WOOD ANATOMY AND RELATIONSHIPS OF DUCKEODENDRACEAE AND GOETZEACEAE

by

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Summary

Duckeodendron has been referred to Solanaceae, Boraginaceae, and Apocynaceae; segregation into its own family is based on its drupoid fruits. Drupoid fruits also characterize Goetzeaceae, which have been placed within Sapotaceae and within Solanaceae by particular authors. Both Duckeodendraceae and Goetzeaceae have intraxylary phloem (a characteristic of Solanaceae but absent from most dicotyledon families) and wood features entirely congruent with the concept that they are closely related to Solanaceae. Wood of Duckeodendron is very similar to that of Notochoeestrum (Solanaceae). Wood of Goetzeaceae is most like wood of the solanaceous genera Grabowskya and Lycium. Duckeodendraceae and Goetzeaceae may be regarded as satellite families of Solanaceae, in accord with the treatment of Hunziker (1979), or could conceivably be treated as subfamilies of Solanaceae. Qualitative and quantitative features are given for wood of Duckeodendron cestroides (Duckeodendraceae) and two species of Goetzeaceae: Espadaea amoena and Henoonia myrtifolia. Wood of Duckeodendron is clearly mesomorphic. Wood of Espadaea is intermediate, and wood of Henoonia is relatively xeromorphic as based on vessel element dimensions, vessel density, and vasicentric tracheid presence.

Key words: Ecological wood anatomy, systematic wood anatomy, Duckeodendraceae, Goetzeaceae, Solanaceae.

Introduction

The present contribution is part of a survey of wood anatomy in tubiflorous dicotyledon families with the view of using wood anatomy to help clarify familial and ordinal groupings. In a recent treatment of the generic constitution of South American Solanaceae, Hunziker (1979) regards Duckeodendraceae, Goetzeaceae, Nolanaceae, and Sclerophylacaceae as families closely related to Solanaceae. This treatment has been followed by Takhtajan (1987). Cronquist's (1981) treatment is the same except that Goetzeaceae was included within Solanaceae (as presumably is Sclerophylacaceae, not mentioned by him). All five families are claimed by Hunziker (1979) to possess intraxylary phloem, a feature regarded as characteristic of Solanaceae (e.g., Metcalfe & Chalk 1950); it is present in Convolvulaceae, although it is absent in other tubiflorous families mentioned as possibly related to Solanaceae, including Cuscutaceae (Metcalfe & Chalk 1950). Wood anatomy supports the idea that Nolanaceae is close to Solanaceae; the family Nolanaceae can be maintained on the basis of flower and fruit morphology and anatomy (Di Fulvio 1969, 1971). Sclerophylacaceae, containing a single genus, is herbaceous and therefore not considered here; the fruit of Sclerophyllum (a carcerule) is distinctive and is the basis for familial segregation (Di Fulvio 1961). Data I have accumulated for a monograph on wood anatomy of Solanaceae, now nearing completion, provide new information for comparisons with Duckeodendraceae and Goetzeaceae. As mentioned below, phylogenetic treatments prior to that of Hunziker (1979) are by no means uniform in placement of Duckeodendraceae and Goetzeaceae, so comparisons from wood anatomy are accordingly important.

Duckeodendron was described as a genus by Kuhlmann (1925). Duckeodendron cen-
troid es Kuhl., the sole species, is a tree from the state of Pará, Brazil. Kuhlmann (1925) at first placed the genus in Solanaceae near Centrum; he compared Duckeodendron to Espadaea (Goetzeaceae) because of similarity in fruits; Duckeodendron has large two-seeded drupes with a fibrous mesocarp. Later, Kuhlmann (1930) placed Duckeodendron in Boraginaceae. Finally, Kuhlmann (1947) decided to segregate Duckeodendron as a sole genus of a new family. When wood of Duckeodendron became available, Record (1933) studied it and pronounced it like that of certain Apocynaceae. Record’s comments have not been reviewed, and the wood of Duckeodendron has therefore been studied to see if Record’s opinion could be supported.

Goetzeaceae consists of four shrubby Antillean genera: Coeloneurum Radlk., Espadaea A. Rich., Goetzea Wyd., and Henoonia Griseb. The family has been even more uncertain with respect to systematic position than Duckeodendraceae. The original description of the family Goetzeaceae by Miers (1869; emended by Airy Shaw 1965) suggested relationship to Sapotaceae. This was refuted by Radlkofer (1888), who studied Henoonia. Absence of laticifers, presence of crystal sand, presence of intraxylary phloem, and conformation of leaf bundles in Goetzeaceae convinced Radlkofer that Henoonia should be transferred to Solanaceae. However, as a result of study of wood of Henoonia both Kramer (1939) and Record (1939) concluded that Henoonia was indeed sapotaceous. More recently, Baehni (1943) on the basis of study of flower and leaf anatomy concluded that Henoonia should be in a segregate family (he did not study Coeloneurum, Espadaea, and Goetzea). The name Henoonia in Goetzeaceae has been replaced by Fuentes (1985) with Bissea. Fuentes claims that Henoonia is a later homonym. However, the difference in spelling of Henonia (Amaranthaceae, Brassicaceae) has not been claimed to be a mere orthographic variant, so pending further discussion, Henoonia is retained here for the genus in Goetzeaceae. The claim by Fuentes and Rodriguez (1984) that continuous variation within Henoonia in Cuba forces recognition of only a single species, H. myrtifolia, is credited here. Thus the family Goetzeaceae consists of Coeloneurum ferrugineum (Spreng.) Urb. (Hispaniola), Goetzea elegans Wyd. (Puerto Rico), G. ekmannii O. E. Schulz (Haiti), Henoonia myrtifolia Griseb. (Cuba); locality data may be obtained from Fuentes (1985), Little et al. (1974), Moscoso (1943), and Sauguet and Liogier (1957).

The woods studied here, one sample of Espadaea and two of Henoonia, are insufficient for demonstrating any generic distinctions, but they do seem sufficient for comment on familial affinity of Goetzeaceae.

The wood anatomy of Duckeodendron, Espadaea, and Henoonia invites comparison to ecology because of the diverse habitats of these genera. Duckeodendron is a rain forest tree (Kuhlmann 1925); Espadaea occurs in moist thickets (Sauguet & Liogier 1957); Henoonia is in coastal scrub and savannah (Fuentes 1985).

Materials and Methods

Wood samples were available in dried form, and were kindly provided from the Samuel J. Record (SJRw) collection of the U.S. Forest Products Laboratory, Madison, Wisconsin, through the courtesy of Donna Christensen and Regis B. Miller. Wood samples were boiled in water, stored in 50% aqueous ethyl alcohol, and sectioned (without any softening) on a sliding microtome. Sections were stained with a safranin-fast green combination to permit discernment of pit details; unstained sections were used for SEM studies of crystal presence. Macerations were prepared by means of Jeffrey’s Fluid and stained in safranin.

In quantitative data, means were derived from 25 measurements per feature except for vessel wall thickness, fibre-tracheid diameter, fibre-tracheid wall thickness, and ray cell wall thickness, in which measurements of a few representative conditions were averaged. Vessel diameter is based on internal (lumen) diameter at widest point. Number of vessels per mm² is based on a count of vessels, not vessel groups. Number of vessels per group is a mean based on the system 1 = a solitary vessel, 2 = a pair of vessels in contact, etc. Vasicentric tracheids are defined as in Carlquist (1985). This usage is essentially that...
of the IAWA Committee on Nomenclature (1964) and agrees closely with the usage of Metcalfe and Chalk (1950). All other wood terms used conform to the usage of the IAWA Committee on Nomenclature (1964).

**Anatomical descriptions**

*Duckeodendron cestroides* Kuhl. (SJRw 22591) (Figs. 1—4). — Growth rings absent in terms of vessels, although radial diameter of fibre-tracheids varies (Fig. 1). Vessels rarely solitary; mean number of vessels per group, 6.0 (Fig. 1). Mean vessel diameter, 187 $\mu$m. Vessels most commonly in radial chains 1–2 vessels wide tangentially. Mean number of vessels per mm$^2$, 10.1. Mean vessel element length, 793 $\mu$m. Mean vessel wall thickness, 3.5 $\mu$m. Perforation plates simple. Lateral wall pitting composed of alternate circular pits with circular apertures, both on vessel–vessel contacts (Fig. 3) and on vessel to fibre-tracheid and vessel to parenchyma contacts; pits about 5 $\mu$m in diameter. All imperforate tracheary elements may be designated as fibre-tracheids, because bordered pits, although they have pit cavities 5–7 $\mu$m in diameter, are sparser than those characteristic of tracheids (Fig. 4); pits of fibre-tracheids on radial walls (Fig. 4), rarely on tangential walls (Fig. 5). Mean fibre-tracheid diameter at widest point, 20 $\mu$m. Mean fibre-tracheid length, 1308 $\mu$m. Mean fibre-tracheid wall thickness, 2.4 $\mu$m. Axial parenchyma occasionally diffuse, but most commonly either in apotracheal bands 1–3 cells wide or vasicentric sheaths 1–3 cells wide (Fig. 1). Axial parenchyma in strands of 4–7, mostly 6, cells. Rays both biseriate and uniseriate, the two types about equal in frequency (Fig. 2). Mean height biseriate rays, 423 $\mu$m. Mean height uniseriate rays, 342 $\mu$m. Both biseriate and uniseriate rays composed of procumbent cells exclusively. Mean ray cell wall thickness, 1.2 $\mu$m. Pits infrequent on horizontal walls, common on tangential walls of ray cells; some pits on tangential walls with borders. Starch remnants present in both axial, and ray parenchyma. No secretory canals observed. Wood nonstoried (Fig. 2).

*Espadaea amoena* (SJRw 16611) (Figs. 6—9). — Growth rings absent (Fig. 6). Mean number of vessels per group, 1.84 (probable vasicentric tracheids excluded, but vessel number probably higher because narrow vessels probably excluded unintentionally). Vessels in diagonal aggregations (Fig. 6). Mean number of vessels per mm$^2$, 31. Mean vessel diameter, 61 $\mu$m. Mean vessel element length, 505 $\mu$m. Mean vessel wall thickness, 4.6 $\mu$m. Perforation plates simple. Lateral wall pitting consisting of alternate circular pits 5 $\mu$m in diameter (Fig. 9, right) with elliptical apertures, on both intervacular and vessel-parenchyma contacts. Most imperforate tracheary elements may be considered fibre-tracheids because the pit cavities are 4 $\mu$m in diameter but pits are distributed sparsely (Fig. 8). Mean fibre-tracheid diameter at widest point, 23 $\mu$m. Mean fibre-tracheid length, 1562 $\mu$m. Mean fibre-tracheid wall thickness, 4.6 $\mu$m. Pits more common on radial than tangential walls (Fig. 8). Splits in fibre-tracheid walls present (Fig. 8). Vasicentric tracheids present (Fig. 9, left). Mean length of vasicentric tracheids, 641 $\mu$m. Axial parenchyma diffuse, diffuse-in-aggregates, in bands 1–2 cells wide, and within the grouping of vessels where parenchyma may be regarded as diffuse rather than vasicentric (Fig. 6). Axial parenchyma strands consisting of 3–5, chiefly 4, cells. Rays both multiseriate and uniseriate, the two types about equally frequent (Fig. 7). Mean height multiseriate rays, 330 $\mu$m. Mean height uniseriate rays, 167 $\mu$m. Mean width of multiseriate rays at widest point, 2.34 cells. Rays composed mostly of procumbent cells; square or upright cells present only at tips of multiseriate rays or in some uniseriate rays. Mean ray cell wall thickness, 3.0 $\mu$m. Tangential walls of ray cells more densely pitted than horizontal walls, borders common on ray cell pits. Crystal sand idioblasts present in rays. Amorphous contents in parenchyma inconspicuously present. Wood nonstoried (Fig. 7).

*Henoonia myrtifolia* (SJRw 16160, previously identified as *H. angustifolia* Urb.) (Figs. 10—15). — Growth rings inconspicuously present, demarcated by a layer of marginal (perhaps initial) parenchyma and by slightly wider vessels (growth ring begins 1/4 distance from bottom of photograph, Fig.
Figs. 1–5. Wood sections of *Duckeodendron cestroides* (SJRw 22591). – 1: Transection; apotracheal parenchyma bands are present. – 2: Tangential section; rays are biseriate and uniseriate. – 3: Intervascular pitting from tangential section. – 4: Fitting on fibre-tracheids, radial section. – 5: Walls of fibre-tracheids showing lack of pitting on tangential walls, tangential section. – Figs 1 & 2, magnification scale above Fig. 1 (divisions = 10 μm); Figs 3–5. scale above Fig. 3 (divisions = 10 μm).
Figs. 6–9. Wood sections of *Espadaea amoena* (SJRw 16611). – 6: Transection; axial parenchyma in diffuse and diffuse-in-aggregate distributions. – 7: Tangential section; multiseriate (mostly biseriate) rays and uniseriate rays about equal in frequency. – 8: Fibre-tracheids from radial section, showing bordered pits and splits in walls. – 9: Vasicentric tracheids (left) and ray cells showing vessel-ray pitting (right) from radial section. – Figs 6 & 7, magnification scale above Fig. 1; Figs. 8 & 9, scale above Fig. 3.
Figs. 10–15. Wood sections of *Henoonia myrtifolia* (SJRw 16160). – 10: Transection; vessels are grouped in diagonal aggregations. – 11: Tangential section; biseriate rays almost as frequent as uniseriate rays. – 12: Tangential section, showing intervacular pitting and a vasicentric tracheid (left). – 13: Bordered pits of fibre-tracheids in sectional view (left) and starch grain remnants in ray cells (right), from radial section. – 14: SEM photograph of crystal sand in ray cells, from radial section. – 15: Ray cells from radial section; sectional view of pits shows them to be bordered. – Figs. 10 & 11, scale above Fig. 1; Fig. 12, 13 & 15, scale above Fig. 3; Fig. 14, bracket = 10 μm.
10). Vessels mostly grouped; mean number of vessels per group, 2.84 (vasicentric tracheids excluded; narrow vessels thereby also probably unintentionally excluded). Vessels in diagonal aggregations (Fig. 10). Mean number of vessels per mm², 62. Mean vessel diameter, 44 µm. Mean vessel element length, 468 µm. Mean vessel wall thickness, 3.9 µm. Perforation plates simple. Lateral wall pitting consisting of circular pits 4–5 µm in diameter, both on intervacular and vessel-parenchyma contacts (Fig. 12). Short grooves interconnecting 2–4 pit apertures present on vessel walls. Most imperforate tracheary elements are fibre-tracheids with sparse pits, pit cavities 4–5 µm in diameter. Mean fibre-tracheid diameter at widest point, 16 µm. Mean fibre-tracheid length, 1051 µm. Mean fibre-tracheid wall thickness, 4.6 µm. Vasicentric tracheids common in vessel aggregations. Mean vasicentric tracheid length, 401 µm. Axial parenchyma diffuse, diffuse-in-aggregates, and in bands 1–2 cells wide (some bands marginal, perhaps initial). Axial parenchyma in strands of 3–4, mostly 4, cells. Rays multiseriate and uniseriate, the former slightly less frequent. Mean multiseriate ray height, 194 µm. Mean uniseriate ray height, 116 µm. Mean width of multiseriate rays, 2.32 cells. Procumbent cells predominant; upright cells present only at tips of multiseriate rays and in some uniseriate rays. Mean ray cell wall thickness, 3.5 µm. Pits common on all ray cell faces, many pits bordered. Crystal sand idioblasts present in rays. Starch remnants present in axial parenchyma and occasional in ray cells. Amorphous deposits occasional in ray cells. Wood nonstoried.

Systematic conclusions

Kuhlmann’s (1925) description of the genus *Duckeodendron* placed it in Solanaeae. After later assigning the genus to Boraginaceae (1930), Kuhlmann (1947) segregated it as Duckeodendraceae. Record (1933) compared wood of *Duckeodendron* to that of Apocynaceae and found support for affinity to that family. A major reason for Record’s opinion was his report of infrequent secretory canals in rays. By studying numerous sections from the same wood block studied by Record, I have been unable to find any secretory canals. Possibly the canals Record saw were, in fact, traumatic rather than characteristic of the species. Banded apotracheal
plus vasicentric parenchyma, characteristic of Duckeodendron, can indeed be found in Apocynaceae, but this combination can also be found in some Solanaceae, such as Notchocestrum (data original). Duckeodendron has homogeneous type I rays, a type not reported in Apocynaceae (Metcalfe & Chalk 1950). Homogeneous type I rays may be found in the solanaceous genera Acniscus p.p., Duboisia, Fabiana, and Grabowskya. Multiseriate rays are usually wider than two cells in Apocynaceae (Metcalfe & Chalk 1950); rays no wider than two cells, as in Duckeodendron, are common in such Solanaceae as Cyphomandra, Fabiana, Lycium, and Notchocestrum. I was able to confirm the presence of intraxylary phloem in Duckeodendron, using twigs from an herbarium specimen. This feature, mentioned for Duckeodendraceae by Hunziker (1979), is congruent with placement of Duckeodendron in or near Solanaceae. Study of Duckeodendron twigs reveals no laticifers or secretory canals. The nonglandular trichomes on stems of Duckeodendron are like those figured by Baehni (1943) for Henoonia. The sum of features now established for Duckeodendron is congruent with placement of Duckeodendraceae near Solanaceae; the distinctive habit and the drupoid fruit (much larger but otherwise similar to those of Goetzeaceae) permit one to recognise Duckeodendraceae.

The original assignment of Espadaea and Goetzea to Sapotaceae (Miers 1869) seems to have been more than adequately countered by the features Radlkofer (1888) reported in Goetzeaceae as indicative of affinity to Solanaceae: presence of crystal sand, presence of intraxylary phloem, and absence of laticifers. The leaf bundle features and trichomes of Goetzeaceae are like those of Duckeodendron and Solanaceae (Radlkofer 1888; Baehni 1943; observations on Duckeodendron original). However, both Kramer (1939) and Record (1939), studying wood anatomy of Henoonia, claimed its wood comparable to that of Sapotaceae and mentioned the genus Bumelia in particular. The distinctive diagonal aggregations of vessels as seen in transection and the presence of crystal sand in woods of both Bumelia and Henoonia may have been persuasive. In addition, both Sapotaceae and Goetzeaceae have vasicentric tracheids and multiseriate rays 2–3 cells wide. However, Goetzeaceae have fibre-tracheids (most Sapotaceae have libriform fibres – the genus Sarcosperma can be said to have tracheids); rays are composed of procumbent cells almost exclusively (upright cells to square cells are common in rays of Sapotaceae); and vessel-ray pits identical to vessel-ray pits (vessel-ray pits tend to be much larger than vessel-vessel pits in Sapotaceae). Fibre-tracheids are much more common in Solanaceae than in Sapotaceae, although this is certainly not conclusive where relationship of Duckeodendraceae and Goetzeaceae to Solanaceae are concerned.

If, however, one compares features of wood of Goetzeaceae to those of Solanaceae (in parentheses in the following – data original and from Metcalfe & Chalk 1950), one finds numerous resemblances: vessels in diagonal aggregations (Grabowskya, Lycium); vessels with grooves interconnecting pit apertures (Notchocestrum, Solanum); vessel-ray pits like those of vessel-vessel pits (Grabowskya, Lycium, Solanum); fibre-tracheids present (Grabowskya, Lycium, and most other genera); vasicentric tracheids present (Grabowskya, Lycium), apotracheal parenchyma diffuse plus diffuse-in-aggregates plus narrow bands (Duboisia, Fabiana, Grabowskya, Lycium, Nicotiana, Solanum); rays 1–3 cells wide, composed primarily of procumbent cells with upright cells only at tips of multiseriate rays and in uniseriate rays (Duboisia, Fabiana, Grabowskya, Lycium); crystal sand idioblasts present in rays (Brugmansia, Grabowskya, Nicotiana, Notchocestrum). The resemblances in wood anatomy between Goetzeaceae and Solanaceae thus seem much more compelling than those that one could cite as common to Goetzeaceae and Sapotaceae. In the above comparisons, the genera Grabowskya and Lycium receive frequent mention. The fruit type of Grabowskya (two woody two-seeded pyrenes embedded in fleshy exocarp) and that of Lycium species with indurate pericarp (one seed in each of the two locules) are close to the fruit type of Goetzeaceae: a one-seeded drupe formed from a unilocular ovary (data from Baehni 1943 and Hunziker 1979). The fruit type of
Duckeodendron is, in general terms, identical to the fruit type of Goetzeaceae, although the large size and the fibrous mesocarp of the fruit of Duckeodendron are different. Goetzeaceae may be worthy of recognition as a family, based on such features as the fruit type, the large cotyledons (smaller than the radicle in Duckeodendraceae, Nolanaceae, Sclerophyllacaceae and Solanaceae) and presence of spinules of pollen grains (absent from pollen grains of the four families just cited): data from Hunziker (1979).

Duckeodendron does share some features with genera of Goetzeaceae—notably the fruit type—but may not be closer to Goetzeaceae than are certain Solanaceae (Grabowskya, Lycium). The solanaceous affinities of Duckeodendraceae and Goetzeaceae seem amply demonstrated. One may choose to follow Hunziker’s treatment of Duckeodendraeae, Goetzeaceae, Nolanaceae, and Sclerophyllacaceae as satellite families near Solanaceae, as has Takhtajan (1987), or one may choose subfamilial status, as did Thorne (1976).

**Ecological conclusions**

Duckeodendron is from a tropical rain forest area; Espadaea occurs in a mesic thicket area (‘maniguas’) in Cuba, whereas Henoonia is native to dry areas: coastal scrub and savannah in Cuba (Kuhlmann 1925; Sauguet & Liogier 1957). The solanaceous affinities of Duckeodendraceae and Goetzeaceae seem amply demonstrated. One may choose to follow Hunziker’s treatment of Duckeodendraeae, Goetzeaceae, Nolanaceae, and Sclerophyllacaceae as satellite families near Solanaceae, as has Takhtajan (1987), or one may choose subfamilial status, as did Thorne (1976).

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**References**


