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Macrophotographic wood atlas of Annonaceae

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In this article, a general description of the microscopic wood anatomy of Annonaceae is given. We provide a description of the wood anatomical features of the family and of all subfamilies and tribes, all from material in the Utrecht Wood collection. Hand-lens images can be an important help in identification, not only at the family level, but also at the level of genera or below, notwithstanding the fact that the number of characters that can be easily observed in end-grain photographs is restricted. The differences are often slight and difficult to summarize in a few words, making illustrations an indispensable tool. Therefore, we provide end-grain photographs of cross-sections of wood of 66 genera and > 90 species of Annonaceae. The variation seen in lens key characters is discussed against the framework of the current phylogenetic tree of the family. Additional remarks on microscopic features are given when appropriate. © 2012 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2012, **169**, 135–189.

ADDITIONAL KEYWORDS: lens key characters – phylogenetic tree – wood anatomy.

INTRODUCTION

Annonaceae as a family is easily recognized not only by its flowers, fruit and vegetative habit, but also by the characteristic wood. The vessels are diffusely arranged, solitary and in short radial multiples. Perforation plates are simple and the alternate intervessel pits are mostly minute or small. Two features of the xylem structure stand out in particular: first, the broad and high multiseriate rays and, second, the numerous narrow parenchyma bands that are visible in transverse sections as more or less continuous tangential lines, perpendicular to the rays. The resulting cobweb- to ladder-like (or reticulate) appearance in cross-sections, often visible even to the naked eye, is found in all Annonaceae, even in the first-formed xylem (Fig. 40A). Even the deviating genus *Tetrameranthus* R.E.Fr., with tetramerous flowers and spirally (rather than distichously) placed leaves, shows this striking structure (Ter Welle, 1985).

The same can be said of species growing in moderate climates or of those with a climbing habit. Although taxa belonging to these categories often deviate in certain characters, the general annonaceous structure is always present.

There is general consensus that Annonaceae forms a natural group, and this is supported by the high homogeneity in wood structure. Various authors over the years have arrived at this conclusion: for example, Solereder (1899, 1908), Moll & Janssonius (1906), Hess (1946), Metcalfe & Chalk (1950), Vander Wijk (1950), Ingle & Dadswell (1953), Vander Wijk & Canright (1956), Gottwald (1977), Ter Welle (1984, 1998) and Metcalfe (1987).

In the APG III classification (APG III, 2009; Stevens, 2001 onwards; http://www.mobot.org/MOBOT/research/APweb/; date of access 25 Sep 2011) Annonaceae is placed in the order Magnoliales with Degeneriaceae, Eupomatiaceae, Himantandraceae, Magnoliaceae and Myristicaceae (Sauquet *et al.*, 2003).With the exception of Himantandraceae, these families show scalariform perforation plates (Degeneriaceae, Eupomatiaceae, Magnoliaceae) and/or reticulate to scalariform intervessel pits (Degeneriaceae, Eupomatiaceae, Magnoliaceae, Myristicaceae). Himantandraceae differs, among other characters, in

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its longer radial rows of vessels, the continuous parenchyma bands and the presence of prismatic crystals. In none of the above-mentioned families, however, is the reticulate parenchyma pattern, characteristic for Annonaceae, found.

A wealth of information is available from North Carolina State University (NCSU; Raleigh, NC, USA) on the website *InsideWood* (http://insidewood.lib.ncsu.edu/search/). This website includes microscopic data, often illustrated, on the wood anatomy of (currently) > 2500 genera belonging to nearly 300 families, and it is a valuable tool for the identification of wood. From a search of the *InsideWood* database applying the International Association of Wood Anatomists (IAWA) wood characters, the combination of wide and high rays (characters 98, 102) and seemingly reticulate parenchyma (characters 86, 87, 88) results in six families. Huaceae, Icacinaceae and Loganiaceae are represented by only one species each. The other three families are represented by more species: Annonaceae (14), Lecythidaceae (7) and Malvaceae (5). In the APG III classification, three of these families (Icacinaceae, Lecythidaceae and Loganiaceae) are found in the asterids, two families (Malvaceae and Huaceae) in the rosids, and Annonaceae is the only one placed in the magnoliids.

When six more features are added in the database search based on our description of Annonaceae, referring to vessel distribution, perforation plates and pits of vessels, rays and fibres (IAWA characters 5, 13, 22, 25, 30, 61) and no mismatch is allowed, a search produces seven hits, four of which are for Annonaceae. This low number is caused by the variation found in most wood anatomical features. When one mismatch is allowed, in order to address this problem, the number of hits for Annonaceae increases greatly (43). Twelve other families, all found in the rosids or asterids, are far less often retrieved, Malvaceae being second best with 14 hits. Annonaceae remains the sole representative of the magnoliids.

Given the wood anatomical differences mentioned earlier, it is not surprising that the families considered to be most closely related to Annonaceae were not found when scanning the *InsideWood* database (only Degeneriaceae is not represented in the database).

Although wood anatomical characters are usually variable at the familial level, the character combination exhibited by Annonaceae is more or less homogeneous. Thus, the suite of wood anatomical characters discussed above renders taxa belonging to this large family easily recognizable and surprisingly distinct from other Magnoliales.

In this article, a general description of the microscopic wood anatomy of the family is given on the basis of data from the literature and personal observations. A few microphotographs are added. For further illustrations of microscopic features, we refer to the website Insidewood (2004 onwards), which includes photographs of transverse and tangential sections of *c*. 35, mainly Neotropical, genera of the Utrecht Wood collection.

In addition to the family description, we provide a survey of end-grain photographs of 66 genera and > 90 species of Annonaceae, all from material in the Utrecht Wood collection, which at present is housed at the Netherlands Centre for Biodiversity Naturalis, Leiden, the Netherlands.

Hand-lens images have somewhat suffered from neglect in past decades, most papers showing microphotographs only. The usefulness and advantages of hand-lens photographs, especially end-grain photographs, are discussed by Westra & Koek-Noorman (2004) in their recent wood atlas of Euphorbiaceae *s.l.* Good examples of atlases of wood photographs through a hand lens, covering a large number of families, are found in Pfeiffer (1926), Lindeman & Mennega (1963) and Ilic (1991).

A preliminary survey of mainly end-grain photographs from a selection of Annonaceae was presented in an informal paper by Westra & Koek-Noorman (2003). They illustrated that, in certain cases, despite the homogeneity within the family, differences observed with a good hand lens can be an important help in identification, particularly at the level of genera or below.

The advantages of the use of a hand lens are obvious: ease, speed and the possibility to observe a relatively large area at a single glance, although the number of characters that can be easily observed in end-grain photographs is restricted. The differences are often slight and difficult to summarize in a few words, and illustrations are indispensable.

The variation seen in lens key characters is discussed against the framework of phylogenetic relationships in the family (Richardson *et al*., 2004; Chatrou *et al*., 2012). To facilitate the comparison, the photographs are arranged according to the clades in figure 1 of Chatrou *et al*., 2012. Additional remarks on microscopic features are given when appropriate.

MATERIAL AND METHODS

Small blocks that had previously been cut to size for microtome sectioning were used for photography. The flat surface left after the cutting of microtome slices was photographed using a Zeiss Luminar 40-mm f/4.5 macro-objective (stopped down ½ stop) on Kodachrome 25 or 64 film. All objects were photographed at a standard reproduction ratio of 5 : 1, as in a previous survey of euphorbiaceous woods (Westra & Koek-Noorman, 2004). The resulting image on the 35-mm frame then corresponds to a rectangle of

± 7.0 × 4.5 mm^2 on the object. In a few cases, an additional photograph was taken at a reproduction ratio of 10 : 1 using a Zeiss Luminar 25-mm f/3.5 objective (also stopped down ½ stop), whenever desirable in a fine grain wood. From the original colour slides, digital scans were made for further processing.

Most figures present about half of the full macro-image, showing a rectangle of *c.* 4.0 × 3.0 mm^2 except for Figs. 2B, 11F, and 25F (2.0 × 1.5 mm^2) In some cases, two photographs of different samples are selected, whenever intraspecific variation made this necessary or desirable. All photographs are cross-sections, and the scale bar equals 500 μm, unless indicated otherwise. For a few species, photographs of tangential or radial sections are included. A few microphotographs are included as an illustration of some anatomical features.

Generic names follow the latest taxonomic insights as compiled by Rainer & Chatrou (2006) and Erkens, Mennega & Westra (2012). An alphabetical list of taxa studied, including all author names, is given in Appendix 1.

RESULTS AND DISCUSSION

Microscopic wood anatomy of Annonaceae

The most recent family treatment of the wood anatomy was published by Metcalfe (1987). This elaborate description was based in part on old literature, and the nomenclature in this publication is to some extent out of date. However, our findings still largely confirm Metcalfe's (1987) description. Here, we present a concise family description, based mainly on our own observations and wood anatomical descriptions forming part of recent taxonomic revisions.

The data presented cover only a part of the family. However, in view of the great homogeneity found so far and the agreement with Metcalfe's (1987) publication, we are convinced that the inclusion of data from more material would not change the description considerably. It should be noted that names occurring in a description, whether as illustrations of features or as exceptions, are intended as examples, and do not represent an exhaustive enumeration.

Despite the homogeneity of annonaceous wood, the general appearance as described in the Introduction may sometimes not be obvious, notably in climbing species and also in the one temperate species that we studied. In climbing species, adaptation is effected through enlargement of the vessel diameter. In *Annona haematantha* Miq. (Fig. 16E) and *Guatteria scandens* Ducke (Fig. 35D) (both New World), the transition is more or less gradual, whereas, in some African examples, it is much more abrupt, e.g. in *Toussaintia hallei* Le Thomas (Fig. 13B) and *Friesodielsia montana* (Engl. & Diels) Steenis (Fig. 12B). It should be noted that tangential parenchyma bands tend to become indistinct in liana wood.

Asimina triloba (L.) Dunal (Fig. 19C), found in the temperate USA and able to withstand cold winters, shows marked ring porous wood in growth rings, and parenchyma bands appear to have vanished here altogether. Their presence can only be detected under high magnification using a microscope.

In the great majority of species, growth rings are absent, or present merely as more or less distinct zones indicated by a change in fibre wall thickness, in the number of parenchyma bands and/or the vessel pattern. This pattern is visible in, among others, *Annona annonoides* (R.E.Fr.) Maas & Westra (Fig. 14E) and *Annona edulis* (Triana & Planch.) H.Rainer (Fig. 15E).

Vessels are solitary and in short radial multiples of two to four (five), rarely more. The percentage of solitary vessels is between 10 and 50%. Deviations from the common pattern include a predominance of solitary vessels (*Guatteria* Ruiz & Pav.) or radial multiples and clusters consisting of up to six (eight) vessels (*Duguetia* A.St.-Hil. *p.p.*, *Malmea* R.E.Fr.). The mean vessel diameter is mostly from *c.* 50 to > 200 μm. Lower or higher mean sizes occur in individual species in several genera.

Mean vessel number is between 10 and 40 per mm^2, but sometimes > 50 per mm^2, e.g. in *Fitzalania* F.Muell., *Sapranthus* Seem. and *Malmea* R.E.Fr. Perforations are simple. Intervessel pits are mostly 2–3(–5) μm, rarely up to 9 μm (*Annona*). Vessel-ray pitting and vessel-parenchyma pitting are comparable, but pits are sometimes slightly larger than intervessel pits.

Parenchyma occurs in one- or two- (three-) cell wide tangential bands, rarely wider, consisting of two- to eight-celled strands. The number of parenchyma bands is < 10–20 per millimetre. Paratracheal parenchyma is absent or present as scanty cells, sometimes as incomplete rings to rarely vasicentric (*Fissistigma* Griff., *Guatteria*, *Tetrameranthus*). Strands are of four to eight cells.

Rays consist of narrow procumbent cells, often mingled with higher procumbent to square cells. Uniseriate rays are scanty, rarely absent, rarely more frequent (*Fitzalania*). Multiseriates are mostly four to eight cells wide, but rays > 10 cells wide are often present. The height is nearly always > 1000 μm, sometimes > 7000 μm. The width is from < 150 μm to ≤ 300 μm, with two (three)–10 cells, occasionally with long uniseriate margins.

Fibres are thin to thick, because of the variation in wall thickness and fibre diameter. Pits are mostly small, simple or with narrow borders, numerous on radial and tangential walls, rarely distinctly bordered, rarely scanty on tangential walls.

Oil cells are observed in the rays of several genera. Their size varies from more or less equal to that of the other ray cells and hardly distinguishable, to more than twice the normal ray cells (*Duguetia*). They may vary from scanty to numerous. Other authors have reported them as present in rays or parenchyma in the following genera: *Cananga* (DC.) Hook.f. & Thomson, *Cleistopholis* Pierre ex Engl., *Cyathocalyx* Champ. ex Hook.f. & Thomson, *Cymbopetalum* Benth., *Diclinanona* Diels, *Duguetia* A.St.-Hil., *Guatteria* Ruiz & Pav., *Hornschuchia* Nees, *Mezzettia* Becc., *Monodora* Dunal, *Xylopia* L.

Crystals are not common, but have been reported as occurring in ray cells as small oblong, square or round crystals [*Fusaea* (Baill.) Saff.] or as druses (*Anaxagorea* A.St.-Hil.). In many other genera, they are present incidentally, mainly in ray cells.

Recognition of genera

Wood characters that may be useful for identification purposes in Annonaceae are the arrangement, diameter and number of vessels, size of intervessel pits, width, height and number of multiseriate rays (Fig. 40C–F), presence or absence of crystals (Fig. 40E, F) and oil cells (Fig. 40C), presence of vasicentric parenchyma (Fig. 40D), and number of parenchyma bands per millimetre.

Only a few genera can be recognized on the basis of one character state or a combination of character states. All studied specimens of *Anaxagorea* have small druses in the ray cells (although sometimes sparse, and not visible with a hand lens; Fig. 40F). Paratracheal parenchyma cells can be found in several genera, but all specimens of the large genus *Guatteria* (with the exception of *G. anomala* R.E.Fr.), including the former small genera *Guatteriella* R.E.Fr., *Guatteriopsis* R.E.Fr. and *Heteropetalum* Benth., have paratracheal parenchyma as narrow vasicentric rings around all vessels (Figs 32A–36A, 40D). In *Fusaea*, small rhombic crystals can be observed in the ray cells (Fig. 40E).

For most genera, however, it is not possible, or hardly so, to find a discriminating group of characters. Although small genera may be rather homogeneous, most large genera show as much variation in wood character states as the family as a whole. An example is *Annona* L. (Figs 14E–18E).

When only end-grain observations are available, the number of characters useful for identification is even more limited. The most important characters here, often in combination of character states, are the following: arrangement, diameter and frequency of vessels, width of multiseriate rays and number of parenchyma bands per millimetre.

Comparing wood anatomy and phylogenetic relationships

As a result of the random distribution of wood anatomical characters in the family, the plotting of lens key characters on a phylogenetic tree (as in Chatrou *et al*., 2012) does not reveal significant differences between the clades. Nevertheless, we have arranged the photographs according to the clades that are recognized as subfamilies and tribes in Chatrou *et al*. (2012). In this way, we show cases of closely related genera that can be distinguished on the basis of wood anatomy, such as the *Sapranthus* alliance (Ter Welle & Van Rooden, 1982) and the *Malmea* alliance (Ter Welle, 1998). *Greenwayodendron oliveri* (Engl.) Verdc. (Fig. 27C) and *Monanthotaxis parvifolia* (Oliv.) Verdc. (Fig. 3F) are incorrectly placed, because previous identifications of the wood samples have been rectified recently, which made placing the photographs in the appropriate tribes impossible.

Malmeoideae

The two major clades of Annonaceae, together containing > 95% of species diversity, are Malmeoideae and Annonoideae (Richardson *et al*., 2004; Chatrou *et al*., 2012). Mainly as a result of the fact that the Utrecht wood collection policy has focused primarily on the Neotropics, Annonoideae is much better represented than Malmeoideae by samples and wood anatomical data. Four of the seven tribes of Malmeoideae (Chatrou *et al*., 2012) are represented in this study: Malmeeae, a Neotropical clade that corresponds well to the *Cremastosperma–Malmea* alliance as identified by van Setten & Koek-Noorman (1992) on the basis of fruit and seed characters, Monocarpieae and Miliuseae. The latter forms a seemingly stray group of some Neotropical (e.g. *Sapranthus*, *Stenanona* Standl., *Desmopsis* Saff.), East African and Malagasy, but mostly Asian, taxa, the relationships of which at present are unresolved to some extent (Chatrou *et al*., 2012; T. Chaowasku *et al*., unpubl. data). Because of the sister group relationship of Miliuseae and the monogeneric tribe Monocarpieae, these are treated together in the description. Tribe Piptostigmatae, an African clade containing five small genera (Couvreur *et al*., 2009; Chatrou *et al*., 2012), is sister to the remaining Malmeoideae and is the fourth tribe sampled. The monogeneric tribes Fenerivieae, Maasieae and Dendrokingstonieae are not taken into consideration here, as wood samples were unavailable.

Piptostigmateae (Fig. 27C)

Genus studied: Greenwayodendron Verdc.

Greenwayodendron oliveri (Engl.) Verdc. is characterized by broad rays and rather numerous bands.

Miliuseae and Monocarpieae (Figs 1A–5F)
Genera studied: Alphonsea Hook.f. & Thomson, *Desmopsis* Saff., *Enicosanthum* Becc., *Fitzalania* F.Muell., *Meiogyne* Miq., *Miliusa* Lesch. ex A.DC., *Mitrephora* (Blume) Hook.f. & Thomson, *Monocarpia* Miq., *Orophea* Blume, *Phaeanthus* Hook.f. & Thomson, *Platymitra* Boerl., *Polyalthia* Blume, *Popowia* Endl., *Pseuduvaria* Miq., *Sapranthus* Seem., *Stelechocarpus* (Blume) Hook.f. & Thomson and *Stenanona* Standl.

The phylogenetic relationships among genera of Miliuseae are generally unclear. Of the genera in our sample, close phylogenetic relationships have been demonstrated among three Asian genera of Miliuseae, *Alphonsea*, *Miliusa* and *Orophea* (Mols *et al*., 2004), and between three Central American genera belonging to the same tribe, *Desmopsis*, *Sapranthus* and *Stenanona* (T. Chaowasku *et al*., unpubl. data).

In their study of the wood anatomy of *Desmopsis* (Fig. 1B–D), *Sapranthus* (Figs 4D–F, 5A) and *Stenanona* (Fig. 5C–E), Ter Welle & Van Rooden (1982) concluded that the three genera could be separated on the basis of the presence vs. absence of uniseriate rays, and quantitative ray characters such as height, width and number and vessel member length. However, they were unable to distinguish this group of three genera from Annonaceae as a whole as the characters '. . . match perfectly the annonaceous wood anatomical character complex' (Ter Welle & Van Rooden, 1982, p. 19).

The same can be said for the tribe Miliuseae. Features normally used in the identification of wood all show a wide variation, e.g. diameter and arrangement of vessels, number and width of rays and number of parenchyma bands [compare, for example, *Enicosanthum* (Fig. 1E: 15% solitary vessels and > 20 parenchyma bands per millimetre) with *Miliusa* (Fig. 2D, E: 40% solitary vessels and < 10 parenchyma bands per millimeter]. As another example, broad rays in, for example, *Enicosanthum* and *Pseuduvaria* (Fig. 4A–C), are in sharp contrast with the narrow rays of, for example, *Alphonsea* (Fig. 1A).

Chaowasku, Zijlstra & Chatrou (2011) concluded that *Fitzalania* is nested within *Meiogyne* on the basis of molecular phylogenetic analyses, and therefore should be considered as a single genus. The wood anatomy of *M. cylindrocarpa* (Burck) Heusden (Fig. 1F) and *F. heteropetala* (F.Muell.) F.Muell. (Fig. 2A, B) is highly similar.

Monocarpia (Fig. 5F), the genus that is sister to Miliuseae, shows an extreme difference between the narrow and wide rays in the specimen examined. Uniseriates are numerous. Multiseriates, although not wide in absolute measurements, are eight- to ten-seriate or more, and are high. Wide rays, however, are scarce: less than one per millimetre. Also taking into account the arrangement of the vessels in numerous clusters and the widely spaced parenchyma bands (only five or six per millimetre), the sister group relationship of *Monocarpia* to Miliuseae is reflected in the wood anatomy, as far as can be judged from the single specimen seen.

Malmeeae (Figs 6A–11C)
Genera studied: Cremastosperma R.E.Fr., *Ephedranthus* S.Moore, *Klarobelia* Chatrou, *Malmea* R.E.Fr., *Mosannona* Chatrou, *Oxandra* A.Rich., *Pseudomalmea* Chatrou, *Pseudoxandra* R.E.Fr., *Bocageopsis* R.E.Fr., *Onychopetalum* R.E.Fr. and *Unonopsis* R.E.Fr.

Within this clade, referred to as South American-centred Clade in Pirie (2005) and Pirie *et al*. (2006), the *Cremastosperma–Malmea* group (*sensu* van Setten & Koek-Noorman, 1992) is sister to a clade comprising *Unonopsis*, *Bocageopsis* and *Onychopetalum* (Pirie *et al*., 2006; Chatrou *et al*., 2012). The last three genera have been demonstrated to be closely related (Pirie *et al*., 2006; Maas, Westra & Vermeer, 2007).

In the *Cremastosperma–Malmea* group, the rays mostly tend to be narrow, with occasionally some broader ones in between. In contrast, broad rays prevail in *Cremastosperma*, especially *C. cauliflorum* R.E.Fr. (Fig. 8C), but much less in *C. microcarpum* R.E.Fr.; in one specimen of this species, they are even lacking (Fig. 8D). Broad rays are also prominent in *Bocageopsis* (Fig. 10A–C), *Onychopetalum* (Fig. 10D) and *Unonopsis* (Figs 10E–11C), although markedly less so in *U. perrottetii* (A.DC.) R.E.Fr. (Fig. 11A).

Vessels, whether solitary or in a radial arrangement, appear to be small in most cases. However, a narrow spacing of the rays may enhance an illusion of vessels looking larger than they truly are, notably in *Ephedranthus guianensis* R.E.Fr. (Fig. 6B) where the rays are so close as to often touch the vessels on both sides. The thin fibre walls in *Cremastosperma microcarpum* R.E.Fr. (Fig. 8D, E) might be related to the wet habitat of this species. Relatively large vessels appear in *Bocageopsis*, *Onychopetalum* and *Unonopsis*. *Unonopsis perrottetii*, again, stands somewhat apart by the smaller vessels and, as indicated before, by the narrower rays.

A (rather) fine banding of the parenchyma prevails in most of the genera, but is indistinct in *Pseudomalmea diclina* (R.E.Fr.) Chatrou (Fig. 7F). In *Bocageopsis*, *Onychopetalum* and *Unonopsis*, however, the banding is rather coarse.

The somewhat aberrant wood of *Unonopsis perrottetii*, as compared with other species of this genus studied here, should be noted. Vegetatively, *U. perrottetii* is distinctive by the slightly falcate, narrow leaves with inconspicuous secondary venation

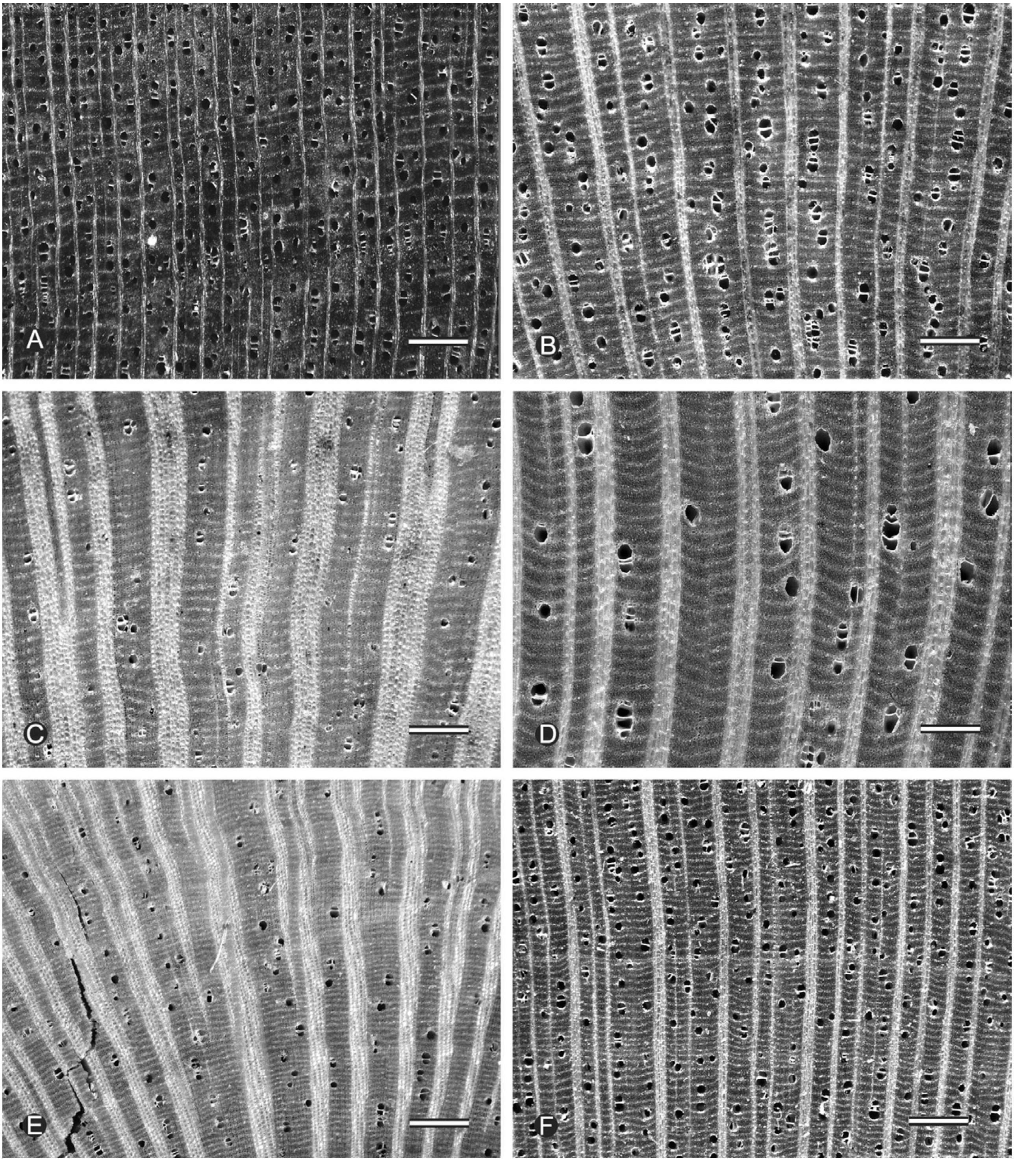

Figure 1. A–F, Miliuseae. A, *Alphonsea mollis* Dunn, Uw 29501; B, *Desmopsis bibracteata* (B.L.Rob.) Saff., Uw 26771; C, *Desmopsis panamensis* (B.L.Rob.) Saff., Uw 24086; D, *Desmopsis* sp., Uw 26193; E, *Enicosanthum macranthum* (King) J.Sinclair, Uw 31869; F, *Meiogyne cylindrocarpa* (Burck) Heusden, Uw 16685.

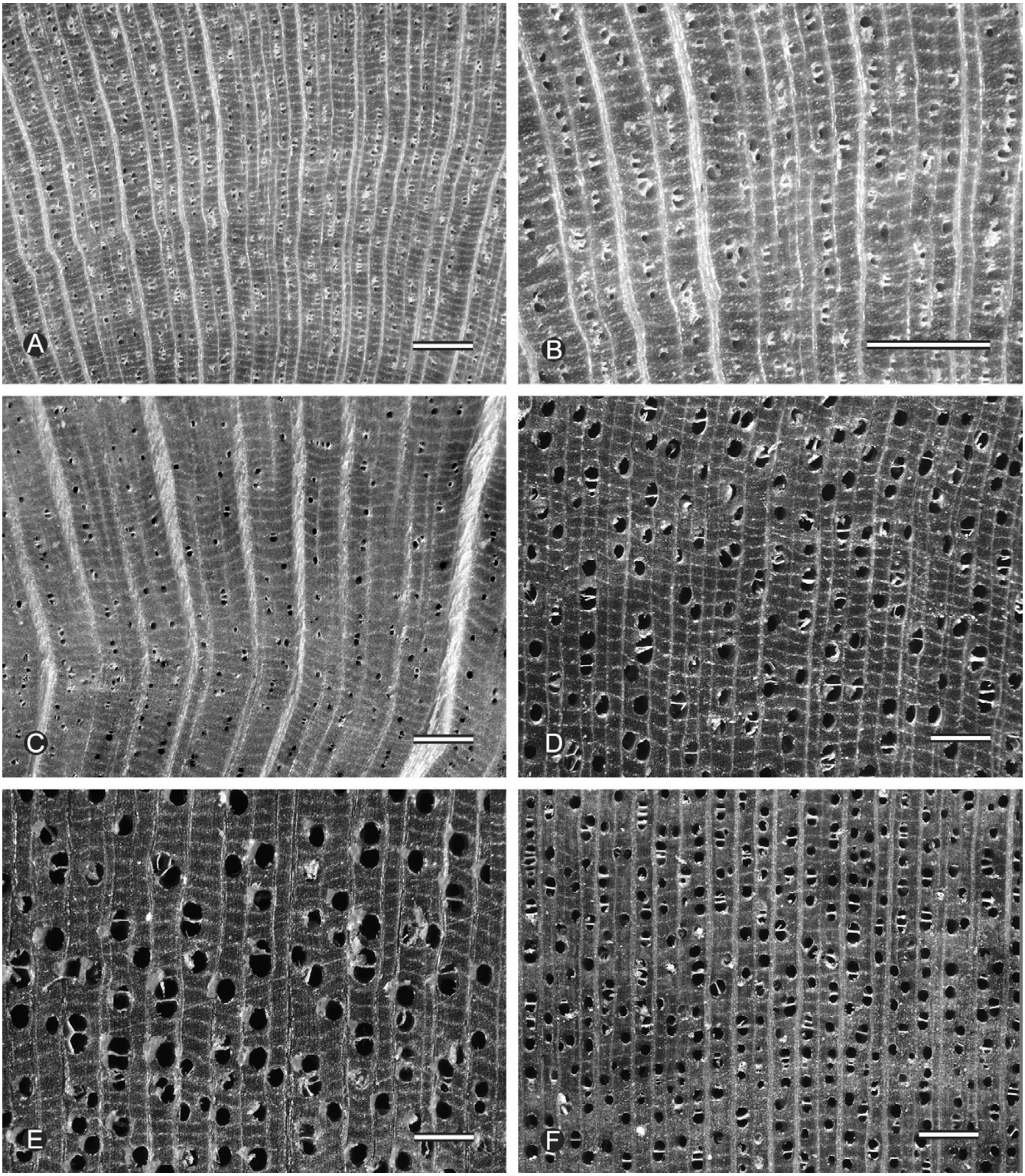

Figure 2. A–F, Miliuseae. A, B, *Fitzalania heteropetala* (F.Muell.) F.Muell., Uw 30384; C, *Orophea creaghii* (Ridl.) Leonar. & P.J.A.Kessler, Uw 32050; D, *Miliusa koolsii* (Kosterm.) J.Sinclair, Uw 18223; E, *Miliusa koolsii,* Uw 18272; F, *Mitrephora thorelii* Pierre, Uw 29514.

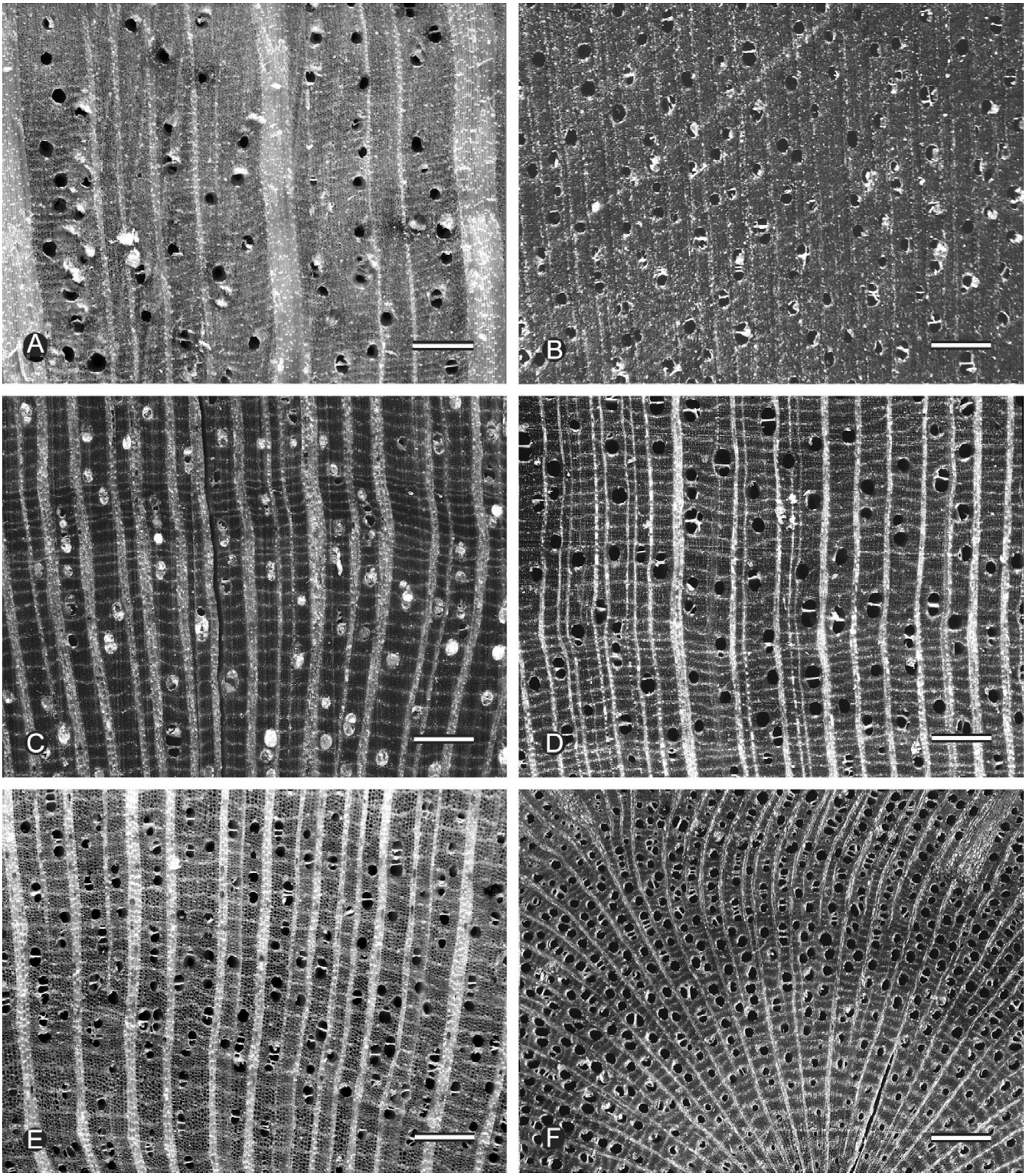

Figure 3. A–E, Miliuseae; F, Uvarieae. A, *Orophea myriantha* Merr., Uw 29493; B, *Phaeanthus ebracteolatus* (C.Presl) Merr., Uw 31376; C, *Platymitra arborea* (Blanco) Kessler, Uw 10744; D, *Polyalthia forbesii* F.Muell. ex Diels, Uw 28711; E, *Polyalthia* sp., Uw 26292; F, *Monanthotaxis parvifolia·* (Oliv.) Verdc., Uw 29499.

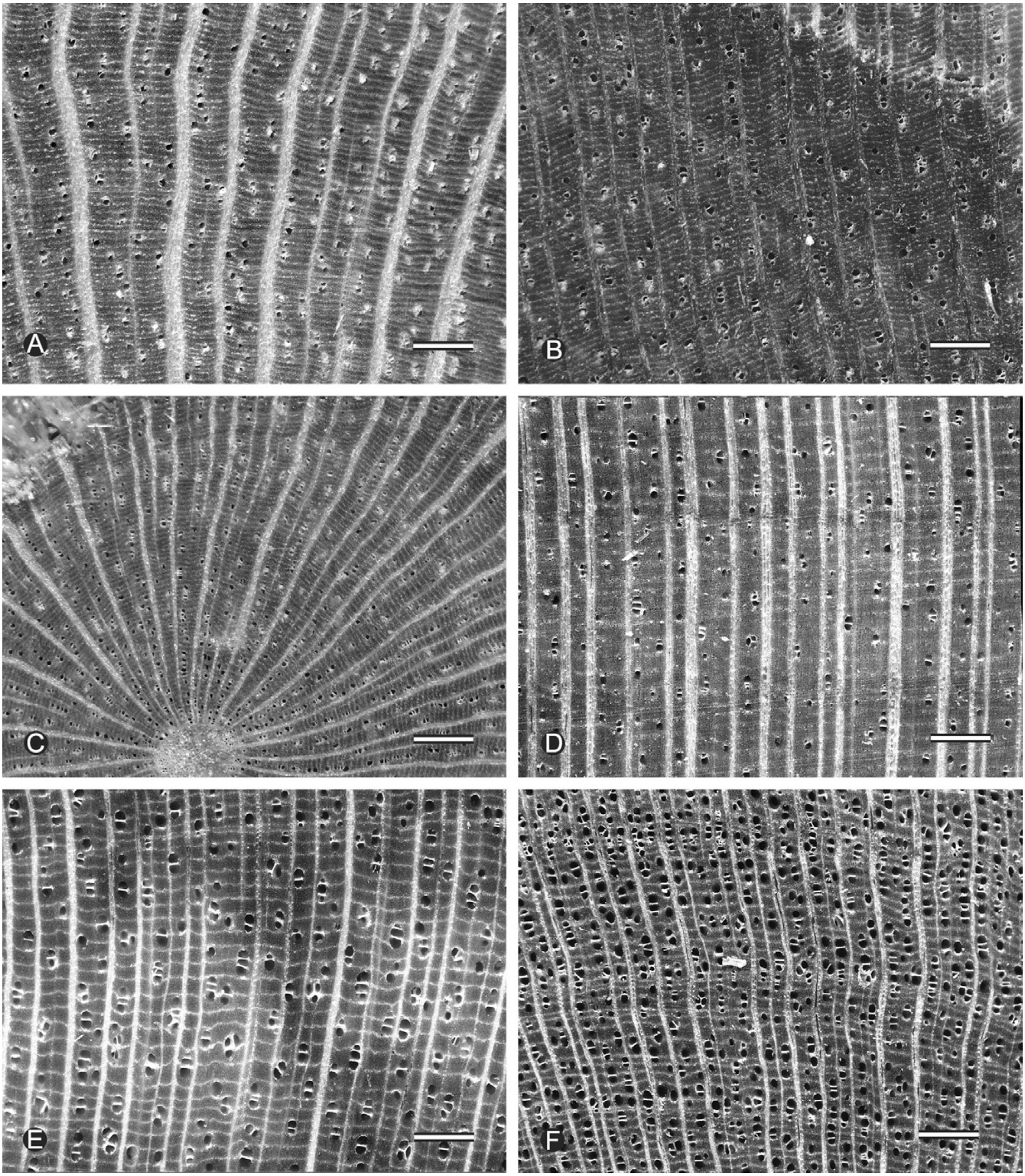

Figure 4. A–F, Miliuseae. A, *Pseuduvaria froggattii* F.Muell., Uw 30394; B, *Pseuduvaria froggattii,* Uw 30408; C, *Pseuduvaria megalopus* (K.Schum.) Y.C.F.Su & Mols, Uw 35942; D, *Sapranthus palanga* R.E.Fr., Uw 26216; E, *Sapranthus palanga,* Uw 26772; F, *Sapranthus violaceus* (Dunal) Saff., Uw 24194.

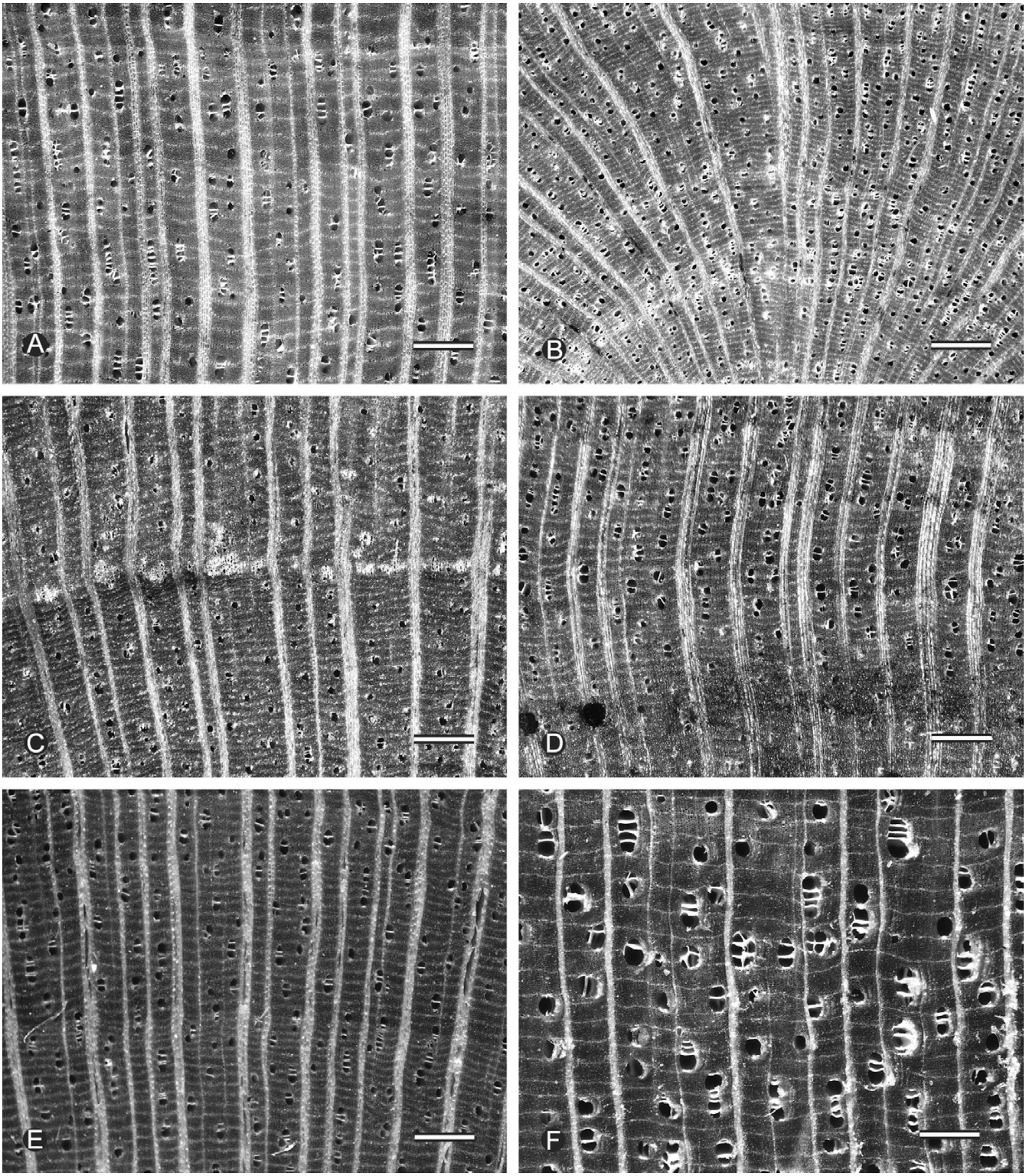

Figure 5. A–E, Miliuseae; F, *Monocarpia*. A, *Sapranthus viridiflorus* G.E.Schatz, Uw 26773; B, *Stelechocarpus cauliflorus* (Scheff.) R.E.Fr., Uw 31305; C, *Stenanona costaricensis* R.E.Fr., Uw 26231; D, *Stenanona panamensis* Standl., Uw 24300; E, *Stenanona stenopetala* (Donn.Sm.) G.E.Schatz, Uw 24298; F, *Monocarpia marginalis* (Scheff.) J.Sinclair, Uw 29515.

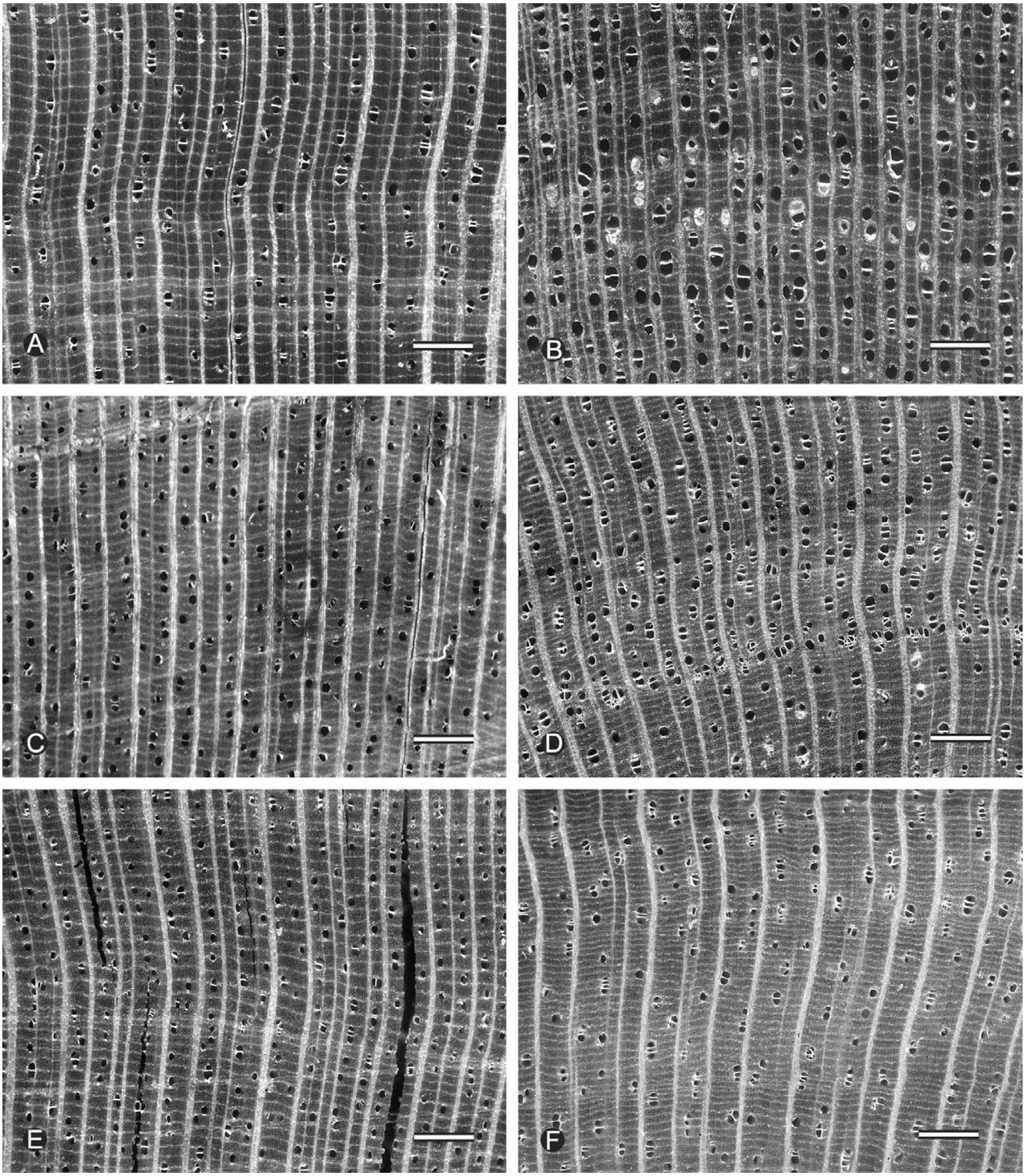

Figure 6. A–F, Malmeeae. A, *Ephedranthus amazonicus* R.E.Fr., Uw 29462; B, *Ephedranthus guianensis* R.E.Fr., Uw 6856; C, *Klarobelia cauliflora* Chatrou, Uw 34863; D, *Klarobelia megalocarpa* Chatrou, Uw 35946; E, *Mosannona* aff. *discolor* (R.E.Fr.) Chatrou, Uw 26395; F, *Mosannona pacifica* Chatrou, Uw 35947.

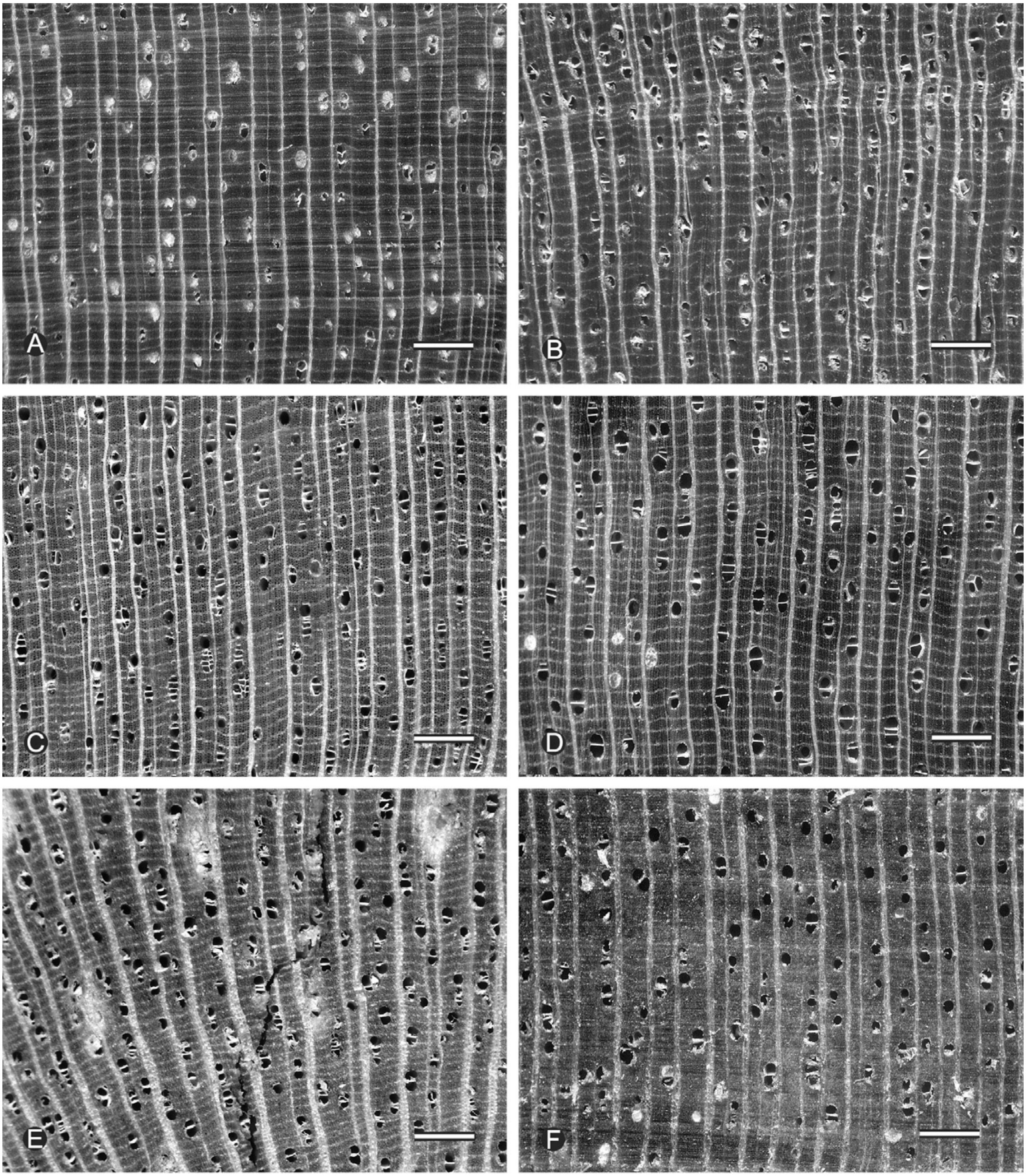

Figure 7. A–F, Malmeeae. A, *Oxandra asbeckii* (Pulle) R.E.Fr., Uw 271; B, *Oxandra asbeckii,* Uw 1916; C, *Oxandra riedeliana* R.E.Fr., Uw 7753; D, *Oxandra riedeliana,* Uw 7793; E, *Pseudomalmea boyacana* (J.F.Macbr.) Chatrou, Uw 31380; F, *Pseudomalmea diclina* (R.E.Fr.) Chatrou, Uw 20084.

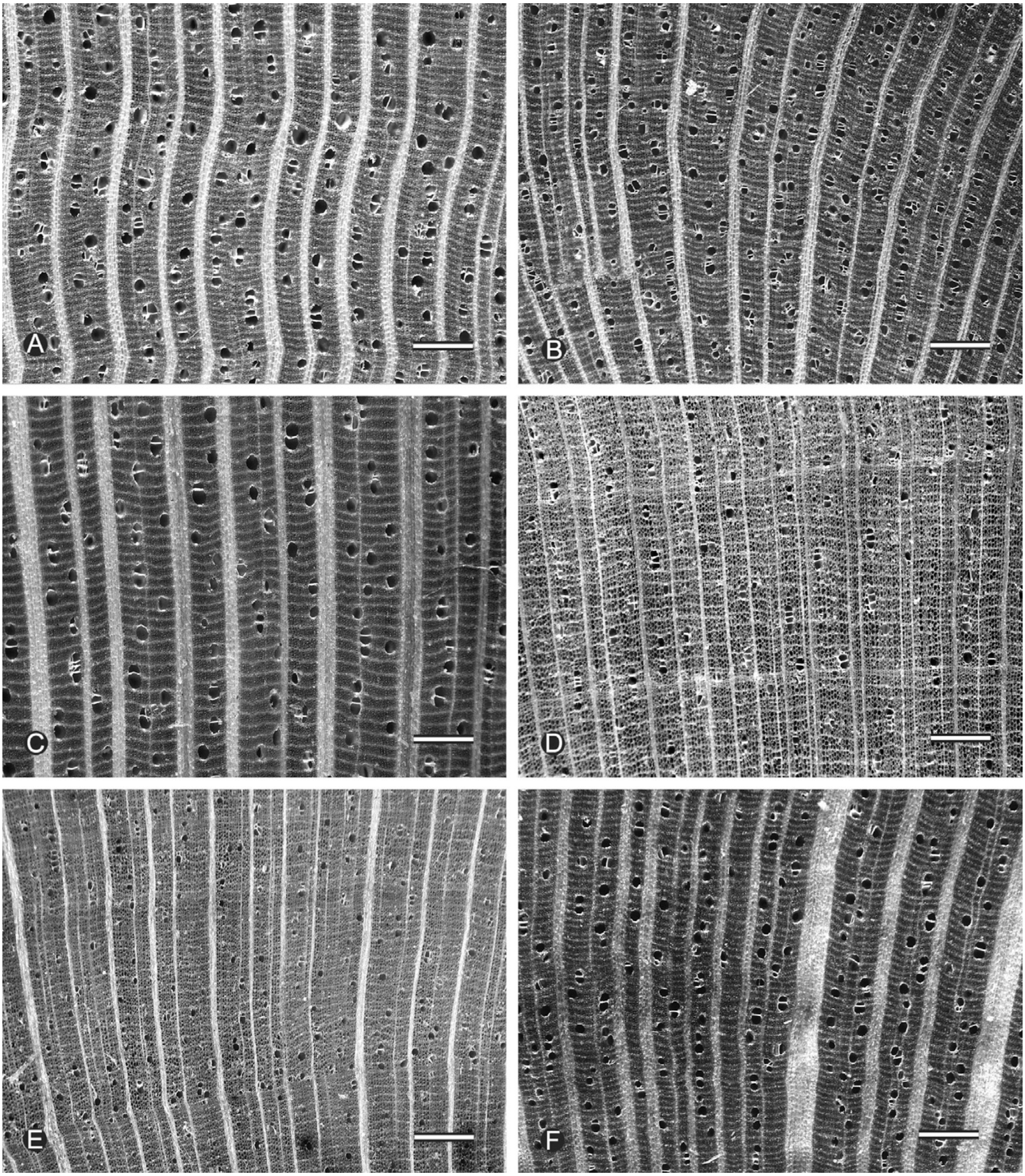

Figure 8. A–F, Malmeeae. A, *Cremastosperma brevipes* (DC.) R.E.Fr., Uw 31466; B, *Cremastosperma brevipes,* Uw 33515; C, *Cremastosperma cauliflorum* R.E.Fr., Uw 30306; D, *Cremastosperma microcarpum* R.E.Fr., Uw 30309; E, *Cremastosperma microcarpum,* Uw 34858; F, *Cremastosperma oblongum* R.E.Fr., Uw 26252.

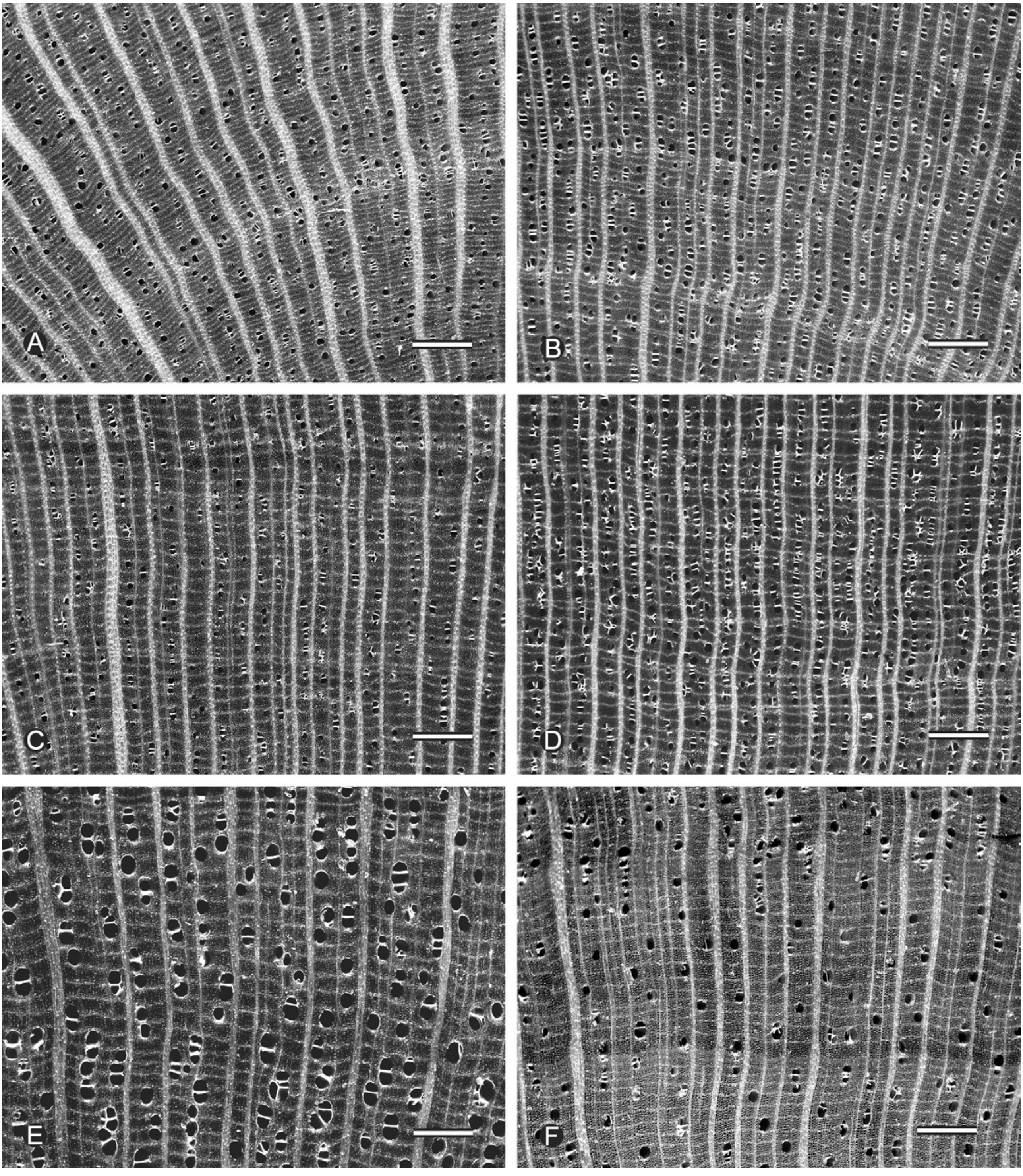

Figure 9. A–F, Malmeeae. A, *Cremastosperma yamayakatense* Pirie, Uw 24523; B, *Malmea dielsiana* R.E.Fr., Uw 30246; C, *Malmea surinamensis* Chatrou, Uw 8543; D, *Malmea surinamensis,* Uw 8629; E, *Pseudoxandra obscurinervis* Maas, Uw 29456; F, *Pseudoxandra polyphleba* (Diels) R.E.Fr., Uw 19657.

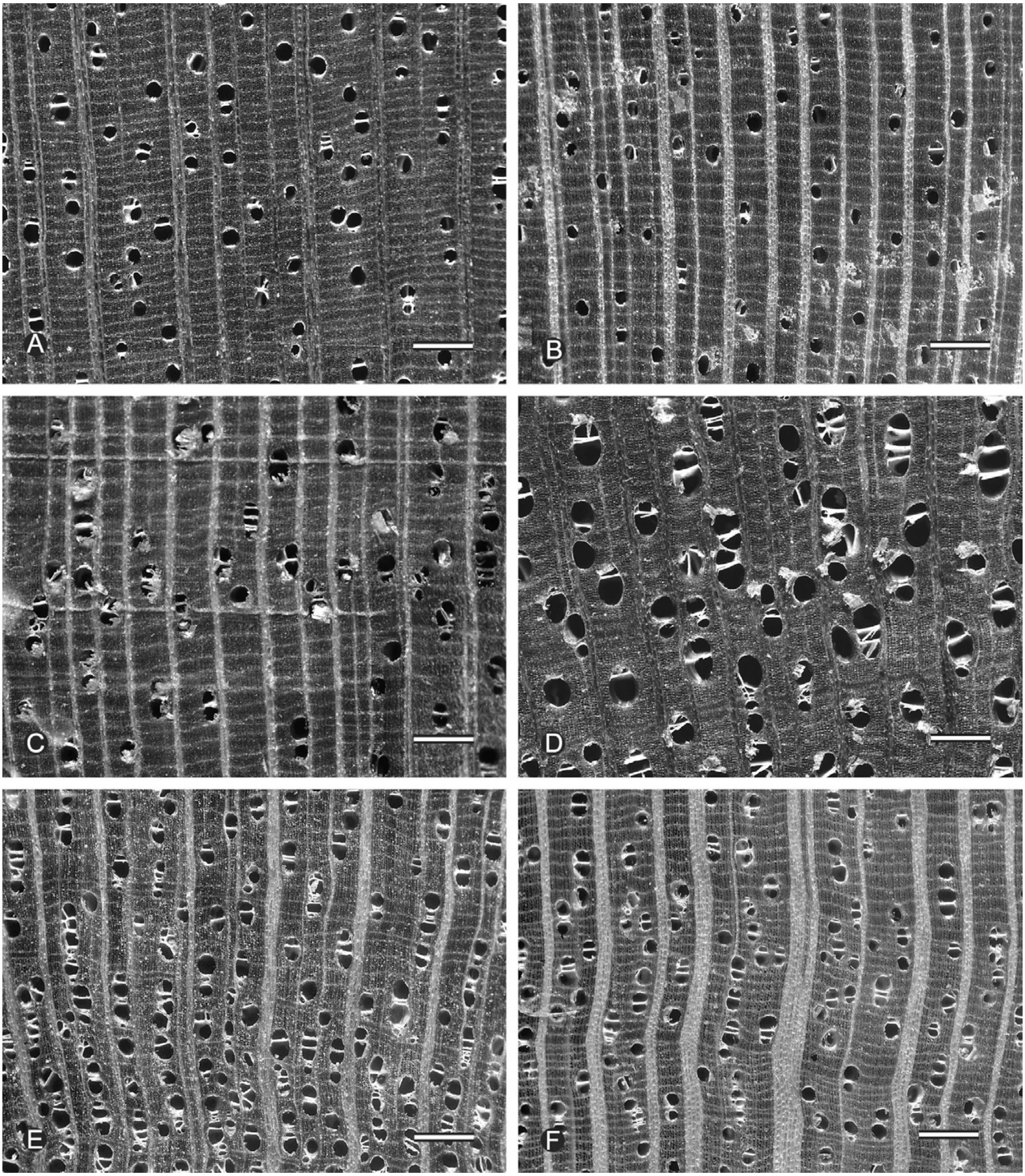

Figure 10. A–F, Malmeeae. A, *Bocageopsis canescens* (Spruce ex Benth.) R.E.Fr., Uw 29474; B, *Bocageopsis multiflora* (Mart.) R.E.Fr., Uw 6796; C, *Bocageopsis multiflora,* Uw 8013; D, *Onychopetalum amazonicum* R.E.Fr., Uw 29457; E, *Unonopsis glaucopetala* R.E.Fr., Uw 2317; F, *Unonopsis guatterioides* (A.DC.) R.E.Fr., Uw 370.

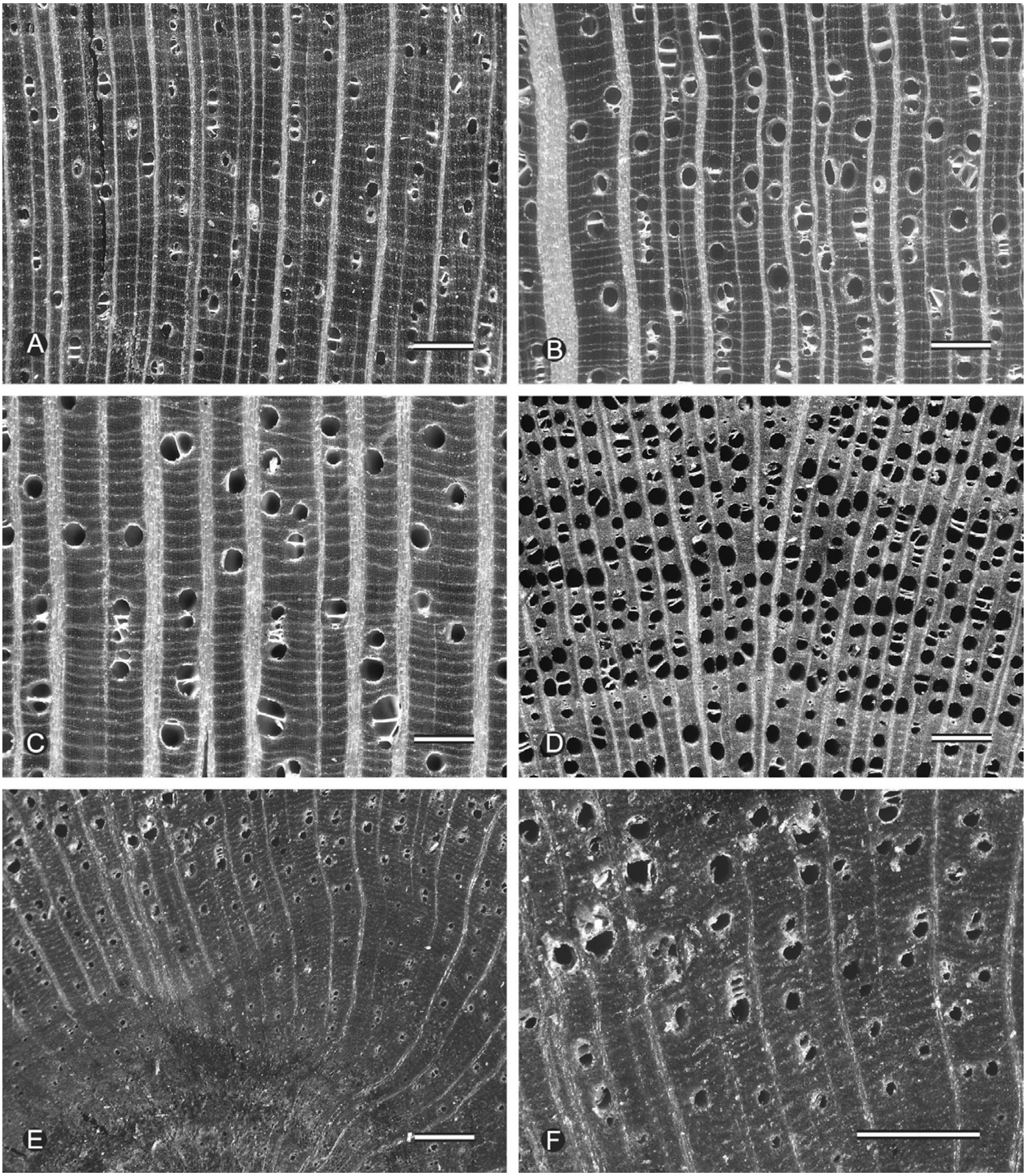

Figure 11. A–C, Malmeeae; D–F, Uvarieae. A, *Unonopsis perrottetii* (A.DC.) R.E.Fr., Uw 772; B, *Unonopsis rufescens* (Baill.) R.E.Fr., Uw 225; C, *Unonopsis sericea* Maas & Westra, Uw 36940; D, *Exellia scamnopetala* (Exell) Boutique, Uw 29528; E, *Fissistigma* sp., Uw 31788; F, *Fissistigma* sp., Uw 31788.

resembling the foliage of *Bocageopsis multiflora* (Mart.) R.E.Fr., rather than that of other *Unonopsis* spp. (Maas *et al*., 2007).

The genera *Klarobelia*, *Malmea*, *Mosannona* and *Pseudomalmea* were formerly treated as one genus, *Malmea*, until Chatrou (1998) convincingly demonstrated their separate status. This is confirmed by more recent research showing the four genera to be polyphyletic (Pirie *et al*., 2006; Chatrou *et al*., 2012). Ter Welle (1998), describing the wood anatomy, concluded that *Malmea s.s.* can be separated from the other three genera by a combination of the prominent radial multiples and the large number of vessels per mm^2 (Fig. 9B–D). In the other three genera, character states overlap in part.

Summarizing, in Malmeeae, an overall tendency seems to prevail towards rather narrow rays and small vessels, often arranged in short to long clusters, but, in contrast, *Onychopetalum*, *Unonopsis* and, to a lesser extent, *Bocageopsis* (and perhaps *Ephedranthus*) tend towards larger vessels.

Annonoideae

In Annonoideae, the large (≥ 100 spp.) genera *Annona*, *Artabotrys* R.Br., *Duguetia*, *Goniothalamus* (Blume) Hook.f. & Thomson, *Guatteria*, *Uvaria* L. and *Xylopia* are found, together with their allies. Although their relative position is not yet fully resolved in the analyses of Chatrou *et al*. (2012) or Erkens, Chatrou & Couvreur (2012), five subclades are recognized.

Monodoreae and Uvarieae (Figs 11D–14D, 40B)

Genera studied: Exellia Boutique, *Fissistigma* Griff., *Friesodielsia* Steenis, *Isolona* Engl., *Monanthotaxis* Baill. (including *Enneastemon* Exell), *Monodora* Dunal, *Toussaintia* Boutique, *Uvaria* L., *Uvariodendron* (Engl. & Diels) R.E.Fr. and *Uvariopsis* Engl.

The genera discussed in this section belong to clade N of Chatrou *et al*. (2012), including Monodoreae and Uvarieae. In their study of syncarpy and other morphological characters, Couvreur *et al*. (2008) discussed the phylogenetic position of *Isolona* and *Monodora* in relation to other African Annonaceae. Both genera were found in their 'African Long Branch clade', now tribe Monodoreae, with, among others, *Uvariastrum* Engl. and *Uvariopsis* Engl. *Monanthotaxis*, *Toussaintia* and *Uvaria* belong to Uvarieae, the sister group of Monodoreae.

The position of *Enneastemon* (Fig. 40B) has been the subject of discussion. The genus was reduced to sectional status under *Monanthotaxis* by Verdcourt (1971) and *E. seretii* (De Wild.) Robyns & Ghesq. was reduced to varietal status as *M. schweinfurthii* (Engl. & Diels) Verdc. var. *seretii* (De Wild.) Verdc. The resemblance between the wood of this species and one of two other available samples of *Monanthotaxis* (*M. poggei* Engl. & Diels, Fig. 12D) is rather weak. However, the wood of *M. schweinfurthii* var. *seretii* is rather similar to that of *Monanthotaxis parvifolia*·(Oliv.) Verdc. (Fig. 3F). These differences almost certainly reflect the taxonomy of *Monanthotaxis*, which is in disarray.

The four samples of *Uvaria* (Fig. 13C–F) show much variation in both the number and diameter of the vessels and in the number and width of the rays. There is some resemblance to *Monodora* (Figs 12E, F, 13A) and *Isolona* (Fig. 12C), with their rather narrow vessels, i.e. often less than half as wide as the distance between two rays, in combination with rather wide rays, notably in *Monodora crispata* Engl. and *M. myristica* (Gaertn.) Dunal. (Fig. 12E, F). *Uvariopsis* (Fig. 14C, D) and, to a lesser extent, *Uvariodendron* (Fig. 14A, B) show a similar combination of characters.

The structure of *Friesodielsia* (Fig. 12A, B), like that of *Toussaintia* (Fig. 13B) and *Exellia* (Fig. 11D), clearly shows the liana habit. *Fissistigma* (Fig. 11E, F) stands out by its vasicentric parenchyma.

Annoneae (Figs 14E–20B)

Genera studied: Annona L., *Anonidium* Engl. & Diels, *Asimina* Adanson, *Diclinanona* Diels and *Goniothalamus* (Blume) Hook.f. & Thomson.

The largest genus in this clade is the Neotropical-African genus *Annona* (now also including *Rollinia* A.St.-Hil. and *Raimondia* Saff.) (Figs 14E–18E). The morphology of the flowers and fruits in *Annona* is variable, and this is paralleled by the range of variation in wood features, which largely parallels that of the family as a whole. The large intervessel pits (7–9 μm) are remarkable. *Anonidium* (Figs 18F, 19A), with its relatively few, large vessels and wide rays, shares the incomplete rings of vasicentric parenchyma with some specimens of *Annona*.

Ter Welle (1995) concluded that it was impossible to distinguish between the closely related genera *Annona*, *Anonidium* and *Rollinia*, then considered a distinct genus. He also did not find any discriminating character, qualitative or quantitative, that would have enabled the recognition of these genera as a separate group within the family. This is mainly because of the large overlap in variation between *Annona* and the family as a whole. Several species have rhombic crystals in rays and axial parenchyma cells (Ter Welle, 1992). In *A.* cf. *densicoma* Mart. (Fig. 15C) and *A. montana* Macfad. (Fig. 17A), the rays vary from narrow to (particularly in *A. montana*) broad. Vessels in *A. montana* are rather large and mostly solitary, and similar (but even larger) in *A. sericea* Dunal. *Annona* cf. *densicoma* has distinctly

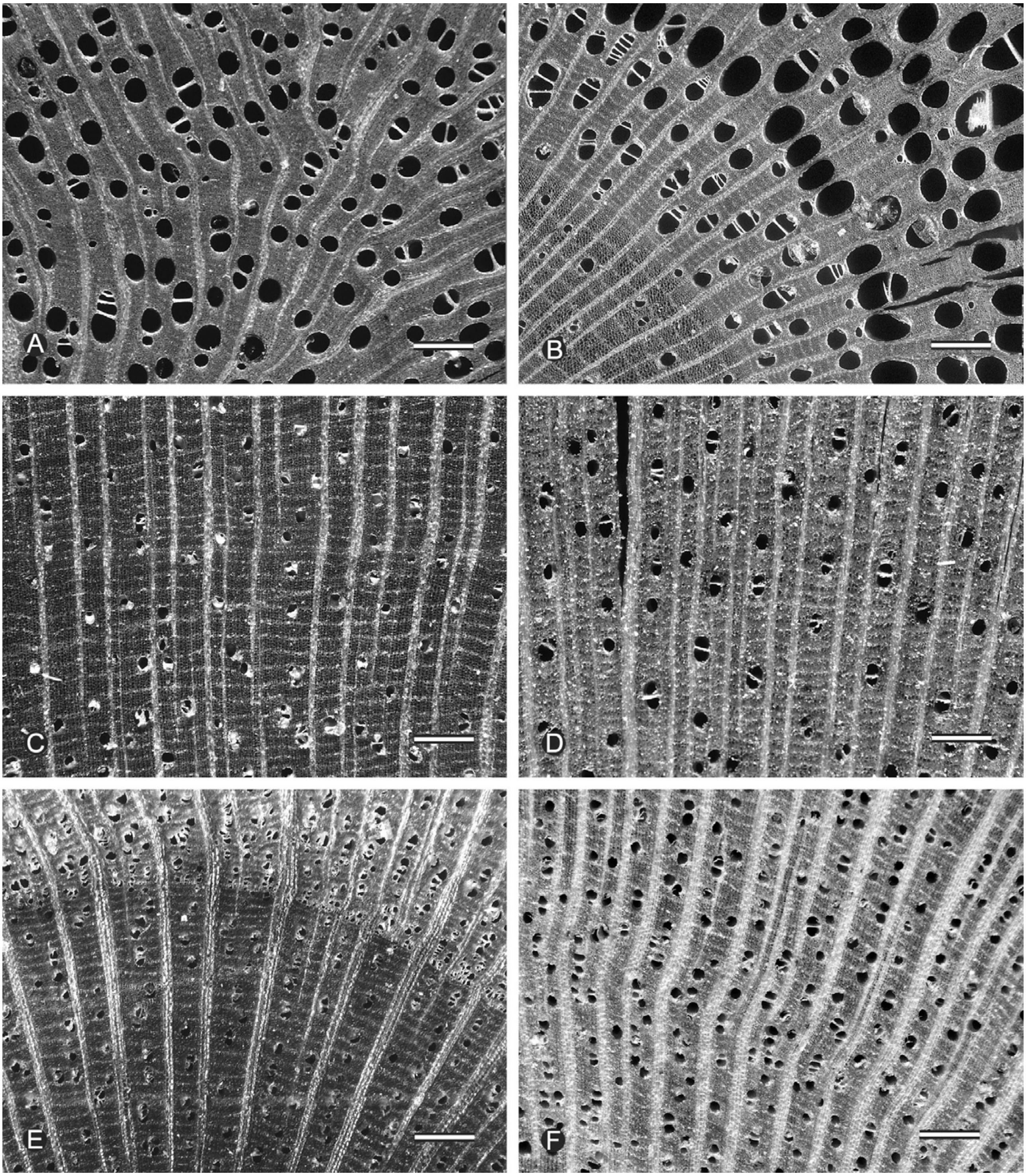

Figure 12. A, B, D, Uvarieae; C, E, F, Monodoreae. A, *Friesodielsia enghiana* (Diels) Verdc., Uw 29536; B, *Friesodielsia montana* (Engl. & Diels) Steenis, Uw 29519; C, *Isolona hexaloba* (Pierre) Engl. & Diels, Uw 29497; D, *Monanthotaxis poggei* Engl. & Diels, Uw 29498; E, *Monodora crispata* Engl. & Diels, Uw 22122; F, *Monodora myristica* (Gaertn.) Dunal, Uw 34652.

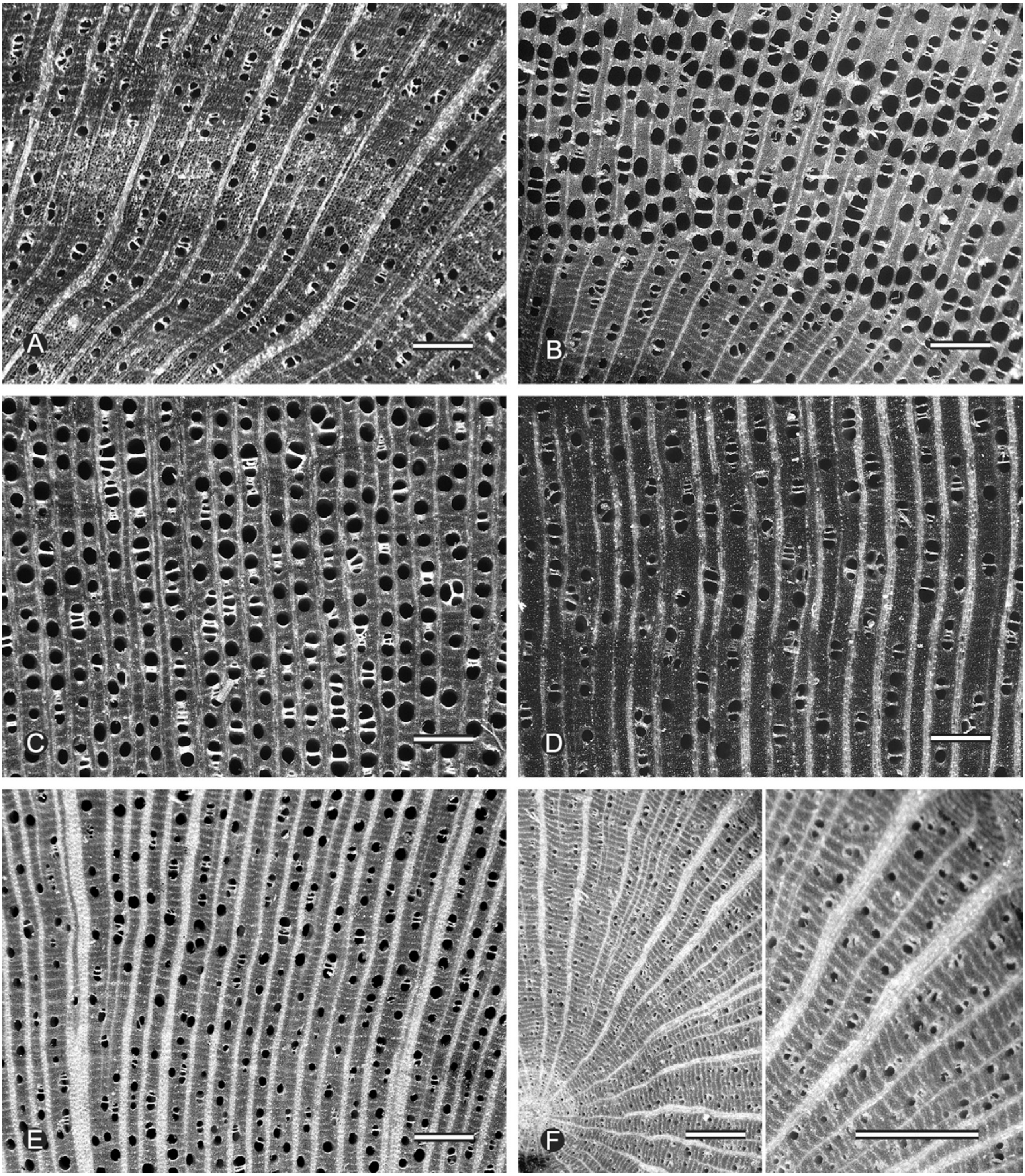

Figure 13. A, Monodoreae; B–F, Uvarieae. A, *Monodora undulata* (P.Beauv.) Couvreur, Uw 29379; B, *Toussaintia hallei* Le Thomas, Uw 29546; C, *Uvaria angolensis* Welw. ex Oliv., Uw 22255; D, *Uvaria chamae* P.Beauv., Uw 25872; E, *Uvaria doeringii* Diels, Uw 22121; F, *Uvaria* sp. (two magnifications), Uw 30698.

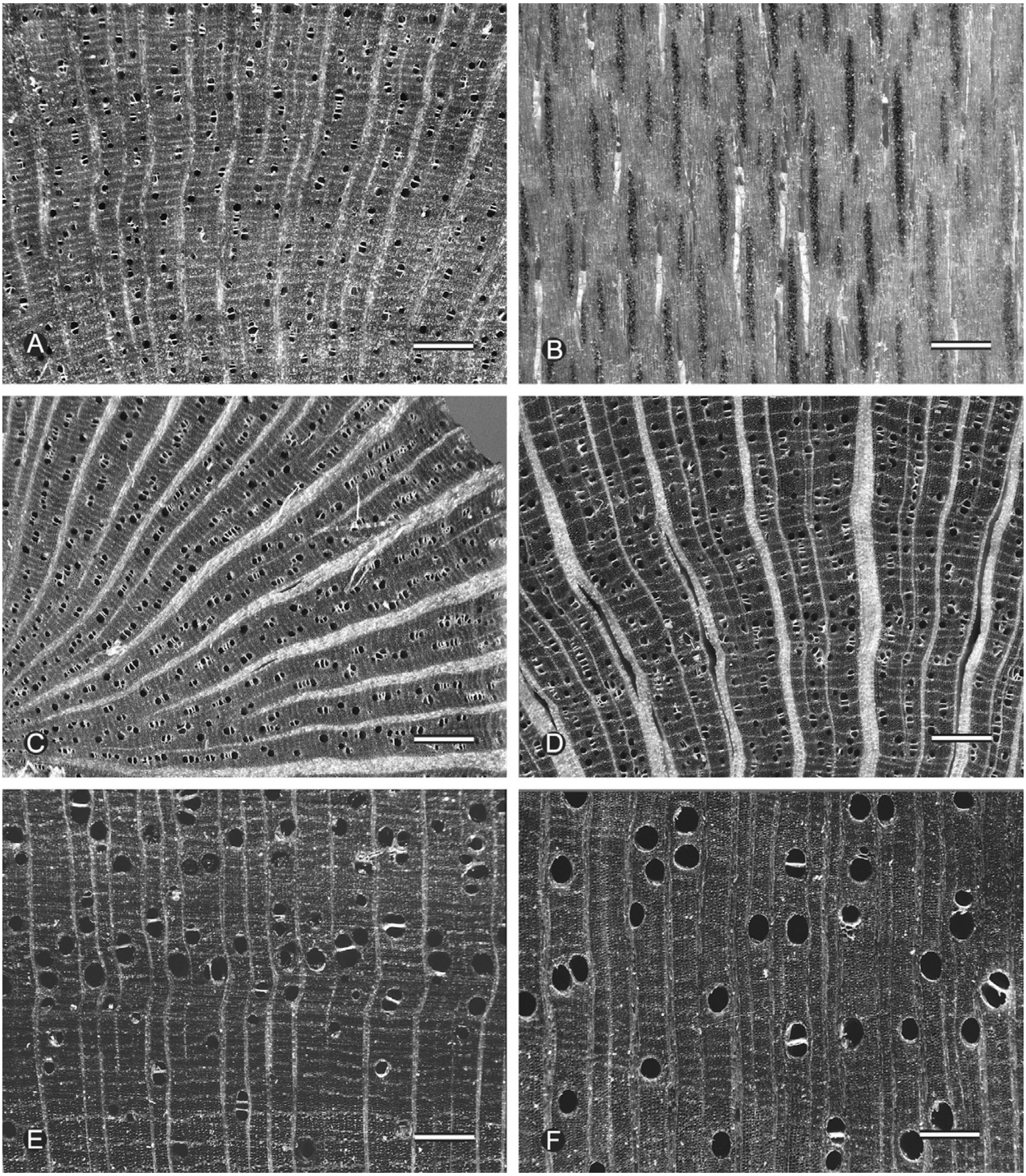

Figure 14. A–D, Monodoreae; E, F, Annoneae. A, *Uvariodendron molundense* (Engl. & Diels) R.E.Fr., Uw 29542; B, *Uvariodendron molundense* (tangential section), Uw 29542; C, *Uvariopsis congolana* (De Wild.) R.E.Fr., Uw 29503; D, *Uvariopsis congolana,* Uw 29511; E, *Annona annonoides* (R.E.Fr.) Maas & Westra, Uw 7989; F, *Annona calcarata* (R.E.Fr.) H. Rainer, Uw 19892.

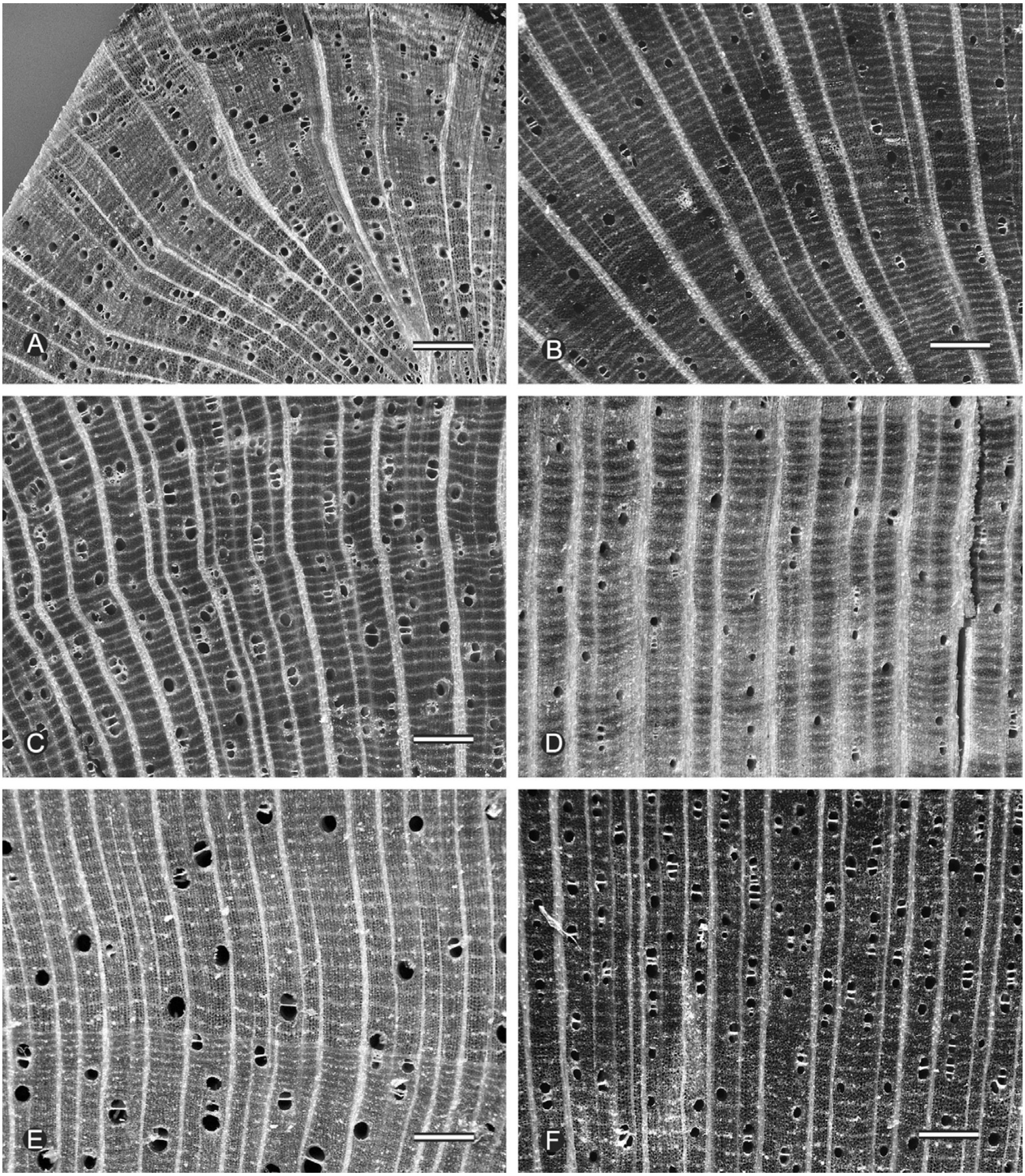

Figure 15. A–F, Annoneae. A, *Annona cherimolioides* Triana & Planch., Uw s.n.; B, *Annona* cf. *cuspidata* (Mart.) H. Rainer, Uw 4050; C, *Annona* cf. *densicoma* Mart., Uw 4012; D, *Annona dolichophylla* R.E.Fr., Uw 30303; E, *Annona edulis* (Triana & Planch.) H.Rainer, Uw 30324; F, *Annona emarginata* (Schltdl.) H.Rainer, Uw 12880.

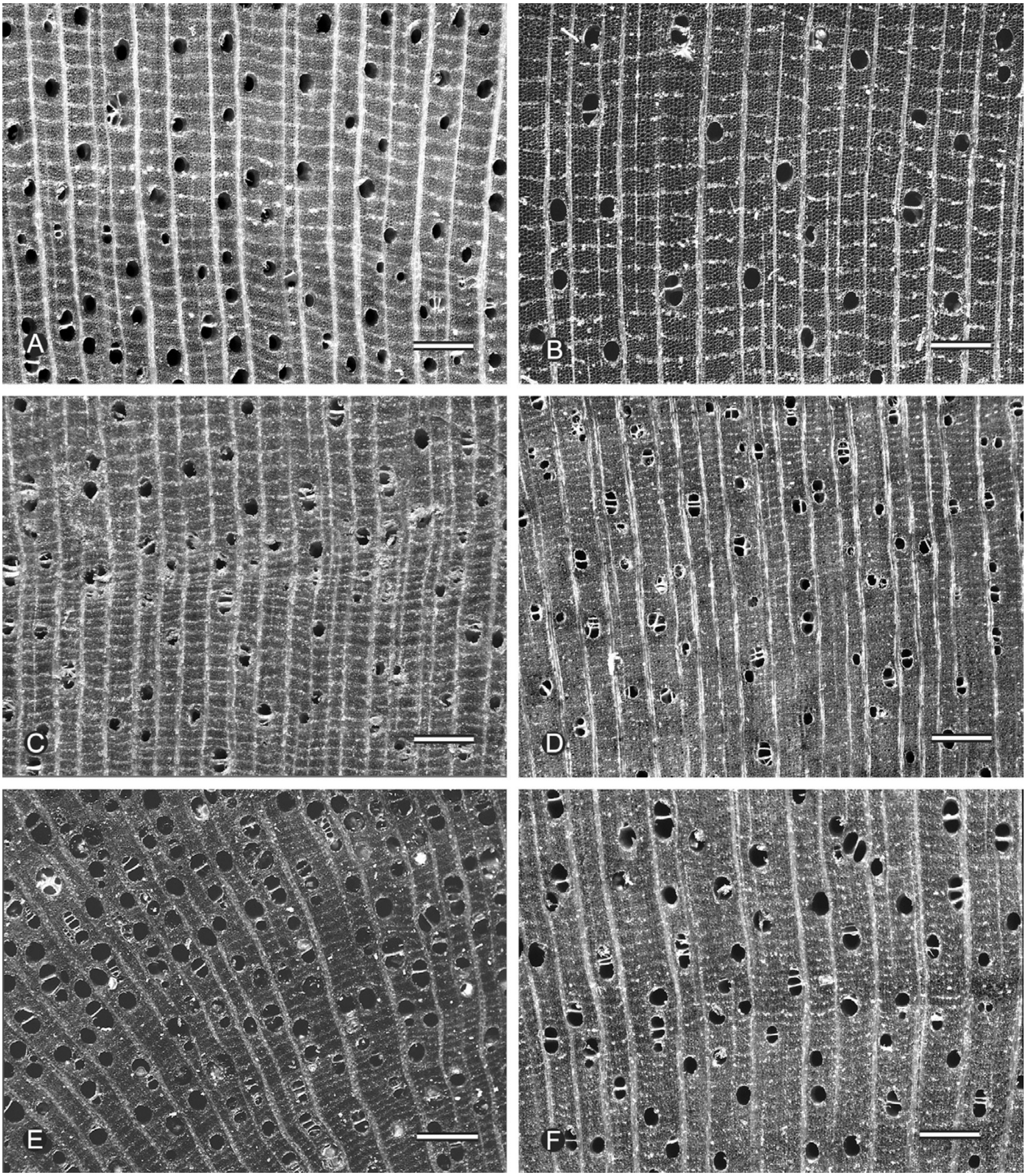

Figure 16. A–F, Annoneae. A, *Annona emarginata* (Schltdl.) H.Rainer, Uw 13209; B, *Annona exsucca* DC., Uw 770; C, *Annona fendleri* (R.E.Fr.) H.Rainer, Uw 35096; D, *Annona glabra* L., Uw 4492; E, *Annona haematantha* Miq., Uw 2572; F, *Annona jucunda* (Diels) H.Rainer, Uw 30279.

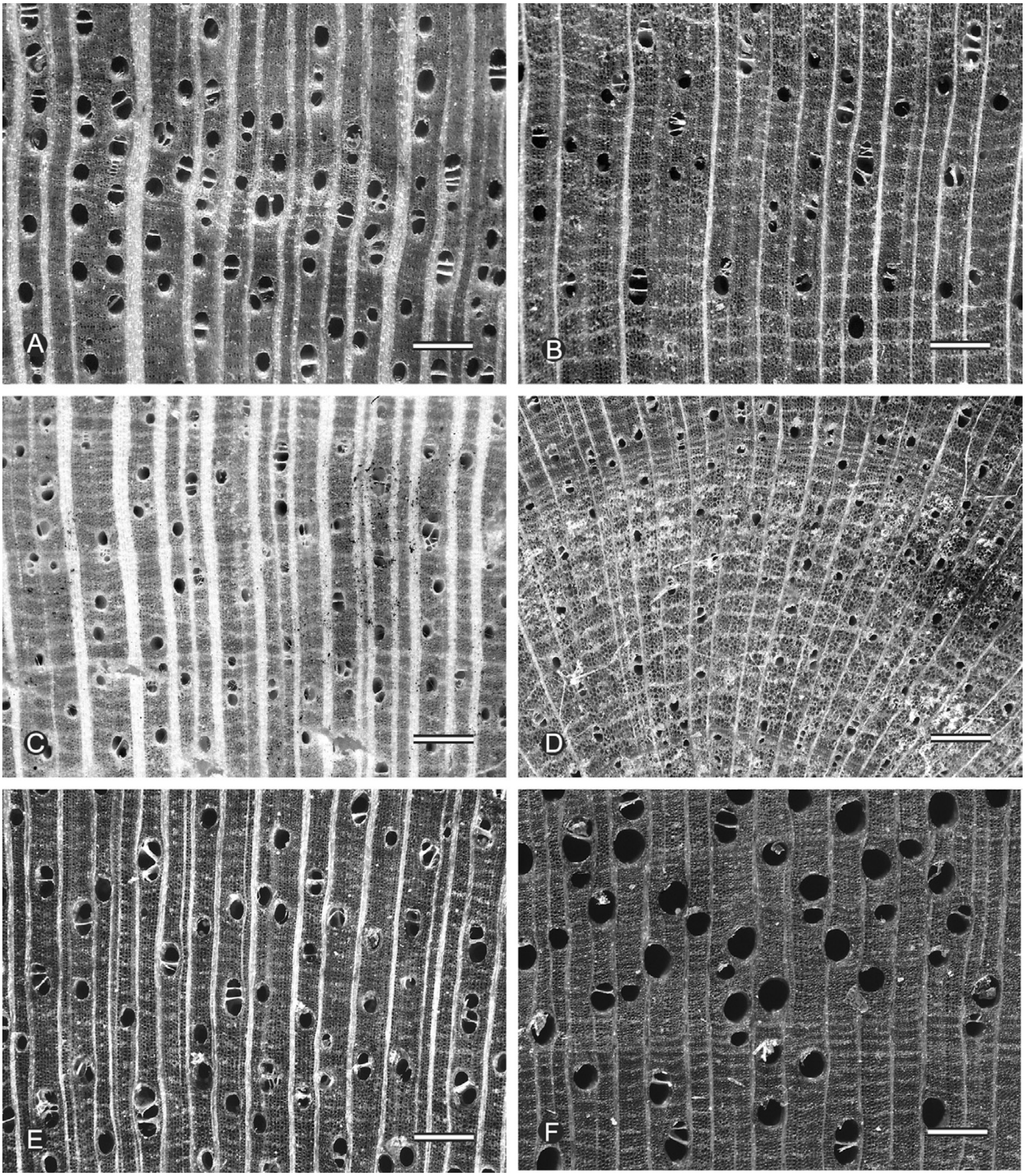

Figure 17. A–F, Annoneae. A, *Annona montana* Macfad., Uw 1465; B, *Annona mucosa* Jacq., Uw 30239; C, *Annona muricata* L., Unw 546; D, *Annona neosericea* H.Rainer, Uw 12501; E, *Annona neoulei* H.Rainer, Uw 30235; F, *Annona neovelutina* H.Rainer, Uw 29435.

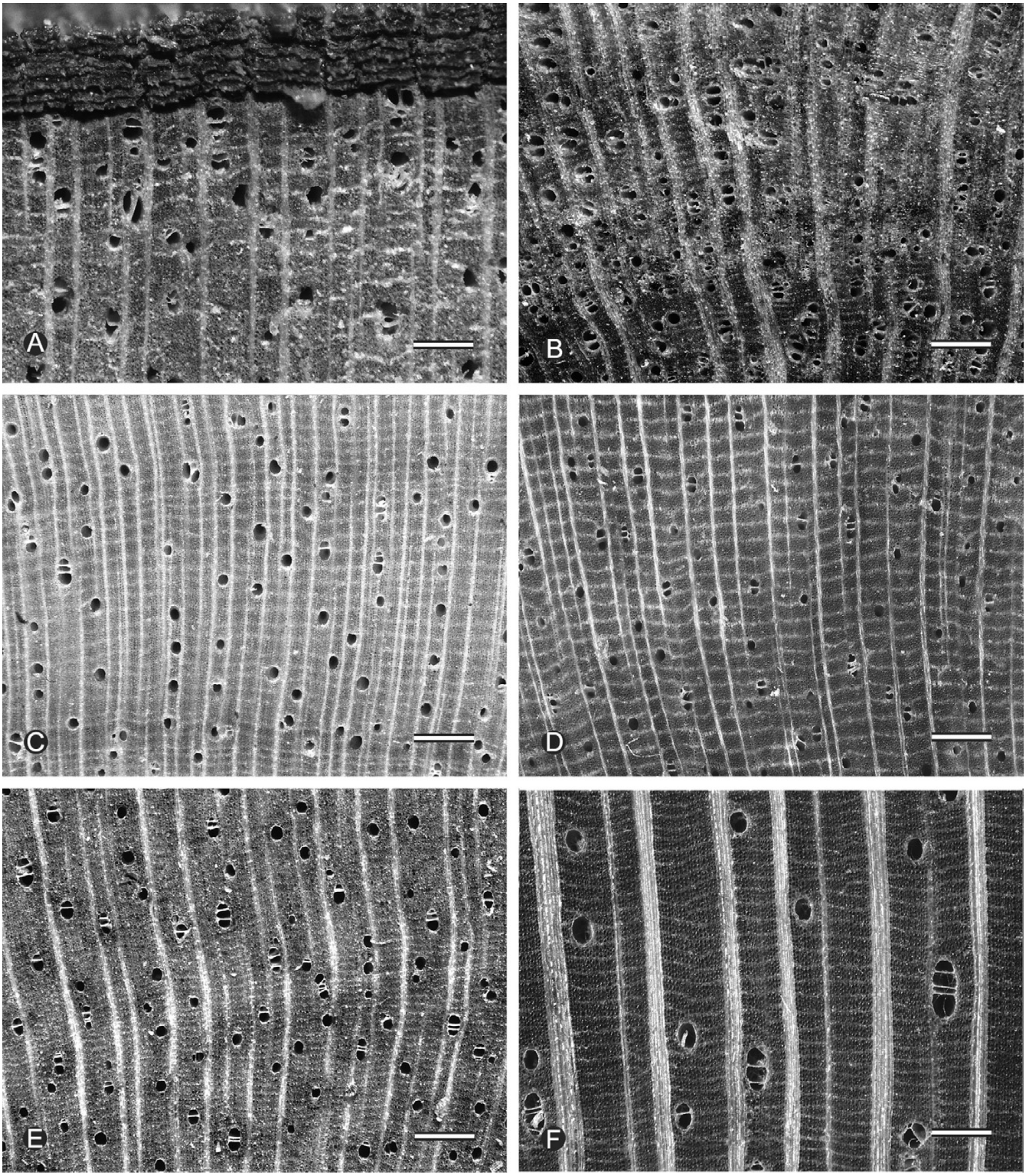

Figure 18. A–F, Annoneae. A, *Annona quinduensis* Kunth, Uw 37079; B, *Annona senegalensis* Persoon, Uw 15581; C, *Annona sericea* Dunal, Uw 32438; D, *Annona sylvatica* A.St.-Hil., Uw 14352; E, *Annona* cf. *williamsii* (Rusby ex R.E.Fr.) H.Rainer, Uw 30255; F, *Anonidium mannii* (Oliv.) Engl. & Diels, Uw 29488.

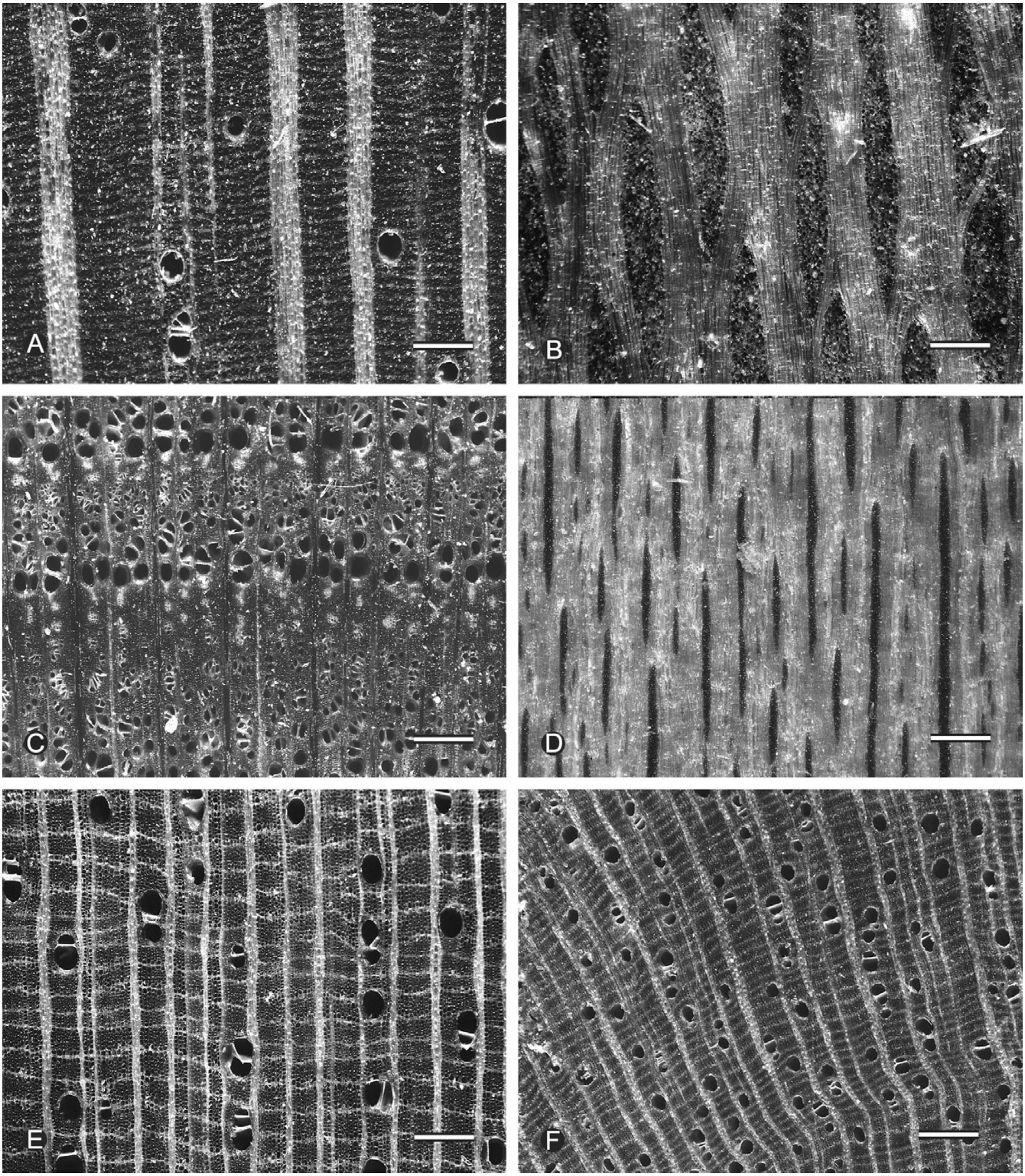

Figure 19. A–F, Annoneae. A, *Anonidium mannii* (Oliv.) Engl. & Diels, Uw 25871; B, *Anonidium mannii* (tangential section), Uw 25871; C, *Asimina triloba* (L.) Dunal, Uw 8474; D, *Asimina triloba* (tangential section), Uw 8474; E, *Diclinanona calycina* (Diels) R.E.Fr., Uw 16135; F, *Diclinanona tessmannii* Diels, Uw 30327.

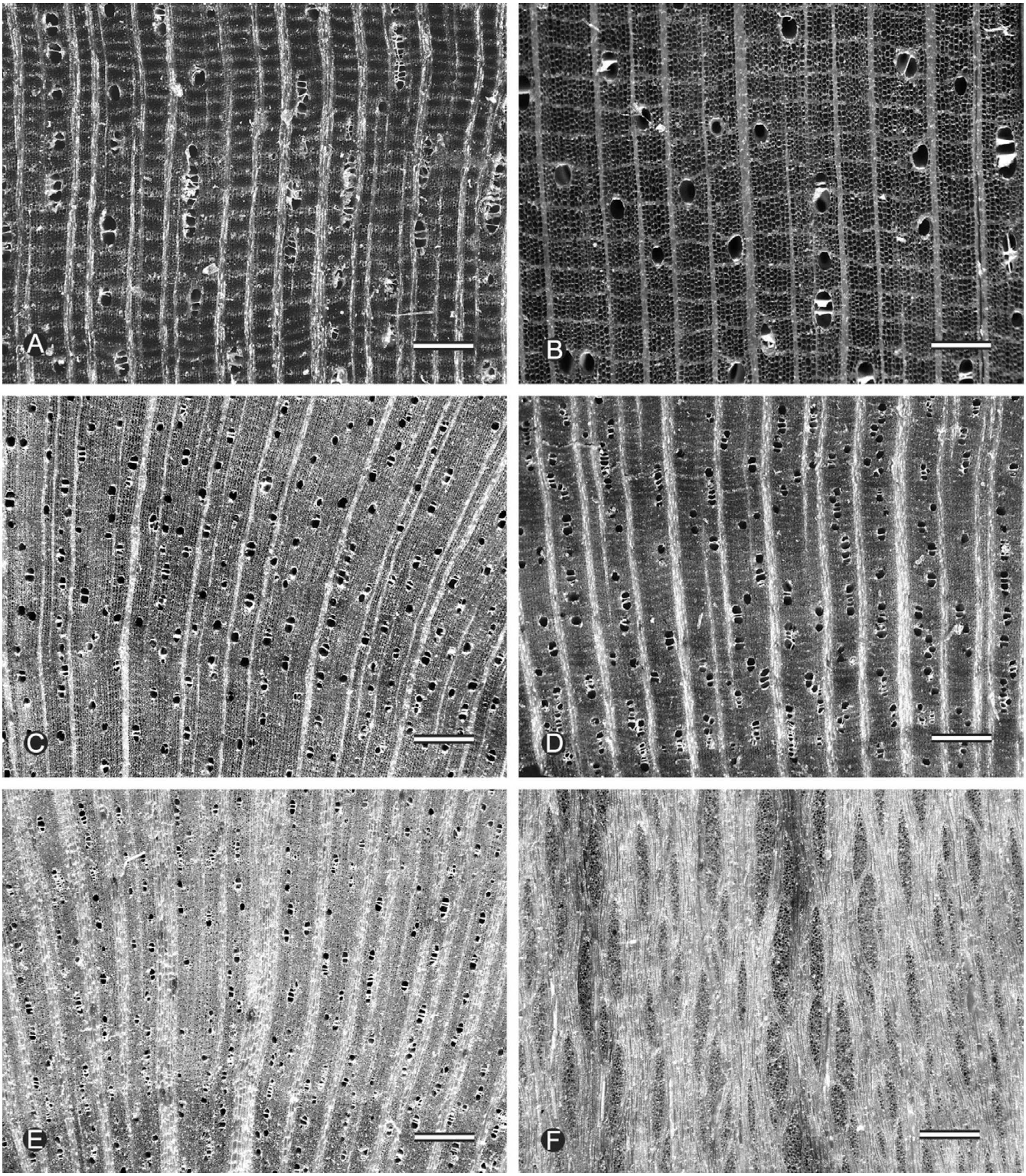

Figure 20. A, B, Annoneae; C–F, Duguetieae. A, *Diclinanona tessmannii* Diels, Uw 30342; B, *Goniothalamus giganteus* Hook.f. & Thomson, Uw 29389; C, *Duguetia argentea* (R.E.Fr.) R.E.Fr., Uw 8182; D, *Duguetia bahiensis* Maas, Uw 31902; E, *Duguetia cadaverica* Huber, Uw 29933; F, *Duguetia cadaverica* (tangential section), Uw 29933.

smaller vessels, mostly in a radial arrangement. The banding pattern of the parenchyma bands is relatively fine in *A.* cf. *densicoma*, but coarse in *A. montana*.

A comparable range of vessel size is seen in species formerly placed in *Rollinia*. The largest vessels are found in *A. calcarata* (R.E.Fr.) H.Rainer (Fig. 14F) and *A. neovelutina* H.Rainer (Fig. 17F). The rays are relatively narrow in *A. emarginata* (Schltdl.) H.Rainer (Figs 15F, 16A), and more variable in *A.* cf. *cuspidata* (Mart.) H.Rainer (Fig. 15B). The banding, however, is rather coarse to very coarse in all former *Rollinia* spp. seen, with (seasonal) variations in *A. edulis* (Triana & Planch.) H.Rainer (Fig. 15E), *A. fendleri* (R.E.Fr.) H.Rainer (Fig. 16C) and *A. neosericea* H.Rainer (Fig. 17D).

Diclinanona (Fig. 19E–20A), a genus recently shown to belong to Annonoideae (T. Chaowasku *et al*., unpubl. data), stands out by relatively low multiseriate rays and thin-walled fibres, in particular along the rays and the parenchyma bands. It has slightly more vessels, sometimes in clusters. The single photographed specimen of *Goniothalamus* (Fig. 20B) has few parenchyma bands: five or six per millimetre.

The wood of *Asimina triloba* (L.) Dunal (Fig. 19C, D), an exceptional species because of its temperate distribution, is ring porous. The small vessels are arranged in large clusters; parenchyma bands are scanty and poorly visible, and are almost restricted to the zones of latewood.

Duguetieae (Figs 20C–26F)

Genera studied: Duguetia A.St.-Hil., *Fusaea* (Baill.) Saff., *Pseudartabotrys* Pellegr.

The wood of *Duguetia* and *Fusaea* was studied by Ter Welle & Du (2003) and Ter Welle (1999), respectively. *Duguetia* (including *Pachypodanthium* Engl. & Diels; Chatrou, Koek-Noorman & Maas, 2000) (Figs 20C–25F), although easily recognized by, among other characters, indument and fruit characteristics, shows a great variation in the wood. Sometimes even within a single species much variation is seen, e.g. in *D. neglecta* Sandwith (Fig. 23A, B). Distinction between species, in spite of all the variation, is not possible, and only extremes might stand out.

Rays vary from broad to very broad in *D. cadaverica* Huber (Fig. 20E, F) to narrow and close together in, for example, *D. latifolia* R.E.Fr. (Fig. 22F) and *D. odorata* (Diels) J.F.Macbr. (Fig. 23C). The banding is very fine in *D. cadaverica*, and fine to rather coarse in the other species.

In most species, vessels are small and radially arranged, in particular in the two flagellate species *D. cadaverica* and *D. flagellaris* Huber (Fig. 22C). In *D. surinamensis* R.E.Fr. (Fig. 25B, C), vessels vary from large and partly solitary to smaller and mainly in clusters. The two African species (out of four) represented here, *D. confinis* (Engl. & Diels) Chatrou (Fig. 21F) and *D. staudtii* (Engl. & Diels) Chatrou (Fig. 24C–E), stand out by having large vessels, notably *D. staudtii*. Oil cells, present in several species of *Duguetia*, are large and conspicuous in the rays of *D. staudtii* (Fig. 24E).

In *Fusaea* (Fig. 26A–E), the vessels, varying from small (*F. peruviana* R.E.Fr., Fig. 26D, E) to moderately large (≤ 100 μm), are arranged in numerous short radial multiples. As a result of the large size of the ray cells, the rays in *Fusaea* are wider than would normally correspond to rays four to eight cells wide. The monotypic genus *Pseudartabotrys* (Fig. 26F) has a climbing habit. The older wood in the centre of the specimen studied is characterized by (rather) large and mainly solitary vessels. In the transition zone to liana-type wood, there is a striking frequency of clusters of smaller vessels.

Xylopieae (Figs 27A, B, 27D–31F)

Genera studied: Artabotrys R.Br. and *Xylopia* L.

This tribe contains two species-rich groups, the pantropical genus *Xylopia* and the Palaeotropical genus *Artabotrys*. In all representatives, the vessel arrangement is partly solitary, partly in short radial multiples.

In *Xylopia*, there are, in general terms, two extremes. That most often seen shows large vessels, sometimes touching the rays on both sides, and widely spaced parenchyma bands, e.g. *X. aromatica* (Lam.) Mart. (Fig. 28A, B), *X. cayennensis* Maas (Fig. 28E), *X. nitida* Dunal (Fig. 30A), *X. papuana* Diels (Fig. 30B) and *X. surinamensis* R.E.Fr. (Fig. 31C). The other tends towards small vessels and numerous parenchyma bands. The most obvious examples of this are *X. cuspidata* Diels (Fig. 28F) and *X. peruviana* R.E.Fr. (Fig. 30E). It is perhaps noteworthy that these two species have stout flowers with comparatively broad petals, whereas most *Xylopia* spp. have elongate flowers with rather narrow petals. It should be added that there is no strong correlation between the vessel, parenchyma and petal characters: for example, in *X. xylantha* R.E.Fr. (Fig. 31F), flowers with broad petals occur with wide vessels and widely spaced parenchyma bands. Narrow rays dominate in a number of species of the first group, thus giving an impression of a finer grain [see, for example, *X. aromatica*, Fig. 28A, B; *X. benthamii* R.E.Fr., Fig. 28D; *X. neglecta* (Kuntze) R.E.Fr., Fig. 29F]. Examples of transitional species are *X. holtzii* Engl., *X. parviflora* (A.Rich.) Benth. and *X. trichostemon* R.E.Fr. (Figs 29D, 30C, 31E), in which relatively small vessels are combined with wide rays and few parenchyma bands. In *X. aethiopica* (Dunal) A.Rich.

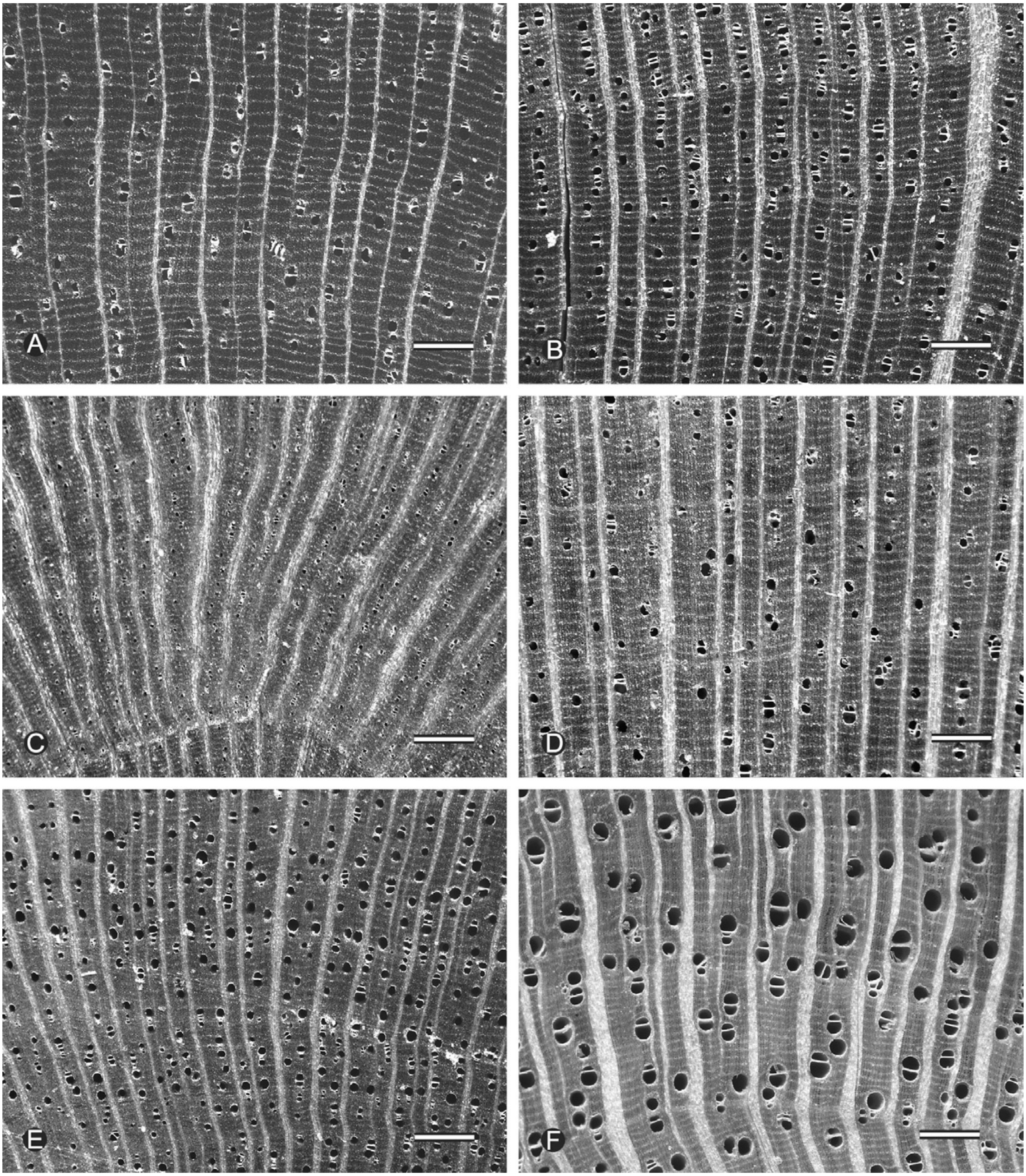

Figure 21. A–F, Duguetieae. A, *Duguetia calycina* Benoist, Uw 761; B, *Duguetia calycina,* Uw 15331; C, *Duguetia cauliflora* R.E.Fr., Uw 3951; D, *Duguetia* cf. *cauliflora,* Uw 4706; E, *Duguetia chrysea* Maas, Uw 36236; F, *Duguetia confinis* (Engl. & Diels) Chatrou, Uw 35931.

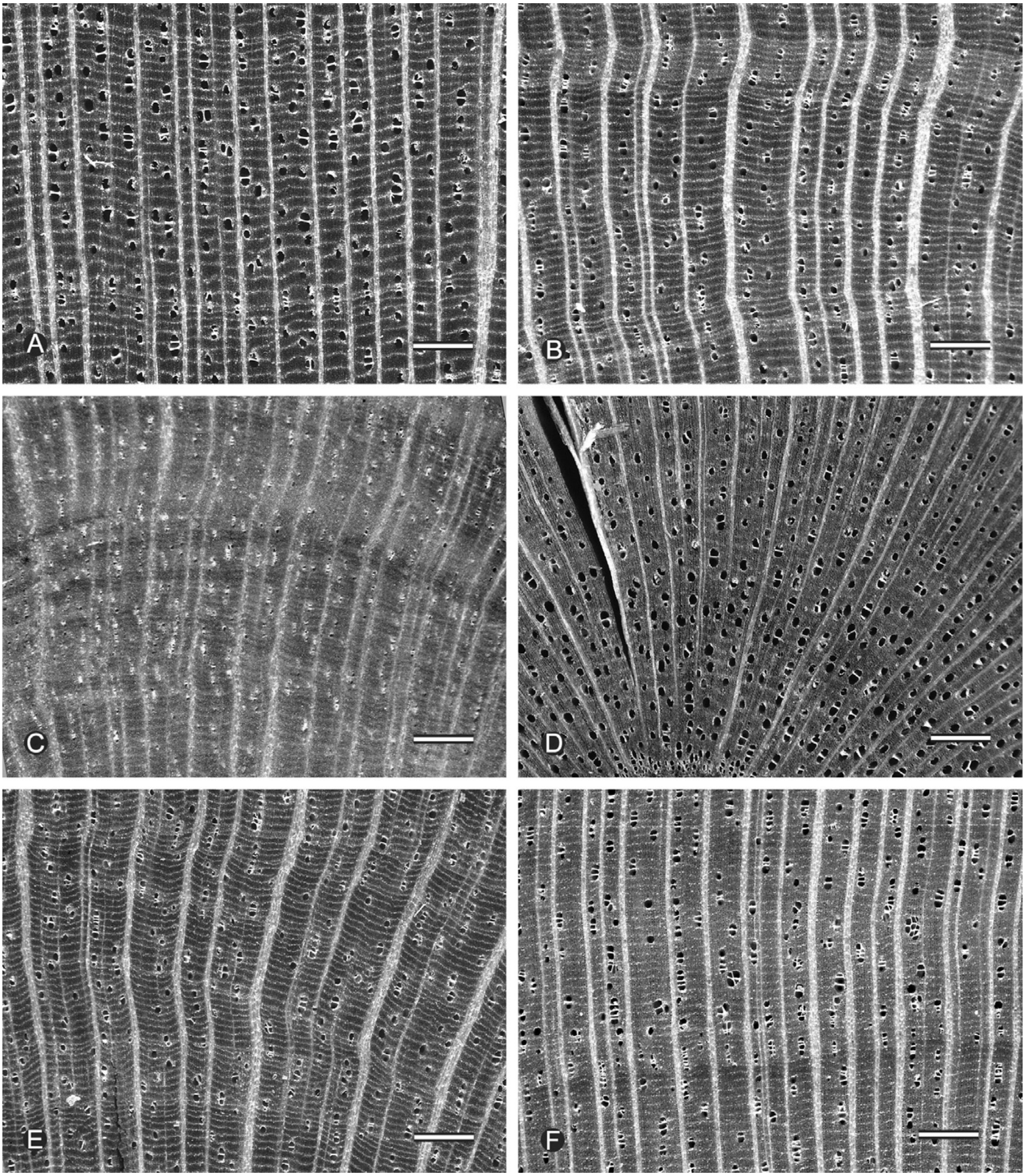

Figure 22. A–F, Duguetieae. A, *Duguetia echinophora* R.E.Fr., Uw 19482; B, *Duguetia eximia* Diels, Uw 29917; C, *Duguetia flagellaris* Huber, Uw 36736; D, *Duguetia furfuracea* (A.St.-Hil.) Saff., Uw 29402; E, *Duguetia granvilleana* Maas, Uw 29888; F, *Duguetia latifolia* R.E.Fr., Uw 7462.

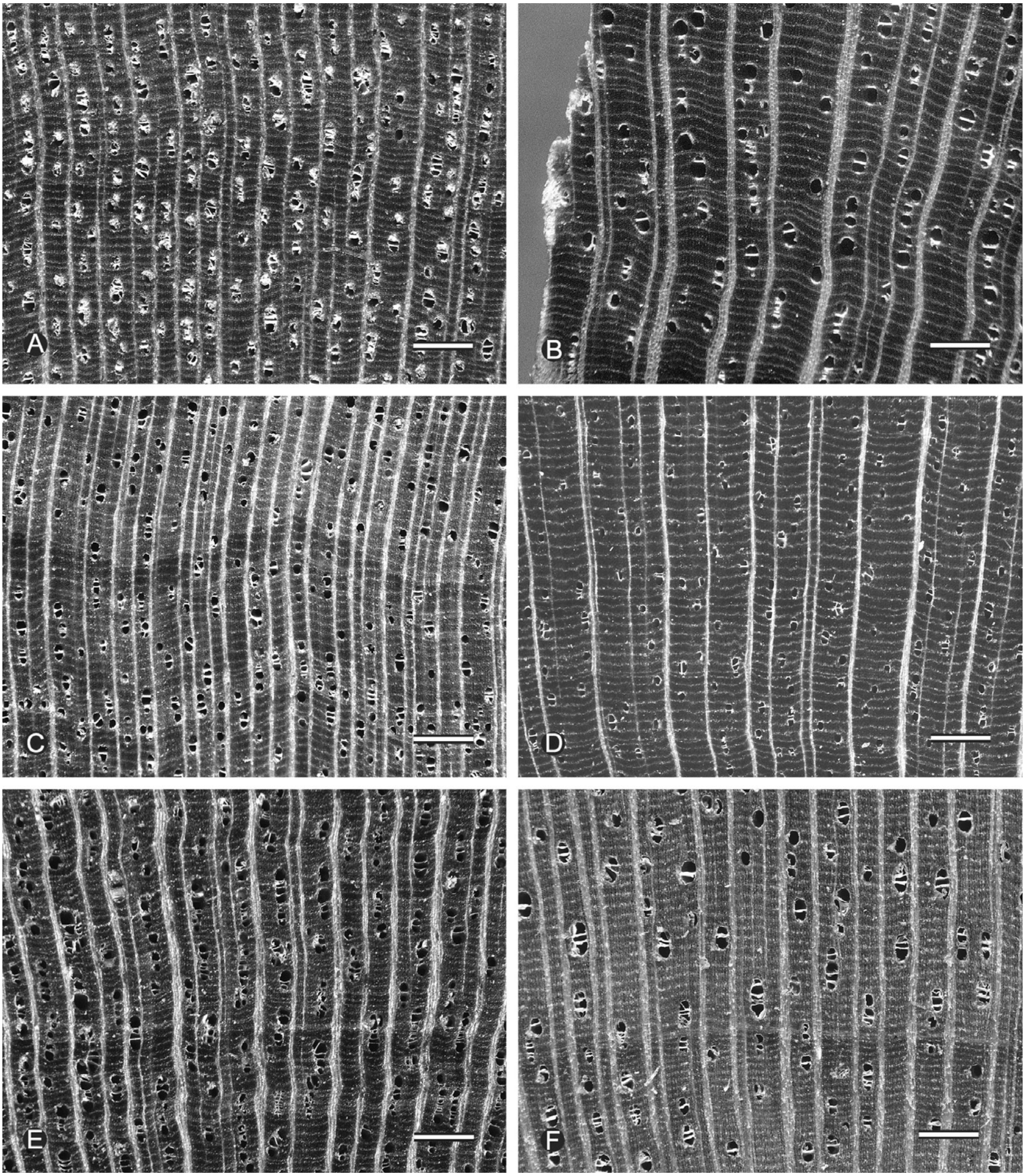

Figure 23. A–F, Duguetieae. A, *Duguetia neglecta* Sandw., Uw 26336; B, *Duguetia neglecta,* Uw 27370; C, *Duguetia odorata* (Diels) J.F.Macbr., Uw 19628; D, *Duguetia pauciflora* Rusby, Uw 762; E, *Duguetia pycnastera* Sandwith, Uw 11121; F, *Duguetia pycnastera,* Uw 30266.

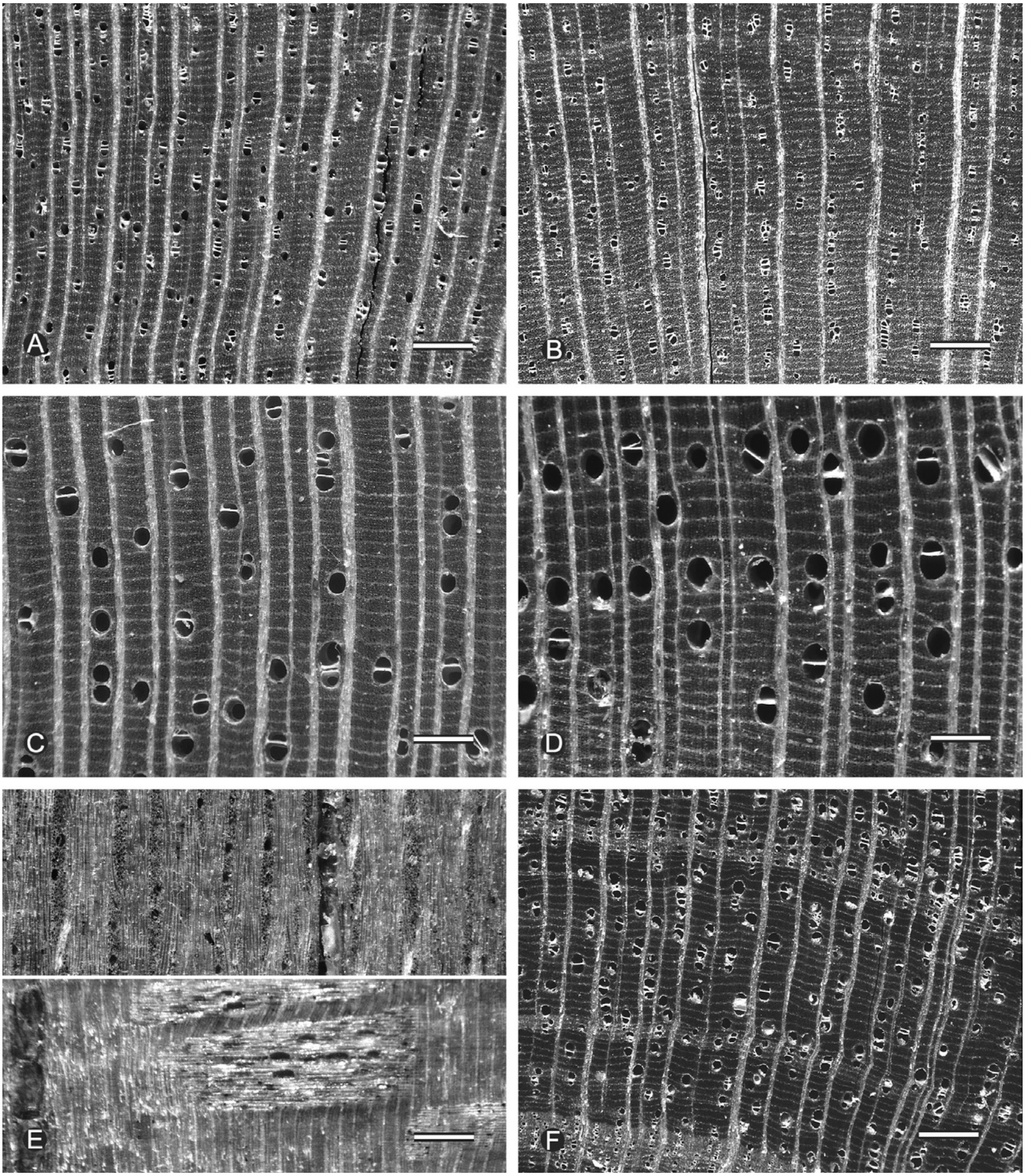

Figure 24. A–F, Duguetieae. A, *Duguetia quitarensis* Benth., Uw 30521; B, *Duguetia riparia* Huber, Uw 17969; C, *Duguetia staudtii* (Engl. & Diels) Chatrou, Uw 6562; D, *Duguetia staudtii,* Uw 29374; E, *Duguetia staudtii* (tangential and radial section), Uw 29374; F, *Duguetia stelechantha* (Diels) R.E.Fr., Uw 16453.

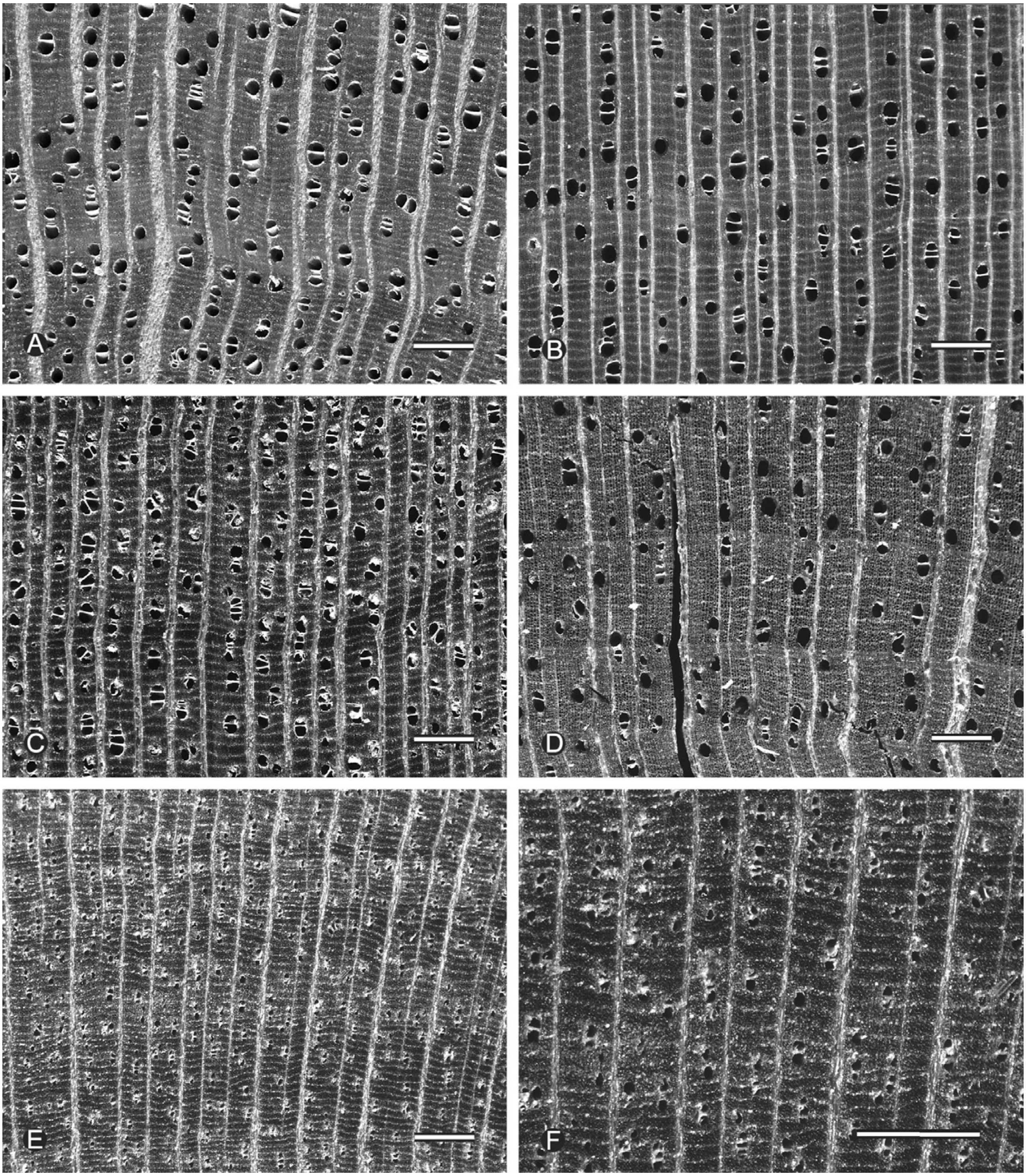

Figure 25. A–F, Duguetieae. A, *Duguetia stenantha* R.E.Fr., Uw 30330; B, *Duguetia surinamensis* R.E.Fr., Uw 7601; C, *Duguetia surinamensis,* Uw 15325; D, *Duguetia uniflora* (DC.) Mart., Uw 8276; E, *Duguetia yeshidan* Sandwith, Uw 36493; F, *Duguetia yeshidan,* Uw 36493.

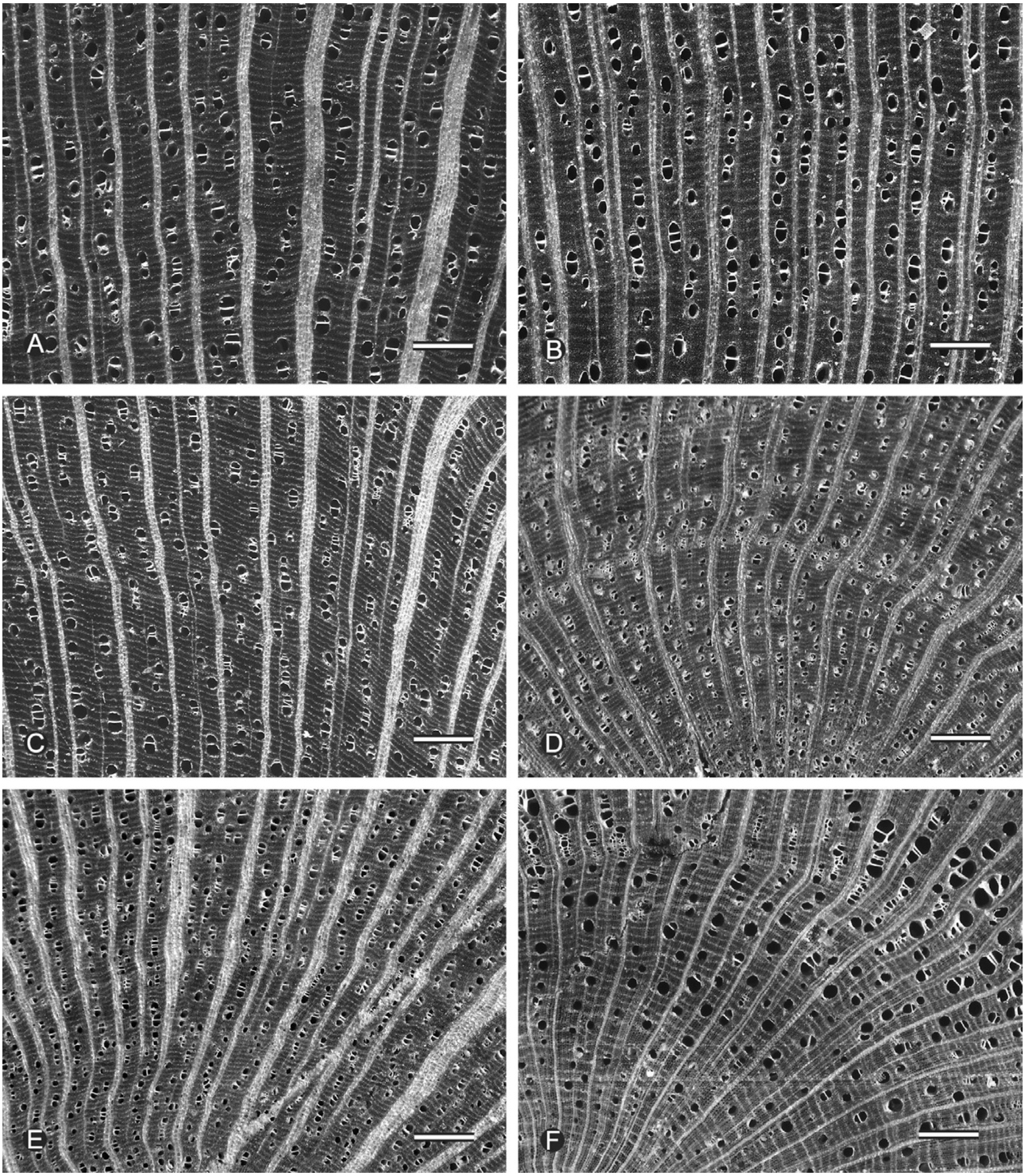

Figure 26. A–F, Duguetieae. A, *Fusaea longifolia* (Aubl.) Saff., Uw 4559; B, *Fusaea longifolia,* Uw 16133; C, *Fusaea longifolia,* Uw 30329; D, *Fusaea peruviana* R.E.Fr., Uw 35939; E, *Fusaea peruviana,* Uw 35940; F, *Pseudartabotrys letestui* Pellegr., Uw 35932.

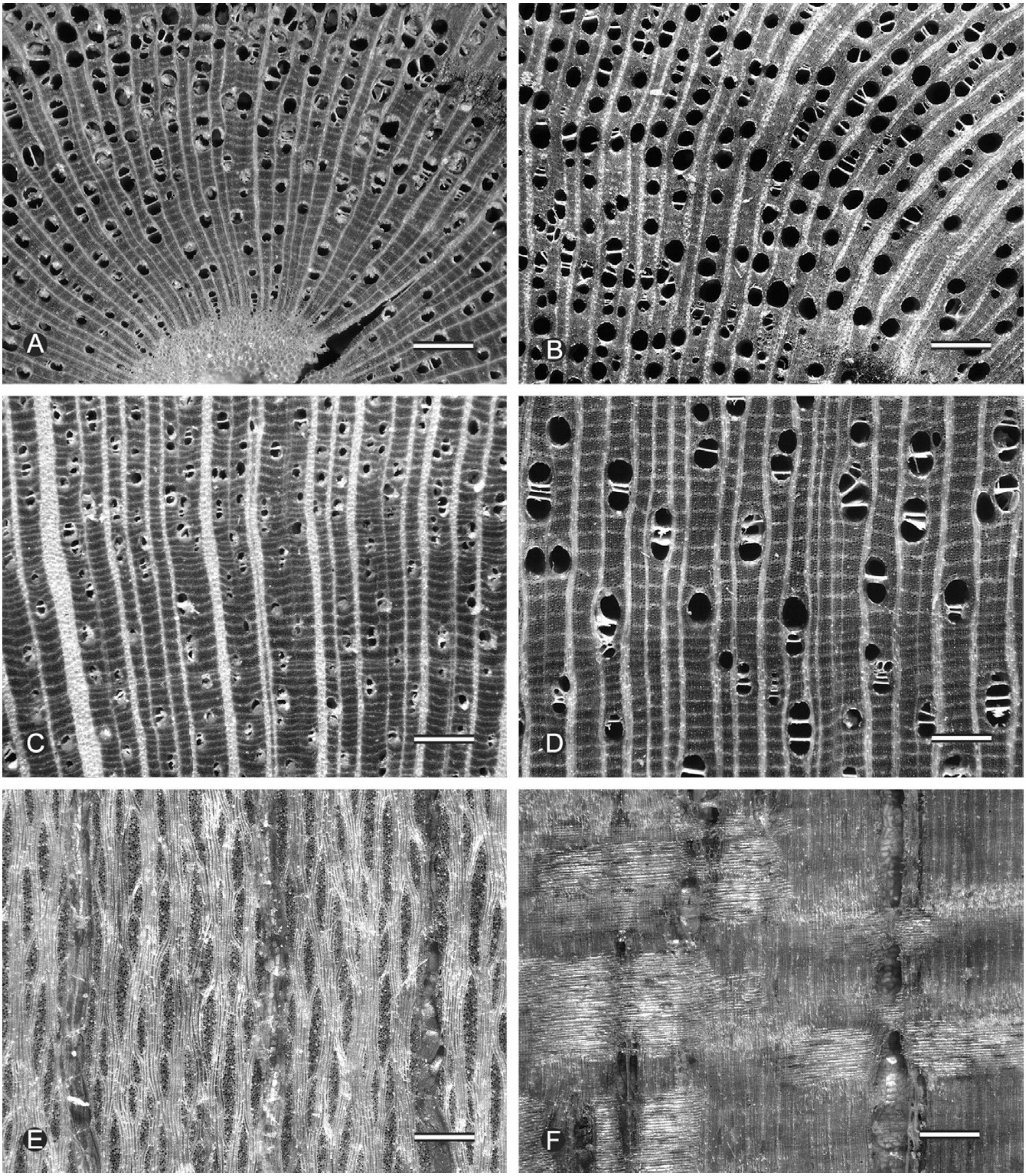

Figure 27. A, B, D–F, Xylopieae; C, Piptostigmateae. A, *Artabotrys insignis* Engl. & Diels, Uw 29509; B, *Artabotrys oliganthus* Engl. & Diels, Uw 22118; C, *Greenwayodendron oliveri* (Engl.) Verdc., Uw 29490; D, *Xylopia aethiopica* (Dunal) A.Rich., Uw 25875; E, *Xylopia aethiopica* (tangential section), Uw 25875; F, *Xylopia aethiopica* (radial section), Uw 25875.

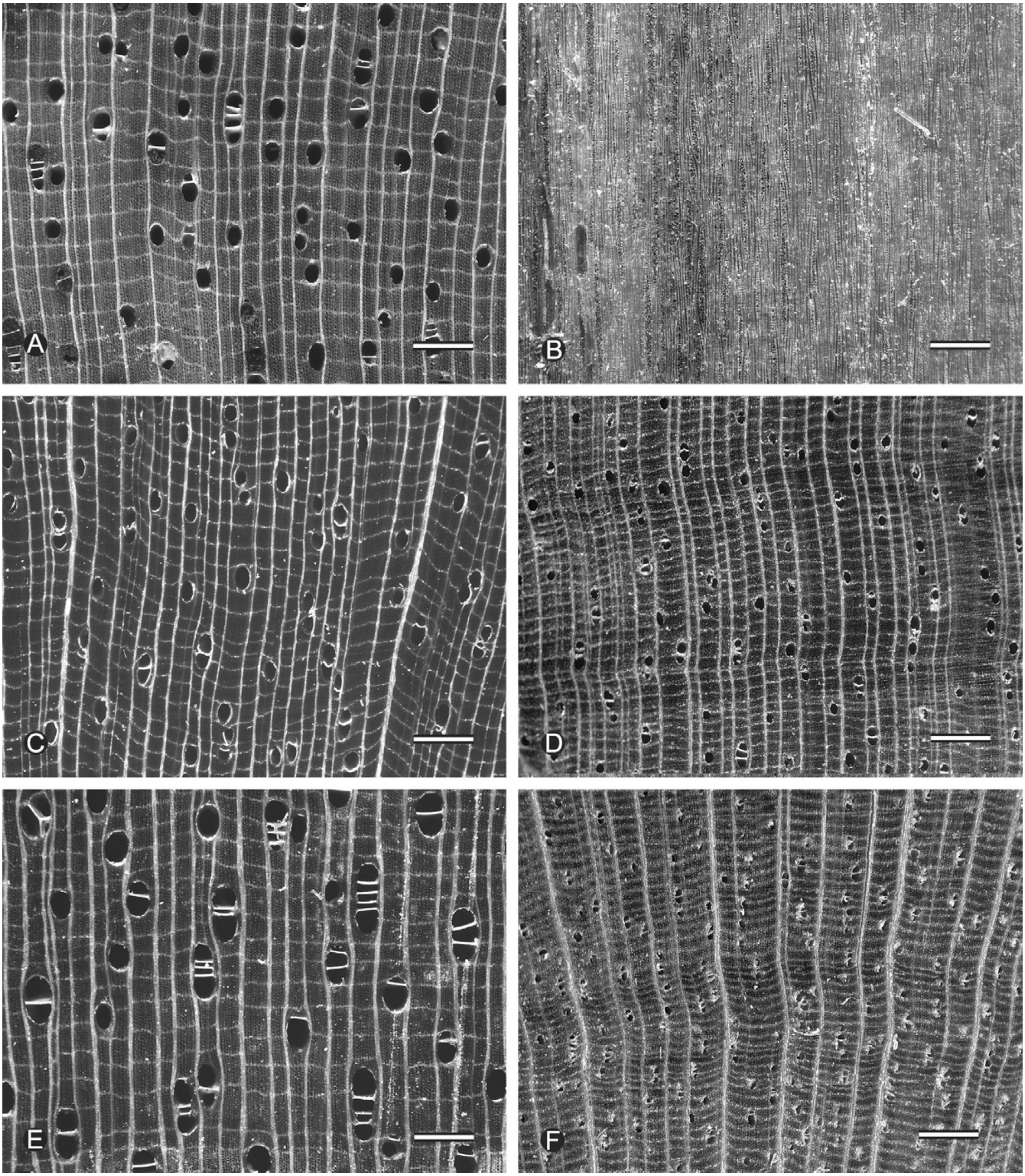

Figure 28. A–F, Xylopieae. A, *Xylopia aromatica* (Lam.) Mart., Uw 773; B, *Xylopia aromatica* (tangential section), Uw 7762; C, *Xylopia amazonica* R.E.Fr., Uw 2563; D, *Xylopia benthamii* R.E.Fr., Uw 9071; E, *Xylopia cayennensis* Maas, Uw 5703; F, *Xylopia cuspidata* Diels, Uw 30325.

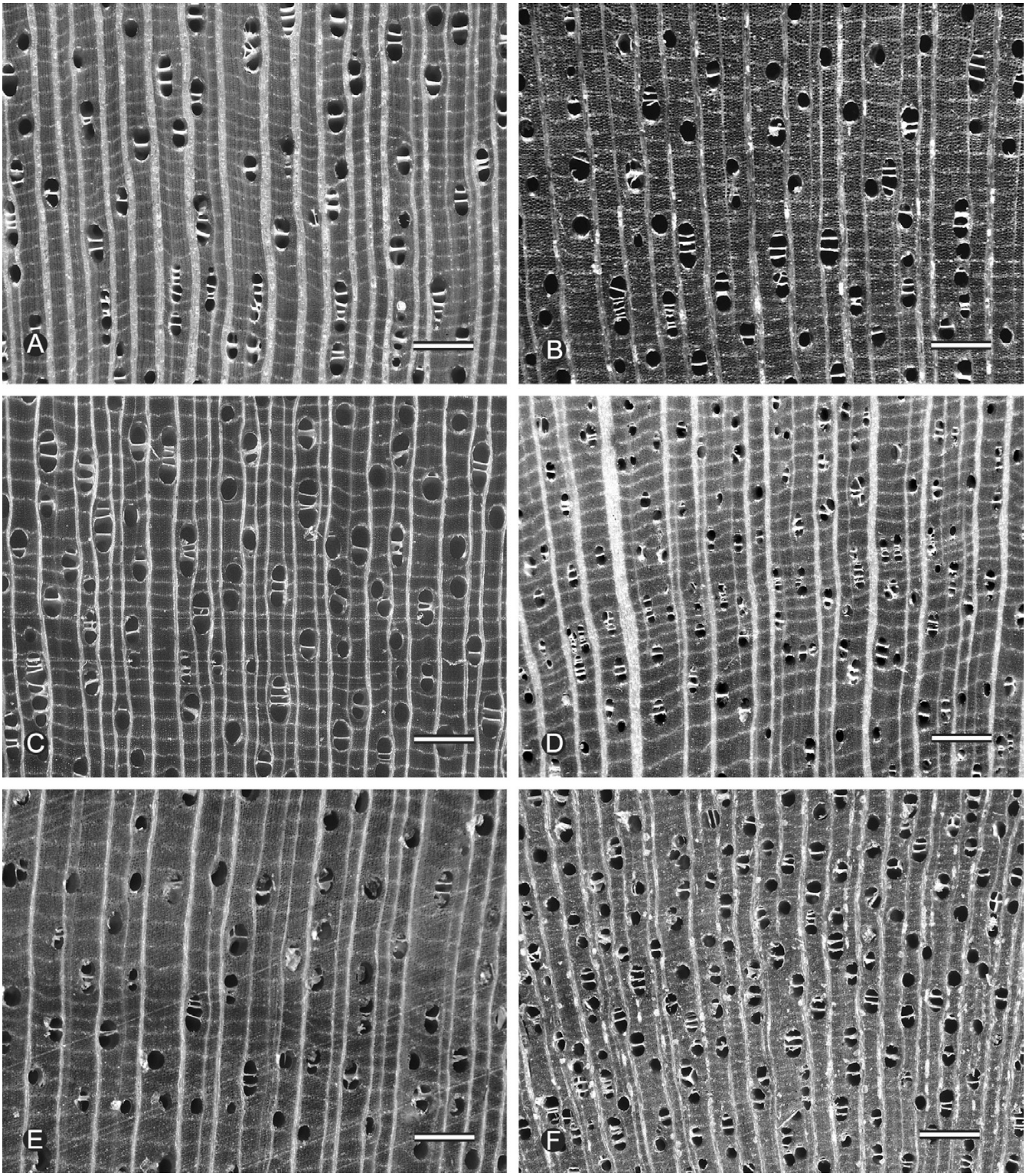

Figure 29. A–F. Xylopieae. A. *Xylopia discreta* (L.f.) Sprague & Hutch., Uw 138a; B. *Xylopia emarginata* Mart. var. *duckei* R.E.Fr., Uw 17208; C. *Xylopia frutescens* Aubl., Uw 775; D. *Xylopia holtzii* Engl., Uw 15600; E. *Xylopia malayana* Hook.f. & Thomson, Uw 32066; F. *Xylopia neglecta* (Kuntze) R.E.Fr., Uw 30331.

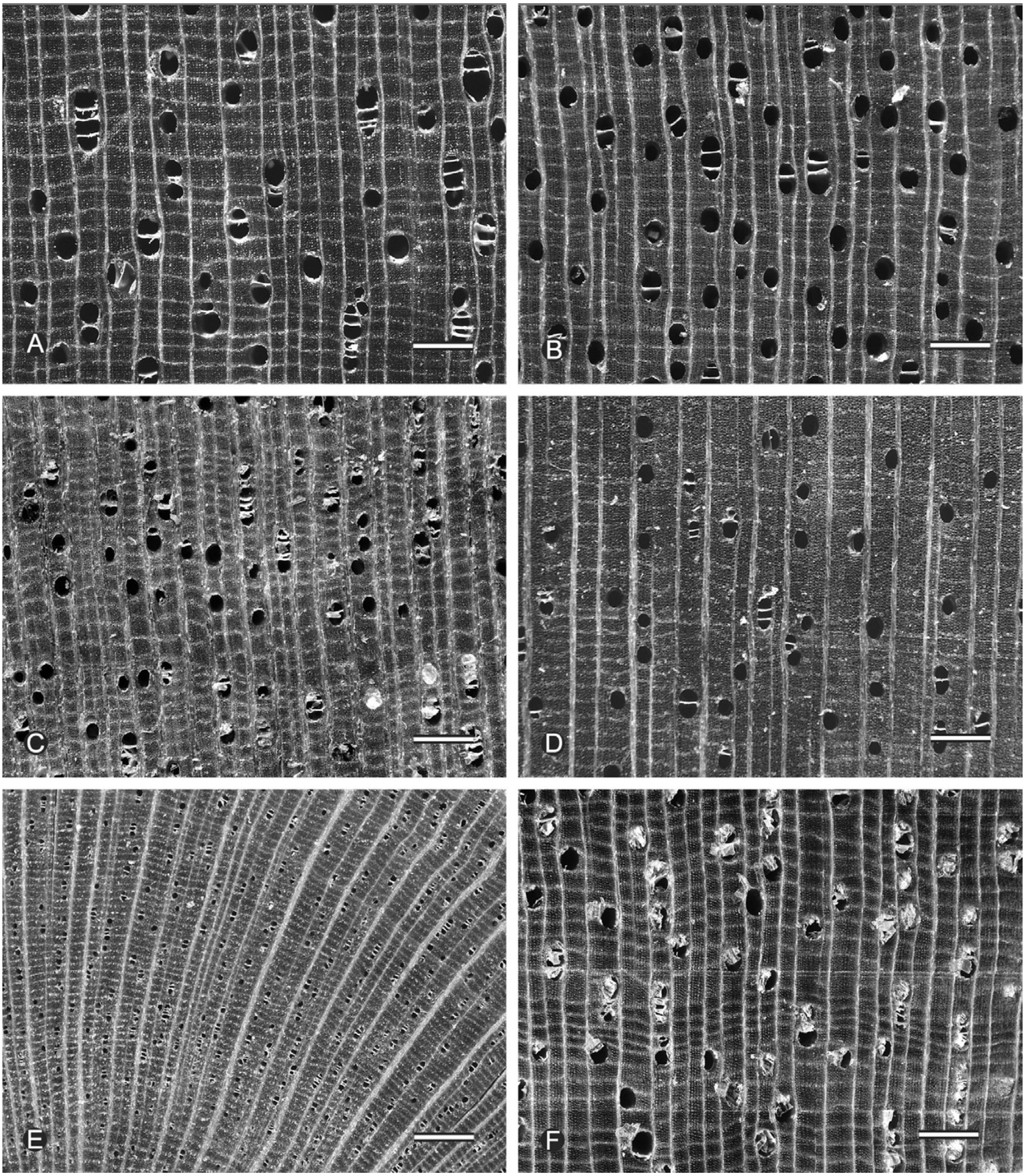

Figure 30. A–F, Xylopieae. A, *Xylopia nitida* Dunal, Uw 11725; B, *Xylopia papuana* Diels, Uw 18227; C, *Xylopia parviflora* (A.Rich.) Benth., Uw 25876; D, *Xylopia peekelii* Diels, Uw s.n.; E, *Xylopia peruviana* R.E.Fr., Uw 30241; F, *Xylopia polyantha* R.E.Fr., Uw 19248.

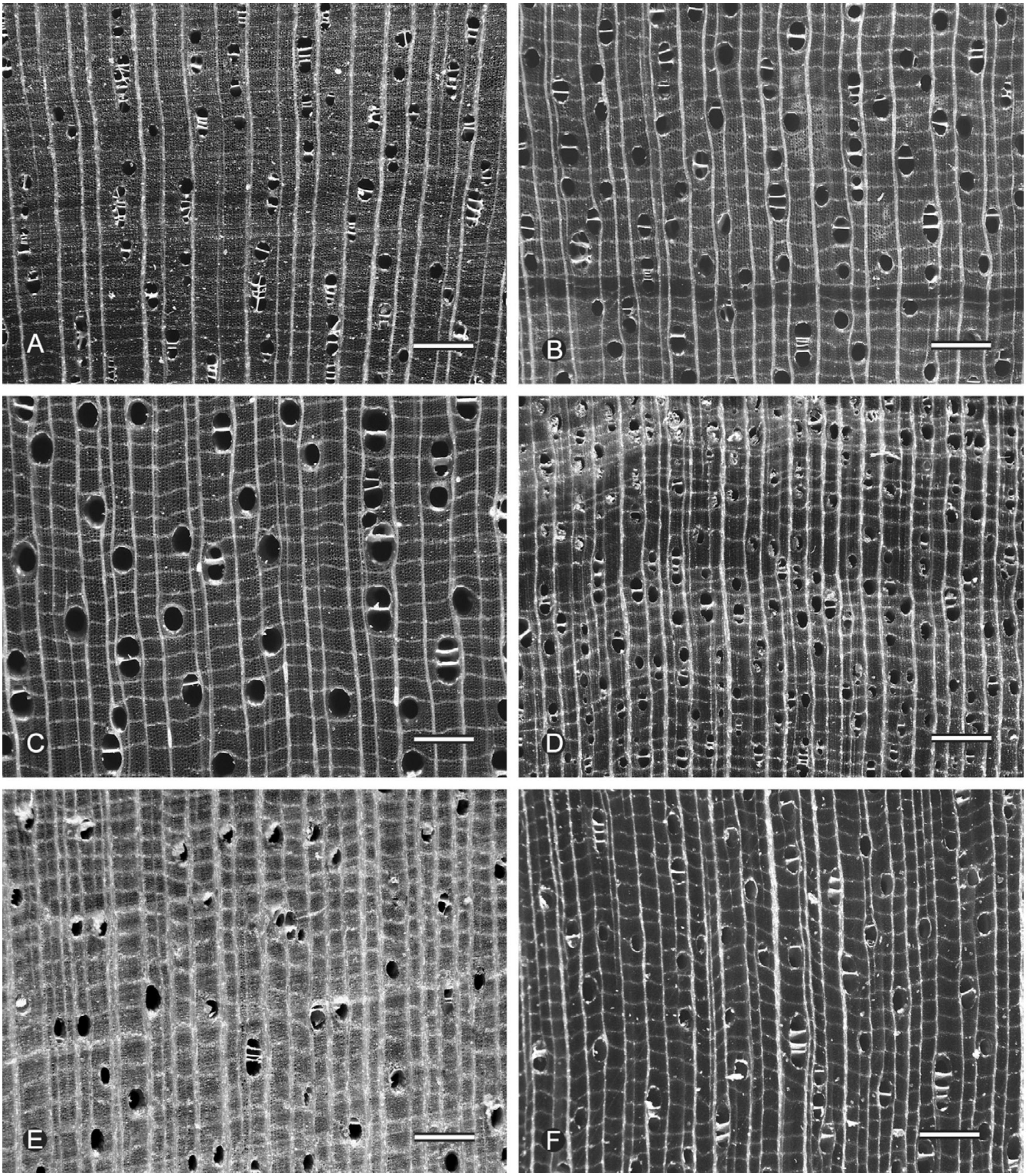

Figure 31. A–F, Xylopieae. A, *Xylopia pulcherrima* Sandwith, Uw 5020; B, *Xylopia quintasii* Engl. & Diels, Uw 9501; C, *Xylopia surinamensis* R.E.Fr., Uw 8875; D, *Xylopia toussaintii* Boutique, Uw 24209; E, *Xylopia trichostemon* R.E.Fr., Uw 20127; F, *Xylopia xylantha* R.E.Fr., Uw 16139.

(Fig. 27D–F), wide vessels in combination with wide rays are found.

Artabotrys oliganthus Engl. & Diels (Fig. 27B) and *A. insignis* Engl. & Diels (Fig. 27A) are climbers, like the large majority of species in the genus. In the photograph of *A. insignis*, a transition from nonliana wood to liana wood can be observed; the nonliana-type wood in the centre looks rather similar to the wood of (many) *Xylopia* spp., as just discussed above: note the large vessel diameter in relation to the space between the rays and the widely spaced parenchyma bands. This would be one of the few synapomorphies for the tribe Xylopieae, consisting of *Xylopia* and *Artabotrys* only, which seem to have few macromorphological characters in common.

Guatterieae (Figs 32A–36A)

Genus studied: Guatteria Ruiz & Pav.

Guatteria appears to be one of the few large genera that shows a recognizable structure, as nearly all species studied so far combine a relatively coarse cobweb formed by a relatively large number of broad rays and rather wide parenchyma bands with large, mostly solitary vessels. Careful observation of smooth end grain surfaces reveals the narrow rings of vasicentric parenchyma around the vessels.

The same pattern of vasicentric parenchyma is found in species that were formerly placed in the small genera *Guatteriella* (Fig. 32E) and *Guatteriopsis* (Fig. 34B), recently united with *Guatteria* (Erkens *et al.*, 2007; Erkens & Maas, 2008), namely *G. campinensis* (Morawetz & Maas) Erkens & Maas and *G. hispida* (R.E.Fr.) Erkens & Maas. In *G. campinensis*, the vasicentric rings are two or three cells wide.

Guatteria anomala R.E.Fr. (Fig. 32B) is a deviating species in inflorescence morphology and in wood anatomy, having vessels no more than 60–80 µm wide, and mostly arranged in multiples or clusters of two to five (to eight) cells. Paratracheal parenchyma is absent or restricted to a few strands only. A rather unusual wood pattern is also seen in *Guatteria heteropetala* Benth. (Fig. 34A), a species long known as *Heteropetalum brasiliense* Benth., but recently shown to belong to *Guatteria* (Erkens & Maas, 2008). The paratracheal parenchyma in *G. heteropetala* is also mostly restricted to a few strands around the narrow vessels. It should be stressed that this character state, although an exception in *Guatteria*, is common in the family as a whole. Thus, it seems to support the position of *G. anomala* and *G. heteropetala* as a link between *Guatteria* and other Annonaceae. *Guatteria scandens* Ducke (Fig. 35D) shows a rather gradual transition from small to large vessels, which (as noted before) betrays a climbing habit. The thin fibre walls in *G. heteropetala*, in combination with the small vessels, are most probably indicative of the wet habitat in which this species is found.

Bocageeae (Figs 36B–37A)

Genera studied: Cymbopetalum Benth., *Froesiodendron* R.E.Fr., *Porcelia* Ruiz & Pav. and *Trigynaea* Schltdl.

In three of the six available specimens of this clade, the vessels are small, 40–50(–60) µm, in contrast with the fourth, *Porcelia* (Fig. 36E, F), with its ≤ 200 µm wide vessels. However, there are two intermediates: the first is a slide of *Porcelia macrocarpa* (Warm.) R.E.Fr. (not photographed), obtained from Universidade Federal do Paraná (Curitiba, Paraná, Brazil: *CEF no. 250*), and the second is a sample of the type collection of *Cymbopetalum schunkei* N.A.Murray (Fig. 36C). Both show vessels ≤ 100 µm, apparently bridging the gap.

Ambavioideae (Figs 37B–38D)

Genera studied: Cananga (DC.) Hook.f. & Thomson, *Cleistopholis* Pierre ex Engl., *Cyathocalyx* Champ. ex Hook.f. & Thomson, *Meiocarpidium* Engl. & Diels, *Mezzettia* Becc. and *Tetrameranthus* R.E.Fr.

This early diverging clade varies in all features mentioned thus far: vessel number and diameter, ray number and width, and number of parenchyma bands. *Tetrameranthus duckei* R.E.Fr. (Fig. 38C) was studied by Ter Welle (1985). As the most notable features, he mentioned the wide and high (≤ 5000 µm) multiseriate rays and the paratracheal, often nearly or fully vasicentric, parenchyma. Vasicentric parenchyma occurs in a minority of the family (e.g. *Guatteria*). Wheeler *et al.* (2004 onwards) indicate the presence of this feature in 15 of *c.* 270 species of Annonaceae included (at the time of writing) in the *InsideWood* database (2004 onwards), including one species each of *Cleistopholis* and *Mezzettia* and three of the five species of *Cyathocalyx*. Although paratracheal parenchyma is present in all five genera of this clade, we cannot confirm the occurrence of vasicentric rings, except in *Tetrameranthus*.

Anaxagoreoideae

Genus studied: Anaxagorea A.St.-Hil. (Figs 38E–40A).

Anaxagorea is sister to all other Annonaceae (Richardson *et al.*, 2004; Chatrou *et al.*, 2012). The wood of *Anaxagorea* is rather uniform, characterized by the frequent presence of broad rays rather wide apart, and small vessels often in a radial arrangement, the multiples and groups consisting of two to six (to eight) vessels. In the family, *Anaxagorea* stands apart by the

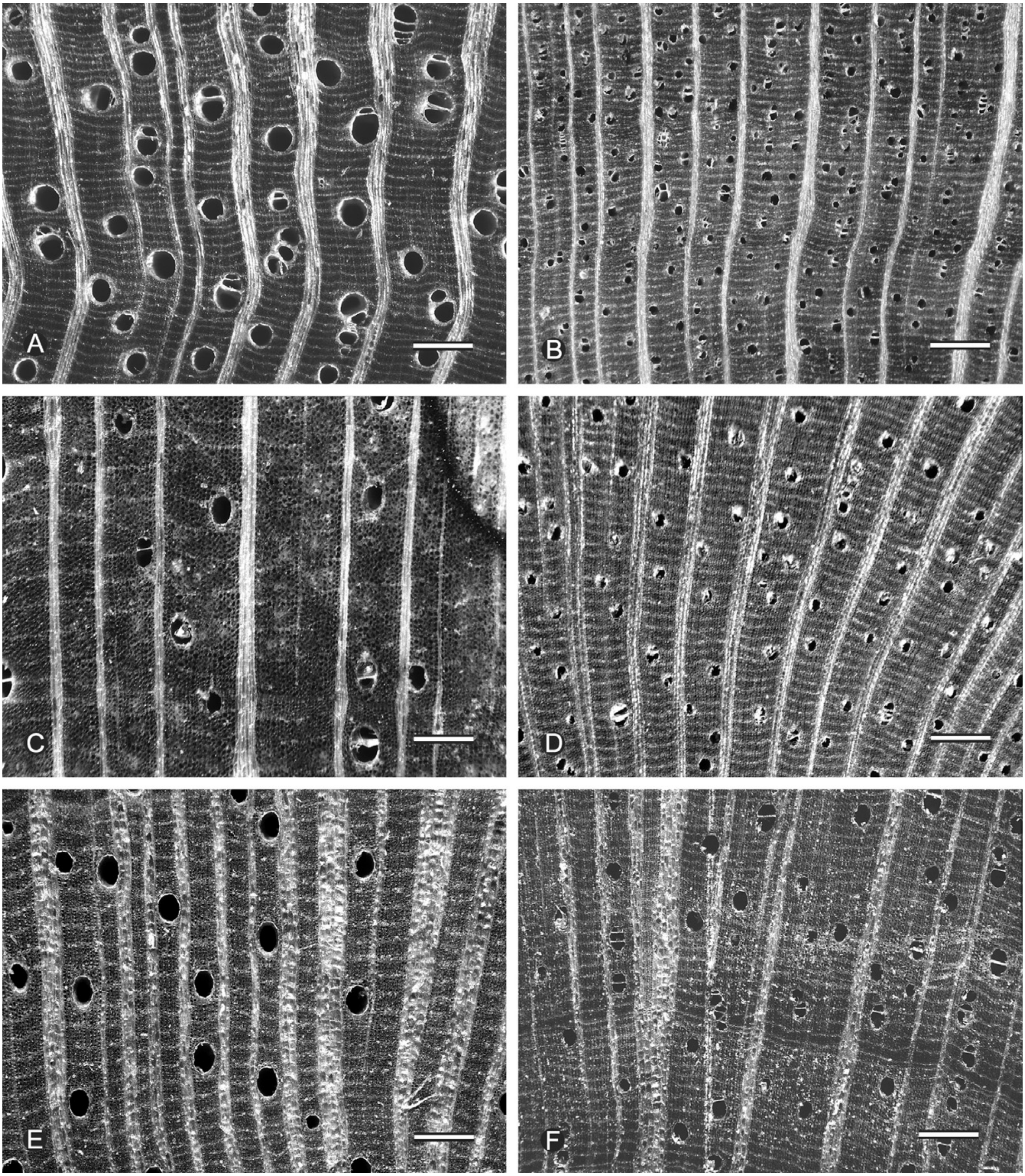

Figure 32. A–F, Guatterieae. A, *Guatteria alta* R.E.Fr., Uw 25132; B, *Guatteria anomala* R.E.Fr., Uw 36880; C, *Guatteria atra* Sandwith, Uw 34267; D, *Guatteria blainii* (Griseb.) Urb., Uw 29375; E, *Guatteria campinensis* (Morawetz & Maas) Erkens & Maas, Uw 29468; F, *Guatteria conspicua* R.E.Fr., Uw 1241.

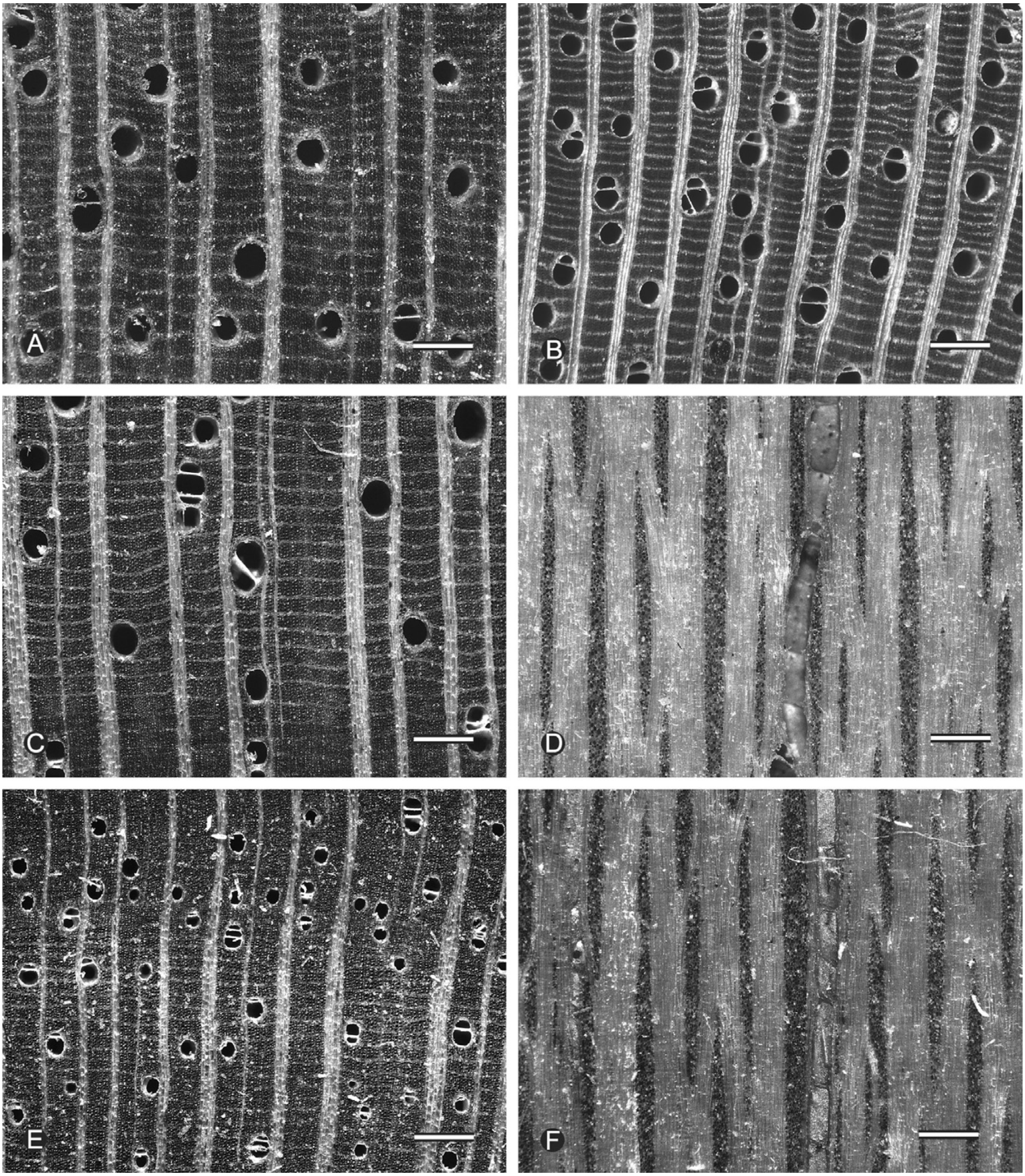

Figure 33. A–F, Guatterieae. A, *Guatteria curvipetala* R.E.Fr., Uw 7806; B, *Guatteria elegantissima* R.E.Fr., Uw 25071; C, *Guatteria discolor* R.E.Fr., Uw 8134; D, *Guatteria discolor* (tangential section), Uw 8134; E, *Guatteria dusenii* R.E.Fr., Uw 13675; F, *Guatteria dusenii* (tangential section), Uw 13675.

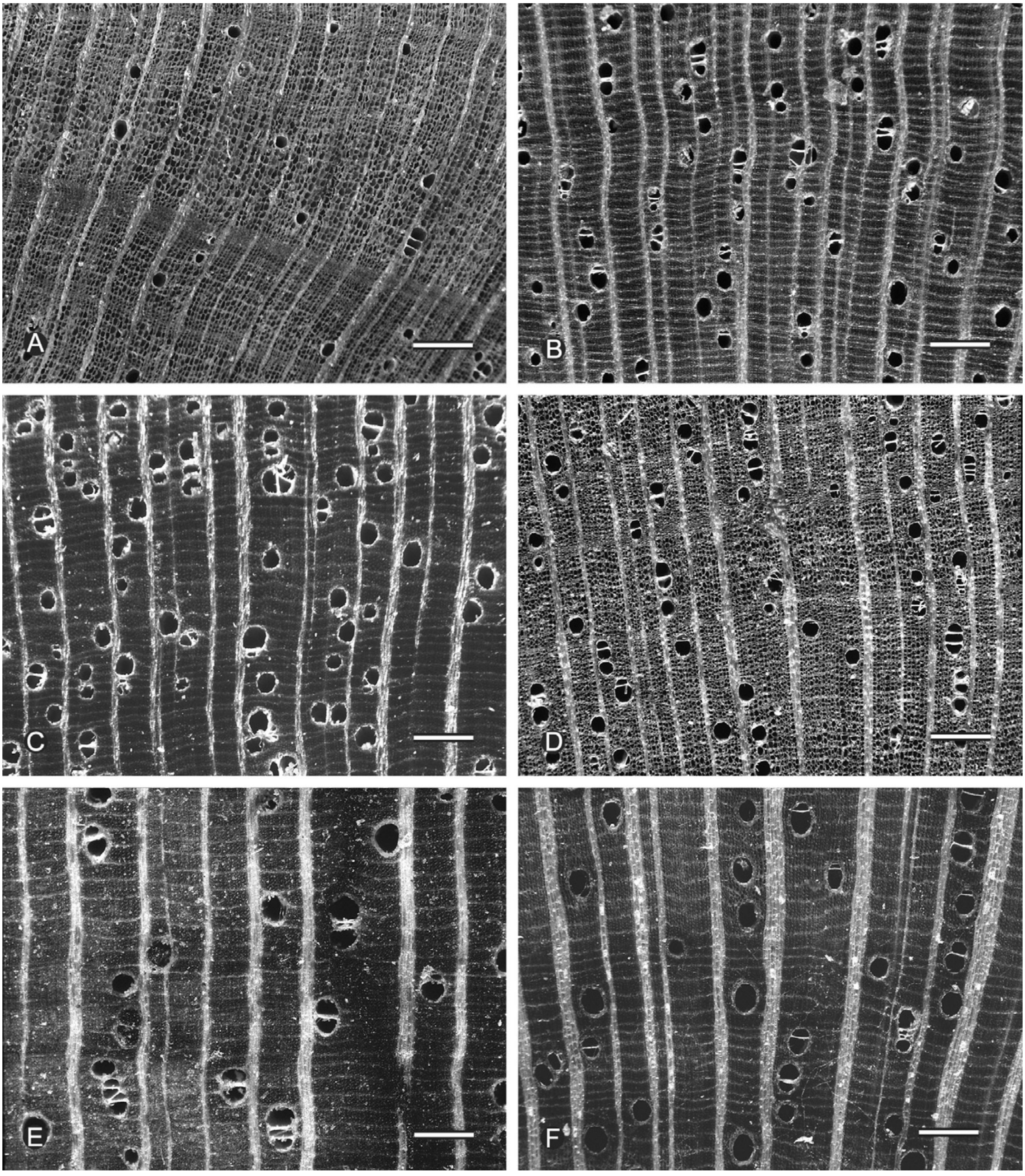

Figure 34. A–F, Guatterieae. A. *Guatteria heteropetala* Benth., Uw 33073; B. *Guatteria hispida* (R.E.Fr.) Erkens & Maas, Uw 29458; C. *Guatteria monticola* R.E.Fr., Uw 34268; D. *Guatteria obovata* R.E.Fr., Uw 29461; E. *Guatteria poeppigiana* Mart., Uw 17242; F. *Guatteria procera* R.E.Fr., Uw 2567.

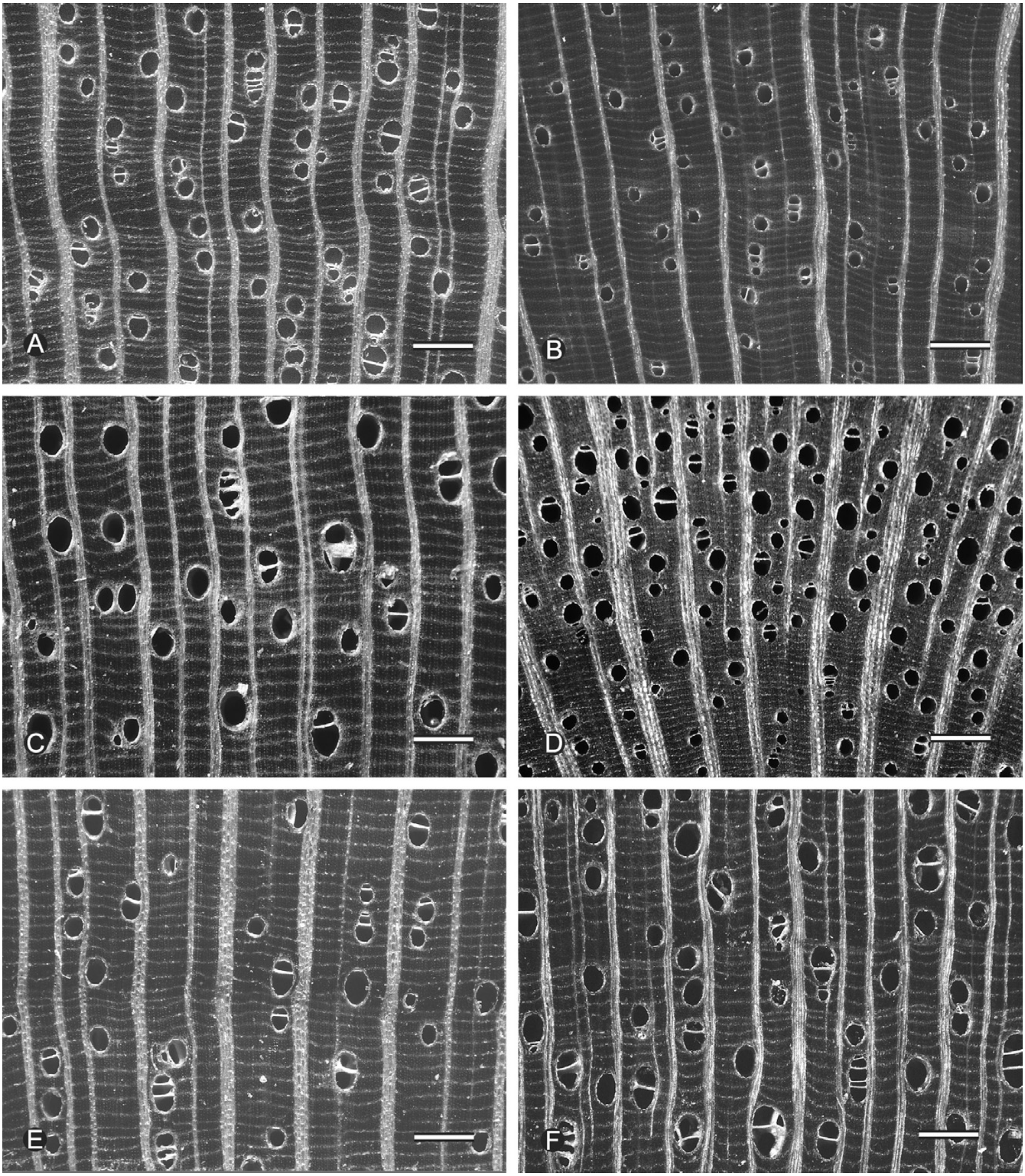

Figure 35. A–F, Guatterieae. A, *Guatteria punctata* (Aubl.) R.A.Howard, Uw 2565; B, *Guatteria punctata*, Uw 2566; C, *Guatteria rubrinervis* R.E.Fr., Uw 34270; D, *Guatteria scandens* Ducke, Uw 24786; E, *Guatteria schomburgkiana* Mart., Uw 254; F, *Guatteria schomburgkiana*, Uw 2568.

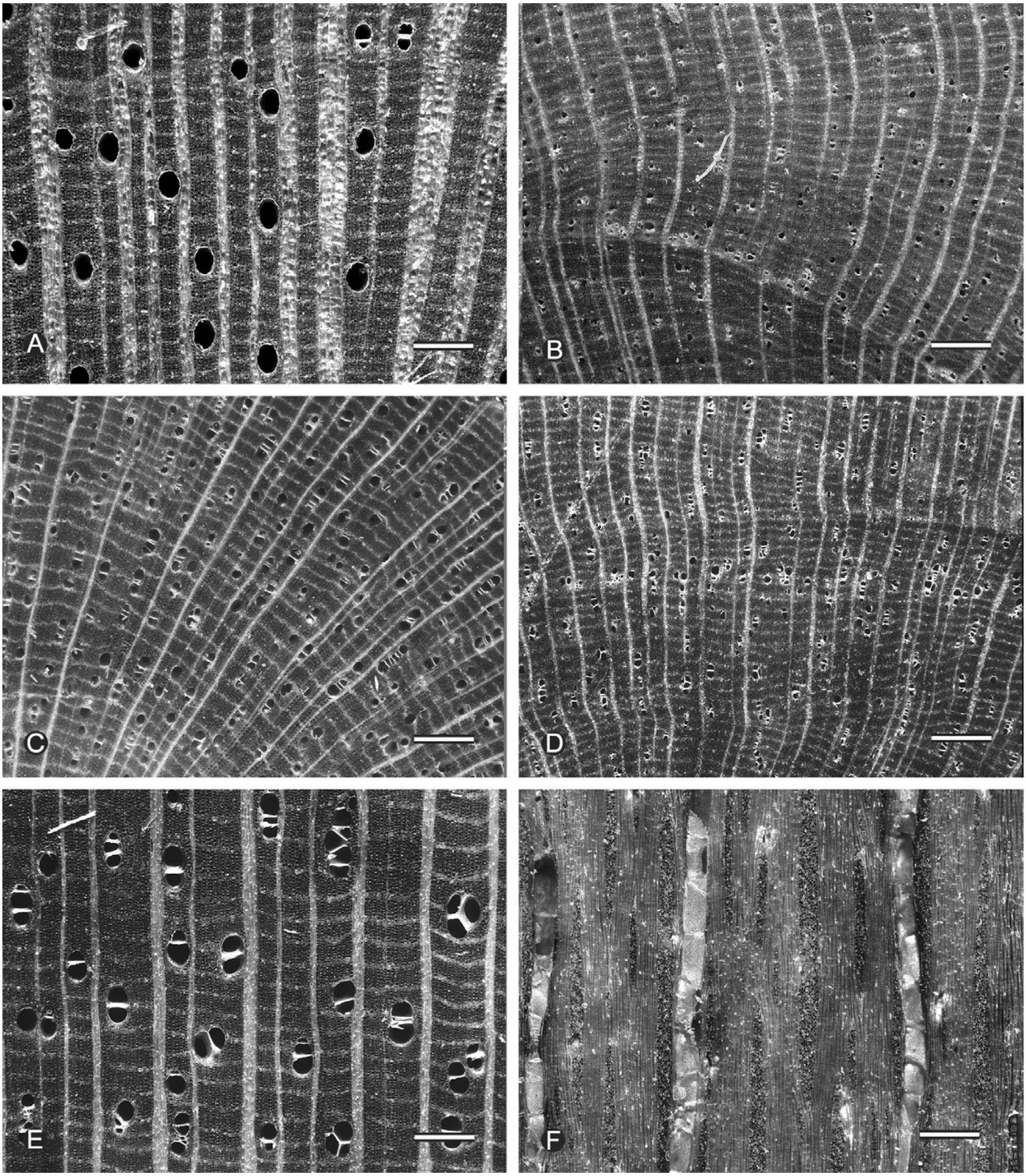

Figure 36. A, Guatterieae; B–F, Bocageeae. A, *Guatteria trichostemon* R.E.Fr., Uw 16119; B, *Cymbopetalum brasiliense* (Vell.) Benth. ex Baill., Uw 8867; C, *Cymbopetalum schunkei* N. A. Murray, Uw 21087; D, *Froesiodendron surinamense* (R.E.Fr.) R.E.Fr., Uw 5015; E, *Porcelia ponderosa* (Rusby) Rusby, Uw 19881; F, *Porcelia ponderosa* (tangential section), Uw 19881.

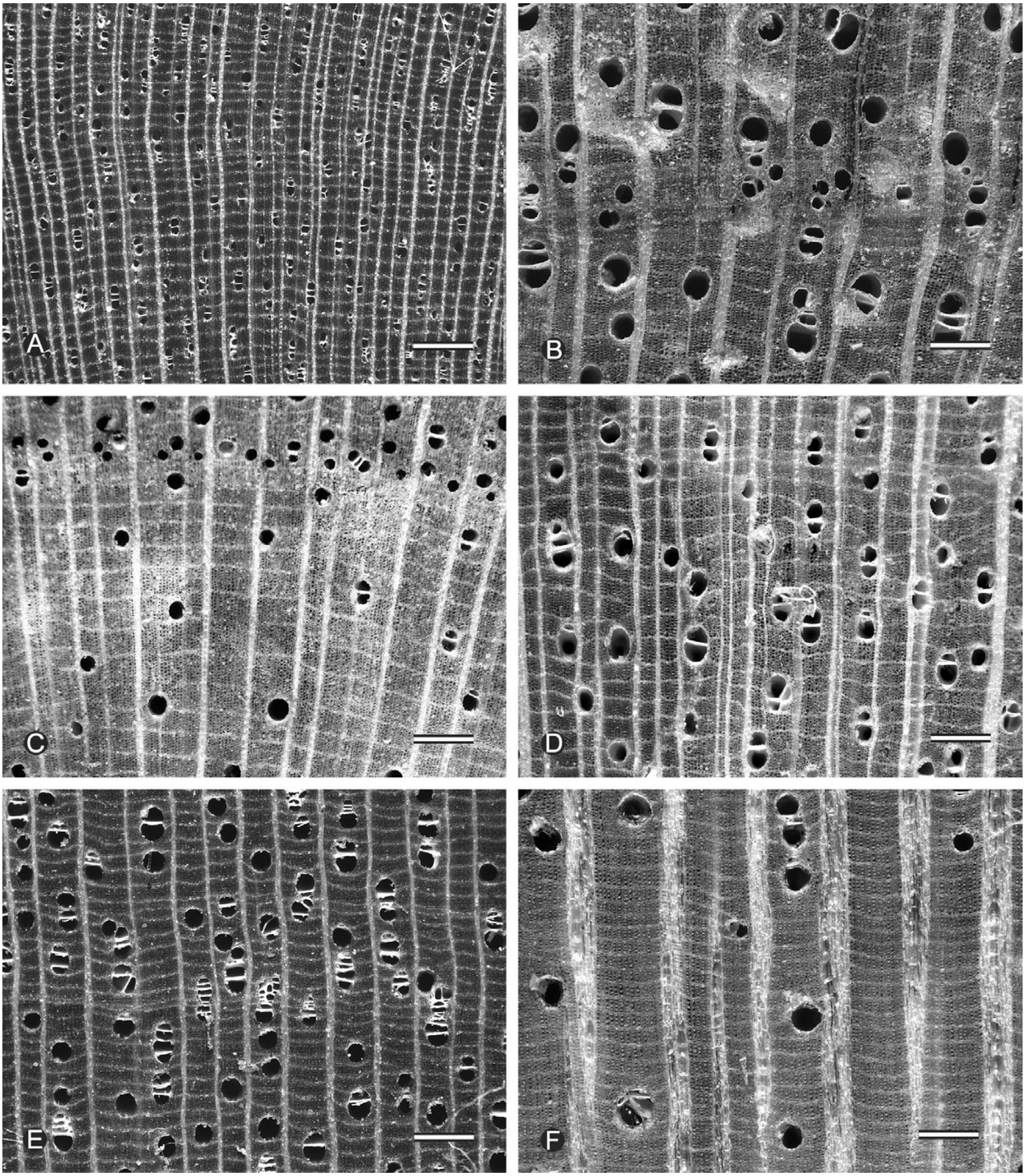

Figure 37. A, Bocageeae; B–F, Ambavioideae. A, *Trigynaea caudata* (R.E.Fr.) R.E.Fr., Uw 764; B, *Cananga* sp., Uw s.n.; C, *Cleistopholis glauca* Pierre ex Engl. & Diels, Uw 29517; D, *Cyathocalyx bancanus* Boerl., Uw 26735; E, *Cyathocalyx subsessilis* Jovet-Ast, Uw 26736; F, *Mezzettia leptopoda* (Hook.f. & Thomson) King, Uw 29504.

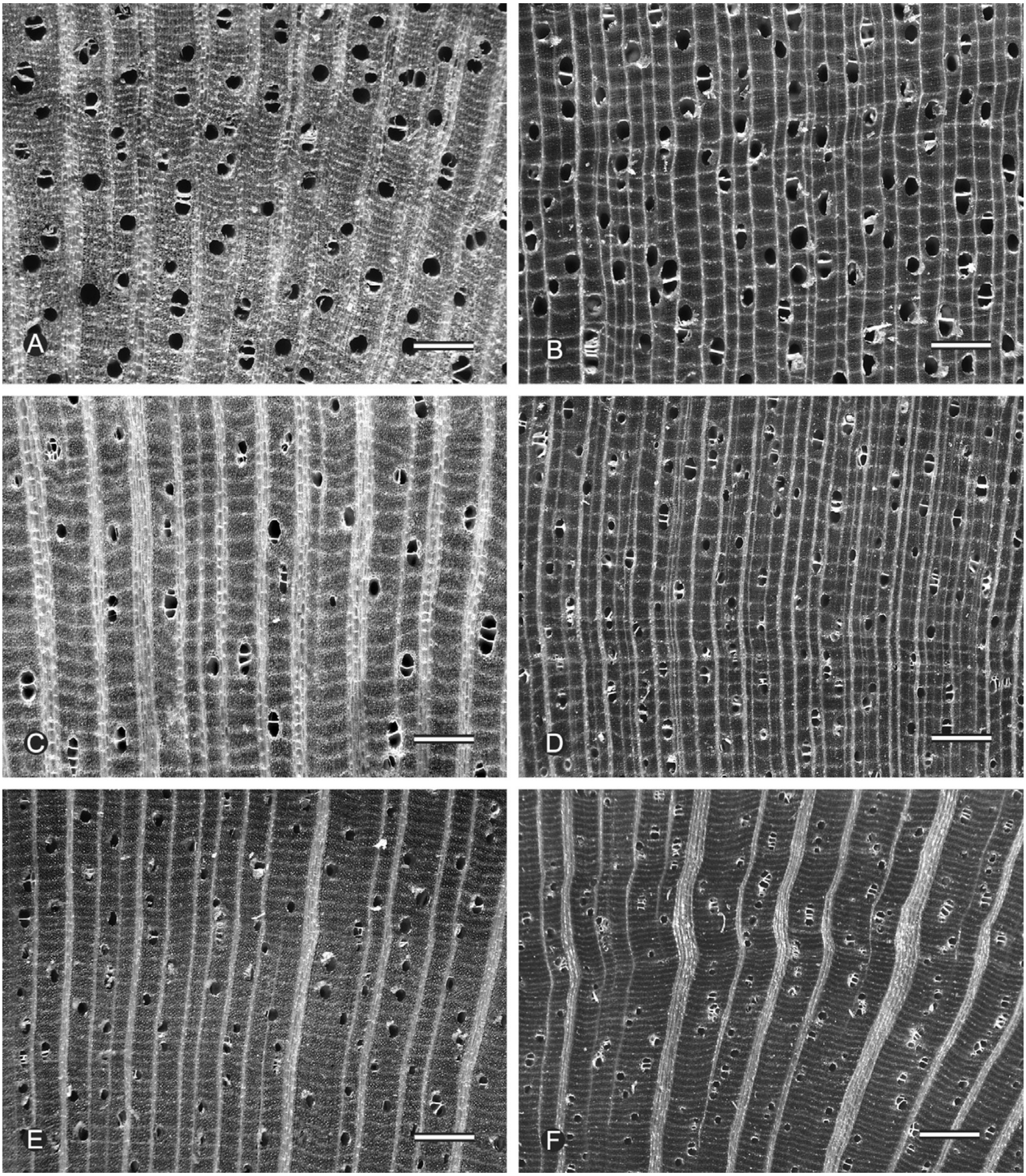

Figure 38. A–D, Ambavioideae; E, F, Anaxagoreoideae. A, *Mezzettia parviflora* Becc., Uw 32051; B, *Mezzettia umbellata* Becc., Uw 29513; C, *Tetrameranthus duckei* R.E.Fr., Uw 26746; D, *Meiocarpidium lepidotum* (Oliv.) Engl. & Diels, Uw 9544; E, *Anaxagorea acuminata* (Dunal) A.DC., Uw 19187; F, *Anaxagorea acuminata*, Uw 21064.

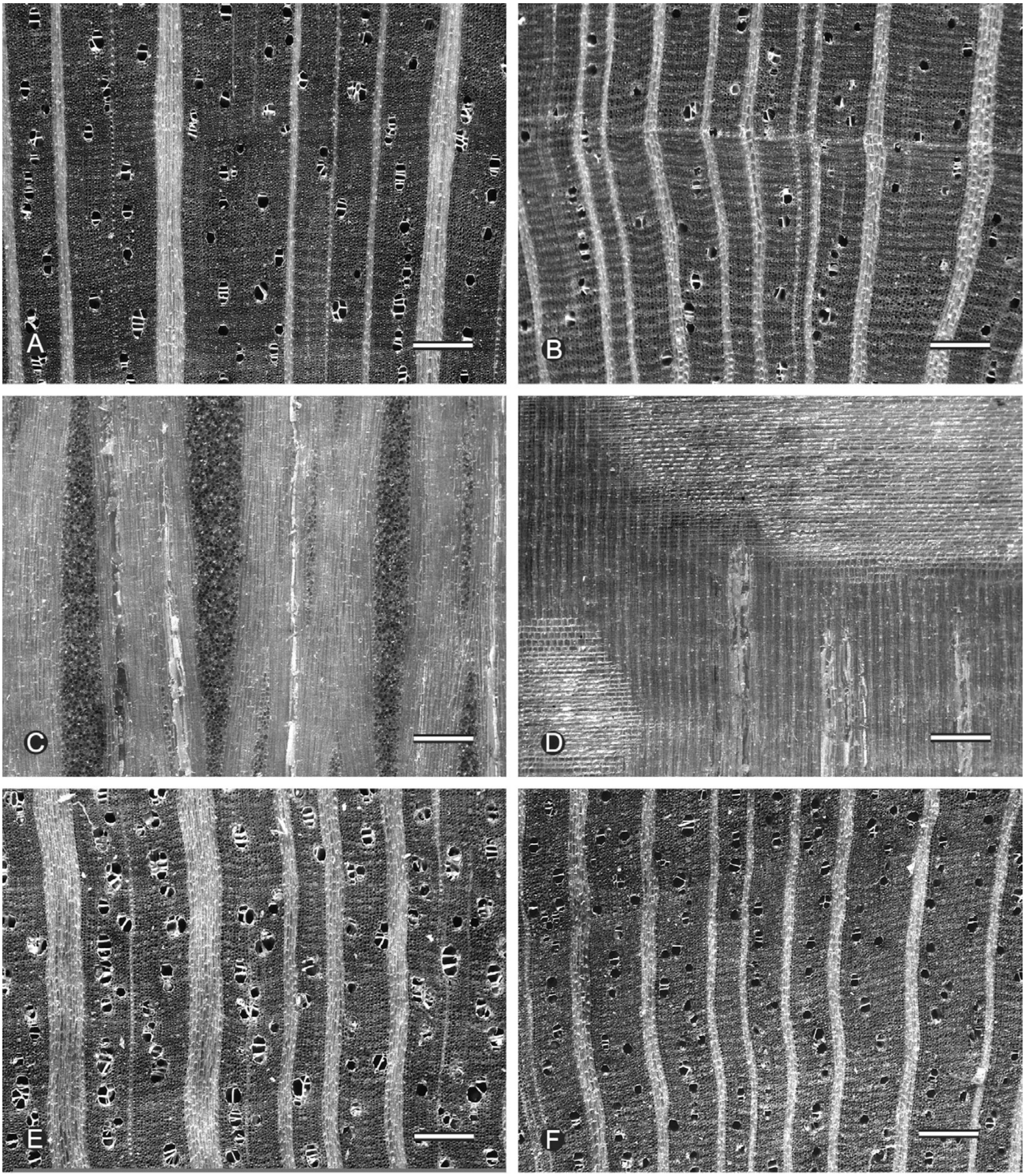

Figure 39. A–F, Anaxagoreoideae. A, *Anaxagorea brevipes* Benth., Uw 19724; B, *Anaxagorea dolichocarpa* Sprague & Sandwith, Uw 2564; C, *Anaxagorea dolichocarpa* (tangential section), Uw 19575; D, *Anaxagorea dolichocarpa* (radial section), Uw 19575; E, *Anaxagorea dolichocarpa*, Uw 20017; F, *Anaxagorea guatemalensis* Standl., Uw 29438.

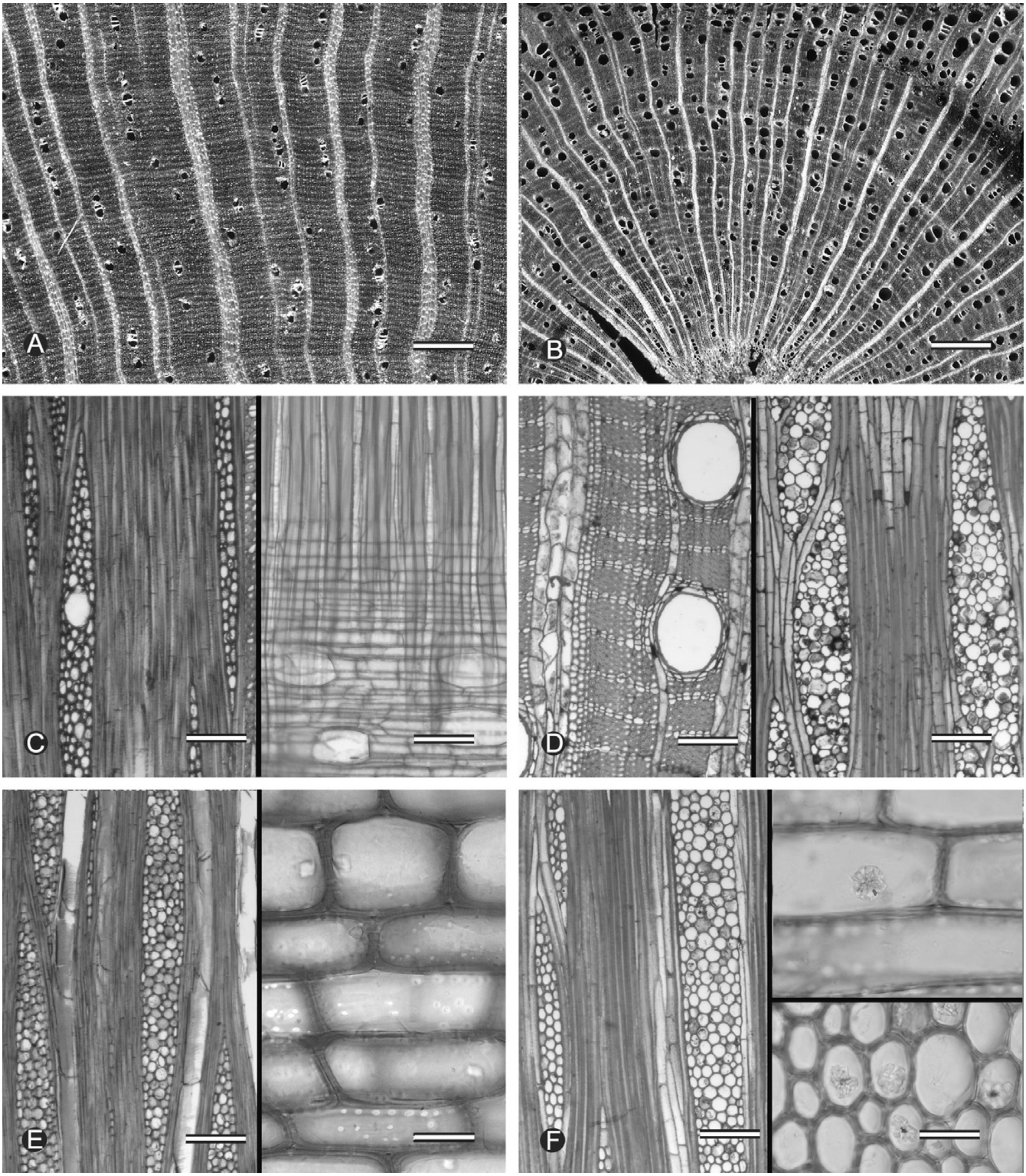

Figure 40. A, *Anaxagorea phaeocarpa* Mart., Uw 23646; B, *Monanthotaxis schweinfurthii* (Engl. & Diels) Verdc.var. *seretii* (De Wild.) Verdc., Uw 29516; C, *Duguetia argentea* (R.E.Fr.) R.E.Fr., Uw 8182, idioblasts in ray cells; left: tangential section, bar = 110 μm; right: radial section, bar = 85 μm; D, *Guatteria maypurensis* Kunth, Uw 2679; left: transverse section, showing vasicentric and reticulate parenchyma, bar = 110 μm; right: tangential section, showing multiseriate rays and axial parenchyma, bar = 110 μm; E, *Fusaea*; left: *F. peruviana* R.E.Fr., Uw 35940, tangential section, bar = 110 μm; right: *F. longifolia* (Aubl.) Saff., Uw 30329, radial section, showing small rhombic crystals in ray cells, bar = 20 μm; F, *Anaxagorea dolichocarpa* Sprague & Sandwith; left: Uw 2564, tangential section, bar = 110 μm; right: Uw 2031, radial section (above) and tangential section (below), showing druses in ray cells, bar = 20 μm.

occurrence of small druses (*c*. 10–15 μm in diameter) in the ray cells of both Neotropical and Palaeotropical species (Ter Welle, 1984).

CONCLUSIONS

Wood anatomical characters that may support phylogenetic conclusions are found at the microscopic level, and not at the macroscopic level. Wood anatomical features may be useful when using a hand lens at the generic level. At the species level, however, the wood anatomy can show great variability, even within one individual, depending on the organ, age, etc. Therefore, wood anatomical characters of Annonaceae can be used to verify plant identifications as long as the above considerations are taken into account.

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REFERENCES

APG III. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society* **161:** 105–121.

Chaowasku T, Zijlstra G, Chatrou LW. 2011. (2029) Proposal to conserve the name *Meiogyne* against *Fitzalania* (Annonaceae). *Taxon* **60:** 1522–1523.

Chatrou LW. 1998. Changing genera: systematic studies in Neotropical and West African Annonaceae. PhD Thesis, Utrecht University.

Chatrou LW, Koek-Noorman J, Maas PJM. 2000. Studies in Annonaceae XXXVI. The *Duguetia* alliance: where the ways part. *Annals of the Missouri Botanical Garden* **87:** 234–245.

Chatrou LW, Pirie MD, Erkens RHJ, Couvreur TLP, Neubig KM, Abbott JR, Mols JB, Maas JW, Saunders RMK, Chase MW. 2012. A new subfamilial and tribal classification of the pantropical flowering plant family Annonaceae informed by molecular phylogenetics. *Botanical Journal of the Linnean Society* **169:** 5–40.

Couvreur TLP, Richardson JE, Sosef MSM, Erkens RHJ, Chatrou LW. 2008. Evolution of syncarpy and other morphological characters in African Annonaceae: a posterior mapping approach. *Molecular Phylogenetics and Evolution* **47:** 302–318.

Couvreur TLP, van der Ham RWJM, Mbele YM, Mbago FM, Johnson DM. 2009. Molecular and morphological characterization of a new monotypic genus of Annonaceae, *Mwasumbia*, from Tanzania. *Systematic Botany* **34:** 266–276.

Erkens RHJ, Chatrou LW, Couvreur TLP. 2012. Radiations and key innovations in a basal angiosperm lineage (Annonaceae; Magnoliales). *Botanical Journal of the Linnean Society* **169:** 117–134.

Erkens RHJ, Chatrou LW, Koek-Noorman J, Maas JW, Maas PJM. 2007. Classification of a large and widespread genus of Neotropical trees, *Guatteria* (Annonaceae) and its three satellite genera *Guatteriella, Guatteriopsis* and *Heteropetalum*. *Taxon* **56:** 757–774.

Erkens RHJ, Maas PJM. 2008. The *Guatteria* group disentangled: sinking *Guatteriopsis, Guatteriella*, and *Heteropetalum* into *Guatteria*. *Rodriguésia* **59:** 401–406.

Erkens RHJ, Mennega EA, Westra LYT. 2012. A concise bibliographic overview of Annonaceae. *Botanical Journal of the Linnean Society* **169:** 41–73.

Gottwald H. 1977. The anatomy of secondary xylem and the classification of ancient dicotyledons. *Plant Systematics and Evolution. Supplementum* **1:** 111–121.

Hess RW. 1946. Identification of New World timbers. Part III. (Annonaceae). *Tropical Woods* **88:** 13–30.

Ilic J. 1991. *CSIRO atlas of hardwoods*. Berlin and Heidelberg: Springer Verlag.

Ingle HD, Dadswell HI. 1953. The anatomy of the timbers of the southwest Pacific. II. Apocynaceae and Annonaceae. *Australian Journal of Botany* **1:** 1–26.

Insidewood. 2004 onwards. Available at: http://www.insidewood/lib.ncsu.edu/search (Accessed 2 January 2012).

Lindeman JC, Mennega AMW. 1963. *Bomenboek voor Suriname. Herkenning van Surinaamse houtsoorten aan hout en vegetatieve kenmerken*. Paramaribo: Dienst's Lands Bosbeheer.

Maas PJM, Westra LYT, Vermeer M. 2007. Revision of the Neotropical genera *Bocageopsis, Onychopetalum*, and *Unonopsis* (Annonaceae). *Blumea* **52:** 413–554.

Metcalfe CR. 1987. *Anatomy of the dicotyledons*, 2nd edn, Vol. **III**. Magnoliales, Illiciales, and Laurales. Oxford: Clarendon Press.

Metcalfe CR, Chalk L. 1950. *Anatomy of the dicotyledons*. Oxford: Clarendon Press.

Moll JW, Janssonius HH. 1906. *Micrographie des Holzes der auf Java vorkommenden Baumarten. I*. Leiden: Brill.

Mols JB, Gravendeel B, Chatrou LW, Pirie MD, Bygrave PC, Chase MW, Kessler PJA. 2004. Identifying clades in Asian Annonaceae: monophyletic genera in the polyphyletic Miliuseae. *American Journal of Botany* **91:** 590–600.

Pfeiffer SJ. 1926. *De houtsoorten van Suriname I*. Amsterdam: Kol. Inst.. Mededeling 22, Afdeeling Handelsmuseum 6.

Pirie MD. 2005. *Cremastosperma* (and other evolutionary digressions). Molecular phylogenetic, biogeographic, and taxonomic studies in Neotropical Annonaceae. PhD Thesis, Utrecht University.

Pirie MD, Chatrou LW, Mols JB, Erkens RHJ, Oosterhof J. 2006. 'Andean-centred' genera in the short-branch clade of Annonaceae: testing biogeographic hypotheses using phylogeny reconstruction and molecular dating. *Journal of Biogeography* **33:** 31–46.

Rainer H, Chatrou LW. 2006. AnnonBase: *world species list of Annonaceae – version 1.1, 12 Oct 2006*. Available at:

http://www.sp2000.org and http://www.annonaceae.org (Accessed 25 Feb 2012).

Richardson JE, Chatrou LW, Mols JB, Erkens RHJ, Pirie MD. 2004. Historical biogeography of two cosmopolitan families of flowering plants: Annonaceae and Rhamnaceae. *Philosophical Transactions of the Royal Society B* **359:** 1495–1508.

Sauquet H, Doyle JA, Scharaschkin T, Borsch T, Hilu KW, Chatrou LW, Le Thomas A. 2003. Phylogenetic analysis of Magnoliales and Myristicaceae based on multiple data sets: implications for character evolution. *Botanical Journal of the Linnean Society* **142:** 125–186.

van Setten AK, Koek-Noorman J. 1992. *Studies in Annonaceae. XVII. Fruits and seeds of Annonaceae: morphology and its significance for classification*. Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung.

Solereder H. 1899. *Systematische Anatomie der Dicotyledonen*. Stuttgart: Enke.

Solereder H. 1908. *Systematische Anatomie der Dicotyledonen. Ergänzungsband*. Stuttgart: Enke.

Stern WL. 1988. Index xylariorum 3. *IAWA Bulletin n.s.* **9:** 203–252.

Stevens PF. 2001 onwards. *Angiosperm phylogeny website*. Version 9, June 2008 [and more or less updated since]. Available at: http://www.mobot.org/MOBOT/research/APweb/ (Accessed 10 September 2011).

Ter Welle BJH. 1984. Wood anatomy. In: Maas PJM, Westra LYT, eds. Studies in Annonaceae. II. A monograph of the genus *Anaxagorea* A. St. Hil. Part 1. *Botanische Jahrbücher fur Systematik, Pflanzengeschichte und Pflanzengeographie* **105:** 82–84.

Ter Welle BJH. 1985. Wood anatomy. In: Westra LYT, ed. Studies in Annonaceae. IV. A taxonomic revision of *Tetrameranthus* R.E. Fries. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen. Series C, Biological and Medical Sciences* **88:** 455–456.

Ter Welle BJH. 1992. Wood anatomy. In: Maas PJM, Westra LYT, collaborators, eds. *Rollinia. Flora Neotropica Monograph* **57:** 21–26.

Ter Welle BJH. 1995. Wood anatomy. In: Westra LYT, ed. Studies in Annonaceae. XXIV. A taxonomic revision of *Raimondia* Safford. *Botanische Jahrbücher fur Systematik, Pflanzengeschichte und Pflanzengeographie* **117:** 276–278.

Ter Welle BJH. 1998. Wood anatomy. In: Chatrou LW, ed. Changing genera: systematic studies in Neotropical and West African Annonaceae. PhD Thesis, Utrecht University, 113–116.

Ter Welle BJH. 1999. Wood anatomy. In: Chatrou LW, He P, eds. Studies in Annonaceae. XXXIII. A revision of *Fusaea* (Baill.) Saff. *Brittonia* **51:** 190–191.

Ter Welle BJH, Du N. 2003. Wood anatomy. In: Maas PJM, Westra LYT, Chatrou LW, collaborators, eds. *Duguetia* (Annonaceae). *Flora Neotropica Monograph* **88:** 25–28.

Ter Welle BJH, van Rooden J. 1982. Systematic wood anatomy of *Desmopsis, Sapranthus* and *Stenanona* (Annonaceae). *IAWA Bulletin n.s.* **3:** 15–23.

Vander Wijk RW. 1950. The comparative morphology of the Annonaceae. PhD Thesis, Harvard University, Cambridge, MA.

Vander Wijk RW, Canright JE. 1956. The anatomy and relationships of the Annonaceae. *Tropical Woods* **104:** 1–24.

Verdcourt B. 1971. Notes on East African Annonaceae. *Kew Bulletin* **25:** 1–34.

Westra LYT, Koek-Noorman J. 2003. Hand lens aspects of annonaceous wood. *Annonaceae Newsletter* **14:** 23–34. Available at: http://www.annonaceae.org/newsletter/ (Accessed 25 February 2012).

Westra LYT, Koek-Noorman J. 2004. Wood atlas of the Euphorbiaceae *sl*. *IAWA Journal Supplement* **4:** 1–110.

APPENDIX 1

Wood samples of Annonaceae studied. Wood collection numbers are indicated by their standard International Association of Wood Anatomists (IAWA) acronym (Stern, 1988). The addition of the capital 'N' indicates material collected in the Netherlands from a cultivated plant. [1]Herbarium vouchers may be deposited elsewhere. If no herbarium voucher exists, the source from which the specimen was obtained is indicated between square brackets. Synonyms are indicated by ' = '. Uw numbers refer to the Utrecht wood collection.

Genus	Species	Collector & nr.[1]	Uw number	Figure
Alphonsea Hook.f. & Thomson	*mollis* Dunn	*[Tw 41668]*	29501	1A
Anaxagorea A.St.-Hil.	*acuminata* (Dunal) A.DC.	*Krukoff 1017*	19187	38E
	acuminata (Dunal) A.DC.	*Irwin et al. 57661 [in Maguire]*	21064	38F
	brevipes Benth.	*Krukoff 5048*	19724	39A
	dolichocarpa Sprague & Sandwith	*Maguire 24605*	2564	39B, 40F
	dolichocarpa Sprague & Sandwith	*Krukoff 4700*	19575	39C, D
	dolichocarpa Sprague & Sandwith	*Krukoff 5532*	20017	39E
	guatemalensis Standl.	*Record 41*	29438	39F
	phaeocarpa Mart.	*W.A. Rodrigues & Coêlho 2460*	23646	40A
Annona L.	*annonoides* (R.E.Fr.) Maas & Westra	*Krukoff 6856*	7989	14E
	calcarata (R.E.Fr.) H.Rainer =*Rollinia calcarata* R.E.Fr.	*Krukoff 5315*	19892	14F
	cherimolioides Triana & Planch. =*Raimondia cherimolioides* (Triana & Planch.) R.E.Fr.	*Madison et al. 4936*	s.n.	15A
	cf. *cuspidata* (Mart.) H.Rainer =*Rollinia cuspidata Mart.*	*Lindeman 5906*	4050	15B
	cf. *densicoma* Mart.	*Lindeman 5861*	4012	15C
	dolichophylla R.E.Fr.	*Maas et al. 6266*	30303	15D
	edulis (Triana & Planch.) H.Rainer =*Rollinia edulis* Triana & Planch.	*Maas et al. 6305*	30324	15E
	emarginata (Schltdl.) H.Rainer =*Rollinia emarginata* Schltdl.	*Lindeman & De Haas 1077*	12880	15F
	emarginata (Schltdl.) H.Rainer =*Rollinia emarginata* Schltdl.	*Lindeman & De Haas 1621*	13209	16A
	exsucca DC.	*Fanshawe 1248 [Forest Dep. Br. Guiana 3984]*	770	16B
	fendleri (R.E.Fr.) H.Rainer =*Rollinia fendleri* R.E.Fr.	*Ll. Williams 10011*	35096	16C
	glabra L.	*Lindeman 6640*	4492	16D
	haematantha Miq.	*Maguire 24470*	2572	16E
	jucunda (Diels) H.Rainer =*Rollinia peruviana* Diels	*Maas et al. 6212*	30279	16F
	montana Macfad.	*Lanjouw & Lindeman 1373*	1465	17A
	mucosa Jacq.	*Maas et al. 6006*	30239	17B
	muricata L.	*Cult. Cantonspark Baarn 431*	N 546	17C
	neosericea H.Rainer =*Rollinia sericea* (R.E.Fr.) R.E.Fr.	*Lindeman & De Haas 221*	12501	17D
	neoulei H.Rainer =*Rollinia ulei* Diels	*Maas et al. 5972*	30235	17E
	neovelutina H.Rainer =*Rollinia velutina* van Marle	*Van der Werff & González 4747*	29435	17F
	quinduensis Kunth =*Raimondia quinduensis* (Kunth) Saff.	*Sánchez et al. 1258*	37079	18A
	senegalensis Persoon	*Schlieben s.n. [Reinbek 1674]*	15581	18B
	sericea Dunal	*Maas et al. 7144*	32438	18C
	sylvatica A.St.-Hil.	*Hatschbach, Lindeman & De Haas 13876*	14352	18D
	cf. *williamsii* (Rusby ex R.E.Fr.) H. Rainer =*Rollinia williamsii* Rusby ex R.E.Fr.	*Maas et al. 6073*	30255	18E
Anonidium Engl. & Diels	*mannii* (Oliv.) Engl. & Diels	*Mildbraed 7*	25871	19A, B
	mannii (Oliv.) Engl. & Diels	*[Tw 362]*	29488	18F
Artabotrys R.Br.	*insignis* Engl. & Diels	*J. Louis 1432*	29509	27A
	oliganthus Engl. & Diels	*Versteegh & Den Outer 666*	22118	27B
Asimina Adans.	*triloba* (L.) Dunal	*[USw 0008638]*	8474	19C, D
Bocageopsis R.E.Fr.	*canescens* (Spruce ex Benth.) R.E.Fr.	*Morawetz 32–7983*	29474	10A
	multiflora (Mart.) R.E.Fr.	*Schulz LBB 8318*	6796	10B
	multiflora (Mart.) R.E.Fr.	*Krukoff 6883*	8013	10C
Cananga (DC.) Hook.f. & Thomson	sp.	*M. Jacobs 8469*	s.n.	37B

APPENDIX 1 *Continued*

Genus	Species	Collector & nr.[1]	Uw number	Figure
Cleistopholis Pierre ex Engl.	*glauca* Pierre ex Engl. & Diels	*A. Sapin 55*	29517	37C
Cremastosperma R.E.Fr.	*brevipes* (DC.) R.E.Fr.	*De Granville et al. 7672*	31466	8A
	brevipes (DC.) R.E.Fr.	*Feuillet et al. 10239*	33515	8B
	cauliflorum R.E.Fr.	*Maas et al. 6271*	30306	8C
	microcarpum R.E.Fr.	*Maas et al. 6281*	30309	8D
	microcarpum R.E.Fr.	*Maas & Chatrou 8222*	34858	8E
	oblongum R.E.Fr.	*Maas et al. 4592*	26252	8F
	yamayakatense Pirie	*Berlin 1588*	24523	9A
Cyathocalyx Champ. ex Hook.f. & Thomson	*bancanus* Boerl.	*D. Normand 623*	26735	37D
	subsessilis Jovet-Ast =*Cyathocalyx sumatranus* Scheff.	*Guigonis 17*	26736	37E
Cymbopetalum Benth.	*brasiliense* (Vell.) Benth. ex Baill.	*Schulz LBB 9304*	8867	36B
	schunkei N.A.Murray	*J. Schunke V. 4829*	21087	36C
Desmopsis Saff.	*bibracteata* (B.L.Rob.) Saff.	*'A.R.G.' 1*	26771	1B
	panamensis (B.L.Rob.) Saff.	*Cooper & Slater 47*	24086	1C
	sp.	*Van Rooden 755*	26193	1D
Diclinanona Diels	*calycina* (Diels) R.E.Fr.	*Krukoff 8346*	16135	19E
	tessmannii Diels	*Maas et al. 6317*	30327	19F
	tessmannii Diels	*Maas et al. 6366*	30342	20A
Duguetia A.St.-Hil.	*argentea* (R.E.Fr.) R.E.Fr.	*Krukoff 7111*	8182	20C, 40C
	bahiensis Maas	*Maas et al. 6987*	31902	20D
	cadaverica Huber	*de Granville et al. 6301*	29933	20E, F
	calycina Benoist	*Fanshawe 141 [Forest Dep. Br. Guiana 2750]*	761	21A
	calycina Benoist	*Oldenburger, Norde & Schulz 478*	15331	21B
	cauliflora R.E.Fr.	*Lindeman 5797*	3951	21C
	cf. *cauliflora* R.E.Fr.	*Lindeman 6991*	4706	21D
	chrysea Maas	*Jansen-Jacobs et al. 5472*	36236	21E
	confinis (Engl. & Diels) Chatrou =*Pachypodanthium confine* Engl. & Diels	*Wieringa & Van Nek 3290*	35931	21F
	echinophora R.E.Fr.	*Fróes 1905 [dir. Krukoff]*	19482	22A
	eximia Diels	*De Granville et al. 6265*	29917	22B
	flagellaris Huber	*Maas et al. 8823*	36736	22C
	furfuracea (A.St.-Hil.) Saff.	*Simonis et al. 85*	29402	22D
	granvilleana Maas	*De Granville et al. 6134*	29888	22E
	latifolia R.E.Fr.	*Krukoff 6068*	7462	22F
	neglecta Sandwith	*Lindeman, Görts-van Rijn et al. 59*	26336	23A
	neglecta Sandwith	*Maas et al. 5887*	27370	23B
	odorata (Diels) J.F.Macbr.	*Krukoff 4805*	19628	23C
	pauciflora Rusby	*Forest Dep. Br. Guiana 3692*	762	23D
	pycnastera Sandwith	*Florschütz & Maas 3091*	11121	23E
	pycnastera Sandwith	*Maas et al. 6183*	30266	23F
	quitarensis Benth.	*Jansen-Jacobs et al. 184*	30521	24A
	riparia Huber	*Oldenburger, Norde & Schulz 1404*	17969	24B
	staudtii (Engl. & Diels) Chatrou =*Pachypodanthium staudtii* Engl. & Diels	*Leeuwenberg 2579*	6562	24C
	staudtii (Engl. & Diels) Chatrou =*Pachypodanthium staudtii* Engl. & Diels	*Mildbraed 6*	29374	24D, E
	stelechantha (Diels) R.E.Fr.	*Maguire et al. 56608*	16453	24F
	stenantha R.E.Fr.	*Maas et al. 6325*	30330	25A
	surinamensis R.E.Fr.	*Krukoff 6258*	7601	25B
	surinamensis R.E.Fr.	*Oldenburger, Norde & Schulz 471*	15325	25C
	uniflora (DC.) Mart.	*Krukoff 7258*	8276	25D
	yeshidan Sandwith	*Jansen-Jacobs et al. 5644*	36493	25E, F
Enicosanthum Becc.	*macranthum* (King) J.Sinclair	*Van Balgooy & Van Setten 5614*	31869	1E
Ephedranthus S.Moore	*amazonicus* R.E.Fr.	*Morawetz 21–13883*	29462	6A
	guianensis R.E.Fr.	*Schulz LBB 8568*	6856	6B
Exellia Boutique	*scamnopetala* (Exell) Boutique	*Hallé & Le Thomas 163*	29528	11D
Fissistigma Griff.	sp.	*Van Balgooy & Van Setten 5553*	31788	11E, F
Fitzalania F.Muell.	*heteropetala* (F.Muell.) F.Muell.	*Morawetz et al. 23–5285*	30384	2A, B

APPENDIX 1 *Continued*

Genus	Species	Collector & nr.[1]	Uw number	Figure
Friesodielsia Steenis	*enghiana* (Diels) Verdc.	*Hallé & Le Thomas 491*	29536	12A
	montana (Engl. & Diels) Steenis =*Friesodielsia soyauxii* (Spague & Hutch.) Steenis	*J. Louis 1267*	29519	12B
Froesiodendron R.E.Fr.	*surinamense* (R.E.Fr.) R.E.Fr.	*Schulz 7396*	5015	36D
Fusaea (Baill.) Saff.	*longifolia* (Aubl.) Saff.	*Lindeman 6742*	4559	26A
	longifolia (Aubl.) Saff.	*Krukoff 8086*	16133	26B
	longifolia (Aubl.) Saff.	*Maas et al. 6320*	30329	26C, 40E
	peruviana R.E.Fr.	*Vasquez & Jaramillo 8506*	35939	26D
	peruviana R.E.Fr.	*Berlin 637*	35940	26E, 40E
Goniothalamus (Blume) Hook.f. & Thomson	*giganteus* Hook.f. & Thomson	*Krukoff 4237*	29389	20B
Greenwayodendron Verdc.	*oliveri* (Engl.) Verdc. =*Artabotrys oliveri (Engl.) Roberty*	*Bamps 2150*	29490	27C
Guatteria Ruiz & Pav.	*alta* R.E.Fr.	*Cuatrecasas 14829*	25132	32A
	anomala R.E.Fr.	*Ishiki, Maas et al. 2194*	36880	32B
	atra Sandwith	*Forest Dep. Br. Guiana 3688*	34267	32C
	blainii (Griseb.) Urb. =*Asimina blainii* Griseb.	*Sintenis 6415*	29375	32D
	campinensis (Morawetz & Maas) Erkens & Maas =*Guatteriella campinensis* Morawetz & Maas	*Morawetz 31–24883*	29468	32E
	conspicua R.E.Fr.	*Lanjouw & Lindeman 455*	1241	32F
	curvipetala R.E.Fr.	*Krukoff 6600*	7806	33A
	discolor R.E.Fr.	*Krukoff 7047*	8134	33C, D
	dusenii R.E.Fr.	*Lindeman & De Haas 2330*	13675	33E, F
	elegantissima R.E.Fr.	*Cuatrecasas 17028*	25071	33B
	heteropetala Benth. =*Heteropetalum brasiliense* Benth.	*D.W. Stevenson 1115*	33073	34A
	hispida (R.E.Fr.) Erkens & Maas =*Guatteriopsis hispida* R.E.Fr.	*Morawetz 12–25883*	29458	34B
	maypurensis Kunth	*A.C. Smith 2452 [Yw 35567]*	2679	40D
	monticola R.E.Fr.	*Wilson-Browne 473 [Forest Dep. Br. Guiana 5882]*	34268	34C
	obovata R.E.Fr.	*Morawetz 16–18883*	29461	34D
	poeppigiana Mart.	*Pires et al. 51863 [in Maguire]*	17242	34E
	procera R.E.Fr.	*Maguire 24684*	2567	34F
	punctata (Aubl.) R.A.Howard	*Maguire 24430*	2565	35A
	punctata (Aubl.) R.A.Howard.	*Maguire 24589*	2566	35B
	rubrinervis R.E.Fr.	*Wilson-Browne 417 [Forest Dep. Br. Guiana 5816]*	34270	35C
	scandens Ducke	*Maas et al. 3600*	24786	35D
	schomburgkiana Mart.	*Stahel 254*	254	35E
	schomburgkiana Mart.	*Maguire 24683*	2568	35F
	trichostemon R.E.Fr.	*Krukoff 8862*	16119	36A
Isolona Engl.	*hexaloba* (Pierre) Engl. & Diels =*Isolona bruneelii* De Wild.	*Dechamps 187*	29497	12C
Klarobelia Chatrou	*cauliflora* Chatrou	*Chatrou et al. 6*	34863	6C
	megalocarpa Chatrou	*Maas et al. 8520*	35946	6D
Malmea R.E.Fr.	*dielsiana* R.E.Fr.	*Maas et al. 6026*	30246	9B
	surinamensis Chatrou	*Daniëls & Jonker 859*	8543	9C
	surinamensis Chatrou	*Daniëls & Jonker 1178*	8629	9D
Meiocarpidium Engl. & Diels	*lepidotum* (Oliv.) Engl. & Diels	*Breteler 2646*	9544	38D
Meiogyne Miq.	*cylindrocarpa* (Burck) Heusden =*Guamia mariannae* (Saff.) Merr.	*Dutton et al. 125*	16685	1F
Mezzettia Becc.	*leptopoda* (Hook.f. & Thomson) King	*[Tw 11543]*	29504	37F
	parviflora Becc.	*Van Balgooy & Van Setten 5653*	32051	38A
	umbellata Becc.	*[Tw 42298]*	29513	38B
Miliusa Lesch. ex A.DC.	*koolsii* (Kosterm.) J.Sinclair	*BW [Nieuw Guinea] 12407*	18223	2D
	koolsii (Kosterm.) J.Sinclair	*BW [Nieuw Guinea] 13267*	18272	2E
Mitrephora (Blume) Hook.f. & Thomson	*thorelii* Pierre	*[Tw 41669]*	29514	2F

APPENDIX 1 *Continued*

Genus	Species	Collector & nr.[1]	Uw number	Figure
Monanthotaxis Baill.	*parvifolia* (Oliv.) Verdc. =*Popowia oliverana* Exell & Mendonça	*Toussaint 120*	29499	3F
	poggei Engl. & Diels	*de Saegher 120 [Tw 28222]*	29498	12D
	schweinfurthii (Engl. & Diels) Verdc. var. *seretii* (De Wild.) Verdc. =*Enneastemon seretii (De Wild.) Rob. & Ghesq.*	*J. Louis 3778*	29516	40B
Monocarpia Miq.	*marginalis* (Scheff.) J.Sinclair	*Tw 17495*	29515	5F
Monodora Dunal	*crispata* Engl. & Diels	*Versteegh & Den Outer 100*	22122	12E
	myristica (Gaertn.) Dunal	*H.T. Beck 1291 [Cult.]*	34652	12F
	undulata (P.Beauv.) Couvreur	*Staudt 40*	29379	13A
Mosannona Chatrou	aff. *discolor* (R.E.Fr.) Chatrou =*Malmea discolor* R.E.Fr.	*Lindeman, Görts-van Rijn et al. 283*	26395	6E
	pacifica Chatrou	*Maas et al. 8531*	35947	6F
Onychopetalum R.E.Fr.	*amazonicum* R.E.Fr.	*Morawetz 11-8983*	29457	10D
Orophea Blume	*creaghii* (Ridl.) Leonar. & P.J.A.Kessler =*Mezzettopsis creaghii* Ridl.	*Van Balgooy & Van Setten 5657*	32050	2C
	myriantha Merr.	*[Tw 18599]*	29493	3A
Oxandra A.Rich.	*asbeckii* (Pulle) R.E.Fr.	*Stahel 271*	271	7A
	asbeckii (Pulle) R.E.Fr.	*Lanjouw & Lindeman 2771*	1916	7B
	riedeliana R.E.Fr.	*Krukoff 6471*	7753	7C
	riedeliana R.E.Fr.	*Krukoff 6585*	7793	7D
Phaeanthus Hook.f. & Thomson	*ebracteolatus* (C.Presl) Merr.	*BFA 18612*	31376	3B
Platymitra Boerl.	*arborea* (Blanco) Kessler =*Alphonsea arborea* (Blanco) Merr.	*[FPRI 484]*	10744	3C
Polyalthia Blume	*forbesii* F.Muell. ex Diels	*BW [Nieuw Guinea] 2553*	28711	3D
	sp.	*Nooteboom & Bhargawa BSI 6331*	26292	3E
Porcelia Ruiz. & Pav.	*ponderosa* (Rusby) Rusby	*Krukoff 5299*	19881	36E, F
Pseudartabotrys Pellegr.	*letestui* Pellegr.	*Wieringa & Van Nek 3273*	35932	26F
Pseudomalmea Chatrou	*boyacana* (J.F.Macbr.) Chatrou	*D. Sánchez et al. 1090*	31380	7E
	diclina (R.E.Fr.) Chatrou	*Krukoff 5632*	20084	7F
Pseudoxandra R.E.Fr.	*obscurinervis* Maas	*Morawetz 32–15883*	29456	9E
	polyphleba (Diels) R.E.Fr.	*Krukoff 4882*	19657	9F
Pseuduvaria Miq.	*froggattii* F.Muell.	*Morawetz et al. 21–27185*	30394	4A
	froggattii F.Muell.	*Morawetz et al. 12–6185*	30408	4B
	megalopus (K.Schum.) Y.C.F.Su & Mols =*Petalolophus megalopus* K.Schum.	*J. & M.S. Clemens 860*	35942	4C
Sapranthus Seem.	*palanga* R.E.Fr.	*Van Rooden 868*	26216	4D
	palanga R.E.Fr.	*Poveda 300*	26772	4E
	violaceus (Dunal) Saff. =*Sapranthus nicaraguensis* Seem.	*Van Rooden 200*	24194	4F
	viridiflorus G.E.Schatz	*Poveda 84*	26773	5A
Stelechocarpus (Blume) Hook.f. & Thomson	*cauliflorus* (Scheff.) R.E.Fr.	*Van Balgooy & Van Setten 5689*	31305	5B
Stenanona Standl.	*costaricensis* R.E.Fr.	*Wilbur & Stone 10706*	26231	5C
	panamensis Standl.	*Cooper 427*	24300	5D
	stenopetala (Donn.Smith) G.E.Schatz. =*Desmopsis stenopetala* (Donn.Smith) R.E.Fr.	*Stevenson 105*	24298	5E
Tetrameranthus R.E.Fr.	*duckei* R.E.Fr.	*Coêlho INPA 69232*	26746	38C
Toussaintia Boutique	*hallei* Le Thomas	*Hallé 4189*	29546	13B
Trigynaea Schltdl.	*caudata* (R.E.Fr.) R.E.Fr.	*Forest Dep. Br. Guiana 7462*	764	37A
Unonopsis R.E.Fr.	*glaucopetala* R.E.Fr.	*Lindeman 3546*	2317	10E
	guatterioides (A.DC.) R.E.Fr.	*Stahel 370*	370	10F
	perrottetii (A.DC.) R.E.Fr.	*Forest Dep. Br. Guiana 4835*	772	11A
	rufescens (Baill.) R.E.Fr.	*Stahel 225*	225	11B
	sericea Maas & Westra	*Soejarto & Rentería 3605*	36940	11C
Uvaria L.	*angolensis* Welw. ex Oliv.	*Cult. RBG Kew 4546.29*	22255	13C
	chamae P.Beauv.	*Kersting 43*	25872	13D
	doeringii Diels	*Versteegh & Den Outer 286*	22121	13E
	sp. cf.	*Edmond s.n.*	30698	13F
Uvariodendron (Engl. & Diels) R.E.Fr.	*molundense* (Engl. & Diels) R.E.Fr.	*Hallé 3264*	29542	14A, B
Uvariopsis Engl.	*congolana* (De Wild.) R.E.Fr.,	*J. Louis 6683*	29503	14C
	congolana (De Wild.) R.E.Fr.,	*J. Louis 3623*	29511	14D

APPENDIX 1 *Continued*

Genus	Species	Collector & nr.[1]	Uw number	Figure
Xylopia L.	*aethiopica* (Dunal) A.Rich.	*Kersting 56*	25875	27D, E, F
	amazonica R.E.Fr.	*Maguire 24818*	2563	28C
	aromatica (Lam.) Mart.	*Forest Dep. Br. Guiana 778*	773	28A
	aromatica (Lam.) Mart.	*Krukoff 6486*	7762	28B
	benthamii R.E.Fr.	*Pires et al. 51825 [in Maguire]*	9071	28D
	cayennensis Maas	*BAFOG 57–1214*	5703	28E
	cuspidata Diels	*Maas et al. 6312*	30325	28F
	discreta (L.f.) Sprague & Hutch.	*Stahel 138a*	138a	29A
	emarginata Mart. var. *duckei* R.E.Fr.	*Pires et al. 51820 [in Maguire]*	17208	29B
	frutescens Aubl. var. *frutescens*	*Forest Dep. Br. Guiana 3656*	775	29C
	holtzii Engl.	*Schlieben 467 [Reinbek 1860]*	15600	29D
	malayana Hook.f. & Thomson	*Van Balgooy & Van Setten 5467*	32066	29E
	neglecta (Kuntze) R.E.Fr.	*Maas et al. 6328*	30331	29F
	nitida Dunal	*Maas LBB 11026*	11725	30A
	papuana Diels	*Schram BW [Nieuw Guinea] 12414*	18227	30B
	parviflora (A.Rich.) Benth. ?	*Kersting 89*	25876	30C
	peekelii Diels	*Craven & Schodde 258*	s.n.	30D
	peruviana R.E.Fr.	*Maas et al. 6013*	30241	30E
	polyantha R.E.Fr. var. *polyantha*	*Krukoff 1204*	19248	30F
	pulcherrima Sandwith	*Schulz 7404*	5020	31A
	quintasii Engl. & Diels	*Breteler 2398*	9501	31B
	surinamensis R.E.Fr.	*Schulz LBB 9323*	8875	31C
	toussaintii Boutique	*[Cult.?] Jardim Ultramar Lisboa 122/16*	24209	31D
	trichostemon R.E.Fr.	*Krukoff 5690*	20127	31E
	xylantha R.E.Fr.	*Krukoff 8750*	16139	31F