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Wood Anatomy of Corynocarpaceae is Consistent with Cucurbitalean Placement

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ABSTRACT. Corynocarpaceae group closely with Coriariaceae and Cucurbitaceae by axial parenchyma types (vasicentric scanty plus apotracheal banded plus ray-adjacent, all in strands of 1–2 cells) and Homogeneous Type II rays. Begoniaceae, Datiscaceae s. s., and Tetramelaceae group on the basis of absence of banded axial parenchyma and subdivision of the vasicentric parenchyma into strands of 3–5 cells. All of the families of Cucurbitales (except Anisophylleaceae) have two unusual features: minimal borders on perforation plates and unusually wide multiseriate rays (not accompanied by uniseriate rays). All of the families except Anisophylleaceae have another unusual feature, storied fusiform cambial initials. Anisophylleaceae have several wood features more primitive than those of other Cucurbitales (tracheids, aliform axial parenchyma, nonstoried cambial initials), but the family is not necessarily excluded from Cucurbitales. Data on wood of Corynocarpaceae are derived from samples of three species of Corynocarpus; possible specific characters are offered.

Corynocarpaceae, a monogeneric family of five species restricted to the southwestern Pacific (including Australia), have proved difficult to place within the natural phylogenetic system. Wagstaff and Dawson (2000) list 13 families cited by various authors as possibly closely related to Corynocarpaceae. Interestingly, none of these 13 families are among the families Wagstaff and Dawson find allied to Corynocarpaceae. DNA sequences provide evidence to Wagstaff and Dawson that Corynocarpaceae belong in Cucurbitales, alongside Coriariaceae (a family that has likewise proved difficult to place), Cucurbitaceae, Begoniaceae, Datiscaceae s. s., and Tetramelaceae (a segregate from Datiscaceae). Anisophylleaceae, composed of four genera traditionally referred to Rhizophoraceae, are also included in Cucurbitales by these authors. A very similar grouping of Corynocarpaceae with the same families of Cucurbitales was proposed by Schwarzbach and Ricklefs (2000). The work of Schwarzbach and Ricklefs was broadly based, incorporating data from chloroplast DNA, nuclear ribosomal DNA, and morphology. Swensen et al. (1998), using DNA sequences from three sources, provide a cladogram in which Cucurbitaceae and Coriariaceae are unresolved and Tetramelaceae, Datiscaceae s. s., and Begoniaceae lie in sequence distal to those two families, but these workers do not include Anisophylleaceae or Corynocarpaceae in their cladogram.

Wood anatomy can reflect systematic relationships very closely in some cases. The pairing of Akaniaceae with Bretschneideraceae (Carlquist 1996) and the inclusion of Lactoridaceae in Piperales (Carlquist 1990) are supported by wood anatomy. One must be cautious in the systematic use of data from wood anatomy, because in large, actively-evolving families that occupy regions with diverse ecology, such as Asteraceae, distinctive wood features of genera and other taxonomic groupings often have ecological rather than systematic significance (Carlquist 1966). Although wood features reflecting habit and ecology occur to some extent in the Curcubitales, most of the features appear related to systematic position. This interpretation is based on the fact that the wood features concerned are not widespread in dicotyledons and, therefore, where they characterize groups of a few genera, are more likely to be synapomorphies than homoplasies.

Groupings defined or redefined with the aid of molecular data increasingly reveal more diversity in floral plan and vegetative habit within a clade than suspected earlier (e.g., Capparales, Caryophyllales s. 1.). In Cucurbitales, Corynocarpaceae are trees with alternate petiolate leaves and flowers with superior ovaries that contain one functional carpel (others vestigial) with apical placentation of the ovule. Coriariaceae are woody to herbaceous, but with a sympodial canelike habit and opposite sessile leaves, and with flowers with superior ovaries composed of 5 or 10 carpels each with a single ovule more axile than apical in attachment. Cucurbitaceae are herbaceous or "softly woody," mostly vining and with alternate petiolate leaves; flowers have inferior ovaries commonly composed of three (in some, one, two, or five) carpels with parietal placentae. The above morphological data are from Cronquist (1981), who offers excellent drawings of *Corynocarpus.*

Data on anatomy of wood and other vegetative portions of *Corynocarpus* have been offered for *C. laevigatus* J. R. & G. Forst. (Metcalfe and Chalk 1950; Patel 1975; Meylan and Butterfield 1978). Wood of *C. cribbianus* (F. M. Bailey) L. S. Sm. and of *C. dissimilis* Hemsl. has been included in the present study, permitting a broader picture of wood of the family than hitherto available. Data on wood of the other families of Cucurbitales as currently defined are available for at least a few species. The sources include Anisophylleaceae (Vliet 1976 plus original data by the second author), Begoniaceae (Carlquist 1985a), Coriariaceae (Carlquist 1985b, Yoda and Suzuki 1992), Corynocarpaceae (original data by the first author), Cucurbitaceae (Carlquist 1992), and Datiscaceae, including Tetramelaceae (Davidson 1976 and original data by the first author), Less comprehensive accounts are cited by Gregory (1994).

MATERIALS AND METHODS

Specimens documenting the woods studied here for *Corynocarpus* are as follows: *C. cribbianus,* B. Gray 3124 (CQTw), Atherton Tableland, Queensland, Australia; C. dissimilis, G. McPherson 5666 (MO), Mt. Dzumac, New Caledonia; *C. laevigatus,* S. Carlquist 1286 (RSA), cultivated in Santa Barbara, California. The specimens (all from Forest Products Laboratory) documenting SEM studies of Anisophyllaceae are as follows: *Anisophyllea laurina* R. Br. ex Sabine, SJRw 9910; *Combretocarpus subrotundatus* (Miq.) Danser, SJRw-23778; *Poga oleosa* Pierre, SJRw 12858; *Polygonanthus amazonicus* Ducke, SJRw 44339a. Specimens documenting the other families illustrated here are cited elsewhere: Cucurbitaceae (Carlquist 1992), Coriariaceae (Carlquist 1985b), and Begoniaceae (Carlquist 1985a).

Wood of Corynocarpus sections with difficulty because the tangential bands of relatively thin-walled axial parenchyma alternate with bands of hard, thick-walled libriform fibers. Sliding microtome sections were successfully prepared for *C. laevigatus* (Figs. 14). However, an alternative method (Carlquist 1982) proved better for wood of the other species of Corynocarpus (Figs. 5–13),as well as for sections of *Acanthosicyos, Coriaria,* and *Begonia* (Figs. 14–20). Sections were stained with a safranin-fast green combination. Macerations were prepared with Jeffrey's Fluid (Johansen 1940) and stained with safranin. Scanning electron microscope (SEM) studies were not feasible because the vessel wall striations of *C. dissimilis* are sparsely distributed within a section. Wood of *C. dissimilis* and *C. laevigatus* was available in liquid-preserved form, and thus presence of starch in axial parenchyma and rays of those species could be demonstrated; the wood sample of *C. cribbianus* was available in dried form.

Scanning electron microscope (SEM) photographs of *Corynocarpus laevigatus* vessels were obtained using an ISI WB-6 SEM. The SEM photographs of four species of Anisophylleaceae were based on sliding microtome sections; photographs were obtained using a JEOL 840 SEM at the Forest Products Laboratory.

Vessel diameter is based on mean lumen diameter; long and short chords were averaged for vessels oval in outline. Terminology is according to the IAWA Committee on Nomenclature (1964), with the exception of the terms pseudoscalariform vessel pits, vasicentric tracheids, ray-adjacent axial parenchyma, intercontinuous rays, and paedomorphic rays (for these, see Carlquist 1988). Data are presented for the *Corynocarpus* species in reverse alphabetical order because more complete observations were available for *C. laevigatus.* A thorough description is given for that species; the descriptions of *C. dissimilis* and *C. cribbianus* that follow include only those details by which those species differ from *C. laevigatus.* The taxonomic treatment of Wagstaff and Dawson (2000) is followed here.

RESULTS

Corynocarpus laevigatus (*Figs. 14, 14–15*). Growth rings minimally distinct. Vessels in multiples (Fig. 1), mean number of vessels per group, 1.38. Mean vessel lumen diameter, 85 µm. Mean vessel wall thickness, 2.6 µm. Mean number of vessels per mm^2, 15.7. Mean vessel element length, 198 µm. Perforation plates simple (Fig. 2), nonbordered or with narrow borders (Fig. 14; Meylan and Butterfield 1978). Lateral wall pitting alternate, whether on vessel to vessel, vessel to axial parenchyma, or vessel to ray contacts. Lateral wall pits of vessels circular to polygonal in outline, pit cavities about 6 µm in diameter, with narrowly lenticular pit apertures. Grooves interconnect pit apertures (Figs. 14, 15). Pairs of ridges (thickenings) may accompany the grooves (Fig. 14) or ridges may weave among the grooves (Fig. 15). Imperforate tracheary elements are all libriform fibers, the pits simple (both simple and

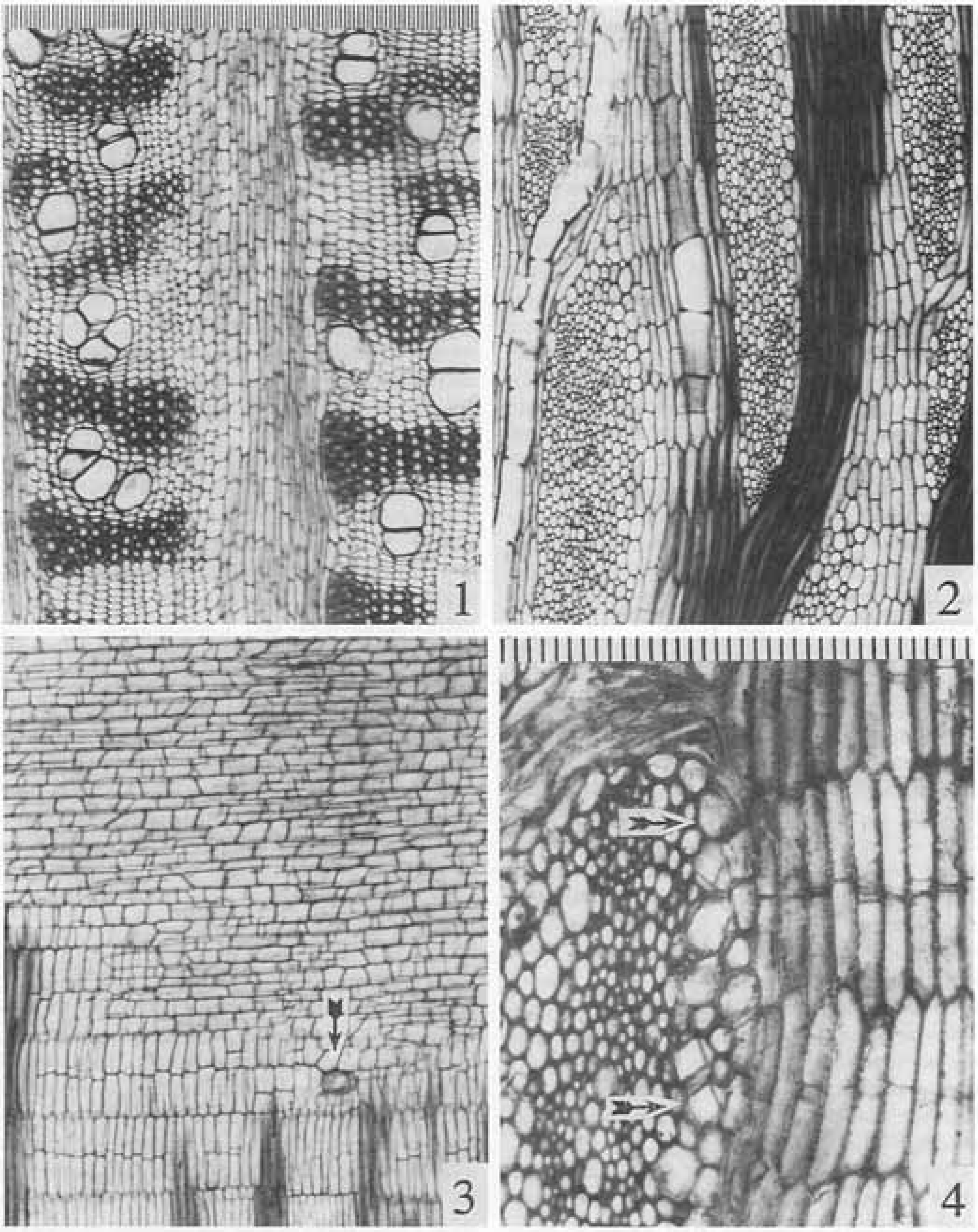

FIG. 1-4. Wood sections of *Corynocarpus laevigatus*. 1. Transection; axial parenchyma bands are wide. 2. Tangential section; rays contain numerous very narrow cells. 3. Radial section; most of area shows procumbent ray cells, axial parenchyma and fibers at bottom; arrow indicates a crystal. 4. Tangential section; axial parenchyma at right; ray at left shows crystals in many of the larger cells between the two arrows. Figs. 1–3, scale above Fig. 1 (divisions = 10 μm; Fig. 4, scale above Fig. 4 (divisions = 10 μm).

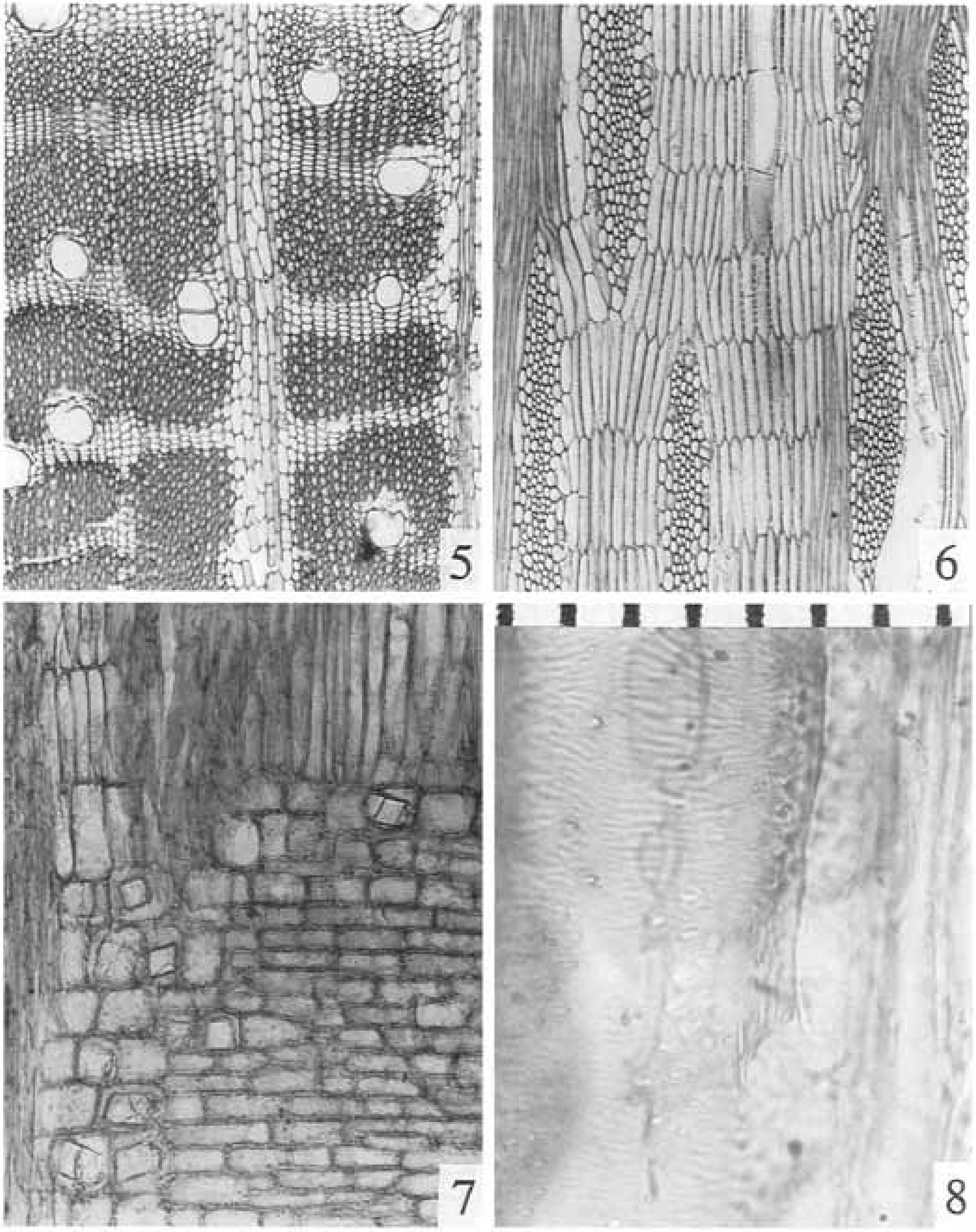

FIG. 5-8. Wood sections of *Corynocarpus dissimilis.* 5. Transection; axial parenchyma bands are narrow. 6. Tangential section; rays have numerous narrow cells; stoned axial parenchyma cells, middle, are mostly not subdivided. 7. Radial section; crystals occur in eight of the ray cells shown. 8. Tangential section; striations (fine horizontal wall thickenings) occur on the sparsely-pitted portion of the vessel. Figs. 5-6, scale above Fig. 1. Fig. 7, scale above Fig. 4. Fig. 8, scale above Fig. 8 (divisions = 10 µm).

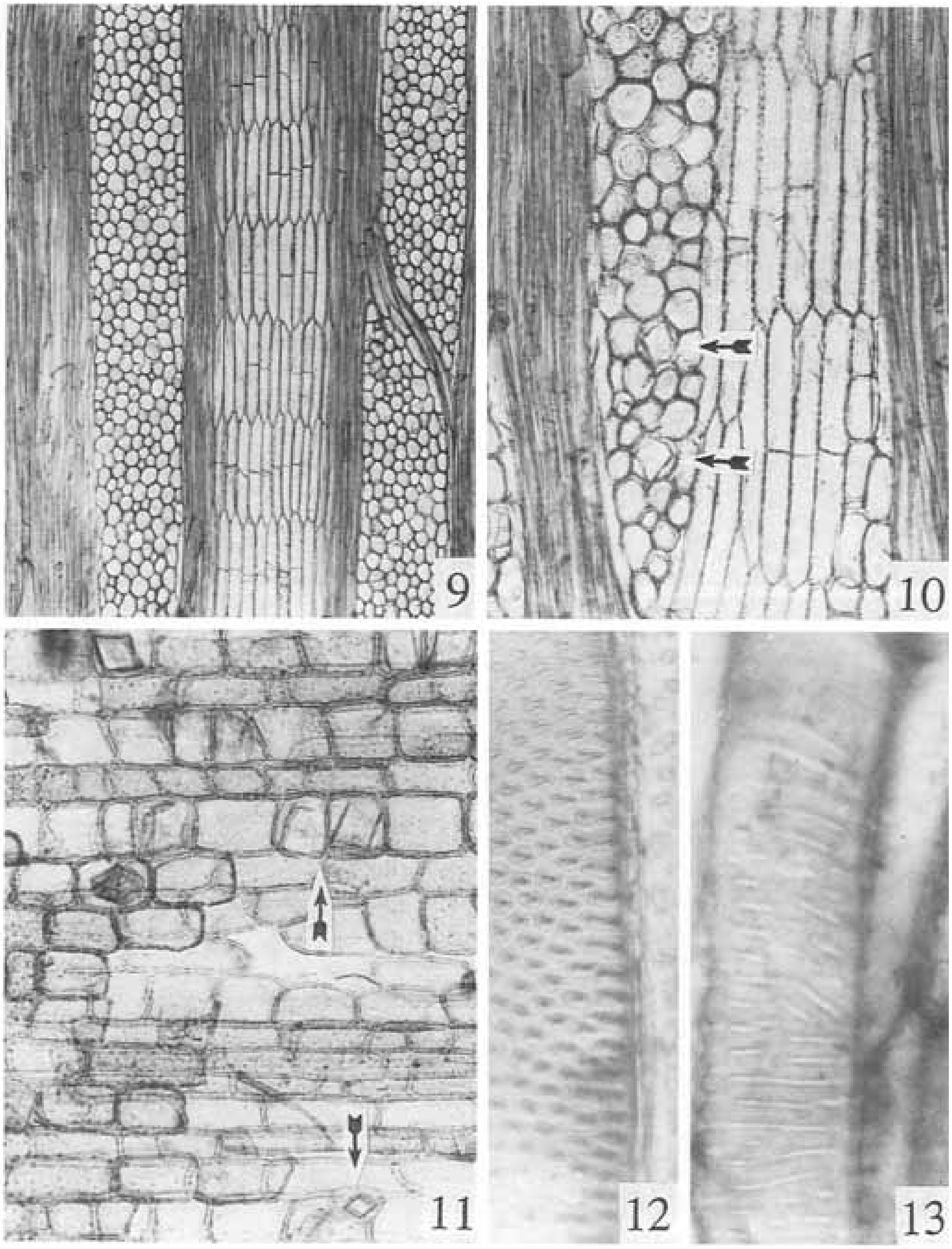

FIG. 9–13. Wood sections of *Corynocarpus cribbianus*. 9. Tangential section; ray cells are not exceptionally narrow. 10. Tangential section; about half of axial parenchyma cells, right, are subdivided; two crystals in ray indicated by arrows. 11. Radial section; rhomboidal crystals in several ray cells; some crystal-bearing cells represent subdivisions into cell pairs (arrows). 12. Vessel wall from tangential section, pits alternate and polygonal in outline. 13. Vessel wall from tangential section, pitting scalariform and transitional. Fig. 9, scale above Fig. 1. Figs. 10–11, scale above Fig. 4. Figs. 12–13, scale above Fig. 8.

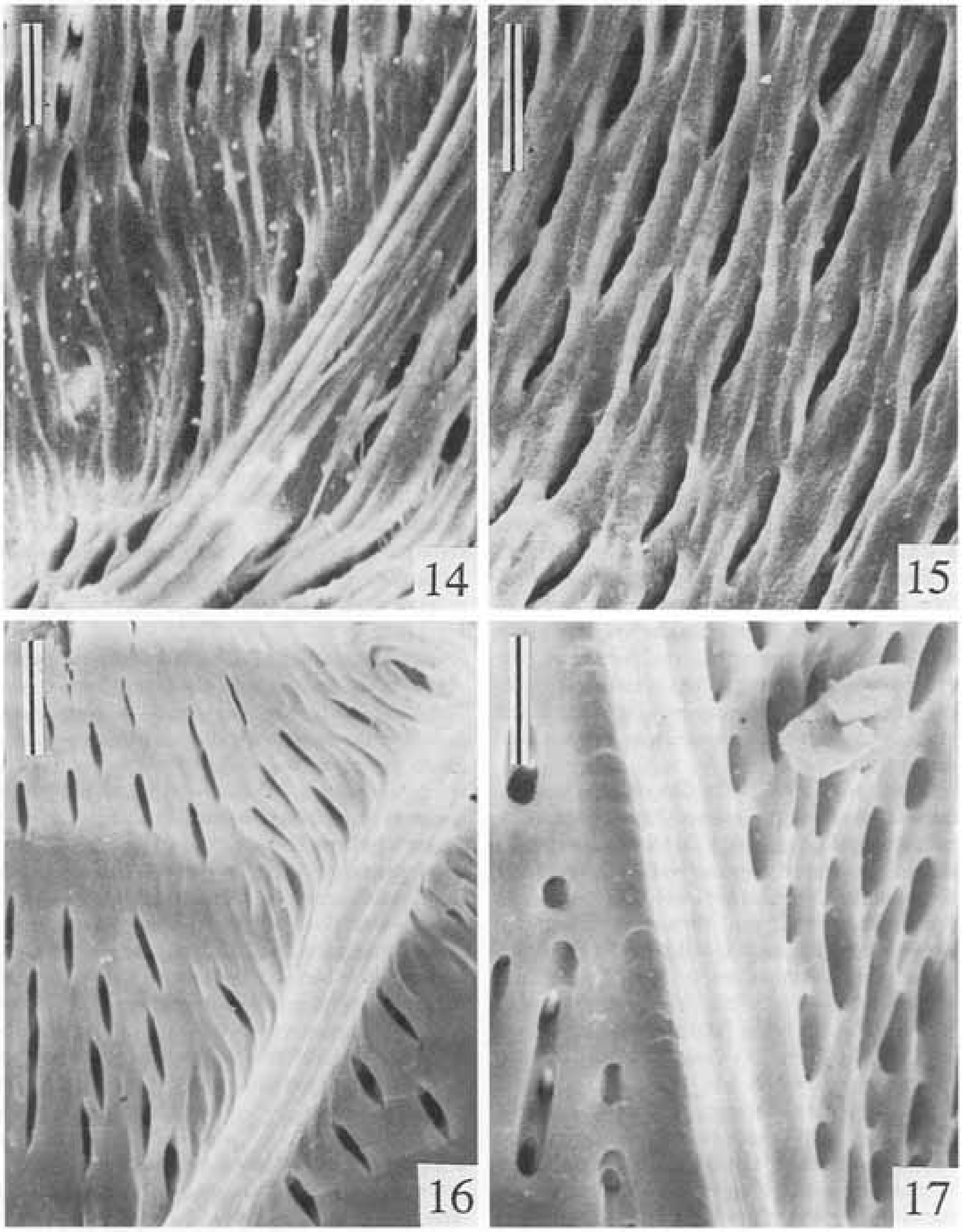

FIG. 14–17, SEM photographs of vessel walls from tangential sections of woods. 14–15. *Corynocarpus laevigatus.* 14. Perforation plate with rounded margins, minimal border; grooves interconnect many pit apertures; pairs of ridges (thickenings) accompany many of the grooves. 15. Grooves accompanied by single thickenings that weave among the grooves. 16. *Anisophyllea laurina;* nonbordered perforation plate; groove interconnects three pits at lower left. 17. *Polygonanthus amazonicus;* perforation plate with rounded margins on either side of a shallow groove; grooves interconnect pit apertures. Scale bars at upper left in each figure = 10 µm.

vestigially bordered pits claimed by Meylan and Butterfield 1978). Mean libriform fiber length, 762 µm. Mean diameter of libriform fibers at widest point, 29 µm. Libriform fiber wall thickness, 3 µm. Axial parenchyma banded, vasicentric scanty, and ray-adjacent. Vessels mostly located in parenchyma bands, but some wholly or partly within the fiber bands; the bands are perhaps best termed apotracheal because vessels are not distributed wholly within axial parenchyma bands. Axial parenchyma chiefly subdivided into strands of two cells (Fig. 2, bottom; Fig. 3, bottom; Fig. 4, right), less commonly not subdivided. Rays multiseriate exclusively (Fig. 2). Ray cells mostly procumbent (Fig. 3), central portions of ray with cells notably narrow as seen in tangential section (Fig. 2). A few upright and square cells present on tips of rays and occasional as sheath cells on ray margins; rays closest to Homogeneous Type II of Kribs (1935). Mean height of rays (all multiseriate), 1225 µm. Mean width of rays at widest point, 13.4 cells. Axial parenchyma storied (Fig. 2), conforming to vessel elements in this respect (libriform fibers not storied because of their marked elongation—more than three times the length of vessel elements). Crystals present in rays, uncommon (Fig. 3) to more abundant (Fig. 4), and present in the wider cells of rays, not in the narrow cells in the central portions of rays. Starch present in rays and in axial parenchyma.

C. dissimilis (*Figs. 5-8*). Growth rings not discernible. Vessels mostly solitary (Fig. 5), mean number of vessels per group, 1.23. Mean vessel lumen diameter, 66 µm. Mean vessel wall thickness, 4 µm. Mean number of vessels per mm^2, 12.1. Mean vessel element length, 222 µm. Portions of vessel wall where pits are sparse bear striations (Fig. 8). Mean lateral wall pit cavity diameter about 5 µm. Bands of fibers relatively wide compared with those of *C. laevigatus* (Fig. 1). Mean libriform fiber length, 996 µm. Mean libriform fiber diameter at widest point, 26 µm. Mean libriform fiber wall thickness, 7 µm. Axial parenchyma cells mostly not subdivided (Fig. 6), occasionally in strands of two cells. Rays with a very few square and upright cells on margins and as sheathing cells, but most ray cells procumbent; narrow cells in central portions of rays (Fig. 6). Mean height of rays, 738 µm. Mean width of rays at widest point, 7.2 cells. Storying conspicuous (Fig. 6). Rhomboidal crystals relatively abundant in the larger ray cells (Fig. 7).

C. cribbianus *(Figs. 9-13).* Growth rings not distinct. Vessels in multiples, mean number of vessels per group, 1.72. Mean vessel diameter, 97 µm. Mean vessel wall thickness, 4 µm. Mean number of vessels per mm^2, 11.3. Mean vessel element length, 204 µm. Lateral wall pits of vessels circular to polygonal in outline (Fig. 12), or, less commonly, scalariform (Fig. 13) to transitional. Shallow grooves interconnect the pit apertures in the circular to polygonal pits. Mean libriform fiber length, 1063 µm. Mean diameter of libriform fibers at widest point, 26 µm. Mean wall thickness of libriform fibers, 6 µm. Axial parenchyma composed of nonsubdivided cells and of strands of two cells in about equal numbers (Fig. 9, 10). Axial parenchyma cells with thicker (about 2.5 µm) walls than in the other species. Rays composed of cells relatively uniform in diameter in tangential sections (Figs. 9, 10), narrow cells not present in central portions of rays. Mean height of rays, 2612 µm. Mean width of rays, 6.6 cells. Ray cell wall thickness, 1.2 µm. Storied structure conspicuous (Figs. 9, 10). Rhomboidal crystals moderately common in rays (Figs. 10, 11), but scattered throughout the ray (probably because narrower cells, which were not observed to contain crystals, are absent in rays of this species). Crystals common in pairs of cells that represent a subdivision of an ordinary ray cell (arrows, Fig. 11).

Cucurbitaceae. Although wood of several species of this family has been studied, *Acanthsicyos horridus* Welw. (Fig. 18–19) has been selected for comparison because it is relatively woody and is thus comparable to representatives of the other families. Vessels are mostly solitary (Fig. 18), with simple minimally bordered perforation plates and alternate lateral wall pitting. Libriform fibers with simple pits are present. Axial parenchyma is of two sorts (Fig. 14): thick-walled vasicentric; and thinner-walled apotracheal, some of which can be designated as ray-adjacent because parenchyma forms a layer a single cell thick in some places between the libriform fiber bands and the rays. Axial parenchyma strands are composed of one to three cells per strand. Rays are all multiseriate with upright cells strongly predominant, therefore Paedomorphic Type II. Rays mostly wider than 10 cells at widest point (Fig. 19). Storying is vague in Fig. 19, although it is shown clearly for the species in Carlquist (1992). Crystals not observed.

Coriariaceae. Coriaria japonica Gray (Figs. 20-22) illustrates features typical for the family. Vessels are grouped (Fig. 20), with simple, nonbordered perforation plates and alternate circular lateral wall pits (grooves interconnecting pit apertures observed in *C. arborea* Lindsay: Carlquist 1985b). Libriform fibers present, pits simple (some pits with vestigial borders in *C. arborea* (Meylan and Butterfield 1978). Axial parenchyma is vasicentric, but also confluent, in apotracheal bands, and some ray-adjacent parenchyma

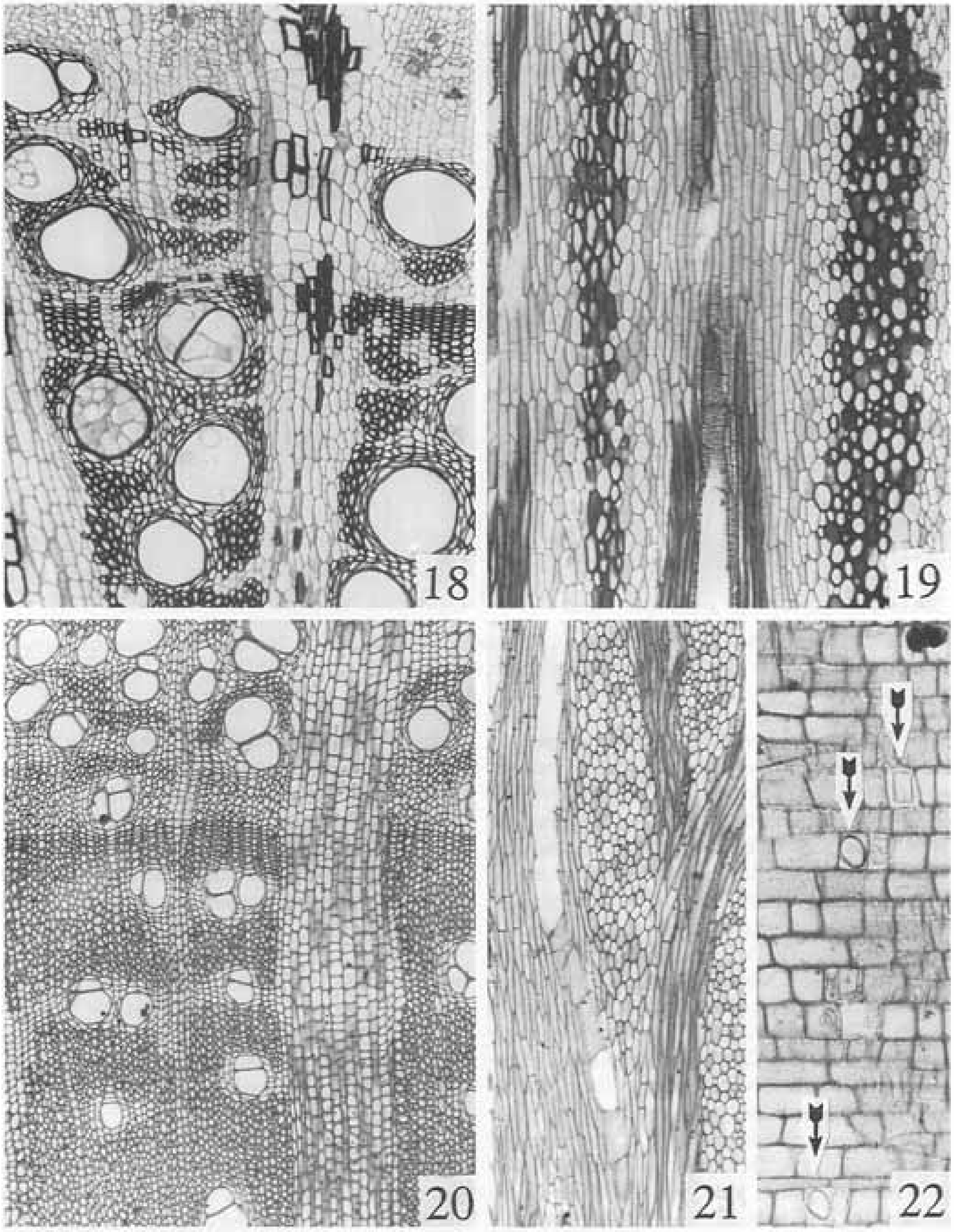

FIG. 18–22. Wood sections of Cucurbitaceae (18–19) and Coriariaceae (20-22). 18–19. Acanthosicyos horridus. 18. Transection; banded axial parenchyma present. 19. Tangential section; central parts of rays consist of dark-staining sclereids. 20-22. *Coriaria japonica.* 20. Transection; banded axial parenchyma present, mostly in upper half of photograph. 21. Tangential section; rays notably wide. 22. Radial section; rhomboidal crystals in several ray cells (arrows). Fig. 18–21, scale above Fig. 1. Fig. 22, scale above Fig. 4.

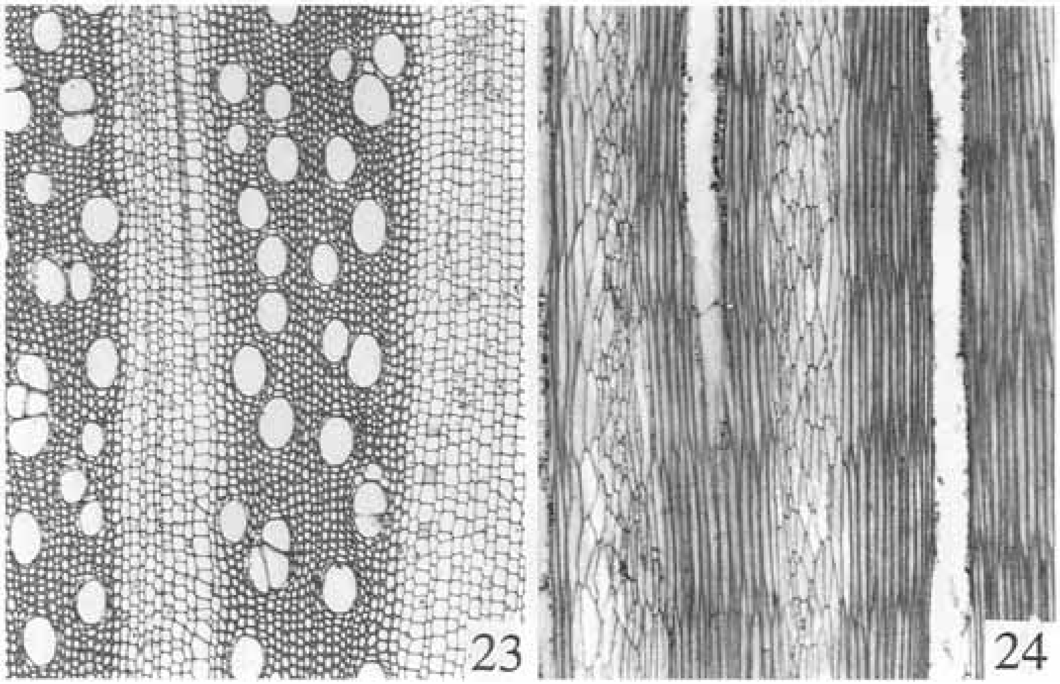

FIG. 23–24. Wood sections of *Begonia parviflora.* 23. Transection; rays notably wide. 24. Tangential section; rays composed of upright cells, libriform fibers clearly storied. Figs. 19–20, scale above Fig. 1.

is present (Fig. 20). Axial parenchyma cells are undivided or in strands of two cells. Rays are multiseriate only (Fig. 21), notably wide, composed mostly of upright cells, and thus closest to Paedomorphic Type 11 (Carlquist 1988). Axial parenchyma, narrow vessels, and vascular tracheids are storied; a few fibers (Fig. 21 lower right) are also storied. Rhomboidal crystals occur singly in some ray cells (Fig. 22).

Begoniaceae. The few species investigated thus far in the family (Carlquist 1985a) have wood very similar to the species illustrated, *Begonia parviflora* Poepp. & Endl. (Figs. 23–24). Vessels are solitary or in small groups (Fig. 23). Perforation plates are simple or nearly so, nonbordered or nearly so. Lateral wall pitting scalariform. Libriform fibers septate or nonseptate, with simple pits. Axial parenchyma vasicentric scanty, typically in strands of four cells; some thin-walled fibriform cells not subdivided into strands but parenchymalike in morphology occur in ray-adjacent positions. Rays more than 10 cells wide (Figs. 23, 24), composed of upright cells (some cells simulating fibers in shape), Paedomorphic Type II. Fibers and axial parenchyma storied, conforming to the vessel element junctures (Fig. 24). Starch common in ray cells, axial parenchyma. Crystals absent in wood.

Datiscaceae s. s. The data below are based on *Datiscus glomerata* (Presl) Baill. Vessels solitary or, more commonly, in multiples, these arranged in tangential bands. Vessels with simple perforation plates, minimally bordered. Lateral walls of vessels with alternate polygonal pits, some elongate and therefore pseudoscalariform, apertures rather widely elliptical. Libriform fibers with simple pits. Axial parenchyma vasicentric scanty, in strands of 2–3 cells. Rays in young stems pluriseriate or uniseriate, but mostly multiseriate, about 8 cells wide, at periphery of larger stems. Ray cells upright in smaller stems, but some procumbent in rays in periphery of older stems, therefore Paedomorphic Type I (Carlquist 1988). Cambium storied at periphery of larger stems. Crystals not observed.

Tetramelaceae. Data are based on the monotypic genera *Octomeles* and *Tetrameles.* Vessel elements mostly solitary, a few in radial pairs. Perforation plates simple, nonbordered or nearly so. Lateral wall pits of vessels oval, alternate with narrow slitlike apertures. Libriform fibers with simple pits on radial walls. Axial parenchyma vasicentric scanty, in strands of 2–16, mostly 6 cells in *Octomeles,* 2-6 cells in *Tetrameles.* Rays multiseriate and uniseriate (uniseriates comprising 20% of the rays present regardless of location in stem), closest to Homogeneous Type I of Kribs (1935). Some multiseriate rays superposed

TABLE I. Wood features of Cucurbitales. Conventions in table: ANIS = Anisophylleacae; CUCU = Cucurbitaceae; CORI = Coriariaceae; CORY = Corynocarpaceae; TETR = Tetramelaceae; DATI = Datiscaceae; BEGO = Begoniaceae; + = present; 0 = absent; (+) occasionally present; min = minimal; ? = report questionable; a = alternate; ab = apotracheal banded; al = aliform; co = confluent; d = diffuse; ft = fiber-tracheids; If = libriform fibers; ra = ray-adjacent; sc = scalariform; t = tracheid; vs = vasicentric scanty; HetII = Heterogeneous Type II; HomII = Homogeneous Type II; PI = Paedomorphic Type I; PII = Paedomorphic Type II.

Feature	ANIS	CUCU	CORI	CORY	TETR	DATI	BEGO
Perforation plate borders	+	min	0	min	+	+	min, +
Lateral vessel pits	a	a	a	a (+sc)	a	a (+ps)	sc
Grooved vessel walls	0	0	+	+	0	0	0
Type imperforate trach. elements	t	If	If (+ft?)	If (+ft?)	If	If	If
Type apotracheal parenchyma	al, co, d	vs, ab, ra	vs, ab, ra	vs, ab, ra	vs	vs	vs
Type of ray	HetII	PII	PII	HomII	HomI	PI	PII
Very wide rays	+	+	+	+	(+)	+	+
Storying	0	+	+	+	+	+	+
Ray crystals	+	0	+	+	0	0	0

and intercontinuous. All axial cells storied; many rays conform to the storied pattern. No crystals observed.

Anisophylleaceae. The data for this family are compiled from the descriptions of Vliet (1976) for *Anisophyllea, Combretocarpus, Poga,* and *Polygonanthus;* data on storying and on vessel features were contributed by the second author. Vessels solitary, less commonly in radial multiples. Perforation plates simple, nonbordered in the first three genera named (Anisophyllea, Fig. 16) or minimally bordered (*Polygonanthus,* Fig. 17) Lateral wall pitting composed of alternate, circular to oval or polygonal pits. Grooves interconnect pit apertures (Fig. 16, lower left; Fig. 17). Imperforate tracheary elements with relatively numerous and large (3–7 µm pit cavity diameter) pits, the elements therefore tracheids sensu IAWA Committee on Nomenclature (1964) and Carlquist (1988). A few "vascular tracheids" reported, these adjacent to vessels and therefore better termed vasicentric tracheids, in *Anisophyllea* and *Polygonanthus* (Vliet 1976). Axial parenchyma aliform or more commonly, aliform confluent, plus scanty diffuse. Parenchyma strands composed of 4–13, mostly 6–9 cells. Rays Heterogeneous Type II of Kribs (1935), composed of procumbent cells with upright tip cells and occasional sheathing cells. Rays mostly either very wide, more than 10 cells in width at widest point, or else biseriate or uniseriate. Storying not present. Solitary crystals reported in axial or ray parenchyma except in Poga; the crystals distributed in the form of chambered crystals in diffuse axial parenchyma in *Anisophyllea, Combretocarpus,* and *Polygonanthus.*

CONCLUSIONS

Distinctions Within Corynocarpaceae. Obviously, material of three of the five species of *Corynocarpus* does not provide data sufficient to establish specific features in wood anatomy. A synoptical study of wood of the five species is desirable. Nevertheless, on the basis of material studied, attention is called to the following distinctive features of *C. laevigatus:* more numerous vessels per group; wider axial parenchyma bands formed of thinner-walled cells; central portions of rays composed of very narrow cells; and crystals restricted to cells in the peripheries of the rays. In C. dissimilis, attention is called to striations on pit-free portions of the vessel wall, narrow bands of axial parenchyma cells, central portions of rays composed of very narrow cells, and crystals restricted to cells in the peripheries of the rays. The wood of C. cribbianus was distinguished by presence of some scalariform and transitional pitting on vessel walls, both axial parenchyma cells and libriform fibers relatively thick-walled, narrow cells lacking in central portions of rays, and crystals throughout the rays (often in ray cells that have subdivided). Ray cells of C. cribbianus are equivalent to the peripheral ray cells in C. dissimilis and *C. laevigatus.*

Composition and Phylesis of Cucurbitales. The features of Table 1 show a high degree of resemblance among the cucurbitalean families with respect to wood features. The most divergent family, Anisophylleaceae, has been placed first because it possess character states traditionally considered as primitive (authors cited as authorities for character state interpretation in dicotyledons at large): presence of tracheids (Metcalfe and Chalk 1950, p. xlv: "fibres with distinctly bordered pits"); aliform and diffuse axial parenchyma (Kribs 1937); Heterogeneous Type II rays (Kribs 1935); and absence of storying (Bailey and Tupper 1918). Character states in the remaining cucurbitalean families are more specialized. Although Cucurbitaceae depart from the Cucurbitales clade before Anisophylleaceae in the scheme of Dawson and Wagstaff (2000), the branch leading to Cucurbitaceae involves only three changes. The cladogram offered by Schwarzbach and Ricklefs (2000) differs from that of Dawson and Wagstaff (2000). More comprehensive data and study of more numerous species may be of assistance in refining ideas on phylogeny with the cucurbitalean clade.

With respect to wood features of probable greater phylogenetic value (Table 1), Coriariaceae, Corynocarpaceae, and Cucurbitaceae form a close grouping. In assessing features of likely phyletic value, one should choose features of more limited occurrence within dicotyledons: these features are less likely to represent homoplasies than are features of wide systematic distribution (e.g., types of vessel grouping). The wood of Coriaria is so similar to that of *Corynocarpus* that one must ate minor features (e.g., greater libriform fiber wall thickness in *Corynocarpus*) to discriminate between wood of the two families. Cucurbitaceae are more diverse than Coriariaceae with respect to wood, a consequence of the habital diversity of Cucurbitaceae. The relatively woody stems of Acanthosicyos predictably have wood much more like that of Corynocarpus than do the secondary xylems of Cucurbitaceae with vining stems or succulent roots. Coriariaceae, Corynocarpaceae, and Cucurbitaceae share unusual wood features such as scanty vasicentric plus banded plus ray-adjacent axial parenchyma (the latter known in very few woods: Carlquist 1988) and Homogeneous Type 11 rays (the Paedomorphic Type II rays of Cucurbitaceae represent a form of Homogeneous Type II found in species with more nearly herbaceous habits). Presence of very wide multiseriate rays (more than 10 cells wide at widest point) combined with absence of uniseriate rays unite the three families. These three families also share storying, but a storying that is not expressed in the libriform fibers because they elongate so greatly (and thus to various degrees, obliterating a storied appearance) during growth.

The wood of Begoniaceae and Datiscaceae s. s., like wood of Cucurbitaceae, has permanently juvenile rays in which upright cells are common (Table 1), but juvenilism is not a feature of phyletic significance. One should look to the character state in woody relatives with less juvenilism for the likely basic condition on which juvenilism has been superimposed. Tetramelaceae do not have permanently juvenile rays. If rays do not clearly unite this trio of families, the nature of axial parenchyma does. Begoniaceae, Datiscaceae, and Tetramelaceae have scanty vasicentric axial parenchyma but lack banded axial parenchyma. Begoniaceae resemble Tetramelaceae closely in having prominently storied fibers. The ontogenetic meaning of this is that in these families, little elongation of the libriform fibers occurs during maturation. Begoniaceae are located close to Tetramelaceae in the cladograms of Dawson and Wagstaff (2000), whereas in that of Schwarzbach and Ricklefs (2000), Datiscaceae s. s. group closely with Begoniaceae. Swensen et al. (1998) group Begoniaceae, Datiscaceae, and Tetramelaceae closely. If wood of Datiscaceae were that of a woody shrub or tree rather than an herb (and thus juvenilistic), its wood pattern might resemble those of Begoniaceae and Tetramelaceae more closely.

Anisophylleaceae differ from the other cucurbitalean families by presence of tracheids, presence of aliform to aliform confluent plus scanty diffuse axial parenchyma, presence of Heterogeneous Type II rays, and absence of storying. These represent more primitive expressions than the character states of these wood features found in the other families of Cucurbitales as defined by Schwarzbach and Ricklefs (2000) or Wagstaff and Dawson (2000). The four genera segregated from Rhizophoraceae as Anisophylleaceae differ from the remaining Rhizophoraceae by possessing alternate circular to polygonal pits on lateral walls of vessels and by having notably wide multiseriate rays (they exceed 10 cells in width at the widest point). These features, however, are found in all of the cucurbitalean families. In addition, Anisophylleaceae differ from Rhizophoraceae in possessing aluminum in wood (Kukachka and Miller 1980); aluminum is apparently lacking in the cucurbitalean families. Reinvestigation of this feature is desirable because in some families studied by Kukachka and Miller (1980), wood samples were few or provided little woody tissue (heartwood shows the aluminum reaction, whereas sapwood typically does not). In Anisophylleaceae, crystal occurrence differs in part (chambered crystals in diffuse axial parenchyma) from solitary crystals in rays found exclusively in the remaining Cucurbitales. Thus, nonbordered or minimally bordered perforation plates as well as wide rays (unaccompanied by uniseriate rays) occur in both Anisophylleaceae and the remaining families referred to Cucurbitales. These features are likely to represent synapomorphies. The other features shared by Anisophylleaceae with the remaining families of Cucurbitales are widely distributed within dicotyledons, and thus are likely to be homoplasies. Nevertheless, the perforation plate and ray features of the families newly included in Cucurbitales are indicative of relationship because they are conservative and not sensitively related to ecology and therefore not likely to evolve numerous times independently within dicotyledons. For example, the only other order in which nonbordered perforation plates are characteristic is Caryophyllales (Carlquist 2000a, 2000b), and Caryophyllales are not adjacent to Cucurbitales in the cladograms cited in the introduction.

Caution must be exercised if only a single species of a family is studied, or if few species provide much wood (e.g., Begoniaceae, Cucurbitaceae), but in the case of paucity of material, presence of a feature is more significant than absence of a character. Features more sensitive to ecology (e.g., sculpturing in vessels walls, grouping of vessels) and, judging from distribution in dicotyledons, more easily evolved in many phylads, are not reliable indicators of relationship (Carlquist 1988). The present paper, therefore, details an instance where wood anatomy character states reflect systematic relationships well. This study also can help to discriminate between those instances in which wood anatomy does illustrate systematic distinctions and those in which wood features are unlikely to be of systematic import because of homoplasic status.

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