THE FLORAL ANATOMY OF THE AURANTIOIDEAE

BY

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INTRODUCTION

A knowledge of the relationships of the cultivated and wild species of the Aurantioideae, as well as of other groups which contain commercially important plants, is desirable from the standpoint of plant improvement by breeding or grafting. Many lines of attack on the problems of relationships are being followed. In recent years the study of the vascular systems supplying the floral organs of numerous dicotyledonous families has come into use as an aid to ascertaining the relationships between various families, as well as between the genera making up these families. While the anatomical evidence has not always been conclusive, it has aided evidence from morphological, ecological, cytological, geographical, and other sources in clearing up some taxonomic problems. The investigation of the floral anatomy of the Leguminosae (Moore, 1936a, 1936b), Polemoniaceae (Dawson, 1936), Primulaceae (Dickson, 1936; Douglas, 1936), Polygonaceae (Laubengayer, 1937), and Boraginaceae (Lawrence, 1937) are examples of such research.

The present study was undertaken in order to ascertain what light could be thrown on the unsettled question of the systematics of the Aurantioideae by anatomical investigations. There has been very little study of the vascular anatomy of the citrous fruits. Among the earlier investigators, Penzig (1887) mentions the bundle traces of a few species in a brief and incomplete way, but makes no attempt to use them in a systematic plan. Saunders (1934) made a study of the vascular

systems of 33 species of rutaceous plants, 5 of which are in the Auran-
tioideae, but facts which may be of systematic value are overlooked in
an attempt to prove her theory of carpel polymorphism. Furthermore,
the 25 genera studied could hardly be considered representative of a
family composed of more than 140 genera.

Taxonomic studies on the Aurantioideae made by early workers,
among them Corea de Serva (1805), Mirbel (1813), De Jussieu (1815),
Roemer (1846), Baillon (1855), Oliver (1861), and Penzig (1887), were
based largely upon the number of stamens, locules and ovules, of the
comparatively few species known at that time. These characters, as
pointed out by Tanaka (1936), may vary even within a single genus. In
later years Engler (1931), Tanaka (1936), and Swingle (in press) have
made use also of such characters as type of inflorescence, type of
leaf, number of leaflets, presence of winged rachis and petiole, num-
ber of thorns on the stems, number and form of floral organs, forma-
tion of pulp vesicles and oil glands, hardening of the rind of fruits,
etc.

Engler (1931), revising his earlier classification (1896), accepts
many of the new genera proposed by Swingle (1914b, 1928) or lists them
as subgenera. The former considers the Aurantioideae to consist of
only one tribe, the Aurantieae, which he divides into the subtribes
Hesperethusinae and Citrinae as shown below.

<div align="center">Hesperethusinae</div>

Glycosmis Correa (1805)	Luvunga Buch. Ham. (1832)
Thoreldora Pierre (1896)	Triphasia Lour. (1796)
Micromelum Blume (1825)	Wenzelia Merrill (1915)
Murraya Konig (1771)	Echinocitrus Tanaka (1928)
Merrillia Swingle (1918)	Monanthocitrus Tanaka (1928)
Clausena Burm. (1768)	Atalantia Correa (1805)
Pleiospermium (Engl.) Swing. (1916)	Lamiofrutex Lauterb. (1924)
Hesperethusa M. Roem. (1846)	Tetracronia Pierre (1893)

Citrinae

Microcitrus Swingle (1915) Swinglea Merrill (1927)
Eremocitrus Swingle (1914) Balsamocitrus Stapf (1906)
Poncirus Raf. (1838) Afraegle (Swing.) Engl. (1915)
Citrus L. (1753) Aeglopsis Swingle (1911)
Fortunella Swingle (1915) Feroniella Swingle (1912)
Citropsis Swing. et M. Kell. (1914) Feronia Correa (1800)
Aegle Correa (1798)

The genera Thoreldora, Tetracronia, Lamiofrutex, Murraya, and

Afraegle are omitted by Tanaka (1930). He considers Thoreldora and

and Tetracronia to be species of Glycosmis, Lamiofrutex a species of

of Atalantia, and Afraegle a section of Balsamocitrus. Chalcas is

is used in preference to the generic name Murraya. Tanaka also recog-

nizes the division of the genus Atalantia by Swingle (1914b) into the

5 separate genera: Atalantia, Severinia, Pamburus, Paramignya, and

Merope. He also adds the genera Oxanthera and Pleurocitrus, both of

which were previously included as species of Citrus. Tanaka's classi-

fication of the genera of the Aurantioideae into 8 tribes is shown be-

low.

Tribe 1. Micromeleae.— Micromelum Blume (1825).
Tribe 2. Clauseneae.— Clausena Burm. f. (1796); Glycosmis
            Correa (1805); Chalcas L. (1797).
Tribe 3. Aegleae.
        Subtribe 1. Merrilliinae.— Merrillia Swingle (1918).
        Subtribe 2. Feroniinae.— Feronia Correa (1800); Feroni-
            ella Swingle (1912).
        Subtribe 3. Balsamocitrinae.— Aegle Correa (1800);
            Aeglopsis Swingle (1911); Balsamocitrus O. Stapf
            (1912).
        Subtribe 4. Swingleinae.— Swinglea Merrill (1918).
Tribe 4. Lavangeae.— Lavanga Buch. Ham. (1891); Pamburus
            Swingle (1916); Pleiospermium Swingle (1916).
Tribe 5. Meropeae.— Triphasia Burm. f. (1760); Echinocitrus
            Tanaka (1928); Merope M. Roemer (1846); Paramignya
            Wight (1838); Wenzelia Merrill (1915).
Tribe 6. Atalantieae.— Atalantia Correa (1800); Severinia
            Tenore (1840); Oxanthera Montrouzier (1860).
Tribe 7. Microcitreae.— Microcitrus Swingle (1915); Eremo-
            citrus Swingle (1914); Monanthocitrus Tanaka (1928);
            Pleurocitrus Tanaka (1929).

Tribe 8. Aurantieae.
    Subtribe 1. Hesperethusinae.— Hesperethusa M. Roem. (1846).
    Subtribe 2. Citropsinae.— Citropsis Swing. et M. Kell.
        (1913).
    Subtribe 3. Poncirinae.— Poncirus Raf. (1833).
    Subtribe 4. Citrinae.— Citrus L. (1753); Fortunella Swing.
        (1915).

Swingle's classification (in press) of the tribes and subtribes of the Aurantioideae does not entirely agree with either of the above. He considers Echinocitrus Brassii a species of Triphasia, and proposes 3 new genera — Burkillanthus (Citrus malaccensis), Clymenia (Citrus polyandra), and Limnocitrus (Pleiospermium littoralis). Swingle's list of the 33 genera making up the orange subfamily is given below. The number of species is given in parenthesis after the name of each genus.

Tribe I. Clauseneae, Remote Citroid Fruit Trees
    Subtribe 1. Micromelinae, Very Remote Citroid Fruit Trees
        i. Micromelum (9)
    Subtribe 2. Clauseninae, Remote Citroid Fruit Trees
        ii. Glycosmis (34)
        iii. Clausena (28)
        iv. Murraya (9)
    Subtribe 3. Merrilliinae, Large-fruited Remote Citroid Fruits
        v. Merrillia (1)
Tribe II. Citreae, Citrous and Citroid Fruit Trees
    Subtribe 1. Triphasiinae, Minor Citroid Fruit Trees
        vi. Wenzelia (4)   )
        vii. Monanthocitrus (1))——— A. Wenzelia Group
        viii. Merope (1)   )
        ix. Oxanthera (3)————————— B. Oxanthera Group
        x. Luvunga (12)   )——— C. Luvunga Group
        xi. Paramignya (14))
        xii. Triphasia (3))
        xiii. Pamburus (2))——————— D. Triphasia Group
        xiv. Severinia (9))
    Subtribe 2. Citrinae, Citrous Fruit Trees
        xv. Pleiospermium (3))
        xvi. Burkillanthus (1))——— A. Primitive Citrus
        xvii. Limnocitrus (1))
        xviii. Hesperethusa (1))
        xix. Citropsis (8))——————— B. Near-Citrous
        xx. Atalantia (10))

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   xxi. Fortunella (3)    )
  xxii. Eremocitrus (1)   )
 xxiii. Poncirus (1)      )
  xxiv. Clymenia (1)      )————————— C. True Citrous
   xxv. Microcitrus (6)   )
  xxvi. Citrus (16)       )
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Subtribe 3. Balsamocitrinae, Hard-shelled Citroid Fruit Trees

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 xxvii. Swinglea (1)————————————— A. Tabog Group
xxviii. Aegle (1)         )
  xxix. Afraegle (4)      )
   xxx. Aeglopsis (1)     )——————— B. Bael Fruit Group
  xxxi. Balsamocitrus (1) )
 xxxii. Feronia (1)       )——————— C. Wood-Apple Group
xxxiii. Feroniella (3)    )
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MATERIALS AND METHODS

The materials upon which this study is based include floral buds, ovaries, and young fruits of the following 94 species comprising 29 genera..

Micromelum minutum (Forst.) Wt. & Arn.
    " compressum (Bl.) Merr.
    " falcatum (Lour.) Tan.
    " integerrimum (Buch.-Ham.) Roem.
    " hirsutum Oliv.
    " ceylonicum Wt.
    " scandens Rechinger
    " pubescens Bl.
Glycosmis citrifolia Lindl.
    " puberula Lindl.
    " chlorosperma Blume
    " Greenei Elmer
    " pentaphylla (Retz.) Correa
    " Craibii Tan.
    " macrantha Merr.
    " cochinchinensis Pierre
Clausena lansium (Lour.)Skeels
    " anisum-olens (Bl.) Merr.
    " anisata Engl.
    " excavata Burm. f.
    " grandifolia Merr.
    " Worcesteri Merr.
    " laxiflora
    " moningerae
    " heptaphylla (Exb.) Wt. & Arn.
    " mollis Merr.
    " Guillaumini Tan.

Clausena inaequalis (DC) Benth.
   "   microphylla
Murraya paniculata Linn.
   "   crenulata (Turcz.) Oliv.
   "   Koenigii Spreng.
Merrillia caloxylon (Ridl.) Swing.
Wenzelia brevipes Merr.
   "   melanesica Swing.
Oxanthera aurantium Tan.
   "   neo-caledonica (Guill.) Tan.
Triphasia trifolia (Burm. f.) P. Wils.
   "   grandifolia Merr.
   "   Brassii (Tan.) Swing.
Luvunga philippinensis Merr.
   "   borniensis Hochr.
   "   scandens (Roxb.) Wall.
   "   villosa
   "   sarmentosa (Bl.) Kurz.
Paramignya Surasiana Craib.
   "   monophylla Wt.
   "   scandens (Griff.) Craib.
   "   hainanensis Swingle
   "   longi-pedunculata Merr.
Severinia buxifolia (Poir.) Tenore
   "   disticha (Bl.) Swing.
   "   linearis (Merr.) Swing.
   "   retusa (Merr.) Swing.
   "   paniculata (Warb.) Swing.
   "   hainanensis Merr. & Chun
   "   trimera (Oliv.) Swing.
Pleiospermium dubium (Bl.) Swing.
   "   alatum (Wt. & Arn.) Swing.
Limnocitrus littoralis (Miq.) Swing.
Burkillanthus malaccensis Swing.
Hesperethusa crenulata (Roxb.) Roem.
Citropsis Schweinfurthii (Engl.) Swing. & M. Kell.
   "   gabonensis (Engl.) Swing. & M. Kell.
   "   angolensis Excell.
   "   mirabilis (A. Chev.) Swing. & M. Kell.
   "   latialata subsp. Gilletiana Swing. & Kell.
Atalantia monophylla (Linn.) DC
   "   racemosa Wt.
   "   Wightii Tan.
Fortunella japonica (Thunb.) Swing.
   "   Hindsii (Champ.) Swing.
   "   margarita (Lour.) Swing.
Eremocitrus glauca (Lindl.) Swing.
Poncirus trifoliata (L.) Raf.
Clymenia polyandra (Tan.) Swing.
Microcitrus australasica (F. Muell.) Swing.

<u>Citrus</u> <u>reticulata</u> Bl.
   "   <u>grandis</u> Osbeck
   "   <u>aurantifolia</u> (Christm.) Swing.
   "   <u>limon</u> (Linn.) Burm. f.
   "   <u>sinensis</u> (Linn.) Osbeck
   "   <u>medica</u> <u>Linn.</u>
   "   <u>macroptera</u> Montr.
   "   <u>ichangensis</u> Swing.
   "   <u>micrantha</u> Wester.
<u>Swinglea</u> <u>glutinosa</u> Merr.
<u>Aegle</u> <u>Marmelos</u> (Linn.) Corr.
<u>Afraegle</u> <u>gabonensis</u> Swing.) Engl.
   "   <u>paniculata</u> (Schum.) Engl.
<u>Aeglopsis</u> <u>Chevalieri</u> Swing.
<u>Feronia</u> <u>limonia</u> Swing.
<u>Feroniella</u> <u>lucida</u> (Scheff.) Swing.
   "   <u>oblata</u> Swing.

Of the 94 species studied, 26 were obtained from trees grown in the University of Maryland Greenhouses and the U. S. D. A. Exhibition Greenhouses, and from preserved material sent in by collectors. The balance were obtained, through the kindness of Dr. W. T. Swingle of the United States Department of Agriculture, from dried herbarium specimens furnished by the following herbariums: University of California, Arnold Arboretum, Gray Herbarium at Harvard University, U. S. National Herbarium, Philippine Bureau of Science, British Museum Herbarium at London, Herbarium of Botanic Gardens at Singapore, Upsala Botanical Museum, U. S. Plant Exploration & Introduction Herbarium, Kew Herbarium, Herbarium of Museum of Natural History at Paris, Botanical Museum Herbarium at Berlin-Dahlem, Rijks Herbarium at Leiden, and University of Aberdeen (Scotland).

The freshly collected buds were fixed in Nawaschin's fluid, and dehydrated and imbedded by Zirkle's butyl alcohol method. The material was sectioned 20 microns thick, and serial sections mounted and stained by the safranin-fast green method. Herbarium specimens had to be given

a softening treatment, slightly modified from the Juel method (1918) of softening and restoring specimens. The buds or fruits were first heated in water below 100° C. for 1-2 hours, then transferred to di- lute ammonia (1 part ammonium hydroxide to 19 parts water) and placed in an oven at 50° C. for 12-24 hours. This treatment softened the flattened specimens and restored them to approximately their original size and shape. After the buds were rinsed thoroughly in running water, the same technique was followed as for fresh material. By this soften- ing treatment sections were obtained which compared favorably with freshly fixed materials, the only apparent difference being the shrunken appearance of the protoplasts.

The drawings, some of which are semi-diagramatic, were made with the aid of a Bausch & Lomb Microprojector. The magnifications are noted in the explanations accompanying the figures.

RESULTS

Floral Structure

A brief description of the floral structure, taken in part from Engler (1931) and in part from actual observations, will aid in an understanding of the anatomical descriptions given below.

The Aurantioideae is a group of trees, shrubs, and woody climbers native to tropical and subtropical Asia, eastern Australia, and Africa. The flowers are typically 3- to 5-parted, regular, mostly perfect, some- times becoming unisexual by abortion. The sepals are free or united, often forming a bowl-shaped calyx. The petals are usually imbricate, seldom valvate, free or somewhat united. The stamens are rarely the same in number as the petals, mostly twice as many or 4-12 times more,

with filaments free or partially fused. The floral axis between the stamens and the ovary is usually enlarged into a ring-, cushion-, or cup-shaped disc or into a gynophore. The ovary is made up of usually 3-5, but sometimes fewer or more numerous carpels, entirely united, mostly with 1-2, but sometimes numerous, ovules in each carpel. The fruit is a berry, chiefly with a pulp consisting of juicy emergences from the carpel walls. Oil glands are found in all parts of the flower, and frequently unusually large oil glands are found at the tips of the sepals, stamens, disc, carpels, or stigma lobes.

Descriptions

TRIBE CLAUSENEAE. The floral organs of the members of this tribe are characterized by the fact that the traces which supply each whorl arise independently from the axis, and display no trace of fusion with each other.

SUBTRIBE MICROMELINAE. Micromelum (Fig. 1-11).-- The vascular tissue of the pedicel is arranged in a varying number of separate bundles. The first bundles to diverge from the axis are the 5 sepal midribs (S), which follow an outwardly ascending course through the receptacle and turn abruptly outward at the base of the sepals, which are fused into a bowl-shaped calyx. In several species lateral sepal traces (LS) are present; these depart from the axis at about the same or a slightly higher level than the sepal midribs and in alternation with them. The 5 petal midribs (P) next diverge in alternation with the sepal midribs and pass horizontally to the petals.

The 10 stamen traces (ST) follow soon after the petal traces, so soon in several species that the antepetalous stamen traces appear

fused with the petal midribs and thus may move outward slightly ahead of the antesepalous stamen traces. The disc is cushion-shaped or stalk-like, and receives from the top of the stamen traces numerous branches (ST'), some of which enter the ovary wall.

The 5 dorsal traces (D) of the carpels diverge on the petal radii, pass upward through the outer carpel walls, giving off several branches (D'), and end just below the 5 large oil glands (OG) at the top of the ovary. The vascular tissue which is left after the departure of the dorsal carpel traces forms 5 traces, each of which represents two fused ventral bundles (V) of two adjacent carpels. Each of these traces passes upward through the ovary axis, sending off branches to ovules in 2 adjacent carpels. At the top of the ovary each fused ventral trace splits into paired bundles, each of which is joined by one or more branches from the dorsal bundles. They then pass upward through the style, the paired bundles alternating with the stylar canals (TT), to the stigma. In some species, some or all of the ventral traces may remain fused for their entire length. In _M. integerrimum_ each of the ventral traces ends just below a large oil gland; however, in most species of _Micromelum_ these abnormally large oil glands are not present in the stigma.

SUBTRIBE CLAUSENINAE. Except for minor differences, the vascular plan throughout the Clauseninae is uniform and is similar to that of _Micromelum_. In _Murraya_ the disc is stalk-like or cushion-shaped, while in _Glycosmis_ and _Clausena_ it is a short, more or less swollen gynophore.

Glycosmis (Fig. 12-13).— The stamen traces do not give off branches in this genus, so that the disc receives no vascular supply except in the case of _G. cochinchinensis_, _G. Eleneri_, and _G. citrifolia_,

where several weak traces (DI) depart from the stele into the disc. The dorsal carpel bundles in most species end at the top of the ovary, and in the case of G. Craibii, G. chlorosperma, and G. Greenii they terminate just below the large oil glands there. However, in G. cochinchinensis and G. macrantha they continue about half way up the style, opposite the stylar canals. Occasionally large oil glands are present also in the stigma (G. macrantha, G. pentaphylla), in which case the ventral traces end adjacent to them.

Clausena (Fig. 14-15).— Several species of Clausena have in the tips of the sepals large oil glands around which the sepal midribs anastomose. Since, as in Glycosmis, the stamen traces do not branch, no vascular tissue is present in the disc, except in C. mollis, where several very weak traces diverge from the axis. At the top of the ovary the dorsal carpel bundles ramify below the large oil glands which are usually present. Some of these branches fuse with the ventral bundles and some pass a short distance up the style. In some species large oil glands are present in the stigma.

Murraya (Fig. 16).— The disc, which is similar to that in Micromelum, derives its vascular supply from branches from the stamen traces; it receives no independent traces from the axis. In most of the species studied, the dorsal traces move up the style opposite the stylar canals and end in or just below the stigma. In M. crenulata, however, the dorsal traces end below the large oil glands at the top of the ovary. The ventral bundles, and in M. Koenigii the dorsal bundles also, terminate below large oil glands in the stigma.

SUBTRIBE MERRILLIINAE. Merrillia.— There is no essential difference between the vascular plan of Merrillia and that of the preceding

groups. The disc, which is like that of Murraya, receives no traces either from the stamens or from the axis. The dorsal carpel bundles enter the style, but pass only a short distance upward.

TRIBE CITREAE. In the Citreae there occurs a fusion of the traces supplying the sepals and petals (with the exception of Microcitrus in the subtribe Citrinae and Afraegle, Aeglopsis, and Aegle in the subtribe Balsamocitrinae). The degree of fusion ranges from the simple union of the sepal midrib with the lateral traces of the two adjacent petals just above it, to the condition where, in addition to this type of adnation, the lateral sepal traces are fused to or arise as branches of the petal midrib just above them.

SUBTRIBE TRIPHASIINAE. In the flowers of this subtribe only the simpler type of fusion, that is the fusion of sepal midrib and lateral petal traces, is commonly present. There are, however, some cases of slight fusion of the petal midrib with the lateral sepal bundles.

A. Wenzelia Group. Wenzelia.— Each of the first 5 bundles to emerge from the stele represents a sepal midrib fused to the lateral petal bundles. As these bundles pass outward below the base of the petals, each gives off two branches which enter the two adjacent petals alternating with the sepal lobes. The petal midribs arise independently from the axis at a slightly higher level, alternating with the sepal midribs. Thus in contrast to the Clauseneae, where the lateral petal bundles are branches of the petal midribs, the petals receive their vascular supply from two different whorls of bundles. The 10 stamen traces next leave the stele, and from the edges of their gaps arise quickly a number of traces which enter the disc and sometimes pass up into the ovary. At the base of the stalked ovary the dorsal carpel

bundles move outward from the axis and run up through the carpel walls, giving off several branches. Some of the branches join the ventral bundles at the top of the ovary. The remaining vascular tissue forms the ventral bundles, which send off branches to the ovules and then, together with the dorsal bundles, pass up through the style to the stigma, where they end in large oil glands. The two ventral bundles of each carpel remain fused until they pass into the style, but at this level they, as well as some of the dorsal bundles may split into two separate bundles. In the style the dorsal bundles occupy a position opposite the stylar canals, while the paired ventral bundles alternate with the stylar canals.

B. Oxanthera Group. Oxanthera.— Due to the fact that there was inadequate material for a study of this genus, no details of the vascular supply will be given here. In general, however, the arrangement of the bundles seems to correspond to that of other genera of this subtribe.

C. Luvunga Group. Luvunga.— The first whorl of bundles, twice as many as the calyx lobes, which diverges from the axis consists of fused sepal midrib-lateral petal bundles alternating with fused lateral sepal-petal midrib bundles. Beneath the base of the petals each sepal midrib sends off 2 lateral branches which enter adjacent petals. The fusion of the lateral sepal-petal midrib bundles is usually only slight and is quite irregular even within a single flower bud. In most cases the lateral sepal traces diverge from the petal midrib close to the axis, or the petal midribs may merely arise from the edges of the gaps left by the lateral sepal traces. However, in L. philippinensis the separation occurs just before the bundles pass below the petals. In L.

villosa the lateral petal traces may branch from the lateral sepal traces or from the sepal midribs. In some species there is an extensive anastomosis of the lateral sepal traces with the sepal midribs, so that it is rather difficult to ascertain from which traces the lateral petal bundles are derived. The origin of the vascular bundles entering the stamens, disc and carpels is similar to that in Wenzelia. The style and stigma were missing from some ovaries, but in those which were present the dorsal and ventral bundles ended adjacent to large oil glands in the stigma.

Paramignya.(Fig. 26).— As in Luvunga, there is a fusion not only of the sepal midrib with the lateral petal traces, but also of the lateral sepal traces with the petal midrib. The divergence of the latter may take place close to the axis or almost beneath the petals. The disc derives its vascular supply from several bundles arising directly from the stele. The disc traces ramify about the large oil glands often present in the disc, as do also the dorsal bundles which arise at a slightly higher level. The dorsal bundles do not enter the style, but ramify about the oil glands at the top of the ovary. Some of the branches from the dorsal bundles fuse with the ventral bundles, which pass up through the style in alternation with the stylar canals and end close to the oil glands in the stigma, around which they may branch.

D. Triphasia Group. Triphasia (Fig. 17-20).— The bundle arrangement in Triphasia, is quite similar to that in Wenzelia. However, in addition to the sepal midribs there are also lateral sepal bundles arising almost at the same level as the latter, and alternating with them. They pass outward, splitting into two branches which enter ad-

jacent sepal lobes. The vascular supply to the disc may arise either as branches of the stamen traces or from the edges of the gaps left by the stamen bundles as they diverge from the stele.

Severinia (Fig. 21-25).— In Severinia a fusion of sepal and petal traces similar to that in Luvunga occurs. However, in all of the species studied, the divergence of the lateral sepal traces from the petal midribs takes place close to the axis, and in one species, S. linearis, there is no such fusion, there being no lateral sepal bundles. The bundles of the cup-shaped disc arise as branches of the stamen traces. The dorsal bundles of the 2 to 3 carpels, after sending branches to the ventral bundles, end just below the large oil glands usually present at the top of the ovary. The fused ventral bundles separate into paired bundles and, alternating with the stylar canals, pass up through the style to the stigma, where they too end close to large oil glands.

SUBTRIBE CITRINAE, A. Primitive Citrous Group. In this group there is a great deal of irregularity in the fusion of the lateral sepal bundles with the petal midribs.

Pleiospermium.— In P. alatum the lateral petal bundles sometimes arise independently and sometimes as branches of the sepal midribs or petal midribs. The lateral sepal bundles and the petal midrib arise from the same bundle group in the axis, but the petal midrib does not send any branches into the calyx. In P. dubium, however, the petal midribs diverge from the axis totally or partially fused with the lateral sepal bundles, from which they quickly separate. The saucer-shaped disc receives branches from the 10 stamen traces. The dorsal

bundles enter the style and pass about half way up to the stigma. The ventral bundles are joined by branches of the dorsal bundles at the top of the ovary and pass up, either as fused or paired ventral bundles, to the stigma, where they end in the large oil glands.

Burkillanthus.— The vascular system of this genus is quite like that of Pleiospermium. However, the lateral sepal bundles diverge from the petal midribs close to the axis and there are no large oil glands in the stigma.

Limnocitrus.— Again in this genus the vascular plan is quite similar to that of Pleiospermium, except that here the dorsal bundles end near the large oil glands at the top of the ovary.

Hesperethusa.— As in Pleiospermium, the amount of fusion of sepal and petal traces is rather irregular. In one bud, two of the lateral petal traces are derived from the sepal midribs, while the rest are branches of the petal midribs. Two of the petal midribs are fused with lateral sepal traces, but the rest are independent. The 8 stamen traces are unbranched, and the disc derives its vascular supply direct-ly from the axis. These disc bundles ramify around the oil glands at the top of the ovary, and the 8 paired ventral bundles end in large oil glands in the stigma.

B. Near-Citrous Group. Species of Citropsis and Atalantia, as a rule, exhibit no fusion of the lateral sepal bundles with the petal midribs.

Citropsis.— The first whorl of bundles to diverge from the axis consists of 4 fused sepal midrib-lateral petal bundles. These are closely followed by a whorl of smaller lateral sepal bundles. In con-

trast to the four preceding genera, there is no fusion whatever of the lateral sepal bundles with the 4 petal midribs, which arise independently. The traces to the ring-shaped disc arise as branches of the stamen bundles; in some species they may also arise at the edges of the stamen gaps or slightly higher up the axis. The dorsal carpel bundles in most species run about half way up the style, opposite the stylar canals, but in C. gabonensis they end below the large oil glands at the top of the ovary. The 4 fused ventral bundles are always joined by branches of the dorsal bundles at the top of the ovary, after which they pass up the style in alternation with the stylar canals, and end in the stigma close to the large oil glands about which they may ramify.

Atalantia (Fig. 27).-- In general, the vascular plan of this genus is the same as that of Citropsis. However, in A. monophylla, after the departure of the sepal midribs a second whorl leaves the axis and represents the fused lateral sepal-lateral petal-petal midrib bundles. Two branches are given off by each of these fused bundles before they pass very far outward, and each of the branches splits into a lateral petal and a lateral sepal bundle below the base of the petals. In A. Wightii some of the sepal midribs give off only one lateral petal bundle, in which case the other lateral petal bundle arises from the petal midrib in the base of the petal. In all of the species studied, the traces to the annular disc diverge from the tops of the stamen bundles. The dorsal carpel bundles pass at least half way up the style, even when (as in A. racemosa)large oil glands are present at the top of the ovary, and in A. monophylla they reach the stigma. The ventral bundles end in the stigma, close to the large oil glands

when these are present (<u>A. racemosa</u>).

C. True Citrous Group. In this group, there is, as in Group B, no fusion of the lateral sepal traces with the petal midribs, except in the case of several species of <u>Citrus</u>. Moreover, in <u>Microcitrus</u>, there is not even fusion of the sepal midribs with the lateral petal traces. In contrast to the two preceding groups the stamen traces are four or more times the petals in number.

<u>Fortunella</u> (Fig. 28).— The arrangement of the vascular bundles is about the same as in <u>Citropsis</u>. The same type of fusion of sepal and petal traces occurs. There are no lateral sepal traces originating directly from the axis. The number of bundles leaving the stele to supply the 15-23 stamens is fewer than the number of stamens, but some of the bundles divide laterally into 2 traces as they pass toward the stamens. In <u>F</u>. <u>margarita</u> only the antepetalous stamen traces branch, but in other species either antepetalous or antesepalous stamen traces may branch. The traces to the annular disc originate from the tops of the stamen bundles. The dorsal carpel bundles in all species enter the short style, and in some species penetrate almost to the stigma. The ventral carpel bundles, as usual, end in the stigma, close to the large oil glands which are commonly present there.

<u>Eremocitrus</u>.— As in the other genera of this group, the first bundles to diverge from the axis are the 5 fused sepal midrib-lateral petal bundles, which separate into their component traces below the petal bases. These are quickly followed by 5 smaller, lateral sepal traces, and then 4 petal midribs leave the stele. As in <u>Fortunella</u>, some of the antepetalous stamen bundles divide after leaving the stele in order to supply the pleiomerous androecium. The antesepalous stamen

bundles do not display any lateral branching. Branches from the tops of the stamen bundles enter the disc. Both the ventral and dorsal carpel bundles enter the style, the latter moving upward opposite the stylar canals and the former in alternation with them. The dorsal carpel bundles end about half way up the style, and the ventral bundles pass up to the stigma.

Poncirus (Fig. 29-33).— The vascular supply to the calyx, corolla, androecium, and disc is the same as in Eremocitrus. At the base of the 6-carpellate ovary the vascular tissue remaining after the departure of the 6 dorsal bundles forms the 6 ventral bundles, which then divide radially so that 2 whorls of 6 bundles each result. Each bundle of the outer whorl takes a position opposite the two placentae of a carpel, and the bundles of the inner whorl move toward the center of the axis. The outer ventral bundles send branches (V') to the outer carpel walls and supply the ovules in the lower part of the ovary, gradually becoming smaller as they pass upward. About half way up the ovary the inner whorl of ventral bundles moves outward to join the outer whorl and supplies the ovules in the upper half of the ovary. Instead of standing opposite the carpels, as did the bundles of the outer whorl, they alternate with them and supply the ovules of one placenta in each of two adjacent carpels, which latter condition is typical of the genera previously described. Near the top of the ovary, branches from the dorsal carpel bundles fuse with the ventral bundles, which then pass upward, in alternation with the stylar canals, to the stigma. The dorsal bundles end at the base of the style.

Clymenia.(Fig. 34-36).— The vascular supply to the calyx and corolla is similar to that for Poncirus and Eremocitrus. As in other

genera, after giving off the lateral petal bundles the sepal bundles form an anastomosing system in the base of the calyx. Each petal receives several lateral petal bundles from each sepal midrib, and one of the 4 petals receives 2 petal midribs from the stele. The occurrence of approximately 100 stamens leads to a great deal more branching of the stamen bundles than has taken place in other genera with more than twice as many stamens as petals. The stamen bundles leave the axis in a single whorl, and as they approach the periphery both the antepetalous and antesepalous stamens branch tangentially and vertically to supply the individual stamens. The filaments separate from the base of the disc in two to three irregular whorls, although the vascular tissue originates in a single whorl of bundles. The annular disc receives some branches from the stamen bundles and some traces directly from the axis. The dorsal bundles of the 17 carpels arise independently from the stele, branch repeatedly as they move upward through the carpel walls, pass up the style one opposite each stylar canal, and end a little below or in the stigma. The remaining vascular tissue at the base of the ovary forms 17 fused ventral bundles which take positions alternating with the carpels and supply placentae of adjacent carpels. About half way up the ovary, branches from the ventral bundles move to the center of the ovary, pass upward and end in a dome of densely cytoplasmic cells beneath the base of the style. At the top of the ovary the ventral bundles divide into two, fuse with branches from the dorsal carpel bundles and pass up the style, in pairs alternating with the stylar canals, to the stigma.

Microcitrus.-- In the species studied there is no fusion whatever of the traces supplying the sepals and petals. The 4 lateral

sepal traces diverge quickly after the sepal midribs, and at a slightly higher level the petal midribs move outward. The lateral petal traces are given off by the petal midribs after they have entered the petals. The short ring-shaped disc derives its vascular supply from the top of the stamen traces, some of which, either antepetalous or antesepalous, branch laterally to enter the 19 or more stamens. The 7 dorsal carpel bundles give off branches as they pass up through the ovary wall, and end about half way up the style. Some of the branches fuse with the paired ventral bundles, which disappear in the stigma.

Citrus (Fig. 37-38).-- In C. micrantha, C. ichangensis, and C. macroptera of the subgenus Papeda the vascular supply to the calyx and corolla exhibits the same type of fusion as in Poncirus and Eremocitrus. However, in C. reticulata, C. grandis, C. aurantifolia, C. limon, and C. sinensis of the subgenus Eucitrus there is not only fusion of the sepal midrib with the lateral petal bundles, but also fusion of the lateral sepal bundles with the petal midrib. When the petal midrib reaches its position beneath the petal base, one or more branches from it continue into the base of the calyx, forming the lateral sepal bundles. The rest of the vascular system differs in no essential way from that of Microcitrus, Eremocitrus, or Fortunella.

SUBTRIBE BALSAMOCITRINAE. In Afraegle, Aeglopsis, and Aegle the sepal and petal midribs arise independently as in the Clauseneae, but differ from them in other ways. In Swinglea, Feronia, and Feroniella, however, fusion of the sepal midribs with the lateral petal bundles occurs, and in Swinglea there is also a slight fusion of the lateral sepal traces with the petal midrib.

A. Tabog Group. Swinglea (Fig. 46).— As mentioned above, the vascular plan of this genus differs markedly from Afraegle, Aeglopsis, and Aegle. The first bundles to leave the stele are the 5 fused sepal midrib-lateral petal bundles. These are soon followed by a whorl of 5 fused lateral sepal-petal midrib bundles, which separate into their component traces shortly after leaving the stele. Some of the lateral petal bundles arise from this second whorl rather than from the sepal midribs. The traces ramifying through the cushion-shaped disc originate both from the 10 stamen bundles and directly from the axis. The antesepalous stamen traces seem to diverge slightly ahead of the antepetalous traces, which supply the 5 shorter stamens. The 8 dorsal carpel bundles, after sending off branches which fuse with the ventral bundles at the top of the ovary, pass upward and end about half way up the style. The fused ventral bundles pass up to the stigma where they ramify about the large oil glands.

B. Bael Fruit Group. Afraegle (Fig. 39-45).— After the departure of numerous traces to the sepals, the remaining bundles come together to form a more or less continuous vascular cylinder, which quickly assumes a pentagonal form as the 5 petal midribs begin to diverge. At a higher level the 15 stamen traces depart from the axis in a single whorl. From the top of the stamen bundles arise branches which ramify through the ring-shaped disc and some of them enter the ovary wall. The dorsal carpel bundles diverge from the axis at the base of the ovary and pass upward through the carpel wall, giving off several branches. Some of the dorsal bundles end in the base of the style, while others pass upward to the base of the stigma. The balance of the vascular tissue forms into the ventral bundles which pass up through the ovary,

giving off branches to the numerous ovules. At the top of the ovary, one to several branches from the dorsal bundles fuse with the ventral bundles, which then pass up through the style to the stigma. In A. paniculata each ventral bundle gives off branches to the series of oil glands which appear at increasing heights to the tip of the stigma. However, in A. gabonensis the ventral bundles pass unbranched to the large oil glands which appear only near the tip of the stigma.

Aeglopsis.— As in Afraegle, the bundles remaining after the sepal traces move outward form an almost continuous stele. After the departure of the petal midribs, a whorl of 8 stamen traces diverges, the trace to each stamen arising independently. The dorsal bundles penetrate the style only for a very short distance, while the ventral bundles pass to the stigma, where they end adjacent to the large oil glands there.

Aegle.— Again in this genus the bundles remaining after the divergence of the sepal midribs form a more or less continuous cylinder, which quickly assumes a square shape as the 4 lateral sepal bundles leave. At a somewhat higher level the 5 petal midribs move outward, followed by a whorl of stamen bundles, many of which, both antepetalous and antesepalous, divide laterally in order to supply the 40 or more stamens. The short columnar disc receives its vascular supply both from branches from the top of the stamen bundles and from traces originating directly from the axis. As in Afraegle and Aeglopsis, the dorsal bundles enter the base of the style, but do not pass upward for any great distance. A little above the base of the ovary the ventral bundles give off several weak branches which move toward the center of the axis and disappear within a short distance. In the stigma the

ventral bundles break up into a number of smaller traces, each of which ends near a large oil gland.

C. Wood-Apple Group. Feronia (Fig. 47-49).— The 5 sepal-lateral petal bundles are the first to depart from the stele. At a slightly higher level the petal midribs diverge independently from the axis, and do not give off any branches to the calyx. The traces to the very short disc come from the gaps left in the stele by the 10 stamen bundles. The 5 dorsal bundles disappear in the base of the style. The 5 ventral bundles are carried outward as the placentae separate to form a 1-loculate ovary with parietal placentae. After fusing with branches from the dorsal bundles at the top of the ovary, the fused ventral bundles separate and pass upward, the pairs alternating with the 5 stylar canals, to the tip of the stigma.

Feroniella.— The vascular supply to the calyx and corolla exhibits the same type of fusion as in Feronia. A whorl of 5 sepal midrib-lateral petal bundles is the first to diverge, and they separate into their component bundles at the periphery of the receptacle. These are soon followed by 5 petal midribs. At the base of the petals there is an anastomosis of the sepal midribs, lateral petal bundles and petal midribs, so that it is difficult to distinguish one from another. The stamens, four times the petals in number, are supplied by an indefinite number of bundles, some of which divide into two bundles very close to the axis. The very short disc receives several weak traces from the axis. The dorsal bundles branch several times as they pass upward through the carpel walls, and end at the top of the ovary. As in Feronia, the ventral bundles, one per carpel, move outward as the placentae separate to form a 1-loculate ovary with parietal placentation. The

fused ventral bundles are joined by branches from the dorsal bundles at the top of the ovary, and enter the style, each separating into a pair of ventral bundles as they pass upward, alternating with the stylar canals, to the tip of the stigma.

DISCUSSION

Relation of Vascular Anatomy to Taxonomy

From the foregoing descriptions it is seen that Swingle's tribe Clauseneae is set off clearly from the tribe Citreae by the fact that in the former group the sepal and petal midribs arise independently from the axis, while in the Citreae the sepal midribs carry out the lateral petal bundles fused to them, and in some species the lateral sepal bundles are fused in varying degrees to the petal midribs. This latter type of fusion may be very slight, the component traces of the bundle separating close to the central cylinder, or the division may take place close to or just beneath the petal bases.

TRIBE CLAUSENEAE.— Although the delimitation of the two tribes on the basis of anatomical evidence is quite definite, the division of the tribes into subtribes and groups is frequently not so clear. As mentioned above, the vascular systems of the genera of the tribe Clauseneae have in common the independent sepal and petal midribs. However, there is little evidence from the vascular systems which would serve as a basis for its subdivision into the three subtribes. The minor differences between the bundle arrangements are not always characteristic of a genus, much less of a subtribe, so that other methods must be used here.

TRIBE CITREAE.— Again in the case of the Citreae it becomes difficult to find a characteristic of the vascular plan which holds true for all the genera of a subtribe. Swingle (in press) bases his division of the tribe into three subtribes on such morphological characters as the presence or absence of pulp vesicles, hard-shelled fruit, and the number of stamens, carpels, and ovules.

SUBTRIBE TRIPHASIINAE.— Although no characteristic of the bundle arrangement of the Triphasiinae is present which would differentiate between this subtribe and the Citrinae, the former may be divided into two groups depending upon the type of fusion of the sepal and petal traces. Wenzelia and Triphasia have in common the absence of fusion of the lateral sepal traces to the petal midrib, which arises independently from the axis. In Luvunga, Paramignya, and Severinia the lateral sepal traces are carried outward by the petal midribs. In some species the division of the bundle into its components takes place close to the axis, while in others the bundle passes outward to the base of the petals before giving off branches to the sepals. This grouping differs from that of Swingle, who, on the basis of morphological characters, places Triphasia and Severinia together in a separate group. The fact that the vascular plan of Triphasia Brassii (Echinocitrus Brassii) differs in no essential way from that of Triphasia trifolia and T. grandifolia lends support to its inclusion by Swingle as a species of Triphasia.

SUBTRIBE CITRINAE, Group A.— This group, which includes Pleiospermium, Burkillanthus, Limnocitrus, and Hesperethusa, is clearly set off from the other two groups by the irregularity of the fusion of sepal and petal traces. In one bud of Pleiospermium alatum, for example,

some lateral petal traces arise directly from the axis, and some arise as branches of the sepal midribs or petal midribs. In _Pleiospermium alatum_ and _Limnocitrus littoralis_ there is no fusion of lateral sepal traces with the petal midrib, in _Pleiospermium dubium_ and _Burkillanthus malaccensis_ the lateral sepal traces diverge from the petal midribs close to the axis, and in a bud of _Hesperethusa crenulata_ two of the petal midribs are fused with lateral sepal traces while three arise independently. On the basis of this anatomical evidence, as well as the occurrence of pulp vesicles, Swingle seems justified in removing _Pleiospermium_ and _Hesperethusa_ from Engler's Hesperethusinae and assigning them a place close to the true citrous fruit trees. _Burkillanthus malaccensis_, which was formerly considered a species of _Citrus_, differs from the latter in having only 10 stamen traces, while in _Citrus_ the more numerous stamen traces divide laterally to supply the 20-25 stamens.

Group B.--- _Citropsis_ and _Atalantia_, comprising Group B, contrast sharply with Group A in not having any fusion of the lateral sepal traces with the petal midribs. _Atalantia_ differs markedly in this respect, as well as in the possession of pulp vesicles, from _Paramignya_, which exhibits fusion of the petal midribs with the lateral sepal traces. These two genera, together with _Merope_, _Severinia_, and _Pamburus_, are considered sections of the genus _Atalantia_ by Engler. However, differences in vascular anatomy, as well as morphological differences, support their recognition as separate genera.

Group C.--- The outstanding difference between the genera of Group C and the preceding groups is the presence of four times as many stamens as petals. Some of the stamen traces divide laterally shortly after

diverging from the axis, and in _Clymenia polyandra_ the stamen bundles branch both laterally and vertically to enter the approximately 100 stamens. The genera of this group, with the exception of several species of _Citrus_, differ from those of Group A in displaying no fusion of lateral sepal traces with the petal midribs. The _Citrus_ subgenus Eucitrus is sharply set off from the subgenus Papeda by the fact that the species of the former group exhibit fusion both of the sepal midribs with the lateral petal bundles and of the petal midribs with the lateral sepal bundles. In _Microcitrus australasica_, however, there is not even fusion of the lateral petal traces with the sepal midribs. The presence of four times as many stamens as petals and more than five carpels, together with other morphological evidence, seem to offer sufficient grounds for including it with this group.

SUBTRIBE BALSAMOCITRINAE.— The members of this subtribe, which are characterized by hard-shelled fruits, may be divided into three groups on the basis of their vascular plans. These groups correspond to the three groups proposed by Swingle (in press). In one group are _Afraegle, Aeglopsis,_ and _Aegle,_ where there is no fusion of sepal or petal traces but the bundles remaining after the divergence of the sepal traces come together in a more or less continuous vascular cylinder, in contrast to the Clauseneae, where the bundles remain separate. _Feronia_ and _Feroniella_ comprise a second group, in which the lateral petal bundles arise as branches of the sepal midribs. _Swinglea glutinosa,_ which is the sole member of the third group, exhibits not only fusion of the sepal midribs with the lateral petal traces, but also fusion of the petal midribs with the lateral sepal traces. The great resemblance of

Swinglea to Pleiospermium and Burkillanthus, in the nature not only of
the vascular systems but also of morphological characters, raises a
question as to the relationship between these two groups,— Balsamocit-
rinae and Citrinae, Group A. From anatomical evidence, it seems reason-
able to suppose that the Balsamocitrinae may represent a side line which
has developed from the Clauseneae independently of the rest of the
Citreae.

It is evident from the foregoing descriptions that the relation-
ships of the Aurantioideae as shown by Engler's system of classifica-
tion do not correspond to the results of this anatomical study. Al-
though Tanaka's classification does appear to show the progressive
development of this subfamily, he does not seem to be justified in set-
ting up eight separate tribes of equal rank. In general, and with the
exceptions noted above, the relationships indicated by a study of the
vascular systems agree with the grouping proposed by Swingle (in press),
who bases his taxonomic ideas on a morphological examination not only
of the flowers and fruits, but also of the vegetative organs of the
plants.

In Table I is presented a summary of the types of vascular systems
found in the various subdivisions of the Aurantioideae. The table is
not intended to indicate a line of descent, but merely shows the trends
in the vascular systems, which, like the morphological changes, may or
may not be a true indication of the phylogeny of the Aurantioideae.

	TRIBE CLAUSENEAE	

	TRIBE CLAUSENEAE	
MICROMELINAE _Micromelum_	CLAUSENINAE _Glycosmis_, _Clausena_, _Murraya_	MERRILLIINAE _Merrillia_

S
P

	TRIBE CITREAE	
	CITRINAE – Group C _Microcitrus_	BALSAMOCITRINAE – Group G _Afraegle_, _Aeglopsis_, _Aegle_

S-LP
P

TRIPHASIINAE – Group A _Wenzelia_	CITRINAE – Group B _Citropsis_, _Atalantia_	BALSAMOCITRINAE – Group C _Feronia_, _Feroniella_
TRIPHASIINAE – Group D _Triphasia_	CITRINAE – Group C _Fortunella_, _Eremocitrus_, _Poncirus_, _Clymenia_, _Citrus_ (Papeda)	

S-LP
P-LS

TRIPHASIINAE – Group D _Severinia_	CITRINAE – Group C _Citrus_ (Eucitrus)	BALSAMOCITRINAE – Group A _Swinglea_
TRIPHASIINAE – Group C _Luvunga_, _Paramignya_	CITRINAE – Group A _Pleiospermium_, _Burkil-_ _lanthus_, _Limnocitrus_, _Hesperethusa_	

Table I. Relation of Vascular Anatomy to Taxonomy. S, sepal midrib independent; P, petal midrib independent; S-LP, sepal midrib and lateral petal bundles fused; P-LS, petal midrib and lateral sepal bundles fused.

Oil Glands

Oil glands occur in all parts of the flower, but in most species conspicuously larger oil glands, several times the normal size, are also present at the tips of the sepals, at the top of the filaments, disc, ovary, or stigma, usually either one or two for each member of the whorl. As pointed out in the foregoing descriptions, wherever a large oil gland appears, one of the principle vascular bundles either ends close to it or sends branches about it. This proximity to the vascular bundles leads one to question the significance of these large oil glands in the life of the plant.

Androecium

In the more primitive _Citrus_ relatives the stamens number only twice that of the petals, and the traces which supply them diverge from the stele independently and in a single whorl. In some species the antesepalous stamens seem to come off first, while in other species the antepetalous stamens seem to leave the axis first and may be slightly fused to the petal midribs. However, there is usually so little difference in the level of departure of the traces that it is impossible to say definitely which diverge first. It is quite evident, nevertheless, that the single whorl of stamens, twice the petals in number, represents two whorls which have been compressed into one, for the antepetalous stamens are usually shorter than the antesepalous stamens, and their filaments may have a different form. Furthermore Penzig (1887), in his study of teratological specimens of _Citrus_, reported buds in which the antesepalous stamens were petaloid while the antepetalous stamens were normal.

A study of the stamen traces of those species of the Citrinae and Balsamocitrinae which have three to four or more times as many stamens as petals shows clearly their origin by the division of members of the originally isomerous androecium. In all species where there is pleiomery of the stamens (except in species of *Afraegle*) some of the stamen bundles branch laterally as they move outward, and in *Clymenia polyandra* there is both lateral and vertical branching of the stamen bundles to supply the numerous stamens. Not all of the bundles branch, however, and since the bundles leaving the axis usually number more than twice the petals, it seems possible that in the expansion of the disc the point of separation of the branches has approached the axis itself, so that they merely arise from the same portion of the vascular cylinder.

Penzig's statement (1887) that in *Poncirus* only the antepetalous stamens branch is borne out by anatomical studies, and in *Fortunella margarita* and *Eremocitrus* the same condition exists. However, in *Citrus* species, in confirmation of Penzig's observations, both antepetalous and antesepalous stamen traces were seen to branch. This condition holds true also in other genera with more than twice as many stamens as petals,-- *Fortunella*, *Clymenia*, *Microcitrus*, *Aegle*, and *Feroniella*. In *Afraegle* no branching is apparent, the divergence of the stamen traces to supply the additional stamens supposedly taking place at the vascular cylinder.

Disc

Moore (1936c), in a review of Saunder's paper (1934), raises the question as to the nature of the disc in the Aurantioideae. Its origin in other families has been discussed by several authors. Dawson (1936), basing her idea on the fact that the disc derives its vascular supply from the stamens, considers the basal disc in the Polemoniaceae a much reduced whorl of stamens. Lawrence (1937) regards it probable that the disc of the Boraginaceae arises from increased proliferation of the swollen base of the ovary. Moore (1936a, 1936b), interpreting the disc in the Phaseoleae as a set of undeveloped stamens, bases his conclusion on the form and position of the disc and the origin of its vascular supply from the stamens.

The form of the disc in the Aurantioideae varies in the several genera. Possibly the simplest form occurs in Glycosmis and some species of Clausena, where the "disc" is merely a swelling of the ovary base or axis between the androecium and gynoecium. The vascular supply consists of a varying number of small traces which arise directly from the vascular cylinder. In several genera, including Micromelum, Paramignya, Merrillia, Burkillanthus, and Swinglea, the disc is stalk-like and derives its traces either as branches of the stamen bundles or directly from the axis. In one species of Paramignya branches of the dorsal carpel bundles pass to the oil glands in the disc. A third type of disc is a ring in which the base of the ovary is sunken, as in Murraya, Wenzelia, Triphasia, Luvunga, Pleiospermium, Limnocitrus, Hesperethusa, Citropsis, Atalantia, Eremocitrus, Poncirus, Clymenia, Fortunella, Citrus, Microcitrus, Afraegle, and Aeglopsis. In Severinia this latter type of disc may be extended upward to form a cup around

the lower part of the ovary. Here again the disc traces may branch from the stamen bundles or come directly from the axis. In some genera,— Aegle, Feronia, Feroniella, and some species of Clausena,— there is little or no enlargement of the axis or constriction at the base of the ovary, so that the disc, if present, must be merged with the ovary base. In these genera the "disc" traces arise either as branches of the stamen bundles or directly from the stele.

Thus it is seen that the disc may vary in form from a swelling of the axis to a cup-like structure surrounding the base of the ovary, and its vascular supply may be derived from the stamens, from the axis, or rarely from the dorsal bundles of the carpels. In no case do the traces arising directly from the axis have a definite orientation in the petal or sepal radii, which would be expected if the "disc" traces supply a whorl of vestigial stamens. Where the disc traces arise as branches of the stamen bundles the radius in which they originate is naturally predetermined. In such cases several small traces arise from each stamen bundle and they ramify throughout the disc. Regardless of their origin some of the disc traces may enter the base of the ovary and pass upward for a short distance in alternation with, or external to, the dorsal carpel bundles. On the basis of this anatomical and morphological evidence it appears improbable that the disc represents a whorl of modified or vestigial floral members. It seems more probable that the disc in the Aurantioideae is, as suggested by Penzig (1887), merely an enlargement of the floral axis between the stamens and the base of the ovary.

Gynoecium

With one exception (<u>Triphasia</u> <u>trifolia</u>) the carpels are antepetal-
ous in position whenever the gynoecium is isomerous, although where the
full number of whorls is present strict alternation of the whorls should
bring them in line with the sepals. This agrees with the findings of a
study of 33 rutaceous species, mostly in other subfamilies than the
Aurantioideae, made by Saunders (1934), who states that "in the complete
Dicotyledon flower the uninterrupted alternation of all the whorls only
occurs when some specific adjustment comes into play which provides a
way of overcoming resistance to expansion, or as we may alternatively
express it, of relieving the congestion which, it may be supposed, nec-
essarily increases towards the centre as each successive whorl, still
surrounded by, and continuous with, the tissue of the earlier whorls,
begins to extend outwards." She explains the antesepalous carpels of
<u>Calodendrum</u> <u>capensis</u> by the "fact that the gynophore becomes disjoined
from, and lies free within, the encircling staminal tube below the level
at which the carpels begin to extend in the radial direction, so that
there is no cumulative congestion effect." Although this explanation
would seem plausible for such genera as <u>Feronia</u> and <u>Feroniella</u>, which
have no discs, it does not explain the antepetalous carpels of such
genera as <u>Micromelum</u>, <u>Glycosmis</u>, <u>Merrillia</u>, <u>Wenzelia</u>, and <u>Paramignya</u>,
where the compression should be relieved by the stalk-like discs or
gynophores.

Style

The stylar canals in the Aurantioideae are the same in number as the carpels and extend from the placentae of each carpel upward through the style to the stigma. They consist of very narrow slits bounded by a single layer of epidermal cells which are more densely cytoplasmic than the parenchyma cells surrounding them. This layer of epidermal cells is continuous from the cluster of "conducting hairs" extending from the epidermis of the placentae, which were noted in several genera by Penzig (1887), to the papillose cells of the stigmatic surface.

This condition, which was also observed in several species by Penzig, is not in agreement with Joshi's statement (1934) that "the stylar canals are either continuous with the ventral traces of the carpels or make their appearance at, and occupy exactly the situation of, such traces." His conclusion that "the stylar canals have been derived from, and represent modified ventral bundles of the carpels" is not in agreement with the above described observations, nor with the fact that in the Aurantioideae the ventral bundles do not disappear after supplying the ovules or merge with the stylar canals, but instead continue upward through the style to the stigma either as fused or paired bundles alternating with the stylar canals. The nature of the stylar canal in the Aurantioideae is then in accord with our previous ideas about transmitting tissue, dating back to Capus (1878) and Gueguen (1900-02), who showed that conduction of the pollen tube is as a rule, effected by the inner faces of the two carpellary margins, and of the placentae which are emergences from these margins.

SUMMARY

An anatomical study of 94 species comprising 29 genera of the Aurantioideae leads to the following conclusions:

1. In the tribe Clauseneae the sepal and petal midribs arise independently from the axis, while in the Citreae, except for _Microcitrus_, _Afraegle_, _Aeglopsis_, and _Aegle_, the sepal midribs are fused to the lateral petal bundles. However the vascular system does not offer such a definite basis for the division of the tribes and subtribes.

2. The fusion of the sepal midrib and lateral petal bundles in _Pleiospermium_, _Hesperethusa_, _Luvunga_, _Triphasia_, _Wenzelia_, and _Atalantia_ demonstrates their closer affinity to the Citrinae than to the Clauseneae.

3. Unusually large oil glands are often present at the tips of the sepals, disc, ovary, stigma, or stamens, and are usually in close association with vascular tissue.

4. That pleiomery of the stamens arises from the division of either antesepalous stamens or both antesepalous and antepetalous stamens is shown by branching of their traces.

5. The disc, which may be a swollen axis, stalk-like, ring-shaped to cup-like, or absent, appears to be merely an enlargment of the floral axis.

6. With the exception of one species, _Triphasia trifolia_, the carpels of isomerous ovaries are antepetalous, although strict alternation of the whorls should make them antesepalous.

7. The stylar canals consist of narrow slits surrounded by epidermal cells and are continuous from the papillose stigmatic cells to the conducting hairs between the placentae. They are not modified ventral carpel bundles.

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Legend: In all drawings the following symbols are used:-

                S, sepal midrib
               IS, lateral sepal bundle
                P, petal midrib
               LP, lateral petal bundle
               ST, stamen bundle
              ST', disc trace arising from stamen bundle
               DI, disc trace arising from axis
                D, dorsal carpel bundle
               D', branch of dorsal carpel bundle
                V, ventral carpel bundle
               V', branch of ventral carpel bundle
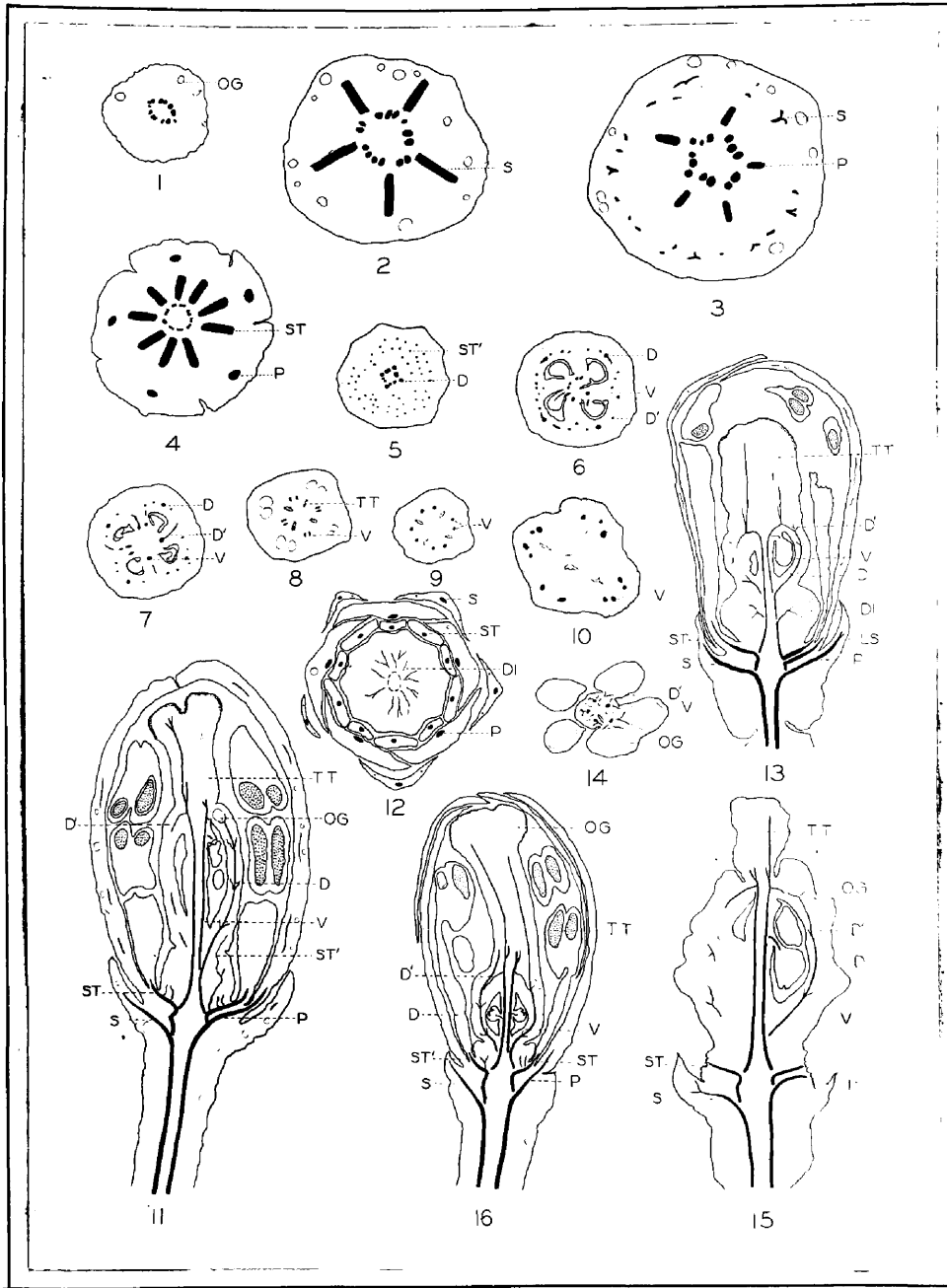   TT, stylar canal
               OG, large oil gland

Fig. 1-11. Micromelum scandens; 1-4, successive cross sections through
receptacle, X 12; 5, cross sect. through disc, X 12; 6-8, successive
cross sect. through ovary, X 12; 9, cross sect. through style, X 12;
10, cross sect. through stigma, X 12; 11, long. sect. of bud, X 7.
Fig. 12-13. Glycosmis citrifolia; 12, cross sect. through disc, X 16;
13, long. sect. of bud, X 11. Fig. 14. Clausena heptaphylla, cross
sect. through top of ovary, X 12. Fig. 15. Clausena grandifolia, long.
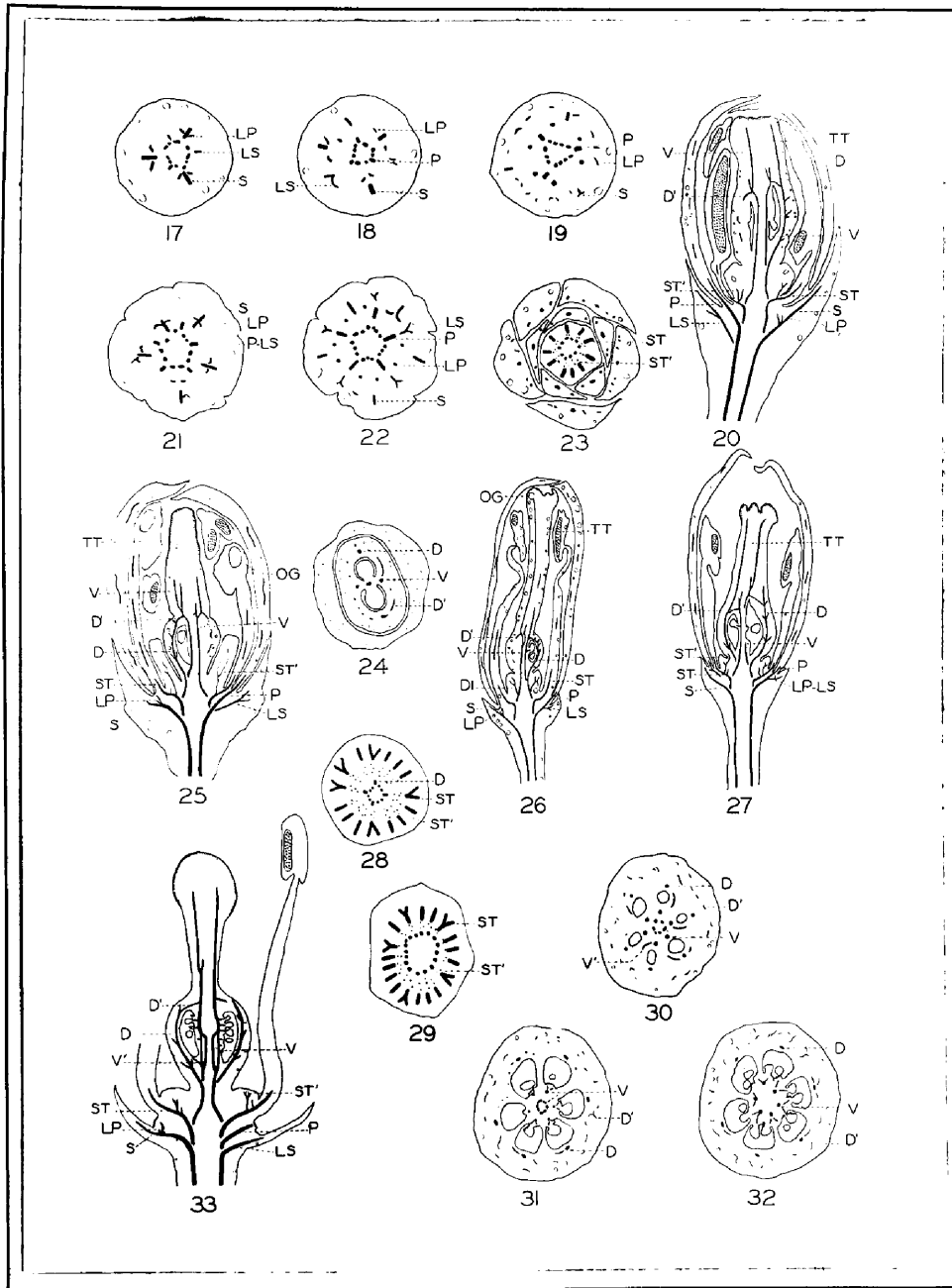sect. of pistil, X 10. Fig. 16. Murraya paniculata, long. sect. of
bud, X 8.

Fig. 17-20. Triphasia trifolia; 17-19, successive cross sect. through receptacle, X 14; 20, long. sect. of bud, X 9. Fig. 21-25. Severinia buxifolia; 21-22, successive cross sect. through receptacle, X 10; 23, cross sect. through base of disc, X 10; 24, cross sect. through ovary and disc, X 10; 25, long. sect. of bud, X 9. Fig. 26. Paramignya Griffithii, long. sect. of bud, X 4. Fig. 27. Atalantia monophylla, long. sect. of bud, X 7. Fig. 28. Fortunella Hindsii, cross sect. through base of disc, X 6. Fig. 29-33. Poncirus trifoliata; 29, cross section through base of disc, X 5; 30-32, successive cross sect. through ovary, X 5; 33, long. sect. of pistil, X 5.
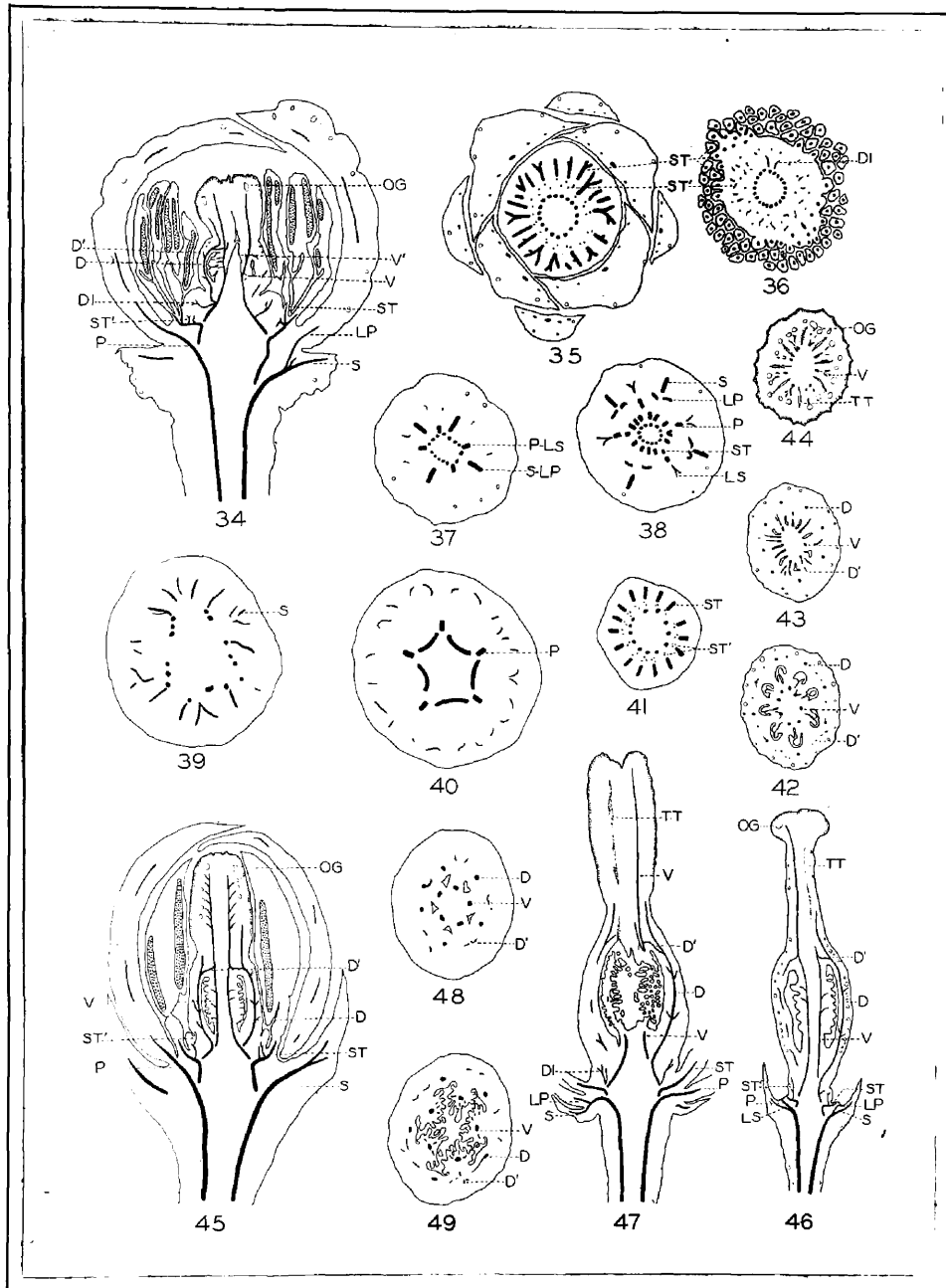
Fig. 34-36. Clymenia polyandra; 34, long. sect. of bud, X 5; 35-36, successive cross sect. through base of disc, X 6. Fig. 37-38. Citrus grandis, successive cross sect. through receptacle, X 6. Fig. 39-45. Afraegle paniculata; 39-43, successive cross sect. through receptacle and ovary, X 8; 44, cross sect. through stigma, X 8; 45, long. sect. of bud, X 7. Fig. 46. Swinglea glutinosa, long. sect. through pistil, X 4. Fig. 47-49. Feronia limonia; 47, long. sect. through pistil, X 5; 48-49, successive cross sect. through base of ovary, X 12.