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WOOD ANATOMY AND RELATIONSHIPS OF NEOWAWRAEA (EUPHORBIACEAE)

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ABSTRACT. Wood anatomy of three specimens of Neowawraea phyllanthoides Rock, a rare and endangered member of Euphorbiaceae endemic to the Hawaiian Islands, is described and compared with woods of other genera of subfamily Phyllanthoideae. Neowawraea has often been associated or synonymized with Drypetes Vahl. Wood of Neowawraea is diffuse porous, perforation plates are simple, imperforate tracheary elements are thin-walled septate fiber-tracheids, rays are heterocellular and crystaliferous, and axial xylem parenchyma is restricted to a few scanty paratracheal and terminal cells. In several respects these results differ from earlier published descriptions of the wood of this taxon; these earlier descriptions are shown to be in error. Further, as described here, wood of Neowawraea differs greatly from that of Drypetes. Accordingly, generic status for Neowawraea is warranted on anatomical grounds and relationship with certain genera of tribe Phyllantheae such as Breynia Forst., Glochidion Forst., or Phyllanthus L. is favored over relationship with Drypetes.

Neowawraea Rock is a monotypic genus of dioecious trees endemic to the Hawaiian Islands. Historically recorded from Kauai, Oahu, Molokai, Maui, and Hawaii (St. John 1973), the species is currently considered in danger of extinction (Fosberg & Herbst 1975). Given its scarcity, and the fact that female flowers have never been described (St. John 1973), it is not surprising that proper understanding of its relationships has yet to be achieved.

Neowawraea phyllanthoides was discovered by Joseph Rock (1913) on rough aa lava flows of Mauna Loa. Rock described this new genus and species on the basis of male flowers and mature fruits, the only material known at that time.
Concerning relationships, Rock stated, "it is evidently related to Phyllanthus"; he also perceived a similarity to the baccate fruits of Bischofia Blume. Pax and Hoffmann (1931) declined to commit an opinion as to relationships, merely placing Neowawraea in a list of doubtful or incompletely described genera. Sherff (1939) transferred this species to Drypetes Vahl, without citing any evidence for this change in status; nevertheless this assignment has generally been followed by subsequent students of the Hawaiian flora (Neal 1965; St. John 1973; Fosberg and Herbst 1975; Carlquist 1980). Webster (1975), in a synopsis of a new classification of Euphorbiaceae, maintained Rock's generic status, but classified Neowawraea with Drypetes and Putranjiva Wall. in his tribe Drypeteae (Griseb.) Hurusawa. Since Putranjiva is often included within Drypetes (Hurusawa 1954; Airy Shaw 1972, 1975, 1980; Willis 1973), Webster's treatment tacitly implies a close relationship between Neowawraea and Drypetes.

In the course of surveying wood anatomy of Drypetes for comparison with several genera of subfamily Oldfieldioideae (Hayden 1980), it became apparent that certain specimens received as "Drypetes phyllanthoides (Rock) Sherff," i.e., Neowawraea, were anatomically discordant with other woods of Drypetes. Furthermore, structures present in the three specimens available for study were also discordant with an earlier published description of the wood of "Drypetes phyllanthoides" (Smith & Ayensu 1964). Accordingly, the following account of wood of Neowawraea phyllanthoides is presented in an effort to clarify the anatomy and relationships of this rare tree.

MATERIALS AND METHODS

Specimens examined are listed in the Appendix; xylarium acronyms follow Stern (1978). Standard techniques were employed in preparation of woods for microscopic examination. Specimens with wide pores were embedded in celloidin (Wetmore 1932) prior to sectioning, others were sectioned without pretreatment.
beyond simple rehydration. Sections were prepared at thicknesses of 15, 20, and 25 µm and were stained with a combination of hematoxylin (either Delafield's or Heidenhain's) and safranin. Macerations were prepared according to Jeffrey's technique (Johansen 1940). Measurements of anatomical structures were made in accordance with the procedures recommended by Tamolang et al. (1963). Numerical values in the description of Neowawraea wood are averages of values from the three specimens studied; values included in parentheses are ranges. The variation from specimen to specimen of some features pertinent to adaptive morphology of xylem is noteworthy; data for these features are presented separately as table 1. Otherwise, pooling of data in the wood description seems justifiable given: (1) the small size of standard wood samples relative to the total amount of wood in a tree and, especially, relative to the dimensional variability of wood elements from different positions in one tree (Panshin & De Zeeuw 1970); (2) the small number of specimens available; and, (3) the relative homogeneity of measurements from the specimens studied other than those features listed in table 1.

WOOD ANATOMY OF NEOWAWRAEA PHYLLANTHOIDES ROCK

Figures. 1--8. Growth rings present, faint, defined by scattered terminal axial xylem parenchyma and tangential alignment of first-formed early wood pores. Porosity diffuse; pore groups 25 percent solitary, 52 percent radial multiples, 22 percent clusters; 3.4 (2--12) pores per multiple pore group; 76 (54--116) pores per mm² (see table 1); pore area 0.114 mm² per mm² cross-sectional area of wood. Pore outlines circular; wall thickness 3 (1--5) µm; tangential diameter 46 (14--95) µm (see table 1). Perforation plates simple; end walls inclined 51 (15--75) degrees from the horizontal. Intervascular pits circular, alternate; diameter 4.5 (2--6.6) µm. Vessel elements 564 (348-797) µm long (see table 1), often
ligulate, containing variable quantities of tannin-like deposits, with tyloses present in Degener et al. 4371.

Fiber-tracheids septate, usually with 3--4 septa per cell, 841 (429--1420) µm long (see table 1); lumen diameter greater than or equal to wall thickness; vertical diameter of pit borders 2.4 (1--4.5) µm.

Rays heterocellular, very numerous, 14 per mm, 22 percent uniseriate, 53 percent multiseriate, 25 percent polymerous. Uniserate rays 18 (13--27) µm wide, 8.5 (3--23) cells or 520 (214--1809) µm tall. Multiserate rays and multiserate portions of polymerous rays 2.8 (2--4) cells or 61 (37--87) µm wide; multiseriate ray height 23 (9--36) cells or 955 (389-2714) µm; polymerous ray height 42 (19--118) cells or 1803 (442-3919) µm. Prismatic crystals and tannin-like deposits frequent. Vessel to ray pits circular and alternate to scalariform.

Axial xylem parenchyma not abundant; distribution scanty paratracheal and widely spaced terminal apotracheal. Parenchyma strand length 7.6 (4--10) cells or 510 (369--663) µm. Vessel to parenchyma pits circular and alternate to widely spaced.

DISCUSSION

Comparison of published data on the wood structure of Neowavrrea (as Drypetes phyllanthoides) with the results reported above reveals several significant differences. Smith & Ayensu (1964) reported the absence of growth rings, a pore distribution of 95 percent solitary and 5 percent radial multiples, scalariform perforation plates with 8 (6--11) bars per perforation, libriform wood fibers (with no mention of septa), and axial xylem parenchyma distribution as diffuse and forming narrow bands; none of these features could be confirmed in our material despite the fact that two of our specimens, USw 18672 and USw 18675, were also studied by Smith & Ayensu. On the other hand,
Smith & Ayensu's data on pore outline, pore diameter, vessel element length, vessel wall thickness, intervacular pitting, imperforate tracheary element length, and ray features conform with our descriptions. All three specimens studied by us (see Appendix) were similar to each other and offered no clue as to the source of results so different from the earlier literature.

Microscope slides of wood of Drypetes at USw were examined in an effort to resolve these discrepancies. As expected, materials labeled "USw 18672" and "18675" were present; these conform with our description of Neowawraea, and differ in the same respects from Smith & Ayensu's description. However, another slide labelled "Drypetes phyllanthoides USw 18315" was also in the collection and the sections on it contain structures that could account for the disputed descriptions from Smith & Ayensu. However, according to data placed on file at USw when this specimen was accessioned from MADw, USw 18315 is actually the African Drypetes gossweilleri S. Moore. Thus, it seems that parts of Smith & Ayensu's (1964) wood description of Neowawraea are erroneous as a result of a mislabelled preparation. Smith & Ayensu's documentation of USw 18672 is also incorrect; the collection number is St. John et al. 11354 (US!), not 11365. It does not seem likely, however, that this second error has any bearing on the erroneous descriptions. Our correction of the errors regarding perforation plates, imperforate tracheary elements, and axial xylem parenchyma of Neowawraea is especially significant since these features have considerable importance in the systematic anatomy of Euphorbiaceae subfamily Phyllanthoideae.

For the most part, woods of Phyllanthoideae can be grouped into two distinct categories or structural syndromes. This was first recognized by Janssonius (1934, 1950), who placed the phyllanthoid genera he studied into the first and third of the four groups he recognized for Javan euphorbiaceous woods. Metcalfe & Chalk (1950) added several genera to these categories, and
referred to them as "Glochidion-type woods" and "Aporosa (sic)-type woods."
As can be seen from table 2 and figures 9--12, these two structural syndromes
are easily distinguished on the basis of perforation plates, imperforate
tracheary element characteristics (see also Bamber 1974), and amount and
distribution of axial xylem parenchyma. *Neowawraea* clearly possesses all
the characteristics of Glochidion-type woods and lacks the defining features
of the Aporusa-type. The significance of our redescription of the wood of
*Neowawraea* is thus apparent; based on Smith & Ayensu's (1964) description,
*Neowawraea* would have fit easily in the Aporusa-type category.

The fact that *Neowawraea* possesses Glochidion-type structure suggests
certain taxonomic conclusions. *Drypetes* possesses Aporusa-type wood, very
different from that of *Neowawraea*; thus Sherff's (1939) union of these genera
is inappropriate and Rock's generic concept should be maintained. Further,
inclusion of *Neowawraea* in Webster's (1975) tribe Drypeteae (consisting of
Drypetes, Putranjiva, and Neowawraea) seems unwarranted. Both Drypetes and
Putranjiva have similar wood structure, as recorded in Metcalfe & Chalk (1950)
and confirmed here; that these entities are very closely related is shown by
the frequent inclusion of Putranjiva in Drypetes (Hurusawa 1954; Airy Shaw
1972, 1975, 1980). As a member of Drypeteae, *Neowawraea* is anatomically out
of place.

The fossil record for phyllanthoid woods offers an interesting perspective
on relationships among woody Phyllanthoideae. Several fossil woods with
Glochidion-type structure have been described from Upper Cretaceous deposits;
these include Paraphyllanthoxylon arizonense from the southwestern United
States (Bailey 1924) and Paraphyllanthoxylon capense, Securinegoxylon
biseriatum, and Bridelioxylon fibrosum from South Africa (Müdel 1962).
Assuming their assignment to Euphorbiaceae is correct, these fossils indicate
that Glochidion-type woods have been in existence for at least 60 million
years. The great antiquity of Glochidion-type wood structure in Euphorbiaceae suggests that extant genera bearing this structural syndrome should not be classified with genera of the Aporusa-type.

A search of Phyllanthoideae for plants more closely related to Neowawraea than Drypetes yields several possible genera, but no single definitive closest relative. Webster (1975) recognizes thirteen tribes within subfamily Phyllanthoideae. Five of the thirteen tribes, Wielandieae Baill. ex Hurusawa, Amanoeae (Pax & Hoffm.) Webster, Dicoelieae Hurusawa, Aporuseae (Lindl. ex Miq.) Airy Shaw, and Drypeteae, can be eliminated on the basis of Aporusa-type wood structure in their constituent genera according to data contained in Metcalfe & Chalk (1950). Five of the remaining tribes can be eliminated by their possession of various unique morphological features (mostly presumed apomorphies) not shared with Neowawraea: Bridelieae Muell. Arg., valvate sepals; Poranthereae (Muell. Arg.) Gruning, porous dehiscence of anthers and herbaceous to ericoid sub-shrub habit; Spondiantheae Webster, biseriate perianth and capsular fruit (probably plesiomorphies); Hymenocardieae (Muell. Arg.) Hutch., samaroid fruits; and Uapaceae (Muell. Arg.) Hutch., globose involucrate inflorescences (morphological data from Pax & Hoffm. 1931).

Three tribes remain: Antidesmeae (Endl.) Hurusawa, with six genera; Phyllantheae Dumort, consisting of 18 genera; and the monotypic Bischofieae Muell. Arg. Bischofia Blume possesses Glochidion-type wood structure, but the genera of Antidesmeae and Phyllantheae are heterogeneous--both Aporusa-type and Glochidion-type woods are found in each (data from Metcalfe & Chalk 1950). Perhaps greater refinement is needed in the classification of these anatomically heterogeneous tribes. As possible relatives of Neowawraea, these three remaining tribes yield Bischofia, Antidesma L., Breynia Forst., Glochidion Forst., and Phyllanthus L., all of which possess Glochidion-type
structure and are widely distributed on Pacific islands. Based on present evidence, wood anatomy offers no means of resolving a candidate for closest relative to Neowawraea from these five genera.

Female flowers and other comparative data for Neowawraea are sorely needed, since the data currently available allows only partial resolution of its relationships. However, present knowledge does allow some speculation concerning relationships with the five genera identified above. Antidesma and Bischofia are excluded routinely from Euphorbiaceae by Airy Shaw (1965, 1967, 1975, 1980; see also Willis 1973), the former on the basis of its unilocular drupaceous fruits with distinctive foveolate-reticulate and often flattened endocarps, and the latter because of its trifoliolate to pinnately compound leaves. Neither of these problematical genera seems especially close to Neowawraea. Only Breynia, Glochidion, and Phyllanthus remain as reasonable relatives of Neowawraea. These three genera are all closely related members of Webster’s tribe Phyllantheae. Breynia and Glochidion differ from Neowawraea by their capsular fruits, and Phyllanthus differs in its uniquely specialized growth habit; thus generic status for Neowawraea within Phyllantheae should present no problem.

Of all the tribes of Phyllanthoideae, Phyllantheae thus seems able to accommodate Neowawraea with the least amount of discord; wood structure and known reproductive features are broadly consistent with such a placement. Classification in Phyllantheae is also consistent with Rock’s (1913) original opinion about the relationships of his genus. However, as noted above, Phyllantheae is anatomically heterogeneous, so its generic composition may be considered provisional at best. Ignorance of female floral structures of Neowawraea further limits the certainty of our conclusions. We therefore tentatively conclude that Neowawraea should be placed in tribe Phyllantheae,
at least until female flowers of Neowawraea and further comparative data for Phyllanthoideae become available.

ACKNOWLEDGMENTS

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LITERATURE CITED


FIGURE CAPTIONS

FIGS. 1--4. Wood structure of Neowawraea phyllanthoides (Webster et al. 13889).
1. Radial multiple and pore cluster, cross-section.
2. Heterocellular ray, radial section.
3. Septate fibers from radial section.
4. Uniseriate and biseriate rays, tangential section. All scales = 50 µm.

FIGS. 5--8. Wood structure of Neowawraea phyllanthoides (Webster et al. 13889).
5. Vessel element from macerated wood.
6. Vessel to ray pitting, radial section.
7. Crystal casts in macerated ray cells.
8. Alternate intervacular pits and multiseriate ray, tangential section. All scales = 50 µm.

FIGS. 9--12. Wood structure of Drypetes (Aporusa-type) and Glochidion (Glochidion-type).
9. Drypetes amazonica (Krukoff 6176), thick-walled fibers and abundant diffuse axial xylem parenchyma, cross section.
10. Drypetes lateriflora (Stern & Brizicky 558), scalariform perforation plates, radial section.
11. Glochidion borneense (Si Boecca 1852), thin-walled fibers, cross section.
12. Glochidion borneense (Si Boecca 1852), rays and septate fibers, radial section. All scales = 50 µm.
APPENDIX. WOOD SPECIMENS EXAMINED

Specimens examined in this study are documented in the following list. Entries for each species include, as available: locality, collector, collection number, xylarium accession number, and location of herbarium voucher.

Bischofia javanica Blume. New Guinea, USw 24030 (L); West Irian, USw 35137 (L); Fiji, Smith 6045, Aw 28452 (A); Sumatra, Si Boeeca 3558, USw 28298 (MICH); New Caledonia, USw 4622; New Caledonia, USw 4626.


Breynia patens Benth. Sumatra, Si Boeeca 1413, USw 27761 (MICH).

Drypetes afzelii Hutch. Liberia, Cooper 315, USw 4895; Ivory Coast, Detienne 135, MADw 36858 (P).

Drypetes alba Poit. Cuba, Gill & Whitford 105, USw 2985 (NY).

Drypetes amazonica Steyermark. Brazil, Krukoff 6176, USw 7532 (NY).

Drypetes cf assamica Pax & Hoffm. Sumatra, Krukoff 4075, USw 6307 (NY).

Drypetes australasica (Muell. Arg.) Pax & Hoffm. New Guinea, Pullen 6845, MADw 29077 (K).

Drypetes aylmeri Hutch. & Dalz. Ivory Coast, Bamps 2390, MADw 32770 (BR).


Drypetes diversifolia Krug & Urban. Florida Keys: Stern 2684 (MARY); Stern et al. 2765 (MARY); Stern et al. 2885 (MARY); Stern et al. 3369 (MARY).

Drypetes dolichocarpa Kanehira. Saipan, Kanehira 2141 (wood no. A2216), MAD-SJRW 26843.


Drypetes lateriflora (Sw.) Krug & Urban. Florida Keys: Stern & Chambers 266, MAD-SJRW 51473 (MAD); Stern & Brizicky 558, MAD-SJRW 51330 (MAD); Stern 2683 (MARY).

Drypetes ovata Hutch. Liberia, Cooper L4, USw 5695 (K).

Drypetes principum (Pax) Hutch. Gold Coast, Vigne 3423, MAD-SJRw 29718 (FH0).

Drypetes sclerophylla Mildbr. Tanganyika, Schlieben 5473 (wood no. 441), MAD-SJRw 30010 (MAD).


Glochidion arborescens Blume. Sumatra, Si Boeeca 7714, USw 29032 (MICH).

Glochidion borneense Boerl. Sumatra, Si Boeeca 1852, USw 27909 (MICH).

Glochidion bracteatum Gillespie. Fiji, Gillespie 3530, MAD-SJRw 25675 (BISH).

Glochidion cuspidatum var. samoanum (Muell. Arg.) Pax. Samoa, Christophersen 3301, MAD-SJRw 26135 (BISH).


Neowawraea phyllanthoides Rock. Hawai‘i, Oahu, Degener et al. 4371, USw 18675 (BISH); Hawaii, South Kona, Kapua, St. John et al. 11354, USw 18672 (BISH); Hawaii, Maui, SW slopes of Haleakala, Webster et al. 13889 (DAV).

Putranjiva roxburghii Wall. West Irian, USw 34683 (L); Trinidad (cultivated), Broadway 9248, AW 22185 (A).
### TABLE 1. Numerical data for some features of wood of *Neowawraea.*

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Mean number of pores per mm² (n = 10)</th>
<th>Mean pore diameter (µm) (n = 50)</th>
<th>Mean vessel element length (µm) (n = 50)</th>
<th>Mean fiber-tracheid length (µm) (n = 50)</th>
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</thead>
<tbody>
<tr>
<td>Degener et al. 4371</td>
<td>54</td>
<td>53</td>
<td>541</td>
<td>857</td>
</tr>
<tr>
<td>St. John et al. 11354</td>
<td>116</td>
<td>35</td>
<td>605</td>
<td>795</td>
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<tr>
<td>Webster et al. 13889</td>
<td>58</td>
<td>50</td>
<td>545</td>
<td>871</td>
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</tbody>
</table>
TABLE 2. Comparison of wood features of *Neowawraea* with other woods of Euphorbiaceae subfam. Phyllanthoideae.

<table>
<thead>
<tr>
<th>Character</th>
<th>Aporusa-type</th>
<th>Neowawraea</th>
<th>Glochidion-type</th>
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</thead>
<tbody>
<tr>
<td>Perforations</td>
<td>scalariform, or mixed scalariform and simple</td>
<td>simple</td>
<td>simple</td>
</tr>
<tr>
<td>Imperforate tracheary elements</td>
<td>non-septate</td>
<td>septate</td>
<td>septate</td>
</tr>
<tr>
<td>Axial xylem parenchyma</td>
<td>thick-walled</td>
<td>thin-walled</td>
<td>thin-walled</td>
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<td>abundant</td>
<td>not abundant</td>
<td>not abundant</td>
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<tr>
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<td>scanty paratracheal, some terminal</td>
<td>scanty paratracheal</td>
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<tr>
<td>Genera investigated</td>
<td>Drypetes</td>
<td>Neowawraea</td>
<td>Bischofia</td>
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<td></td>
<td>Putranjiva</td>
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<td>Breynia</td>
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<td></td>
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<td></td>
<td>Glochidion</td>
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