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## Wood Anatomy of *Amanoa* (Euphorbiaceae)

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## WOOD ANATOMY OF AMANOEA (EUPHORBIACEAE)

by

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### Summary

Wood anatomy of 29 specimens of seven species of *Amanoa* from tropical Africa, South America, and the Caribbean is described. The wood is diffuse-porous with most vessels in short radial multiples. Vessel elements are notably long, have simple perforation plates and small, alternate intervessel pits; tyloses are present in heartwood. Libriform wood fibres bear thick walls. Axial parenchyma distribution is diffuse and diffuse-in-aggregates. Chambered crystalliferous axial parenchyma is common. Rays are heterocellular, narrow, and very tall. The species examined, all from moist lowland forests, have similar wood structure. Wood of *Amanoa* resembles that of other primitive Euphorbiaceae.

**Key words:** *Amanoa*, Euphorbiaceae, Phyllanthoideae, wood anatomy.

### Introduction

*Amanoa* Aublet is a genus of perhaps 15 species found in the humid tropics of western Africa and the Americas. It is characterised by unisexual petal-bearing flowers produced in densely bracted axillary clusters and explosively dehiscent globose fruits. *Amanoa* is a member of Euphorbiaceae subfamily Phyllanthoideae and it is the type genus of the small tribe Amanoeae (Pax & Hoffm.) Webster. Amanoeae may be distinguished from the closely related Wielandiae Baillon ex Hurusawa by persistent stipules and coarsely sculpted pollen grains. The only other genera that have been placed in Amanoeae are *Actephila* Blume from Australasia (Pax & Hoffmann 1922, 1931; Webster 1975) and *Pentabrachium* Muell. Arg. from West Africa (G.L. Webster, pers. comm.). Further, *Croizatia* Steyermark has been discussed as a possible link between *Amanoa* and subfamily Oldfieldioideae (Webster et al. 1987). Never-

theless, relationships of *Amanoa* to other bi-ovulate euphorbs remain unclear (see discussion).

Although three species have been named from Africa, one of these, *A. schweinfurthii* Baker & Hutchinson, is known only from the type collection and recent study of herbarium specimens shows the other two to be broadly sympatric and morphologically intergradant (Hayden unpublished). Consequently, all African material studied here is referred to *A. bracteosa* Planchon. The genus is more speciose in the neotropics where 13 species can be distinguished (Hayden 1990). Wood samples of six neotropical species were available for study.

Wood of *Amanoa* has received cursory examination by several authors (Kribs 1928; Record 1938; Hayden 1980; Mennega 1987). However, detailed descriptions and published illustrations are lacking. The present study of wood structure in *Amanoa* was undertaken in concert with ongoing monographic studies of the genus to provide evidence concerning the relationships of this still poorly understood genus.

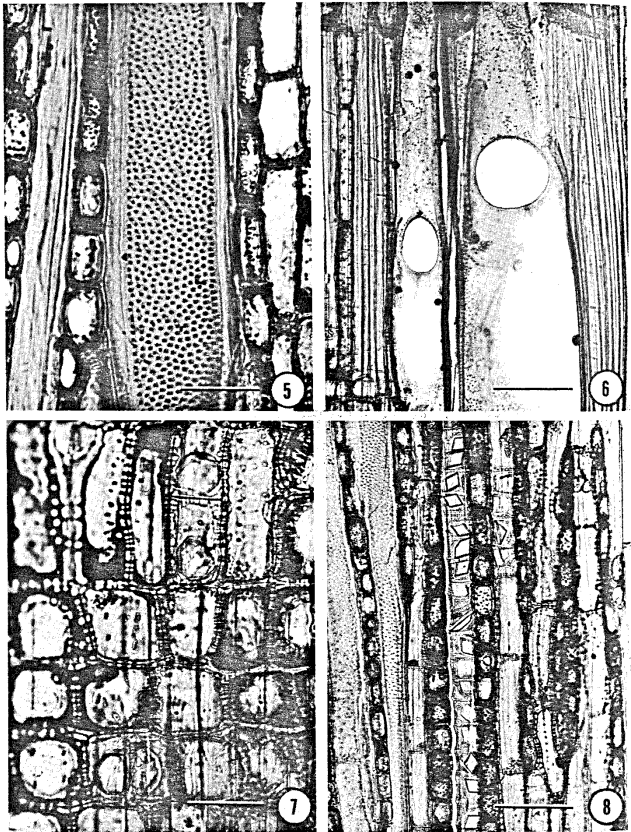
### Materials and Methods

Specimens of *Amanoa* examined in this study are listed and documented in Appendix I. Two specimens of putatively related genera were also consulted for comparative purposes: *Actephila javanica* Miq., Sumatra, Rahmat si Boeea 4324, USW 28512 (MICH); and *Pentabrachium reticulatum* Muell. Arg., Cameroon, Zenker 1688, USW 31260 (K).

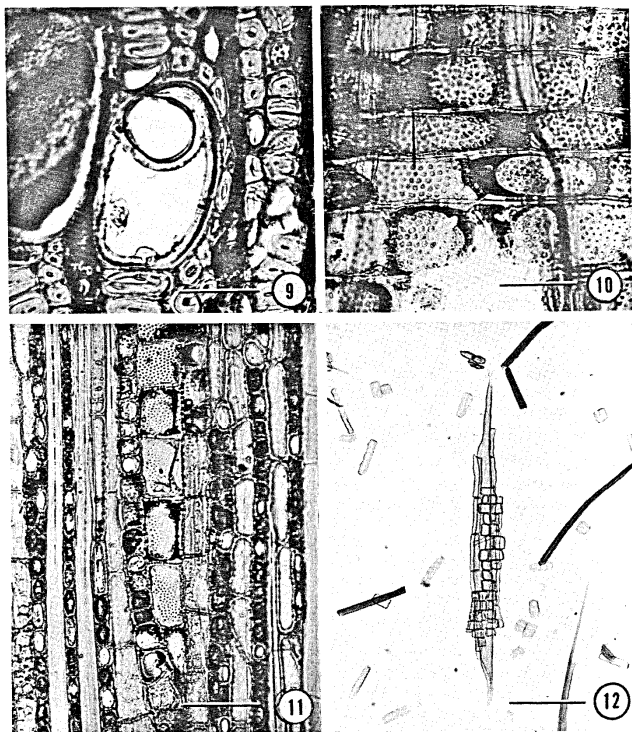
Woods were softened prior to sectioning by refluxing for at least 48 hours in a 10 percent aqueous solution of Aerosol OT. Most woods were sectioned unembedded; however, a few specimens were embedded in cel-

Table 1. Selected dimensional data ( $\mu\text{m}$ , mean  $\pm$  standard deviation) for wood of *Amanoa*. Duplicate data for certain specimens were obtained by independent observers as an internal check of accuracy. An asterisk (\*) indicates a specimen from a small branch.

Species / Specimen	Pore diameter	Vessel element length	Fibre length
<i>A. bracteosa</i> Planch.			
King 241	107 $\pm$ 24	1040 $\pm$ 175	1946 $\pm$ 295
PRFw 18603	100 $\pm$ 25	969 $\pm$ 156	1847 $\pm$ 294
Walker 141	137 $\pm$ 24	953 $\pm$ 154	2069 $\pm$ 257
	133 $\pm$ 29	994 $\pm$ 243	2072 $\pm$ 234
Letouzy 12546	149 $\pm$ 25	1084 $\pm$ 198	2237 $\pm$ 208
	148 $\pm$ 33	1069 $\pm$ 221	2510 $\pm$ 338
<i>A. caribaea</i> Kr. & Urb.			
CTFw 4723 = Uw 29582	133 $\pm$ 29	1218 $\pm$ 257	2333 $\pm$ 300
CTFw 17324 = Uw 27734	139 $\pm$ 27	1060 $\pm$ 220	2198 $\pm$ 256
CTFw 28162 = Uw 27806	132 $\pm$ 25	1254 $\pm$ 230	2440 $\pm$ 233
	135 $\pm$ 31	1358 $\pm$ 310	2384 $\pm$ 279
<i>A. congesta</i> W.J. Hayden			
Maguire et al. 47742	99 $\pm$ 15	1117 $\pm$ 243	2211 $\pm$ 238
	103 $\pm$ 17	1127 $\pm$ 252	2700 $\pm$ 260
Maguire et al. 47755	109 $\pm$ 17	1025 $\pm$ 176	1738 $\pm$ 194
	110 $\pm$ 22	1204 $\pm$ 183	1946 $\pm$ 173
<i>A. guianensis</i> Aublet			
BAFOG Serv. Forest. 117M	132 $\pm$ 22	1096 $\pm$ 171	2340 $\pm$ 234
BAFOG Serv. Forest. 248M	136 $\pm$ 28	940 $\pm$ 188	1936 $\pm$ 194
BAFOG Serv. Forest. 1324	154 $\pm$ 20	1022 $\pm$ 203	2175 $\pm$ 218
	148 $\pm$ 30	1105 $\pm$ 215	2301 $\pm$ 186
Cuatrecasas 19879	95 $\pm$ 17	968 $\pm$ 249	2161 $\pm$ 252
	93 $\pm$ 22	1185 $\pm$ 276	2344 $\pm$ 241
For. Dept. Br. Guiana 3454	119 $\pm$ 20	1025 $\pm$ 170	1998 $\pm$ 181
Krukoff 1916	116 $\pm$ 17	1133 $\pm$ 229	2348 $\pm$ 231
Krukoff 5113	81 $\pm$ 18	1386 $\pm$ 274	2325 $\pm$ 295
Krukoff 6370	127 $\pm$ 27	948 $\pm$ 164	1790 $\pm$ 269
Lanjouw & Lindeman 410	114 $\pm$ 19	937 $\pm$ 191	2258 $\pm$ 328
Lanjouw & Lindeman 501	109 $\pm$ 24	1043 $\pm$ 199	2110 $\pm$ 196
Lindeman 4495*	80 $\pm$ 16	903 $\pm$ 172	1974 $\pm$ 321
Lindeman 5091	118 $\pm$ 17	985 $\pm$ 227	2174 $\pm$ 243
Maguire (Irwin) et al. 55553	113 $\pm$ 26	1076 $\pm$ 246	2151 $\pm$ 257
Sabatier & Prevost 2109	144 $\pm$ 25	986 $\pm$ 173	1968 $\pm$ 153
Stahel 28	107 $\pm$ 21	1076 $\pm$ 178	2176 $\pm$ 245
	107 $\pm$ 22	1049 $\pm$ 180	2112 $\pm$ 239
<i>A. nanayensis</i> W.J. Hayden			
Ellenberg 2785	95 $\pm$ 14	1077 $\pm$ 211	2162 $\pm$ 249
	84 $\pm$ 19	1139 $\pm$ 210	2352 $\pm$ 287
Ellenberg 2846	131 $\pm$ 23	1086 $\pm$ 215	2258 $\pm$ 209
	120 $\pm$ 26	1172 $\pm$ 205	2282 $\pm$ 218
<i>A. oblongifolia</i> Muell. Arg.			
Krukoff 7015	105 $\pm$ 24	1046 $\pm$ 241	1990 $\pm$ 230
<i>A. sinuosa</i> W.J. Hayden			
Krukoff 1489	111 $\pm$ 21	988 $\pm$ 205	2042 $\pm$ 289
<i>A. sp.</i>			
BAFOG Serv. Forest. 36N	128 $\pm$ 21	1175 $\pm$ 201	2298 $\pm$ 232
	123 $\pm$ 30	1216 $\pm$ 265	2368 $\pm$ 266



Figs. 5–8. Wood of *Amanoa*. – 5: *A. guianensis*, Stahel 28, intervessel pits, tangential section. – 6: *A. guianensis*, Stahel 28, simple perforation plates, radial section. – 7: *A. nanayensis*, Ellenberg 2846, crystalliferous ray cells, radial section. – 8: *A. guianensis*, Stahel 28, axial parenchyma with and without crystals, tangential section. – Scale bars of 5 & 8 = 50  $\mu\text{m}$ ; of 6 & 7 = 100  $\mu\text{m}$ .



Figs. 9–12. Wood of *Amanoa*. – 9: *A. bracteosa*, PRFw 18603, tylosis in vessel, transverse section. – 10: *A. guianensis*, Stahel 28, vessel-ray pits, radial section. – 11: *A. congesta*, Maguire et al. 47755, rays and axial parenchyma, tangential section. – 12: *A. oblongifolia*, Krukoff 7015, vessel element, macerated wood. – Scale bar of 9 = 50  $\mu\text{m}$ ; of 10 & 11 = 100  $\mu\text{m}$ ; of 12 = 300  $\mu\text{m}$ .

### Discussion

With few exceptions, the specimens of *Amanoa* examined are remarkably homogeneous qualitatively. As noted in the description, three specimens have unusually abundant crystalliferous axial parenchyma, two

specimens lack such cells, and only two specimens possess prismatic crystals in the rays. None of these departures from the usual were found consistently in conspecific specimens. The high proportion of uniseriate rays report-

1987). The small intervessel pits and simple perforation plates can be considered apomorphic, but these features are so widespread in phyllanthoid woods with *Aporusa*-type structure and in subfamily Oldfieldioideae (Hayden 1980) that only a very general inclusion with other *Aporusa*-type woods can be supported. Similarly, while the evolutionary status of polymerous rays is unknown, these rays, too, are widespread in both uniovulate and biovulate Euphorbiaceae (Metcalf & Chalk 1950; Hayden 1980; Mennega 1987) and contribute little towards resolution of relationships. Thus, despite the general wood and floral resemblances between *Amanoa* and Wielandiacae there is no compelling evidence of particularly close relationships among these plants.

Composition of tribe Amanoeae has been problematic (see the introduction). Mennega (1987) has already argued that wood of *Actephila* differs significantly from that of *Amanoa* in several respects, especially in its septate fibres, scarce axial parenchyma restricted to a few paratracheal cells, a preponderance of erect ray cells, and presence of sheath ray cells. These differences, confirmed in the single specimen of *Actephila* cited above, and in concert with indications from leaf architecture (Levin 1986) and pollen (Köhler 1965), argue against retention of *Actephila* in tribe Amanoeae. The specimen of *Pentabrachium* studied is anatomically similar to *Actephila* (see also Mennega 1987). Thus, inclusion of *Pentabrachium* in tribe Amanoeae cannot be supported by wood structure. The wood of *Croizatia* is presently unknown.

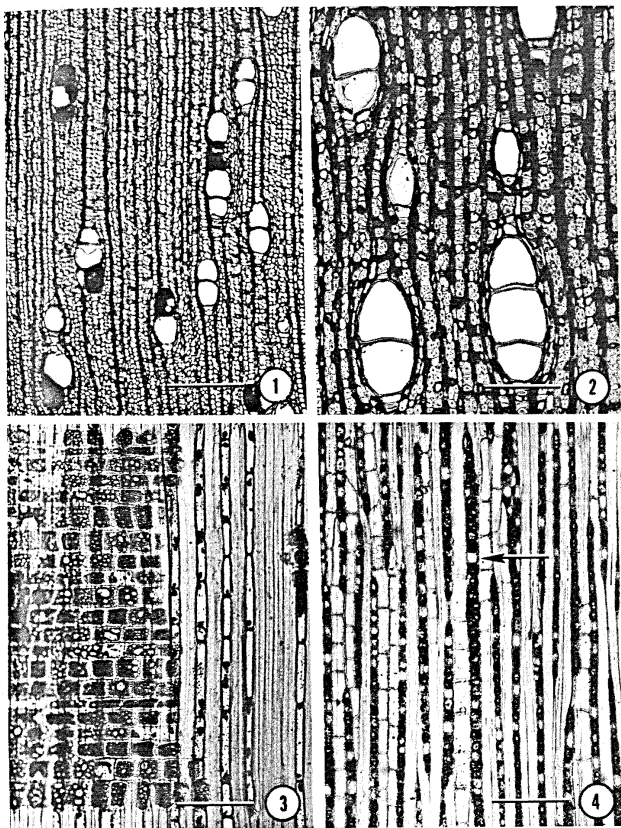
In summary, woods of *Amanoa* species are homogeneous. Wood anatomy is consistent with the hypothesis that *Amanoa* is an early derivative of ancestral elements of the biovulate portion of Euphorbiaceae. Although there are euphorb woods with more primitive features (*Blotia*, for example), *Amanoa* wood is not sufficiently specialised to support any particular relationship beyond a general association with other biovulate euphorbs with *Aporusa*-type wood. In terms of their wood structure, neither *Actephila* nor *Pentabrachium* seem closely related to *Amanoa*.

### Acknowledgements

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Figs. 1-4. Wood of *Amanoa*. — 1: *A. caribaea*, CTFW 4723, pore distribution, transverse section. — 2: *A. oblongifolia*, Krukoff 7015, diffuse-in-aggregates distribution of axial parenchyma, transverse section. — 3: *A. caribaea*, CTFw 17324, heterocellular ray and axial parenchyma, radial section. — 4: *A. congesta*, Maguire et al. 47755, rays, including polymerous ray (arrow), and axial parenchyma, tangential section. — Scale bar of 1 = 500  $\mu$ m; of 2-4 = 200  $\mu$ m.

loidin (Wetmore 1932). Sections were stained in Delafield's hematoxylin, and counterstained with safranin. Macerations were prepared by treatment in equal parts of 10 percent nitric and 10 percent chromic acids, followed by several rinses in water, staining in safranin, dehydration in tert-butyl alcohol, and clearing in toluene.

Numerical data reported for vessel diameter, vessel element length, and fibre length are based on 50 measurements of each feature per specimen; all other features for which averages are reported are based on 10 measurements or counts per specimen. The following description is based upon specimens judged to exemplify mature wood structure for the genus.

## Results

Growth rings are absent; the wood is diffuse-porous, without large scale repetitive pattern of vessel distribution (Fig. 1). Vessels are mostly solitary or in short radial multiples of two or three (rarely more) cells (Figs. 1, 2); clusters may constitute 0–10 percent of pore groups; pore grouping indices range from 1.6 to 2.7. Vessels have rounded outlines. Perforation plates are simple (Fig. 6) and occur on moderately inclined end walls; average end wall angles range from  $32 \pm 8$  to  $60 \pm 11$  degrees from horizontal. Vessel walls vary from 4–6  $\mu\text{m}$  thick and bear minute to small circular alternate intervessel pits (Fig. 5), the average vertical diameters of which range from 3–6  $\mu\text{m}$ . Vessel-ray pits (Fig. 10) resemble intervessel pits. Vessels lack helical thickenings. Average values for tangential diameter of vessels (including walls) range from a low of  $81 \pm 18 \mu\text{m}$  to a high of  $154 \pm 20 \mu\text{m}$  (Table 1). The average number of vessels per  $\text{mm}^2$  ranges from 4–14 (to 28 in wood of a small branch, Lindeman 4495); however, most specimens fall within the range of 6–10. Vessel elements are mostly very long (Fig. 12), with average values ranging from  $937 \pm 131$  to  $1386 \pm 274 \mu\text{m}$  (Table 1). Tyloses (Fig. 9) are present, but not abundant, in heartwood specimens.

Imperforate tracheary elements are non-septate, thick-walled, libriform wood fibres (Figs. 2–4). Average fibre lengths range from  $1738 \pm 194$  to  $2510 \pm 338 \mu\text{m}$  (Table 1).

Values for the ratio of fibre to vessel element length fall mostly in the range of 1.9–2.2.

Axial parenchyma is diffuse and diffuse-in-aggregates (Fig. 2). Parenchyma strands may consist solely of large cells (Fig. 3) or a mixture of large and chambered crystalliferous cells (Fig. 8). Large cells are relatively thin-walled, average 85–115  $\mu\text{m}$  tall, and appear empty or contain variable amounts of tannin deposits. Small cells average 28–40  $\mu\text{m}$  tall and have sclerified walls that enclose a single prismatic crystal (Fig. 8). Parenchyma strands may consist of 8–16 large cells, or more if chambered. Crystalliferous axial parenchyma is especially abundant in several specimens: Krukoff 1916, 5113 (both *A. guianensis*), and King 241 (*A. bracteosa*); on the other hand, these cells appear to be completely absent in Cuatrecasas 19879 and Lanjouw & Lindeman 501 (both *A. guianensis*).

Rays are uniseriate, multiseriate, and polymerous (cf. the 'polymerer Holzstrahl' of Braun 1970, vertically fused rays of Menega 1987, or interconnected rays of Carlquist 1988) (Figs. 4, 8, 11). Genus-wide averages show each ray type to be present in roughly equal proportions with a range of 12–50 percent for any ray type in most specimens. Uniseriate rays, however, are especially frequent in Ellenberg 2785 and 2846 (both *A. nanayensis*), constituting 83 and 65 percent, respectively, of all rays. Uniseriate rays average from 18 to 26  $\mu\text{m}$  wide. Multiseriate portions of rays are largely biseriate, occasionally 3 cells wide, and average maximum widths from individual specimens have a range of 26–41  $\mu\text{m}$ . Ray heights are extremely variable. Shortest rays observed, by ray type, are 33  $\mu\text{m}$  for uniseriate, 82  $\mu\text{m}$  for multiseriate, and 221  $\mu\text{m}$  for polymerous rays. Tallest rays, whether uniseriate, multiseriate, or polymerous, routinely reach heights over 1 mm tall, and often up to 6 mm. Rays are heterocellular, consisting of mostly procumbent cells with rows of square or erect cells scattered throughout the ray (Fig. 3). Average number of rays per mm ranges from 13–16. Amber-coloured deposits are common in ray cells. Although ray cells usually lack crystals, two specimens, Maguire et al. 47742 and Ellenberg 2785, have sporadic ray cells containing single prismatic crystals (Fig. 7).



ed for the Ellenberg collections here referred to *A. nanayensis* might prove to be a species-specific wood feature. Unfortunately, herbarium vouchers of both of the Ellenberg collections are sterile and their identification to species is somewhat tentative (pers. obs.). Otherwise, no clear discontinuities of a qualitative nor quantitative nature were noted from species to species.

African *Amanoa*, formally comprising section *Strobilanthus* Pax, have large inflorescence bracts that nearly enclose the flowers. In contrast, flowers of New World species are well-exserted from smaller bracts. In terms of wood structure, African and New World specimens are similar and argue for maintenance of both groups in the same genus. Pax & Hoffmann (1922) distinguished two groups of species in the Americas. Section *Imraya* Krug & Urban (1897) was erected to accommodate *A. caribaea* Krug & Urban based on its pedicellate staminate flowers, with all other species known at the time referred to section *Amanoa* ('*Eumanoa*'). Nothing unique to the wood structure of *A. caribaea* was found in this study, so its segregation from the remainder of neotropical species cannot be supported by wood anatomy.

The homogeneity of wood structure surveyed here is not surprising, given that the species studied share the same general habitat, lowland rain forest, often being found in swamps, along riverbanks, or in periodically flooded forest. These species seem constrained to a single ecological milieu with the consequence that adaptation and common descent result in similar wood features. *Amanoa cupatensis* Huber, a shrub less than 2 m in height, would have offered a most interesting comparison with the species studied, had wood samples been available.

Woods of subfamily Phyllanthoideae exhibit a strikingly diverse range of structures (Mennega 1987) that permit significant evolutionary inferences. According to Mennega (1987) many genera of tribe Wielandieae have extremely primitive wood structure. Indeed, the wood of *Blotia* Leandri, by virtue of the extreme length of its vessel elements, scalariform perforations with numerous bars, and very high and wide rays, is notable as perhaps the most primitive wood of all Euphorbiaceae.

It is, no doubt, significant that woods of Wielandieae possess so many primitive features, because flowers in this tribe, like *Amanoa* (but unlike most Euphorbiaceae) retain a biseriate perianth (both sepals and petals).

For the most part, woods of other genera of Phyllanthoideae fall into two groups (*Aporusa*-type and *Glochidion*-type), representing different degrees of divergence from the primitive structure exemplified by *Blotia*; these two groups were first recognised by Metcalfe and Chalk (1950) and were also employed by Mennega (1987), despite the fact that her detailed study included a number of genera with minor and a few with major divergences from these two structural syndromes. Woods of the *Aporusa*-type were originally characterised by Metcalfe and Chalk (1950) as having thick-walled nonseptate fibres, abundant axial parenchyma and scalariform (or mixed scalariform and simple) perforation plates; Mennega (1987) also included some genera with exclusively simple perforation plates in this group. In contrast, woods with *Glochidion*-type structure have thin-walled septate fibres, no to (at most) a few paratracheal strands of axial parenchyma, and simple perforation plates. Overall, *Glochidion*-type woods manifest a greater degree of divergence from primitive structure than do the *Aporusa*-type woods.

*Amanoa* is a good match for other *Aporusa*-type woods, although it does differ from the original formulation of this syndrome in having simple perforation plates. Overall, *Amanoa* bears a reasonable similarity to woods of Wielandieae as described by Mennega (1987), sharing great length of vessel elements, extremely small intervessel pits, moderately to extremely high rays that are at most two or three cells wide (*Blotia* excepted), numerous polymerous (vertically fused) rays, and simple perforation plates (some Wielandieae only). Further, *Amanoa* and Wielandieae also share petals in flowers, a feature, as noted above, that is absent in most other Euphorbiaceae. If any of these wood or flower features were interpretable as synapomorphic for *Amanoa* and Wielandieae, a close relationship could be hypothesised. However, long vessel elements, tall rays, and petal-bearing flowers are likely to prove plesiomorphic for Euphorbiaceae (Mennega 1987; Webster et al.

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## APPENDIX

Specimens of *Amanoa* examined. Citations for each specimen include: collector and field number, xylarium and xylarium accession number, and location of herbarium vouchers (in parentheses). Xylarium acronyms follow Stern (1988).

- A. bracteosa* Planch. (incl. *A. strobilacea* Muell. Arg.). Cameroon: Letouzy 12546, CTFw 20898. Gabon: Walker 141, CTFw 5410. Sierra Leone: King 241, FHOW 15022; PRFw 18603.
- A. caribaea* Krug & Urban. Guadeloupe: CTFw 4723 = Uw 29582; CTFw 17324 = Uw 27734; CTFw 28162 = Uw 27806.
- A. congesta* W.J. Hayden. Brazil. Amapa: Maguire et al. 47742 (= Irwin & Westra 47742), Uw 16880 = USw 39187 (NY, US); Maguire et al. 47755 (= Irwin & Westra 47755), Uw 16883 = USw 39180 (B, GH, K, MO, NY, U, US).
- A. guianensis* Aublet. Brazil. Amazonas: Krukoff 5113, Uw 19767 (A, BM, F, MO, NA, NY, U, US); Krukoff 6370, Uw 7670 = USw 7670 (A, B, BM, F, G, MO, NY, U, US). Maranhao: Krukoff 1916, Uw 19489. Colombia. Valle: Cuatrecasas 19879, Uw 24954 = USw 33416. French Guiana: BAFOG Service Forestier 117M, Uw 5202 (CAY, U); BAFOG Service Forestier 248M, Uw 5323 (CAY, U); BAFOG Service Forestier 1324, Uw 5812; Sabatier & Prevost 2109, Uw 32746. Guyana: Forest Dept of British Guiana 3454, Uw 863 (NY); Maas & Westra 3618, Uw 24790 (F, K, MO, NY, U). Surinam: Lanjouw & Lindeman 410, Uw 1216 (U); Lanjouw & Lindeman 501, Uw 1255 (K, NY); Lindeman 4495, Uw 3127 (U, US); Lindeman 5091, Uw 3625 (U); Lindeman 5128, Uw 3468; Lindeman 5133, Uw 3471 (U); Maguire et al. 55553 (= Irwin et al. 55553), Uw 21029 (F, K, MO, NY); Mennega 267, Uw 2993 (A, U); Stahel 28, Uw 28 (A, AAU, B, CAY, GH, NY, U).
- A. nanayensis* W.J. Hayden. Peru. Loreto: Ellenberg 2785, Uw 8757 (U); Ellenberg 2846, Uw 8789 (U).
- A. oblongifolia* Muell. Arg. Brazil. Amazonas: Krukoff 7015, Uw 8105 = USw 8105 (A, B, BM, F, K, NY, U, US).
- A. sinuosa* W.J. Hayden. Brazil. Matto Grosso: Krukoff 1489, Uw 19372 (A, BM, F, G, K, MO, NY, U, US).
- A. sp.* French Guiana. BAFOG Service Forestier 36N, Uw 5535.