WOOD AND BARK ANATOMY OF BUCHENAVIA EICHL. (COMBRETACEAE)¹

by

Veronica Anyyallossy Alfonso² and Hans Georg Richter³

Summary

Wood and bark structure of Buchenavia (Combretaceae) was studied for infrageneric variation and taxonomic utility. Despite its wide neotropical distribution Buchenavia has a homogeneous wood anatomy, axial parenchyma distribution being the most variable feature. The presence or absence of septate fibres and presence and location of silica grains in ray and/or axial parenchyma might eventually allow recognition of individual species or species groups. Bark anatomy offers no diagnostic features for species differentiation. Wood and bark structure of Buchenavia (15 species studied) intergrades fully with that of neotropical Terminalia (5 species studied), thus corroborating results of studies on morphology (Exell & Stace 1963) and leaf anatomy (Stace, personal communication, 1989) which postulate a very close relationship between the two genera.

Key words: Wood anatomy, bark anatomy, taxonomy, Buchenavia, Terminalia, Combretaceae.

Introduction

The present study was undertaken to contribute to the general taxonomy of Buchenavia, particularly under the aspect of combined wood and bark anatomy. Increasingly, the latter is employed in differentiating taxa of similar or nearly identical wood structure, and has proven a useful complementary element in taxonomic studies (e.g. Alfonso 1983; Chattaway 1955a–c; Esau & Cheadle 1984; Karstedt & Parameswaran 1976; Richter 1981a, b, 1985, 1990; Trockenbrodt 1989; Trockenbrodt & Parameswaran 1986).

Wood and bark structure of 15 species (23 samples) of Buchenavia and 5 species (8 samples) of neotropical Terminalia were examined to see if they – either singly or in combination – provided useful features for distinguishing between Buchenavia and Terminalia. Buchenavia and Terminalia are known to have similar wood anatomy. Bark anatomy might provide a means of distinguishing between the two genera, and between Buchenavia species.

The genus Buchenavia Eichl. was established in 1866 (Exell & Stace 1963) by the German botanist A.W. Eichler (1839–1887) who was co-editor of Flora Brasiliensis. His original treatise of Buchenavia included eight species. More recently Buchenavia has been studied by Exell & Stace (1963, 1966) and Alwan Al-Mayah & Stace (1985).

In their 1963 revision Exell & Stace recognised 24 validly described species. In a forthcoming monograph of neotropical Combretaceae to be published in Flora Neotropica (Stace, in print) the number of valid species is reduced to 21.

Buchenavia is part of the tribe Terminaliaceae of the family Combretaceae and most closely related to Terminalia (Exell & Stace 1963). Stace (pers. comm., 1989) reports that there are no absolute vegetative differences between Buchenavia and Terminalia while differences in flower and fruit are always clear-cut.

¹ Dedicated to Professor Dr. Drs. mult. h. c. Walter Liese on the occasion of his 65th birthday (31 January 1991).
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Buchenavia is confined to but fairly widespread in tropical America from the Caribbean to southern Brazil, with the largest number of species concentrated in northern continental South America (Guyanas, Amazon valley, see map). The genus is represented by small shrubs to large trees from about three to fifty metres tall, the former growing mostly in frequently inundated lowland forests, the latter more in upland rain forests (Exell & Stace 1963).

As the wood of Buchenavia species is very similar to that of Terminalia in appearance and gross structure they cannot be easily separated and are traded jointly as one group of commercial timbers. They are used mainly in internal and external construction, as railway sleepers, cross arms, posts, and for furniture (Mainieri et al. 1983).

There are various descriptions of the wood anatomy of Buchenavia (e.g. Détienne & Jacquet 1983; Lindeman & Mennega 1963; Mainieri et al. 1983); however, only Van Vliet (1979) has discussed the wood structure of Buchenavia as part of a comparative study of the whole family.

The bark structure of some combretaceous taxa (Bucida, Combretum, Terminalia) was first described by Moeller (1882). More recently, taxonomic aspects were highlighted by Den Outer and Fundtler (1976) who discussed the bark structure of Strephonema pseudocola in relation to other taxa of Combretaceae of African origin (Buchenavia not included). Zahir (1959) described bark of Terminalia catappa and T. myriocarpa from Hawaii; Roth (1981) described bark of Buchenavia capitata, Terminalia guyanensis and T. amazonia, all from Venezuela.

**Material and Methods**

Tables 1 (Buchenavia) and 2 (Terminalia) list the species studied and gives information on origin, collectors’, herbarium and wood collection numbers. For most (9 of the 15) Buchenavia and (4 of the 5) Terminalia species only one sample was available for examination.

Microscopic sections 10–15 μm in thickness were prepared from all wood specimens following common laboratory procedures, stained with malachite green (transverse and tangential) and safranin (radial), and subsequently mounted permanently in a synthetic medium (‘Permoun’). Bark material was sectioned after penetration with polyethylene glycol (DP 1500); individual sections of 10 to 25 μm thickness, protected by scotch tape or a hardened layer of commercial nail polish. The 'scotch tape' method follows the procedures outlined by Rupp (1964), modified by Wilhelm (1975) and Kruse (1977). The staining of the sections is done while still adhering to the tape. In the other case, microtome sections from the PG-impregnated block are glued to a cover glass by means of a thin layer of colourless nail polish. Further processing (staining, dehydration, mounting) is done with the sections firmly adhering to the cover glass. The sections were double-stained with malachite green and hematoxylin or, in few cases, with astra blue and chrysoidine/acidine red. Macerations were prepared with Jeffrey’s solution (equal parts of 10% acetic solution of nitric and chromic acid) and stained with safranin (wood) or double-stained with chrysoidine/acidine red and astra blue (bark).

Quantitative data are based on 10 (vessel pit diameter), 25 (diameter and length of vessel elements, fibre diameter wood/bark), 30
The terms used in wood and bark descriptions adhere to the character lists proposed by IAWA (1989) and Trockenbrodt (1990), respectively.

### Wood description

**General:** Heartwood light brown to yellowish, not well differentiated from the lighter coloured sapwood; grain straight to slightly wavy; texture fine to medium; surface non-fluorescent; without specific odour or taste. Growth increments more or less distinct.

**Anatomy:** Vessels arranged in a diffuse-porous pattern, approaching semi-ring-porous in *B. ochropurumna*; solitary and in radial multi-

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<tr>
<td><em>B. amazonia</em> Alwan &amp; Stace*</td>
<td>Guyana</td>
<td>Sébatier &amp; Prévost 2179</td>
<td>Uw 32810</td>
</tr>
<tr>
<td><em>B. capitata</em> (Vahl) Eichl.</td>
<td>Brazil, PA</td>
<td>—</td>
<td>MGw 4154</td>
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<tr>
<td>idem</td>
<td>Brazil, AM</td>
<td>Kubitzki 75-87</td>
<td>RBHW 16699</td>
</tr>
<tr>
<td>idem</td>
<td>Surinam, Rio Pará</td>
<td>B. B. S. 91 (sterile)</td>
<td>Uw 686</td>
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<tr>
<td><em>B. congesta</em> Ducke</td>
<td>Brazil, AM</td>
<td>W. Rodrigues, INPA 15008</td>
<td>INPAw X-2581</td>
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<td><em>B. grandis</em> Ducke</td>
<td>Brazil, AM</td>
<td>—, Museu Goeldi 55715</td>
<td>MGw 2938</td>
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<tr>
<td>idem (received as <em>B. huberi</em>)</td>
<td>Brazil, AM</td>
<td>Loureiro, Coelho &amp; Mello</td>
<td>INPAw X-2657</td>
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<tr>
<td>idem</td>
<td>Brazil, AM</td>
<td>Alfonso 5267</td>
<td>Uw 7754</td>
</tr>
<tr>
<td><em>B. kleinii</em> Exell ?</td>
<td>Brazil, PR</td>
<td>Lindeman &amp; De Haas 2350</td>
<td>Uw 13694</td>
</tr>
<tr>
<td>idem</td>
<td>Brazil, AM</td>
<td>Krukoff 6472</td>
<td>INPAw X-6800</td>
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<td><em>B. macrophylla</em> Eichl.</td>
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<td>Lima &amp; Chagas, INPA 13306</td>
<td>INPAw X-1612</td>
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<td>W. Rodrigues &amp; Coelho 6770, INPA 15234</td>
<td>INPAw X-3091</td>
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<tr>
<td>idem</td>
<td>Brazil, AM</td>
<td>Coelho &amp; Lima 380, INPA 81230</td>
<td>INPAw X-6800</td>
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<tr>
<td><em>B. oxycarpa</em> (Mart.) Eichl.</td>
<td>Brazil, AM</td>
<td>W. Rodrigues 2254, INPA 8665</td>
<td>INPAw X-891</td>
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<tr>
<td>idem</td>
<td>Brazil, PA</td>
<td>Kubitzi 82-47</td>
<td>RBHW 19170</td>
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<td><em>B. pallidovirens</em> Cuatrec.</td>
<td>Columbia</td>
<td>Rooden et al. 545</td>
<td>Uw 25612</td>
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<td><em>B. parvifolia</em> Ducke</td>
<td>Brazil, AM</td>
<td>Loureiro, Coelho &amp; Mello, INPA 14449</td>
<td>INPAw X-2626</td>
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<td>idem</td>
<td>Brazil, AM</td>
<td>W. Rodrigues 5466, INPA 14135</td>
<td>INPAw X-2017</td>
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<tr>
<td><em>B. rabeilloana</em> Mattos</td>
<td>Brazil, SP</td>
<td>Kuhlmann s.n., SP 157742</td>
<td>SPw 43</td>
</tr>
<tr>
<td><em>B. sericocarpa</em> Ducke*</td>
<td>Brazil, AM</td>
<td>Krukoff 6916 (type)</td>
<td>Uw 8044</td>
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<tr>
<td><em>B. suaveolens</em> Eichl.</td>
<td>Brazil, AM</td>
<td>Kubitzi 75-87a</td>
<td>RBHW 16683</td>
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<tr>
<td><em>B. tomentosa</em> Eichl.</td>
<td>Brazil, MT</td>
<td>—, INPA 15839</td>
<td>INPAw X-3278</td>
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<tr>
<td><em>B. viridiflora</em> Ducke</td>
<td>Guyana</td>
<td>BAFOG 1313</td>
<td>Uw 5801</td>
</tr>
<tr>
<td>idem</td>
<td>Brazil, AM</td>
<td>W. Rodrigues &amp; Loureiro 65</td>
<td>INPAw X-3571</td>
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* Specimens without bark.

(rays/mm, ray height in mm and number of cells) and 50 (number of vessels/mm) and fibre length wood/bark) individual counts, respectively. In all cases but vessel pit diameter the statistical requirements of minimum number of measurements \(N = t^2 \times s^2 / \bar{E}^2\); where \(t = \) student, \(s = \) standard deviation, \(\bar{E}^2 = (0.1 \times X)^2\), according to Freese (1967) were fulfilled. The numerical values given in the description are the ranges of species means accompanied by overall minimum and maximum values between brackets. Specific collection numbers are cited for species with multiple samples to indicate that this is the only sample(s) that showed this particular feature.

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Table 1. Specimens examined of the genus *Buchenavia* Eichl.

- *B. amazonia* Alwan & Stace*
- *B. capitata* (Vahl) Eichl. idem
- *B. congesta* Ducke
- *B. grandis* Ducke idem (received as *B. huberi*)
- *B. kleinii* Exell ?
- *B. macrophylla* Eichl.
- *B. ochropurumna* Eichl. idem
- *B. oxycarpa* (Mart.) Eichl.
- *B. pallidovirens* Cuatrec.
- *B. parvifolia* Ducke idem
- *B. rabeilloana* Mattos
- *B. sericocarpa* Ducke*
- *B. suaveolens* Eichl.
- *B. tomentosa* Eichl.
- *B. viridiflora* Ducke idem

- Specimens without bark.
Table 2. Specimens examined of the genus *Terminalia* L.

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<tr>
<td><em>T. amazonia</em> (Gmel.) Exell</td>
<td>Venezuela</td>
<td>—, Museu Goeldi 31909</td>
<td>MGw 779</td>
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<tr>
<td>idem*</td>
<td>Brazil, PA</td>
<td>N.T. Silva 3412</td>
<td>BCTw 13254</td>
</tr>
<tr>
<td>idem*</td>
<td>Guatemala</td>
<td>Inv.For.El Petn 9512</td>
<td>RBHw 12861</td>
</tr>
<tr>
<td>idem*</td>
<td>Surinam</td>
<td>Stahel 93a</td>
<td>RBHw 18688</td>
</tr>
<tr>
<td><em>T. argentea</em> Mart. &amp; Eichl.</td>
<td>Brazil, MG</td>
<td>Heringer &amp; Filho 4032, RB 93481</td>
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<td><em>T. brasiliensis</em> Eichl.</td>
<td>Brazil, PA</td>
<td>—</td>
<td>MGw 396</td>
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<tr>
<td><em>T. guianensis</em> Aubl.</td>
<td>Brazil, PA</td>
<td>—, Museu Goeldi 90567</td>
<td>MGw 3233</td>
</tr>
<tr>
<td><em>T. cf. tanibouca</em> Smith</td>
<td>Brazil, MA</td>
<td>—</td>
<td>MGw 2279</td>
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* Specimens without bark.

Examples of 2, rarely up to 5, exceptionally up to 10 in *B. tomentosa*; tangential diameter (40–) 60–220(–280) μm, frequency variable, (1–) 4–22(–33) vessels/mm²; vessel element length (155–)310–630(–800) μm; perforation plates simple; intervessel pits 6–10(–11) μm in diameter (axial dimension), alternate, circular to polygonal in outline, ventured; vessel-ray pits similar to intervessel pits in size and shape, mostly circular, simple or with much reduced borders. Helical thickenings throughout body of narrow vessel elements observed only in *B. grandis* (Uw 7754, Fig. 14) and *B. suaveolens*; thin-walled tyloses and yellowish to brown gum deposits in vessels of *B. oxyarpa*.

Fibres thin to very thick-walled, the latter only at growth increment borders (Figs. 2, 4); length (570–)920–1630(–2180) μm, diameter (10–)15–19(–32) μm; pits simple to minutely bordered, few fibres with distinctly bordered pits in *B. amazonia* (Fig. 11), *B. capitata* (RBHw 16699), *B. congesta*, *B. grandis* (MGw 2938), *B. parvifolia*, *B. suaveolens*; septa present in some fibres of *B. capitata* (Uw 686), *B. oxyarpa* (Fig. 12) and *B. seriocarpa*.

Parenchyma predominantly paratracheal aliform to confluent with a large variation in the degree of confluence: lozenge-aliform in *B. parvifolia* (INPAw X-2017, Fig. 1) and *B. viridiflora*; confluent well-developed in *B. amazonia*, *B. capitata*, *B. congesta*, *B. grandis* (Fig. 3), *B. kleinii*, *B. parvifolia* (INPAw X-2626), *B. rabelloana*, *B. seriocarpa*, *B. suaveolens*, *B. tomentosa*; with marked confluence grading into conspicuously banded parenchyma in *B. macrophylla*, *B. ochropurpurna*, *B. oxyarpa* (Fig. 6) and *B. pallidovirens*; marginal or seemingly marginal parenchyma present in *B. amazonia*, *B. capitata*, *B. grandis* (INPAw X-2657, Uw 7754), *B. ochropurpurna*, *B. pallidovirens*, *B. parvifolia* (INPAw X-2626), *B. rabelloana* (Fig. 2), *B. seriocarpa*, *B. suaveolens*, *B. tomentosa* and *B. viridiflora*, poorly developed in *B. capitata* (MGw 4154) and *B. congesta*; diffuse parenchyma generally present in small quantities, absent in *B. capitata* (MGw 4154), *B. grandis* (INPAw X-2657), *B. ochropurpurna* (INPAw X-3091), *B. oxyarpa* and *B. pallidovirens*.

Rays exclusively uniseriate (including locally biseriate rays) in most species (Fig. 9) with a small portion (7–23%) of biseriate rays in *B. congesta* and *B. macrophylla*; predominantly biseriate with few triseriates (≅ 2%) in *B. tomentosa* (Fig. 10); very variable in height, (100–)180–350(–710) μm; all cells procumbent or body cells procumbent with one marginal row of square/upright cells; usually with reddish-brown gum deposits.

Inorganic inclusions: prismatic crystals present in the majority of *Buchenavia* species; occasionally also styloids (Fig. 18) in *B. amazonia*, *B. congesta*, *B. kleinii*, *B. ochropurpurna* (INPAw X-3091), *B. oxycar-
pa (INPAw X-891), B. pallidovirens, B. rabeloana, often surrounded by a distinct sheath; predominantly in non-chambered ray cells (one crystal per cell, Fig. 19); exclusively associated with axial parenchyma (chambered cells) in B. capitata (MGw 4154, Fig. 17) and B. kleini; in both radial and axial parenchyma in B. amazonia, B. congesta, B. macrophylla, B. ochroprumna (INPAw X-6800), B. rabeloana, B. tomentosa; no crystals observed in B. capitata (RBHw 16699), B. oxyacarpa (RBHw 19170), B. seriocarpa, B. viridiflora.

Globular silica grains in axial parenchyma of B. macrophylla, B. ochroprumna (INPAw X-6800, Fig. 15), B. seriocarpa; in both rays (Fig. 16) and axial parenchyma of B. capitata (RBHw 16699).

Traumatic canals observed in B. capitata, B. rabeloana (Fig. 13) and B. tomentosa.

Growth increments: When present delimited by tangential zones of thick-walled, radially flattened fibres in B. kleini, B. parvijolia (INPAw X-2017; Fig. 1, see arrow); also in combination with marginal parenchyma as in B. capitata (Fig. 4), B. rabeloana (Fig. 2), B. suaveolens, B. viridiflora; in some instances associated with a marked difference of vessel diameter between early and latewood, e.g. in B. ochroprumna (Fig. 5).

Bark description

General: Dark brown to reddish brown externally, locally with grey to whitish areas; surface smooth to fissured in a reticulate pattern; fissures usually narrow, longitudinal and transverse, often cutting fairly deep into the rhytidome layers; of varying thickness (0.2–1 cm) in function of bole diameter/age.

Anatomy: Bark regularly stratified from cambium towards periphery; strata formed by multisierate tangential bands of phloem parenchyma and conducting cells (sieve tubes and companion cells) alternating with rows of sclerenchymatic cells (Figs. 20, 21, 23; see also Fig. 24 for same feature in Terminalia brasiliensis).

Phloem parenchyma arranged in 2- to 4-seriate tangential bands in all species; cells with large and circular simple pits.

Sieve tubes (and companion cells) solitary or in small groups of 2 or 3, with little variation throughout the genus, interspersed with parenchyma cell strata; cells irregular in outline (Fig. 26), about 30–50 μm in diameter and 500–600 μm in length; sieve plates horizontal to inclined, simple and compound in one and the same or different elements (Fig. 28), with 3–6 sieve areas, each with sieve pores of 2–3 μm in diameter; lateral sieve areas present.

Phloem rays similar to xylem rays in composition and dimensions (Fig. 22); with considerable numbers of intercellular spaces in specimens of B. capitata, B. parvijolia (Fig. 33), B. rabeloana and B. viridiflora; dilated towards the periphery due to tangential cell division and/or inflation (Figs. 20, 21); dilatation in some instances well developed, resulting in considerable distortion of the tissue arrangement in the outer bark; when in contact with 'sclerified cells' (see below) some ray cells become sclerified and develop branches ('branched ray sclereids', Figs. 39, 40) gradually growing into intercellular spaces as observed in B. congesta and B. rabeloana (see also Figs. 41, 42 for same feature in Terminalia).

Phloem fibres (Fig. 29, maceration) arranged in regular 1- to 3-seriate continuous tangential bands in B. capitata (Fig. 20), B. congesta, B. grandis (MGw 2938), B. ochroprumna, B. oxyacarpa, B. suaveolens; in small, tangentially arranged groups of less regular and frequent occurrence in B. grandis (INPAw X-2657), B. macrophylla, B. pallidovirens, B. parvijolia, B. rabeloana, B. tomentosa, B. viridiflora; fibre length varying from (440–)730–1910(–2340) μm; diameter variable from (12–)17–25(–35) μm; fibres frequently gelatinous in all species (Fig. 27, short arrow).

'Sclerified cells': cells of considerable dimensions in transverse section (radially larger than tangentially) with thick, polylamellate (Fig. 32), generally gelatinous walls (Fig. 27, long arrow); axially elongated due to pronounced apical growth, varying from very long and thin (i.e. fibre-like, Fig. 30) to wide-bodied and short (Fig. 31); length (330–)540–1070(–1320) μm and (30–)40–

(text continued on page 135)
Legends of Figures 1-42:

Figs. 1-6. Buchenavia, wood, transverse sections, × 44. – 1: B. parvifolia, lozenge-aliform parenchyma; growth ring boundaries indicated by thicker-walled and radially flattened fibres (arrow). – 2: B. rabelloana, aliform with some confluent and marginal parenchyma; growth ring boundaries marked by thick-walled, radially flattened fibres and marginal parenchyma. – 3: B. grandis, aliform, confluent and marginal parenchyma. – 4: B. capitata, aliform, confluent and marginal parenchyma; growth ring boundaries marked by thick-walled fibres and marginal parenchyma. – 5: B. ochroprumna, aliform parenchyma with pronounced confluence; growth ring boundaries associated with change in vessel diameter. – 6: B. oxycarpa, parenchyma with pronounced confluence forming bands.

Figs. 7 & 8. Terminalia guianensis, wood. – 7: Transverse section, aliform, confluent and marginal parenchyma, traumatic canals (arrows), × 44. – 8: Tangential section, uniseriate rays with crystals, × 110. — Figs. 9-11. Buchenavia, wood, tangential section. – 9: B. grandis, uniseriate rays, × 110. – 10: B. tomentosa, predominantly biseriate, also triseriate rays, × 44. – 11: B. amazonia, fibres with large bordered pits, × 440. — Fig. 12: B. oxycarpa, wood, radial section, septate fibres (arrows), × 440. — Fig. 13: B. rabelloana, wood, transverse section, traumatic canals, × 44.


Figs. 20–23. Buchenavia, bark. – 20: B. capitata, transverse section, stratified, phloem parenchyma alternating with phloem fibres (arrow); dilated rays (D); periderm (P), × 60. – 21: B. grandis, transverse section, stratified, phloem parenchyma alternating with 'sclerified cells' (arrows); dilated ray (D); periderms (P), × 44. – 22: B. ochroprumna, tangential section, uniseriate rays, druses in chambered cells, × 110. – 23: B. pallidovirens, transverse section, earlier formed phloem with predominantly phloem fibres (white radial line), and last formed phloem with only 'sclerified cells' (black radial line), × 44. — Fig. 24. Terminalia brasiliensis, bark, transverse section, stratified, phloem parenchyma alternating with 'sclerified cells' (arrows); periderm (P), × 44.

Figs. 25–34. Buchenavia, bark. – 25: B. capitata, transverse section, druses in seriate strands, large druse (centre), polarised light, × 110. – 26: B. rabelloana, transverse section, sieve element(s), × 440. – 27: B. ochroprumna, transverse section, gelatinous fibres (short arrow) and 'sclerified cells' (long arrow), × 220. – 28: B. macrophylla, macerated, sieve element with sieve plates – compound at one end, simple at the other, × 220. – 29: B. congesta, macerated, phloem fibre, × 44. – 30: Idem, macerated, long and thin 'sclerified cell', × 44. – 31: B. macrophylla, macerated, short and wide-bodied 'sclerified cells', × 44. – 32: Idem, transverse section, 'sclerified cells' with thick, polylamellate walls, × 440. – 33: B. parvifolia, radial section, ray with intercellular spaces, × 440. – 34: Idem, phellem cells with large simple pits, × 375.

Figs. 35–40. Buchenavia, bark. – 35: B. capitata, transverse section, periderm with thin-walled phelloderm cells (ph), and stratified phellem (pe) with organic contents in some cells (arrow), × 110. – 36: B. suaveolens, phellem cells with U-shaped wall thickenings (arrows), × 110. – 37: B. ochroprumna, phellem cells with evenly thickened cell walls (long arrow) alternating with one row of very thin-walled cells (short arrow), × 110. – 38: B. grandis, lenticel, × 110. – 39 & 40: B. rabelloana, macerated, branched ray sclereids, × 220. — Figs. 41 & 42. Terminalia, bark, branched ray sclereids (arrows), × 220. – 41: T. amazonia, macerated. – 42: T. brasiliensis, tangential section.
90(–140) μm, respectively; arranged in regular, 1–3-seriate tangential bands and accompanied by few phloem fibres in *B. capitata* (RBHw 16699), *B. grandis* (INPAw X-2657), *B. macrophylla*, *B. pallidovirens* (Fig. 23), *B. parvifolia*, *B. rabelloana*, *B. suaveolens*, *B. tomentosa*, *B. viridiflora*; in small groups and of more sporadic occurrence in *B. congesta*, *B. grandis*, *B. ochrophyllum*, *B. oxycarpa* (INPAw X-891).

Inorganic inclusions: Druses located in chambered parenchyma cells (Fig. 22) which are arranged in short tangential lines (cross section, Fig. 25), present in all species except *B. rabelloana*; druse-bearing parenchyma strands decreasing in frequency with distance from cambium (in *B. rabelloana* chambered parenchyma cells were also observed but without druses); in the outer, dilated portion of the phloem very large druses in isolated, inflated parenchyma cells occur in most species (Fig. 25), absent in *B. congesta*, *B. grandis* (MGw 2938), *B. parvifolia*, *B. viridiflora*; other crystal types and silica not observed.

Organic, presumably phenolic contents present in parenchymatous tissue of all species (Fig. 35).

Periderm very consistent in arrangement and composition throughout the genus. Radial depth varies from 110–830 μm; the number of periderms per radial distance was impossible to quantify because of interspersed collapsed phloem tissue obscuring the boundaries.

Phellem stratified, composed of one to several rows of rectangular cells with either all walls evenly thickened (Fig. 37) or U-shaped thickenings (Fig. 36); transverse walls with very large simple pits in some species such as *B. capitata* (MGw 4154), *B. grandis*, *B. ochrophyllum*, *B. parvifolia* (Fig. 34), *B. tomentosa*, *B. viridiflora*; alternating with usually one, occasionally several rows of very thin-walled cells (Fig. 37). Phellem poorly developed, composed of few rows (1–6) of thin-walled cells (Fig. 35). Lenticels observed only in *B. capitata*, *B. grandis* (INPAw X-2657, Fig. 38) and *B. parvifolia*. Rhytidome persistent in all species, encompassing 1–2 periderms and including parts of the collapsed phloem.

**Terminalia** (Figs. 7, 8, 24, 41, 42)

The secondary xylem and phloem of neotropical *Terminalia* (5 species, 8 samples) examined is essentially identical to that of *Buchenavia*. Also, the features observed agree very well with those reported by Van Vliet (1979) and thus do not warrant a separate description. Differences are few and largely restricted to quantitative features such as vessel dimensions. Slight differences were also observed in parenchyma distribution, frequency, size and location of crystals, presence of 'sclerified cells' in bark, etc.; whenever appropriate, these differences will be considered in the following discussion.

**Discussion**

The wood anatomy of the species of *Buchenavia* and neotropical *Terminalia* examined in this study is remarkably homogeneous. However, there are variations in type and frequency of axial parenchyma, location of crystals, presence/absence of silica and septate fibres, and growth increment borders. These features may prove to be useful for identifying species or species groups.

Détienne & Jacquet (1983) describe considerable variation of axial parenchyma for neotropical *Terminalia* and use it in their species identification key. Axial parenchyma arrangement is also useful identifying species or species groups in *Buchenavia* (Table 3). Only *B. oxycarpa* lacks both marginal and diffuse parenchyma; *B. macrophylla*, *B. ochrophyllum*, *B. oxycarpa*, *B. pallidovirens* show confluent to banded, only *B. viridiflora* a typically aliform-lozenge parenchyma. Considerable within-species variation in just parenchyma is observed in specimens of *B. parvifolia* and *Terminalia amazonia* (Table 4). Thus, although some *Buchenavia* species appear to have characteristic parenchyma distribution, the same individual pattern(s) also occur(s) in *Terminalia*, a fact which renders this feature somewhat ambiguous diagnostically for species identification within and attribution to these two taxa.

Détienne and Jacquet (1983) found localisation and type of crystals to be of diagnostic significance in *Terminalia*. Judging from the present study only the occurrence of pris...
Table 3. Variation of selected qualitative and quantitative wood characters in *Buchenavia*.

<table>
<thead>
<tr>
<th>Species</th>
<th>Coll. nr.</th>
<th>Parenchyma distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>aliform lozenge</td>
</tr>
<tr>
<td><em>B. amazonia</em></td>
<td>Uw 32810</td>
<td></td>
</tr>
<tr>
<td><em>B. capitata</em></td>
<td>MGw 4154</td>
<td></td>
</tr>
<tr>
<td></td>
<td>RBHw 16699</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Uw 686</td>
<td></td>
</tr>
<tr>
<td><em>B. congesta</em></td>
<td>INPAw X-2381</td>
<td></td>
</tr>
<tr>
<td><em>B. grandis</em></td>
<td>MGw 2938</td>
<td></td>
</tr>
<tr>
<td></td>
<td>INPAw X-2657</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Uw 7754</td>
<td></td>
</tr>
<tr>
<td><em>B. kleinii?</em></td>
<td>Uw 13694</td>
<td></td>
</tr>
<tr>
<td><em>B. macrophylla</em></td>
<td>INPAw X-1612</td>
<td></td>
</tr>
<tr>
<td><em>B. ochropumma</em></td>
<td>INPAw X-3091</td>
<td></td>
</tr>
<tr>
<td></td>
<td>INPAw X-6800</td>
<td></td>
</tr>
<tr>
<td><em>B. oxycarpa</em></td>
<td>INPAw X-891</td>
<td></td>
</tr>
<tr>
<td></td>
<td>RBHw 19170</td>
<td></td>
</tr>
<tr>
<td><em>B. pallidovirens</em></td>
<td>Uw 25612</td>
<td></td>
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<td><em>B. parvifolia</em></td>
<td>INPAw X-2626</td>
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<tr>
<td></td>
<td>INPAw X-2017</td>
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</tr>
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<td><em>B. rabelloana</em></td>
<td>SPw 43</td>
<td></td>
</tr>
<tr>
<td><em>B. sericocarpa</em></td>
<td>Uw 8044</td>
<td></td>
</tr>
<tr>
<td><em>B. suaveolens</em></td>
<td>RBHw 16683</td>
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</tr>
<tr>
<td><em>B. tomentosa</em></td>
<td>INPAw X-3278</td>
<td></td>
</tr>
<tr>
<td><em>B. viridiflora</em></td>
<td>Uw 5801</td>
<td></td>
</tr>
<tr>
<td></td>
<td>INPAw X-3571</td>
<td></td>
</tr>
</tbody>
</table>

+ = present; - = absent; ( ) = character poorly developed; r = ray; p = axial parenchyma; cp = chambered strands.
matic crystals in chambered parenchyma strands in *B. capitata* and *B. kleinii* appear to constitute a diagnostic feature. The remaining data on crystals (presence/absence, type, location) assembled here for *Buchenavia* (Table 3) and *Terminalia* (Table 4) are ambiguous in that

a) crystals are present in all but one (*B. seriocarpa*, only one sample) of the species examined. This observation agrees with Van Vliet’s (1979) description of the same species, cited there as *B. acuminata* but since reduced to synonymy according to Stace (pers. comm., 1989);

b) in several species (*B. capitata, B. oxycarpa, B. viridiflora*) crystals are present in some, absent in other specimens;

c) crystal size is a continuum from isodiametric to intermediate (prismatic) and elongate (styloids) within and between specimens/species.

Clearly, the small sample size of only one specimen for most species and considerable within species variation does not allow definite conclusions about the diagnostic significance of crystalline inclusions in *Buchenavia*.

Four *Buchenavia* species (*B. capitata* except *Uw* 686, *B. kleinii, B. oxycarpa, B. suaveolens*) have average diameters of ≤ 100 µm (see Table 3). Van Vliet (1979) and Détienné and Jacquet (1983) have found similar values for the latter two species. However, as vessel diameter is also a function of sample diameter (age) no taxonomic significance is attributed to this quantitative character. The same holds true for ray width. Only the predominantly biseriate rays in *B. tomentosa* might warrant a clear separation from the remaining species with predominantly uniseriate rays.

Silica was observed in some *Buchenavia* species, not in *Terminalia*. The absence of

*) The material of *B. kleinii* examined by Van Vliet (Lindeman & De Haas 2355 = Uw 13699) originates, according to the collectors, from the same group of trees as the material used here (Lindeman & De Haas 2350 = Uw 13694). As the vouchers of both specimens are sterile, doubts have since been raised as to the correct generic attribution, and its relegation to *Terminalia* was proposed informally (Lindeman, pers. comm.). Despite this uncertainty it was decided to maintain the original designation (*B. kleinii*) for the benefit of both consistency and comparison with Van Vliet’s account.

### Table 4. Variation of selected qualitative wood characters in *Terminalia* L.

<table>
<thead>
<tr>
<th>Species</th>
<th>Parenchyma distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>aliform lozenge</td>
</tr>
<tr>
<td><em>T. amazonia</em></td>
<td></td>
</tr>
<tr>
<td>MGw 779</td>
<td>-</td>
</tr>
<tr>
<td>BCTw 13254</td>
<td>+</td>
</tr>
<tr>
<td>RBHw 12861</td>
<td>+</td>
</tr>
<tr>
<td>RBHw 18688</td>
<td>+</td>
</tr>
<tr>
<td><em>T. argentea</em></td>
<td></td>
</tr>
<tr>
<td>RBHw 3540</td>
<td>-</td>
</tr>
<tr>
<td><em>T. brasiliensis</em></td>
<td></td>
</tr>
<tr>
<td>MGw 396</td>
<td>-</td>
</tr>
<tr>
<td><em>T. guianensis</em></td>
<td></td>
</tr>
<tr>
<td>MGw 3233</td>
<td>-</td>
</tr>
<tr>
<td><em>T. tanibouca</em></td>
<td></td>
</tr>
<tr>
<td>MGw 2279</td>
<td>-</td>
</tr>
</tbody>
</table>

+ = present; - = absent; ( ) = character poorly developed; r = ray; p = axial parenchyma; cp = chambered parenchyma strands.
silica in *Terminalia* was previously noted by Van Vliet (1979, 43 species), Ter Welle (1976) and Détienne and Jacquet (1983). Sili-

caca was observed in one sample of *B. capitata* (RBHw 16699) and *B. ochroprunna* (INPAw X-6800), in *B. macrophylla*, and *B. serio-
carpa* (Table 3). Van Vliet (1979) observed silica in *B. seriocarpa*, Ter Welle (1976) and Détienne and Jacquet (1983) report silica ab-
sent in *Buchenavia*. Some authors consider silica to be an important and consistent diag-
nostic character at the various taxonomic lev-

els (Richter 1981a, 1985; Ter Welle 1976; Ter Welle & Détienne 1986). The inconsist-
tency of its occurrence in *Buchenavia* species (vide *B. capitata*, *B. ochroprunna*) poses

serious difficulties of interpretation: In *B. capitata* the voucheredi specimen RBHw 16699 is the only one with silica while, ac-

cording to Benoist (1931, cited by Van Vliet 1979), Détienne and Jacquet (1983) and Ter Welle (pers. comm., cited by Van Vliet 1979), silica is absent in this particular species. Con-

sequently, these observations raise some doubt as to the correct identification of the specimen labeled *B. capitata* and, for that

matter, *B. ochroprunna*.

Septate fibres were observed in one sam-
ples of *B. capitata* (Uw 686), in *B. oxycarpa* and *B. seriocarpa*, reported for the latter also by Van Vliet (1979). Détienne and Jacquet (1983) report non-septate fibres in *B. capitata* and *B. oxycarpa*. Yet, the within species in-

consistency (e.g. *B. capitata*) does not at present make septate fibres a viable taxon-

omic character. Within *Terminalia amazonia* (Table 4) septate fibres are of constant occu-

rence.

Helical thickenings were found by Van Vliet (1979) in vessel elements and axial pa-

renchyma of *B. grandis* (syn. *B. huberi*); an additional species (*B. suaveolens*, narrow vessel elements only) is reported here (Table 3). Distinctly bordered pits in fibre walls, not previ-

ously described for *Buchenavia*, were observed occasionally in *B. amazonia, B. capitata* (RBHw 16699), *B. congesta, B. par-
vifolia* and *B. suaveolens*.

The bark anatomy of the taxa studied is as homogeneus as the wood anatomy. Separat-
ing *Buchenavia* and *Terminalia* by bark struc-
ture appears impossible. The most remark-
able feature of both *Buchenavia* and *Ter-

mali* bark is the regular occurrence (and fre-

quency) of the so-called 'sclerified cells' (see bark description). This neutral term was cho-

sen provisionally because of the unknown ontogeny of these cells. Though often but by

no means always resembling fibres in general appearance (shape, dimensions), these ele-

ments differ from normal phloem fibres by the sclerified, i.e. polylamellate, pitted and

very thick walls, and the ovoid transverse section (larger diameter radially). This cell

type, already observed by several authors in the bark of various taxa, is known under an

array of different denominations: 'fibrous sclerotic cells' (Shimakura 1936), 'fibre-

sclereids' (Holdheide 1951; Santos 1960), 'fibres' (Chattaway 1955c, 1959), 'sclereids'

(Srivastava 1963), 'sclerotic phloem fibres' (Parameswaran 1980). Only a thorough on-

togenetic study will reveal whether they are of parenchymatous origin or derived directly

from fusiform cambial initials, and will give rise to an appropriate terminology. Perhaps

even both forms develop in different taxa.

'Sclerified cells' are present in all *Buche-

navia* and *Terminalia* species studied with varying frequency between and within indi-

vidual species. They may already occur at the age of two years (Holdheide 1951), and their propor-

tion increases with age (Chattaway 1955c). In *B. pallidovirens*, the scleren-

chymatic tissue of the younger phloem con-

sists predominantly of phloem fibres, while in the older phloem strata only 'sclerified

cells' occur. Hence, frequency variation can-

not be used as a diagnostic feature for species differen-
tiation, even when the exact age of the material studied is known.

Phloem fibres are arranged in continuous tangential bands in some species, and in tan-
gentially arranged groups in others. Richter (1981a) observed similar differences in sclereid arrangement in *Cinnamomum* (Laura-
ceae) and used this as one of several argu-
ments for separating different species groups in this genus. However, the little material of *Buchenavia* studied here makes attaching
diagnostic value to this character premature.

Many of the observations made by Roth (1969, 1981) on the bark structure of one
species of *Buchenavia* and two species of *Terminalia* cannot be corroborated by the present study: Not only *Terminalia* (Roth 1969) but also *Buchenavia* bark features small druses in crystalliferous parenchyma strands in the non-collapsed phloem, and large druses in inflated cells in the collapsed phloem; in both genera wall thickenings of phellem cells are of the same type (i.e. ‘U’-shaped) rather than ‘U’-shaped in *Terminalia* and inverted in *Buchenavia* as reported by Roth (1969); ray dilatation and ray sclereids were observed in *Terminalia* and *Buchenavia* bark while Roth (1969, 1981) lists these features as absent in both taxa.

Moeller (1882) described axial parenchyma cells with large and simple pits for *Terminalia*; the same type of wall pitting can be observed in parenchymatous phellem cells of *Buchenavia*.

Branched ray sclereids observed in *B. congesta*, *B. rabelloana*, *T. amazonia* and *T. brasiliensis* constitute an interesting phenomenon. The rather bizarre looking sclereids differentiate from ray cells in direct contact with the axially oriented 'sclerified cells'. They differ from regular ray sclereids by forming slender and pointed branches that grow into and gradually fill intercellular spaces. The sclerification of ray tissue elements in such contact areas has been reported by many authors (Moeller 1882; Holdheide 1951; Chattaway 1955c, 1959; Zahur 1959; Parameswaran & Liese 1970; Richter 1981, 1990; Trockenbrodt 1989). Branched sclereids differentiating apparently from axial parenchyma are described and illustrated in Esau (1969). However, a reference to branched ray sclereids has not been found in the literature consulted.

Finally, there is little variation within and between *Buchenavia* species or between *Buchenavia* and *Terminalia* in stratification of non-collapsed and collapsed phloem, type of sieve element and sieve plate, ray dilatation, structure of periderm and rhytidome.

**Conclusions**

Wood and bark anatomy alone do not allow distinguishing *Buchenavia* from neotropical *Terminalia*. The similarity in wood and bark structure of these two genera is not surprising as Exell & Stace (1963, 1966) found the morphology of vegetative organs and leaf anatomy (Stace, pers. comm., 1989) to be similar and indicative of a close relationship between the two genera.

There appears to be considerable intra-specific variation and overlap in wood anatomical characters within *Buchenavia*. Consequently, different species cannot always be reliably distinguished using wood and/or bark anatomy at the present state of knowledge. This contrasts Van Vliet's (1979) contention that species of *Buchenavia* are distinguishable using wood anatomical characters. Studies of more vouchedered material per species are necessary to determine which, if any, wood and bark features are diagnostic of *Buchenavia* species. Silica and septate fibres (wood) and fibre arrangement (bark) appear to be the most promising features for further study.

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