Botanical Journal of the Linnean Society, 2008, **158**, 569–583. With 21 figures

Systematic and phylogenetic value of wood anatomy in Heteromorpheae (Apiaceae, Apioideae)

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Received 29 December 2007; accepted for publication 13 May 2008

The wood anatomy of all four woody genera of the tribe Heteromorpheae (Apiaceae, subfamily Apioideae) has been described and compared, based on 40 wood samples (representing nine species of *Anginon*, one species of *Glia*, three species of *Heteromorpha* and two species of *Polemannia*). The four genera were found to be relatively similar in their wood anatomy. Helical thickenings on the vessel walls occur in all species investigated and appear to represent an ancestral character state and a symplesiomorphy for the tribes Bupleurieae and Heteromorpheae. Each of four genera has a diagnostically different combination of character states relating to the diameter of vessels, size of intervessel pits, length of fibres, presence and arrangement of banded axial parenchyma, size of rays and ray cells, and presence of septate fibres and crystals in the ray cells. The occurrence of marginal axial parenchyma in *Anginon* and *Glia* may be an additional synapomorphy for these taxa. Variation in the wood anatomy of 31 samples from nine species of *Anginon* is not correlated with habitat (Fynbos or Succulent Karoo Biomes), but instead appears to reflect adaptations to seasonal aridity found in both ecosystems. © 2008 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2008, **158**, 569–583.

ADDITIONAL KEYWORDS: crystals – diagnostic characters – ecological patterns – helical thickenings – phylogeny – secondary phloem.

INTRODUCTION

The tribe Heteromorpheae M.F.Watson & S.R.Downie has been described recently (Downie *et al.*, 2001) to accommodate a group of five African genera that form a distinct, early-branching clade in several molecular systematic studies of Apiaceae subfamily Apioideae (Plunkett, Soltis & Soltis, 1996a, b; Downie & Katz-Downie, 1999; Downie *et al.*, 2001). The five genera originally included in the tribe are *Anginon* Raf. (12 species of shrubs or small trees from southern Africa), *Dracosciadium* Hilliard & B.L.Burtt (two non-woody species from the Drakensberg region of southern Africa), *Glia* Sond. (one shrub from the Fynbos region of the Cape), *Heteromorpha* Cham. & Schltdl. (seven species of shrubs and trees from sub-Saharan Africa and a small part of Yemen in the Arabian Peninsula, but with a centre of diversity in southern Africa) and *Polemannia* Eckl. & Zeyh. (three closely related species of shrubs and small trees from the eastern parts of South Africa and Lesotho). A molecular systematic study by Calviño *et al.* (2006) suggested that the limits of the tribe should be expanded to include *Pseudocarum* C.Norman (one species in Africa and one in Madagascar), the as yet undescribed Socotran genus '*Oreofraga*' and four genera endemic to Madagascar (i.e. *Andriana* B.-E.van Wyk, *Cannaboides* B.-E.van Wyk, *Pseudocannaboides* B.-E.van Wyk and *Tana* B.-E.van Wyk). However, no detailed evidence has yet been published to support and motivate the inclusion of the Madagascan genera. Information on the wood anatomy of Heteromorpheae, however, remains scanty and is insufficient to formulate any meaningful interpretations about relationships

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*Corresponding author. E-mail: bevanwyk@uj.ac.za within the tribe, or to enable a comparison of the anatomical features with the phylogenetic trees generated by molecular analyses. To date, published results are available for only a single species, *Heteromorpha arborescens* (Spreng.) Cham. & Schltdl (Metcalfe & Chalk, 1950; Rodriguez, 1957; Oskolski, 2001). Rodriguez's (1957) general conclusion was that *Heteromorpha* is remarkable in terms of the presence of the longest vessel elements within Apiaceae (only matched by those of *Steganotaenia araliacea* Hochst.) as an ancestral state for this family. The latest revisions and phylogenetic studies of *Anginon* (Allison & Van Wyk, 1997; Van Wyk, Allison & Tilney, 1997) and *Heteromorpha* (Winter & Van Wyk, 1995) included aspects of leaf anatomy and, especially, fruit anatomy, but the stem anatomy and secondary xylem were not investigated.

The fact that Heteromorpheae, as originally circumscribed, represents a monophyletic lineage (Downie *et al.*, 2001), and that four of the five genera of the Heteromorpheae clade (those originally assigned to the tribe) are predominantly woody (shrubs and trees), provides, for the first time, the opportunity to describe and interpret what appears to be the ancestral condition of woodiness in Apioideae. As no defining morphological synapomorphies are as yet known for the tribe, we investigated the possibility of shared derived characters in their wood anatomy. We also wished to interpret and compare salient wood anatomical features of other woody members of the predominantly herbaceous (non-woody) Apioideae and the more distantly related family Araliaceae (in which woodiness is a common feature). The goal of the article was to contribute to the evaluation of the overall value of wood anatomy in the interpretation of new hypotheses of phylogenetic relationships based on molecular evidence. The aim was therefore to determine how wood anatomical characters in the subfamily Apioideae should be interpreted from a phylogenetic point of view.

MATERIAL AND METHODS

All but two of the 40 wood samples examined were collected over a period of 15 years during extensive field studies by the authors and several collaborators (Table 1). Authorities for the names are given in Table 1 and are not repeated in the text. Voucher specimens were deposited at JRAU, LE, MO, NOU, P, PRE and various other institutions, as shown in Table 1. Two samples of *Heteromorpha arborescens* were obtained from the wood collections of the Royal Botanic Gardens, Kew (Kw 16 060, collected in May 1894 by G. Volkens in Tanzania) and the University of Utrecht (Uw 15 556, collected in Tanzania). Mature wood was examined (taken from stems with a secondary xylem radius of more than 5 mm), but juvenile samples were also studied in some species.

Standard procedures for the study of wood structure (Carlquist, 1988) were employed to prepare sections and macerations for light microscopic investigations. Specimens for scanning electron microscopy were prepared according to the methods of Exley, Meylan & Butterfield (1977). The standardized descriptive terminology and measurements proposed by Carlquist (1988) and the IAWA List of Microscopic Features for Hardwood Identification (IAWA Committee, 1989) were followed throughout, except that the vertical dimension of the diameter of intervessel pits was also recorded.

In the formal descriptions below, the collector's numbers of the samples are given with the names of the collector: AO, A. Oskolski; BdV, B. de Villiers; BvW, B.-E. van Wyk; IA, I. Allison; PL, P. P. Lowry II; PW, P. J. D. Winter.

RESULTS

WOOD STRUCTURE (APPENDIX; FIGS 1–21)

Anginon *(nine of 12 species examined)*

Growth ring boundaries indistinct [*A. fruticosum* (BvW3535d) (Fig. 1), *A. verticillatum* (IA189a–c; IA191), *A. pumilum* (IA153, IA155), *A. ternatum* (IA198), *A. paniculatum* (IA196)] or distinct, marked by zones or rings of more numerous vessels and also by differences in vessel diameter between latewood and earlywood [*A. paniculatum* (BvW3025a, c, AO39-06), *A. difforme* (IA183, IA186, IA200, IA201), *A. swellendamense* (IA199), *A. intermedium* (IA194), *A. jaarsveldii* (IA167)] up to semi-ring-porous condition in *A. verticillatum* (IA174, IA179, IA181), *A. paniculatum* (BvW3025c, AO39-06), *A. difforme* (IA183, IA185) (Fig. 4) and *A. swellendamense* (AO32–06), by marginal parenchyma [all samples except *A. fruticosum* (BvW3535d) and *A. verticillatum* (IA189a–c)] or by zones of somewhat radially flattened fibres [*A. difforme* (IA185), *A. fruticosum*, *A. intermedium*, *A. paniculatum* (IA196a, IA197), *A. pumilum* (IA153, IA155), *A. swellendamense* (IA89, IA119b, AO32-06) (Fig. 2), *A. ternatum* (IA198), *A. verticillatum*].

Vessels angular, rarely rounded in outline, narrow (tangential diameter usually less than 40 μm) to somewhat wider [up to 55 μm in *A. difforme* (IA183)], numerous [vessel frequency from 78 mm^{-2} in *A. paniculatum* (BvW3025c) to 442 mm^{-2} in *A. fruticosum* (IA86)]. Vessels in clusters and radial multiples of 2–15, commonly fused into larger groupings [up to 33 in *A. fruticosum* (BvW3535d) and *A. swellendamense* (IA199)]; sometimes arranged into tangential and diagonal bands [*A. paniculatum* (IA197), *A. swellendamense* (IA89, IA119b, AO32-06)] or into more or less

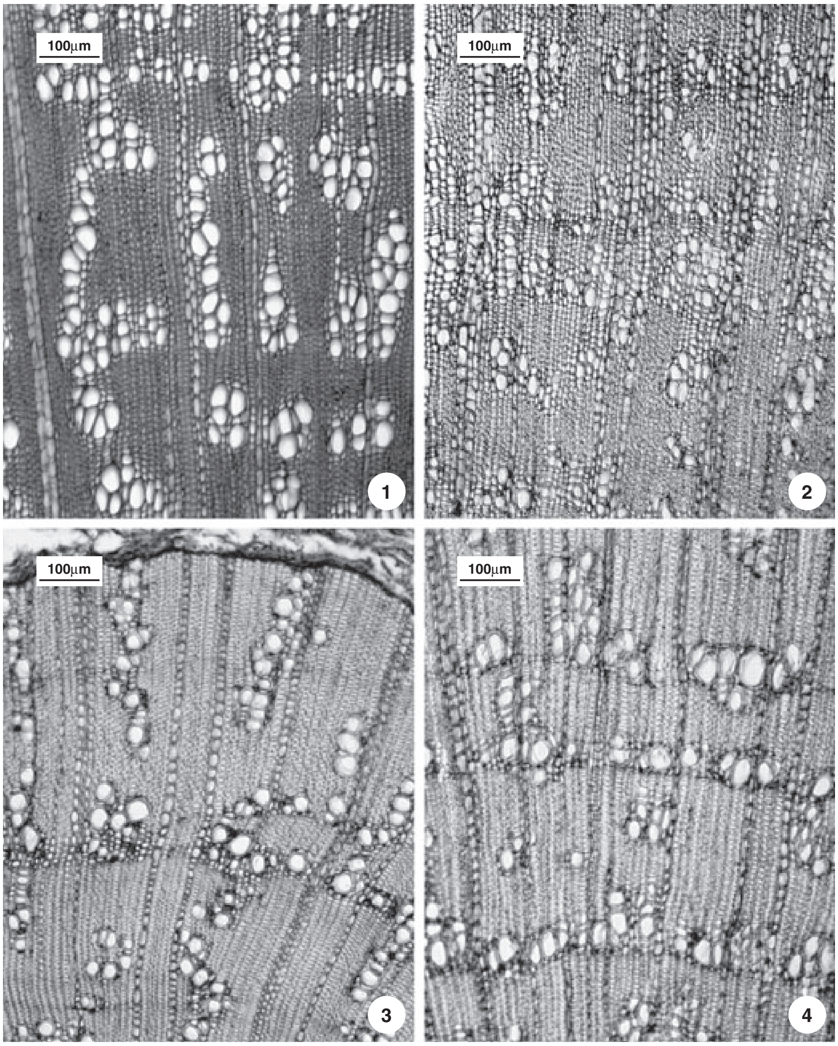
Table 1. Wood and bark samples of the genera of members of the tribe Heteromorpheae. Provinces in South Africa are abbreviated (NC, Northern Cape Province; WC, Western Cape Province). Habitat classification for *Anginon* species is given according to the biomes in Mucina & Rutherford (2006). All voucher specimens are housed at the herbarium of the University of Johannesburg (JRAU)

Species	Collector's number and herbarium	Locality/source and quarter degree square reference	Habitat
Anginon difforme (L.) B.L.Burtt	I. Allison 183 (JRAU)	South Africa, NC, top of Nababiepsberg (2917DB)	Succulent Karoo
Anginon difforme	I. Allison 185 (PRE)	South Africa, NC, top of Nababiepsberg (2917DB)	Succulent Karoo
Anginon difforme	I. Allison 186 (NBG)	South Africa, NC, top of Nababiepsberg (2917DB)	Succulent Karoo
Anginon difforme	I. Allison 200 (JRAU)	South Africa, WC, Tradouw Pass (3319DC)	Fynbos
Anginon difforme	I. Allison 201 (PRE)	South Africa, WC, Tradouw Pass (3319DC)	Fynbos
Anginon fruticosum I.Allison & B.-E.van Wyk	B.-E. van Wyk 3535d (JRAU)	South Africa, WC, top of Hex River Pass (3319BD)	Fynbos
Anginon fruticosum	I. Allison 86 (NBG)	South Africa, WC, top of Hex River Pass (3319BD)	Fynbos
Anginon intermedium I.Allison & B.-E.van Wyk	I. Allison 194 (PRE)	South Africa, NCP, Kamiesberg Pass (3018AC)	Fynbos
Anginon jaarsveldii B.L.Burtt	I. Allison 167 (K)	South Africa, NC, Pella Mountain (2919AA)	Desert
Anginon paniculatum (Thunb.) B.L.Burtt	A. Oskolski 39-06 (LE)	South Africa, WC, Olifants River, N of Citrusdal (3218BD)	Fynbos
Anginon paniculatum	B.-E. van Wyk 3025a (JRAU)	South Africa, WC, road between Citrusdal and Clanwilliam (3218BD)	Fynbos
Anginon paniculatum	B.-E. van Wyk 3025c (JRAU)	South Africa, WC, road between Citrusdal and Clanwilliam (3218BD)	Fynbos
Anginon paniculatum	I. Allison 196 (JRAU)	South Africa, WC, between Baievlei and Pendoringkraal (3118DB)	Succulent Karoo
Anginon paniculatum	I. Allison 197 (PRE)	South Africa, WC, between Baievlei and Pendoringkraal (3118DB)	Succulent Karoo
Anginon pumilum Allison & B.-E.van Wyk	I. Allison 153 (GRA)	South Africa, WC, De Hoop road, 2 km from turn-off to Ouplaas (3420AD)	Fynbos
Anginon pumilum	I. Allison 154 (JRAU)	South Africa, WC, De Hoop road, 2 km from turn-off to Ouplaas (3420AD)	Fynbos
Anginon pumilum	I. Allison 155 (PRE)	South Africa, WC, De Hoop road, 2 km from turn-off to Ouplaas (3420AD)	Fynbos
Anginon pumilum	I. Allison 158a (BOL)	South Africa, WC, De Hoop Nature Reserve, near entrance gate (3420AD)	Fynbos
Anginon pumilum	I. Allison 158c (JRAU)	South Africa, WC, De Hoop Nature Reserve, near entrance gate (3420AD)	Fynbos
Anginon swellendamense (Eckl. & Zeyh.) B.L.Burtt	I. Allison 89 (JRAU)	South Africa, WC, top of Hex River Pass (3319BD)	Succulent Karoo
Anginon swellendamense	I. Allison 119a (JRAU)	South Africa, WC, Worcester (3319CB)	Succulent Karoo
Anginon swellendamense	I. Allison 199b (JRAU)	South Africa, WC, Burger Pass (3319DB)	Succulent Karoo

Table 1. *Continued*

Species	Collector's number and herbarium	Locality/source and quarter degree square reference	Habitat
Anginon swellendamense	A. Oskolski 32-06 (LE)	South Africa, WC, Karoo Desert National Botanic Garden, Worcester (3319CB)	Succulent Karoo
Anginon ternatum Allison & Van Wyk	I. Allison 198 (GRA)	South Africa, WC, Gifberg Pass	Fynbos
Anginon verticillatum (Sond.) B.L.Burtt	I. Allison 174 (PRE)	South Africa, NC, South Africa, top of Numeesberg (2816BD)	Succulent Karoo
Anginon verticillatum	I. Allison 179 (K)	South Africa, NCP, top and upper eastern slopes of Ploegberg (2817CA)	Succulent Karoo
Anginon verticillatum	I. Allison 181 (NBG)	South Africa, NC, top and upper eastern slopes of Ploegberg (2817CA)	Succulent Karoo
Anginon verticillatum	I. Allison 189a (JRAU)	South Africa, NC, top of Nababiepsberg (2917DB)	Succulent Karoo
Anginon verticillatum	I. Allison 189b (JRAU)	South Africa, NC, top of Nababiepsberg (2917DB)	Succulent Karoo
Anginon verticillatum	I. Allison 189c (JRAU)	South Africa, NC, top of Nababiepsberg (2917DB)	Succulent Karoo
Anginon verticillatum	I. Allison 191 (JRAU)	South Africa, NC, Kamiesberg Pass (3018AC)	Fynbos
Glia prolifera (Burm.f.) B.L.Burtt	A. Oskolski 38-06 (LE)	South Africa, WC, Citrusdal, Middelberg (3218DB)	
Heteromorpha arborescens (Spreng.) Cham. & Schltdl. (variety unknown)	Museum of Economic Botany, Royal Botanical Gardens, Kew (Kw10606)	Tanzania (exact locality unknown)	
Heteromorpha arborescens (variety unknown)	Wood Collection, National Herbarium Nederland, Utrecht (Uw15556)	Tanzania (exact locality unknown)	
Heteromorpha arborescens var. *abyssinica* (A.Rich.) H.Wolff	B. de Villiers 74 (JRAU)	South Africa, Mpumalanga Province, Pilgrim's Rest (2430DD)	
Heteromorpha arborescens var. *abyssinica*	P.P. Lowry II 4805 (MO, P)	Zimbabwe, Manicaland, Bvumba Mts., Bunga Forest Reserve	
Heteromorpha pubescens Burtt Davy	P.J.D. Winter 65 (JRAU)	South Africa, Mpumalanga Province, Sudwala Caves area (2530CC)	
Heteromorpha stenophylla Welw. ex Schinz var. *transvaalensis* (Schltr. & H.Wolff) P.J.D.Winter	P. J.D. Winter 57a (JRAU)	South Africa, Mpumalanga Province, Pilgrim's Rest (2430DD)	
Polemannia montana Schltr. & H.Wolff	P.J.D. Winter 186 (JRAU)	South Africa, Wakkerstroom (2730AC)	
Polemannia simplicior Hilliard & B.L.Burtt	B.-E. & C.M. van Wyk 2879 (JRAU)	South Africa, Free State Province, Golden Gate National Park, Diepkloof (2828DD)	

distinct radial [*A. fruticosum* (BvW3535d), *A. verticillatum* (IA179), *A. difforme* (IA185)] and/or dendritic [*A. difforme* (IA183, IA185), *A. fruticosum* (BvW3535d), *A. pumilum* (IA158c), *A. swellendamense* (IA89), *A. verticillatum* (IA179)] pattern. Solitary vessels not numerous [most common in *A. pumilum* (IA153) (Fig. 3)]. Vessel walls 2–4 μm thick. Tyloses not found. Vessel elements (120–)210–400(–530) μm long.



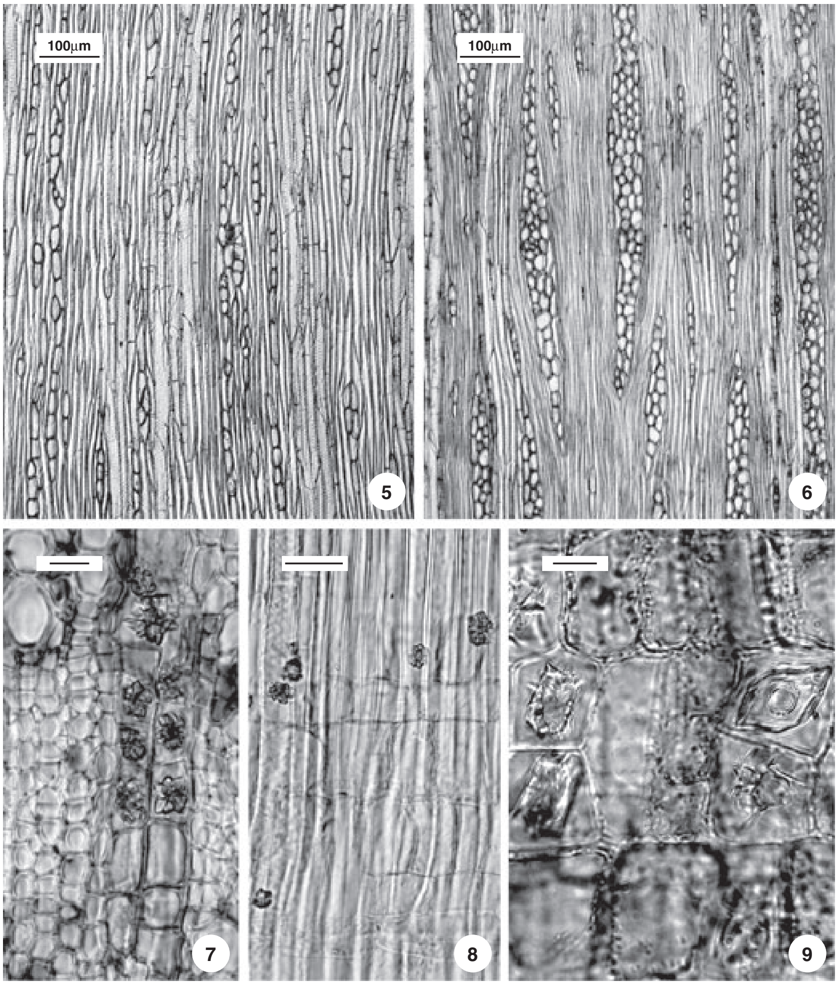
Figures 1–4. Transverse sections of wood of *Anginon*. Scale bars, 100 µm. Fig. 1. *Anginon fruticosum* (BvW3535d) showing indistinct growth ring boundaries; radial to dendritic patterns of vessel arrangement. Fig. 2. *Anginon swellendamense* (IA89) showing distinct growth ring boundaries, marked by radially flattened fibres and marginal parenchyma; groups of vessels tend to be arranged in tangential patterns. Fig. 3. *Anginon pumilum* (IA153) showing distinct growth ring boundaries, marked by a band of marginal parenchyma or by zones of radially flattened fibres; radial to dendritic patterns of vessel arrangement. Fig. 4. *Anginon difforme* (IA183) showing distinct growth ring boundary, marked by wider vessels arranged into rings (semi-ring-porous wood) and by lines of marginal parenchyma.

Perforation plates simple (see Fig. 18). Intervessel pits mostly transitional to alternate (sometimes scalariform) in *A. difforme* (IA186, IA200, IA201), *A. paniculatum* (BvW3025, AO39-06) and *A. pumilum* and mostly alternate (sometimes transitional) in other taxa (Fig. 18), 3–5(–6.5) µm in vertical size, mostly with rounded margins and slit- or lens-like apertures. Vessel-ray and vessel-axial parenchyma pits similar to intervessel pits in size and shape, half-bordered; mostly with distinct borders. Helical thickenings throughout body of vessel elements are common (Fig. 18).

Few vascular tracheids found in *A. verticillatum* (IA174).

Fibres libriform, moderately thick-walled to thick-walled, fibre walls 2–4(5) µm thick [up to 6 µm thick in *A. difforme* (IA183)], with few simple to minutely bordered pits, with slit-like apertures in radial walls. Septate fibres occurring rarely [not found in *A. paniculatum* (IA196) and *A. pumilum*].

Axial parenchyma scanty paratracheal [mostly solitary strands near vessels in *A. difforme* (IA186, IA200, IA201), *A. paniculatum* (BvW3025, AO39-03), *A. swellendamense* (IA199), *A. ternatum*, *A. verticil-*

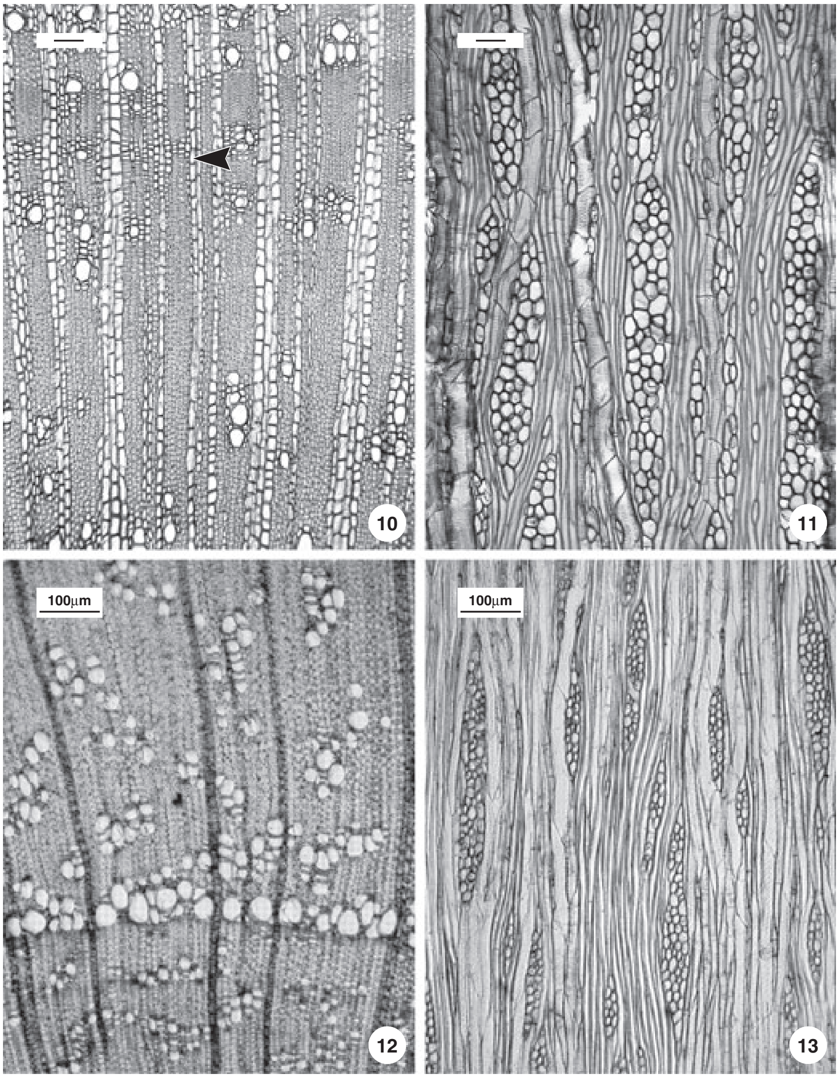


Figures 5–9. Figs 5, 6. Tangential sections of wood of *Anginon*. Scale bars, 100 µm. Fig. 5. *Anginon pumilum* (IA158c) showing rays composed mostly of square and upright cells with a few procumbent cells. Fig. 6. *Anginon swellendamense* (IA89) showing rays composed of procumbent cells with long uniseriate portions and incomplete sheaths of square and upright cells. Figs 7–9. Calcium oxalate crystals in ray cells of *Anginon*. Fig. 7. Transection of wood of *Anginon difforme* (IA201) showing druses. Scale bar, 20 µm. Fig. 8. Radial section of wood of *Anginon intermedium* (IA194) showing druses. Scale bar, 20 µm. Fig. 9. Radial section of wood of *Anginon paniculatum* (IA197) showing prismatic crystals and druses. Scale bar, 10 µm.

latum (IA174, IA191), and in incomplete sheaths in other species], scanty diffuse in solitary strands (*A. pumilum*) and marginal, forming interrupted [*A. verticillatum* (IA174, IA179, IA181), *A. pumilum* (IA153, IA155, IA158a, c), *A. difforme* (IA185), *A. swellendamense* (IA119b)] or continuous [*A. difforme* (IA183, IA186, IA200, IA201), *A. jaarsveldii*, *A. paniculatum* (BvW3025, AO39-03), *A. swellendamense* (IA199), *A. verticillatum* (IA181, IA189a–c)] lines, or one- to three-seriate bands [*A. pumilum* (IA154), *A. swellendamense* (IA89)]. Strands composed of (2–)3–4(–6) cells.

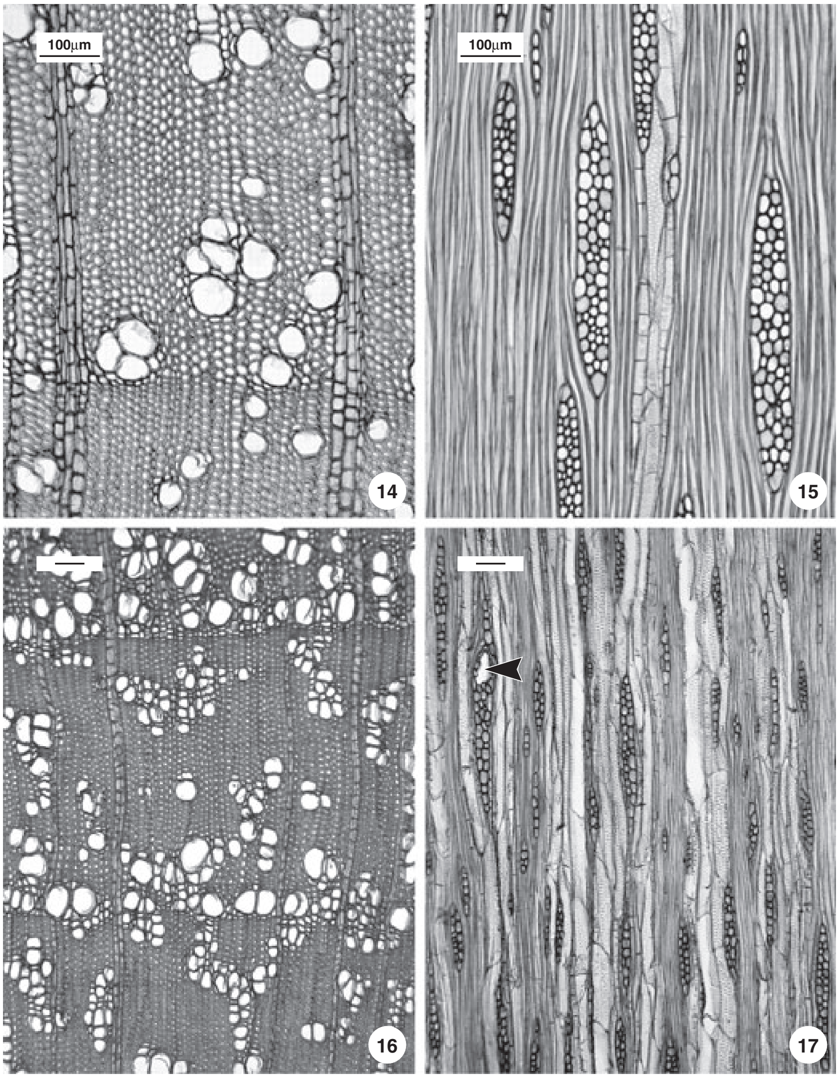
Rays 8–12 mm^{-1} [from 5 mm^{-1} in *A. paniculatum* (AO39-06) up to 24 mm^{-1} in *A. pumilum* (IA158a)], uni- and multiseriate [mostly uniseriate in *A. pumilum* (IA153, IA155, IA158a) (Fig. 5), *A. fruticosum* (IA86), *A. verticillatum* (IA181, IA189c)], up to three cells in width in *A. difforme* (IA185), *A. pumilum* and *A. verticillatum* (IA181, IA189c) and up to four to five cells in width in other taxa [up to six cells in width in *A. swellendamense* (IA89) (Fig. 6)]. Ray cells small, commonly less than 20 µm in tangential size [up to 31 µm in *A. intermedium* (IA194) and 33 µm in *A. paniculatum* (BvW3025c)]. Ray height commonly less than 1 mm, but more than 1 mm in *A. difforme* (IA183, IA186, IA200, IA201), *A. jaarsveldii*, *A. paniculatum* (BvW3025, AO39-03, IA197) and *A. swellendamense* (IA89).

Multiseriate rays composed of procumbent, square and upright cells mixed throughout the ray [almost



Figures 10–13. Figs 10, 11. Wood structure of *Glia prolifera* (AO38-06). Scale bars, 100 μm. Fig. 10. Transverse section showing distinct growth ring boundary, marked by radially flattened fibres and interrupted lines of marginal parenchyma; axial parenchyma scanty, paratracheal and banded (arrow). Fig. 11. Tangential section showing rays composed of square, upright and procumbent cells mixed throughout the ray. Figs 12, 13. Wood structure of *Polemannia simplicior* (B&MvW 2879). Scale bars, 100 μm. Fig. 12. Transverse section showing distinct growth ring boundary, marked by radially flattened fibres; dendritic pattern of vessel arrangement. Fig. 13. Tangential section showing rays composed mostly of procumbent cells; square and upright cells form short uniseriate portions and occur as solitary sheath cells.

exclusively of square and upright cells in *A. difforme* (IA183), *A. jaarsveldii*, *A. pumilum* (IA153, IA154, IA155), *A. verticillatum* (IA174, IA181, IA189a–c)], with long uniserial portions (up to 12 marginal rows) and with incomplete [*A. fruticosum* (BvW3535d), *A. paniculatum*, *A. swellendamense*] to complete [*A. paniculatum* (AO39-06)] sheaths of square and upright cells. Uniseriate rays composed mostly of square and upright cells, but procumbent cells also present. Radial canals present in *A. verticillatum* (IA174, IA189b, IA189c, IA198), rather small (10–30 μm in diameter), bordered by numerous small epithelial cells, commonly with yellow content. Druses of calcium oxalate (Figs 7, 8) occur in upright and square ray cells in all species studied [but not found in some samples of *A. difforme* (IA186), *A. paniculatum* (IA197), *A. pumilum* (IA153, IA154, IA155) and *A. verticillatum* (IA189b,c)]; rhombic crystals found in upright and square ray cells in *A. paniculatum* (IA197) (Fig. 9).



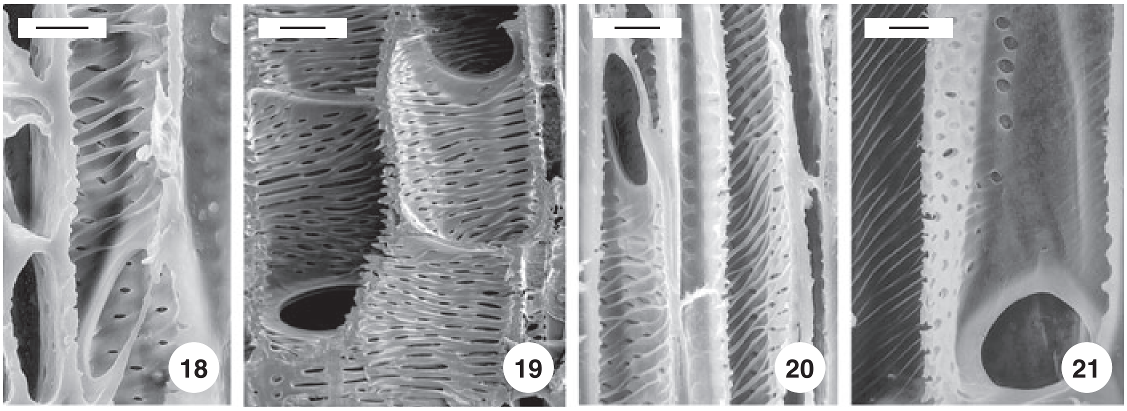
Figures 14–17. Figs 14, 15. Wood structure of *Heteromorpha arborescens* (Uw 15 556). Scale bars, 100 µm. Fig. 14. Transverse section showing distinct growth ring boundary, marked by radially flattened fibres. Fig. 15. Tangential section showing rays composed mostly of procumbent cells; square and upright cells form short uniseriate portions and occur as solitary sheath cells. Fig. 16, 17. Wood structure of *Heteromorpha stenophylla* (PW57a). Scale bars, 100 µm. Fig. 16. Transverse section showing distinct growth ring boundary, marked by radially flattened fibres, line of marginal parenchyma and a difference in vessel diameter between latewood and earlywood (semi-ring-porous wood); diagonal to dendritic patterns of vessel arrangement. Fig. 17. Tangential section showing rays composed mostly of procumbent cells; square and upright cells form uniseriate portions and occur as solitary sheath cells; radial canal (arrow).

Glia *(one species)*
Growth ring boundaries indistinct, marked by zones of somewhat radially flattened fibres and by interrupted lines and bands of marginal parenchyma (Fig. 10).

Vessels angular, rarely rounded in outline, narrow (up to 51 µm in tangential diameter), numerous (67 mm^{-2}), solitary and in clusters and radial multiples of 2–12. Vessel walls 2.6–3.7 µm thick. Tyloses not found. Vessel elements (96–)225(–350) µm long.

Perforation plates simple (see Fig. 19). Intervessel pits (Fig. 19) mostly scalariform and transitional to alternate (sometimes fully alternate), 4–5(–7.4) µm in vertical size, mostly with rounded margins and slit- or lens-like apertures. Vessel-ray and vessel-axial parenchyma pits similar to intervessel pits in size and shape, half-bordered; mostly with distinct (sometimes indistinct) borders. Helical thickenings throughout body of vessel elements common (Fig. 19).

Vascular tracheids not found.



Figures 18–21. Scanning electron micrographs of vessel elements showing simple perforation plates and helical thickenings on the vessel walls. Fig. 18. *Anginon paniculatum* (IA199) showing alternate intervessel pitting. Scale bar, 10 µm. Fig. 19. *Glia prolifera* (AO38-06) showing intervessel pitting scalariform and transitional to alternate. Scale bar, 20 µm. Fig. 20. *Polemannia montana* (PW186) showing alternate intervessel pitting. Scale bar, 10 µm. Fig. 21. *Heteromorpha arborescens* (Uw15556) showing alternate intervessel pitting. Scale bar, 10 µm.

Fibres libriform, moderately thick-walled to thick-walled, fibre walls 2.4–4(8.8) µm thick, with few simple to minutely bordered pits, with slit-like apertures in radial walls. Septate fibres not found.

Axial parenchyma scanty paratracheal (mostly in complete sheaths one to three cells wide near the vessels) or banded (sometimes marginal) in interrupted lines and two- to five-seriate bands (Fig. 10), rarely diffuse in solitary strands. Strands composed of (3–)4–5(–7) cells.

Rays 4–8 mm^{-1}, uni- and multiseriate of two to seven cells in width, ray cells rather large (13–44 µm in tangential size). Ray height commonly exceeding 1 mm (up to 1.8 mm).

Multiseriate rays (Fig. 11) composed mostly of square and upright cells, and also of a few procumbent cells mixed throughout the ray, with short uniserial portions (up to five marginal rows) as well as with complete or incomplete sheaths of square and upright cells. Uniseriate rays composed mostly of square and upright cells, but procumbent cells also occur. Radial canals absent. Crystals not found.

Polemannia *(two of three species examined)*
Growth ring boundaries indistinct in *P. montana* and distinct in *P. simplicior*, marked by zones of somewhat radially flattened fibres, and in *P. simplicior*, by differences in vessel diameter between latewood and earlywood up to semi-ring-porous condition (Fig. 12).

Vessels angular, rarely rounded in outline, narrow (tangential diameter less than 34 µm), numerous (vessel frequency from 275 mm^{-2} in *P. montana* to 414 mm^{-2} in *P. simplicior*), mostly in clusters and radial multiples commonly fused into larger groupings of up to 20 vessels in *P. simplicior* and up to 33 vessels in *P. montana*, arranged into distinct diagonal to dendritic patterns, more distinctly so in *P. simplicior* (Fig. 12). Vessel walls 0.9–3.6 µm thick. Tyloses not found. Vessel elements (170–)290–300(–440) µm long.

Perforation plates simple (see Fig. 20). Intervessel pits (Fig. 20) alternate (rarely transitional to alternate), 2.4–5.3 µm in vertical size, mostly with rounded margins and slit- or lens-like apertures. Vessel-ray and vessel-axial parenchyma pits similar to intervessel pits in size and shape, half-bordered; mostly with indistinct borders. Helical thickenings throughout body of vessel elements common (Fig. 20).

Vascular tracheids not found.

Fibres libriform, moderately thick-walled to thick-walled, fibre walls 1.4–4.5 µm thick, with few simple to minutely bordered pits, with slit-like apertures in radial walls. Septate fibres not found.

Axial parenchyma scanty paratracheal, mostly in solitary strands (sometimes in uniseriate incomplete sheaths) near the vessels, consisting of fusiform cells (found in *P. simplicior*) and strands of two to five cells.

Rays 4–12 mm^{-1}, uni- and multiseriate of two to four cells in width (up to six cells in *P. simplicior*), ray cells small (6–18 µm in tangential size). Ray height commonly less than 1 mm, but few rays more than 1 mm occurring in *P. simplicior*.

Multiseriate rays (Fig. 13) composed of procumbent body cells and upright and square cells forming 1–2(–3) marginal rows in *P. simplicior* or of procumbent, square and upright cells mixed throughout the ray with long uniserial portions (up to 12 marginal rows) in *P. montana*. Upright and square sheath cells solitary in *P. simplicior* or in incomplete sheaths by some multiseriate rays in *P. montana*. Uniseriate rays composed mostly of square and upright cells, but procumbent cells also occurring. Radial canals absent. Crystals not found.

Heteromorpha *(three of seven species examined)*
Growth ring boundaries rather indistinct in *H. arborescens* (Kw16 060, PL4805) and distinct in other taxa, marked by zones of somewhat radially flattened fibres (Fig. 14), by lines of marginal parenchyma (in *H. pubescens* and *H. stenophylla*) and by differences in vessel diameter between latewood and earlywood up to semi-ring-porous condition [especially distinct in *H. arborescens* (BdV74), *H. pubescens* and *H. stenophylla* (Fig. 16)].

Vessels angular, rarely rounded in outline, rather narrow (tangential diameter less than 84 μm) and numerous [vessel frequency varies from 49 mm^{-2} in *H. arborescens* (Uw15 556) to 265 mm^{-2} in *H. stenophylla*], mostly in clusters and radial multiples [up to six in *H. arborescens* (Uw15 556) and up to ten in *H. arborescens* (Kw10 606)], commonly fused into larger groupings of up to 18 vessels in *H. arborescens* (BdV74) and up to 32 vessels in *H. stenophylla*, arranged into tangential to diagonal bands in both varieties of *H. arborescens* (especially distinct in BdV74), or into diagonal to dendritic patterns in *H. stenophylla* (Fig. 16). Vessel walls 1.5–5.0 μm thick. Tyloses not found. Vessel elements (200–)310–490(–660) μm long.

Perforation plates simple (Fig. 21). Intervessel pits (Fig. 21) alternate (rarely opposite and transitional from scalariform to alternate), 4.4–9.3 μm in vertical size, mostly with rounded margins and slit- or lens-like apertures. Vessel-ray and vessel-axial parenchyma pits similar to intervessel pits in size and shape, half-bordered; mostly with indistinct borders. Helical thickenings throughout body of vessel elements common (Fig. 21).

Vascular tracheids found in *H. arborescens* [Kw16 060], *H. pubescens* and *H. stenophylla*.

Fibres libriform, moderately thick-walled to thick-walled, fibre walls 1.4–4.5 μm thick, with few simple to minutely bordered pits, with slit-like apertures in radial walls. Septate fibres common in *H. arborescens* [BdV74; Uw15 556], *H. pubescens* and *H. stenophylla* and occurring in other samples.

Axial parenchyma scanty paratracheal, mostly in solitary strands (sometimes in uniseriate incomplete sheaths) near the vessels, and marginal in continuous lines (in *H. pubescens* and *H. stenophylla*), consisting of strands of three to seven cells.

Rays 4–7 mm^{-1}, uni- and multiseriate [mostly uniseriate in *H. arborescens* (Kw16 060) and *H. pubescens*], of two to three cells in width in *H. pubescens* and *H. arborescens* (PL4805), and up to four to five cells in width in other samples, ray cells small to rather large (7–33 μm in tangential size). Ray height commonly less than 1 mm, but few rays more than 1 mm occurring in *H. arborescens* (Kw16 060; BdV74) and *H. stenophylla*.

Multiseriate rays composed of procumbent body cells, and upright and square cells forming 1–2(–4) marginal rows and occurring as solitary sheath cells in *H. arborescens* (BdV74, Uw15 556) (Fig. 15) and *H. stenophylla* (Fig. 17) or of procumbent, square and upright cells mixed throughout the ray with long uniserial portions (up to 20 marginal rows) in *H. arborescens* (Kw16 060) and *H. pubescens*. Uniseriate rays composed mostly of square and upright cells, but procumbent cells also occurring. Radial canals bordered by few epithelial cells found in *H. stenophylla* (Fig. 17). Crystals not found.

COMPARISON OF WOOD STRUCTURE OF *ANGINON* FROM DIFFERENT HABITATS

The material of *Anginon* examined here is sufficiently representative to analyse the variation of its wood structure in relation to habitat. The distributions of the species studied are more or less confined to one of the three major biomes of the western part of South Africa (Mucina & Rutherford, 2006), namely Fynbos, Succulent Karoo and Desert (Table 1). Fynbos is the most humid, with a mean annual precipitation of 483 mm and a mean annual moisture stress of 77% (defined as the percentage of days in the year when evaporation demand is more than double the soil moisture supply) (Mucina & Rutherford, 2006). However, Fynbos also occurs in some very low rainfall areas, usually with a strong seasonal pattern of wet winter and arid summer. Succulent Karoo has a much lower annual rainfall than Fynbos (mean annual precipitation of 168 mm and a mean annual moisture stress of 81%) (Mucina & Rutherford, 2006) but shares the characteristic pattern of winter rain and summer aridity with Fynbos. The narrow stretch along the Orange River on the border of Namibia is defined by Mucina & Rutherford (2006) as part of the Desert Biome, but only one species (*A. jaarsveldii*) occurs there.

A comparison between the *Anginon* wood samples collected in Fynbos and those collected from Succulent Karoo has been carried out on the basis of the data listed in the Appendix. The lack of replications necessitated the exclusion of the single sample of *A. jaarsveldii* (representing the Desert Biome) from the analysis. The statistical significance of the between-group differences of the mean values was estimated using the *t*-test (STATISTICA 6.0 package). The mean values of the wood characters which may be of ecological interest are noted in Table 2.

No statistically significant ($P < 0.1$) differences in any wood features were observed between the

Table 2. Comparison of the mean values of certain wood characters of *Anginon* samples from Fynbos and Succulent Karoo, using the *t*-test

Character	Fynbos			Succulent Karoo
	Mean	*t* value	*P* value	Mean
Radius of sample (mm)	6.8 ± 1.36	1.51	0.142	8.8 ± 0.65
Mean length of vessel elements (μm)	283.9 ± 12.12	0.10	0.922	285.5 ± 10.07
Mean length of fibres (μm)	420.1 ± 12.95	0.02	0.981	420.4 ± 11.49
Number of vessels per mm^2	224.1 ± 28.62	1.69	0.110	277.5 ± 25.27
Mean number of vessels per group	3.6 ± 0.28	1.43	0.164	4.22 ± 0.27
Maximum number of vessels per group	17.1 ± 1.70	0.79	0.438	19.2 ± 1.73
Mean diameter of vessels (μm)	21.6 ± 1.71	0.61	0.546	20.6 ± 0.85
Mean width of multiseriate rays (cells)	2.5 ± 0.17	0.48	0.636	2.6 ± 0.09
Mean width of multiseriate rays (μm)	32.4 ± 3.37	0.37	0.756	31.2 ± 1.47
Mean height of multiseriate rays (mm)	0.62 + 0.070	0.85	0.402	0.57 ± 0.025
Maximum height of multiseriate rays (mm)	1.7 ± 0.27	0.37	0.756	1.6 ± 0.13
Number of multiseriate rays per mm	5.4 ± 0.65	0.61	0.547	5.9 ± 0.43
Number of uniseriate rays per mm	4.9 ± 1.28	0.92	0.364	4.0 ± 0.33

samples from the two biomes. In addition, the growth ring types and the pattern of vessel arrangement were visually compared between the samples of the three different biomes. No correspondence between the variation of these wood features and the biome types was found.

DISCUSSION

The studied genera of Heteromorpheae show a set of characters that is typical for all other woody members of the family investigated to date, such as exclusively simple perforation plates, rather short vessel elements and scanty paratracheal axial parenchyma (Metcalfe & Chalk, 1950; Rodriguez, 1957; Oskolski, 2001). All these taxa, however, share a remarkable wood feature, namely the presence of helical thickenings on the vessel walls. Within Apiaceae, this character has also been reported for *Bupleurum* L., *Melanoselinum* Hoffm. (Rodriguez, 1957; Schweingruber, 1990) and for the woody African (Cape) species of *Peucedanum* L. (A. R. Magee, A. A. Oskolski and B.-E. van Wyk, University of Johannesburg, unpubl. data). According to molecular data (Downie & Katz-Downie, 1999; Plunkett *et al.*, 2004), *Bupleurum* forms a separate clade from other Apioideae, and the *Heteromorpha* clade (i.e. this genus with *Anginon*, *Glia* and *Polemannia*) is again sister to this combined clade (i.e. *Bupleurum* and all other Apioideae), whereas *Melanoselinum* (Lee & Downie, 2000) and African *Peucedanum* (Winter *et al.*, 2008) are not closely related to each other or to that alliance. Therefore, the helical thickenings on the vessel walls may be suggested to be an ancestral condition for Apioideae that is symplesiomorphic for Heteromorpheae and *Bupleurum*, and is probably the result of secondary reversals in *Melanoselinum* and African *Peucedanum*. This interpretation is supported by the fact that the helical thickenings on the vessel walls are also present in *Astrotricha* DC. (Oskolski, 1996), belonging to one of the early-branching lineages of Araliaceae (Wen *et al.*, 2001; Lowry *et al.*, 2004). *Astrotricha* is also characterized by its two-winged mericarps with free, bifurcating carpophores, which are unique in Araliaceae but typical for Apiaceae (Liu *et al.*, 2006).

Generally, the wood structure in Heteromorpheae is rather uniform, and the genera under study can be distinguished mainly on the basis of quantitative characters (Table 3). *Heteromorpha* differs from the three other genera by having wood with wider vessels and longer fibres and by the presence of numerous septate fibres. Scalariform intervessel pitting, large ray cells and wide bands of axial parenchyma not associated with the growth ring boundaries appear to be diagnostic features for *Glia*. In addition, *Heteromorpha* and *Glia* share larger intervessel pits than the other two genera. The occurrence of calcium oxalate crystals allows a distinction to be made between the wood of *Anginon* and that of the other genera. Crystals in ray cells occur in all species of *Anginon*, although they were not found in some wood samples of this genus. However, *Anginon* and *Glia* share marginal parenchyma, which may be interpreted as an additional synapomorphy of the two taxa (in addition to bottle-shaped fruit epidermal cells with heavily cutinized outer walls; Van Wyk *et al.*, 1997). This character can be used to distinguish *Anginon* from *Polemannia*: the two genera are similar

Table 3. Diagnostic and phylogenetically important wood features of the studied genera of the tribe Heteromorpheae (+, present; –, absent)

	Anginon	*Glia*	*Polemannia*	*Heteromorpha*
Size of some intervessel pits > 7 µm	–	+	–	+
Diameter of some vessels > 60 µm	–	–	–	+
Mean length of fibres > 500 µm	–	–	–	+
Tangential width of some ray cells > 40 µm	–	+	–	–
Marginal axial parenchyma	+	+	–	±
Non-marginal bands of axial parenchyma	–	+	–	–
Septate fibres	Solitary	–	–	Numerous
Occurrence of crystals in ray cells	+	–	–	–

in their wood structure, but the latter is devoid of marginal parenchyma.

Rodriguez (1957) reported that *H. arborescens* has the longest vessel elements in woody Apiaceae; the mean length is 502 µm, which corresponds to that found in many Araliaceae (Oskolski, 2001). Our results confirm his findings: the mean length of the vessel elements in the three samples of *H. arborescens* examined exceeded 400 µm (up to 495 µm in Kw16 060). As the shortening of vessel elements is regarded as a major trend of wood evolution (Bailey & Tupper, 1918; Baas & Wheeler, 1996), these data are in good agreement with the results of molecular phylogenetic studies (Downie & Katz-Downie, 1999; Chandler & Plunkett, 2004; Plunkett *et al.*, 2004), which suggest a early-branching position of the 'woody South African clade I' (which corresponds to the currently recognized Heteromorpheae) (Downie & Katz-Downie, 1999) with respect to other Apioideae, and for *Heteromorpha* relative to the other members of this clade.

The common occurrence of numerous septate fibres can be suggested as another ancestral trait of the family that has been retained in *Heteromorpha*. Septate fibres are common in Araliaceae, including lineages such as *Osmoxylon* Miq. and *Astrotricha* DC. (Plunkett *et al.*, 2004), but they are not typical for Apiaceae (Oskolski, 2001). The loss of septate fibres seems to have been part of the course of evolution within Heteromorpheae: they occur only rarely in *Anginon* and appear to be altogether absent in *Polemannia* and *Glia*.

Vessel elements in *H. pubescens* and *H. stenophylla* are distinctly shorter than in *H. arborescens*; the mean lengths in these two species are within the range for this parameter for *Anginon* spp. and many other woody Apiaceae (Rodriguez, 1957). We speculate that the observed differences in the vessel element lengths within *Heteromorpha* could be the result of the more derived phylogenetic positions of *H. pubescens* and *H. stenophylla* [see the morphological cladogram for *Heteromorpha* species presented by Winter & Van Wyk (1995)]. These two species also differ from *H. arborescens* by their smaller and more numerous vessels, larger groups of vessels (up to 32 per group in *H. stenophylla*) and the presence of marginal parenchyma. These features of *H. pubescens* and *H. stenophylla* appear to agree with their shrubby or suffrutescent habit, in contrast with the tree-like *H. arborescens*, a trend also seen in other groups (Carlquist, 1988).

All the species studied here share a set of wood characters that is typical for Mediterranean and xerophytic plants, i.e. narrow and numerous vessels in groupings and helical thickenings on vessel walls (Baas & Schweingruber, 1987; Carlquist, 1988). However, no ecological trends in the variation of any wood features within *Anginon* have been observed. It is probable that the basic level of hydraulic efficiency of vessels in all *Anginon* species is not conditioned by annual rainfall, but is sufficiently high to provide a reliable water supply and to prevent air embolisms during the driest season.

Our detailed study of several members of Heteromorpheae has led to the following conclusions:

1. Wood anatomical characters have some value in distinguishing between genera, especially if unique combinations of characters are taken into account.
2. The genera included in Heteromorpheae are similar in their wood anatomy, supporting the idea (thus far based only on molecular evidence) that they are related.
3. The species show the ancestral states of wood structure in Apioideae as a whole, and may have retained the original condition from which modifications have occurred in other woody Apioideae, by reductions and/or reversals.
4. The diversity in wood structure is not correlated with habitat (at least not in *Anginon*).

ACKNOWLEDGEMENTS

Research conducted by the first author was supported by a grant from the Russian Foundation of Basic Research (RFFI, no. 06-04-48 003a). The authors are also grateful to E. S. Chavchavadze for valuable consultations and to Hester Roets for her help in preparing the illustrations from digital images. Assistance was provided to the first and second authors by the following: the Botanical Museum, V. L. Komarov Botanical Institute, St. Petersburg, Russia and the Department of Botany and Plant Biotechnology, University of Johannesburg, South Africa.

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APPENDIX

WOOD ANATOMICAL CHARACTERS OF TRIBE HETEROMORPHEAE

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Anginon difforme [IA183]	7	278 ± 13.2 132–456	4.3/6.0	214	26 ± 2.0 11–55	4.7/15	7.2	362 ± 9.8 240–504	2.4/4	0.76/2.8	5.0	2.6	7.6	15.5/22
A. difforme [IA185]	5	280 ± 10.2 193–398	4.0/6.0	344	19 ± 1.1 7–32	5.3/22	4.5	473 ± 15.0 344–804	2.1/3	0.55/1.7	4.9	4.7	9.6	10.9/14
A. difforme [IA186]	8	280 ± 10.3 193–381	3.7/5.3	146	22 ± 1.2 9–37	2.7/9	12.9	395 ± 12.1 279–689	2.3/4	0.45/1.7	6.2	4.8	11.0	12.8/17
A. difforme [IA200]	10	219 ± 8.4 135–299	3.5/5.0	302	20 ± 0.9 11–35	3.7/15	5.8	354 ± 11.4 213–492	2.7/4	0.67/2.2	6.9	3.5	10.4	13.6/17
A. difforme [IA201]	7	276 ± 9.2 164–377	3.8/4.6	274	17 ± 0.6 10–23	3.2/16	10.8	410 ± 10.9 279–558	2.8/5	0.79/2.9	7.8	2.6	10.4	11.5/16
A. fruticosum [BvW3535d]	15	309 ± 9.0 234–422	4.0/5.3	555	25 ± 1.0 14–36	7.4/33	3.8	452 ± 8.4 295–541	2.3/4	0.56/1.4	4.4	4.4	8.8	13.9/20
A. fruticosum [IA86]	8	231 ± 8.8 139–320	4.1/4.7	442	15 ± 0.5 9–19	3.6/20	6.8	436 ± 9.9 312–558	2.6/4	0.62/1.8	5.9	6.8	12.7	13.6/20
A. intermedium [IA194]	6	308 ± 12.2 197–467	3.2/4.3	335	20 ± 1.2 11–33	4.1/26	6.3	507 ± 18.1 312–869	2.4/4	0.42/0.8	3.9	3.8	7.7	17.2/31
A. jaarsveldii [IA167]	5	317 ± 11.3 192–468	4.5/5.9	145	24 ± 1.4 12–38	3.3/12	8.2	417 ± 11.3 276–600	2.3/4	1.02/2.9	6.0	2.5	8.5	17.8/23
A. paniculatum [AO39-06]	16	313 ± 7.8 214–436	4.7/6.3	77	29 ± 1.5 11–47	3.2/10	7.6	467 ± 9.4 319–616	3.8/6	0.67/1.5	4.6	0.3	4.9	16.0/23
A. paniculatum [BvW3025a]	8	334 ± 11.3 213–430	3.9/5.7	249	29 ± 1.5 19–46	4.9/16	3.2	436 ± 11.9 328–623	2.3/4	0.60/1.4	4.3	4.1	8.4	14.0/19
A. paniculatum [BvW3025c]	10	294 ± 12.2 189–451	4.7/5.6	78	28 ± 1.2 16–40	3.2/13	12.4	473 ± 13.0 325–616	2.9/5	1.14/3.4	5.3	2.2	7.5	22.1/34
A. paniculatum [IA196]	10	285 ± 10.0 193–422	3.4/4.1	245	14 ± 0.4 10–21	3.6/14	8.2	411 ± 12.9 262–672	3.0/5	0.64/1.9	6.9	2.8	9.7	15.0/20
A. paniculatum [IA197]	10	216 ± 7.9 156–300	3.8/5.0	216	17 ± 0.7 12–27	4.2/13	3.9	337 ± 7.0 252–420	3.6/5	0.67/2.9	7.7	2.4	10.1	13.6/17
A. pumilum [IA153]	3	321 ± 14.4 211–490	3.3/5.2	304	15 ± 0.9 7–26	4.0/23	5.4	465 ± 12.4 342–650	2.1/3	0.57/1.2	1.7	7.1	8.8	9.6/12
A. pumilum [IA154]	3	311 ± 12.7 189–443	4.0/5.5	299	22 ± 1.1 11–34	4.8/27	4.6	430 ± 8.9 308–547	2.1/3	0.43/0.8	4.6	3.5	8.1	12.4/16
A. pumilum [IA155]	3	285 ± 10.6 155–396	3.5/5.0	190	24 ± 1.5 11–48	2.1/11	23.2	369 ± 10.7 228–528	2.2/3	0.39/1.0	4.2	6.5	10.7	9.4/14
A. pumilum [IA158a]	4	239 ± 7.4 180–320	3.7/5.1	170	16 ± 0.7 8–23	2.6/20	19.4	407 ± 8.4 328–574	2.3/3	0.46/1.5	8.9	15.0	23.9	20.9/29
A. pumilum [IA158c]	4	247 ± 7.0 180–328	3.9/6.1	298	18 ± 0.9 9–31	4.2/20	5.9	398 ± 11.8 230–558	2.2/3	0.50/1.3	6.04	4.7	10.8	17.9/25
A. swellendamense [IA89]	10	256 ± 11.7 156–396	3.1/4.6	413	18 ± 0.6 10–26	5.9/26	2.6	375 ± 12.8 228–564	3.6/6	0.80/2.3	7.3	2.2	9.5	15.9/22
A. swellendamense [IA199]	10	212 ± 7.6 127–291	3.0/3.6	311	18 ± 0.6 13–24	5.0/33	5.7	346 ± 10.0 180–492	2.9/5	0.40/1.3	8.3	1.4	9.7	17.6/26
A. swellendamense [IA119]	10	258 ± 12.0 168–408	3.6/4.7	227	17 ± 1.1 7–30	3.2/16	11	317 ± 9.8 204–516	2.7/5	0.47/1.0	8.9	3.3	12.2	14.1/19
A. swellendamense [AO32-06]	6	283 ± 7.1 179–398	4.4/6.5	109	24 ± 0.8 11–36	3.1/10	7.6	422 ± 12.1 302–667	2.5/4	0.72/2.1	4.8	1.9	6.8	16.2/26
A. ternatum [IA198]	15	262 ± 8.9 156–389	3.4/4.5	241	25 ± 0.8 15–37	2.8/12	7.3	419 ± 9.8 312–590	2.6/5	0.62/2.2	9.7	5.5	12.5	7.5/10
A. verticillatum [IA174]	6	275 ± 9.4 172–402	3.5/5.2	379	21 ± 1.1 14–36	4.6/26	6.6	457 ± 10.5 312–574	2.4/5	0.46/1.0	4.4	4.4	8.9	12.9/16
A. verticillatum [IA179]	5	314 ± 13.0 119–422	3.3/4.2	352	16 ± 0.6 10–23	4.1/16	5.8	450 ± 10.9 344–623	2.9/5	0.58/1.6	5.8	3.7	9.5	15.9/22
A. verticillatum [IA181]	5	280 ± 8.7 176–402	3.5/5.2	245	24 ± 1.4 13–43	3.8/14	6.7	479 ± 15.9 328–771	2.1/3	0.47/1.3	2.4	5.6	8	12.6/16
A. verticillatum [IA189a]	10	332 ± 11.0 204–444	4.2/5.0	254	21 ± 1.3 11–41	5.4/27	5.2	420 ± 12.3 228–564	2.7/5	0.51/1.3	5.0	5.5	10.5	14.6/20
A. verticillatum [IA189b]	10	364 ± 14.9 144–528	4.2/5.2	215	23 ± 1.4 13–47	5.0/28	3.2	429 ± 10.9 312–564	2.5/4	0.58/1.7	5.8	3.9	9.8	15/19

APPENDIX *Continued*

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14
A. verticillatum [IA189c]	10	398 ± 14.1 228–528	3.5/4.8	177	27 ± 1.3 16–41	2.6/11	15.1	473 ± 15.9 276–696	2.2/3	0.60/1.1	3.0	6.0	9	14.8/19
A. verticillatum [IA191]	10	290 ± 11.7 193–484	3.5/4.3	131	20 ± 1.1 10–33	3.3/14	7.8	449 ± 11.9 328–689	2.7/5	0.54/1.0	7.8	4.7	12.5	10.0/18
Glia prolifera [AO38-06]	8	225 ± 9.5 96–351	5.6/7.4	67	28 ± 1.5 16–51	2.4/12	15.9	377 ± 7.4 279–465	3.7/7	0.78/1.8	4.9	1.1	6.0	26.3/44
Heteromorpha arborescens [Kw10606]	9	495 ± 14.1 376–656	6.6/8.6	117	42 ± 1.1 20–64	2.3/10	18.5	669 ± 11.9 499–842	2.4/4	0.42/1.2	1.8	4.9	6.7	15.3/21
H. arborescens [Uw15556]	20	368 ± 18.1 204–512	7.3/8.7	49	50 ± 1.1 24–84	1.9/6	26.2	627 ± 15.8 406–811	3.3/5	0.41/0.7	4.2	0.5	4.7	17.0/25
H. arborescens [BdV74]	23	437 ± 12.1 302–590	8.1/9.3	124	39 ± 1.7 22–80	6.5/18	2.3	748 ± 14.8 516–937	3.6/5	0.33/1.1	4.4	0.3	4.7	15.0/24
H. arborescens [PL4805]	12	407 ± 16.1 244–552	6.0/7.7	121	36 ± 1.5 21–65	2.7/12	12.4	643 ± 19.7 406–1061	2.1/3	0.23/0.5	3.2	2.8	6.0	17.4/34
H. pubescens [PW65]	6	309 ± 10.8 226–394	6.1/7.7	247	32 ± 2.4 12–79	4.0/16	6.3	526 ± 13.1 345–781	2.1/3	0.33/0.9	2.4	2.8	5.2	14.6/22
H. stenophylla [PW57a]	7	336 ± 9.5 218–475	5.7/7.4	265	28 ± 2.1 10–63	7.1/32	2.0	547 ± 11.3 331–681	2.5/5	0.29/1.2	4.7	2.1	6.8	14.1/23
P. montana [PW186]	10	292 ± 9.4 216–444	3.5/5.2	275	20 ± 1.2 8–34	7.3/33	3.4	437 ± 8.9 324–540	2.4/4	0.42/1.4	3.6	4.3	7.9	13.7/18
Polemannia simplicior [B&MvW 2879]	6	300 ± 9.2 168–444	4.1/5.3	414	20 ± 0.8 9–33	4.5/20	6.5	427 ± 11.3 276–564	3.2/6	0.26/0.7	5.2	2.7	7.9	11.0/14

Characters: 1, radius of wood sample (mm); 2, length of vessel elements (mean and minimum–maximum, µm); 3, vertical size of intervessel pits (mean/maximum); 4, vessel frequency (per mm^2); 5, tangential diameter of vessels (mean and minimum–maximum, µm); 6, mean greatest number of vessels in a vessel group; 7, percentage of solitary vessels; 8, mean length of libriform fibres (mean and minimum–maximum, µm); 9, width of multiseriate rays (mean/maximum cells); 10, height of multiseriate rays (mean/maximum, mm); 11, number of multiseriate rays per mm; 12, number of uniseriate rays per mm; 13, total number of rays per mm; 14, tangential size of ray cells (mean/maximum, µm).