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Wood and bark anatomy of *Steganotaenia* and *Polemanniopsis* (tribe Steganotaenieae, Apiaceae) with notes on phylogenetic implications

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The wood and bark structure of the distinctive southern African genera *Polemanniopsis* (including the newly described species *P. namibensis*) and *Steganotaenia* have been described. To allow for comparisons with the traditional subfamily Saniculoideae, a shrubby species of *Eryngium* from the Juan Fernández Islands was also studied. *Polemanniopsis* and *Steganotaenia* were recently considered as two closely related genera forming a new tribe Steganotaenieae of subfamily Saniculoideae (Apiaceae), whereas *Eryngium* is commonly recognized as a member of Saniculoideae. *Eryngium* differs significantly from the other two genera in the smaller size of intervessel pits, sclerification and radial dilatation in collapsed secondary phloem, the absence of crystals in the phelloderm cells and the occurrence of druse crystals in secondary phloem ray cells. *Steganotaenia* and *Polemanniopsis* share features, including the presence of marginal axial parenchyma, the occurrence of radial secretory canals in secondary xylem, dilatation of the secondary phloem by axial parenchyma stretching, cortical periderm initiation and the presence of chambered phelloderm cells containing druse crystals. These characters (especially the occurrence of chambered crystalliferous cells in phelloderm, which has not yet been reported for Apiaceae) support both the monophyly and the isolated position of the Steganotaeniae. No reliable synapomorphic features could be found to support a relationship with Saniculoideae. *Steganotaenia* is remarkable in the presence of axial secretory canals in the phelloderm: these structures have not yet been found in the periderm of any member of Apiales. Our results do not provide any support for the suggestion that the woody habit in the three genera examined was derived from herbaceous ancestors secondarily. *Botanical Journal of the Linnean Society*, 2010, **163**, 55–59.

ADDITIONAL KEYWORDS: Apiales – chambered crystaliferous cells – *Eryngium* – periderm – phelloderm – Saniculoideae – secretory canals.

INTRODUCTION

Polemanniopsis B.L.Burtt and *Steganotaenia* Hochst. are two distinctive taxa of woody Apiaceae endemic to the African continent. The former genus comprises two shrubby species: *Polemanniopsis namibensis* B-E. van Wyk, A.Burke & Mannh. is endemic to a small desert area in southern Namibia (Van Wyk *et al.*, 2010), whereas *Polemanniopsis marlothii* (H.Wolff) B.L.Burtt is restricted to two known localities in the western part of South Africa (Cedarberg Mountains and the Richtersveld). Both are woody shrubs with summer–deciduous, hysteranthous leaves; the former is ≤ 0.6 m high, whereas the latter is ≤ 4 m. In *Steganotaenia*, *Steganotaenia araliacea* Hochst is a deciduous shrub or small tree ≤ 10 m tall which is widespread in the tropical parts of Africa, whereas two other species of this genus, *S. hockii* (C.Norman) C.Norman and *S. commiphoroides* Thulin, are both found only in East Africa (Ethiopia and Somalia).

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On the basis of DNA sequence data, *Polemanniopsis* and *Steganotaenia* were proposed to be 'sister taxa and that this clade is sister to Apiaceae subfamily Saniculoideae' (Downie & Katz-Downie, 1999). Van Wyk (2001) agreed that these two genera share several synapomorphies and added that they are 'basal' (i.e. early branching) in Apioideae. Some of their morphological characters were described by Liu, Van Wyk & Tilney (2004) 'as potential synapomorphies, not only between *P. marlothii* and *S. araliacea*, but also between them and Saniculoideae'.

Subfamily Saniculoideae (Calviño & Downie, 2007) have a unique fruit structure (Liu, Van Wyk & Tilney, 2003), which includes a non-lignified endocarp, outgrowths on the mericarp, large secretory ducts (rib oil ducts) which are invariably situated in the ribs (intrajugal), and a complete absence of vallecular and commissural vittae. The transfer of *Steganotaenia* from subfamily Apioideae to Saniculoideae was supported by Liu, Van Wyk & Tilney (2006), based on the presence of irregular vittae and druse crystals in the fruits and by Calviño *et al*. (2006), based on molecular evidence. Convincing molecular evidence for a sister-group relationship between *Polemanniopsis* and *Steganotaenia* was reported by Calviño & Downie (2007), who formally described a new tribe, Steganotaenieae C.I.Calviño & S.R.Downie, to accommodate them. A reconsideration of relationships amongst the early divergent lineages of Apioideae (the so-called 'protoapioids') and Saniculoideae has recently shown that several African genera (*Choritaenia* Benth., *Marlothiella* H.Wolff, *Lichtensteinia* Cham. & Schltdl., *Phlyctidocarpa* Cannon & Theobald) are anomalous in their morphology and that the traditional classification system requires modification (Magee *et al*., 2010). Especially noteworthy is the co-occurrence of large rib oil ducts and vittae in *Phlyctidocarpa* and some species of *Alepidea* Delar. (Yembaturova *et al*., in press). The conclusion was that these taxa represent isolated relicts that are as distinctive as the traditional concept of Saniculoideae. A new tribal classification system was proposed, in which the circumscription of Apioideae was extended to include the Saniculoideae (as tribe Saniculeae W.D.J.Koch) and several other early divergent lineages (Magee *et al*., 2010). It was argued that there are no morphological or anatomical features available for use as diagnostic characters or synapomorphies to support a hierarchical relationship between these phylogenetically isolated tribes.

An anatomical study can be useful to support evidence obtained from other sources of taxonomic information (Metcalfe & Chalk, 1950; Rodríguez, 1957; Guyot, 1966; Chuang, 1970; Theobald, 1971; Lotova & Timonin, 2005; Oskolski *et al*., 2007). This study was carried out to evaluate the taxonomic value of anatomical characters in exploring the relationships between the two woody southern African genera representing Steganotaenieae and their possible affinity with Saniculoideae. To date, published results on wood anatomy are available only for *Steganotaenia araliacea* (Metcalfe & Chalk, 1950; Rodríguez, 1957; Dechamps, 1977). Moreover, a fossil wood from the lower Pleistocene of Ethiopia has been placed by Dechamps (1977) near this species under the name *Steganotaenioxylon araliaceum* R.Dechamps. However, the bark structure of *Steganotaenia* remains unknown and nothing has been published on the wood and bark anatomy of the two *Polemanniopsis* spp.

For comparison of bark and wood characters, *Eryngium bupleuroides* Hook & Arn., a shrub or small tree that is endemic to Juan Fernández Islands (Bernardello *et al*., 2001), was also studied. This species was chosen as one of few truly woody representatives of Saniculoideae other than Steganotaenieae. Some data on the wood structure of *E. bupleuroides* were recorded by Rodríguez (1957); an anatomical investigation of the young stem of this species was made by Lemesle (1926).

A detailed study of Steganotaenieae was considered necessary because there is little known about Saniculoideae and putative relatives in Africa. According to Burtt (1991), a study of southern African Apiaceae, especially of the woody elements, would lead to greater insight into relationships in the family as a whole. Recent molecular systematic studies by Calviño *et al*. (2006), Calviño & Downie (2007), Calviño, Martínez & Downie (2008), Nicolas & Plunkett (2009) and Magee *et al*. (2010) have all shown that the woody African Apiaceae are critical to a better understanding of the early diverging lineages of subfamilies Mackinlayoideae, Saniculoideae and Apioideae. Most of these genera and species are geographically highly localized and hitherto poorly studied.

MATERIAL AND METHODS

The origin of the material used is listed in Table 1. Fresh material was fixed for at least 24 h in formalin–acetic acid–alcohol (FAA) and dry fragments were rehydrated before fixing in FAA.

The wood sample of *E. bupleuroides* was obtained from the wood collection (Uw) of the National Herbarium of the Netherlands. Two wood samples of *S. araliacea* were obtained from the Economic Botany Collection (Kw) at the Royal Botanic Gardens, Kew; one sample of this species was collected by A. A. Oskolski and B.-E. van Wyk from a cultivated plant in the Pretoria National Botanical Garden. Other

Table 1. Material of woody southern African Saniculoideae used for bark (b) and wood (w) anatomical studies

Taxon	Voucher specimen	Number of the sample in wood collection	Locality	Plant parts studied
Eryngium bupleuroides Hook.	Meyer 9648, U	Kw 15018	Chile, Juan Fernández Islands	b, w (dry)
Polemanniopsis marlothii (H.Wolff) B.L.Burtt	Pimenov 83, MW		South Africa, Northern Cape Province, Cederberg mountains, North of Citrusdal	w
Polemanniopsis marlothii	Oskolski 40-06, LE		South Africa, Northern Cape Province, Cederberg mountains, North of Citrusdal	b, w (FAA*)
Polemanniopsis namibensis B.-E.van Wyk, A.Burke & Mannh.	Mannheimer 2769, JRAU		Namibia, Kaukausib Fountain	b, w (dry)
Steganotaenia araliacea Hochst.	Welwitsch 2517, K	Kw 10608	South-west tropical Angola	w
Steganotaenia araliacea	Meikle 1057, K	Kw 10611	Nigeria	w
Steganotaenia araliacea	Seidel 1193, PRE		South Africa, Pretoria, National Botanical Garden, cultivated	b (fresh, FAA), w (70% alcohol)

*FAA, formalin–acetic acid–alcohol.

wood samples were obtained from the collectors listed in Table 1. Voucher specimens are deposited at JRAU, K, LE, MN, PRE and various other institutions.

The bark samples were collected from the same plants as the wood samples (Table 1). The fresh bark samples of *P. marlothii* and *S. araliacea* were cut from branch tips without a visible periderm layer and from other stem parts on which the bark was mature, having a more or less a thick periderm. The bark structure of *E. bupleuroides* and *P. namibensis* was examined from the dried bark of wood samples. The single bark sample studied of *Polemanniopsis namibensis* (Mannheimer 2769) had a wide zone of collapsed secondary phloem and remnants of cortical parenchyma. Neither the epidermis nor cortical collenchyma was examined. The epidermis and cortex were not been examined for *Eryngium bupleuroides* (Meyer 9648) [but their anatomical structure was briefly described by Lemesle (1926)].

Both fresh and dried bark samples were fixed in FAA for at least 24 h, before being stored in 70% alcohol (Johansen, 1940). Transverse, tangential and radial bark and wood sections of 15–30 μm thick were made using a freeze microtome (Ernst Leitz GMBH, Wetzlar, Germany) or a sledge microtome (R. Jung AG, Heidelberg, Germany). Standard preparation procedures were used for wood, light microscopic studies and macerations (Carlquist, 2001). The sections were then stained according to either one of two methods: in toluidine blue for 1 min, before being thoroughly washed with water or with a 1:1 alcian blue/safranin mixture. The sections were mounted in Euparol mounting fluid. The measurements of wood and bark elements were carried out by using UTHSCSA ImageTool version 3 (Brent Dove, 1996–2002) software.

All sections were photographed with a JVC KY-F1030 digital camera, connected to a Leitz Wetzlar Orthoplan light microscope. The terminology used to describe the wood structure follows the recommendations of the International Association of Wood Anatomists (IAWA) Committee (1989) and Carlquist (2001). Measurements were carried out according to Carlquist (2001), except for the recording of the vertical dimension diameter of intervessel pits. The bark descriptions follow Trockenbrodt (1990). Sheath parenchyma is used to describe parenchyma which is associated with the axial secretory canals (Roth, 1981) and axial phloem parenchyma is the term used for parenchyma which is associated with companion cells and sieve tubes. 'Elongated sclerified cells' is the

Figures 1–4. Figures 1 and 2. Wood structure of *Steganotaenia araliacea* (Welwitch 2517). Scale bars, 100 μm. Fig. 1. Transverse section showing the indistinct growth ring boundary, marked by a zone of thin-walled fibres; paratracheal axial parenchyma in 1- to 3-seriate sheaths near vessels. Fig. 2. Tangential section showing rays composed mostly of procumbent cells; radial secretory canals. Figures 3 and 4. Wood structure of *Eryngium bupleuroides*. Scale bars, 100 μm. Fig. 3. Transverse section showing the indistinct growth ring boundary, marked by somewhat radially flattened fibres. Fig. 4. Tangential section showing rays composed mostly of procumbent cells; square and upright cells form short uniseriate portions and occur as solitary sheath cells; radial canals (arrows).

Table 2. Wood and bark anatomical characters of *Eryngium*, *Polemanniopsis* and *Steganotaenia**

	1	2	3	4	5	6	7	8	9	10	11	12	13
Eryngium bupleuroides (Meyer 9648)	12	222 ± 12.3 151–338	243 ± 10.6 140–344	4.2/4.9	57	41 ± 0.9 20–60	1.8/7	29	386 ± 8.0 281–515	3.0/5	0.43/0.85	2.0	4.0
Polemanniopsis marlothii (Oskolski 40-06)	5	272 ± 9.4 194–362	312 ± 15.7 185–581	6.0/7.5	60	44 ± 3.2 13–85	1.7/12	31	371 ± 13.0 208–541	2.3/3	0.31/0.62	2.6	4.7
Polemanniopsis marlothii (Pimenov 83)	5	–	290 ± 9.9 204–468	6.3/8.0	42	49 ± 1.6 22–81	2.0/6	22	400 ± 9.6 276–540	2.6/5	0.27/0.74	4.3	6.0
Polemanniopsis namibensis (Mannheimer 2769)	2	163 ± 10.1 88–243	312 ± 13.9 165–479	5.1/6.3	153	41 ± 3.2 13–75	2.9/10	11	386 ± 13.5 212–740	1.2/3	0.24/0.44	6.3	1.3
Steganotaenia araliacea (Welwitsch 2517)	50	–	455 ± 18.6 256–620	7.9/9.9	9	115 ± 2.9 56–168	1.8/6	30	684 ± 18.9 515–998	4.1/7	0.42/1.11	0.4	5.2
Steganotaenia araliacea (Meikle 1057)	22	–	426 ± 18.4 220–660	6.6/7.6	17	107 ± 1.8 68–136	2.1/7	20	649 ± 16.0 452–811	3.9/5	0.56/1.17	0.3	4.2
Steganotaenia araliacea (Seidel 1193)	11	247 ± 24.5 95–581	462 ± 14.9 282–602	4.8/6.8	56	66 ± 2.9 34–92	2.6/12	18	524 ± 17.7 218–692	2.5/4	0.24/0.51	2.0	6.1

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

term used to describe fibre-like sclereids, which form fusiform axial phloem parenchyma cells when secondarily differentiated. The fibre-like sclereids do not fit the definitions of fibres or sclereids given by Trockenbrodt (1990).

Wood and bark fragments were also embedded in glycol methacrylate (GMA) according to a modification of the Feder & O'Brien (1968) method. Transverse, tangential and radial (wood, bark) sections of *c*. 5 μm thick were cut by using a Porter Blum MT-1 ultramicrotome. Wood and bark sections were then stained with toluidine blue before being mounted in Entellan.

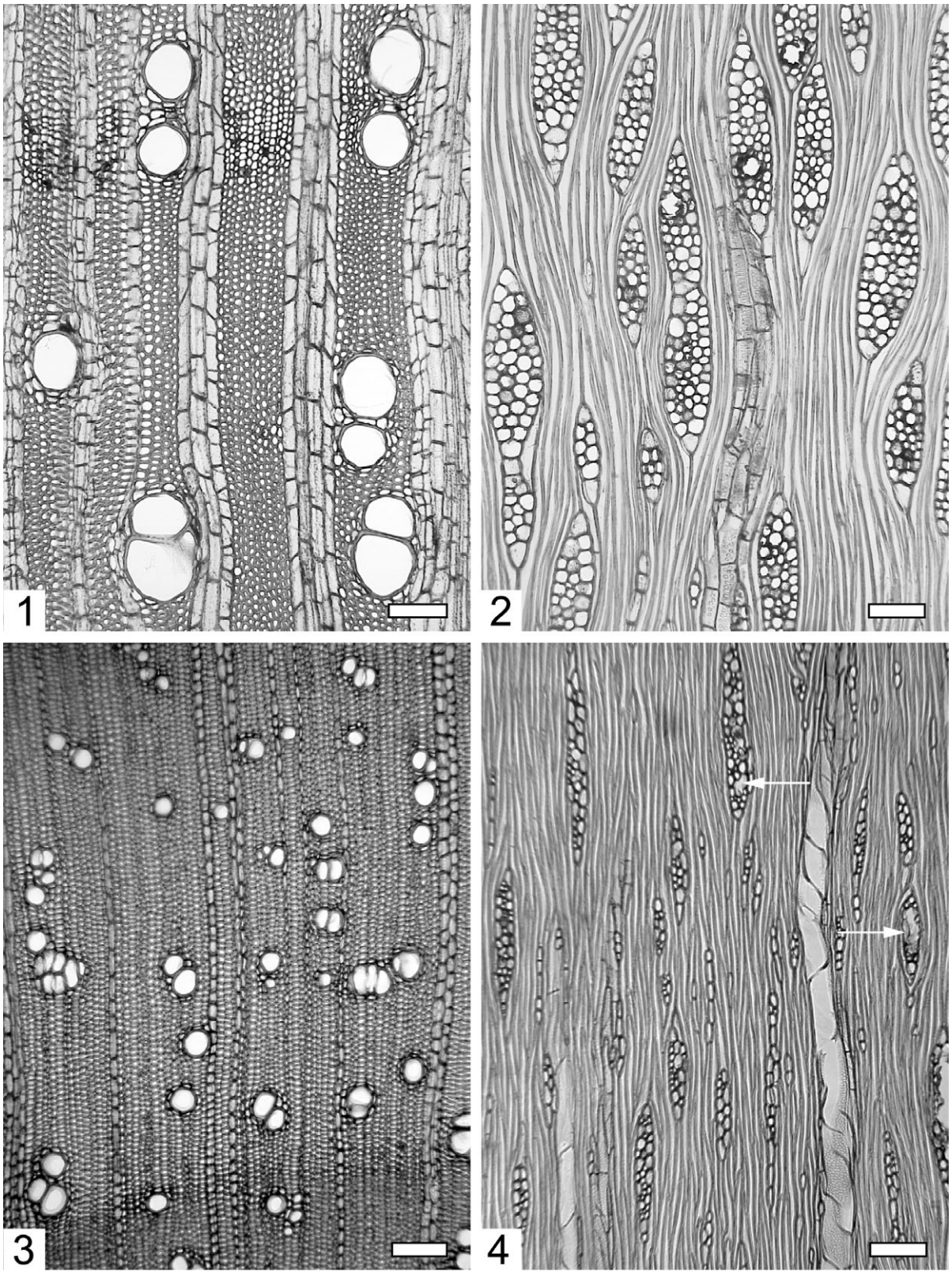
RESULTS

The qualitative characters of wood and bark for the taxa under study are given in Table 2. Transverse sections of the wood of *E. bupleuroides*, *P. marlothii*, *P. namibensis* and *S. araliacea* are shown in Figure 1, followed by the tangential sections in Figure 2. Figure 3 shows bark transverse sections and Figure 4 the bark tangential sections.

WOOD STRUCTURE (FIGS 1, 2)

Growth ring boundaries are indistinct to distinct, marked by zones of thin-walled fibres in *S. araliacea* (M1057, W2517) (Fig. 1), by interrupted lines of marginal axial parenchyma and by zones of somewhat radially flattened fibres in *E. bupleuroides* (Fig. 3) or by continuous lines (*P. namibensis*) or 2- to 5-seriate (up to 10-seriate) bands of marginal axial parenchyma in *P. marlothii* (Fig. 5).

Vessels are rounded or angular in outline, rather narrow in both *Polemanniopsis* spp. and *E. bupleuroides* (≤ 85 μm in tangential diameter in *P. marlothii*) and somewhat wider in *S. araliacea* [≤ 90 μm in (S1191) and ≤ 168 μm in (W2517)], not numerous in *S. araliacea* [9–17 per mm^2, ≤ 56 per mm^2 (S1193)] to more numerous in other species [up to very numerous (153 per mm^2) in *P. namibensis*], solitary or in clusters or radial multiples of two to eight (up to 14 in *P. namibensis*). Vessel walls are 2–4 μm thick in *P. namibensis* and 2–8 μm thick in other species [≤ 10 μm in *S. araliacea* (M1057)]. Some vessels contain tyloses in *S. araliacea* (S1193). Vessel elements are relatively long in *S. araliacea* [(220–)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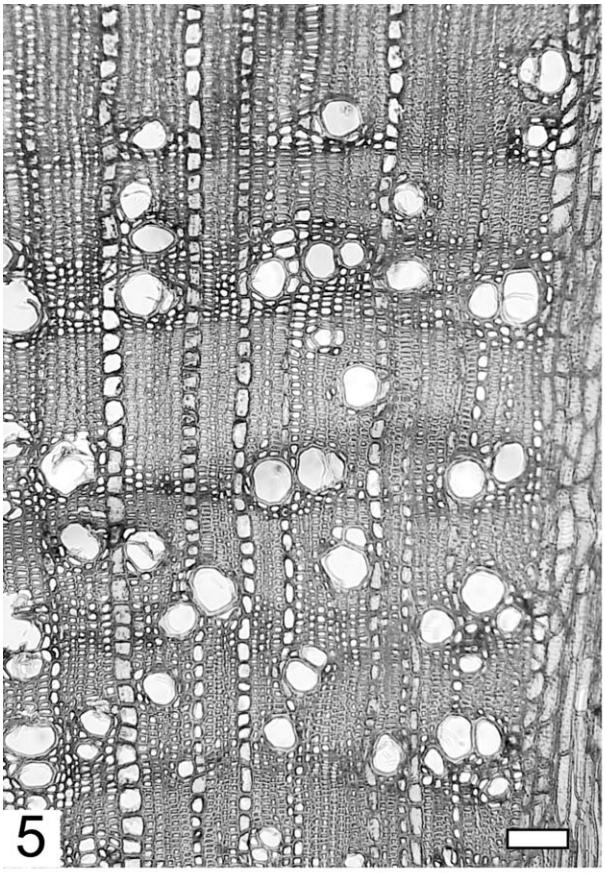
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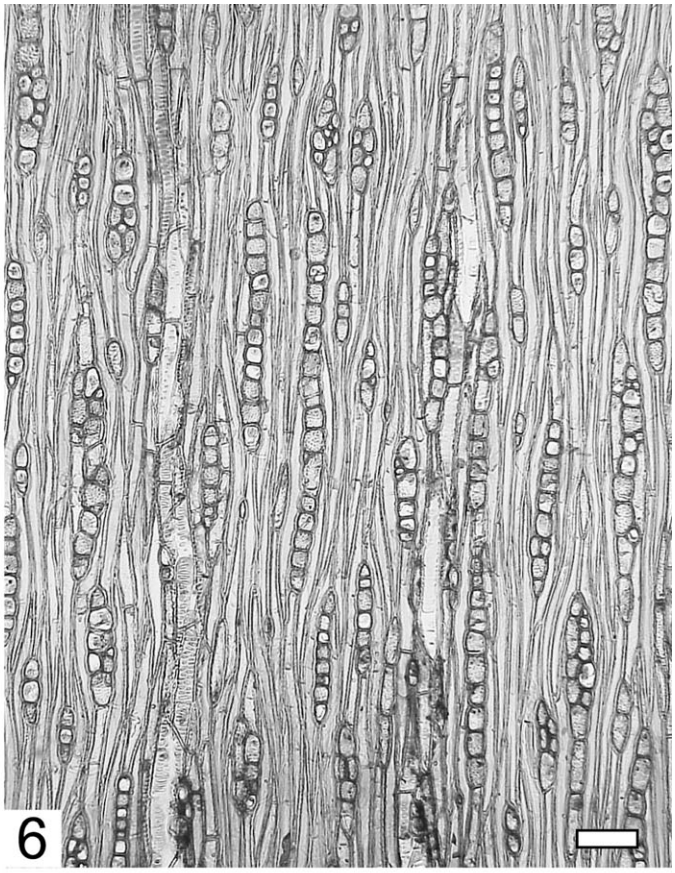
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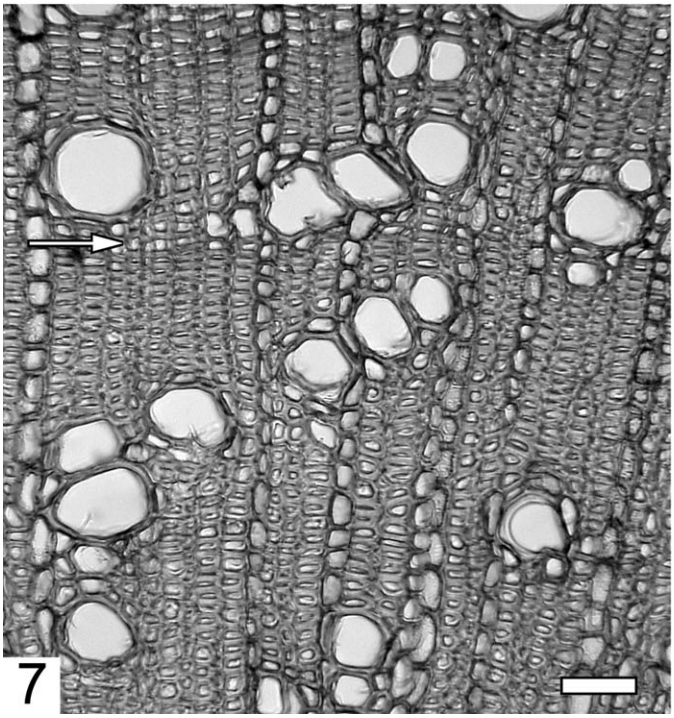
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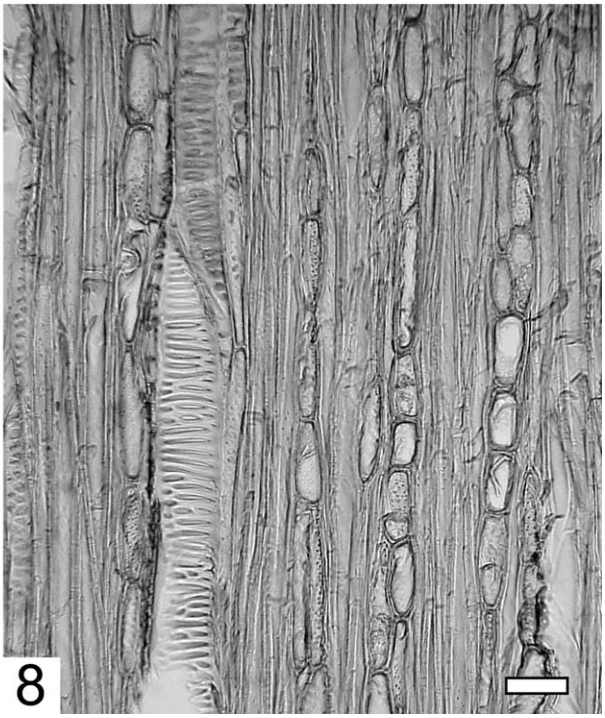
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Figures 5–8. Figures 5 and 6. Wood structure of *Polemanniopsis marlothii* (Oskolski 40-06). Scale bars, 100 μm. Fig. 5. Transverse section showing the indistinct growth ring boundary, marked by 2- to 5-seriate bands of axial parenchyma; paratracheal axial parenchyma in complete and incomplete 1-seriate sheaths near vessels. Fig. 6. Tangential section showing mostly uniseriate (sometimes 2- to 3-seriate) rays composed mostly of procumbent cells. Figures 7 and 8. Wood structure of *Polemanniopsis namibensis*. Scale bars, 50 μm. Fig. 7. Transverse section showing continuous 1- to 2-seriate band of axial parenchyma (arrow); paratracheal axial parenchyma in complete and incomplete 1-seriate sheaths near vessels. Fig. 8. Tangential section showing uni- and 2-seriate rays composed of procumbent, square and upright cells; square and upright cells form short uniseriate portions and occur as solitary sheath cells; intervessel pitting is scalariform and transitional to alternate.

420–460 (–660) μm in length] and somewhat shorter in other species.

Perforation plates are simple [occasionally with single vestigal bars in *S. araliacea* (S1193) and *P. namibensis*]. Intervessel pits are mostly alternate and transitional to scalariform (occasionally opposite or scalariform) in *S. araliacea*, *P. marlothii* (P83) and *E. bupleuroides*, mostly transitional in *P. marlothii* (AO40-06) or mostly scalariform (sometimes opposite and alternate) in *P. namibensis* (Fig. 8), 3–5 μm in vertical size in *E. bupleuroides* (Fig. 4) and 4–6(–8) μm in other species [up to 6–10 μm in *S. araliacea* (W2517)], with rounded (sometimes polygonal) borders in *S. araliacea*, and mostly polygonal borders in other species, with slit- or lens-like apertures. The shape and size of vessel-ray and vessel-axial parenchyma pits are similar to those found in the intervessel pits or somewhat smaller than the latter. Parenchyma pits are half-bordered, with distinct or indistinct borders. Helical thickenings are absent.

Vascular tracheids are absent. Fibres are libriform, mostly thin-walled (1–4 μm thick) in *P. marlothii* (P83) or mostly moderately thick walled [(1–)2–5(–8) μm thick] in other species, with a few simple to minutely bordered pits. Slit-like apertures are present in radial walls. Septate fibres are rarely found in either *Polemanniopsis* species.

Axial parenchyma is scanty paratracheal, mostly in complete (rarely incomplete) 1– to 2–seriate sheaths near the vessels [up to 3–seriate (Fig. 1) in *S. araliacea* (W2517)] and banded (sometimes marginal) in short interrupted lines and 2- to 3-seriate bands in *E. bupleuroides*, in continuous lines in *P. namibensis*, in continuous lines and 2– to 5–seriate (up to 10-seriate) bands in *P. marlothii* (Fig. 5). Axial parenchyma strands are composed of 2–4(–6) cells.

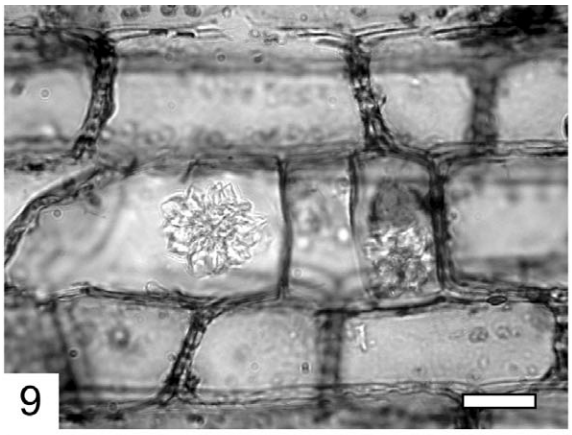
Rays are 4–8(–9) per mm in *S. araliacea* and *E. bupleuroides* and (3–)4–11(–12) in *P. marlothii* and *P. namibensis*, mostly uniseriate (rarely 2– to 3–(4–) seriate) in *P. namibensis* and *P. marlothii* (Fig. 6) and 2–5 cells width in other species [up to seven in *S. araliacea* (W2517). Tangential ray size is 15–50 μm. Ray height reaches 1.2 mm in *S. araliacea* (M1057, W2517) and does not exceed 0.8 mm in other samples. Multiseriate rays in *S. araliacea* are mostly composed of procumbent cells (Fig. 2); upright and square cells occur in marginal rows (one to three) or as solitary sheath cells; in other species, multiseriate rays are mostly composed of square and upright cells with procumbent cells mixed throughout the ray and arranged into incomplete (sometimes complete in *E. bupleuroides*) sheaths, with short (up to three marginal rows in *P. namibensis* and *E. bupleuroides*) or long (up to ten marginal rows in *P. marlothii*) uniseriate portions. Uniseriate rays are composed of all procumbent, square and upright cells in *S. araliacea* and of square and upright cells with few procumbent cells in other species (Fig. 8). Radial secretory canals occur in all species except *P. namibensis* (Figs 2, 4). Druses and prismatic crystals are common in upright, square and sometimes also in procumbent ray cells in *E. bupleuroides*; druses occur also in procumbent ray cells in *S. araliacea* (W2517) (Fig. 9) and *P. namibiensis*. Crystalliferous ray cells are mostly chambered.

BARK STRUCTURE (FIGS 14–22)

The epidermis is formed by a single layer of extremely radially flattened (in *P. marlothii* also isodiametric) thin-walled cells. Druses are rarely present in the epidermal cells in *S. araliacea*.

Cortical collenchyma is lamellar, in a single layer (Fig. 10) of large cells (20–50 μm in tangential size) in *S. araliacea* or consisting of two to four layers of smaller cells (tangential size 15–35 μm) in *P. marlothii*. Cortical parenchyma is formed by six to 20 layers (five to nine layers in *P. namibensis*) of isodiametric or somewhat axially elongated thin-walled parenchyma cells (tangential size is 15–50 μm in *S. araliacea* and 15–35 μm in *P. marlothii*). Druses are sometimes present in cortical parenchyma cells (Fig. 10). Axial secretory canals in the cortex are 50–90 μm in tangential diameter in *S. araliacea* and 30–130 μm in *P. marlothii*, lined by a single (sometimes incomplete double) layer of six to nine epithelial cells. Primary phloem fibres are thick-walled, aggregated into small groups of three to 15.

Dilatation of the cortical tissue is mostly effected by tangential cell stretching; however, in *S. araliacea* it can also occur as a result of anticlinal divisions of the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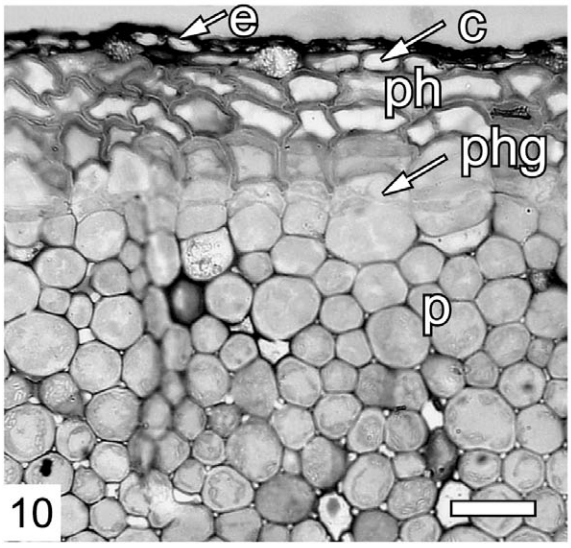
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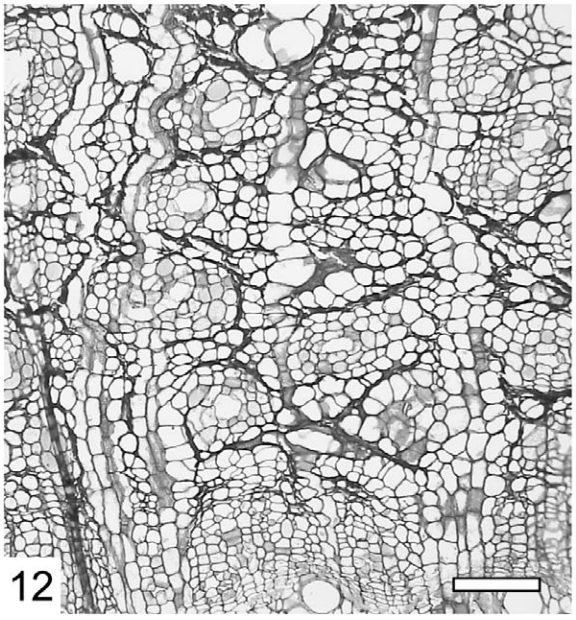
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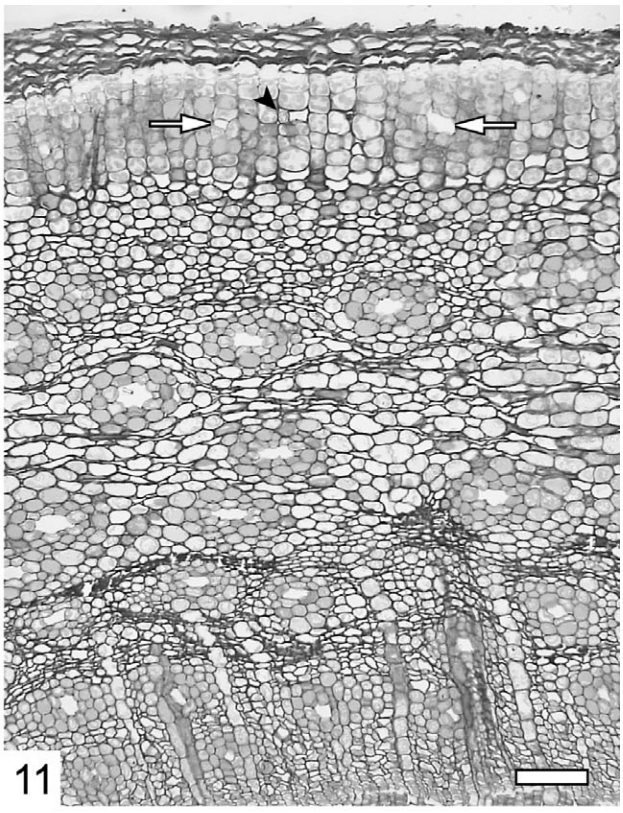
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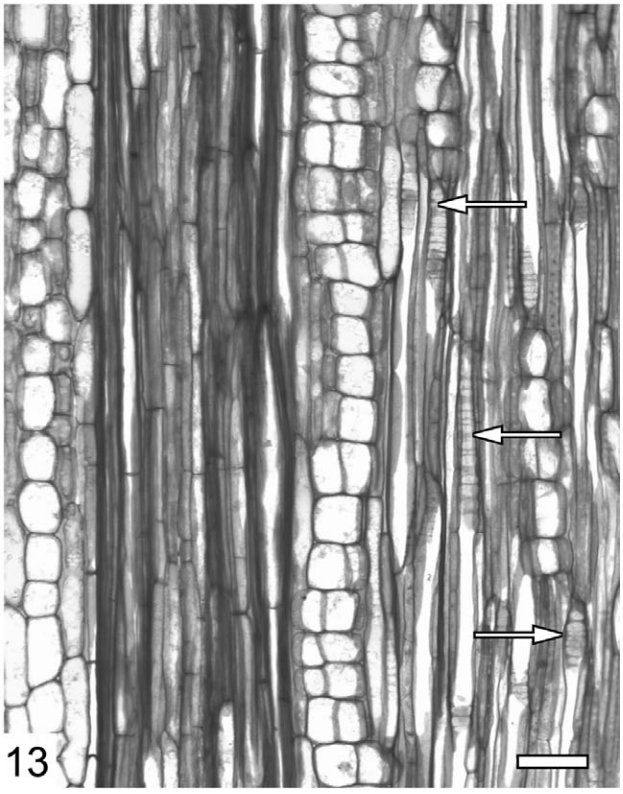
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Figures 9–13. Fig. 9. Druses in chambered procumbent cell of secondary xylem ray in *Steganotaenia araliacea* (Welwitsch 2517). Scale bar, 20 μm. Figures 10–13. Bark structure of *Steganotaenia araliacea* (Seidel 1193). Fig. 10. Transverse section of young stem showing epidermis (e), cortical collenchyma in a single layer (c), cortical parenchyma (p) and the early stage of periderm initiation in the cell layer right below the collenchyma (phg, phellogen; ph, phellem); druses in cells of cortical collenchyma and cortical parenchyma. Scale bar, 50 μm. Fig. 11. Transverse section of bark showing periderm, cortical parenchyma and secondary phloem; axial secretory canals in phelloderm (arrows), cortical parenchyma and secondary phloem; chambered crystalliferous cell in phelloderm (arrowhead). Scale bar, 100 μm. Fig. 12. Transverse section of secondary phloem showing axial secretory canals with sheaths of axial parenchyma. Scale bar, 100 μm. Fig. 13. Tangential section of secondary phloem showing uniseriate and 2- to 3-seriate rays composed mostly of square and procumbent cells; compound sieve plates with numerous sieve areas (arrows). Scale bar, 50 μm.

cortical parenchyma cells, forming tangentially directed strands (two to five cells). Axial secretory canals in the dilated cortex are enlarged to a diameter of 100–270 μm, lined with eight to 17 epithelial cells. Druses are rarely present in the dilated cortex.

Periderm initiation is cortical in *S. araliacea* (Fig. 10) and *P. marlothii* (Fig. 15) (its origin was not observed in *P. namibensis* and *E. bupleuroides*); phellogen is initiated in the second cell layer (in *P. marlothii* also in third one) right below the epidermis. Phellem is composed of eight to 20 (up to 50 in *S. araliacea*) layers of strongly radially flattened cells with thicker outer walls in *S. araliacea* or with thin walls in other species. Phelloderm is composed of three to 15 (up to 20 in *P. marlothii*) layers of thin-walled radially flattened cells. Druses occur in phelloderm cells in all species under study except *E. bupleuroides*; some of the crystalliferous phelloderm cells are subdivided into two or three chambers in *S. araliacea* (Fig. 11) and *P. marlothii* (Fig. 14), and into two to seven chambers in *P. namibensis* (Fig. 18).

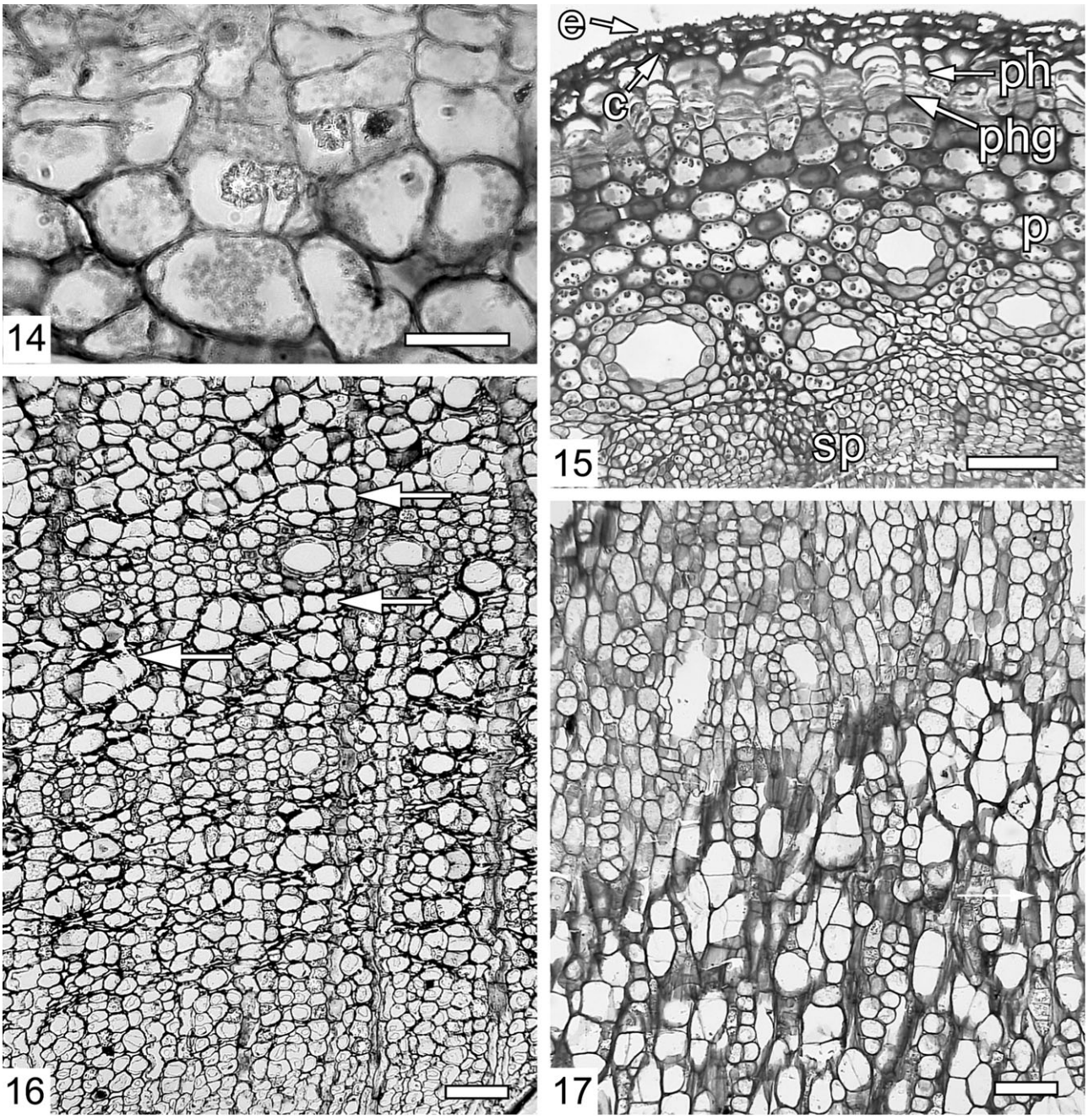
Axial secretory canals are present in the phelloderm in *S. araliacea* (Fig. 11). In the phelloderm of young stems, these canals are 10–70 μm in tangential diameter, lined by a single layer of four to seven epithelial cells. Secretory canals in mature bark are larger with a tangential diameter of 40–130 μm, lined by a single or incomplete double layer of four to nine epithelial cells.

Secondary phloem is composed of sieve elements, companion cells and axial parenchyma cells which also contain axial secretory canals with sheaths of axial parenchyma (Fig. 12). Axial scretory canals in secondary phloem are solitary or arranged in tangential rows (Fig. 16) of two to 10 (up to seven in *P. namibensis*, up to 12 canals in *S. araliacea*). Transition from non-collapsed to collapsed secondary phloem is distinct. Dilatation of the secondary phloem is mostly effected by tangential stretching of rays and anticlinal divisions of ray cells, forming very wide (to 15-seriate) rays in *E. bupleuroides* (Figs 20, 22) or by tangential stretching and anticlinal divisions of axial parenchyma cells, forming tangentially directed strands of two to nine cells (Fig. 16) in other species.

Sieve tube members are 10–30 μm wide (up to 40 μm in *P. marlothii*), 90–245 μm long in *P. namibensis* and longer in other species (up to 95–580 μm long in *S. araliacea*) (Table 2). Sieve plates are compound with four to eight sieve areas in *E. bupleuroides*, five to 10 in *P. marlothii*, four to 14 in *P. namibensis* and six to 16 sieve areas in *S. araliacea* (Fig. 13), located on oblique cross walls. Axial parenchyma cells are mostly fusiform, sometimes in strands of two or three cells in *E. bupleuroides*, or in strands of two to eight cells in *P. namibensis* and two to 10 cells in others species. Druses rarely occur in axial parenchyma cells in *S. araliacea* but are common (especially in collapsed secondary phloem) in *P. marlothii* and *P. namibensis*; their crystalliferous cells are mostly chambered, sometimes subdivided into numerous chambers (up to 14 in *P. namibensis*). Crystalliferous cells are absent in axial parenchyma of *E. bupleuroides* but the sclerified axial parenchyma cells (thick-walled fibre-like sclereids or strands of two or three sclereids) occur in its collapsed secondary phloem (Fig. 20).

Axial secretory canals are present throughout the secondary phloem, lined by a single (sometimes incomplete double) layer of three to 10 epithelial cells, which is accompanied by 1- to 3-seriate sheaths of axial parenchyma (Figs 12, 16, 20). The diameter of the axial secretory canal lumina is 50–140 μm in *P. marlothii* and 30–70 μm in other species. Axial parenchyma sheaths near axial secretory canals consist of strands of three to five thin-walled cells (up to eight cells in *P. marlothii* and up to 12 cells in *E. bupleuroides*).

Secondary phloem rays are uni- and biseriate in *P. namibensis* and uni- and 2- to 4-seriate in other species (up to 5-seriate in *P. marlothii* and 6-seriate in *E. bupleuroides*). Both uni- and multiseriate rays in *S. araliacea* (Fig. 13), *P. marlothii* (Fig. 17) and *E. bupleuroides* (Fig. 21) are mostly composed of square and procumbent cells, upright and square cells occur as solitary sheath cells (*S. araliacea*) or forming one or two marginal rows (*E. bupleuroides*). In *P. namibensis*, both uni- and multiseriate rays are composed of upright and square cells, with a few procumbent cells mixed throughout the ray (Fig. 19).



Figures 14–17. Bark structure of *Polemanniopsis marlothii* (Oskolski 40-06). Fig. 14. Transverse section of phelloderm showing chambered cells with druses. Scale bar, 20 μm. Fig. 15. Transverse section of young stem showing epidermis (e), cortical collenchyma in two layers (c), cortical parenchyma (p) with wide axial secretory canals, the early stage of periderm initiation in the cell layer right below the collenchyma (phg, phellogen; ph, phellem) and secondary phloem (sp.). Scale bar, 50 μm. Fig. 16. Transverse section of secondary phloem showing axial secretory canals with sheaths of axial parenchyma arranged into tangential rows; tangentially directed strands of two to five cells formed by anticlinal divisions of axial parenchyma cells during their dilatation (arrows). Scale bar, 50 μm. Fig. 17. Tangential section of secondary phloem showing uniseriate and 2- to 3-seriate rays composed mostly of square and procumbent cells. Scale bar, 50 μm.

Dilated rays are enlarged mostly by anticlinal divisions of ray cells up to 8-seriate in *S. araliacea* and up to 15-seriate in *E. bupleuroides* (Fig. 22), or mostly by tangential stretching of ray cells in *P. marlothii* (dilatation of rays was not observed in *P. namibensis*). Numerous druses and sometimes prismatic crystals are found in ray cells in *E. bupleuroides*; moreover, druses occur rarely in ray cells in *S. araliacea* and *P. namibensis*. Radial secretory canals are 45–130 μm in tangential diameter in *S. araliacea* and 35–80 μm in tangential diameter in *E. bupleuroides* (Fig. 21), lined by a single layer of four to seven epithelial cells, not found in both *Polemanniopsis* spp.

DISCUSSION

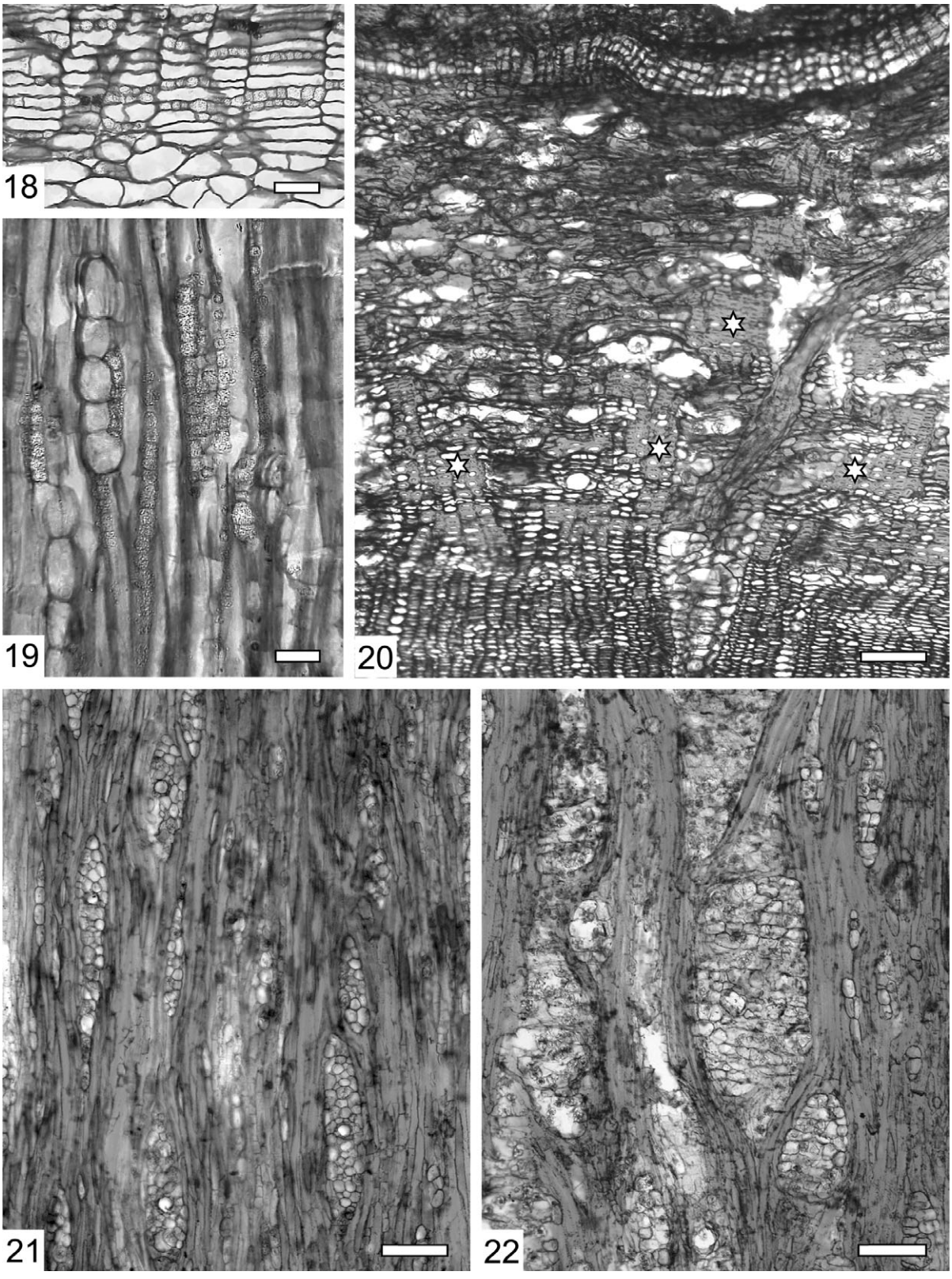
Steganotaenia, *Polemanniopsis* and *Eryngium* show wood and bark characters which are common in woody Apiaceae (Metcalfe & Chalk, 1950; Rodríguez, 1957; Oskolski, 2001; Oskolski & Van Wyk, 2008). Such characters include exclusively simple perforation plates, scanty paratracheal axial parenchyma and the presence of axial secretory canals in the cortex and secondary phloem [their presence in the cortex has been reported by Lemesle (1926) in *E. bupleuroides* and in many other species of *Eryngium*]. At the same time, the three genera under study can be clearly distinguished from each other on the basis of their stem anatomy (Table 3).

Eryngium bupleuroides differs markedly from *Steganotaenia* and *Polemanniopsis* in the smaller size of intervessel pits, sclerification and radial dilatation (tangential stretching of rays) in collapsed secondary phloem, the absence of crystals in the phelloderm cells and the occurrence of druse crystals in secondary phloem ray cells. According to Lemesle's (1926) data, *E. bupleuroides* (unlike *S. araliacea* and *P. marlothii*) also shows subepidermal periderm initiation, although this feature is not characteristic for the whole genus: cortical periderm initiation was reported by this author for *E. carlinoides* Boiss. The three genera under study share features including marginal axial parenchyma, the presence of radial canals in secondary xylem and the cortical initiation of periderm (at least in some members of these genera). This combination of characters can also be found in others members of Apiaceae (Metcalfe & Chalk, 1950; Rodríguez, 1957; Oskolski, 2001) and therefore has limited taxonomic value. As for the fossil wood of *Steganotaenioxylon* described by Dechamps (1977), more information is required to make definite conclusions about its relationships to extant Apiaceae.

Steganotaenia and *Polemanniopsis* share features including the presence of marginal axial parenchyma, the occurrence of radial secretory canals in secondary xylem, dilatation of secondary phloem by axial parenchyma stretching (without any remarkable expansion of rays), cortical periderm initiation (in the second or third cell layers below the epidermis) and the presence of chambered phelloderm cells containing druse crystals. The last character is especially distinctive: chambered crystalliferous phelloderm cells have not yet been reported in Apiaceae (Metcalfe & Chalk, 1950; Rodríguez, 1957; Kotina & Oskolski, 2007), Araliaceae or Myodocarpaceae (Kolalite *et al*., 2003; Oskolski *et al*., 2007). Other characters listed occur sporadically in other groups of Apiaceae, but the combination of these wood and bark features is distinctive; it confirms the close relationships between *Steganotaenia* and *Polemanniopsis* suggested by molecular (Downie & Katz-Downie, 1999; Calviño

Table 3. Diagnostic and phylogenetically important wood and bark anatomy features of the taxa studied

	Steganotaenia araliacea	*Polemanniopsis marlothii*	*Polemanniopsis namibensis*	*Eryngium bupleuroides*
Marginal axial parenchyma	+	+	+	+
Radial secretory canals in wood	+	+	–	+
Chambered crystalliferous cells in wood rays	+ (very rare)	–	–	+
Initiation of periderm	Cortical	Cortical	?	Subepidermal (Lemesle, 1926)
Chambered crystalliferous cells in phelloderm	+	+	+	–
Axial secretory canals in phelloderm	+	–	–	–
Tangential stretching of rays in dilated secondary phloem	–	–	–	+
Sclerification of axial parenchyma in collapsed secondary phloem	–	–	–	+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Figures 18–22. Figures 18 and 19. Bark structure of *Polemanniopsis namibensis*. Scale bars, 50 μm. Fig. 18. Transverse section of phelloderm showing chambered cells with druses. Fig. 19. Tangential section of secondary phloem showing uniseriate rays composed mostly of square cells; strands of axial parenchyma cells with druses. Figures 20–22. Bark structure of *Eryngium bupleuroides*. Scale bar, 100 μm. Fig. 20. Transverse section of bark showing axial secretory canals, sclerified axial parenchyma (asterisks) and tangentially expanded rays in dilated secondary phloem. Fig. 21. Tangential section of non-collapsed secondary phloem showing uniseriate and 2- to 5-seriate rays composed mostly of square and procumbent cells; radial secretory canals. Fig. 22. Tangential section of non-collapsed secondary phloem showing dilated rays enlarged mostly by anticlinal divisions of ray cells.

et al., 2006; Calviño & Downie, 2007) and carpological (Liu *et al*., 2003, 2004) data. Therefore, our results confirm an isolated position of tribe *Steganotaeniae* (Calviño *et al*., 2006; Calviño & Downie, 2007; Nicolas & Plunkett, 2009; Magee *et al*., 2010). However, they do not provide any reliable synapomorphic features for including the tribe in an expanded Saniculoideae, as proposed by Calviño & Downie (2007).

Despite the similarities between the two genera, *Steganotaenia* is distinct from *Polemanniopsis* (and from *Eryngium*) in its longer vessel elements (mean length > 400 μm), the predominance of procumbent cells in the ray composition and the presence of axial secretory canals in the phelloderm. With *Heteromorpha* Cham. & Schltdl. (Rodríguez, 1957; Oskolski & Van Wyk, 2008), this genus has the longest vessel elements found in woody Apiaceae. In as much as the shortening of vessel elements is regarded as a major trend in wood evolution (Bailey & Tupper, 1918; Baas & Wheeler, 1996), these data are in good agreement with results obtained from molecular phylogenetics (Calviño & Downie, 2007), which suggested a sister group position of *Steganotaenia* and *Polemanniopsis* in relation to Saniculoideae *sensu stricto* (although the relationships between this pair of genera have not been clarified by molecular analysis). *Heteromorpha* belongs to the 'woody South African clade I' (Downie & Katz-Downie, 1999) corresponding to tribe Heteromorpheae M.F.Watson & S.R.Downie, the first diverging branch of Apioideae (Plunkett *et al*., 2004; Magee *et al*., 2010).

The presence of axial secretory canals in the phelloderm is another remarkable feature of *Steganotaenia*. Although axial secretory canals are present in the cortex and secondary phloem of an overwhelming majority of Apiaceae and Araliaceae examined to date (Solereder, 1899; Lemesle, 1926; Metcalfe & Chalk, 1950; Kolalite *et al*., 2003; Oskolski *et al*., 2007; Kotina & Oskolski, in press), the presence of these structures in the periderm has not yet been reported within Apiales. Secretory canals in the phelloderm have also been recorded in *Lannea coromandelica* (Houtt.) Merr. of Anacardiaceae (Venkaiah & Shah, 1984). This feature probably occurs in other flowering plants, but we were unable to find other references to its occurrence in other taxa.

Polemanniopsis namibensis can be distinguished from *P. marlothii* by the predominance of scalariform intervessel pits and the presence of uniseriate rays, unlike the mostly alternate intervessel pitting and 2- to 4-seriate rays in *P. marlothii*. Furthermore, the vessel frequency in *P. namibensis* is considerably higher (153 vessels per mm^2) than in *P. marlothii* (42–60 vessels per mm^2; Table 2). The differences between the *Polemanniopsis* spp. are probably related to differences in their habitats (extremely dry desert for *P. namibensis* and relatively humid fynbos for *P. marlothii*), i.e. corresponding to a common ecological trend in wood anatomy (Carlquist, 2001).

Cladograms based on molecular data (Calviño *et al*., 2006) suggest that the woody habit in the three genera examined (and in other woody Apiaceae) is derived from a herbaceous ancestor. Our results cannot confirm this suggestion. Wood anatomical data has uncovered a few cases of a secondary origin of the woody habit in Apiaceae, as in *Azorella* Lam. (Ternetz, 1902), *Myrrhidendron* J.M.Coult. & Rose and *Nirarathamnos* Balf.f. (Oskolski, 2001). The examined species of *Steganotaenia*, *Polemanniopsis* and *Eryngium*, however, did not show any anatomical traits of secondary woodiness [paedomorphic features *sensu* Carlquist (1962, 2001, 2009) such as pseudoscalariform intervessel pitting, raylessness, etc. are not present]. The sampling in this study is not sufficient to explore the apparent incongruence between molecular and morphological evidence fully. An accurate comparative study of the habit transformations and of the diversity of stem structure within *Eryngium* (the largest taxon of protoapioids with a wide range of habits) is desirable to try and solve this problem.

CONCLUSION

The wood anatomy of *Steganotaenia* and *Polemanniopsis* shows some taxonomically useful similarities and differences at generic and species level (such as the unique presence of secretory canals in the periderm of *Steganotaenia*), but no evidence could be found that the woodiness of these taxa is secondarily derived. The bark anatomy revealed two interesting potential synapomorphies for tribe Steganotaenieae,

namely the cortical periderm initiation (not subepidermal as in other Apiaceae) and the presence of chambered crystalliferous cells in the phelloderm.

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