Wood anatomy of the endemic woody Asteraceae of St Helena I: phyletic and ecological aspects

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Quantitative and qualitative data are given for samples of mature wood of all eight species of woody Asteraceae, representing three tribes, of St Helena I. The quantitative features of all except one species are clearly mesomorph, corresponding to their mesic central ridge habitats. Commidendrum rugosum has more xeromorphic wood features and occurs in dry lowland sites. Commidendrum species are alike in their small vessel pith and abundant axial parenchyma. Melanodendrum agrees with Commidendrum in having fibre dimorphism and homogeneous type II rays. The short fibres in both genera are storied and transitional to axial parenchyma. Elongate crystals occur in ray cells of only two species of Commidendrum, suggesting that they are closely related. Wood of Commidendrum and Melanodendrum is similar to that of the shrubby genus Felicia, thought closely related to Commidendrum on molecular bases. Commidendrum and Melanodendrum have probably increased in woodiness on St Helena, but are derived from shrubby ancestors like today's species of Felicia. Petrorium wood is paedomorphic and indistinguishable from that of Bidens, from which Petrorium is likely derived. The two senecionid species (Senecio leucadendron = Pladaroxylon leucadendron; and Senecio redivivus = Lachanodes arborea, formerly Lachanodes prenanthiflora) also show paedomorphic wood. Wood of the various St Helena Asteraceae is consonant with relationship to African or South American ancestors that reached St Helena via long distance dispersal. Derivation from genera of Pacific islands or Austro-Malaysian regions is considered less likely. However, DNA evidence is needed to clarify origins, times of colonization on St Helena and divergence from closest relatives, and the nature of evolutionary patterns.

ADDITIONAL KEY WORDS: Astereae — Compositae — dispersal — ecological wood anatomy — Heliantheae — insular woodiness — paedomorphosis — phytogeography — Senecioneae.

INTRODUCTION

Eight species of woody Asteraceae, representing three tribes, are endemic to St Helena I. (Melliss, 1875; Ashmole & Ashmole, 2000; Cronk, 2000). Seven of these are trees, but C. rugosum differs from its congener in being a shrub up to 1 m tall (Cronk, 2000). The St Helena Asteraceae have attracted attention because of their arboreal status, although woodiness of various degrees is not really rare in species of the family, especially those of subtropical and tropical areas. However, the St Helena Asteraceae include trees once prominent and common on the island, but now mostly scarce; their disappearance and subsequent conservation efforts are discussed by Ashmole & Ashmole (2000) and Cronk (2000).

Wood anatomy can offer only limited phylogenetic evidence. Increasingly, molecular data offer invaluable evidence of taxonomic relationships, their degree and even timing. A preliminary classification of the family based on cladistic study of macromorphological features has been offered by Bremer (1987), and cladograms based on analysis of DNA have been presented by Jansen, Michaels & Palmer (1991). These have superseded earlier schemes. The St Helena Asteraceae do not belong to basal groups of the family. Bremer (1987) and Jansen et al. (1991) find mutisioids (especially the barnadesioids, often now segregated as the outgroup to the remainder of the family) and other tribes of the subfamily Lactucoideae to represent older elements within Asteraceae.

The floras of the Macaronesian islands (offshore islands of Africa in the north Atlantic) have been thought by some to be relictual in nature (e.g. Cronk, 1987, 1992). However, the reverse hypothesis, that 'woody herbs' of the Macaronesian islands are secondarily woody and have evolved that and other
features relatively recently on the islands, was espoused by Carlquist (1965, 1974). Recent studies in which DNA analysis is presented cladistically, have supported the idea of secondary woodiness and autochthonous evolution in Macaronesia in relatively recent times in such genera as *Echium*, *Gonospermum* and *Sonchus* (Böhle, Hilger & Martin, 1996; Francisco-Ortega et al., 1995, Francisco-Ortega et al. 1996; Francisco-Ortega, Jansen & Santos-Guerra 1996; Francisco-Ortega et al., 2001; Kim et al., 1996). The flora of St Helena can be viewed against the background of these studies, although DNA-based analysis on the St Helena flora is needed. Paedomorphosis in wood anatomy (Carlquist, 1962), despite earlier scepticism (Mabberley, 1975) has proved a reliable indicator to discriminating between primary and secondary woodiness (see Carlquist, 1980, 1988, 2001). The geographical relationships of the St Helena flora are of critical importance, because the distance of this island from the African coast makes long-distance dispersal a mechanism that must be considered. The St Helena flora (Cronk, 2000) is relatively depauperate and does not contain any conifers or primitive angiosperms, and thus appears typical of what is expected on a remote volcanic island (with favourable ecology). The data from wood anatomy does bear on geographical relationships, and some comments can be offered even though the best evidence will be provided by DNA analysis. Cronk (1992: 95) gives geographical affinities for the woody genera of St Helena Asteraceae (reproduced by Ashmole & Ashmole, 2000). None of these claimed affinities include Africa, although Noyes & Rieseberg (1999) find that the African genera *Felicia* and *Amellus* branch from the base of the Asteraceae they analyse, just before *Comnindendrum*.

Even if studies of wood anatomy cannot yield the broader results of the phylogenetic relationships that DNA studies can offer, wood anatomy remains a sensitive indication of specific and generic similarities and differences. More significantly, wood anatomy tells much about the ecology of a species (Carlquist, 1975), and thus is worth investigation on this basis alone. The St Helena climate is diverse, being dry on scrubby slopes near the shoreline and quite moist in dense fern forest along the summit ridge (Ashmole & Ashmole, 2000; Cronk, 2000). Vessel features of the wood anatomy of the St Helena Asteraceae provide quantitative reflections of this diversity in ecology.

**MATERIAL AND METHODS**

Wood samples for six of the species of species of St Helena Asteraceae were provided by the Royal Botanic Gardens, Kew, from collections made by J. C. Melliss (c. 1875, s.n.). These include *Comnindendrum robustum* (Roxb.) DC., *C. spurium* (G. Forst.) DC., *Lachanodes arborea* (Roxb.) B. Nord., *Melanodendrum integrifolium* (G. Forst.) Hook. f., *Petriobium arboreum* (J.R. & G. Forst.) R. Br., and *Plodoroxylon leucadendron* (G. Forst.) Hook. f. The generic names *Lachanodes* and *Plodoroxylon* are used here in accordance with Cronk (2000), although these two monotypic genera may well be abandoned in favour of *Senecio* when DNA studies of them have been made. Material of *Comnindendrum rugosum* (Dryand.) DC. was also provided by the Royal Botanic Gardens, Kew; material was harvested from their living collections of endangered St Helena species by Tim Upson (s. n.). The material of *Comnindendrum rotundifolium* (Roxb.) DC. was provided by the Samuel J. Record collection under the number Yw-29783 when that collection was housed at Yale University. All of the above wood samples were taken from larger stems of mature plants, and thus are comparable with each other and with mature wood of other species. Material of *Felicia amelloides* Voss, obtained from a commercial source, was cultivated in my home garden.

Dried wood samples were boiled in water and stored in 50% aqueous ethanol (material of *Felicia amelloides* was taken from a living plant and preserved in 50% ethanol). Sections were prepared with a sliding microscope and stained with a safranin-fast green combination. Some sections were left unstained, air-dried between clean slides, attached to aluminum stubs, and examined with scanning electron microscopy (SEM). Wood portions of each species were macerated with Jeffrey's Fluid and stained with safranin.

Vessel diameter was measured as mean vessel lumen diameter. Figures for vessel grouping are means based on the convention: a solitary vessel = 1, a pair of vessels in contact = 2, etc. Vessel grouping varies within sections, and in some illustrations the degree of vessel grouping is not representative (Figs 1, 5). Terminology follows that of the IAWA Committee on Nomenclature (1984). Fibre dimorphism occurs in six of the species, and in some, subdivision of the shorter fibres into strands illustrates a transition into formation of axial parenchyma. Note should be taken that the term 'subdivided fibre' here indicates a fibroform strand of cells, each of which is surrounded by a secondary wall, and does not in any way refer to septate fibres. Septate fibres were not observed in any species of the present study. Libriform fibres are not subdivided into strands unless that condition is specifically stated. For simplicity, paratracheal axial distributions are described separately from the distributions of shorter fibres, even if the shorter fibres are quite parenchyma-like. The difficulty of distinction (i.e. lack of wider difference between two length classes of libriform fibres) demonstrates clearly that fibre dimorphism is a path for origin of axial parenchyma, as claimed earlier (Carlquist, 1968, 1961). Further comments on this phenomenon are offered by Baas & Zweypfenning.
Figures 1–4. Wood sections of *Commidendrum robustum*. Fig. 1. Transverse section (TS); tangential bands of wider fibres above centre. Fig. 2. Tangential longitudinal section (TLS); most rays are multiseriate. Fig. 3. SEM photograph of vessel wall, showing elongate pit apertures and grooves connecting pit apertures. Fig. 4. SEM photograph of ray cells from TLS; numerous elongate prismatic crystals are present in ray cells. Figs 1, 2, scale bar (in Fig. 1) = 100 μm; Figs 3, 4, scale bar = 10 μm.
Mean libriform fibre length was measured from macerations, and includes both shorter and longer fibres in species with fibre dimorphism.

RESULTS

COMMIDENDRUM ROBUSTUM
(Figs 1–4)

Growth rings not clearly demarcated, probably present in the form of shorter, wider fibres (Fig. 1). Vessels mostly solitary (Fig. 1). Mean number of vessels per group, 1.96. Mean number of vessels per mm², 32. Mean vessel element length, 213 μm. Perforation plates simple. Lateral wall pitting of vessels alternate to transitional. Pit apertures of vessels often elongate and coalescent into grooves (Fig. 3). Mean axial pit cavity diameter, 2.3 μm. Mean vessel wall thickness, 3.0 μm. Libriform fibres dimorphic, the shorter wider fibres mostly distributed as tangential bands (Figs 1, 2). Mean libriform fibre length, 602 μm. Mean wall thickness of libriform fibres, 2.5 μm. Axial parenchyma scanty to abundant vasicentric. Axial parenchyma in strands of two cells. Multiseriate rays somewhat more abundant than uniseriate rays (Fig. 2). Ray cells procumbent, except for a few square cells at tips of multiseriate rays. Mean height of multiseriate rays, 258 μm. Mean width of multiseriate rays at widest point, 3.1 cells. Mean height of uniseriate rays, 73 μm. Mean wall thickness of ray cells, 0.8 μm. Ray cell pits mostly simple. Shorter fibres and axial parenchyma indistinctly storied (Fig. 2). Elongate crystals present in ray cells (Fig. 4). Dark-staining deposits in axial parenchyma cells (Fig. 1) and ray cells (Fig. 2).

COMMIDENDRUM ROTUNDIFOLIUM
(Figs 5, 6–12)

Growth rings not readily evident, perhaps present in relation to some of the tangential bands of shorter fibres (Fig. 5). Vessels solitary or grouped (Fig. 5). Mean number of vessels per group, 1.68. Mean vessel lumen diameter, 53 μm. Mean number of vessels per mm², 35. Mean vessel element length, 224 μm. Perforation plates simple. Lateral wall pitting of vessels alternate with some grooves interconnecting pit apertures. Mean axial diameter of pit cavities, 2.3 μm. Mean vessel wall thickness, 3.2 μm. Libriform fibres dimorphic. Mean length of libriform fibres, 552 μm. Mean wall thickness of libriform fibres, 2.4 μm. Axial parenchyma commonly abundant vasicentric, less commonly scanty vasicentric (Fig. 5). Axial parenchyma in strands of 1 or 2 cells (Figs 6, 12). Multiseriate rays more common than uniseriate rays (Fig. 6). Rays composed of procumbent cells almost exclusively; a few square cells at tips of multiseriate rays. Mean height of multiseriate rays, 239 μm. Mean width of multiseriate rays at widest point, 3.7 cells. Mean height of uniseriate rays, 42 μm. Mean ray cell wall thickness, 1.0 μm. Most ray cell pits non-bordered. Shorter fibres and axial parenchyma storied, although not clearly so in all places (Fig. 6). Crystals absent in rays. No deposits observed in ray cells or axial parenchyma.

COMMIDENDRUM RUGOSUM
(Figs 9–11)

Growth rings not evident (but growth ring absence probable because of cultivated provenance of specimen). Vessels mostly grouped (Fig. 9). Mean number of vessels per group, 2.04. Mean vessel lumen diameter, 24 μm. Mean number of vessels per mm², 101. Mean vessel element length, 166 μm. Perforation plates simple. Lateral wall pits of vessels alternate, circular to slightly oval. Inconspicuous grooves interconnect some pit apertures. Axial pit cavity diameter, 2.3 μm. Mean vessel wall thickness, 2.8 μm. Libriform fibres dimorphic, the shorter, wider fibres few in number. Axial parenchyma abundant to scanty vasicentric. Axial parenchyma strands of one or two cells. Multiseriate and uniseriate rays about equally frequent (Fig. 10). Rays composed of procumbent cells almost exclusively, square cells present only at tips of multiseriate rays. Mean height of multiseriate rays, 161 μm. Mean width of multiseriate rays at widest point, 3.0 cells. Mean height of uniseriate rays, 56 μm. Mean ray cell wall thickness, 1.0 μm. Most ray cell pits non-bordered. Shorter libriform fibres vaguely storied. Crystals present in ray cells (Fig. 11). No deposits observed in axial or ray parenchyma.

COMMIDENDRUM SPURIIUM
(Figs 7, 8, 13)

Growth rings not clearly demarcated, possibly indicated by tangential bands of shorter fibres (Fig. 7). Vessels mostly grouped (Fig. 7). Mean number of vessels per group, 2.36. Mean vessel lumen diameter, 46 μm. Mean number of vessels per mm², 22. Mean vessel element length, 184 μm. Perforation plates simple. Lateral wall pitting of vessels circular to oval, alternate. Grooves interconnect pit apertures. Axial diameter of vessel pits, 2.3 μm. Mean vessel wall thickness, 3.0 μm. Libriform fibres dimorphic, the shorter, wider fibres distributed in tangential and radial bands (Fig. 7). Mean libriform fibre length, 510 μm. Mean libriform fibre wall thickness, 2.3 μm. Axial parenchyma abundant vasicentric (Fig. 7). Axial parenchyma in strands of two cells, but more commonly undivided. Multiseriate rays more common than uniseriate rays (Fig. 8). Rays composed of procumbent cells except for tip cells of multiseriate rays, which vary from square to rhomboid shapes (Fig. 13). Mean
Figures 5-8. Wood sections of Comminidendrum. Figs 5, 6. C. rotundifolium. Fig. 5. TS; vasicentric parenchyma around vessel groups is abundant. Fig. 6. TLS; wider parenchymalike fibres are adjacent to vessel at left. Figs 7, 8. C. spurium. Fig. 7. TS; short parenchymalike fibres form tangential and radial bands adjacent to vessels and vessel groups. Fig. 8. Tangential section; multiseriate rays are short and composed of procumbent cells. Figs 5–8, magnification as in Fig. 1.
Figures 9–13. Wood sections of Commidendrum. Figs 9–11. *C. rugosum*. Fig. 9. TS; vessels notably narrow. Fig. 10. TLS; most libriform fibres in this view are long, narrow and thick-walled, although a few wide short fibres (near right edge) are present. Fig. 11. SEM photograph of elongate prismatic crystals from TLS. Fig. 12. *C. rotundifolium*, radial section, showing band of axial parenchyma cells running vertically. Fig. 13. *C. spurium*, TLS showing predominantly procumbent shape of ray cells. Figs 9, 10, magnification as in Fig. 1; Fig. 11, scale bar = 5 μm; Figs 12, 13, scale bar = 40 μm.
height of multiseriate rays, 56 µm. Mean width of multiseriate rays at widest point, 3.1 cells. Mean height of uniseriate rays, 56 µm. Mean wall thickness of ray cells, 1.0 µm. Some pits on tangential walls of ray cells bordered. Shorter fibres and axial parenchyma storied, sometimes irregularly (Fig. 8). Crystals absent in ray cells. Deposits absent in ray and axial parenchyma.

**MELANODENDRUM INTEGRIFOLIUM**

(Figs 14-17).

Growth rings absent (Fig. 14). Vessels mostly grouped (Fig. 14). Mean number of vessels per group, 2.56. Mean vessel lumen diameter, 53 µm. Mean vessel element length, 300 µm. Perforation plates simple. Lateral wall pitting of vessels oval and alternate (Fig. 16), transitional (Figs 16, 17) or pseudoscalariform (Fig. 17). Axial diameter of vessel wall pits, 5 µm. Grooves interconnecting pit apertures present. Mean vessel wall thickness, 2.5 µm. Libriform fibres dimorphic, but the shorter fibres are only slightly thinner-walled than the longer libriform fibres. Mean libriform fibre length, 502 µm. Mean libriform fibre wall thickness, 2.0 µm. Axial parenchyma scanty vasicentric (Fig. 14). Axial parenchyma in strands of two cells. Multiserate rays more numerous than uniseriate rays (Fig. 15). Ray cells predominantly procumbent, a few square or upright cells present at tips of multiserate rays. Mean height of multiserate rays, 141 µm. Mean width of multiserate rays at widest point, 2.6 cells. Mean height of uniseriate rays, 74 µm. Shorter libriform fibres indistinctly storied (Fig. 15). Crystals absent in ray cells. No deposits present in axial or ray parenchyma cells.

**PETROBIUM ARBOREUM**

(Figs 18-21)

Growth rings absent (Fig. 18). Vessels solitary or in short radial clusters (Fig. 18). Mean number of vessels per group, 1.48 µm. Mean vessel lumen diameter, 67 µm. Mean number of vessels per mm², 11. Mean vessel element length, 329 µm. Perforation plates predominantly simple, but a very small number of perforation plates with numerous slender bars present (not illustrated). Lateral wall pitting of vessels circular and alternate or transitional, axial diameter of pit cavities, 5 µm. Mean vessel wall thickness, 5.0 µm. Libriform fibres dimorphic, the shorter fibres thinner walled and often subdivided into strands of two cells and therefore definable as axial parenchyma (Fig. 19). Mean length of libriform fibres, 764 µm. Mean wall thickness of longer libriform fibres, 5 µm; mean wall thickness of shorter fibres/axial parenchyma, 2.3 µm. Axial parenchyma scanty vasicentric, intercontinuous with bands representing fibre dimorphism (Figs 20, 21). Multiserate rays present exclusively (Fig. 19). Upright, square, and procumbent cells about equally abundant throughout rays. Mean height of multiserate rays, 1033 µm. Mean width of multiserate rays at widest point, 3.7 cells. Mean wall thickness of ray cells, 1.3 µm. Some borders present on pits of tangential walls of ray cells. Axial parenchyma and shorter fibres storied (Fig. 19); longer libriform fibres indistinctly storied. Crystals absent in rays. Deposits absent in axial parenchyma, but some resin-like deposits observed in vessels.

**PLADAROXYLON LEUCADENDRON**

(SENECIO LEUCADENDRON)

(Figs 22, 23)

Growth rings absent. Vessels solitary or in small clusters (Fig. 22). Mean number of vessels per group, 1.89. Mean vessel lumen diameter, 63 µm. Mean number of vessels per mm², 21. Mean vessel element length, 306 µm. Perforation plates simple. Lateral wall pits of vessels circular to oval, alternate. Mean axial diameter of pit cavities, 5 µm. Vessel wall thickness, 3.0 µm. Libriform fibres monomorphic, mean length 572 µm. Mean libriform fibre wall thickness, 3.5 µm. Axial parenchyma scanty vasicentric (Fig. 22). Axial parenchyma in strands of two to three cells. Multiserate rays predominant, uniseriate rays uncommon (Fig. 23). Procumbent, square and upright cells about equally common throughout rays. Mean height of multiserate rays, 987 µm. Mean width of multiserate rays at widest point, 4.8 cells. Mean height of uniseriate rays, 153 µm. Mean wall thickness of ray cells, 1.1 µm. Most ray cell pits simple. Libriform fibres indistinctly storied (Fig. 23). Deposits seen in a few vessels (Fig. 22).

**LACHANODES ARBOREA (SENECIO REDIIVUS)**

(Figs 24-27)

Growth rings absent (Fig. 24). Vessels solitary or in radial clusters (Fig. 24). Mean number of vessels per group, 1.84. Mean vessel lumen diameter, 53 µm. Mean number of vessels per mm², 49. Mean vessel element length, 360 µm. Perforation plates simple, but a very few aberrant plates with numerous very fine bars present. Lateral wall pitting of vessels alternate (Fig. 25). Lateral wall pitting of vessel circular to oval, alternate (Fig. 26), transitional (Fig. 26) or pseudoscalariform (Fig. 27). Axial diameter of vessel pit cavities about 5 µm. Mean vessel wall thickness, 2.1 µm. Libriform fibres monomorphic, mean length, 739 µm. Mean libriform fibre wall thickness, 3.5 µm. Multiserate rays predominant, only a few uniseriate rays present (Fig. 25). Procumbent cells present in central portions of rays, but square and upright cells common throughout multiserate rays. Mean height of multiserate rays, 1143 µm. Mean width of multiserate rays at widest point, 6.3 cells. Mean height of uniseriate rays, 106 µm. Mean wall thickness of ray cells, 1.2 µm.
Figures 14–17. Wood sections of *Melanoderon integrifolium*. Fig. 14. TS; vessel density is low. Fig. 15. TLS; most libriform fibres are wide, short; some fibres are indistinctly storied. Figs 16, 17. Vessel wall portions from radial sections. Fig. 16. Alternate and transitional pitting; axial parenchyma on either side of vessel. Fig. 17. Alternate, transitional, and pseudoscalariform pitting on vessel wall. Figs 14, 15, magnification as in Fig. 1. Figs 16, 17, scale bar in Fig. 16 = 20 μm.
Figures 18-21. Wood sections of *Petrosium arboreum*. Fig. 18. TS; vessels mostly in radial clusters. Fig. 19. TLS; axial parenchyma and parenchymalike fibres to left of centre. Figs 20, 21. TS showing distribution of wider, shorter libriform fibres. Fig. 20. Strand of wider fibres apotracheal, between vessels. Fig. 21. Wider fibres in a radial strip, to the right of the vessels. Figs 18, 19, magnification as in Fig. 1; Figs 20, 21, magnification as in Fig. 12.
Figures 22–27. Wood sections of Senecioneae. Figs 22, 23, *Pladaxylon leucadendron* (*Senecio leucadendron*). Fig. 22. TS; vessels wide, density low. Fig. 23. TLS; rays multiseriate. Figs 24–27. *Lacharodes arborea* (*Senecio redivius*). Fig. 24. TS; vessels narrow, density high. Fig. 25. TS; multiseriate rays notably wide. Fig. 26. Pitting alternate. Fig. 27. Some pitting alternate (right edge of vessel) but most pitting pseudoscalariform. Figs 22–25, magnification as in Fig. 1; Figs 23, 27, magnification as in Fig. 16.
Ray cell pits mostly simple. Libriform fibres indistinctly storied (Fig. 25). No crystals observed in wood cells. No deposits observed in axial or ray parenchyma.

SYSTEMATIC, GEOGRAPHICAL AND HABITAL CONCLUSIONS

Commidendrum and Melanodendrum are closely paired in the treatment of Hoffmann (1890). This closeness is evidenced in wood anatomy by the presence of fibre dimorphism (for a discussion of this concept in Asteraceae, see Carlquist, 1958, 1961, 1988, 2001). The shorter, wider, thinner-walled fibres in the two genera are wider and also, in general, more clearly storied than the longer, narrower, thicker-walled fibres. The shorter fibres of Commidendrum and Melanodendrum are morphologically transitional to axial parenchyma. In all species of both genera, grooves interconnect pit apertures in vessel walls. Further, Commidendrum and Melanodendrum share homogeneous Type II rays (for definition, see Carlquist, 1988, 2001), whereas most Asteraceae have heterogeneous or paedomorphic rays. Generic characters shared by the species of Commidendrum include relatively abundant (for the family) paratracheal axial parenchyma and vessel wall pits with small cavity diameter (c. 2.3 μm). In Melanodendrum, in contrast, paratracheal axial parenchyma is scanty, and vessel pits are larger (c. 5 μm). The present treatment of the two genera is justified, therefore. Commidendrum rugosum shares with C. robustum the unusual feature of elongate crystals in ray cells, and is probably an indicator of close relationship between the two species. The quantitative vessel features of C. rugosum differ from those of the other species and relate to differences in ecology, discussed below.

Sections of moderately small stems of Felicia amelloides reveal the same qualitative features seen in Commidendrum and Melanodendrum, although the wood of F. amelloides is somewhat more juvenile because of sample size. A close relationship between Felicia and the two St Helena genera of Asteraceae is justified on the basis of wood anatomy. Wood of Felicia was studied because Noyes & Rieseberg (1999), in a DNA-based cladogram of Asteraceae, place Felicia and Amellus as basal (but adjacent) to Commidendrum. The affinities of Commidendrum and Melanodendrum seem clearly to lie with the African genera of Asteraceae Felicia and Amellus, although DNA data from a larger number of genera of Asteraceae would, of course, be desirable. Hoffmann (1890) recognized 50 species of Felicia, all shrubs, mostly from southern Africa. The woody (albeit non-arborescent) nature of Felicia, and the opposite leaves of Felicia and Amellus are shared with Commidendrum and Melanodendrum. The two St Helena genera appear to have had woody ancestry, as indicated by lack of paedomorphic features (see Carlquist, 1962, 1988, 2001) in the wood. An increase in stature from shrubs to trees during evolution of Commidendrum and Melanodendrum on St Helena would be consistent with data available. If paedomorphosis were present in these woods, one would hypothesize evolution from herbaceous or near-herbaceous to woody, rather than increase in plant size within an already woody (i.e. shrubby) phylad. Cronk (1992) had suggested relationship between the pair of St Helena genera and Austromalesian genera of Asteraceae such as Olearia. This relationship would seem unlikely on the basis of distance between the Austromalesian localities of Olearia and St Helena, because long-distance dispersal must be hypothesized for St Helena. St Helena is a volcanic island, and no connection to any continental land mass has ever been demonstrated (Ashmole & Ashmole, 2000). Long-distance dispersal of the St Helena Asteraceae by oceanic drift, as suggested by Ashmole & Ashmole (2000) is unlikely, because no Asteraceae have been demonstrated to have achenes viable after soaking in seawater. Olearia is not the most likely relative: its wood differs from that of Commidendrum and Melanodendrum by lacking fibre dimorphism and by having heterogeneous rays (Carlquist, 1960).

The family Asteraceae is probably basically woody (Carlquist, 1966), a conclusion reached by cladistic studies using macromorphology (Bremer, 1987) and molecular data (Jansen et al., 1991). However, some phylads of Asteraceae have probably changed from moderately woody to herbaceous, judging from cladograms available (Bremer, 1987; Jansen et al., 1991). Some herbaceous phylads of Asteraceae have developed secondary woodiness, a phyletic trend indicated by cladograms such as those of Böhle et al., 1996; Francisco-Ortega et al., 2001; Kim et al., 1996 and others cited in the Introduction. Paedomorphism in wood has proved to be a viable indicator of secondary woodiness (Carlquist, 1980, 1988, 2001). Although paedomorphism in wood is not indicated in the Commidendrum–Melanodendrum line, it does occur in the species discussed below.

Although a few anatomical data on Petrobiurn were presented earlier (Carlquist, 1957), no wood data were presented then or in the survey of Heliantheae (Carlquist, 1958). The wood description given above is the first to be offered. The wood of Petrobiurn exhibits a number of distinctive features. One of these is fibre dimorphism: the longer fibres are vaguely storied, the shorter fibres more clearly storied. The short fibres, although not subdivided, are distributed in bands and strands and could be considered transitional to axial parenchyma. A survey of my wood sections of Bidens,
Fitchia and Oparanthus reveals that Petrobium possesses no features not also seen in these genera. Fitchia and Oparanthus are likely derivatives of Bidens that has colonized Pacific islands, whereas Pacific insular species of Bidens represent one or more (probably several) later colonizations. Petrobium is very likely also a derivative of Bidens that has reached St Helena either from Africa or South America by long-distance dispersal, probably via migratory birds. Oparanthus and Petrobium share quadrimerous disk corollas, but this single feature is not an indicator of close relationship. Cronk (1992) hypothesized a relationship between Oparanthus and Petrobium, but the distance between St Helena and the Polynesian localities of Oparanthus alone would lead one to doubt this. Shannon & Wagner (1997) offer the quote “Carlquist (1974: 417, 450) has stated that the south Atlantic Petrobium and the Polynesian lineage which gave rise to both Oparanthus and Fitchia were presumably independently derived from a Bidens-like ancestor, an hypothesis with which we agree.” I see no reason to depart from this conclusion. Hopefully, molecular data will soon identify precise pathways within this alliance.

The mean vessel element length of Petrobium (329 μm) is higher than the mean figure for vessel elements of Asteraceae from mesic habitats, 282 μm (Carlquist, 1966). Upright cells occur in multiseriate rays of Petrobium, and are not restricted to tips and a marginal cell layer of the rays as is typical in truly woody plants. Rather, the upright cells comprise at least half of the ray tissue. The long vessel elements, occasional perforation plate with fine bars, and ray histology of Petrobium correspond to criteria of xylary paedomorphosis in wood of dicotyledons (Carlquist, 1962), and indicate probable secondary woodiness for Petrobium.

The St Helena Senecioneae have been placed into two monotypic genera, Lachanodes and Pladaroxylon. Hoffmann (1890) treated the two species within the section Arborei of Senecio, along with species from Fernando Po, Cameroons, and E. Africa. Mabberley (1975) placed the two species within Senecio, but claimed that “they resemble nothing in Africa”, without detailing the reasons for his assertion. Mabberley (1975) further claimed that the two St Helena species show similarities to “woody Senecioneae of the South American Islands”, although the islands are not specified. Perhaps Robinsonia on the Juan Fernandez Islands was hinted as the relative, but it was not specified. Mabberley (1874) believed that the “pachycaulous” habit of the St Helena Senecioneae is primitive within the tribe. Cronk (1987) mentioned Lordhowea of New Zealand as a possible close relative for both St Helena senecionids. Cronk (1992) claims South America and Australasia as source areas for the St Helena Senecioneae, but does not offer evidence for this interpretation. Unfortunately, the large size of the genus Senecio will delay accurate determination of the affinities of the St Helena species by means of DNA analysis. Pending the outcome of such studies, I see no reason to exclude Africa as a source area for the St Helena I. Senecioneae. Certainly Africa or continental South America is closer than the Juan Fernandez Islands or Australasia, and the St Helena flora and fauna (Melliss, 1875) are congruent with those of other oceanic islands, so that a source area close to St Helena should be expected unless there is persuasive evidence to the contrary.

There is a report of pollen of Asteraceae in an early Pliocene deposit 9 Myr BP on St Helena I. (Muir & Baker, 1968). Evidence now shows that the family must have begun with barnadesioid in South America (Bremer, 1987; Jansen et al., 1991). Asteraceae, Heliantheae and Senecioneae appeared appreciably later, as indicated and the dating of the St Helena pollen grains referred to Asteraceae are correct, there is no assurance that these grains belong to phylads of Asteraceae that currently occupy St Helena I. Moreover, there is no evidence for an unbroken occupancy of St Helena by those or other Asteraceae. We need 'molecular clock' data on the St Helena Asteraceae. Molecular data will prove more powerful than any other data set in clarifying relationships, timing of colonization and evolutionary change in the St Helena Asteraceae.

Secondary woodiness on islands is now widely accepted (Wagner & Funk, 1995; Francisco-Ortega et al., 1995, 1996, 2001; Rahn, 1996; Böhle et al., 1996; Kim et al., 1996). Although selection for features that avoid inbreeding is obviously a factor important to plant evolution on islands (Carlquist, 1974), other factors may be of greater significance in evolution of woody growth forms on islands. If Asteraceae, Lamiaceae and other families are considered alongside an appreciable number of herbaceous species, increased woodiness is evident in species of areas of Mediterranean-type climates with minimal frost, such as those of southern California, southern Europe or in areas of cloud forest in the Andes. Böhle et al. (1996) omit mention of secondary woodiness on continental areas such as those where inbreeding is not a problem, and consequently, their concept that avoidance of inbreeding is the selective factor that leads to increased woodiness.
on Macaronesian islands is dubious. These authors even go so far as to declare growth forms of some of the Canarian Echium species as "non-adaptive", without giving any evidence for this designation.

ECOLOGICAL CONCLUSIONS
All of the the woody St Helena Asteraceae except for Commidendrum rugosum occur in wet forest (Ashmole & Ashmole, 2000; Cronk, 2000). Commidendrum rugosum occurs in lowlands, especially in steep valleys above the coast, and may have commonly occurred on lowland flats in earlier times (Cronk, 2000). Vessel features of woods tend to be a sensitive indicator of ecology, as shown for the southern California flora by Carlquist & Hoekman (1985). The mesomorphy ratio (vessel diameter times vessel element length divided by number of vessels per mm² of transection) is the figure that proved most useful in that study. Carlquist & Hoekman (1985) report figures for this ratio for woods of desert shrubs (21), chaparral (87), and sage scrub areas (81) of southern California. Mesomorphy ratios are also given for woody plants of riparian area (106) and for mesic woodland areas (1950). The lowest mesomorphy ratio value among the woods of St Helena I. Asteraceae is that of Commidendrum rugosum (39), which is in line with the values cited for shrubs from dry areas of southern California. Mesomorphy ratio values for woods of the remaining St Helena Asteraceae are: C. robustum (300); C. rotundifolium (339); C. spurium (385); Melanodendrum integrifolium (611); Petroleum arboreum (2003); Lachanodes arborea (389); and Pladaroxylon leucadendron (918). The range from 300 to 2003 is not as great as it may seem; any value of 300 or above indicates a definitely mesic habitat, and the higher values may be correlated with larger leaf size, which in turn tends to be associated with wider vessels that permit greater transpiration. Because there are no weather stations in the various localities where the St Helena species of Asteraceae occur, it is impossible to determine whether there are correlations between the mesomorphy ratio values of 300 and above and soil moisture of the various summit ridge localities of St Helena.

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