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### WHAT IS THE PRIMITIVE FLORAL STRUCTURE OF ARALIACEAE?

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"THE GENERA OF Araliaceae that are most remote from Umbelliferae are *Plerandra*, *Tetraplasandra*, and their near relatives; in general, these are the genera that are distinguished by a greater number of stamens or carpels. In an arrangement where the Umbelliferae follow the Araliaceae, one would have to place these genera at the beginning of the family. Since we can observe within the Araliaceae a very gradual transition from species with many stamens and carpels to those characterized by 5 stamens and 2 carpels, it is not improbable that we have here a reduction series and that the forms placed at the beginning of the generic sequence also represent the oldest types of the family." (Harms, 1894, p. 21, 22.)

"A few of the Araliaceae have ten or more petals, stamens, and carpels in a regular, symmetrical arrangement. These polymerous types have sometimes been regarded as primitive within the family, but they more probably have undergone a secondary increase in the number of parts of each kind. Pentamerous flowers are here regarded as primitive in the family and order." (Cronquist, 1968, p. 278.)

The first quotation, translated rather freely from Harms's monograph of the Araliaceae, cautiously expresses a view that has long prevailed concerning floral evolution in the family. H.-L. Li, in his revision of the Chinese Araliaceae, put it more emphatically. Of *Tupidanthus*, he wrote: "Its primitiveness . . . as indicated by the numerous stamens, ovary-cells, and styles, is unquestionable." Baumann-Bodenheim (1955), a leading student of fruit structure in Araliaceae and Umbelliferae, recognized a five-stage reduction series from the many-carpellate ovary to the pseudomonomerous ovary. As far as we know, Cronquist is the first author to question the "unquestionable" primitiveness of the polymerous flower in this alliance.

Ordinarily, primitive floral characters might be sought in genera with primitive wood characters; experience shows such an association of characters occurs fairly often. However no wood anatomist has yet carried out a thorough investigation of the Araliaceae, and the limited data available suggest no simple relationship between floral characters and xylem



characters. The most detailed observations to date (Rodriguez, 1957) show advanced xylem characters in temperate herbs (*Aralia californica*, *A. hispida*) and in the vine *Hedera helix*, where one would expect to find specialization, but primitive xylem characters such as scalariform perforation plates and heterogeneous rays are distributed among genera that differ greatly with respect to numbers of floral parts. Of course, future work on the wood anatomy of Araliaceae may reveal correlations with floral structure that are not now apparent. It should be kept in mind, however, that at least some of the Araliaceae have evolved through repeated radiation on oceanic islands, radiation apparently accompanied by complex changes in growth habit (e.g., trees to shrubs and back to trees again; see Carlquist, 1965, p. 191). If such changes were sufficiently widespread, the usual trends of wood evolution might be difficult or impossible to find in this family.

Since associated xylem characters are not presently of value for assessing the evolutionary status of polymeric flowers, we looked for an association between vascular characters—more specifically, vascular characters of the gynoecium—and the number of floral parts. One basic tenet of evolutionary plant morphology is that flowers with sepals, petals, stamens, and carpels united in various ways have evolved from flowers with all appendages free. Similarly, a flower in which all of the principal vascular bundles are separate is more primitive than one in which the principal bundles are variously united. In a group with inferior ovaries, the degree of union between dorsal carpel bundles and peripheral bundles (supplying epigynous appendages) may differ in different taxa, thus providing an indication of evolutionary advancement (Eames & MacDaniels, 1947, *Figure 167*; Eyde, 1967, *Figures 5–8*). Baumann (1946) found that the Araliaceae differ among themselves in this regard,<sup>1</sup> but his observations were not detailed enough for our purpose; so we surveyed the family to establish the taxonomic distribution of the differences. Simultaneously, and for like reasons, we examined our material for differences in the position and the degree of union of ventral bundles.

#### MATERIAL, METHOD

TABLE 1 lists the collections from which our observations are taken, together with the manner of preparation. Whenever possible, we used fluid-preserved specimens, usually flowers, occasionally fruits. Some we collected ourselves; others were obtained from helpful colleagues (see acknowledgments); for the most part, however, we had to make do with herbarium material, as indicated in the table. Herbarium specimens of most Araliaceae carry a great many flowers or fruits; so a few can usually be taken for anatomical study without detriment to the collection. In most cases, we removed two to four flowers for serial sectioning and

<sup>1</sup> Baumann (later known as Baumann-Bodenheim) had his own manner of describing the derived form of the gynoecial vascular system. Where we say the dorsal carpel bundles are united with peripherals, he would say the carpel bundles are absent (Baumann, 1946, p. 63 and *Table 1*).



a similar number for clearing; however, we occasionally made our observations from a single flower, found nothing of much interest, and declined to remove others from the sheet.

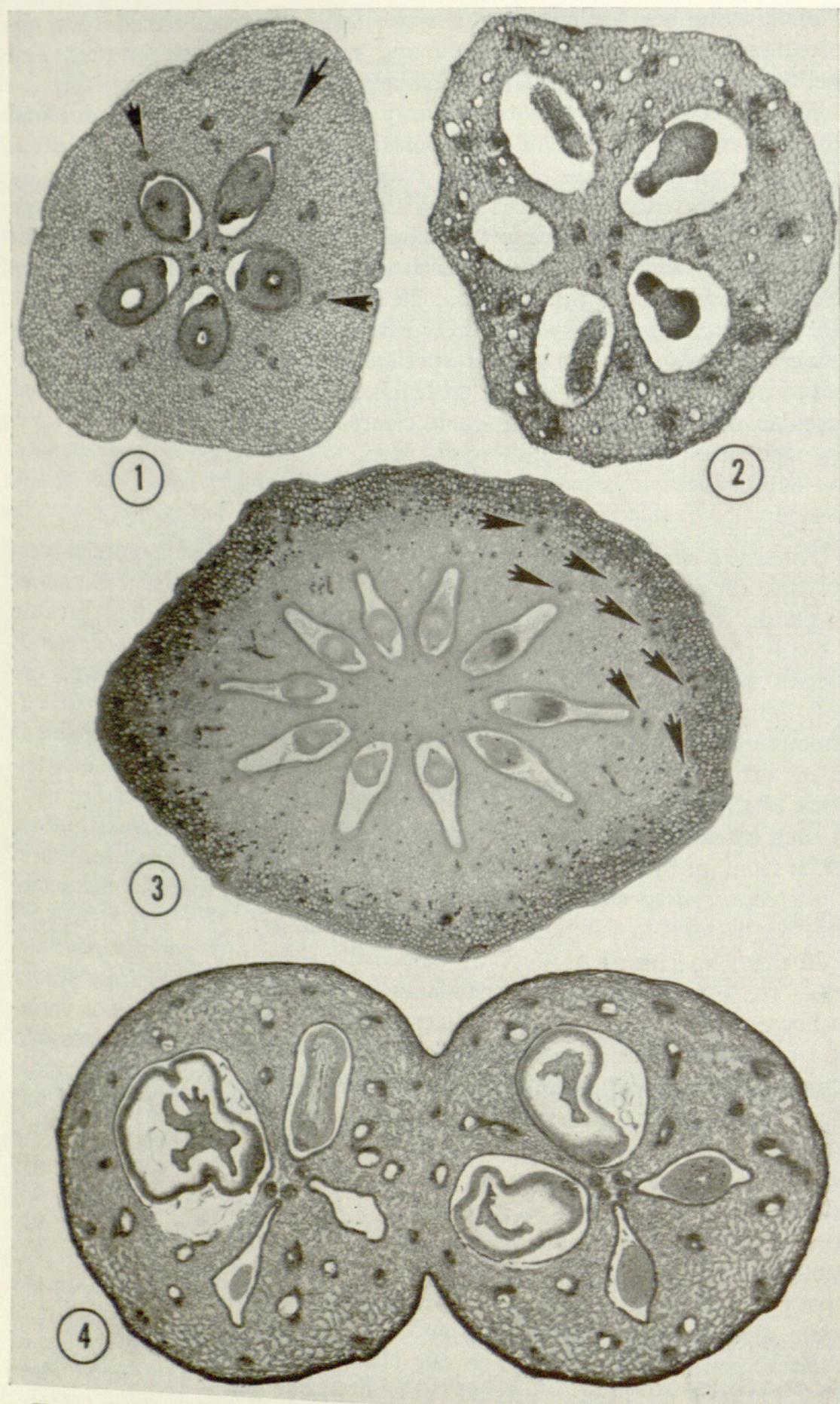
We sectioned the flowers transversely, supplementing with longitudinal sections only in the case of *Tetraplasandra* (on which we have written a separate paper; Eyde & Tseng, 1969). We cleared whole flowers by treating them with NaOH and chloral hydrate, then passed them through an ethanol series into toluene for examination. If this treatment did not reveal the vascular system in sufficient detail, we next transferred the cleared flowers from toluene to melted paraffin, cast the paraffin into blocks, and cut the blocks into pieces with a razor blade, using a dissecting microscope to orient the smaller specimens. When we subsequently dissolved away the paraffin matrix with toluene, the cut pieces often showed vascular detail not visible in whole cleared flowers.

### OBSERVATIONS

TABLES 2 and 3 summarize the important features of gynoecial vasculature for each of the examined species; the tables also list the number of petals, stamens, and carpels for each. Sepals are not listed because the calyx is often poorly developed or lacking in Araliaceae. In TABLE 2, species are arranged in four groups, according to whether their flowers are best described as polymeric, 5-merous in all whorls, 5-merous with 2-merous gynoecium, or 5-merous with 1-locular gynoecium. Assignment is rather arbitrary in some cases, but most species fall readily into one or another of these groups. Literature citations accompany a few of the entries; in such cases, the vascular characters are not our own observations but are taken from an illustration or from descriptive comments in the cited work. *Tetraplasandra* species vary so greatly with respect to meristic characters that we decided to list them separately (TABLE 3).

In many species of Araliaceae — especially those with polymeric flowers — the number of floral appendages in each whorl varies from flower to flower. Obviously, we could not expect to establish the limits of variation for such species by examining only a few flowers of each (moreover, some of the flowers had petals or stamens missing); therefore, the counts given in TABLE 2 rely heavily on published descriptions. Several of our entries for petals and stamens of *Oreopanax* species are based on Smith's (1941) generic description in *North American Flora*, in which flowers are said to be "5 (rarely 4- or 6)-merous." In general, Smith's treatment does not give the numbers of floral parts for individual species. We use quotation marks wherever we have made no count of our own. For the most part, however, we did make one or more counts which fell within the limits given in the literature; in such cases we list the literature limits without quotation marks. When our count deviated from the counts of other authors, we usually expanded the literature limits to accommodate our observation. For instance, Clarke's treatment of *Schefflera* (*Heptapleurum*)  *khasiana* in Hooker's *Flora of British India* (see generic de-





FIGURES 1-4. Transverse sections through inferior ovaries of Araliaceae.  
FIGURE 1. *Oreopanax nitidus*, Cuatrecasas 27539; dorsal carpel bundles (arrows)



scription, vol. 2, p. 727) would indicate that the flowers are completely 5–6-merous, but we count 9 ovary locules, so our entry in the GYNŌECIUM column of TABLE 2 is 5–9 to accommodate Clarke's count as well as our own.

In two cases, however, we list only our own count, because we are not confident that the specimens are correctly identified. One of these is *Boerlagiodendron novo-guineense*: our preparation has 12 carpels, whereas Harms (1894, p. 31) lists this species among those with "Fruchtknotenächer 7–9." The other is *Gastonia boridiana*, reportedly 8–10-carpellate (Harms, 1938a), but 15-carpellate in our preparation.

It is not always easy to characterize the degree of union between dorsals and peripherals. To be sure, there are taxa (*Peckeliopanax*, for instance) in which all dorsals are distinctly separate, even in sections taken near the base of the ovary; and there are others in which the dorsals are intimately united with peripherals up to the summit of the ovary. But there are also taxa in which the dorsals are united with peripherals in the lower part of the ovary and free from the peripherals in the upper part. To complicate matters further, the several dorsals within a single gynoeceum may be free in varying degree.<sup>2</sup> At first we planned to use only two symbols, + for united and – for separate, in the DORSALS column of our tables, but we found we needed a third symbol (int) for the many taxa that are intermediate. Of course, the addition of a third category did not eliminate uncertainties attributable to poorly differentiated vascular bundles, to less than satisfactory preparations, or to omissions in the works of other authors. These uncertainties are indicated by question marks.

Characters of the ventral bundles are treated in two vertical columns, one expressing the degree of union of each pair of bundles, the other their position. In most species, the pairs are readily characterized as separate or united (if the separation is at the placental level only, a frequent condition, we consider the ventrals united), but an intermediate designation was necessary in certain cases. The ventral supply of a few species is anomalous. In *Meryta sinclairii*, for instance, it consists of a complex of slender anastomosing strands with no apparent symmetry. In *Tetraplasandra racemosa* the ventral system is seen in cross section as a series of vascular patches arranged in a circle, with most patches containing several discrete xylem strands. The ventral system of *Plerandra vitiensis* has a somewhat similar appearance, but only in the upper half of the

<sup>2</sup>This is true of our specimens of *Hedera helix*, for instance. Apparently, other authors have observed little or no union of dorsals and peripherals in this species (Eames & MacDaniels, 1947, p. 352; Philipson, 1967).

united with peripheral bundles, duplex ventral bundles heterocarpellous (i.e., aligned with the septa, see also FIGURE 10);  $\times 26$ . FIGURE 2. *Oreopanax* aff. *oerstedianus*; somewhat oblique section; ventral bundles fewer than carpels, appear to be homocarpellous;  $\times 53$ . FIGURE 3. *Schefflera quinduensis*; dorsal bundles (inner arrows) and peripheral bundles (outer arrows) separate, ventral bundles anomalous (see text);  $\times 20$ . FIGURE 4. *Hedera helix*; double ovary (see also FIGURE 8); ventrals on left are fewer than carpels;  $\times 13$ .



TABLE 1. Collections, Preparations

SPECIES	COLLECTOR'S NAME & NUMBER *	LOCALITY	PREPARATION <sup>b</sup>
<i>Acanthopanax giraldii</i> Harms	Purdom 445 (US) Wilson 1971 (A) Ching 887 (GH) Ching 20481 (A) Wilson 379a (US) Steward, Chiao, & Cheo 258 (A) Henry 4832 (GH) Wilson 1977 (A)	Shensi Szechwan Szechwan Chekiang Hupeh Kweichow Hupeh Hupeh	hfl, xs, cl hfl, xs hfr, xs hfl, xs hfl, cl hfr, xs hfl, xs hfr, xs
<i>Acanthopanax gracilistylus</i> W. W. Sm.			
<i>Acanthopanax henryi</i> (Oliv.) Harms			
<i>Acanthopanax innovans</i> (Sieb. & Zucc.) Franch. & Sav. = <i>Evodiopanax innovans</i> (Sieb. & Zucc.) Nakai	Wilson 6998 (A) Haio 2916 (A) Wilson 1967 (A)	Japan Korea Hupeh	hfl, xs hfl, xs hfl, xs
<i>Acanthopanax koreanus</i> Nakai			
<i>Acanthopanax leucorrhizus</i> (Oliv.) Harms			
<i>Acanthopanax senticosus</i> (Rupr. & Maxim.) Harms	Skvortzov s.n. (A)	Manchuria	hfl, xs
<i>Acanthopanax sessiliflorus</i> (Rupr. & Maxim.) Seem.	Smith 303 (A) Wilson 1968 (A) Giraldi s.n. (A) Suzuki "480003" (A) Muroi 3658 (A) Handel-Mazzetti 796 (A) Henry 2253 (GH) cult., U.S. Natl. Arbor. cult., U.S. Natl. Arbor. Rahmat si Toroes 5440 (A)	Hopeh Hupeh Shensi Japan Japan Hunan Hupeh	hfl, xs hfl, xs hfr, xs hfl, xs hfr, xs hfl, xs hfr, xs pfl, xs, cl pfl, xs, cl hfl, xs
<i>Acanthopanax setchuensis</i> Harms ex Diels			
<i>Acanthopanax spinosus</i> (L.f.) Miq.			
<i>Acanthopanax trifoliatum</i> (L.) Merr.			
<i>Aralia elata</i> (Miq.) Seem.			
<i>Aralia spinosa</i> L.			
<i>Aralidium pinnatifidum</i> Miq.		Sumatra	



<i>Arthrophyllum ahernianum</i> Merr.	<i>Williams 1557</i> (GH)	Philippines	hfl, xs
<i>Arthrophyllum diversifolium</i> Bl.	<i>Ramos &amp; Edano 44446</i> (A)	Philippines	hfl, xs
<i>Astrotricha floccosa</i> DC.	collector unknown (A)	Singapore	hfl, xs, cl
<i>Boerlagiodendron novo-guineense</i> (Scheff.) Harms	<i>Johnson &amp; Constable 36621</i> (A)	Australia	hfl, cl
<i>Boerlagiodendron tetrandrum</i> C. T. White	<i>Clemens 440</i> (A)	New Guinea	hfl, xs
<i>Brassaiopsis hispida</i> Seem.	<i>Walker 260</i> (A)	Solomon Is.	hfl, xs
<i>Cheirodendron kauaiense</i> Kraj.	<i>Yü 20875</i> (A)	Yunnan	hfl, xs
<i>Cheirodendron trigynum</i> (Gaud.) Heller	<i>Hitchcock 15336</i> (US)	Hawaii	hfl, cl, xs
	<i>Degener, Greenwell, &amp; Murashige 20348</i> (US)	Hawaii	hfl, xs, cl
<i>Cussonia paniculata</i> Eckl. & Zeyh.	<i>Burchell 2400</i> (K)	South Africa	hfl, cl
<i>Delarbrea lauterbachii</i> Harms	cult., Bogor Bot. Gard. XIII. J. 117		
<i>Delarbrea paradoxa</i> Vieill.	<i>Lecard s.n.</i> (A)	New Caledonia	pf, xs
<i>Dendropanax chevalieri</i> (Vig.) Merr.	<i>Norton 1363</i> (US)	Fukien	hfl, cl
<i>Dendropanax gonatopodus</i> (Donn. Sm.) A. C. Sm.	<i>Pittier 16066</i> (US)	Costa Rica	hfl, xs, cl
<i>Dendropanax querceti</i> Donn. Sm.	<i>Standley 43039</i> (US)	Costa Rica	hfl, xs, cl
<i>Didymopanax attenuatus</i> (Sw.) March.	<i>Cooley 8337</i> (GH)	Windward Is.	hfl, cl
	<i>Proctor 17992</i> (A)	Windward Is.	hfr, xs
<i>Didymopanax morototoni</i> (Aubl.) Decne. & Planch.	<i>Jiménez 3665</i> (US)	Dominican Rep.	hfl, xs, cl
	<i>Gentle 2647</i> (A)	Brit. Honduras	hfl, xs
<i>Diplopanax stachyanthus</i> Hand.-Mazz.	<i>Tsang 22361</i> (A)	Kwangsí	hfl, xs
<i>Dizygotheca elegantissima</i> (Veitch) Vig. & Guill.	<i>Franc 2350</i> (A) (US)	New Caledonia	hfl, xs, cl
<i>Eremopanax angustata</i> Baill.	<i>Guillaumin, Baumann, &amp; Hurlimann 15064</i> (A)	New Caledonia	hfl, xs
<i>Fatsia japonica</i> (Thunb.) Decne. & Planch.	<i>Takeuchi 402</i> (US)	Japan	hfl, xs, cl
<i>Gamblea ciliata</i> C. B. Clarke	<i>Kingdon-Ward 21093</i> (A)	Burma	hfl, xs
<i>Gastonia boridiana</i> Harms	<i>Brass &amp; Versteegh 13139</i> (A)	New Guinea	hfl, xs



TABLE 1. Collections, Preparations (continued)

SPECIES	COLLECTOR'S NAME & NUMBER <sup>a</sup>	LOCALITY	PREPARATION <sup>b</sup>
<i>Gastonia cutispungia</i> Lam.	Brown, Britton, & Wortley 1674 (NY)	Bermuda (cult.)	hfr, xs, cl
<i>Gastonia papuana</i> Miq.	Neth. Ind. For. Serv. bb 27220 (A)	South Moluccas New Guinea	hfl, xs, cl hfl, xs, cl pfl, xs, cl hfl, xs
<i>Harmsioplanax harmsii</i> K. Schum.	Hoogland & Schodde 7307 (US) cult., Arlington, Va.	Kwangsi	hfr, xs
<i>Hedera helix</i> L.	Ching 8055 (A)	Kwangsi	hfr, xs, cl
<i>Heteroplanax chinensis</i> (Dunn) Li	Tsang 24584 (A)	Hainan	hfl, xs
<i>Heteroplanax fragrans</i> (Roxb.) Seem.	Wang 36212 (A)	Seychelles	pfl, xs; pfr, xs, cl
<i>Indokingia crassa</i> Hemsl.	Liang 63839 (A)	Szechuan	hfl, cl
<i>Kaloplanax pictus</i> (Thunb.) Nakai	Fosberg 51970 (US)	Queensland	hfr, xs
<i>Kissodendron australianum</i> (F. Muell.) Seem.	Wilson 1962 (US)	New Guinea	hfl, cl
<i>Mackinlaya celebica</i> (Harms) Philipson	White 11717 (A)	Yunnan	hfl, xs
<i>Macropanax undulatus</i> (Wall.) Seem.	Clemens 7820 (A)	Cuba	hfl, xs
<i>Megaloplanax rex</i> Ekm.	Yü 20163 (A)	Yunnan	hfl, cl
<i>Merrillioanax listeri</i> (King) Li	Ekman 17551 (GH)	New Zealand	hfl ♀, xs, cl
<i>Meryta sinclairii</i> Seem.	Tsai 54386 (A)	New Caledonia	hfl, cl
<i>Myodocarpus involucratus</i> Dubard & Vig.	Walker 5391 (US)	Michigan	hfl, xs
<i>Oplopanax horridus</i> (J. E. Sm.) Miq.	McKee 2048A (US)	Montana	hfr, xs
	Cooper 28 (GH)	Alaska	hfl, cl
	Clemens s.n. (GH)		
	Anderson 935 (US)		
<i>Oreoplanax floribundus</i> (H.B.K.) Decne. & Planch.	Cuatrecasas 27411 (US)	Colombia	pfl, xs, cl
<i>Oreoplanax nitidus</i> Cuatr.	Cuatrecasas 27424 (US)	Colombia	pfl, xs, cl
	Cuatrecasas 27539 (US)	Colombia	pfl, xs, cl







TABLE 1. Collections, Preparations (continued)

SPECIES	COLLECTOR'S NAME & NUMBER <sup>a</sup>	LOCALITY	PREPARATION <sup>b</sup>
<i>Schefflera racemosa</i> (Wight) Harms	<i>Theobald &amp; Grube</i> 2369 (US)	Ceylon	pfr, cl
<i>Schefflera robusta</i> (A.C. Sm.) A. C. Sm.	<i>Smith</i> P2291 (A)	Costa Rica	hfl, xs
<i>Schefflera sciodaphyllum</i> (Sw.) Harms	<i>Proctor</i> 22250 (GH)	Jamaica	hfl, xs
<i>Schefflera umbellata</i> (N.E. Br.) Vig.	<i>Pinkus</i> 153 (GH)	Venezuela	hfr, xs
<i>Schefflera</i> sp. ined.	<i>Hladik</i> 330, Co.	Panama	pfr, xs, cl
<i>Sciadodendron excelsum</i> Griseb.	<i>Allen</i> 1604 (GH) (US)	Panama	hfl, xs, cl
<i>Sinopanax formosanus</i> (Hayata) Li	<i>Wilson</i> 9734 (A)	Taiwan	hfl, xs
<i>Stilbocarpa lyallii</i> Armstr.	<i>Walker</i> 4903 (US)	New Zealand	hfl, xs, cl
<i>Stilbocarpa polaris</i> (Hornbr. & Jacquinet) A. Gray	collector unknown (GH)	?	hfl, xs
<i>Tetrapanax papyriferus</i> (Hook.) K. Koch	<i>Steward, Chiao, &amp; Cheo</i> 740 (A)	Kweichow	hfr, xs
<i>Tetraplasandra gymnocarpa</i> (Hillebr.) Sherff	<i>Wilson</i> 10895 (US)	Taiwan	hfl, cl
	<i>Rock &amp; Wilder</i> 8827 (A)	Hawaii	hfl, xs
	<i>Degener &amp; Martinez</i> 11920 (US)	Hawaii	hfl, xs, ls, cl
	<i>Hopeman s.n.</i> (US 690486)	Hawaii	hfl, cl
<i>Tetraplasandra hawaiiensis</i> A. Gray	<i>Degener &amp; Wiebke</i> 2181 (A)	Hawaii	hfr, xs; hfl, cl
	<i>Degener</i> 24153 (US)	Hawaii	hfl, xs, ls
	<i>Rock</i> 10026 (US)	Hawaii	hfl, cl
	<i>Hillebrand s.n.</i> (US 809489)	Hawaii	hfr, cl
<i>Tetraplasandra kaalae</i> (Hillebr.) Harms	<i>Degener, Murashige, &amp; Kerr</i> 21018 (US)	Hawaii	hfl, xs, ls, cl
<i>Tetraplasandra kavaensis</i> (H. Mann) Sherff	<i>Rock</i> 12510 (US)	Hawaii	hfl, xs, ls, cl
<i>Tetraplasandra lanaiensis</i> Rock	<i>Rock</i> 8088 (GH)	Hawaii	hfl, xs
	<i>Munro s.n.</i> (US 1091161)	Hawaii	hfl, cl
	<i>Rock</i> 8666 (A)	Hawaii	hfl, xs
<i>Tetraplasandra meiandra</i> (Hillebr.) Harms	<i>Degener</i> 12988 (US)	Hawaii	hfl, xs, ls
	<i>Degener, Lam, &amp; Clay</i> 19550 (US)	Hawaii	hfl, ls







ovary; at lower levels there are paired xylem patches in the septal radii, as in *Plerandra solomonensis*. *Schefflera quinduensis* shows an anomaly that we found nowhere else in the family: the ventral system is a double series (FIGURE 3), arranged so that each septal radius has two well defined vascular strands, one internal to the other. Another species of *Schefflera*, *S. khasiana*, also has supernumerary bundles in the center of its gynoeceum, but they are not so symmetrically arranged with respect to the septa.

Ventral bundles can be united, or merely associated in pairs, in either of two ways: if the united bundles belong to adjacent carpels, the union is heterocarpellous; the union is homocarpellous if the united ventrals belong to the same carpel.<sup>3</sup> Since homocarpellous ventrals lie on the same radii as the dorsal bundles and heterocarpellous ventrals are on the septal radii (FIGURE 1), the two types of union are readily distinguished. Occasionally, however, one finds flowers in which the duplex ventral bundles are fewer than the carpels; the bundles may then be arranged asymmetrically with respect to the septa and to the dorsal bundles. This is the case in our material of *Hladik 551* (*Oreopanax* aff. *oerstedianus*, FIGURE 2) and we are therefore uncertain as to the original position of the ventrals, although they appear more homocarpellous than heterocarpellous. It is also true of *Reynoldsia sandwicensis*, and of some specimens of *Hedera helix* (FIGURE 4), but in these species the asymmetry does not obscure the true position of the ventrals. Our uncertainty concerning the position of the ventrals in *Harmsiopanax harmsii* and in *Cheirodendron kauaiense* is due to the difficulty of following weakly differentiated vascular bundles in sectioned herbarium flowers.

Baumann (1946) supposed homocarpellous ventrals to be the usual condition in araliaceous flowers (see his Figure 3, showing a "typical" gynoeceum in cross section), even attributing this type of venation—quite wrongly—to *Schefflera* and to *Polyscias*. Actually, the heterocarpellous condition is far more common. We have found homocarpellous ventrals only in *Trevesia*, *Aralia*, *Panax*, *Stilbocarpa*, *Harmsiopanax*, *Mackinlaya*, and certain species of *Oreopanax* and *Acanthopanax*.

Miscellaneous observations on the lateral bundles of the carpels, on crystal complement, and on secretory structures are covered in the discussion section.

## DISCUSSION, CONCLUSIONS

**Polymery is primitive.**—If our criteria for recognizing advancement are reliable, the question posed as our title is answered unequivocal-

<sup>3</sup>Hall (1954) coined these terms as "homocarpous" and "heterocarpous," but homocarpy, heterocarpy, and their adjectival derivatives have an older and more appropriate application (see van der Pijl, 1969, p. 82); hence the altered spelling. In his elaborate system for describing fruits, Baumann-Bodenheim (1955, p. 483) used "homocarpellate" and "heterocarpellate" to express symmetry and asymmetry of external form, but as far as we know no other author has followed his system; so our use of similar terms in a different sense should cause no confusion.



ly by the data in the tables. Ventral bundles retain their individuality only in certain species with polymeric flowers and nowhere else, even if we should count the intermediate (int) cases as having paired ventrals. Group A also has the largest proportion of taxa with discrete dorsal bundles: nine of the 11 Group A genera that we examined have one or more species with free dorsals. One of the two exceptions, *Boerlagiodendron*, is recognizably specialized by virtue of its sympetalous corollas. It is possible that the Group A genera missing from our survey (TABLE 4) contain a few additional species with advanced vascular characters. The insertion into Group A of additional taxa with derived vasculature would not alter our principal conclusion, however, that this group retains within it the primitive floral characters of the family.

Group B has relatively few species with discrete dorsal bundles, and these species belong to only four of the 15 genera listed. *Schefflera*, the only one of the four with species in both Group A and Group B, appears to be least advanced. Specialized characters found in the other three genera include capitate inflorescences (in *Oreopanax*), simple leaves (in *Dendropanax*), and prickly stems (in *Acanthopanax*).

No one doubts that 2-merous gynoecea are derived; therefore the preponderance of fused bundles in Group C serves to support our use of vascular characters as a guide to evolutionary advancement. This part of the table is not, however, without surprises. One unexpected finding is that *Tetrapanax*, with many specialized features, has markedly discrete dorsal bundles. It is less surprising to find discrete dorsals in the ovary wall of *Didymopanax*, for Frodin (ms)<sup>4</sup> merges *Didymopanax* with *Schefflera*, where discrete dorsals are not out of place. The relatively primitive vascular system of *Delarbreia*, together with its peculiar secretory structures and its geographic isolation on New Caledonia, place this genus (and its allies *Porospermum* and *Myodocarpus*) on an evolutionary line that diverged from other Araliaceae perhaps as long ago as the Cretaceous Period.

Comparison of species within certain genera provides additional evidence that our criteria are valid and that separate vascular bundles tend to occur in polymeric flowers. In *Plerandra*, the two typical species *P. vitiensis* and *P. solomonensis* have very primitive vasculature, as would be expected if polymeric flowers are primitive. The exception is *P. insolita*, which we assume to be a specialized member of the genus because of its highly modified inflorescence (see Smith & Stone, 1968, p. 477). In *Tetraplasandra*, the polymeric species *T. paucidens* and *T. hawaiiensis* have the least specialized gynoeceal vasculature; *T. racemosa*, the only other polymeric species examined, has an anomalous ventral supply, in keeping with its somewhat isolated position<sup>5</sup> within the genus.

<sup>4</sup>D. G. Frodin kindly allowed us to xerograph his impressive handwritten manuscript "The Complex of *Cephaloschefflera*" and to cite it here. The work is an interim report, written as part of Frodin's preparation for the doctorate in the Botany School of Cambridge University.

<sup>5</sup>As its name indicates, *Tetraplasandra racemosa* bears its flowers in racemes, rather than in umbels. Sherff (1952) considered it a separate monotypic genus.



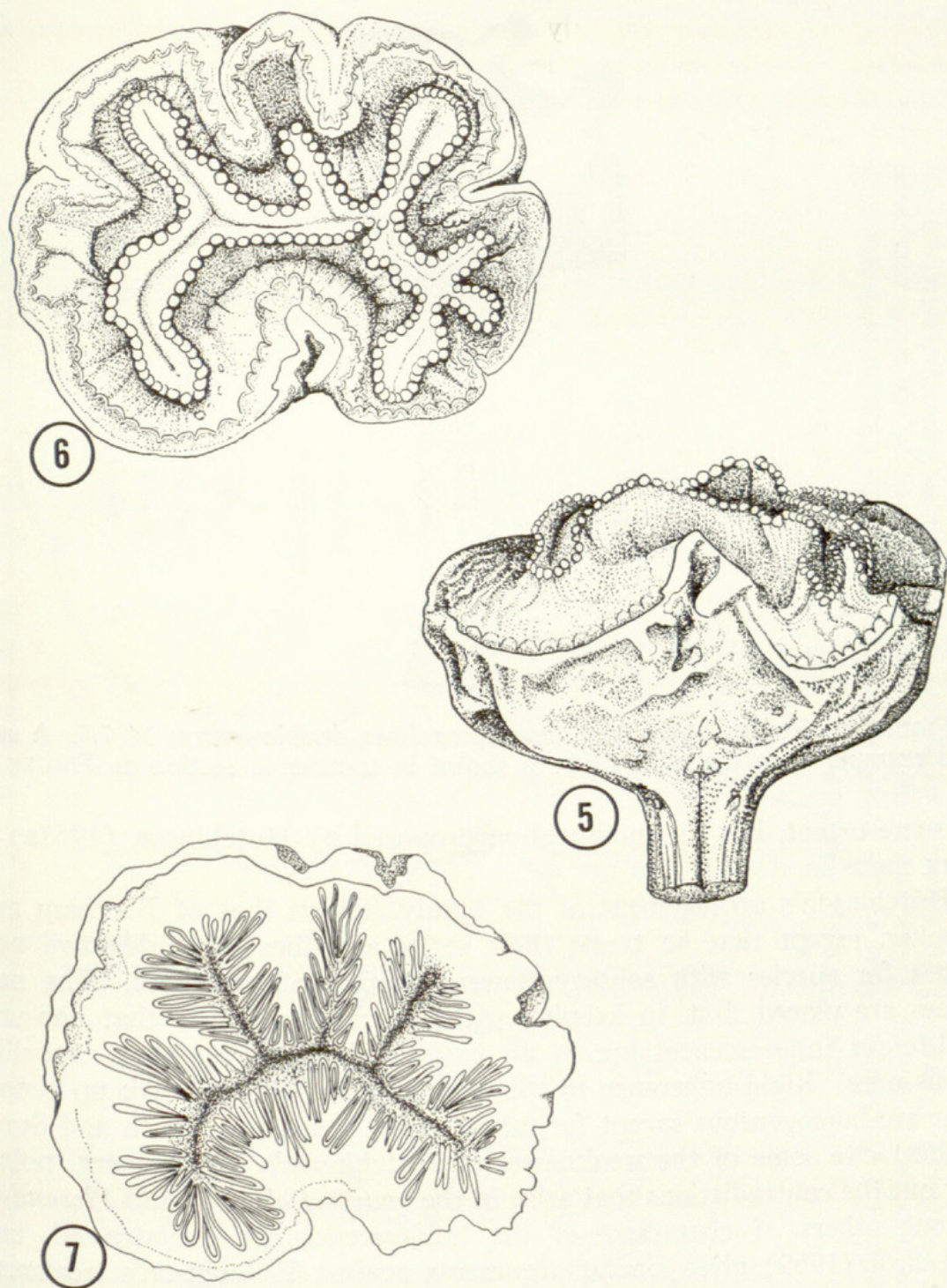
Meristic differences are similarly associated with vascular differences in *Reynoldsia*. The Hawaiian species *R. sandwicensis*, ecologically specialized and belonging to a derived flora, has fewer carpels than *R. pleiosperma* and other extra-Hawaiian species; it also has the more specialized vascular system of the two species we examined. Another genus with vascular characters that vary according to the species is *Schefflera*. Although *Schefflera* exhibits no simple relationship between meristic characters and the union of bundles (see our earlier comments on *Didymopanax*), neither does it contradict our conclusions. That is, the 5-merous examples in our study are not collectively more primitive than the polymerous examples.

Although we believe the tables demonstrate beyond reasonable doubt the derivation of 5-merous flowers from polymerous flowers, we also recognize that at least a few Araliaceae have undergone a secondary increase in the number of floral parts. Certain species of *Plerandra* and *Tetraplasandra*, for instance, have a much greater number of stamens than their nearest allies, suggesting that evolution has progressed from "many" to "even more." The outstanding example, however, is *Tupidanthus calyptratus* (the only species of *Tupidanthus*). In this species, high polymery of the flower is associated with at least two specialized features: climbing habit and a calyptrate corolla so highly modified that no sutures distinguish its components. Furthermore, the flowers with the highest numbers of stamens and carpels tend to have a grotesque, fasciated appearance (FIGURES 5-7). Observing this, Delpino (1883, p. 215) and Rippa (1904) were reminded of the double flowers that occur occasionally in *Hedera helix* (FIGURES 4 and 8), and Rippa went so far as to propose that *Tupidanthus* is nothing but a *Plerandra* with double flowers.<sup>6</sup> This opinion was overlooked or ignored by Li (1942), who selected *T. calyptratus* as the most primitive living araliad.

**Subdividing the family.** — Our support of the long-entrenched concept of polymery as primitive in Araliaceae is not an endorsement of any of the several systematic treatments incorporating that concept. Indeed, we are convinced that no author has yet subdivided the family in a way that

<sup>6</sup>"... una *Plerandra*, i cui fiori sono normalmente e stabilmente divenuti doppi mediante la fusione di 2 fiori..." In support of this notion, Rippa figured a flower of *Tupidanthus* with one pedicel, two congenitally united ovaries, two androecial circles (side by side), and two sets of stigmas. We doubt that Rippa's explanation is completely correct, however. The word "fusion," and Rippa's use of the term "atavism" for his figured flower, seem to imply a gradual phyletic union, beginning with the close approximation of flowers and proceeding through intermediate stages in which the pedicels and then the ovaries are united. The fasciation of flowers in *Tupidanthus* is more likely caused by mutations that broaden the floral meristem. Such changes are known to play a major role in the fasciation of cultivated tomato fruits (Houghtaling, 1935; Luckwill, 1943; Zielinski, 1945). If this is true, Rippa's double flower is an extreme case of a derived condition rather than a throwback to an earlier condition. Furthermore, the supposed propinquity of *Tupidanthus* and *Plerandra* has been questioned: Frodin (ms) considers *Tupidanthus* more closely related to *Scheffleropsis subintegra* Craib (which is actually a *Schefflera*, *Paratropia* group, according to Frodin) than to any species of *Plerandra*.





FIGURES 5-7. A fruit of *Tupidanthus calypttratus*, Henry 12298,  $\times 1.5$ . FIGURE 5. Viewed from side. FIGURE 6. Viewed from above. FIGURE 7. Cut transversely through upper part of locules, most of which are sterile. No attempt was made to represent all of the more than 200 stigmatic lobes and pyrenes.

shows evolutionary alliances. Harms (1894/1897), whose monograph is still the most complete — though it should not be used without also consulting his supplementary contributions covering the next 30 years — divided the Araliaceae into three principal groups. Earlier, Bentham and Hooker (1867) had recognized five main groups (as series), and Viguier (1906) later recognized 10 groups. Each of these treatments is artificial



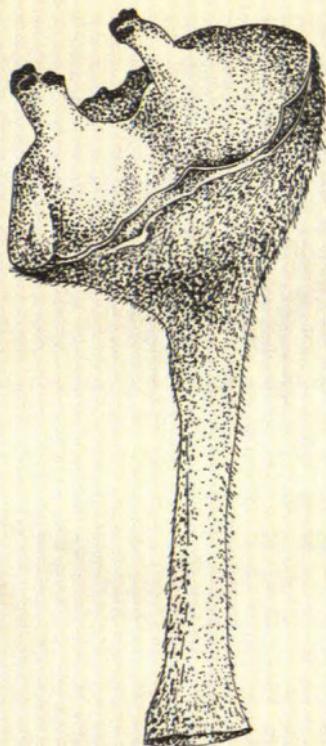


FIGURE 8. *Hedera helix*; fruit developing from double ovary;  $\times 7.5$ . A second example from the same plant is shown in transverse section as FIGURE 4.

to some extent, but the modification proposed by Hutchinson (1967a) is even more so.

Hutchinson's arrangement of the family follows that of Bentham and Hooker, except that he treats their series as tribes and adds two new tribes for species with solitary flowers in the inflorescences. The new tribes are placed first, in keeping with Hutchinson's view that non-umbelliferous inflorescences are in all cases more primitive than umbelliferous ones. Rigid adherence to this view obliges him to break up genera that are homogeneous except for inflorescence structure. Smith and Stone (1968) cite some of the weaknesses of Hutchinson's arrangement, pointing out the contradictions that arise in the genera *Polyscias* and *Plerandra*, among others, if characters of the inflorescence are overstressed, and Bernardi (1969) gives similar arguments against Hutchinson's treatment as it pertains to Madagascan araliads. Perhaps no genus confounds Hutchinson's emphasis on the inflorescence more effectively than *Meryta*, for the plants are dioecious, with staminate and carpellate inflorescences sometimes differing markedly. Hutchinson's key (1967a, p. 55), if applied to *M. sinclairii* and *M. choristantha*, would put carpellate plants in the tribe Cussonieae, staminate plants in the tribe Panaceae.

The floral characters customarily used to subdivide the Araliaceae yield groups that are only slightly more satisfactory than groups based on characters of the inflorescence. For instance, Viguier (1906) and Hutchinson (1967a) have placed together the genera in which some or all species have polyandrous flowers. In both arrangements, *Octothea*, with three whorls of stamens, and *Dizygotheca*, with one whorl of stamens, are



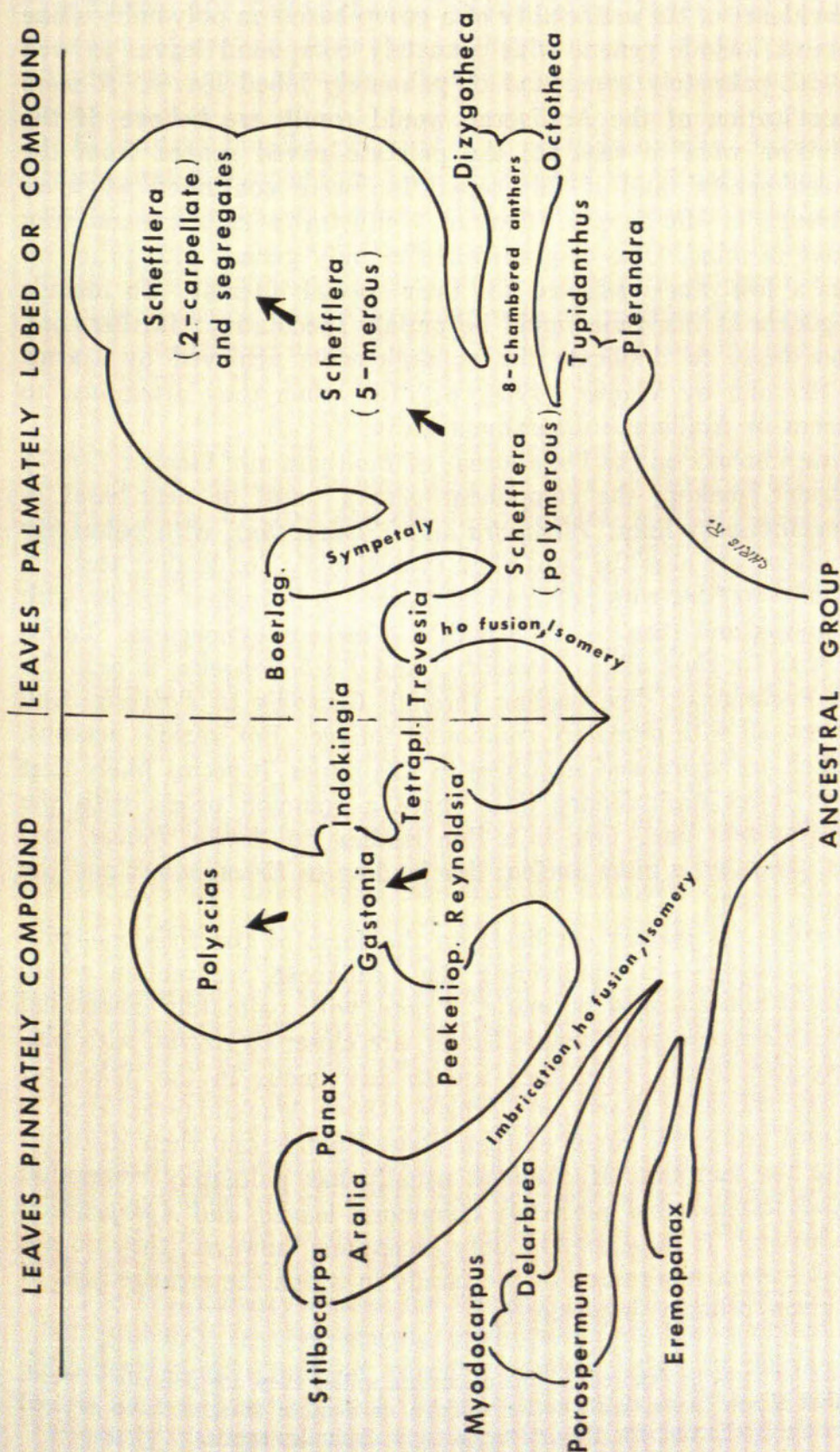


FIGURE 9. Suggested lineages within the Araliaceae. Most of the genera on the left side of the diagram have pinnately compound leaves; *Panax* and *Stilbocarpa* are exceptions. Those on the right have palmately lobed or palmately compound leaves (occasionally unifoliate in *Schefflera*). Flowers of the ancestral group are thought to have been moderately polymorous, with a pair of ventral bundles for each carpel. Within the Araliaceae, imbrication of petals appears to be a derived condition. A principal feature of the diagram is that it divides the Plerandreae of earlier authors (see text).



assigned to different tribes. Yet these two genera are anatomically alike (Viguier, 1906, p. 136); they both occur in New Caledonia; and they share the 8-chambered condition of the anther found nowhere else in the family (Viguier, 1906, *Figures 26 & 41*).

Further evidence of the artificiality of a group based on polyandry alone is that it must include genera with pinnately compound leaves as well as genera with palmately compound or palmately lobed leaves. A more natural classification of the Araliaceae would result, we believe, if the primary division were to separate the palmate-leaved genera from the pinnate-leaved genera, and if this separation were continued wherever possible throughout the family. FIGURE 9 illustrates in a general way what we have in mind. The diagram includes only genera with primitive flowers plus a few others selected for their special interest. To include additional genera at this time would be unduly speculative; furthermore, we have no desire to duplicate the entanglements achieved by Harms (1894, p. 23) and by Viguier (1906, p. 176) when they attempted to link all genera of Araliaceae diagrammatically.

Our diagram breaks up the Plerandreae of Bentham and Hooker (1867) and of Viguier, making the component genera basal or near-basal in two main evolutionary lines. *Plerandra* and *Tupidanthus*, with palmately compound leaves, are near the base of an evolutionary line leading through the species of *Schefflera* with polymerous flowers to *Schefflera* species with 5-merous flowers and then to those with a 2-merous gynoecium. *Tetraplasandra*, with its close allies *Reynoldsia* and *Peckeliopanax*, is near the base of an evolutionary line leading through *Gastonia* to *Polyscias* and its derivatives, all with pinnately compound foliage. For various reasons, some of which are mentioned elsewhere in this paper, it seems likely that at least two lesser evolutionary lines share a common origin with the *Reynoldsia-Gastonia* line. One is a line leading to *Aralia*, *Panax*, and *Stilbocarpa*, the other a more ancient line leading to *Eremopanax* and the *Myodocarpus* group.

While arguing for greater emphasis on the form of the foliage — pinnate versus palmate — in subdividing the Araliaceae, we remain aware that certain exceptions must be made. *Panax*, with palmately compound leaves, and *Stilbocarpa*, with simple leaves, are closer to *Aralia*, with pinnately compound leaves, than they are to any genus in the *Schefflera* alliance. Also, the three genera of Harms's (1894) Mackinlayeae seem to form a natural group, by virtue of their clawed petals and their distribution, despite the fact that *Mackinlaya* usually has palmately compound leaves, *Pseudosciadium* has pinnately compound leaves, and *Apiopetalum* has simple leaves.<sup>7</sup> If these are the only exceptions, however, they do not greatly complicate a subdivision of the family in which the arrangement of leaflets is given primary importance.

<sup>7</sup> Simple leaves must be ignored in this discussion unless they are palmately lobed. It is clear that simple leaves with entire margins or dentate margins have evolved repeatedly in the Araliaceae, for they occur in very dissimilar species.



**Position of ventral bundles and its significance.**— From what is known of evolutionary trends in angiosperms, it is reasonable to assume that the syncarpous, inferior gynoecium of Araliaceae evolved from an apocarpous superior gynoecium, as we have indicated diagrammatically in FIGURE 10. Other changes shown in the figure are: reduction in the number of carpels, reduction in the number of ovules per carpel, homocarpellous union of ventral bundles, and heterocarpellous union of ventrals.

If ventral bundles were always positioned with diagrammatic symmetry and if the position, once established, could not change, taxonomists would have a superb tool for classification. Species with homocarpellous ventrals would perforce be assigned to a different evolutionary line from those with heterocarpellous ventrals. In reality, however, such a simple interpretation cannot be presented without qualification. One complication, already mentioned under OBSERVATIONS, is that the locules occasionally outnumber the ventral bundles; in such cases the designations "homocarpellous" and "heterocarpellous" may be difficult or impossible to apply. Another complication is that there are taxa in which the apparent position of the ventrals changes with the level of the cross section. In scanning a series of cross sections from *Hedera* or from *Fatsia*, for instance, one observes that the ventral bundles are heterocarpellous through the lower levels of the gynoecium but converge in the upper half of the gynoecium into a central plexus; just below the insertion of the ovules they become reestablished as discrete bundles in the homocarpellous position. Singh's (1954) drawings of transverse and longitudinal sections show these changes very nicely for *Hedera nepalensis*.

The diversity of ventral vasculature within *Oreopanax* and *Acanthopanax* is the most bothersome complication of all. *Oreopanax* has not been monographed. It appears to us to be an artificial genus, and this could account, at least in part, for its vascular heterogeneity. *Acanthopanax*, on the other hand, has had the attention of Harms (1918) and of Li (1942). We are satisfied that in this case the vascular variations occur within a group of related species. Among the Group B species of *Acanthopanax* that we have examined, *A. henryi* and *A. leucorrhizus* seem least aberrant: the ventral bundles are in the heterocarpellous position except for a narrow asymmetric-to-homocarpellous region in the vicinity of ovular insertion. In *A. senticosus*, the ventrals are heterocarpellous below the locules, homocarpellous near the ovules, and asymmetrically arranged at intermediate levels. The ventral supply of *A. setchuenensis* and *A. giraldii* can be either heterocarpellous or homocarpellous; that is, both patterns are found in the same species. In this respect, these two species differ from all others in our study.

The evolutionary causes for this variation in the ventral vascular supply probably involve genetic modification of the direction of vascular differentiation. Data on vascular differentiation in flowers are scanty. It is known, however, that the procambium develops acropetally and continuously in some carpels, including those of certain primitive angiosperms



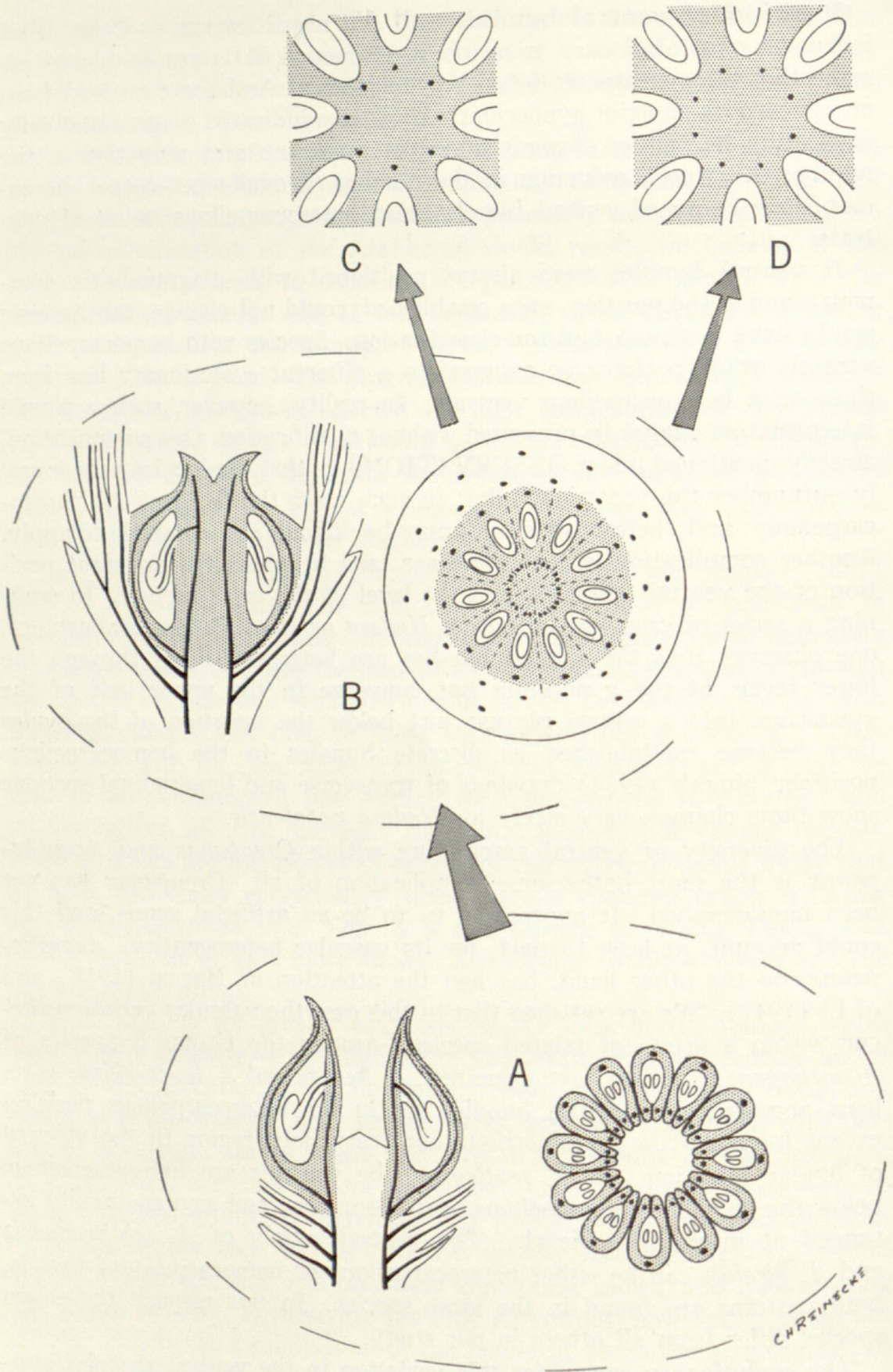


FIGURE 10. Origin of homocarpellous and heterocarpellous ventrals according to orthodox concepts of floral evolution. (A) Polymeric, apocarpous gynoecium with two ventral bundles and two or more ovules per carpel. (B) Later stage—primitive for Araliaceae—with united carpels, inferior ovary,



(Tucker, 1959, 1961; Tucker & Gifford, 1964). In the gynoecia of other species, however, procambial differentiation is basipetal or bidirectional, (summarized by Esau, 1954, and Tucker, 1959; *see also* Paterson, 1961). We conjecture that the ventral bundles of primitive Araliaceae developed acropetally and that subsequent genetic changes have introduced varying degrees of basipetal differentiation—from the ovule toward the receptacle—in certain taxa. Basipetally differentiating procambial strands would tend to be in the homocarpellous position because of the more or less median insertion of the single fertile ovule, and the junction of these homocarpellous strands with acropetally differentiating heterocarpellous strands would necessarily be a region of asymmetry or anastomosis. This conjecture is in keeping with our observation that the ventral bundles are always heterocarpellous in Araliaceae with polymorous flowers (*Trevesia* excepted), whereas the mixed or transitional condition occurs only in a few Group B taxa. The existence of these few transitional forms suggests the manner in which the homocarpellous pattern could have arisen here and there among the 2-carpellate (Group C) Araliaceae. Similar reasoning can be invoked to explain the diversity found in the Umbelliferae, in which the ventral bundles can be in either position (Jackson, 1933; Tseng, 1967), apparently without regard to major taxonomic groupings.

This is not to say that the hypothetical sequence in FIGURE 10 is completely incorrect or that the position of the ventrals has no taxonomic value. We suspect that the change from B to C illustrates fairly accurately the origin of the homocarpellous condition in *Trevesia*, because the flowers of this genus do not seem greatly advanced, and because one may find specimens in which the original paired condition of the ventrals is partially retained (Eyde, 1967, *Figure 11*). These pairs are always in the homocarpellous position, with no indication of secondary complexity; therefore, we have constructed FIGURE 9 so as to make *Trevesia* an early evolutionary offshoot of the *Schefflera* line. For like reasons FIGURE 9 shows the early divergence of a line leading to *Aralia*, *Stilbocarpa*, and *Panax* (perhaps *Harmsiopanax* belongs here too). Homocarpellous vasculature seems primary in this case—we have seen no exceptional or ambivalent specimens—and agrees with other features such as the form of the style and the estivation of the corolla in linking these genera together. Parenthetically, it should be added that differences in ventral vasculature may have value for distinguishing genera and species of Araliaceae even if the phylogenetic concepts expressed in FIGURE 10 should eventually prove false.

**Additional characters.**—While recording the vascular characters listed in TABLES 2 and 3, we scanned our serial sections for other features

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single ovule per carpel; ventral bundles still in pairs. At still later stages, the paired ventrals unite as homocarpellous ventrals (C) or as heterocarpellous ventrals (D). This sequence explains the origin of some, but not all, ventral vascular systems in Araliaceae.



TABLE 2. Gynoecial vasculature and meristic characters in selected Araliaceae

Symbols in the DORSALS column show whether the dorsal bundles are predominantly separate from the peripheral bundles, —; united with the peripherals, +; or intermediate for this character, int. Similar symbols indicate the separation or union of paired ventrals, the ultimate form of union being a solitary central strand, ce. Pairing or union of ventrals may be homocarpellous, ho, or heterocarpellous, he; see FIGURE O. Other abbreviations identify anomalous vasculature, anom; asymmetry, asym; and items that are not applicable, NA. Further explained in text.

	VENTRALS					
	DORSALS	UNION	POSITION	COROLLA	ANDROECIUM	GYNOECIUM
GROUP A, FLOWERS MORE OR LESS POLYMEROUS						
<i>Tupidanthus calypttratus</i>	—	+?	he	NA	many	up to 200+
<i>Plerandra vitiensis</i>	—	—	he	5	75-ca. 175	11-13
<i>Plerandra insolita</i>	+	+	he	"4-6"	"50-75"	9-12
<i>Plerandra solomonensis</i>	—	—	he	5	many	9
<i>Peekeliopanax spectabilis</i>	—	+?	he	6-12	25-66	6-22
<i>Boerlagiodendron</i> <i>novo-guineense</i>	+	int	he	11	11	12
<i>Boerlagiodendron</i> <i>tetrandrum</i>	+	—	he	4	4	8
<i>Reynoldsia pleiosperma</i>	—	+	he	10-11	10-11	20-22
<i>Reynoldsia sandwicensis</i>	+	+	he	8-12	8-12	7-12
<i>Indokingia crassa</i>	—	int	he	NA	up to 100	14-18
<i>Gastonia boridiana</i>	—	int	he	?	?	15
<i>Gastonia papuana</i>	—	int	he	5-9	7-55	6-12
<i>Gastonia cutispongia</i>	—?	+	he	"10-12"	"10-12"	9-12
<i>Trevesia</i> sp.	—	+	ho	7-12	7-12	7-12
<i>Sciadodendron excelsum</i>	+	+	he	9-10	9-12	9-12
<i>Megalopanax rex</i>	—	+	he	7-10	7-10	7-10
<i>Schefflera quinduensis</i>	—	+	he			
<i>Schefflera digitata</i>	—	+	(anom) he	8-9 "5 or more"	8-9 "5 or more"	8-10 6-10 (or more?)
<i>Schefflera khasiana</i>	—	+	he			
<i>Schefflera racemosa</i>	+	+	(anom) he	5-6 5-7	5-6 5-7	5-9 5-9
GROUP B, FLOWERS MORE OR LESS 5-MEROUS						
<i>Schefflera decaphylla</i>	—	+	he	5	5	5
<i>Schefflera sciadophyllum</i>	—	+	he	5	5	5
<i>Schefflera bangii</i>	+	+	he	5	5	5
<i>Schefflera robusta</i>	+	+	he	5	5	5
<i>Schefflera</i> sp. (Hladik 330)	+	+	he	5	5	5
<i>Schefflera umbellata</i>	+?	+	he	5	5	5
<i>Oreopanax capitatus</i> (Baumann- Bodenheim, 1955)	?	+	ho	4-6	4-6	5-10
<i>Oreopanax obtusifolius</i>	—	+	ho	4-6	4-6	5-7
<i>Oreopanax xalapensis</i>	+	+	he	4-6	4-6	4-6
<i>Oreopanax nitidus</i>	int	+	he	5	5	5
<i>Oreopanax sectifolius</i>	—	+	he?	5	5	5
<i>Oreopanax</i> aff. <i>oerstedianus</i>	—	+	ho? (asym)	5	5	5



TABLE 2. Gynoecial vasculature and meristic characters in selected Araliaceae  
(continued)

	DORSALS	VENTRALS		COROLLA	ANDROECIUM	GYNOCICIUM
		UNION	POSITION			
<i>Oreopanax floribundus</i>	int	+	he	5	5	4-5
<i>Dendropanax chevalieri</i>	—	+	he	5	5	5-6
<i>Dendropanax querceti</i>	—	+	he	5	5	4-5
<i>Dendropanax gonatopodus</i>	int	+	he	5	5	5-6
<i>Aralia elata</i>	+	+	ho	5-6	5-6	5-6
<i>Aralia spinosa</i>	+	+	ho	5	5	5
<i>Dizygotheca elegantissima</i>	+	+	he	5	5	5
<i>Pentapanax castanopsidicola</i>	+	+	he	5	5	5
<i>Pentapanax subcordatus</i>	+	+	he	5	5	5
<i>Pseudopanax crassifolius</i>	+	+	he	5	5	5
<i>Fatsia japonica</i>	int	+	he	5	5	5
<i>Hedera helix</i>	int	+	he	5	5	3-5
<i>Hedera nepalensis</i> (Singh, 1954)	+	+	he	5	5	5
<i>Acanthopanax senticosus</i>	—	+	asym	5	5	5
<i>Acanthopanax leucorrhizus</i>	int	+	he	5	5	5
<i>Acanthopanax</i> <i>setchuenensis</i>	+	int	he or ho	5	5	5
<i>Acanthopanax henryi</i>	int	+	he	5	5	3-5
<i>Acanthopanax giraldii</i>	—	+	he or ho	5	5	3-5
<i>Gamblea ciliata</i>	+	+	he	4-5	4-5	3-5
<i>Cheirodendron kauaiense</i>	+	+	he?	5	5	3-5
<i>Cheirodendron trigynum</i>	+	+	he	5-6	5-6	2-5
<i>Meryta sinclairii</i>	+		anom	4-6	4-6	3-6
<i>Stilbocarpa polaris</i>	+	+	ho	5	5	3-5
<i>Polyscias nodosa</i>	+	+	he	5	5	5
<i>Kissodendron</i> <i>australianum</i>	+	+	he	5	5	3-5
GROUP C, GYNOCICIUM 2-LOCULAR						
<i>Polyscias multijuga</i>	+	+	he	5-6	5-6	2
<i>Polyscias grandifolia</i>	+	+	he	5	5	2
<i>Tieghemopanax elegans</i> (Baumann, 1946)	+	+	he	5	5	2
<i>Panax trifolius</i>	+	+	ho	5	5	3
<i>Panax quinquefolius</i>	int	+	ho	5	5	2
<i>Oplopanax horridus</i>	int	+	he	5-6	5-6	2-3
<i>Didymopanax attenuatus</i>	—	+	he	5	5	2-3
<i>Didymopanax morototoni</i>	—	+	he	5	5	2
<i>Brassaiopsis hispida</i>	int	+	ce	5	5	2
<i>Macropanax undulatus</i>	int	+	ce	5	5	2
<i>Pseudopanax arboreus</i>	int	+	he	5	5	2
<i>Pseudopanax davidii</i>	+	+	ce	5	5	2
<i>Acanthopanax gracilistylus</i>	—	+	he	5	5	2
<i>Acanthopanax sessiliflorus</i>	—	+	he	5	5	2
<i>Acanthopanax koreanus</i>	int	+	ce	5	5	2
<i>Acanthopanax spinosus</i>	int	+	he	5	5	2
<i>Acanthopanax trifoliatum</i>	int	+	he	5	5	2
<i>Acanthopanax innovans</i>	—	+	ho	5	5	2
<i>Kalopanax pictum</i>	+	+	he	5	5	2
<i>Merrillioanax listeri</i>	int	+	he	5	5	2



TABLE 2. Gynoecial vasculature and meristic characters in selected Araliaceae  
(continued)

	VENTRALS			COROLLA	ANDROECIUM	GYNOECIUM
	DORSALS	UNION	POSITION			
<i>Cussonia paniculata</i>	+	+	he	5	5	2
<i>Heteropanax chinensis</i>	+	+	he	5	5	2
<i>Heteropanax fragrans</i>	+	+	he	5	5	2
<i>Astrotricha floccosa</i>	+	+	he	5	5	2
<i>Mackinlaya celebica</i>	+	+	ho	5-6	5-6	2
<i>Mackinlaya macrosciadea</i> (Baumann-Bodenheim, 1955)	+	+	ho	5-6	5-6	2
<i>Harmsiopanax harmsii</i>	+	+	ho?	5	5	2
<i>Harmsiopanax aculeatus</i> (Philipson, 1970)	+	+	ho	5	5	2
<i>Delarbrea lauterbachii</i>	—	+	he	5	5	2
<i>Delarbrea paradoxa</i>	?	+	he	5	5	2
<i>Myodocarpus involucratus</i>	int	+	ho?	5	5	2
<i>Porospermum michieanum</i>	+	+	ho or ce	5	5	2
<i>Stilbocarpa lyallii</i>	+	+	ho	4-5	5	2
<i>Tetrapanax papyriferus</i>	—	+	he	4	4	2
GROUP D, GYNOECIUM 1-LOCULAR						
<i>Diplopanax stachyanthus</i>	—	+	NA	5	5-10	1
<i>Arthrophyllum ahernianum</i>	—	+	NA	5	5	1
<i>Arthrophyllum diversifolium</i>	—	+	NA	5	5	1
<i>Eremopanax angustata</i>	—	+	NA	5	5	1
<i>Aralidium pinnatifidum</i>	—	+	NA	5	5	1

TABLE 3. Gynoecial vasculature and meristic characters in Tetraplasandra  
[Symbols and abbreviations as in TABLE 2]

	DORSALS	VENTRALS		COROLLA	ANDROECIUM	GYNOECIUM
		UNION	POSITION			
<i>T. paucidens</i>	—	int	he	8-9	20-40+	9-11
<i>T. hawaiiensis</i>	int	int	he	6-8	20-30	6-13
<i>T. racemosa</i>	+		anom	"5-6"	"10-20 (rarely 5)"	11-14
<i>T. pupukeensis</i>	int	+	he	6-10	ca. 20	5-7
<i>T. waialealae</i>	int	+	he	5-7	20-28	6
<i>T. kavaiensis</i>	+	+	he	6-9	6-9	2-5
<i>T. kaalae</i>	+	+	he	6	12-18	3-4
<i>T. meiandra</i>	+	+	he	5-8	5-8	2-5
<i>T. lanaiensis</i>	int	+	he	5-6	10-14	3
<i>T. micrantha</i>	+	+	he	8	7-8	2-4
<i>T. gymnocarpa</i>	NA	+	he	5-9	5-9	2-5

that would distinguish taxa or suggest evolutionary trends. We especially wanted to learn whether secretory canals, known to have taxonomic utility in the Umbelliferae, might aid in classifying the Araliaceae. Since many of our observations are based on herbarium flowers, with no con-



trol over developmental stages or quality of preservation, it would be pointless to attempt a description of secretory structures of each species, but a few generalizations can be made.

We found, for instance, that the number of secretory canals can differ greatly in gynoecia of different species, even closely related species. *Heteropanax fragrans* has an abundance of canals, whereas *H. chinensis* has few. Canals are abundant in flowers of *Acanthopanax senticosus*, rare in *A. giraldii* and *A. sessiliflorus*, confined to the vicinity of major vascular bundles in *A. koreanus*, and lacking in *A. leucorrhizus* and *A. setchuenensis*.

Secretory canals have a prominent place in the phylogenetic speculations of Baumann and Tikhomirov. Tikhomirov (1961) called the secretory structures of Araliaceae "rebernye kanal'tsy" (costal canals), indicating that they are found only in association with vascular bundles. If this were a reliable generalization it would tend to support his contention that *Hydrocotyle* and *Centella*, with closely associated canals and bundles, resemble Araliaceae more than they resemble apioid Umbelliferae.<sup>8</sup> We have found, however, that canals are associated with bundles in only a limited number of Araliaceae (examples occur in *Acanthopanax*, *Aralia*, *Oplopanax*, *Panax*, *Tetrapanax*). Baumann (1946) concluded from his studies that the ancestral Araliaceae were without secretory structures (see his summarizing table), but we see no evidence in support of this view. All of the polymeric flowers that we examined contained secretory canals, and the canals are scattered; that is, they have no noticeable tendency to accompany major vascular bundles. We failed to find secretory structures in the flowers of a very few species belonging to Groups C and D; viz., *Diplopanax stachyanthus*, certain species of *Acanthopanax*, *Aralidium pinnatifidum*, and *Stilbocarpa lyallii*.<sup>9</sup> *Aralidium* and *Stilbocarpa* would be considered advanced by any reasonable standards.

Our evidence indicates very emphatically that the gynoecia of ancestral Araliaceae were well supplied with scattered secretory canals, that the canals have been lost in a few of the derived taxa, and that they have been localized in others, including the Umbelliferae. In umbelliferous fruits the canals may be confined to ridges formed by major vascular bundles (*Hydrocotyloideae*) or to the grooves alternating with the ridges; some Umbelliferae have canals in both positions. Many older works call all of these canals vittae, whereas modern authors tend to use a separate

<sup>8</sup> Tikhomirov also claimed, as Håkansson (1952, p. 43) did, that the locules of Araliaceae lack the second, abortive ovule commonly found in locules of apioid Umbelliferae (but not in locules of *Hydrocotyle* and *Centella*). This is a puzzling error, for Harms's (1894, p. 8) monograph says abortive ovules (zurückgebliebende Samen) are not uncommon in Araliaceae, and other authors have confirmed the observation. Philipson (1970), who found vestigial ovules in all of the 30 or so genera of Araliaceae that he examined, suggests that the abortive structures take part in the transmission of pollen tubes (see also Håkansson, p. 34).

<sup>9</sup> Grushvitskii et al. (1969) also found no secretory structures in *Stilbocarpa lyallii*, but attributed this to the poor quality of their material. We are somewhat uncertain about *Diplopanax*, for our observations were hindered by a darkly staining substance in the floral tissues.



term for canals that run with, and external to, the peripheral vascular bundles: extravasale Sekretkanäle (Baumann, 1946); ěkstrafastsikul'yarnye kanal'tsy, rebernye kanal'tsy (Tikhomirov & Galakhova, 1965); companion canals (Tseng, 1967). Companion canals develop somewhat differently from canals that do not accompany bundles (Kovács & Sárkány, 1968). This suggests that the two kinds of canals could contain different substances. It should be noted, however, that Lassányi & Lörincz (1970) report no histochemical differences between "pith canals" and "canals of the phloem" in stems of coriander.

Flowers of Araliaceae differ not only with regard to the distribution of secretory canals, but also with regard to the form and the distribution of calcium oxalate crystals. A survey of the family for crystals is beyond the scope of this article, but a few observations will serve to illustrate the diversity available for future taxonomic research. We found no crystals in the developing fruit wall of *Oplopanax horridus*, *Panax trifolius*, *Peckeliopanax spectabilis*, or *Tetraplasandra gymnocarpa*; in contrast, scattered druses are abundant in the young fruit wall of *Boerlagiodendron novo-guineense*, *Plerandra vitiensis*, *Tetraplasandra hawaiiensis*, *Trevesia* sp., and *Tupidanthus calyptratus*. The druses in *Tetrapanax papyrifera* are localized, mainly in the depressions that run longitudinally across the endocarp. Some of the araliads have two kinds of crystals, rhomboidal crystals in a narrow zone adjoining the endocarp tissue and druses scattered in the tissues external to this zone; examples are *Dizygotheca elegantissima*, *Plerandra solomonensis*, and *Tetraplasandra paucidens*. In *Delarbrea* and *Porospermum*, as in the related genus *Myodocarpus* (Baumann, 1946, Figure 2), druses are especially abundant in the ovarian septum. A similar concentration of druses occurs in the commissural region of certain Umbelliferae (Tseng, 1967, p. 39).

Our survey has not by any means exhausted the potential taxonomic utility of the gynoecial vascular system. Each carpel of an araliaceous gynoecium commonly has two or more conspicuous bundles in addition to the dorsal bundle and the ventral bundles. In some taxa, these intermediate or lateral carpel bundles are found in the septa between the locules (*Oreopanax obtusifolius*, *Trevesia* sp.; Eyde, 1967, Figures 9 & 11); in others they occupy a more peripheral position, where they may alternate symmetrically with the dorsal bundles (*Fatsia japonica* is an example; see Baumann, 1946, Figure 24). Intermediate bundles, like dorsal bundles, can be either separate from the peripheral bundles or united with them. In a few of the 2-carpellate taxa, the dorsal and the several intermediate bundles are arranged in a distinct circle around the endocarp tissue (*Delarbrea*, *Tetrapanax*). Some of the other 2-carpellate Araliaceae, such as *Astrotricha floccosa*, show the typical umbelliferous vascular pattern, in that there are 10 conspicuous bundles in the wall of the inferior ovary, each clearly representing the union of a carpel bundle with a peripheral bundle.

We do not wish to leave the subject of gynoecial vasculature without commenting on a feature that may prove useful in distinguishing the Um-



belliferae — at least the apioid Umbelliferae — from the Araliaceae. In both families, it is common for intermediate carpel bundles (lateral bundles of Umbelliferae) to turn inward through the upper part of the ovary and join the ventral bundles. The junction may take place at the level of ovular insertion (*Panax*) or very close to this level. In Araliaceae, the usual position of the junction is above the attachment of the ovule, but in the apioid Umbelliferae the junction is usually below the attachment of the ovule. The characteristic pattern for Araliaceae is shown in Philipson's (1967, p. 147) diagrams of *Hedera helix* and *Pseudopanax arboreus*; the pattern for Umbelliferae is exemplified by Jackson's (1933, p. 123) diagrams of *Osmorhiza longistylis*.

#### Ancestry and affinities of the Araliaceae-Umbelliferae complex.

—Taxonomic opinion is divided as to the nearest allies of the Araliaceae and Umbelliferae.<sup>10</sup> Thorne (1968), Hutchinson (1967a, 1969), and Takhtajan (1969) adhere to the traditional concept of a close tie with Cornaceae. Others oppose this view (Eyde, 1967; Cronquist, 1968; Hegnauer, 1969; Philipson, 1970). We remain with the opposition, for our evidence indicates that the ancestral Araliaceae had, in addition to polymeric flowers, compound (probably pinnately compound) leaves and a normal ventral vascular system, features not found in *Cornus* or in any of the genera that can confidently be allied with *Cornus*.

According to Cronquist (1968, p. 278), the Araliaceae "would be perfectly at home in the Sapindales" — and close to Burseraceae — if the ovaries were superior instead of inferior. At his suggestion, we ran *Tetraplasandra gymnocarpa* through Hutchinson's (1967b) key to plant families: because of its hypogynous flowers, the species came out in Burseraceae as Cronquist predicted it would. Of course, the key could be adjusted quite easily to place *T. gymnocarpa* where it belongs, and we mention this point only to emphasize the similarity of certain Araliaceae to the Burseraceae. Secretory canals provide one link between the two families, pinnately compound leaves another. The ovules of Burseraceae are oriented in the same manner as those of the Araliaceae, but there are usually two fertile ovules per locule, a more primitive condition than that found in the Araliaceae. In other respects, the Burseraceae are more advanced. Vessel members of Burseraceae are always simply perforate (Metcalf & Chalk, 1950), and none of the species have polymeric flowers. The seeds lack endosperm. Also, the ventral carpel bundles of the few burseraceous flowers that have been examined anatomically (Narayana, 1960a, 1960b) are united in the heterocarpellous position. From the mixture of primitive and advanced characters, it appears that neither family can be derived from the other. If the Araliaceae and the

<sup>10</sup> The Araliaceae and Umbelliferae have sometimes been linked with Pittosporaceae on anatomical grounds. Hegnauer (1969) and Jay (1969) recently revived this view, citing chemical similarities. The differences in floral structure separating Pittosporaceae from Araliaceae and Umbelliferae are so great, however, that we cannot envision a close common ancestry.



Burseraceae are allied, as the evidence indicates, both must have arisen from a common ancestral group. It then follows that the Araliaceae are also allied with the Rutaceae, for the affinity of Burseraceae to Rutaceae is well established. The addition of Rutaceae to the discussion makes Araliaceae seem even more "at home in the Sapindales" (Rutales of some authors), for a few of the Rutaceae have moderately polymerous flowers, and scalariform perforation plates have been observed in rutaceous woods (Solereider, 1908). The ventral bundles of Rutaceae with syncarpous gynoecia may be separate (*Coleonoma*) or united in either the homocarpellous (*Skimmia*) or the heterocarpellous position (*Ruta*; see illustrations in Gut, 1966).

The likelihood of a connection with Rutaceae recalls a suggestion put forward by Ehrlich and Raven (1967). Citing Dethier's (1941) finding that certain Rutaceae and certain Umbelliferae contain the same essential oils attractive to swallowtail butterflies, these authors suggested that the two families might share "a closer ancestral tie than had been suspected." Although a chemical link between Rutaceae and Umbelliferae seems to support our arguments, it also raises a question: Why have these essential oils not been found in Araliaceae? (At least one of them, methyl chavicol, occurs in Burseraceae; Roberts, 1923.) Of course, the answer may simply be that no systematic search for these compounds has yet been undertaken in the Araliaceae.

W. R. Philipson, whose recent work on Araliaceae has been directed toward delimiting troublesome genera, sent us one of his manuscripts (Philipson, 1970) as we were finishing our own. Independently, Philipson has made some of the same observations on gynoecial vasculature that we report. He also includes an interesting analysis of staminal vasculature which strengthens the case for the primitiveness of polymery in the Araliaceae. Our general conclusions are similar to his, with one main exception; Philipson suggests that the ancestral araliads had racemose inflorescences, and he mentions a number of taxa that he thinks may retain an indication of the original racemose condition. We believe at least some of Philipson's examples actually represent a secondary loss of umbels. For instance, Li's (1942) illustration of the spike-like inflorescence of *Diplopanax* shows most flowers in clusters of two and three, suggesting a previously umbellate condition. Moreover, there are associated characters in *Diplopanax* that also indicate advancement: the leaves are simple and entire, and the gynoecium is 1-locular. In *Cuphocarpus*, another of Philipson's examples (see also Hutchinson, 1967a, 1969), the partially racemose inflorescence is associated with 4-mery of the corolla and androecium, as well as a 1-locular gynoecium. Similarly, the racemose condition in *Pseudopanax* is associated with an advanced floral vascular system, heterophylly, and dicliny or polygamy. On the other hand, two of the genera that Philipson mentions, *Tetraplasandra* and *Schefflera*, exhibit independent indications of primitiveness; therefore we agree that the racemose or partially racemose inflorescences occurring in these genera may never have passed through an earlier umbellate stage.



We suspect, however, that some of the ancestral Araliaceae had more loosely branched inflorescences than the term "racemose" would indicate. The panicles of *Reynoldsia pleiosperma* and the more or less paniculate inflorescences of certain *Tetraplasandra* species suggest the manner in which various early Araliaceae may have borne their flowers.

Our conclusions concerning the ancestral characters of the Araliaceae agree well with current phytogeographic concepts in that the taxa we consider most primitive are all tropical. Moreover, many of them are found in southeast Asia and on islands of the western Pacific, that is, in the region believed to be "the cradle of the flowering plants" (Takhtajan, 1969; Smith, 1970).

### SUMMARY

This investigation was undertaken in response to conflicting claims concerning the relative antiquity of polymery and 5-mery in Araliaceae. Assuming the degree of fusion of vascular bundles should be least in the least advanced flowers, we surveyed gynoecial vasculature throughout the family using standard clearing and sectioning methods. If the initial assumption is correct our findings show that 5-merous flowers are derived from polymerous flowers. Older taxonomic treatments err, however, in making *Tupidanthus* most primitive because of its highly polymerous flowers; in this genus, as in certain species of *Plerandra*, floral parts have increased. Furthermore, most treatments mistakenly place all polyandrous genera in the same subdivision of the family. We believe the polyandrous forms belong to two main evolutionary lines, one with pinnately compound leaves, the other with palmately lobed or palmately compound leaves. Position of ventral carpel bundles is of theoretical interest and may prove to be an aid to classification. In most Araliaceae the ventral bundles alternate with the locules. There are several taxa, however, in which the ventrals are aligned with the locules, and the genus *Acanthopanax* includes species that exhibit both patterns, apparently indicating the manner in which one type of ventral vascular system can be converted to the other. We judge that the ancestral Araliaceae had pinnately compound leaves, that at least some of the inflorescences were paniculate, and that the flowers were well supplied with secretory canals. We agree with others who have suggested an evolutionary link with Burseraceae and Rutaceae.

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TABLE 4. Genera not included in survey: meristic characters and comments

	COROLLA	ANDROECIUM	GYNOECIUM	
				GROUP A, FLOWERS MORE OR LESS POLYMEROUS
<i>Plerandropsis</i>	10	many	10	1 sp.; Tonkin. Separated from <i>Plerandra</i> by divided calyx lobes, palmately lobed leaves.
<i>Octotheca</i>	5	15	15-20	1 or 2 spp.; New Caledonia. Separated from <i>Dizygotheca</i> by 3 whorls of stamens.
<i>Woodburnia</i>	5	5	8-13	1 sp.; Upper Burma. Small prickly tree with palmately compound leaves, long calyx lobes, large flowers. Probably related to <i>Trevesia</i> (Harms, 1907).
<i>Osmoxylon</i>	8-10	8-10	8-10	2 spp.; New Guinea, Moluccas. Flowers sessile in heads.
<i>Geopanax</i>	8-10	8-10	5-10	1 sp.; Seychelles. Frodin (ms) unites this with <i>Schefflera</i> ( <i>Sciadaphyllum</i> group).
				GROUP B, FLOWERS MORE OR LESS 5-MEROUS
<i>Hederopsis</i>	5	5	5	2 spp.; Malay Peninsula. 3-foliolate leaves; connate styles.
<i>Bonino fatsia</i>	5	5	5	2 spp.; Bonin Is. Related to <i>Fatsia</i> .
<i>Apiopetalum</i>	5	5	2-4	4 spp.; New Caledonia. Clawed petals, as in <i>Mackinlaya</i> and <i>Pseudosciadium</i> .
				GROUP C, GYNOECIUM 2-LOCULAR
<i>Sciadopanax</i>	5	5	2-3	3 spp.; Madagascar. Related to <i>Polyscias</i> .
<i>Bonnierella</i>	5	5	2	1 or 2 spp.; Society Is. Related to <i>Polyscias</i> .
<i>Palmervandenbroekia</i>	5	5	2	1 sp.; New Guinea. Intermediate between <i>Kissodendron</i> and <i>Polyscias</i> .
<i>Motherwellia</i>	5	5	2	1 sp.; Australia. Woody climber; 3-foliolate (sometimes only 1 leaflet). Linked to <i>Aralia</i> by imbricate petals.



<i>Cephalalaria</i>	5	5	2	1 sp.; Australia. Related to <i>Motherwellia</i> and <i>Aralia</i> (Harms, 1896, p. 22).
<i>Seemannaralia</i>	5	5	2	1 sp.; South Africa. 5-lobed palmate leaves. Segregated from <i>Cussonia</i> .
<i>Pseudosciadium</i>	5	5	2	1 sp.; New Caledonia. Pinnate leaves; unusual articulation of flower. Supposedly related to <i>Mackinlaya</i> , <i>Apiopetalum</i> .
<i>Wardenia</i>	5	5	2	1 sp.; Perak. Small armed tree with simple leaves. For cross section of fruit, see Philipson, 1970.
GROUP D, GYNOCERIUM 1-LOCULAR				
<i>Cuphocarpus</i>	4	4	1	5 spp. (Bernardi, 1966); Madagascar. Pinnately compound leaves, unusual inflorescence (Hutchinson, 1969, p. 129). Related to and possibly derived from <i>Polyscias</i> .



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**Note added in proof.** While reading galley proofs for this article, we received two additional contributions by W. R. Philipson, "The Malesian species of *Gastonia*" (Blumea 18: 490-495. 1970) and "A redefinition of *Gastonia* and related genera" (*Ibid.* 497-505). Philipson redefines *Gastonia* to include *Indokingia*, *Peekeliopanax*, and the extra-Hawaiian tetraplasandras. His findings make synonyms of certain entries in our tables: *Tetraplasandra paucidens* = *Gastonia papuana*, and *G. boridiana* = *Peekeliopanax spectabilis*, now *G. spectabilis* (Harms) Philipson. If *Tetraplasandra* is to include only Hawaiian species, it should occupy a slightly more advanced position than *Gastonia* in our FIGURE 9; otherwise our conclusions are not affected.

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