), Gauthier and Arros (1963) state that it is not impossible to interpret the stamens as a contraction of telomes, but then as constituting an organ that is bilaterally symmetrical.

I am also inclined to think that the monothecous stamens of the families under consideration are flattened syntelomic structures; as a matter of fact, the flattening can be seen to take place during ontogeny. Furthermore the innervation is generally fan-like, with a tendency to prominence in two lateral directions; this may indicate potential subdivision in, again, two equal halves. In *Durio kutejensis* some of these flattened thecae may form a kind of imperfectly compound flattened structure. In teratological cases, such as the double *Hibiscus rosa-sinensis* and *Althaea rosea* flowers, the vegetative character is, for some unknown reason, markedly advanced in the somewhat petaloid stamens.

However this may be, the most important phenomenon, the series of dichotomous divisions, remains intact. These even occur partly free instead of being shifted into the underlying tissues. To quote Zimmermann's remarks (1959) on the paper by Van der Pijl: 'The general construction takes place by forking and (in *Ricinus*) the reduction of the mesome is partly released'. Here I would add the release of the incorporation of the mesomes into the receptacle, an incorporation that is most evident in Tiliaceous flowers where, in the vascular bundle supply, it may even retain proof of a strictly dichotomous mesome division (*Erinocarpus nimmonii*) or of a striking basal dichotomy (*Adansonia digitata*).

Moreover, according to Parkin (1951), connective protrusions represent a primitive feature and, since they show that the pollen sacs are not placed apically, they favour the classic view of the stamens. In my opinion, however, Parkin was dealing rather with the apical arrest in the development of entire anthers, including the pollen sacs, that can take place after a completely fertile anther has originated. An instance of this we found in *Apeiba echinata.* On the other hand, in *Camptostemon philippinense* real protrusions may be present, not in every stamen, but only in those in which the division, anatomically present, is not entirely effectuated in the external form. In that case evidently an apical part of the connective tissue may remain sterile.

Conclusions

Since the rise of the telome theory (Zimmermann, 1930, 1959, 1964) the question as to the nature of stamens and the androecium has been answered in two different ways. The classic theory maintains that the stamens are sporophylls bearing marginal sporangia. The lesser reduction is to be found in the three-trace sporophylls in *Magnoliaceae, Nymphaeaceae, Annonaceae, Himantandraceae, Degeneriaceae,* and other families (Eames, 1961). As Ozenda (1952), who has committed himself to this theory, rightly remarks, the idea that this less reduced but most foliar structure represents primitiveness in stamens rests entirely upon the putative primitive position of these families among the Angiosperms. In contrast to this theory there is the telome theory, by which stamens can be explained as contracted ramification systems of telomes with apical sporangia and dichotomous divisions (Wilson, 1937, 1942). Moreover, as a natural implication, fascicles of stamens can be supposed to have arisen by the failure or release of mesome reduction in the contracted ramification system. This opinion is based on ancient fossil land plants. According to Lam (1948) phyllosporous as well as stachyosporous stamens occur in the Angiosperms.

On the other hand, to offer an interpretation of the stamen fascicles the classic theory requires extraneous hypotheses. One of the most important among the classic explanations is that advanced by Čelakovsky (1894) and at present underscored by Eames (1961), namely, the possible connation into fascicles of simple stamens, each of which is homologous with a foliage leaf. This is essentially the same interpretation as that given by von Goebel (1930) and Edlin (1934), who assume the fasciculation of separate members in favoured places in certain sectors of the flower. The opinion of Corner (1946) as described above, also runs practically parallel. I agree with Eames (1961) that ontogeny, in revealing fascicles arising as a mound with individual stamens developing on the surface, is believed to show evidence of branching but that organs phylogenetically fused also arise congenitally united. And, indeed, since I have found congenital and postgenital reduction, or only a temporary break in development, of alternisepalous stamens or groups of stamens in the *Tiliaceae,* I fully believe that this process of favouring definite floral sectors may play a certain part in the androecium structure. In fact, under the force of reduction the annularity of the androecium might be limited to merely the initial stage of the development of its originally component parts. The most important objection, however, is that, proceeding from the classic point of view, I cannot conceive how a putative connation of stamens could successively take place in pairs; such repetition would be indispensable to the establishment of fascicles of stamens showing a series of dichotomous subdistal free or congenitally fused parts. We have learned to regard the monothecous stamen as the unit constituting the androecia in *Malvaceae* and many *Bombacaceae.*

A second explanation arising from the classic theory but not necessarily presupposing an initial annular arrangement of stamens is offered by those who simply speak of chorisis (of five stamens), that is, of the multiplication of stamens by splitting and intercalation (Duchartre, 1845, and Frank, 1876). Recently Rendle (1959) assumed that in *Malvaceae* the multitude of stamens is caused by the multiplication of five antepetalous stamens, since if there are five stamens, these are located in front of the petals. According to my interpretation, however, these five stamens in *Malvaceae* represent the only stamens of the major sides of antesepalous staminal lobes left and they are not precisely in front of the petals.

A third important classic interpretation, allied to the preceding one, was offered by Payer (1857) and Van Tieghem (1875), who interpreted the splitting stamens as centrifugally branching sporophylls or compound staminal leaves. Dickson (1864) and Eichler (1875) supported this theory. It should be added that since it is not flat, Van Tieghem hesitated to homologize the compound sporophyll with a vegetative leaf. In 1886 von Goebel accepted an antepetalous leaf that is branched on the margin in *Tilia* and *Malvaceae* but later, as stated above, he changed his opinion. Both Goethart (1890) and von Goebel (1886) found the expression serial chorisis, used by Duchartre (1845) for the *Malvaceae*, incorrect; there is no series of dichotomies starting from a single stamen primordium but, on the contrary, a successive appearance of stamen primordia. Hofmeister (1868) and Sachs (1874) also concluded that there are five compound microsporophylls with marginal, occasionally dorsal (*Sparmannia*) stamens. All these authors considered the meiomerous androecia to be primitive. The authors who accepted these microsporophylls as being located antepetalously assumed a previous reduction of an antesepalous outer whorl (Firbas, 1962, as well). In another attempt to rescue the law of alternation Hofmeister and Sachs, in contrast to all others, assumed that in *Malvaceae* the branched sporophylls alternate with the petals. To a certain degree the present study proves this view to be correct.

Chadefaud (1955, 2) stands apart in so far as he accepted multibranched floral parts in the androecium as well as in other floral regions. Zimmermann (1959) drew attention to the dichotomous ramifications in the aquatic *Batrachium* leaves to show that the dichotomies in *Ricinus* may probably due to reversion.

In my opinion the above explanations that homologize stamens with lateral or, occasionally, dorsal parts of compound foliage leaves, are valid to the extent to which they refer to similar processes that may have formed (compound) vegetative leaves during evolution.

How can we now on the basis of our interpretations reconcile these conflicting views, which presuppose a homology with either a modified (compound) leaf or a contracted ramification system? On this question it is interesting to note that Goethart (1890), in dealing with the stamen fascicle primordia in *Malvaceae*, preferred to speak of indifferent organs, neither purely caulomic nor phyllomic. He refrained from coming to a conclusion, looking forward to the time when more should be known about the phylogeny of caulomes and phyllomes.

Our own conclusion is that slightly flattened monothecous or bithecous stamens can be arranged on a system of mesomes that may be either partly free and thereby distinctly dichotomous or partly (in *Tiliaceae* entirely) congenitally fused and thereby less distinctly dichotomous. These systems form together five three-trace groups, each trace corresponding with a part of the groups, one median upper and two outer lateral parts. These subgroups may still retain characteristics of a more spatial dimension as a separate branching system, for instance in *Bombax* and *Pachira*. In other *Bombacaceae*, *Malvaceae*, and *Sterculi-*

aceae, however, the three-trace groups are increasingly flat, forming staminal lobes, cladosporophyllic in nature, that generally are sterile in the distal regions. Furthermore we must recall that in some species, e.g. *Ochroma lagopus*, only a few thecae are formed; these recede into sessility on the margins of the staminal lobes. Finally a stage is reached in which the margins of the lobes each immediately form a continuous theca, as, for instance, in *Chorisia crispiflora*, *Ceiba* spp., and, with intermediate transverse partitions, in *Fremontia californica*. Consequently in these families the most flat staminal lobes each develop wholly into a single bithecous stamen, with apical sterilization and a three-trace branching innervation. These are exactly the characteristics that are regarded as primitive by the classic theory.

In this way, since it is possible to demonstrate a series of transitions between more branching and more foliar formations, in a natural group of taxa the telomic and classic views come into line. Speculation about the direction of evolution, about whether here the branching is due to retention or reversion,cannot have any influence on the conclusion. If there is a reversion it works by ancient processes. Therefore it is accepted here that the branching is primitive. Recently Meeuse (1965) stated that in his opinion fascicles of stamens reduce to single stamens. It is obvious that my conclusions agree with his. Further, it follows from this study that the reduction works not only through simple loss of the individual parts but also by means of congenital fusion and incorporation into the receptacle. The study shows, moreover, that during the reduction the foliar characters gradually become more prominent. The stachyosporous and phyllosporous characters in androecia may not only be distributed over different taxa; in the natural group of *Malvales* families they are gradatingly connected. Lam (1959, 1) foresaw that there might prove to be intermediate organs; these he proposed to call stachyophylls (1959, 2). He recognized the female Coniferous scales as cladosporophylls (1948). In the course of my investigations I have found this kind of structure in the *Malvales* androecia but I should prefer to name them transitory rather than intermediate structures. It would seem just possible that the three-trace stamens of *Lauraceae*, in which the lateral traces supply lateral glandular parts by means of profuse branching, represent similar transitory stages between three-trace branching systems and three-trace foliar stamens. These have been described by Kasapligil (1951) and Sastri (1965).

Finally, it follows that in *Malvales* a bithecous stamen may occur as a structure of two different ranks, namely, either as one of the members forming the staminal lobes or as a stamen homologous with an entire staminal lobe.

SUMMARY

In order to test the applicability of the telome and the classic theories to the nature of stamens a study was made of flowers in *Malvaceae*, *Bombacaceae*, *Sterculiaceae*, *Tiliaceae*, and *Elaeocarpaceae* with respect to their ultimate form, their development, and the vascular course of their androecia. The customary dissecting, clearing, and microtomy techniques were used. A chapter on the interpretation of the vascular bundle course in floral morphology has been added.

In each flower the stamens are considered to be arranged in five groups, which may be fused more or less laterally. The groups have a three-trace vascular system the laterals of which may be commissural. Only a few *Tiliaceae* have ten groups.

Whereas in most *Tiliaceae* and *Elaeocarpaceae* the groups are antesepalous, in *Malvaceae*, *Bombacaceae*, and *Sterculiaceae* they are either antesepalous, antepetalous, or intermediate, depending on the variation of a spiral growth in the floral apex. If there is no such growth the groups are antepetalous. Spiral growth is revealed by an oblique course of the vascular bundle traces and the asymmetrical form of the petals and stamen groups.

The stamen groups may have many stamens *(Tiliaceae)* or bear fewer stamens in a fan-like arrangement, in which case they are called either staminal lobes *(Malvaceae* and *Bombacaceae)* or, if they are less well-developed, phalanges *(Sterculiaceae* and many *Elaeocarpaceae)*. Since they have their own group primordia, which show a certain phyllotaxis, the stamen groups are considered to be individual in nature. Moreover, in *Bombax* and allied genera and in some *Malvaceae* the apical regions of the staminal lobes originate free and are phyllomic in appearance.

Three parts can be distinguished in each stamen group: one median upper and two lateral outer parts, corresponding with the three-trace vascular system. The upper part is often formed by a few stamens in *Tiliaceae* and by a single stamen or a staminodial part in *Bombacaceae* and *Sterculiaceae*; in *Malvaceae* it is reduced. Judging by the sub-group primordia, here called staminal buttresses, the lateral parts are considered to have a certain individuality; in some *Malvaceae* and very markedly so in *Pachira* spp. the staminal buttresses arise on the staminal lobes to form the lateral parts of the stamen groups. The parts have many stamens, arranged spatially (in *Tiliaceae* and *Pachira* spp.), or fewer stamens occurring as simple rows (mainly in *Malvaceae* and *Sterculiaceae)*. Between the two an intergradated series of forms can be found, e.g., in *Bombax* and allied genera and in some *Malvaceae*. In some cases the lateral parts are formed by a single stamen or even a single theca.

The position of the carpels depends upon the position of the stamen groups. The carpels alternate with those regions of the stamen groups the development of which is the most advanced when the carpel primordia arise.

The parts of the groups as well as the groups as a whole may formerly have been freer but they have been reduced by congenital fusion and partial incorporation in the main floral axis. Evidence for this interpretation is provided by some Tiliaceae with ten freer stamen groups that may be visible either when mature *(Mollia speciosa)* or only in an early phase of development *(Colona* spp.). In *Mollia speciosa* the antepetalous groups are collaterally double, so that they may be regarded as the lateral parts of triple arrangements. In the *Colona* spp. the antepetalous groups are obscured during ontogeny by secondary receptacular growth. Moreover, if at the same time reduction occurs in the median line of these groups, their lateral parts are assimilated by the adjoining antesepalous groups. What can happen during ontogeny (postgenitally) may equally well happen (congenitally) before the primordia become visible externally.

The stamens may represent slightly flattened syntelomic structures. Depending on the time the division process begins, in *Malvaceae* and *Bombacaceae* a monothecous stamen primordium can be more or less deeply divided, forming two equal halves with facing xylem. In *Malvaceae* this dividing process may operate up to three times in succession; the products of the division are all arranged in one plane. Still further divisions may occur in *Adansonia digitata* and *Durio* spp.; in that case the results are arranged spatially, though in *Durio* not in an adaxial median direction. The mesomes occur either free, especially in *Durio*, or fused. This successive pairing of mesomes cannot be explained by connation of stamens. Under the influence of reduction superficial division gives rise to a bithecous stamen. Partitioned pollen sacs can be considered as due to imperfect division. The nature of several kinds of sterile extensions has been discussed. In *Sterculiaceae* and *Tiliaceae* the stamens of many species are resupinate.

In some species the lateral margins of the staminal lobes form only a few sessile thecae *(Matisieae)*. In still others *(Fremontia californica, Chorisia* and *Ceiba* spp.) each margin immediately forms a single continuous theca each, the primordial staminal lobes being distinctly foliar in appearance. In this way each entire staminal lobe forms a single flattened bithecous stamen with a sterile apical part and a three-trace vascular system. It is precisely these characteristics that the classic theory regards as primitive in stamens. Moreover, it follows that in *Malvales* bithecous stamens can be structures of two different ranks.

Consequently in the androecia of this group of taxa a series of transitions exists between more branched and more foliar formations. In this series reduction operates by the loss of parts, by congenital fusion, by incorporation and by flattening. The androecial parts are neither fully stachyosporous nor fully phyllosporous; they are transitory between the two.

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