

136; Yu-Shih Liu 1283, 1885; Yunnan, Tsai 53322, 54334, 54598, 55334, 55982, 56614, 58519, 58667, 59122; Yü 17774, 19949; Forrest 15683 (TYPE), 17583, 18075, 26224, 26272; Henry 10694; Sikong, Chiao 1286, 1704. INDO-CHINA, Tonkin, Chapa, Pételot 5929.

Data on the type number, Forrest 15683, taken from Notes, Roy. Bot. Gard. Edinburgh 17:152. 1930: "Shrub or tree of 30 or 40 ft. Flowers creamy-white. In open thickets on the Shweli-Salween divide. Lat. 25°30' N. Alt. 10,000 ft. July 1917." This species has flowers as large as those of *Turpinia pomifera* (Roxb.) DC. The leaflets, although acuminate, have not the elongate apex which marks most of the collections of the latter species. The fruits are scarcely at all fleshy and not nearly so large as in *T. pomifera* (Roxb.) DC. Indeed, it would seem that this species is the explanation of why *T. pomifera* (Roxb.) DC. and *T. cochinchinensis* (Lour.) Merr. (*T. nepalensis* Wight & Arn.) have been confused in China. *Turpinia affinis*, although readily separated from *T. cochinchinensis* (Lour.) Merr. in the flowering state by the open lax inflorescence with flowers almost twice as large, is somewhat difficult to distinguish in the more nearly mature fruits. In all the specimens cited we have been able to see, around the subsistent bases of the styles, some remnants of the pubescence which is readily seen on the pistil in the flower. The leaves usually have 5-9, sometimes 11, leaflets, a little broader than in the related species and more closely serrate.

***Turpinia cochinchinensis*** (Lour.) Merr. Jour. Arnold Arb. 19:43. 1938.

*Triceros cochinchinensis* Lour. Fl. Cochinch. 184. 1790.

*Turpinia nepalensis* Wight & Arn. Prodr. 156. 1834.

INDIA: Nepal, Wallich 4277; Assam, Khasia, Hooker f. & Thomson; Khasia and Jaintia Hills, Ruse 137. BURMA: Thandaung, Dickason 5143; Kachin Hills, Shaik Mokim. INDO-CHINA: Annam, Mt. Bana, Clemens 3791; Tonkin, Petelot 4242. CHINA: Yunnan, Henry 11612, A,B,H,I; Tsai 54310, 54504, 54625, 56367, 56400, 56912, 58789, 58887, 58985; Forrest 7476, 8474, 11857, 11888, 15758, 17867, 17893, 26410, 26521; Rock 2924, 7200; Wang 73075, 76313, 77381; Yü 18195.

*Turpinia cochinchinensis* (Lour.) Merr. shows considerable variation. Amongst the material cited are specimens with 3-foliolate leaves, 3- and 5-foliolate leaves, but most have 5-foliolate leaves. The species is not an easy one to define. It blends into *T. montana* (Blume) Kurz and *T. glaberrima* Merr. on the one hand, and on the other it is not easy to distinguish from *T. affinis* in fruit. Its best character is the somewhat

stiff compact inflorescence and small flowers. In *T. montana* (Blume) Kurz the netted venation of the leaves is much more distinct, the serrations are closer, and the inflorescence is longer and distinctly lax.

***Turpinia glaberrima*** Merr. Lingnan Sci. Jour. 7: 312. 1931, l.c. 14: 27. 1935.

CHINA: Kwangsi, *Ko* 55847; Kwangtung, *Tsiang* 1701, 2715; *Taam* 176, 579; Hong Kong, *C. Wright*; Hainan, *How* 70303, 71654, 73218; *Wang* 36220, 36510; *Liang* 63626, 64285, 64286, 64719; *Chun & Tso* 43958, 43682, 43918, 44396; *McClure* (C.C.C. 8497). INDO-CHINA: along Kwangtung-Tonkin border, Taai Wong Mo Shan, *Tsang* 27226.

This species needs to be studied in the field; it is perplexingly inconstant. Some numbers have the leaves 1- and 3-foliolate, other 3- and 5-foliolate, or all 5-foliolate, a single number which we interpret as a young growing shoot of this species has 9-11-foliolate leaves. Some specimens are disturbingly close to *Turpinia montana* (Blume) Kurz, yet none has as long an inflorescence as that species; further, although the secondary venation is fairly distinct, the leaves are mostly firmer. Other collections are scarcely separable from *T. cochinchinensis* (Lour.) Merr. since we have removed *T. affinis* from that complex. Possibly more material of the three species will lead to the reduction of this.

***Turpinia glaberrima*** Merr. var. *stenophylla* var. nov.

A forma typica differt foliulis angustioribus 4.5-6(-10) cm. longis, 1.5-2 cm. latis, plerumque rhachi brevior.

CHINA: Kwangtung, along the Kwangtung-Tonkin Border, Fang Ch'eng District, *Tsang* 26739 (TYPE); Kwangsi, Sup-man-ta Shan, *Liang* 69616, 69632.

These specimens are all fruiting material. The type of the variety has leaves small enough to belong to *Turpinia parviflora* Craib, described from Siam. We have no material so named, and Craib points out that it is very closely allied both to *T. parva* Koord. & Val. and to *T. nepalensis* Wight & Arn. Both the latter species have a fairly large inflorescence; the inflorescence in both *T. glaberrima* Merr. and var. *stenophylla* is mostly shorter than the leaves.

***Turpinia montana*** (Blume) Kurz, Jour. As. Soc. Bengal 46(2): 182. 1875; Koord. Exkursionfl. Java 2: 528. 1912; Koord. & Val. Atlas. Baumart. Java 1: fig. 92. 1913; Merr. Contr. Arnold Arb. 8: 93. 1934, Jour. Arnold Arb. 19: 42. 1938.

*Zanthoxylum montanum* Blume, Bijdr. 248. 1825.

*Turpinia parva* Koord. & Val. Meded. Lands Plant. 61: 249 (Bijdr. Boomsoort. Java 9: 249). 1903.

*Turpinia gracilis* Nakai, Jour. Arnold Arb. 5: 79. 1924. For further synonymy, consult Koorders (1912) and Merrill (1934).

CHINA: Yunnan, Szemao, *Henry* 12039, *b, c*; Fo-Hai, *Wang* 73601, 73694, 73813, 74654, 74797, 77154; Nan-Chiao, *Wang* 75050, 75136, 75181; Che-li Hsien, *Wang* 75497, 75693, 78111, 79504, 79713. INDO-CHINA: Tonkin, *Pételot* 5959; Annam, Mt. Bana, *Clemens* 3894; Cambodia, *Pierre* 907. SUMATRA: on trail from Kabajakan to Tretel, *W. N. & C. M. Bangham* 887. JAVA: *Hallier*; *Kuntze* 4498.

*Turpinia montana* (Blume) Kurz appears to be the most widely ranging species of the genus. It is a small tree with very slender and lax panicles as long as, or usually longer than, the leaves; the scarcely crowded flowers are small (half-open bud 2 mm. diameter) with ciliate petals and rounded anthers  $\pm$  0.5 mm. long; the fruit is 7-8 mm. diameter. The venation of the chartaceous leaves is perhaps more obvious than in any other known species.

***Turpinia montana* (Blume) Kurz var. *borneensis* var. nov.**

Foliolis usque 14 cm. longis et 5 cm. latis; fructibus usque 1.5 cm. diametro.

BORNEO: Sarawak, *Native collector* 2379; Mount Kinabalu, Penibukan, *Clemens* 31369, 31657, 40996, alt. 4000-8000 ft.; Tenompok, *Clemens* 28840, 29391 *bis* (TYPE), 29391, 30070, alt. 5000 ft.

The leaflets, although larger than in *Turpinia montana* (Blume) Kurz, somewhat broader and more rounded-cuneate at the base, are similar in texture and venation to those of the species. In the few inflorescences at our disposal we have not found any floral differences worth noting. The fruit is larger in some cases, but the seeds are few and the pericarp is thin. When more and better prepared material is at hand this may prove to be a distinct species.

***Turpinia laxiflora* Ridl. Jour. As. Soc. Straits Branch 82: 179. 1920, Fl. Malay Pen. 1: 512, 1922.**

MALAY PENINSULA: Perak, Larut, *Dr. King's collector* 5640 (Chanderiang). SUMATRA: Asahan, *Krukoff* 4425; *Rahmat Si Boeea* 6689, 6871, 6894, 7198; Simaloer, *Achmad* 559.

The distinguishing features of this species are the long lax panicles and the small (7-10 mm. diameter) dry fruits. In the specimens at hand all the dried fruits are wrinkled. This may be on account of their not

being mature, or because of the thin pericarp ( $\pm 0.5$  mm. thick). The leaves are very much like those of *Turpinia latifolia* Ridl.

***Turpinia Versteeghii* sp. nov.**

Arbor  $\pm 21$  m. alta glabra, tantum inflorescentia minute pubescens; petiolo 6–8 cm. longo, rhachi 5–8 cm. longa; stipulis caducis; foliis 1–3-jugis; stipellis in stipellam unam intrapetiolularem recurvatim connatis; foliolis coriaceis ovatis vel ellipticis, 9–17 cm. longis, 4.5–8.5 cm. latis, basi subrotundatis vel leviter cuneatis, apice breviter acuminatis, acumine  $\pm 1$  cm. longo, margine inconspicue serrulatis interdum revolutis, subnitidis; venis primariis utrinsecus 8, utrinque manifestis, patulis deinde curvatim adscendentibus; reticulo subobscuro; petiolulis 1–1.5 cm. longis, terminali 2–4 cm. longo; paniculis ad maturitatem 20–30 cm. longis, ramis subadscendentibus; floribus 3–4 mm. diametro; sepalis oblongis rotundatis ciliatis; petalis obovato-oblongis ciliatis; filamentis 2.5 mm. longis, basi 0.6–0.8 mm. latis, apice subulatis; antheris elliptico-ovatis 0.8 mm. longis minute apiculatis; disco dentato; ovario glabro; stylis glabris; ovulis in loculo 6–8; baccis obsolete trilobis 1.5 cm. diametro; pericarpio 2 mm. crasso.

NETHERLANDS NEW GUINEA: Bernhard Camp, Idenburg River, *Brass & Versteegh 13586* (TYPE), April 1939, alt. 300 m., frequent in primary rain-forest (tree 21 m. high, 39 cm. diameter; bark grey-brown, scaly, fissured; fruit green); 2 km. southwest of Bernhard Camp, Idenburg River, *Brass & Versteegh 13532*, April 1939, alt. 700 m., frequent in primary rain-forest (tree 26 m. high, 50 cm. diameter; fruit green). NORTHEASTERN NEW GUINEA: Sattelberg, *Clemens 3089*, May 1936, alt.  $\pm 1000$  m. (flowers white).

The species is marked by the large and inconspicuously serrulate leaflets; the fruit lacks the protruding base of the styles so well marked in the other New Guinean species. Probably *Clemens 3358* and *4041* from Yunzaing also belong here. Both are fragmentary specimens.

***Turpinia papuana* sp. nov.**

Arbor  $\pm 20$  m. alta praeter inflorescentiam puberulam glabra; petiolo 3–6 cm. longo, rhachi 2–5 cm. longa; foliis 1–2-jugis (in una collectione 1–5-foliolatis); stipulis caducis; stipellis in stipellam unam intrapetiolularem recurvatim connatis; foliolis coriaceis oblongis vel ellipticis, 7–11(–15) cm. longis, 2.7–4(–7) cm. latis, basi obtusis, apice acuminatis, acumine 1–2 cm. longo, margine serrulatis; venis primariis utrinsecus circiter 8 patulo-adscendentibus, reticulo inconspicuo; inflorescentiis in fructu usque 18 cm. longis, juvenilibus ad nodos multibracteatis,

bracteis minute foliiformibus; baccis subglobosis vel subtrilobis, 1.5 cm. diametro, apice remote 3-tuberculatis; ovulis 1-2 in uno loculo; pericarpio 2-2.5 mm. crasso.

NETHERLANDS NEW GUINEA: 18 km. southwest of Bernhard Camp, Idenburg River, *Brass & Versteegh 11994* (TYPE), February 1939, alt. 2160 m., frequent tree of the primary forest, on the slope of a ridge (tree 20 m. high, 37 cm. diameter; bark grey; fruit green); 15 km. southwest of Bernhard Camp, Idenburg River, *Brass & Versteegh 11960*, January 1939, alt. 1750 m., occasional tree in primary forest, on ridge (tree 17 m. high, 36 cm. diameter; bark grey; fruits brown); Bele River, 18 km. northeast of Lake Habbema, *Brass & Versteegh 11143*, November 1938, alt.  $\pm$  2400 m., occasional in primary forest (tree 17 m. high; 33 cm. diameter; bark grey; fruits green-brown). NORTHEASTERN NEW GUINEA: Ogeramnang, *Clemens 6405*, May 1937, alt.  $\pm$  1750 m.

Although we are handicapped by the lack of flowers, this material seems to be relatively uniform, differing from *Turpinia Versteeghii* in the smaller leaves with less rounded bases and definitely serrulate margins. The fruits are 3-pointed at the apex and in each locule are only 1-2 ovules. In *T. Versteeghii* there are 6-8 ovules in each locule.

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THE COMPARATIVE MORPHOLOGY OF THE ICACINACEAE  
IV. RAYS OF THE SECONDARY XYLEM

I. W. BAILEY AND R. A. HOWARD

*With four plates*

INTRODUCTION

WE have shown in the preceding papers of this series that a segregation of the Icacinoideae into three categories, upon the basis of their nodal anatomy and vessel structure, serves to differentiate their imperforate tracheary elements and wood parenchyma into three general levels of increasing structural specialization. It is of interest in this connection to determine whether the salient trends of phylogenetic modification of the rays tend to parallel those that occur in the other elements of the secondary xylem.

Kribs' (6) statistical investigations of the wood of large stems indicate that the primitive ray structure in dicotyledons is of the so-called heterogeneous I type. Woods with this primitive structure are characterized by having two types of rays, (1) vertically extensive, high-celled, uniseriate rays and (2) multiseriate rays with relatively long, high-celled, uniseriate extensions. Barghoorn's (4) recent detailed studies of ray ontogeny in the various families of the dicotyledons demonstrate that in structurally less modified plants both the first-formed and the later-formed secondary xylem have rays of the heterogeneous I type. In young stems, the first-formed multiseriate rays extend outward from the gaps or interfascicular parts of the stele, whereas in young roots they arise opposite the strands of primary xylem rather than between them. The first-formed uniseriate rays of young stems extend outward from the fascicular parts of the stele.

The original uniseriate and multiseriate rays are very extensive vertically, but are dissected into lower rays during subsequent stages of the lateral enlargement of the stem. During these stages of ontogeny, the multiseriate rays commonly undergo a more or less conspicuous increase in width, due either to an increase in the size or the number of

their constituent cells. New uniseriate and multiseriate rays are formed by the cambium, the multiseriate rays arising by lateral enlargement of the uniseriate ones.

As Kribs' (6) and Barghoorn's (4 & 5) investigations have shown, there are various trends of morphological deviation from this primitive type of ray structure. The most significant of these are (1) increase in the size or the number of the multiseriate rays, (2) reduction in the height or the number of the uniseriate rays, (3) reduction in the size or the number of the multiseriate rays and (4) changes in the form and the orientation of the constituent cells of the rays. Certain of these trends of phylogenetic modification are first detectable in the later stages of the ontogeny of the stem or root. Thus, many dicotyledons tend to retain relatively primitive types of ray structures in the first-formed secondary xylem after the rays of the outer wood have become more or less extensively modified. On the contrary, the phylogenetic reduction or elimination of multiseriate rays frequently progresses in an inverse direction, viz. from the earlier toward the later stages of the ontogeny of the secondary body. Under these circumstances, the outer secondary xylem exhibits more primitive types of ray structure than does the first-formed secondary xylem. Therefore, in dealing with rays, it is essential to keep in mind that "the phylogenetic modification of rays is achieved by consecutive series of increasingly modified ontogenies," Barghoorn (4).

#### GROUP I. ICACINOIDEAE

##### **Trilacunar Icacineae: Vessels with scalariform perforations**

The first-formed rays of the secondary xylem of *Calatola*, *Citronella*, *Dendrobangia*, *Emmotum*, *Oecopetalum*, *Ottoschulzia*, *Pennantia Cunninghamii* Miers and *Platea latifolia* Bl. are of the primitive heterogeneous I type. The vertically very extensive multiseriate rays vary somewhat in width, in number and in the shape of their constituent cells. The ontogenetic changes that these rays undergo during subsequent enlargement of the stem fluctuate considerably and give rise in the later-formed wood to different ray patterns that are characteristic of the various genera and species.<sup>1</sup> Thus, in *Oecopetalum guatemalense* Howard, the multiseriate rays tend to retain a slender form, consider-

<sup>1</sup>In this paper, the rays are described and illustrated as seen in tangential longitudinal sections of the xylem. For illustrations of transverse sections of the wood of various representatives of the Icacinoideae, the reader is referred to the plates in the preceding papers of this series, Bailey and Howard (1, 2 and 3).

able height and relative wide spacing in the later-formed wood, *Fig. 1*. Similar widely spaced, high multiseriate rays are formed in *Emmotum holosericeum* Ducke, but they are much broader and are characterized by having a sclerotic modification of their constituent cells. The broadening of the multiseriate rays is much exaggerated in *Ottoschulzia cubensis* (Wright) Urb., *Fig. 7*, and the uniseriate rays are reduced in height and are composed of vertically shortened cells. In the allied genus, *Poraqueiba*, as in various species of *Quercus* and *Casuarina*, the huge multiseriate rays of *P. sericea* Tul. exhibit various stages of phylogenetic dissection into so-called aggregate rays, *Fig. 8*.

There is considerable widening and dissection of the multiseriate rays in the later-formed wood of *Platea latifolia* Bl. and *Pennantia Cunninghamii* Miers, and many of the lower multiseriate rays exhibit a fusiform outline in tangential sections, *Fig. 2*. Such a tendency for widening and dissection of the multiseriate rays is emphasized in various species of *Citronella*, *Fig. 6*, and is associated with a conspicuous increase in the number of multiseriate rays and a corresponding decrease in the number of uniseriate ones. A similar increase in the number of multiseriate rays at the expense of the uniseriate ones occurs in the wood of *Calatola*, *Fig. 5*, and certain species of *Apodytes*, but in these plants the multiseriate rays retain a more slender form.

The first-formed secondary xylem of *Anisomallon*, *Pittosporoides*, *Cassinopsis*, most species of *Apodytes*, *Platea excelsa* Bl. and *P. philippinensis* Merr. exhibits various stages of the reduction in width, height and number of the multiseriate rays. As these rays are reduced in width, their constituent cells frequently tend to become more elongated vertically and thus to resemble the cells of the unmodified uniseriate rays. The multiseriate rays of the later-formed wood tend to be reduced in height and width, but not in number. In *Anisomallon* and *Platea*, *Fig. 3*, they are higher and relatively widely spaced, whereas in *Apodytes*, *Fig. 4*, they commonly are lower and are very numerous per unit area. Their cells still differ from those of their uniseriate extensions, and from the cells of the independent uniseriate rays, in being radially rather than vertically elongated. This trend of phylogenetic specialization in ray structure, which progresses from the earlier toward the later stages of ontogeny, culminates in other families of the dicotyledons in the elimination of multiseriate rays from the entire secondary xylem. In the Group I Icacinioideae, it progresses only as far as the elimination of multiseriate rays from the first-formed secondary xylem of certain species. Modified forms of relatively primitive heterogeneous I type rays are retained in the later-formed wood.

## GROUP II. ICACINOIDEAE

**Trilacunar Icacineae: Vessels of the secondary xylem with scalariform-porous perforations**

There are three major trends of phylogenetic specialization in the rays of the Group II Icacinoideae. The first of these occurs in *Leptaulus*. In this genus, as in *Apodytes* of the Group I Icacinoideae, there is an obvious tendency to reduce the number of multiseriate rays in the first-formed secondary xylem of the internodal parts of the stem. There is likewise a concomitant tendency to reduce the height and width of the multiseriate rays in the later-formed secondary xylem, but in *Leptaulus*, there is, in addition, a more pronounced tendency for reduction in the height of the uniseriate rays. This leads to the formation of a heterogeneous II type of ray structure, in which the numerous, low, fusiform multiseriate rays have relatively short uniseriate extensions.

The second trend of structural specialization occurs characteristically in *Gonocaryum*, *Discophora*, *Stemonurus*, *Gastrolepis*, *Urandra* and *Medusanthera*. In the wood of these genera, *Figs. 9, 10 & 11*, as in that of certain species of *Citronella*, *Fig. 6*, there is a conspicuous tendency for enlargement of the multiseriate rays, but the concomitant reduction in the number of the uniseriate rays is carried much farther than in the Group I Icacinoideae. There is, however, a considerable range of variability in the various species of these genera which illustrates different stages of this salient trend of structural specialization.

The first-formed secondary xylem of *Gonocaryum* usually has rays of the heterogeneous I type, but the number of uniseriate rays varies considerably in different species and in different parts of the same plant. Similar types of ray structure occur in the first-formed secondary xylem of *Gastrolepis austro-caledonica* (Baill.) Van Tiegh., *Lasianthera africana* Beauv., various species of *Stemonurus* and *Discophora*, and certain less modified representatives of *Urandra*, e.g. *U. Ammui* Kanehira and *U. celebica* (Val.) Howard. In other species of *Urandra* and *Stemonurus*, as in *Medusanthera*, the uniseriate rays are much reduced in number, even in the first-formed part of the secondary body.

The enlargement of the multiseriate rays in the later-formed parts of the secondary xylem is not perfectly synchronized with reduction in the height and the number of the uniseriate rays. Thus, in *Gonocaryum*, *Fig. 9*, and *Stemonurus*, *Fig. 10*, the multiseriate rays frequently are as large and numerous as in comparable material of *Urandra*, *Fig. 11*, and *Medusanthera*, but the uniseriate rays are less reduced in height and

in number. In general, the phylogenetic reduction of the uniseriate rays tends to progress from the later-formed toward the first-formed secondary xylem. Therefore, species having a more normal heterogeneous I type of ray structure in the first-formed part of the secondary xylem tend to retain a higher ratio of uniseriate rays in the subsequently formed wood.

A third trend of specialization in the ray structure of the Group I Icacinioideae occurs in *Cantleya corniculata* (Becc.) Howard, *Grisollea Thomassetii* Hemsl. and *Stemonurus Merrittii* Merr. There are more or less numerous, narrow multiseriate, as well as uniseriate, rays in the first-formed secondary xylem of these plants. During subsequent enlargement of the stem, these rays are dissected into lower ones and most of the uniseriate rays widen to form multiseriate ones. Thus, the later-formed secondary xylem is characterized by having numerous, relatively small multiseriate rays and very few uniseriate ones, *Fig. 12*. In *Grisollea Thomassetii* and *Stemonurus Merrittii*, the cells of the remaining uniseriate rays and of the much abbreviated uniseriate extensions of the multiseriate ones are reduced in height. Therefore, in the outer wood of these species, the rays are very nearly of the so-called homogeneous type.

### GROUP III. ICACINOIDEAE

#### **Unilacunar Icachineae: Vessels of the secondary xylem with porous perforations**

The later-formed secondary xylem of *Mappia*, *Nothapodytes* and *Merrilliodendron*, *Fig. 13*, resembles that of various species of *Calatola*, *Fig. 5*, and *Apodytes*, *Fig. 4*, in having very numerous, closely spaced, narrow multiseriate rays, as well as many high-celled uniseriate ones. Furthermore, in these genera as in *Apodytes*, there is a conspicuous tendency for reduction in the width of the multiseriate rays in the secondary xylem. On the contrary, the wood of *Desmostachys Vogelii* Stapf, *Fig. 15*, resembles that of *Oecopetalum*, *Fig. 1*, in having widely spaced, relatively high multiseriate rays, but it differs from the wood of this genus in its much modified uniseriate rays which are composed of a few unusually high cells. In the wood of *Alsodeiopsis*, *Fig. 14*, as of *Poraqueiba*, *Fig. 8*, there is a conspicuous phylogenetic tendency for the dissection of large multiseriate rays into so-called aggregate rays. In *A. Staudtii* Engl., *Fig. 14*, this trend of specialization has progressed to a stage comparable to that in various species of the betulaceous genera, *Alnus*, *Corylus* and *Carpinus*.

The subscandent and scandent representatives of the unilacunar

Icacineae exhibit various stages in the modification of relatively large, widely spaced multiseriate rays. Certain of these trends of phylogenetic specialization progress from the first-formed, toward the subsequently formed, secondary xylem and, therefore, may be studied in stems of herbarium specimens.<sup>2</sup> In such material of *Rhaphiostylis*, the rays are of the heterogeneous I types, and the multiseriate rays extend outward from the interfascicular parts of the stele. A somewhat similar type of ray structure occurs in young stems of *Rhyticaryum elegans* Schellenb. and *R. onocarpum* Sch. & Lautb., but the multiseriate rays tend to be composed of vertically much elongated cells. On the contrary, there is a more or less conspicuous retardation in the formation of multiseriate rays in *Leretia* and *Lavigeria*. The first-formed secondary xylem, particularly of the internodal parts of the stem, is characterized by having numerous high-celled uniseriate and biseriate rays. The multiseriate rays arise abruptly at varying distances from the primary body, frequently from aggregations of narrow rays. This abrupt transition from small-rayed to wide-rayed wood appears to occur at the beginning of a new growth layer. In *Lavigeria*, it coincides with the transition zone between the normal and the large-vesselled anomalous secondary xylem, and the multiseriate rays are composed of very thin-walled, much modified cells. The wood of *Pleurisanthes* is characterized by an evident phylogenetic tendency for the replacement of multiseriate rays by aggregate rays. The first-formed secondary xylem of *Icacina* and *Humirianthera* has numerous high-celled uniseriate, or uniseriate and biseriate rays, but no large stems are available for determining whether multiseriate or aggregate rays are formed during the later-stages of the enlargement of the stem.

#### Iodeae, Sarcostigmataeae, and Phytocreneae

In most species of these highly specialized tribes of climbing plants, there is a more or less conspicuous tendency for the elimination of multiseriate rays from the first-formed secondary xylem. The least modified types of ray structure occur in the young stems of certain representatives of the Iodeae, e.g. *Hosiea sinense* (Oliv.) Hemsl. and Wils. and *Mappianthus iodoides* Hand.-Mazz. There are a few widely separated multiseriate rays in the former species which extend outward from gaps in the primary body. The latter species resembles *Leretia* in having multiseriate rays which commonly arise abruptly at some

<sup>2</sup>Larger stems of several of these genera are not available at present in existing collections.

distance from the stele. The first-formed and more nearly normal secondary xylem of most species of *Iodes* and *Polyporandra* is characterized by having multiseriate rays with or without varying numbers of biseriate or aggregate rays. This type of ray structure predominates throughout relatively thick stems of the Sarcostigmateae, *Fig. 16*, but not of the Iodeae, where much modified multiseriate rays with very thin-walled cells are retained in the later-formed anomalous wood. In the Phytocreneae, multiseriate rays usually are eliminated from young stems except for pairs of wide rays which flank the inwardly projecting strands of phloem.

#### INTERRELATIONS BETWEEN THE SALIENT TRENDS OF MORPHOLOGICAL SPECIALIZATION IN VESSELS, TRACHEIDS, WOOD PARENCHYMA AND RAYS

We have demonstrated in the preceding papers of this series that the Group I Icacinoideae are characterized by having primitive types of vessels, tracheids and wood parenchyma. They obviously have, in addition, a high ratio of relatively primitive heterogeneous I type rays. On the contrary, the Group III Icacinoideae, which have highly specialized vessels, imperforate tracheary elements and wood parenchyma, exhibit a high ratio of much modified types of ray structures. The Group II Icacinoideae, which show various transitional stages of the modification of the vessels, tracheids and wood parenchyma, likewise illustrate various trends of structural deviation from the primitive heterogeneous I type of rays.

It should be emphasized again in this connection, however, that although the salient lines of phylogenetic specialization in vessels, tracheids, wood parenchyma and rays tend in general to be correlated, the *rates* of these evolutionary modifications are not perfectly synchronized in all cases. Thus, in any particular species or genus; the changes in the rays may have been retarded or accelerated in relation to the specializations of the vessels, tracheids or wood parenchyma.

#### Group I Icacinoideae

In the case of the Group I Icacinoideae, the most primitive *combination* of structural characters occurs in *Oecopetalum*. The vessel members of *Platea* are structurally somewhat more primitive than those of *Oecopetalum*, but there is an obvious incipient tendency in *Platea* for the vessels to aggregate in radial clusters and for reduction in the number of multiseriate rays in the first-formed secondary xylem, par-

ticularly of the internodal parts of the stem. The most modified vessel members of the Group I Icacinoideae occur in *Emmotum*, *Ottoschulzia* and *Poraqueiba*, and in these genera the tracheids, wood parenchyma and rays likewise exhibit varying degrees of morphological specialization. In *Emmotum holosericeum* Ducke, the parenchyma is transitional to scanty abaxial paratracheal, and there is a conspicuous enlargement and sclerotic modification of the multiseriate rays in the later-formed wood. In *Ottoschulzia cubensis* (Wright) Urb., the parenchyma is transitional to narrow-banded apotracheal, the bordered pits of the tracheids are reduced in size and the multiseriate rays are greatly enlarged. In *Poraqueiba sericea* Tul., the huge multiseriate rays exhibit various stages of dissection into so-called aggregate rays, but the tracheids have remained more or less unmodified.

All of the remaining representatives of the Group I Icacinoideae, with the exception of certain species of *Citronella*, have retained a primitive type of parenchyma distribution, and all of them, with the exception of *Pennantia*, have relatively unmodified types of tracheids. In *Pennantia*, the bordered pits of the tracheids, as of the vessels, are considerably reduced in size, but the wood parenchyma and rays are of essentially primitive types. Certain species of *Citronella* resemble *Emmotum* in having parenchyma that is transitional to scanty abaxial paratracheal. In these species, there are concomitant tendencies for specialization of the vessels and for increasing the size and number of the multiseriate rays at the expense of the uniseriate ones. Although there is a high degree of morphological stability in the tracheids and wood parenchyma of *Anisomallon*, *Apodytes*, *Cassinopsis*, *Dendrobangia* and *Pittosporopsis*, there are obvious trends of specialization in the rays of these genera that are more or less closely synchronized with minor specializations of the vessels. For example, the reduction in the height of the multiseriate rays in the later-formed wood, and in their number in the first-formed secondary xylem, have progressed farther in various species of *Apodytes* than in *Anisomallon*. The vessel members of the latter genus are in general somewhat less modified than those of *Apodytes*.

### Group II Icacinoideae

There are at least two, and possibly three, entirely independent lines of coordinated specializations in the Group II Icacinoideae. In the genus *Leptaulus*, the simple porous perforations of the vessels arise primarily by reduction in the number, and a concomitant increase in the size, of the scalariform perforations. The parenchyma is transitional to very scanty diffuse and abaxial paratracheal, the bordered pits of the slender,

thick-walled tracheids are reduced in size, and the numerous uniseriate and narrow multiseriate rays are much reduced in height. On the contrary, in the remaining representatives of the Group II Icacinoideae, the simple porous perforations of the vessels arise by the elimination of more or less numerous bars between the scalariform perforations or, to express the matter ontogenetically, by the cells not forming such secondary wall thickening during tissue differentiation. More or less closely correlated with increasing specialization of the vessels in these plants are conspicuous tendencies for reduction in the number of uniseriate rays, for increase in thickness of the walls of the imperforate tracheary elements, for reduction in the size of their bordered pits, and for modifications in the distribution of wood parenchyma.

The least modified combinations of structural characters occur in species of *Gonocaryum* and *Stemonurus* which have small isolated vessels and relatively high ratios of scalariform and transitional types of perforations. The tracheids have relatively large bordered pits, the parenchyma is either diffuse or transitional to narrow-banded apotracheal, and there is less reduction of the uniseriate rays, particularly in the first-formed parts of the secondary xylem. There is, however, a more or less conspicuous tendency for increase in the size of the multiseriate rays in the later-formed wood of various species of these genera. This tendency for enlargement of the multiseriate rays is accentuated in *Medusanthera* and the uniseriate rays are much reduced in number even in the first-formed secondary xylem. The vessels tend to occur in clusters and have a very low ratio of vestigial scalariform perforations. The imperforate tracheary elements have excessively thickened walls and their bordered pits are much reduced in size. The wood parenchyma is transitional to irregularly banded types in which the vessels are partly or completely embedded.

*Discophora*, *Gastrolepis*, *Urandra* and *Cantleya* are characterized by a tendency for enlargement of the pits in the lateral walls of the vessels, but the structural features associated with this aberrant trend of specialization fluctuate considerably in the different genera. Thus, in *Discophora* the parenchyma is abundant and transitional between diffuse and narrow banded apotracheal, whereas in the other genera it is scanty paratracheal and vestigial diffuse. The large, very thick-walled, imperforate tracheary elements of *Cantleya corniculata* (Becc.) Howard have large bordered pits, whereas those of *Discophora*, *Gastrolepis* and particularly of *Urandra* are reduced in size. The vessels of *Cantleya* are isolated in distribution, whereas those of *Discophora*, *Gastrolepis* and *Urandra* are more or less extensively aggregated into clusters. There is

a conspicuous tendency for reduction of the uniseriate rays in all of these genera, but the multiseriate rays in the wood of *Cantleya* differ from those of *Discophora*, *Gastrolepis* and *Urandra*, as well as of *Gonocaryum*, *Stemonurus* and *Medusanthera*, in being relatively low and very narrow. Similar small, but more numerous and nearly homogeneous, multiseriate rays occur in herbarium material of *Grisollea* and in the wood of *Stemonurus Merrittii* Merr. However, in the latter plant, the numerous, small vessels tend to occur in radial clusters, the parenchyma is scanty diffuse and abaxial paratracheal, and the slender thick-walled tracheids have small but conspicuous bordered pits. The pits in the lateral walls of vessels of this plant, as of *Grisollea*, are of small size.

### Group III Icacinoideae

The structural specializations of the stems of most of the Group III Icacinoideae are obviously complicated by the acquisition of a scrambling or climbing habit of growth. Therefore, it is essential to differentiate trends of phylogenetic modification that occur in trees and shrubs of normal habit of growth from those that are characteristic of subscandent and scandent plants. It should be noted, in addition, that the most reliable means of differentiating the Group III from the Group II Icacinoideae is by their unilacunar nodes. Although the vessels of the non-scandent unilacunar Icacinoideae have prevalingly porous perforations and in general are composed of shorter vessel members, they are only slightly more advanced morphologically than the vessels of such highly modified representatives of the Group II Icacinoideae as *Medusanthera*, where the ratio of vestigial scalariform perforations is very low.

The vessels of *Mappia*, *Nothapodytes* and *Alsodeiopsis* tend to occur in radial grouping. The wood parenchyma is abundant and transitional to irregular-banded apotracheal and scanty paratracheal. The slender thick-walled imperforate tracheary elements are of reduced length and are provided either with very small bordered pits, *Alsodeiopsis*, or with simple pits, *Mappia* and *Nothapodytes*. In the latter genera, there are numerous uniseriate and multiseriate rays, but the multiseriate rays are reduced in size throughout both the first-formed and later-formed secondary xylem. In *Alsodeiopsis*, there is a conspicuous tendency for the dissection of large multiseriate rays into so-called aggregate rays, and for their elimination from the first-formed secondary xylem. The vessels of *Merrilliodendron* are very large and widely spaced. The wood parenchyma is very abundant and is transitional to loosely banded apotracheal and vasicentric. The numerous uniseriate and small multiseriate rays are closely spaced. The cells of both the rays and the wood

parenchyma are large, resembling those that occur in *Discophora* and *Medusanthera*. The thick-walled imperforate tracheary elements have conspicuously bordered pits.

The vessels in the wood of *Desmostachys Vogelii* Stapf, as in the first-formed secondary xylem of various subscandent and scandent representatives of the unilacunar Icacineae, are reduced in number and exhibit a tendency to occur at least periodically in more or less loosely organized tangential or concentric grouping. The parenchyma fluctuates in abundance and distribution, being transitional between banded apotracheal and paratracheal. The thick-walled imperforate tracheary elements have small conspicuously bordered pits. The widely spaced multiseriate rays resemble those of *Oecopetalum*, but the uniseriate rays of the later-formed secondary xylem are composed of only a few, vertically much extended cells.

The scrambling or climbing representatives of *Humirianthera*, *Icacina*, *Lavigeria*, *Leretia*, *Pleurisanthes*, *Rhaphiostylis* and *Rhyticaryum*, as of the Iodeae, Sarcostigmateae and Phytocreneae, exhibit various peculiar and aberrant trends of structural specialization that are correlated with the acquisition of a climbing habit of growth. The most significant of these are tendencies for lateral enlargement and shortening of the vessel members, for the development of curious short tracheids having relatively thin walls and numerous much enlarged bordered pits, for the reduction of banded apotracheal parenchyma to paratracheal types, for the reduction of widely spaced multiseriate rays in the first-formed secondary xylem either to narrow rays or to aggregates of narrow rays, and for either the elimination of multiseriate rays from the later-formed wood, *Sarcostigma*, or their modification into sheets of much modified cells, Iodeae, Phytocreneae and *Lavigeria*.

It should be emphasized, in conclusion, that there is a very wide range of structural variability in different parts of these climbing plants. The material available at present is too fragmentary to serve as a basis for more than a preliminary investigation of their major trends of structural specialization. Extensive collections, particularly of older and larger stems, are essential for making reliable detailed comparisons between the various genera.

#### SUMMARY

There is a high ratio of relatively primitive heterogeneous rays in the Group I Icacinoideae.

On the contrary, the Group III Icacinoideae have a high ratio of more or less specialized types of ray structures.

The Group II Icacinoideae are transitional and exhibit various trends of morphological deviation from the primitive heterogeneous I type of ray structure.

The interrelations between the salient trends of morphological specializations in the vessels, tracheids, wood parenchyma and rays of the Icacinoideae are discussed in some detail.

Although these trends of specialization tend in general to be more or less closely correlated, the rates of the evolutionary modifications in one category of these tissue cells not infrequently are retarded or accelerated in relation to the changes that are occurring in the other tissue cells.

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#### DESCRIPTION OF PLATES

##### PLATE I

- FIG. 1. *Ocotepealum guatemalense* Howard, *Sketch 2080*. Tangential longitudinal section of the wood, showing typical, heterogeneous I type of ray structure.  $\times 50$ .
- FIG. 2. *Platea latifolia* Bl., *Y. U. 30522*. Tangential longitudinal section of the wood, showing heterogeneous I type of ray structure.  $\times 50$ .
- FIG. 3. *Platea species*, *Y. U. 20201*. Tangential longitudinal section of the wood, showing modified heterogeneous I type of ray structure.  $\times 50$ .
- FIG. 4. *Apodytes dimidiata* E. Mey., *Y. U. 14833*. Tangential longitudinal section of the wood, showing much modified heterogeneous I type of ray structure.  $\times 50$ .



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