



# 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 annonaecous 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 & Menega (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



$\pm 7.0 \times 4.5 \text{ mm}^2$  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  $\frac{1}{2}$  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.*  $4.0 \times 3.0 \text{ mm}^2$  except for Figs. 2B, 11F, and 25F ( $2.0 \times 1.5 \text{ mm}^2$ ). 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  $\mu\text{m}$ , 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 *Gutteria 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, *Annonaannonoides* (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 (*Gutteria* 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  $\mu\text{m}$ . Lower or higher mean sizes occur in individual species in several genera.

Mean vessel number is between 10 and 40 per  $\text{mm}^2$ , but sometimes > 50 per  $\text{mm}^2$ , e.g. in *Fitzalania* F.Muell., *Sapranthus* Seem. and *Malmea* R.E.Fr. Perforations are simple. Intervessel pits are mostly 2–3(–5)  $\mu\text{m}$ , rarely up to 9  $\mu\text{m}$  (*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., *Gutteria*, *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  $\mu\text{m}$ , sometimes > 7000  $\mu\text{m}$ . The width is from < 150  $\mu\text{m}$  to  $\leq$  300  $\mu\text{m}$ , 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 vascentric 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 vascentric 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 *Crematosperma*–*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.

#### *Piptostigmatae* (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 millimetre)]. 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. Uniseriate rays are numerous. Multiseriate rays, 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:* *Crematosperma* 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 *Crematosperma*–*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).

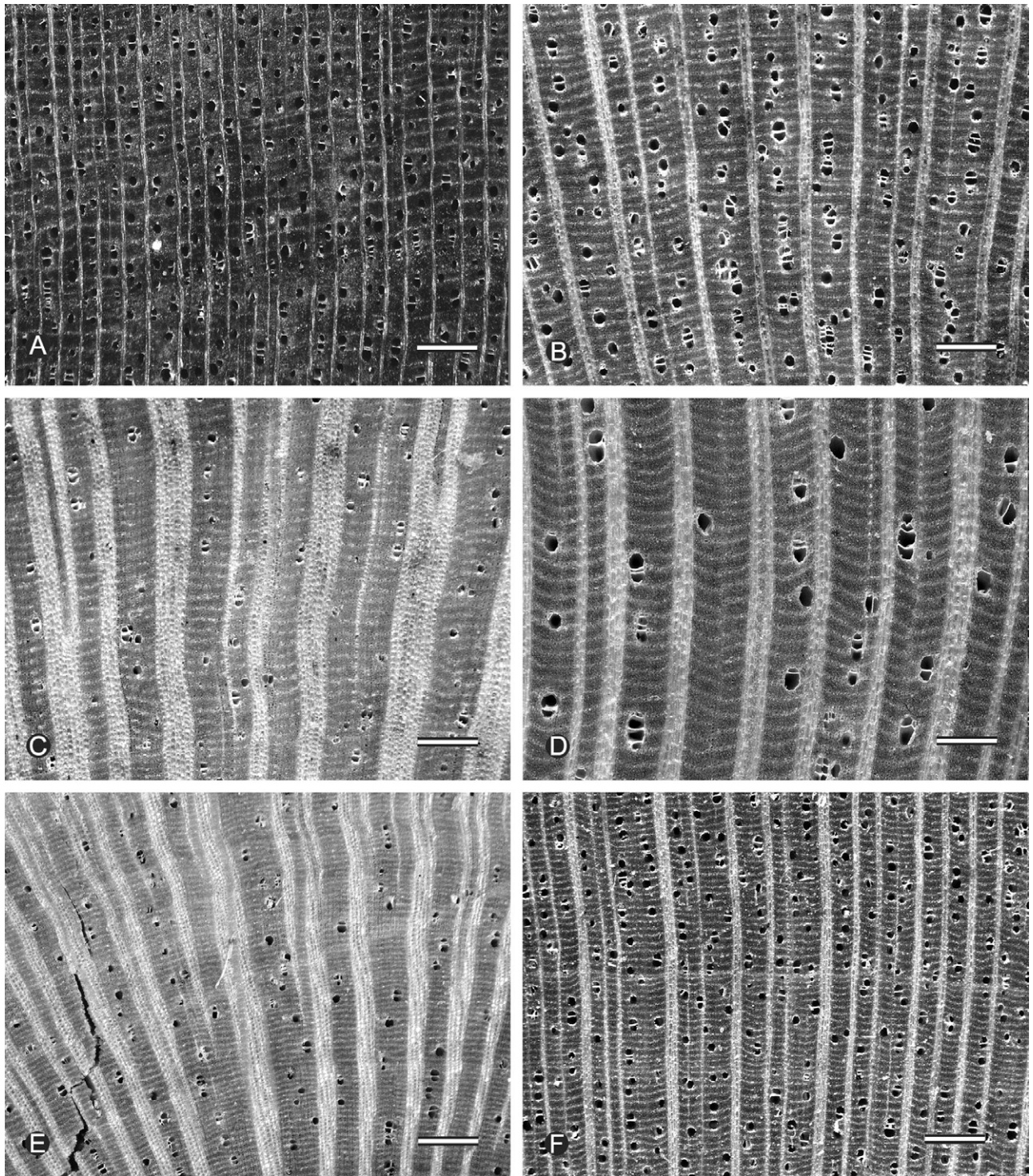
In the *Crematosperma*–*Malmea* group, the rays mostly tend to be narrow, with occasionally some broader ones in between. In contrast, broad rays prevail in *Crematosperma*, especially *C. cauliflorum* R.E.Fr. (Fig. 8C), but much less in *C. microcarpum* R.E.Fr.; in one specimen of this species, they 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 *Crematosperma 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.

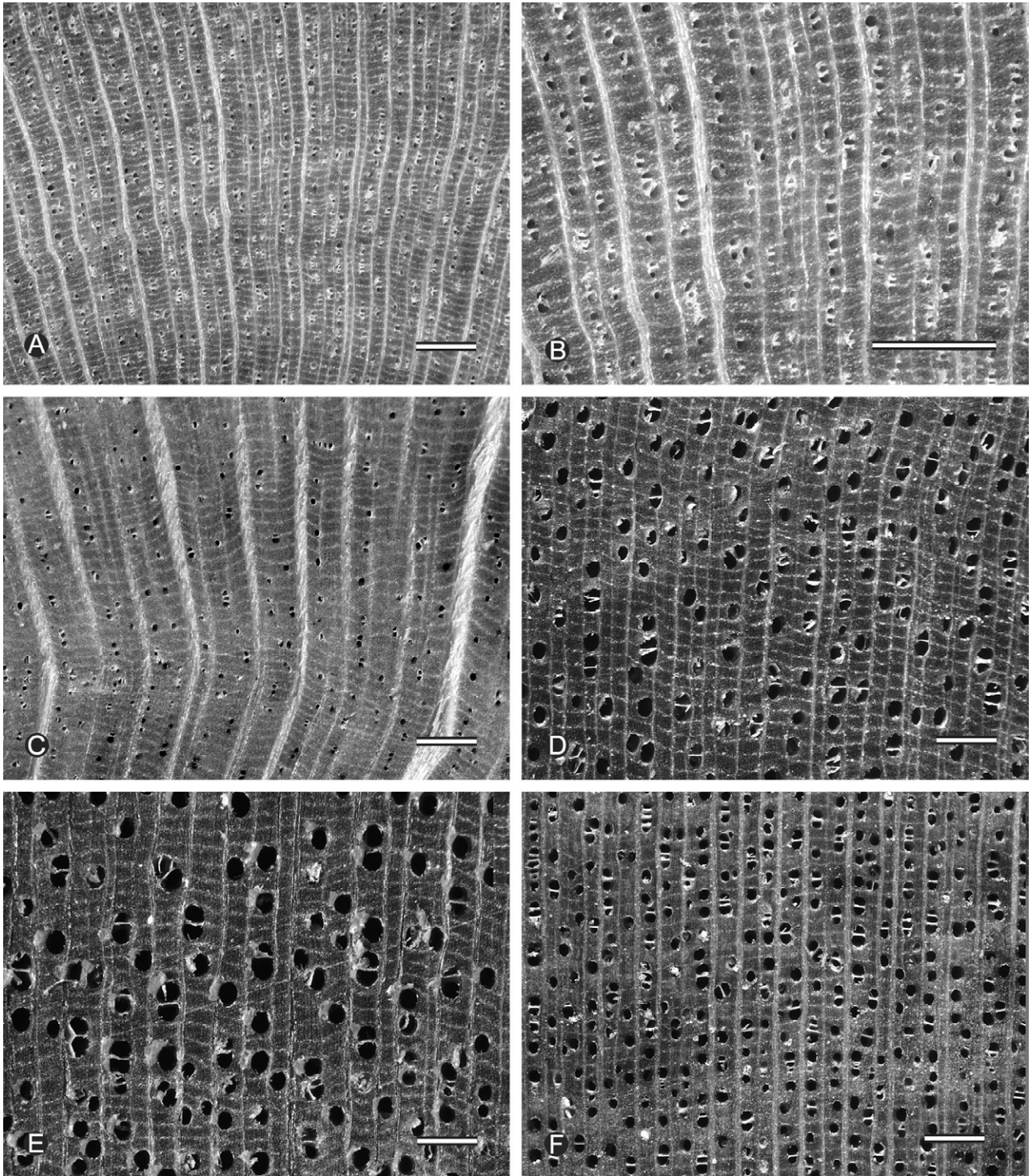
The somewhat aberrant wood of *Unonopsis perrottetii*, as compared with other species of this genus studied here, should be noted. Vegetatively, *U. perrottetii* is distinctive by the slightly falcate, narrow leaves with inconspicuous secondary venation





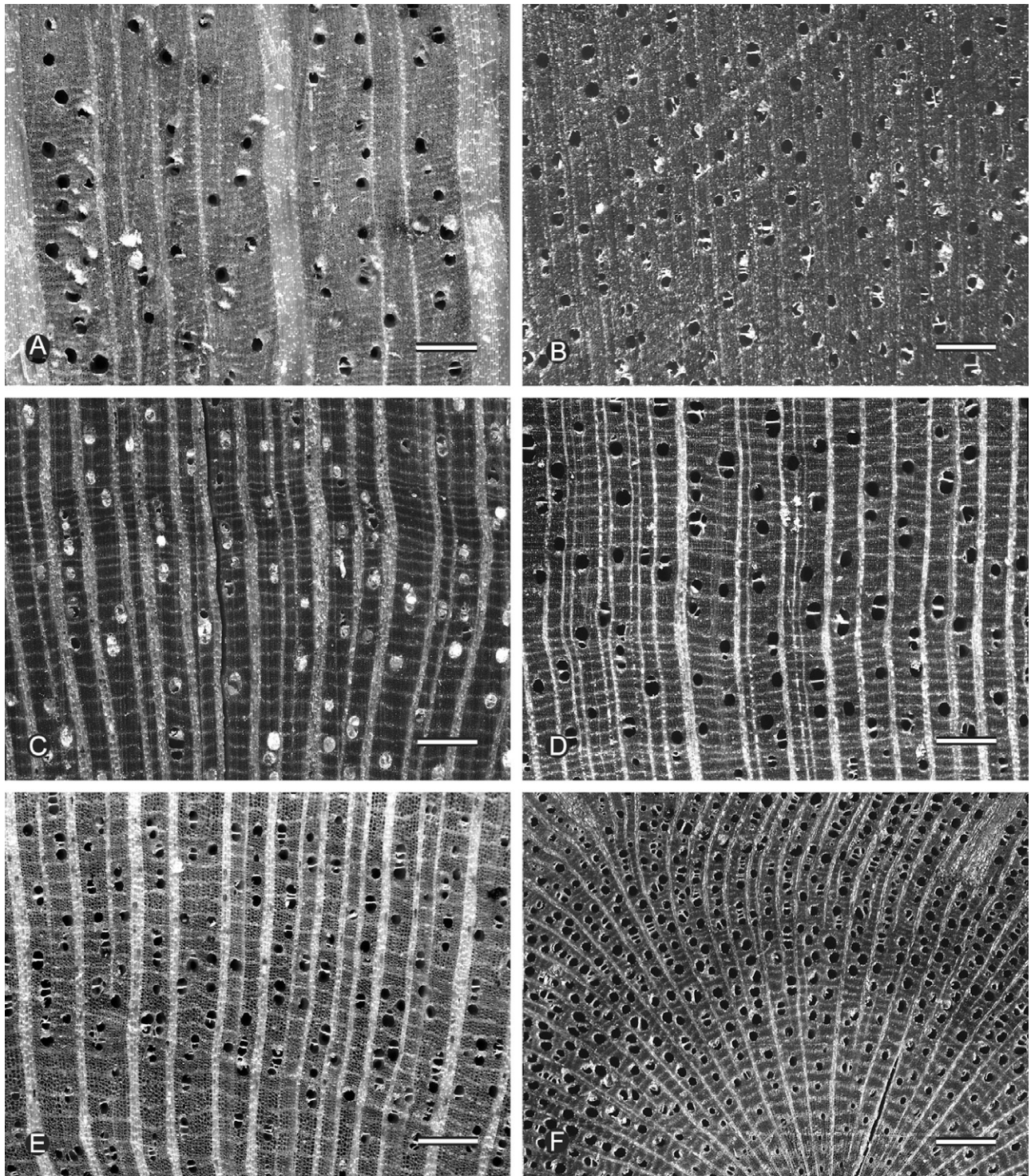
**Figure 1.** A–F, Miliuseae. A, *Alphonsea mollis* Dunn, Uw 29501; B, *Desmopsis bibracteata* (B.L.Rob.) Saff., Uw 26771; C, *Desmopsis panamensis* (B.L.Rob.) Saff., Uw 24086; D, *Desmopsis* sp., Uw 26193; E, *Enicosanthum macranthum* (King) J.Sinclair, Uw 31869; F, *Meiohyne cylindrocarpa* (Burck)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





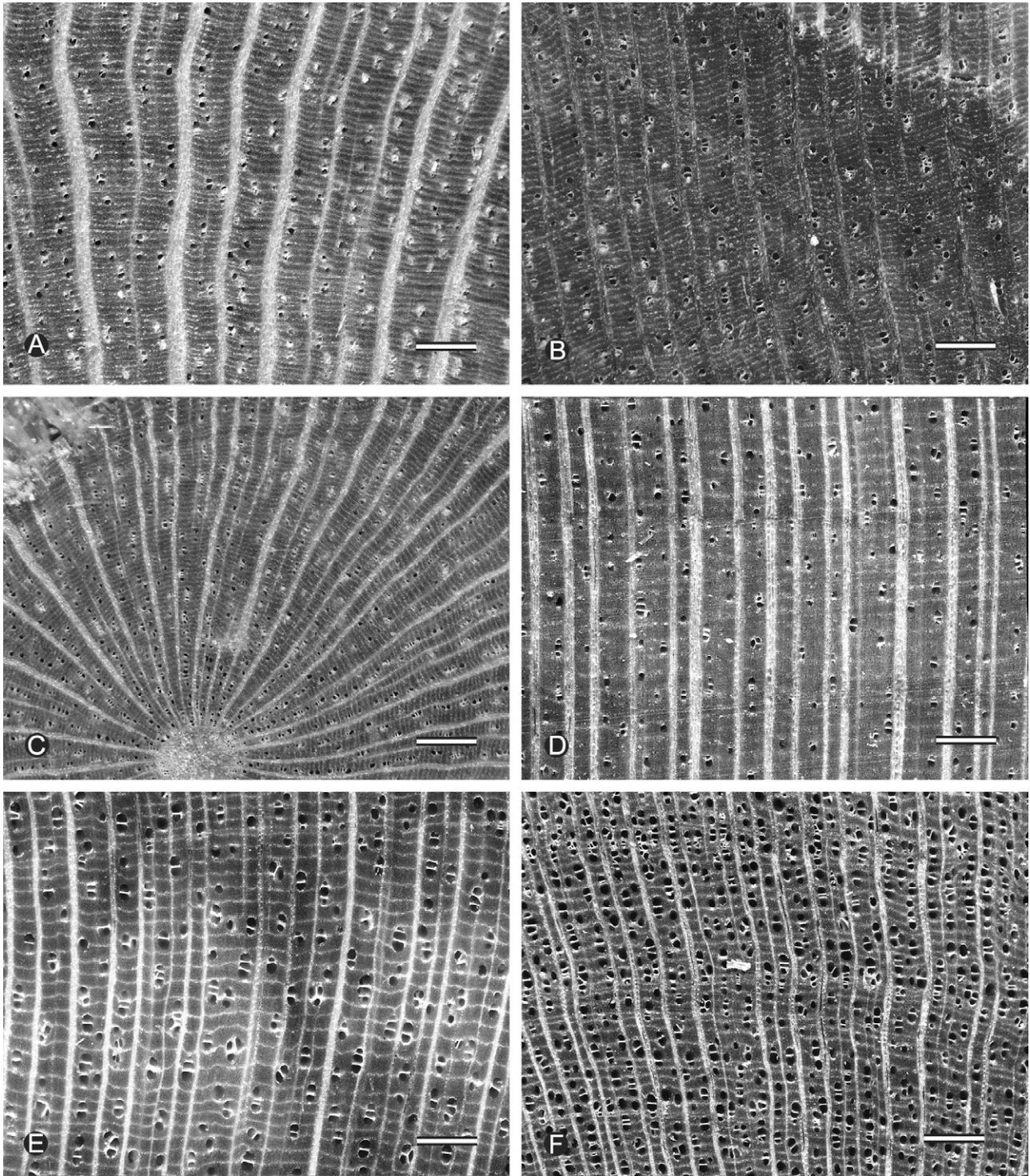
**Figure 2.** A–F, Miliuseae. A, B, *Fitzalania heteropetala* (F.Muell.) F.Muell., Uw 30384; C, *Orophea creaghii* (Ridl.) Leonar. & P.J.A.Kessler, Uw 32050; D, *Miliusa koolsii* (Kosterm.) J.Sinclair, Uw 18223; E, *Miliusa koolsii*, Uw 18272; F, *Mitrephora thorelii* Pierre, Uw 29514.





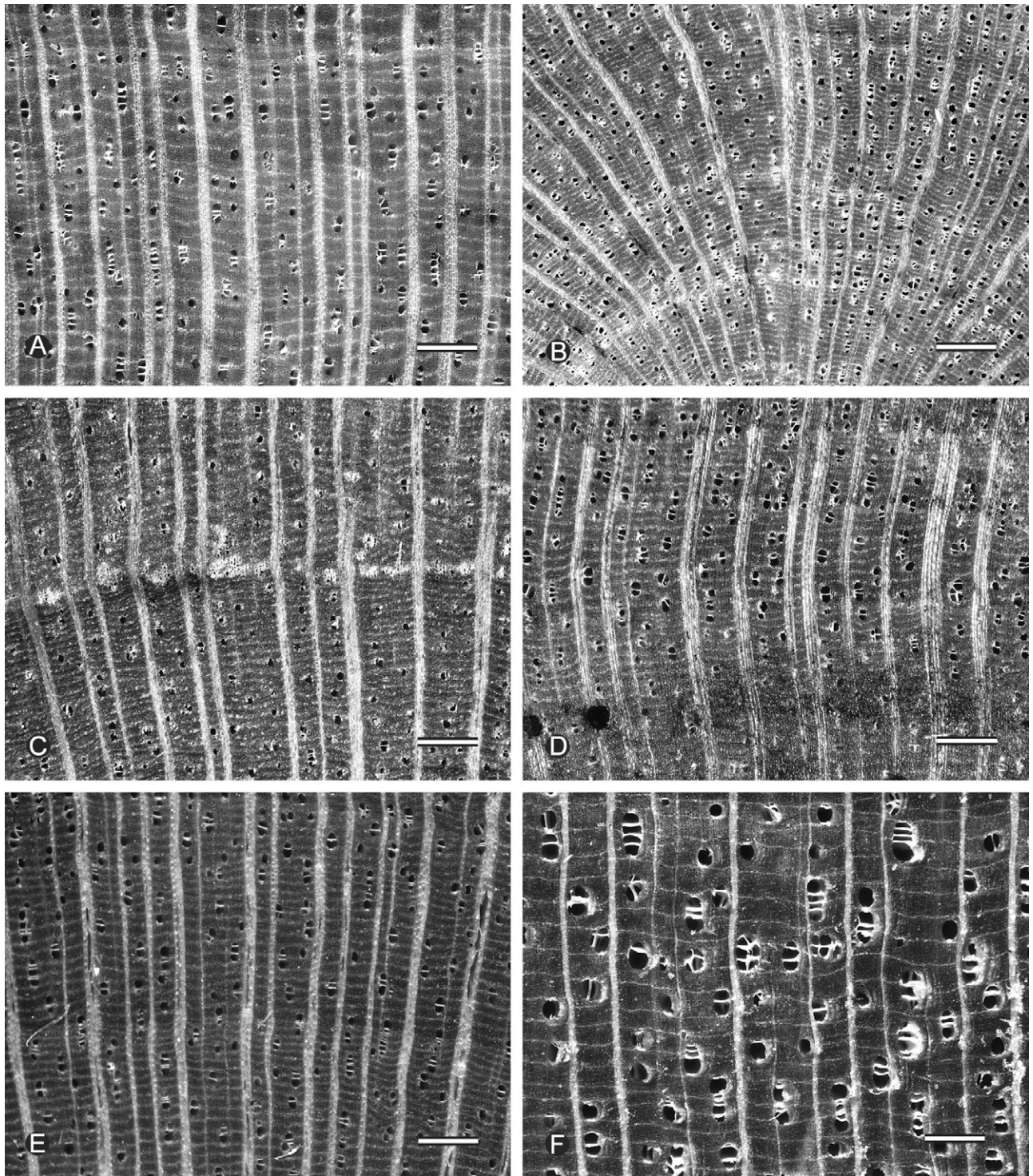
**Figure 3.** A–E, Miliuseae; F, Uvarieae. A, *Orophea myriantha* Merr., Uw 29493; B, *Phaeanthus ebracteolatus* (C.Presl) Merr., Uw 31376; C, *Platymitra arborea* (Blanco) Kessler, Uw 10744; D, *Polyalthia forbesii* F.Muell. ex Diels, Uw 28711; E, *Polyalthia* sp., Uw 26292; F, *Monanthotaxis parvifolia*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





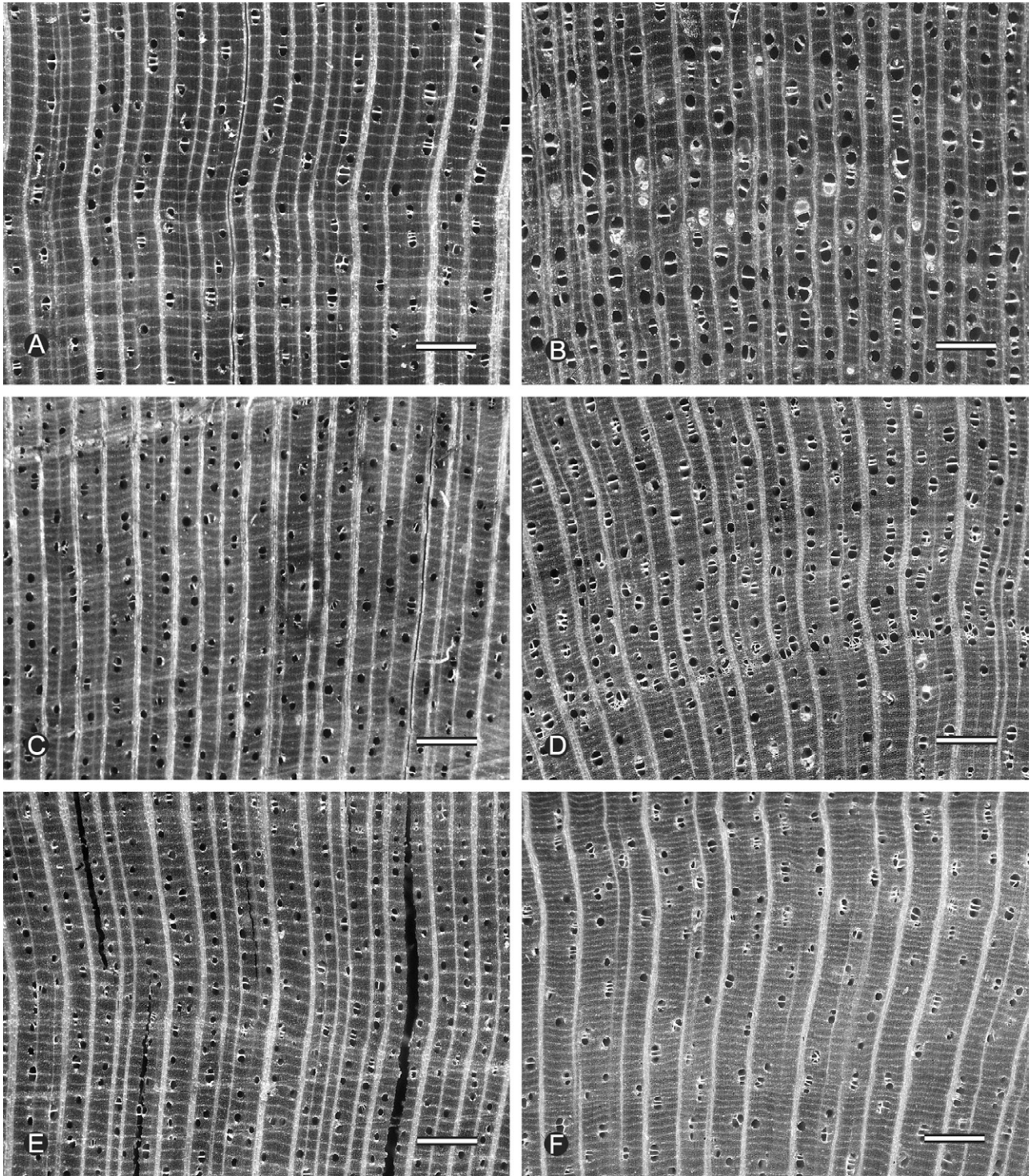
**Figure 4.** A–F, Miliuseae. A, *Pseuduaria froggattii* F.Muell., Uw 30394; B, *Pseuduaria froggattii*, Uw 30408; C, *Pseuduaria megalopus* (K.Schum.) Y.C.F.Su & Mols, Uw 35942; D, *Sapranthus palanga* R.E.Fr., Uw 26216; E, *Sapranthus palanga*, Uw 26772; F, *Sapranthus violaceus* (Dunal) Saff., Uw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





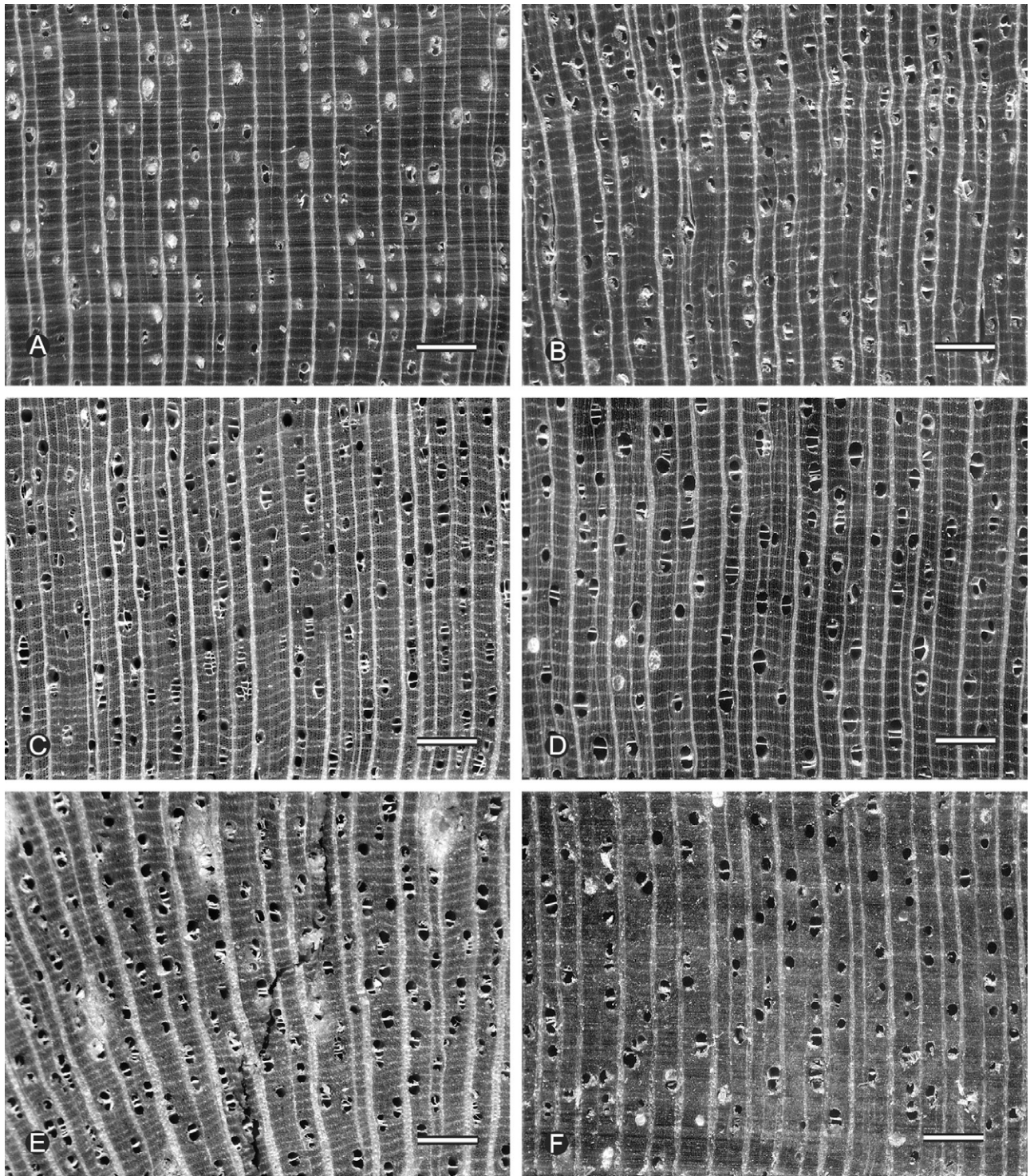
**Figure 5.** A–E, Miliuseae; F, *Monocarpia*. A, *Sapranthus viridiflorus* G.E.Schatz, Uw 26773; B, *Stelechocarpus cauliflorus* (Scheff.) R.E.Fr., Uw 31305; C, *Stenanona costaricensis* R.E.Fr., Uw 26231; D, *Stenanona panamensis* Standl., Uw 24300; E, *Stenanona stenopetala* (Donn.Sm.) G.E.Schatz,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





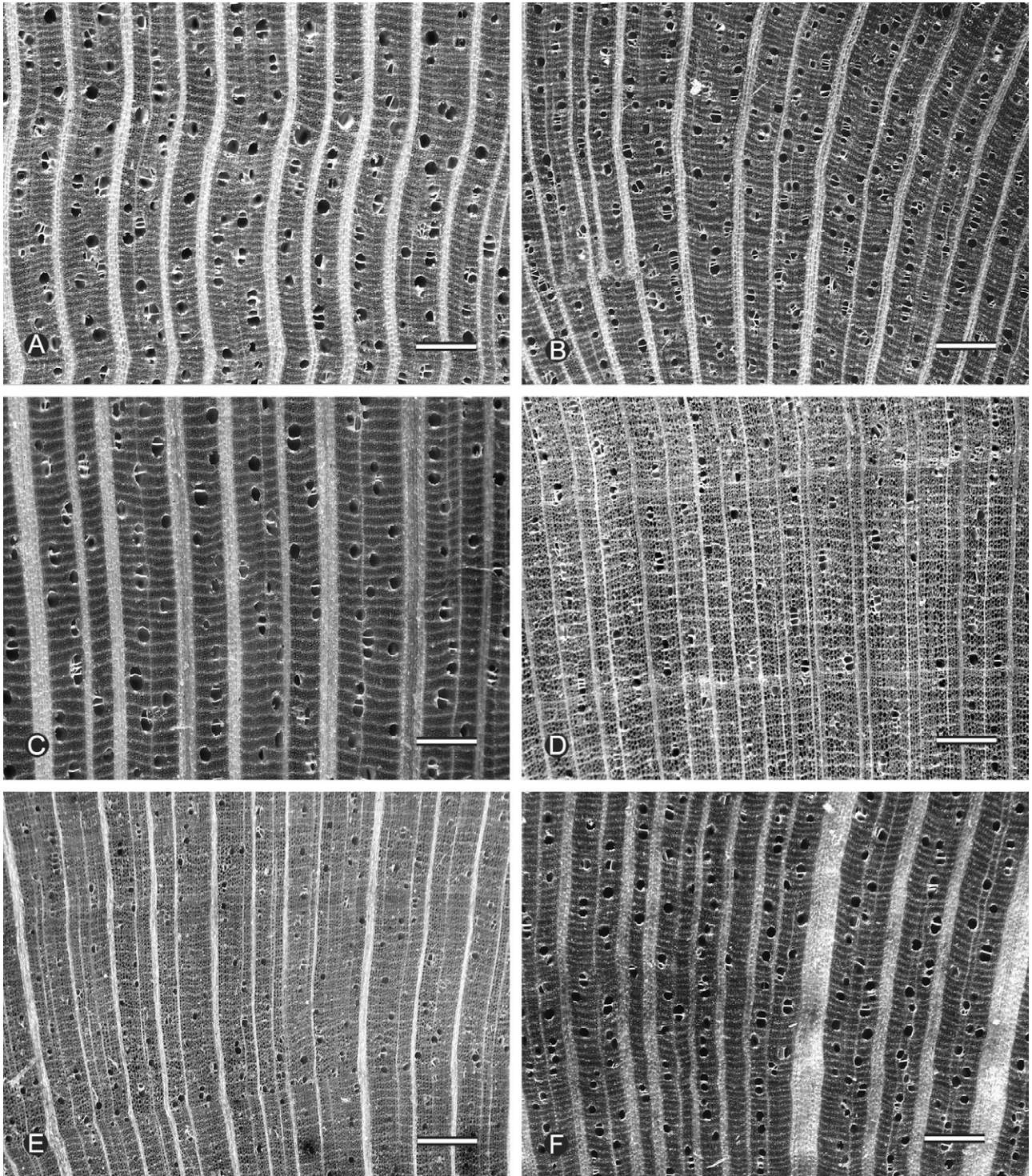
**Figure 6.** A–F, Malmeae. A, *Ephedranthus amazonicus* R.E.Fr., Uw 29462; B, *Ephedranthus guianensis* R.E.Fr., Uw 6856; C, *Klarobelia cauliflora* Chatrou, Uw 34863; D, *Klarobelia megalocarpa* Chatrou, Uw 35946; E, *Mosannonna* aff. *discolor* (R.E.Fr.) Chatrou, Uw 26395; F, *Mosannonna pacifica*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





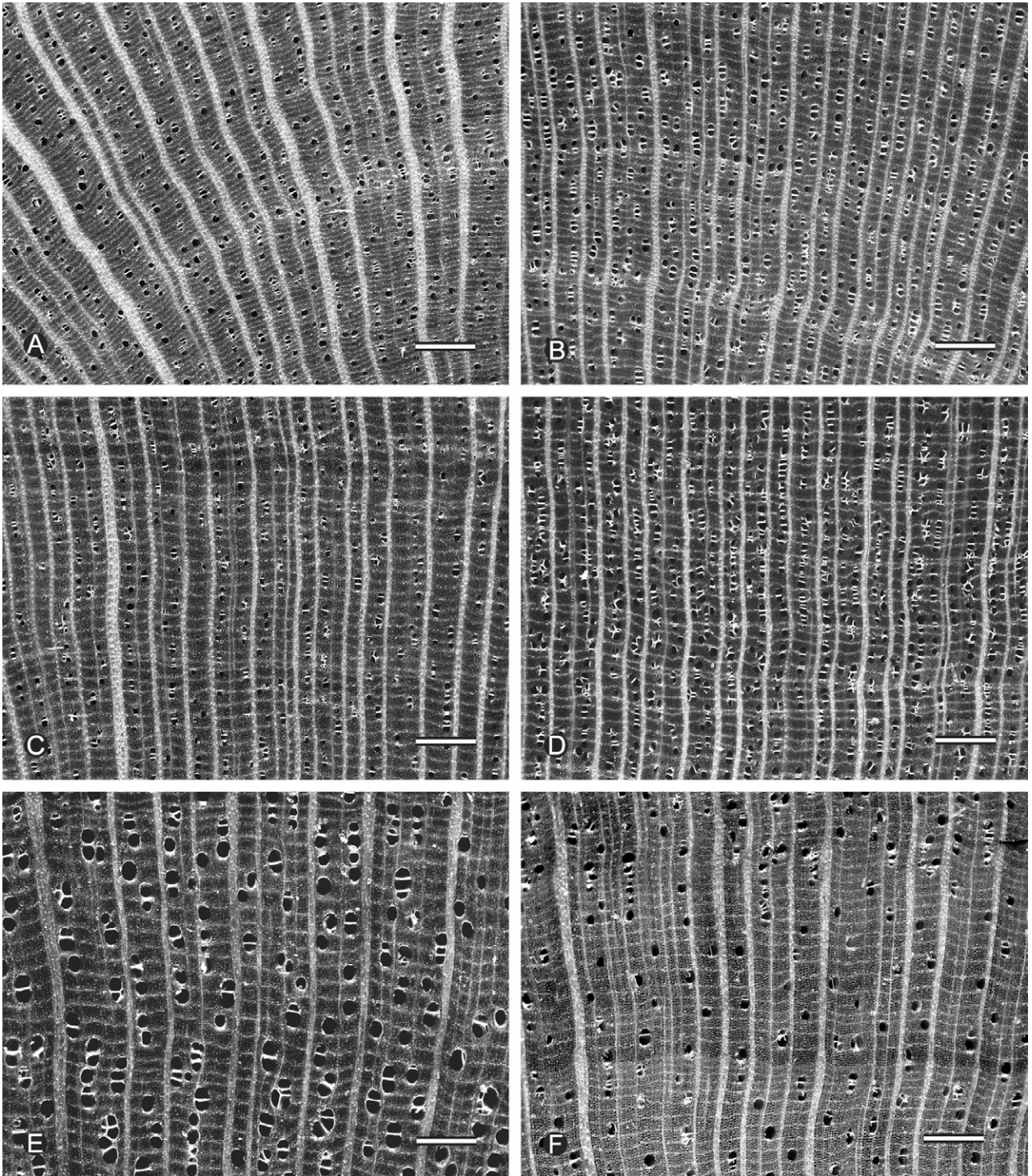
**Figure 7.** A–F, Malmeeae. A, *Oxandra asbeckii* (Pulle) R.E.Fr., Uw 271; B, *Oxandra asbeckii*, Uw 1916; C, *Oxandra riedeliana* R.E.Fr., Uw 7753; D, *Oxandra riedeliana*, Uw 7793; E, *Pseudomalmea boyacana* (J.F.Macbr.) Chatrou, Uw 31380; F, *Pseudomalmea diclina* (R.E.Fr.) Chatrou, Uw 20084.





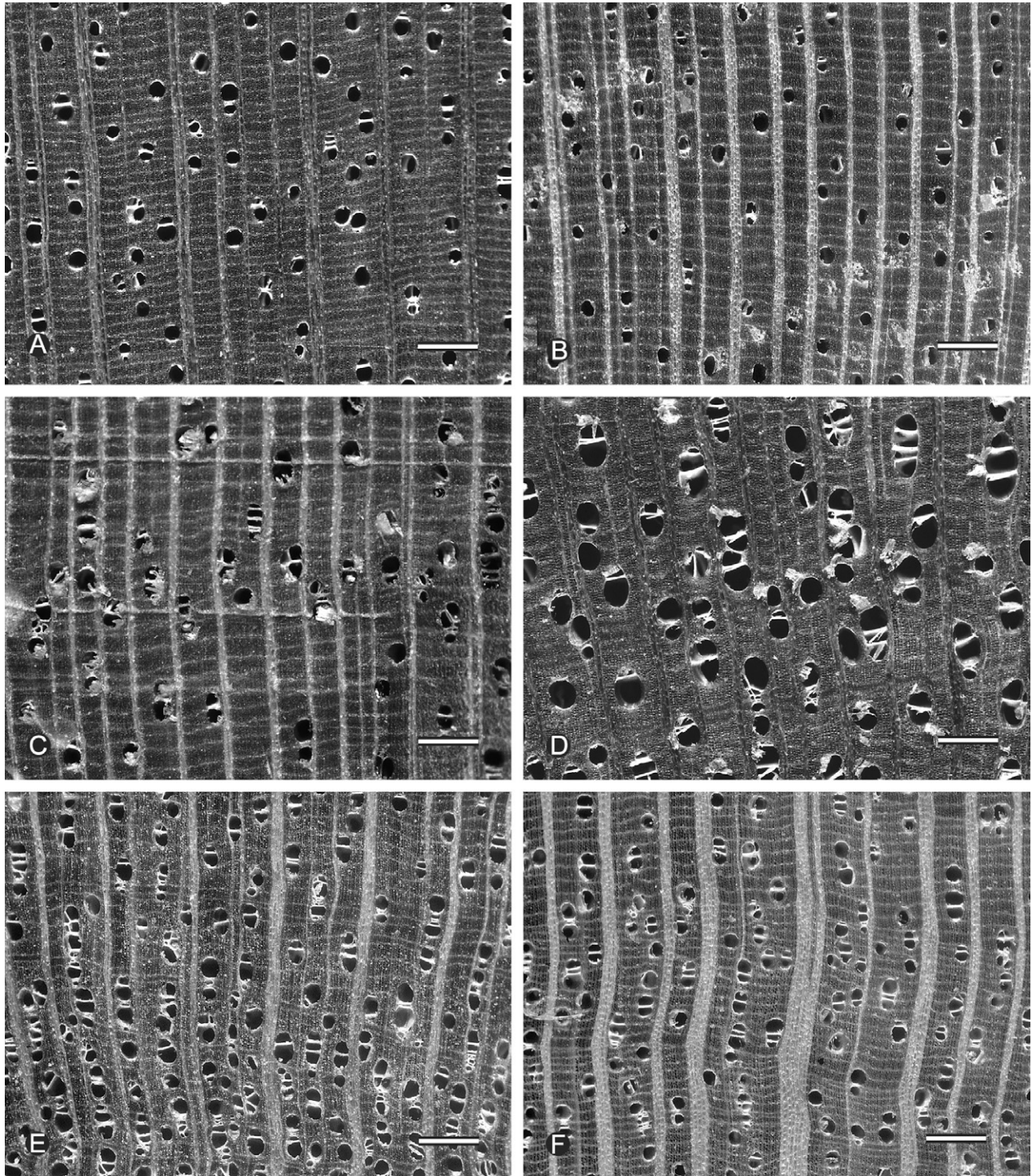
**Figure 8.** A–F, Malmeae. A, *Crematosperma brevipes* (DC.) R.E.Fr., Uw 31466; B, *Crematosperma brevipes*, Uw 33515; C, *Crematosperma cauliflorum* R.E.Fr., Uw 30306; D, *Crematosperma microcarpum* R.E.Fr., Uw 30309; E, *Crematosperma microcarpum*, Uw 34858; F, *Crematosperma oblongum* R.E.Fr., Uw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





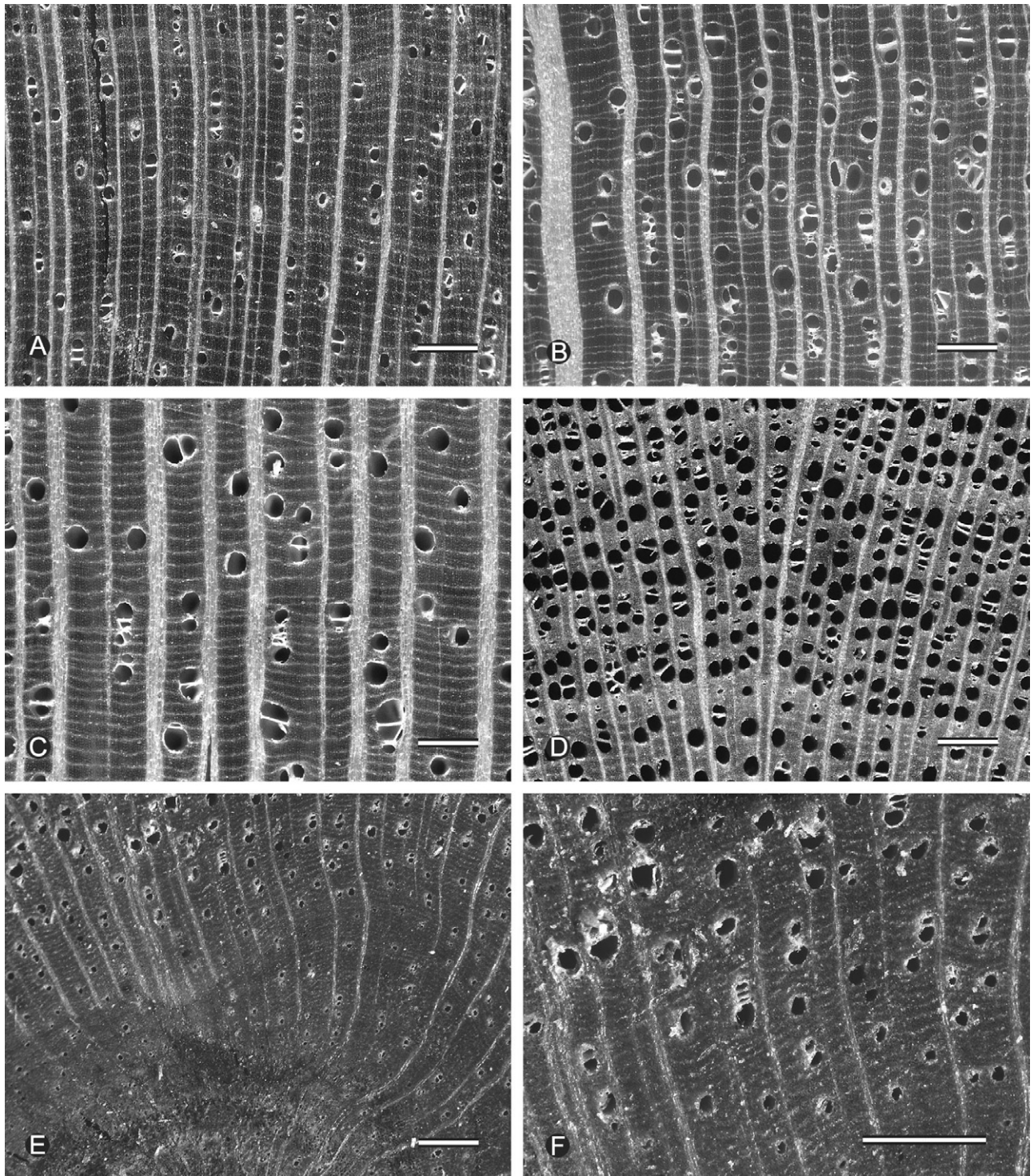
**Figure 9.** A–F, Malmeae. A, *Crematosperma yamayakatense* Pirie, Uw 24523; B, *Malmea dielsiana* R.E.Fr., Uw 30246; C, *Malmea surinamensis* Chatrou, Uw 8543; D, *Malmea surinamensis*, Uw 8629; E, *Pseudoxandra obscurinervis* Maas, Uw 29456; F, *Pseudoxandra polyphleba* (Diels) R.E.Fr., Uw 19657.





**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, Malmeaeae; 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<sup>2</sup> (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 ( $\geq 100$  spp.) genera *Annona*, *Artabotrys* R.Br., *Duguetia*, *Goniothalamus* (Blume) Hook.f. & Thomson, *Gutteria*, *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., *Uvariendron* (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, *Uvariendron* (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.

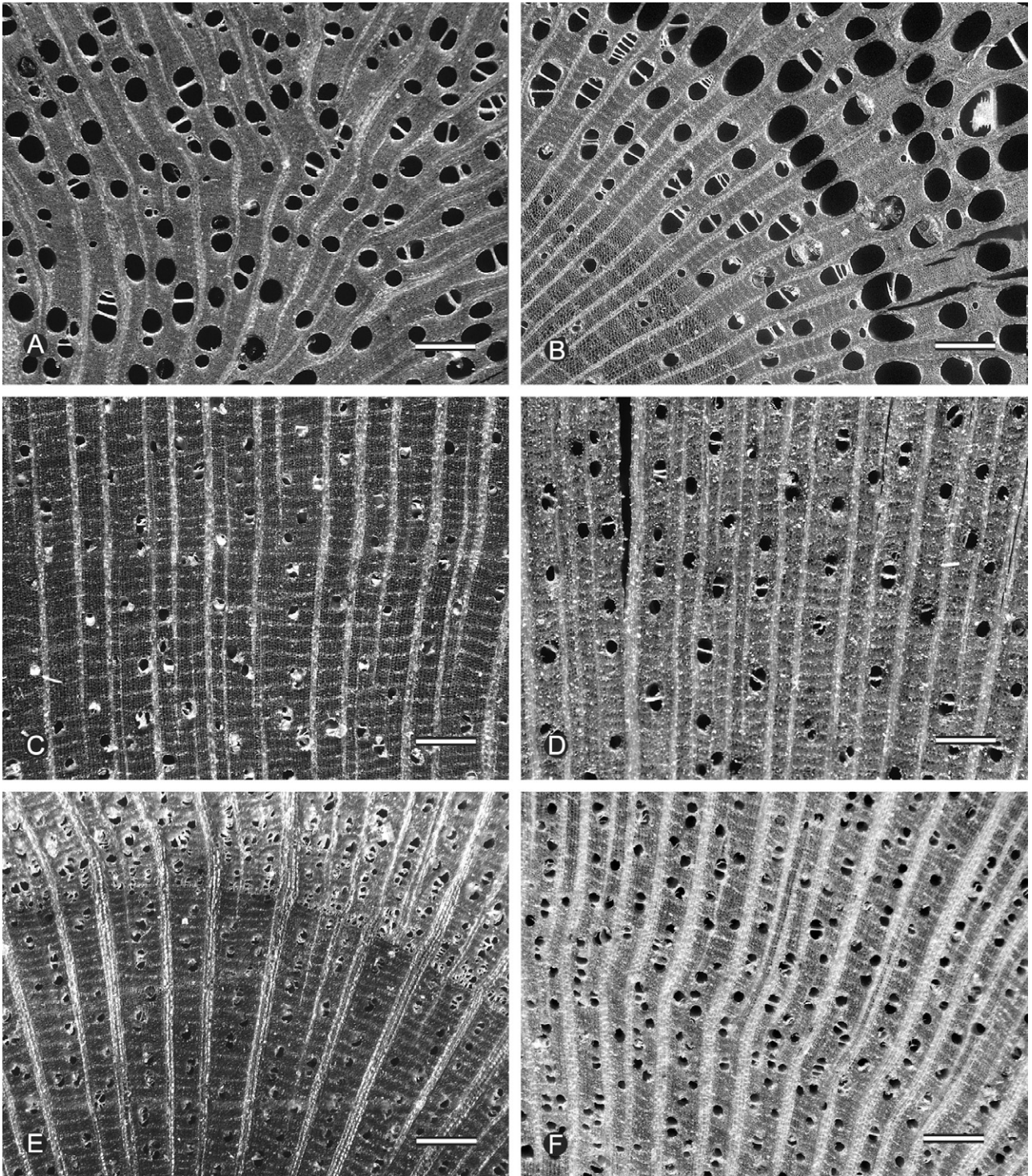
#### Annoneae (Figs 14E–20B)

*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  $\mu$ m) 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*.

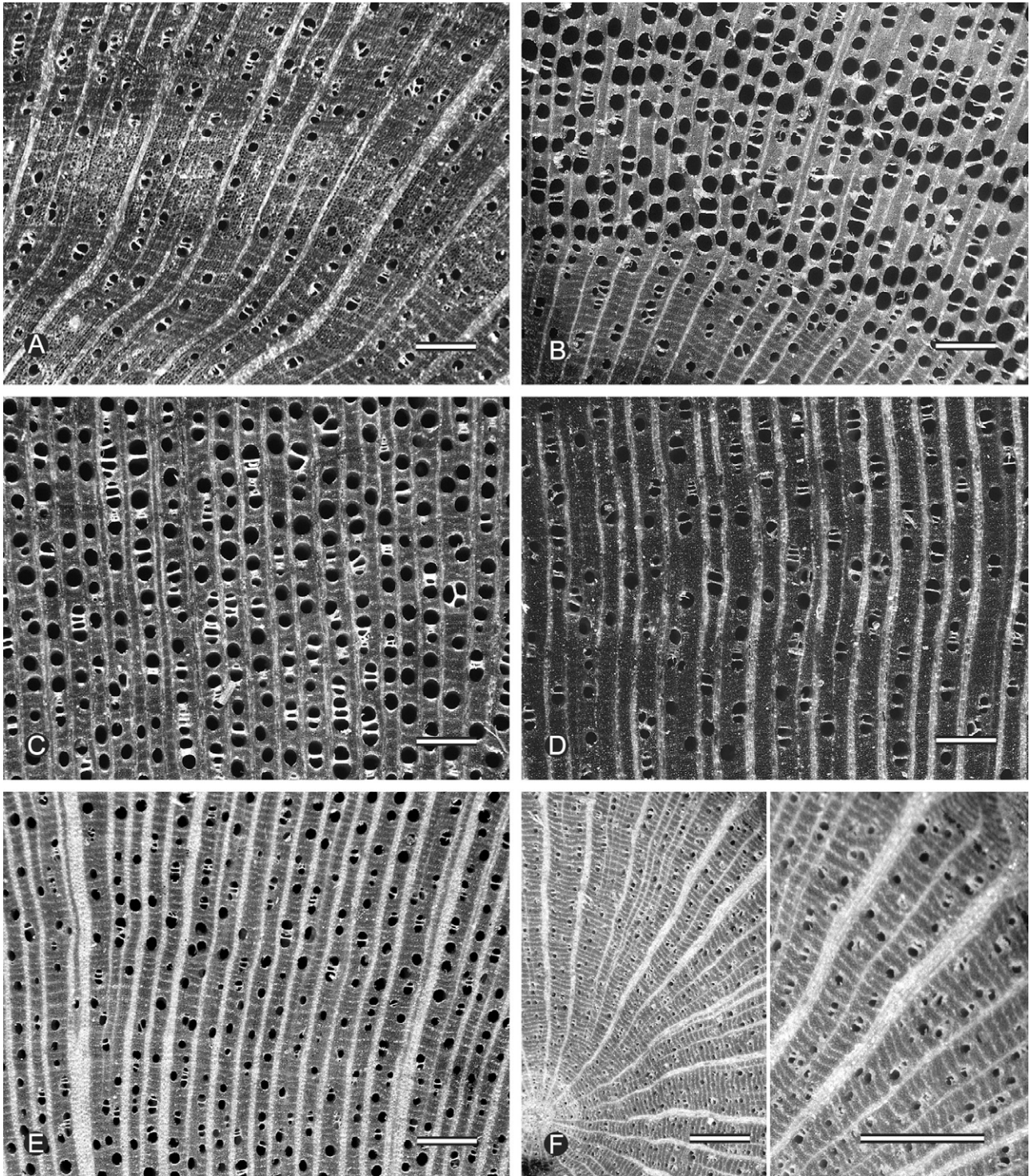
Ter Welle (1995) concluded that it was impossible to distinguish between the closely related genera *Annona*, *Anonidium* and *Rollinia*, then considered a distinct genus. He also did not find any discriminating character, qualitative or quantitative, that would have enabled the recognition of these 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





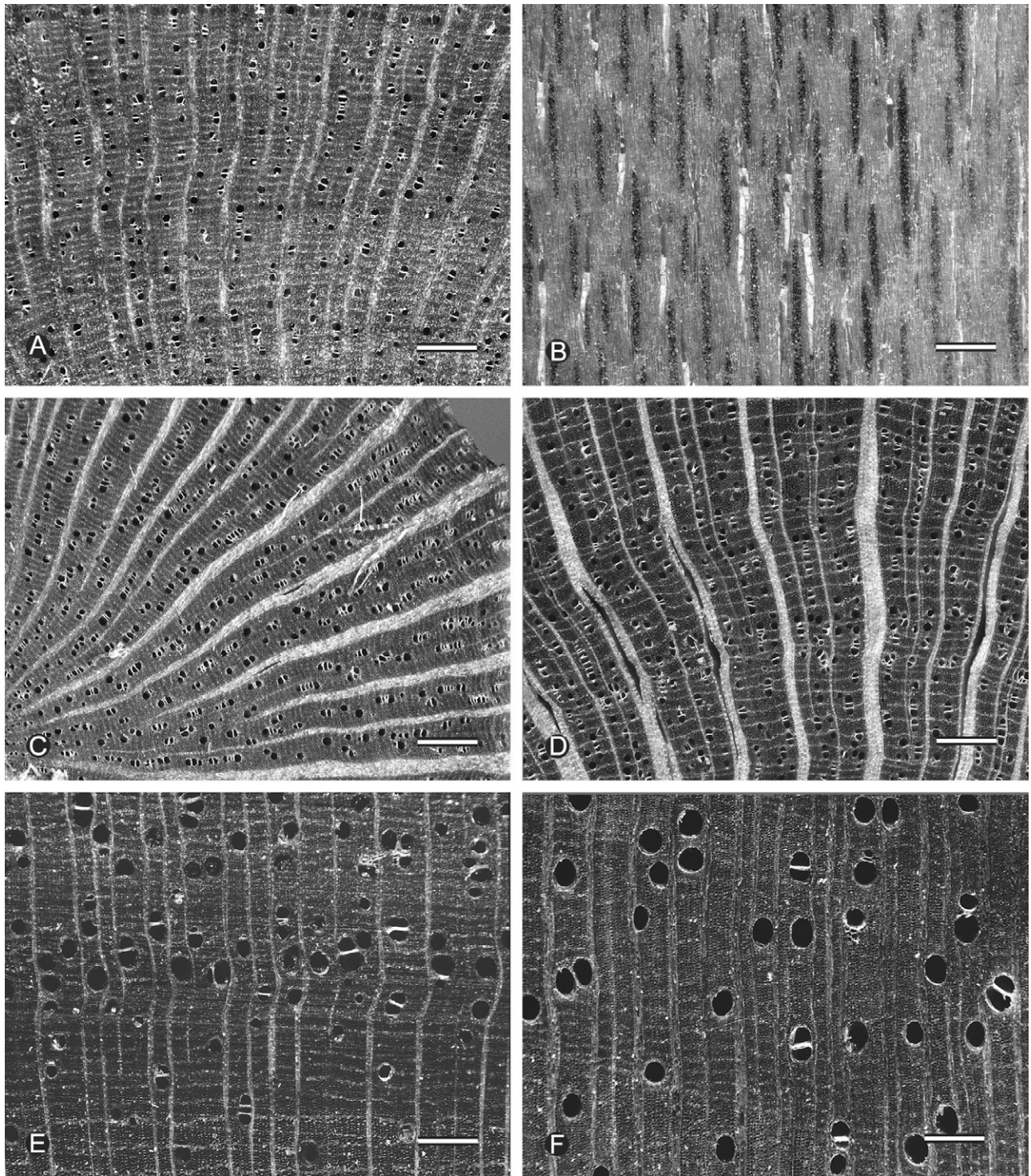
**Figure 12.** A, B, D, Uvarieae; C, E, F, Monodoreae. A, *Friesodielsia enghiana* (Diels) Verdc., Uw 29536; B, *Friesodielsia montana* (Engl. & Diels) Steenis, Uw 29519; C, *Isolona hexaloba* (Pierre) Engl. & Diels, Uw 29497; D, *Monanthotaxis poggei* Engl. & Diels, Uw 29498; E, *Monodora crispata*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





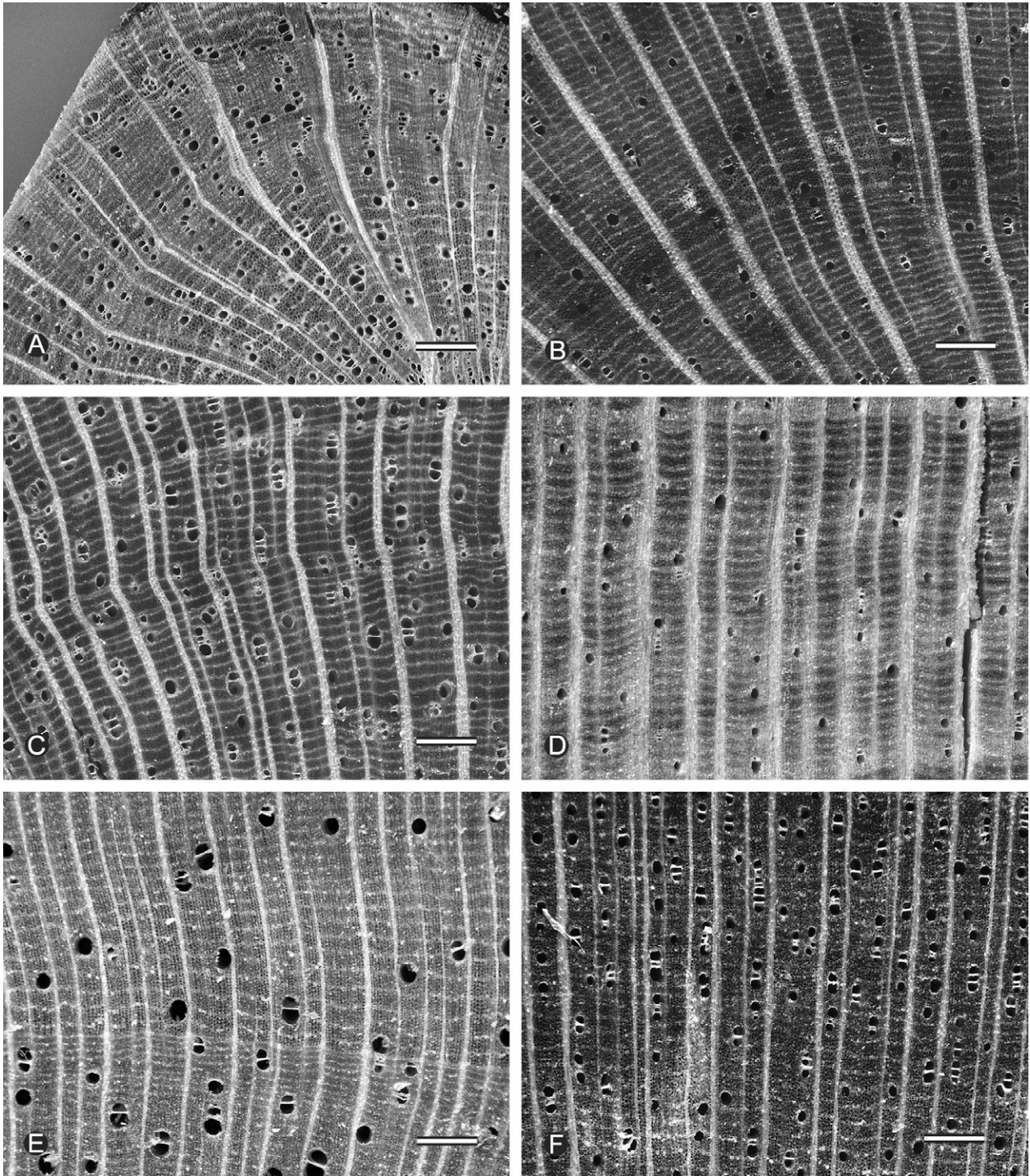
**Figure 13.** A, Monodoreae; B–F, Uvarieae. A, *Monodora undulata* (P.Beauv.) Couvreur, Uw 29379; B, *Toussaintia hallei* Le Thomas, Uw 29546; C, *Uvaria angolensis* Welw. ex Oliv., Uw 22255; D, *Uvaria chamae* P.Beauv., Uw 25872; E, *Uvaria doeringii* Diels, Uw 22121; F, *Uvaria* sp. (two magnifications),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





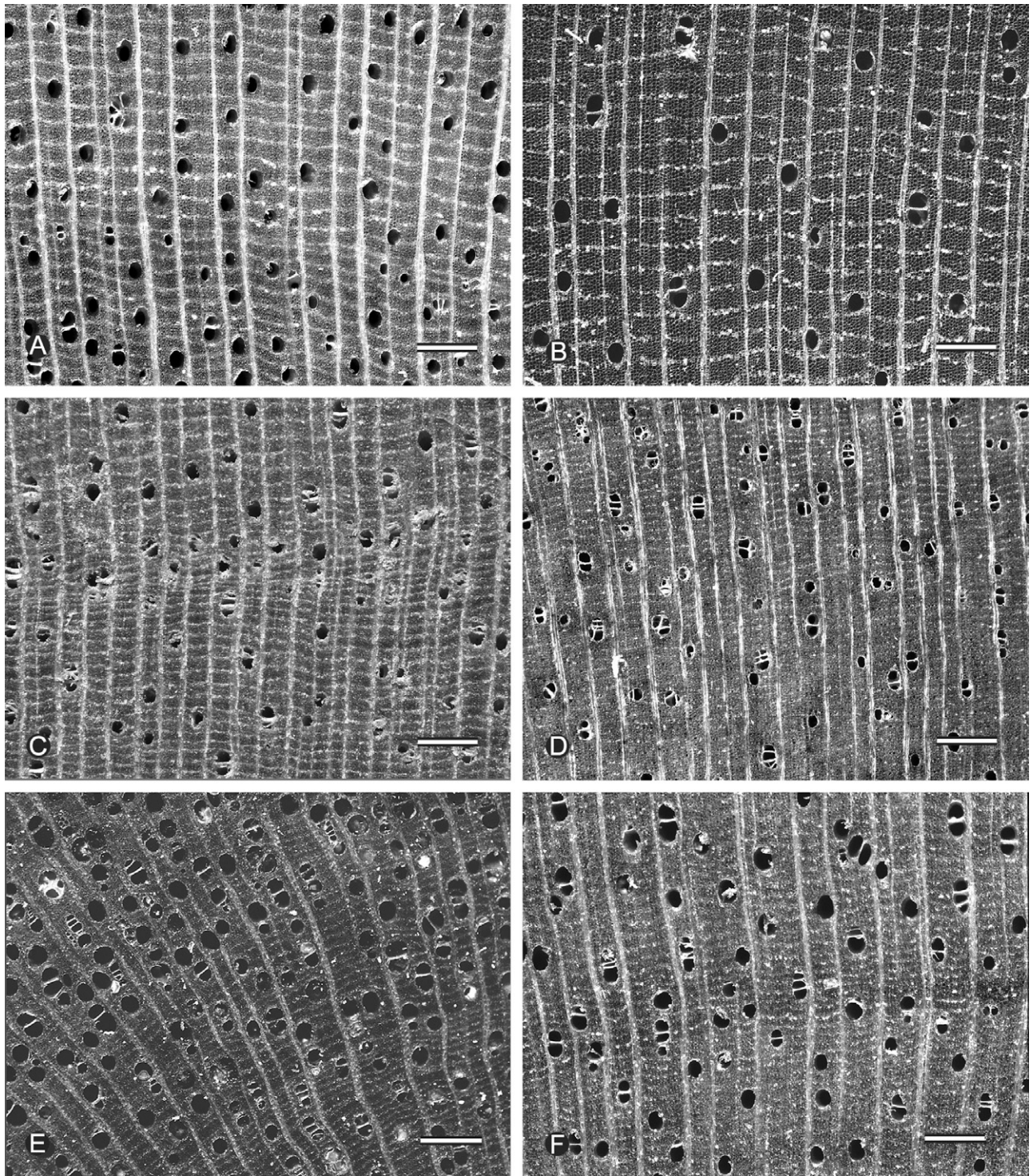
**Figure 14.** A–D, Monodoreae; E, F, Annoneae. A, *Uvari dendron molundense* (Engl. & Diels) R.E.Fr., Uw 29542; B, *Uvari dendron molundense* (tangential section), Uw 29542; C, *Uvariopsis congolana* (De Wild.) R.E.Fr., Uw 29503; D, *Uvariopsis congolana*, Uw 29511; E, *Annonaannonoides* (R.E.Fr.) Maas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





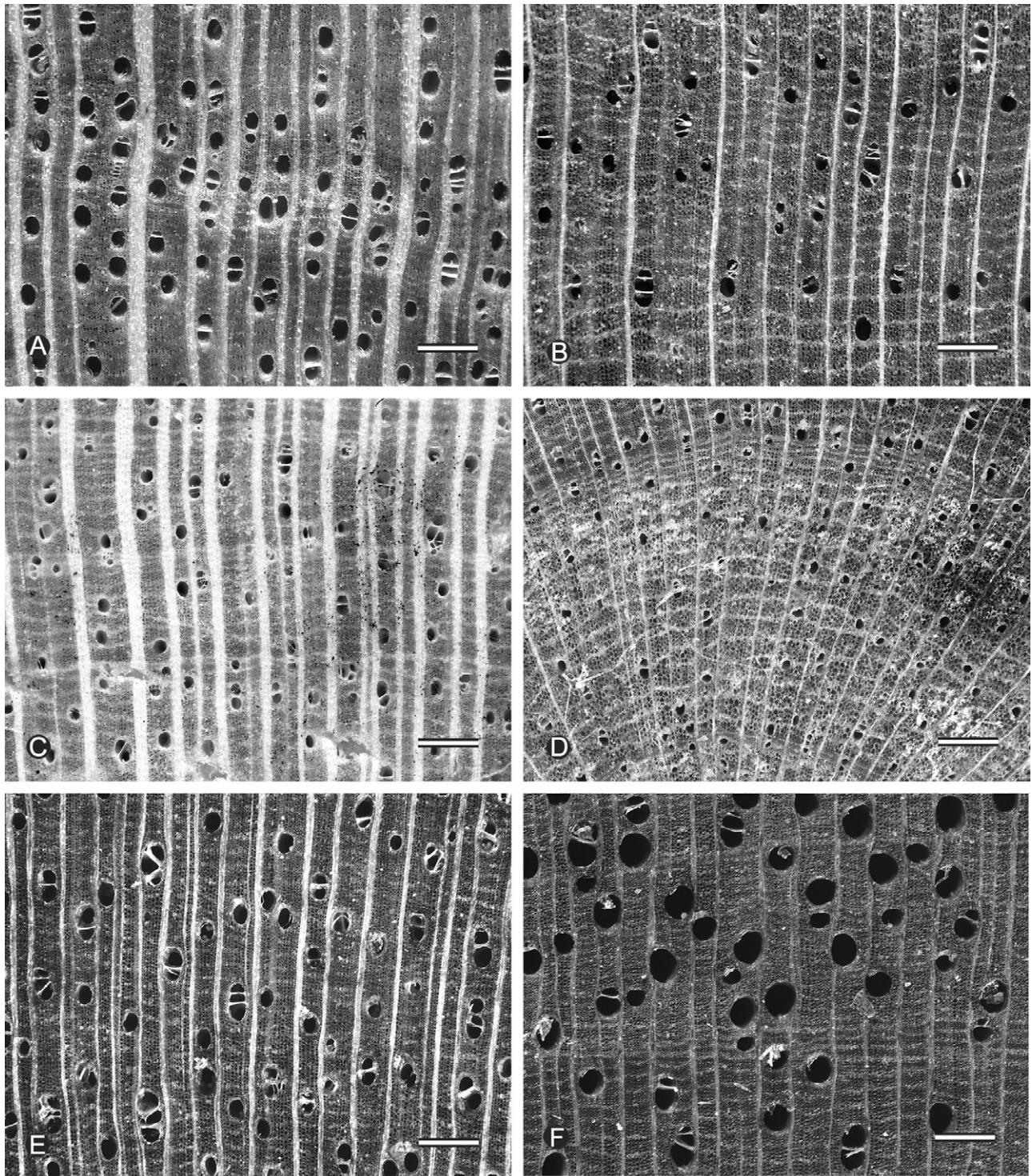
**Figure 15.** A–F, Annonaceae. A, *Annona cherimolioides* Triana & Planch., Uw s.n.; B, *Annona* cf. *cuspidata* (Mart.) H. Rainer, Uw 4050; C, *Annona* cf. *densicoma* Mart., Uw 4012; D, *Annona dolichophylla* R.E.Fr., Uw 30303; E, *Annona edulis* (Triana & Planch.) H.Rainer, Uw 30324; F, *Annona emarginata*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





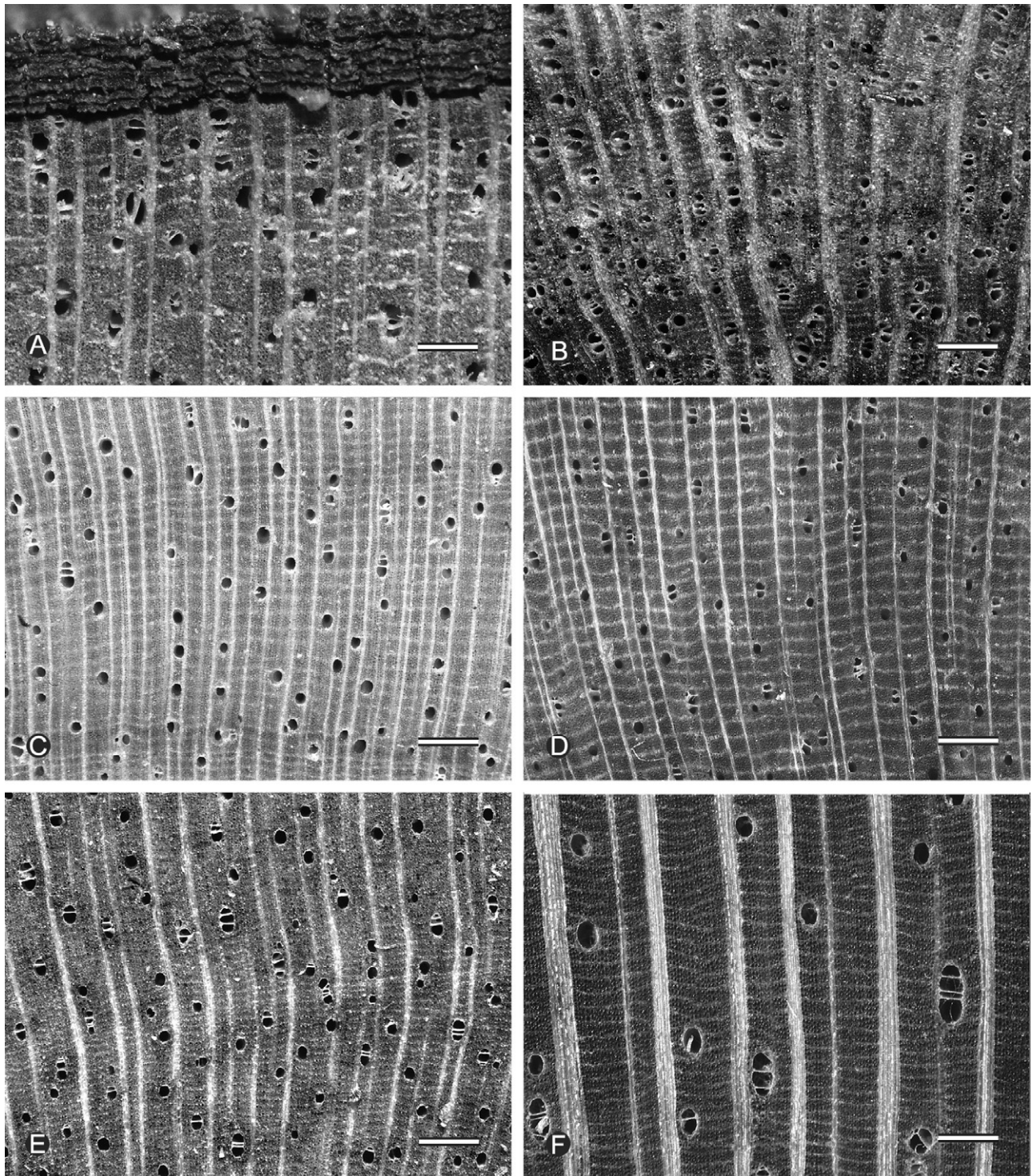
**Figure 16.** A–F, Annoneae. A, *Annona emarginata* (Schtdl.) H.Rainer, Uw 13209; B, *Annona exsucca* DC., Uw 770; C, *Annona fendleri* (R.E.Fr.) H.Rainer, Uw 35096; D, *Annona glabra* L., Uw 4492; E, *Annona haematantha* Miq., Uw 2572; F, *Annona jucunda* (Diels) H.Rainer, Uw 30279.





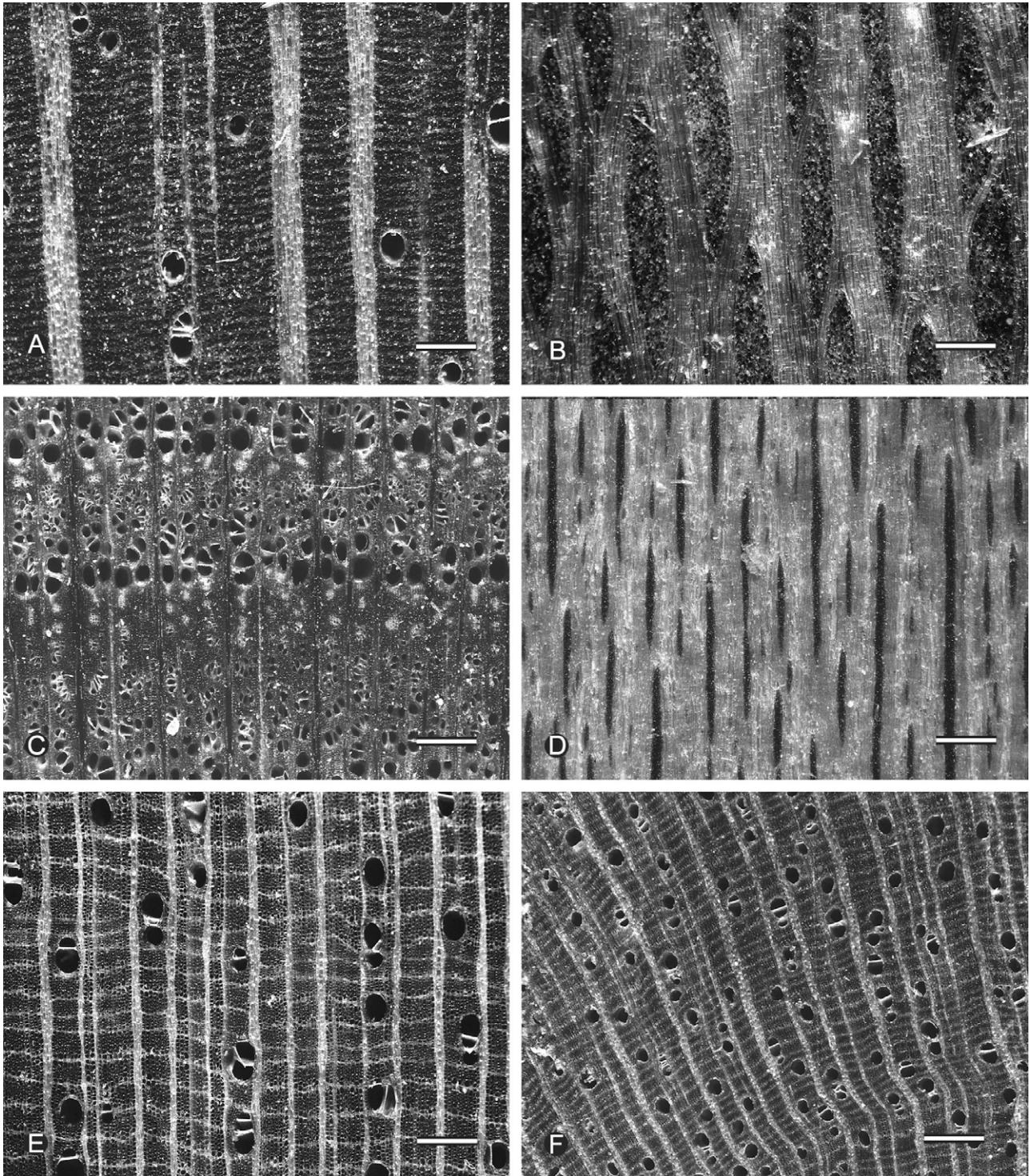
**Figure 17.** A–F, Annoneae. A, *Annona montana* Macfad., Uw 1465; B, *Annona mucosa* Jacq., Uw 30239; C, *Annona muricata* L., Unw 546; D, *Annona neosericea* H.Rainer, Uw 12501; E, *Annona neoulei* H.Rainer, Uw 30235; F, *Annona neovelutina* H.Rainer, Uw 29435.





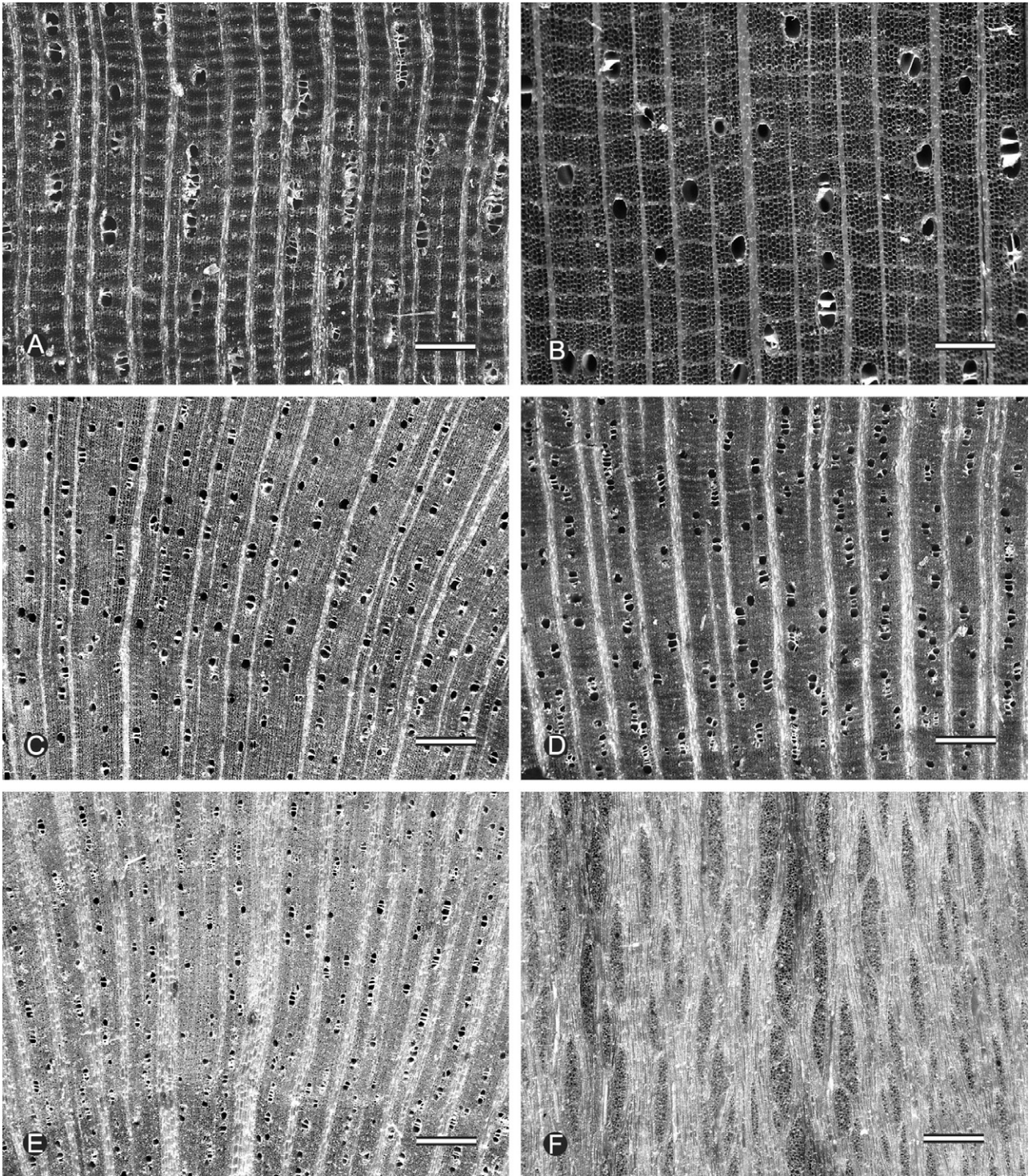
**Figure 18.** A–F, Annoneae. A, *Annona quinduensis* Kunth, Uw 37079; B, *Annona senegalensis* Persoon, Uw 15581; C, *Annona sericea* Dunal, Uw 32438; D, *Annona sylvatica* A.St.-Hil., Uw 14352; E, *Annona* cf. *williamsii* (Rusby ex R.E.Fr.) H.Rainer, Uw 30255; F, *Anonidium mannii* (Oliv.) Engl. &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





**Figure 19.** A–F, Annonaceae. 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. neo-sericea* 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 ( $\leq 100 \mu\text{m}$ ), 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.

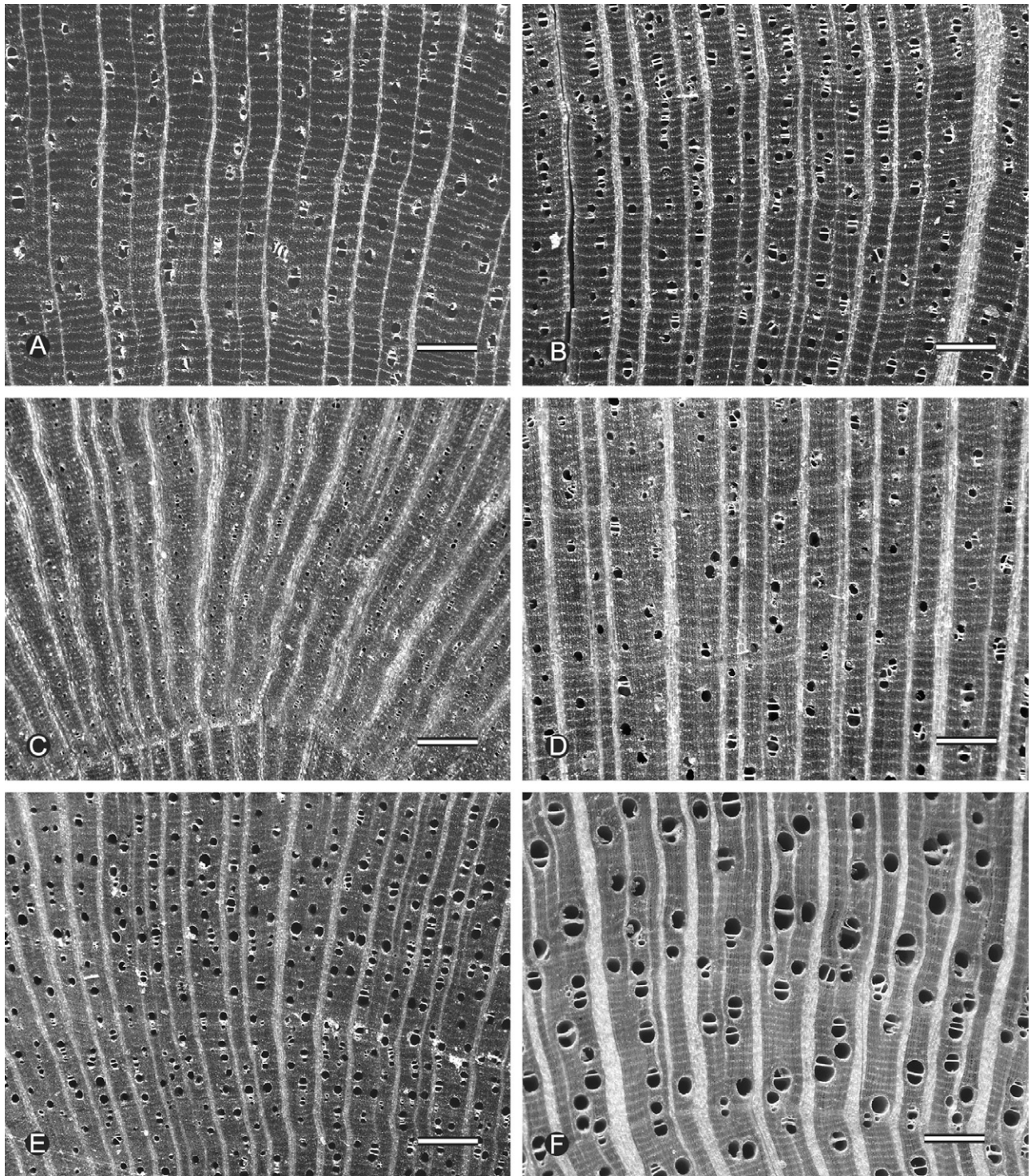
#### *Xylopieae* (Figs 27A, B, 27D–31F)

*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.

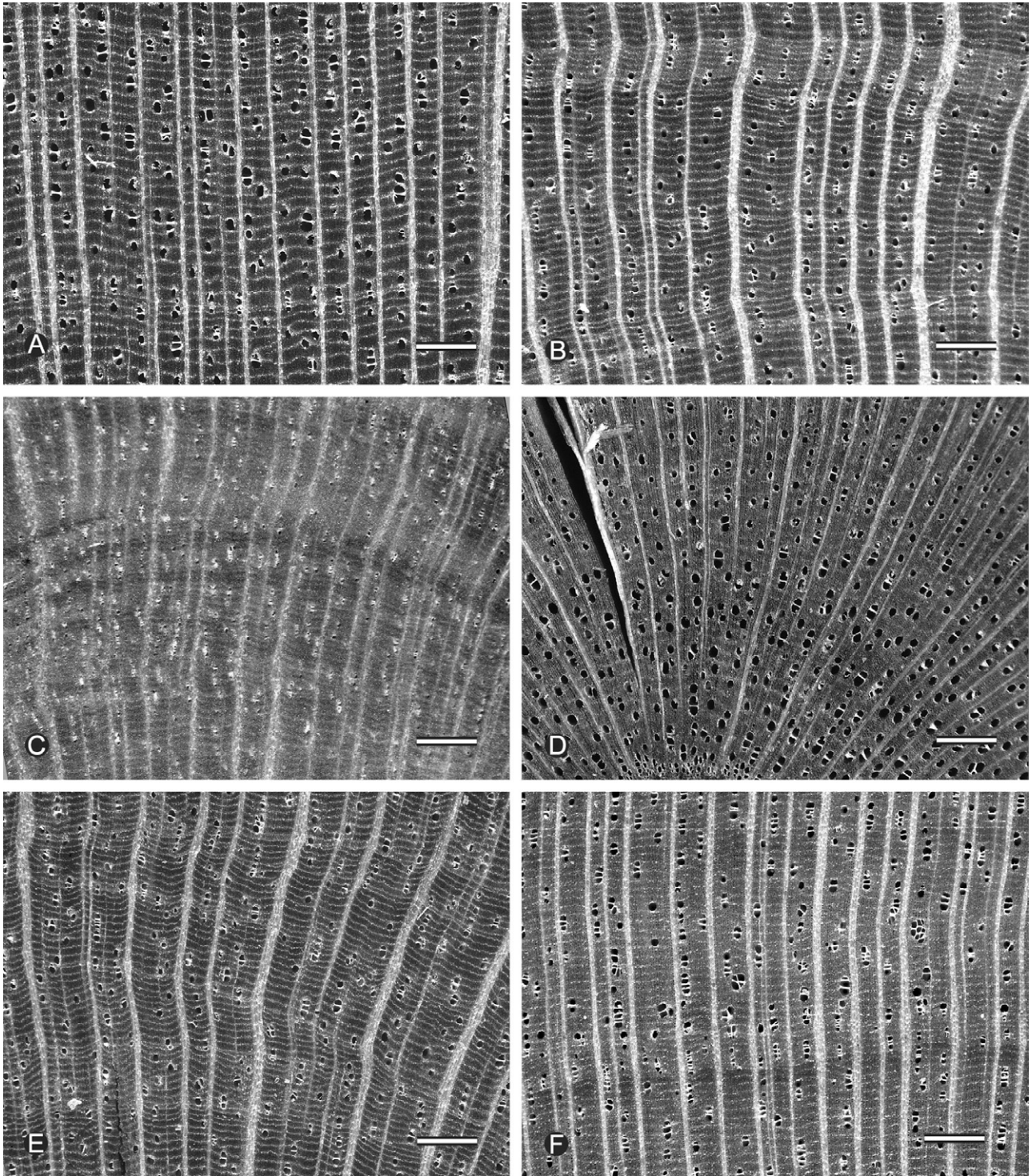
In *Xylopia*, there are, in general terms, two extremes. That most often seen shows large vessels, sometimes touching the rays on both sides, and widely spaced parenchyma bands, e.g. *X. aromatica* (Lam.) Mart. (Fig. 28A, B), *X. cayennensis* Maas (Fig. 28E), *X. nitida* Dunal (Fig. 30A), *X. papuana* 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.





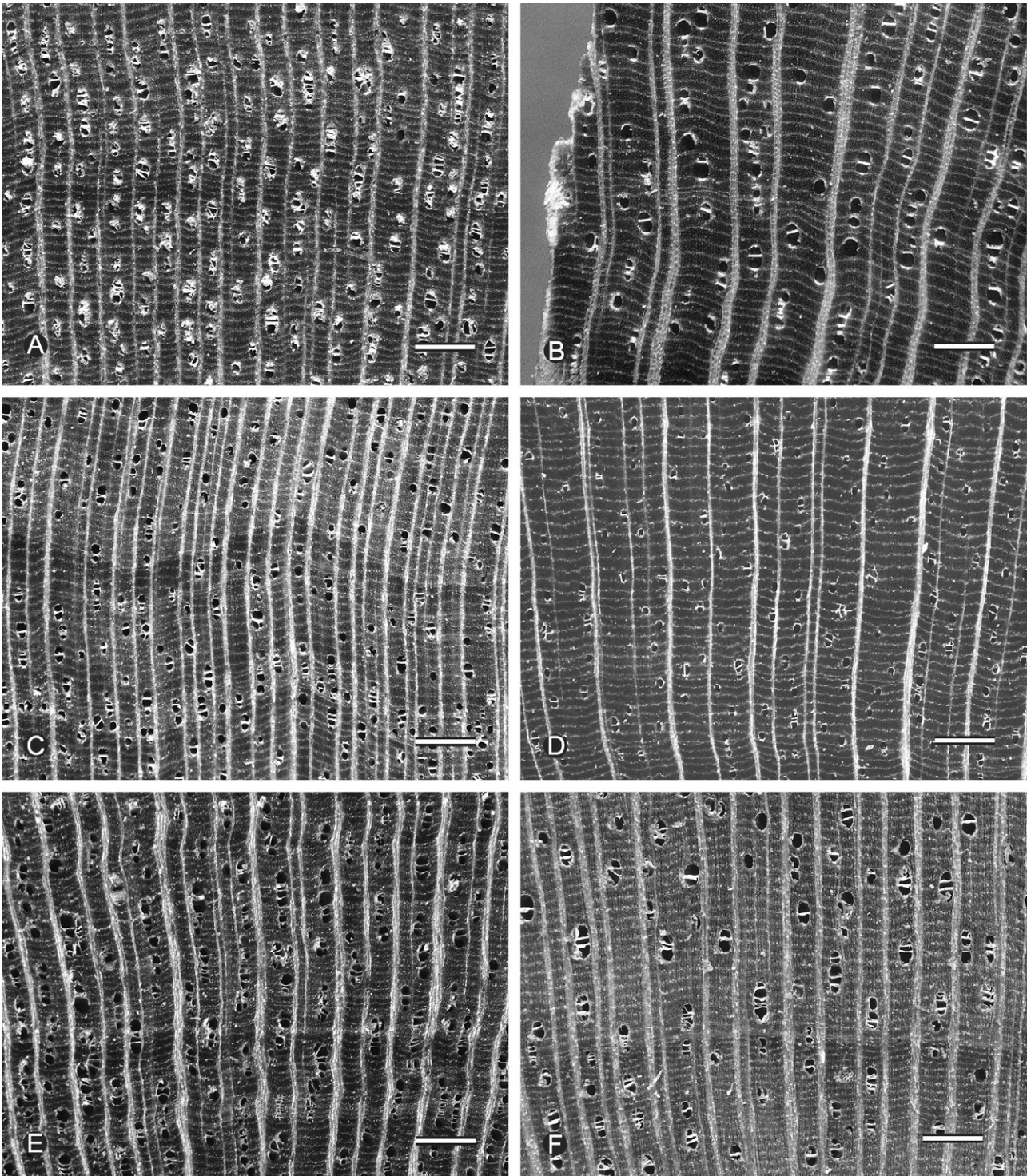
**Figure 21.** A–F, Duguetieae. A, *Duguetia calycina* Benoist, Uw 761; B, *Duguetia calycina*, Uw 15331; C, *Duguetia cauliflora* R.E.Fr., Uw 3951; D, *Duguetia* cf. *cauliflora*, Uw 4706; E, *Duguetia chrysea* Maas, Uw 36236; F, *Duguetia confinis* (Engl. & Diels) Chatrou, Uw 35931.





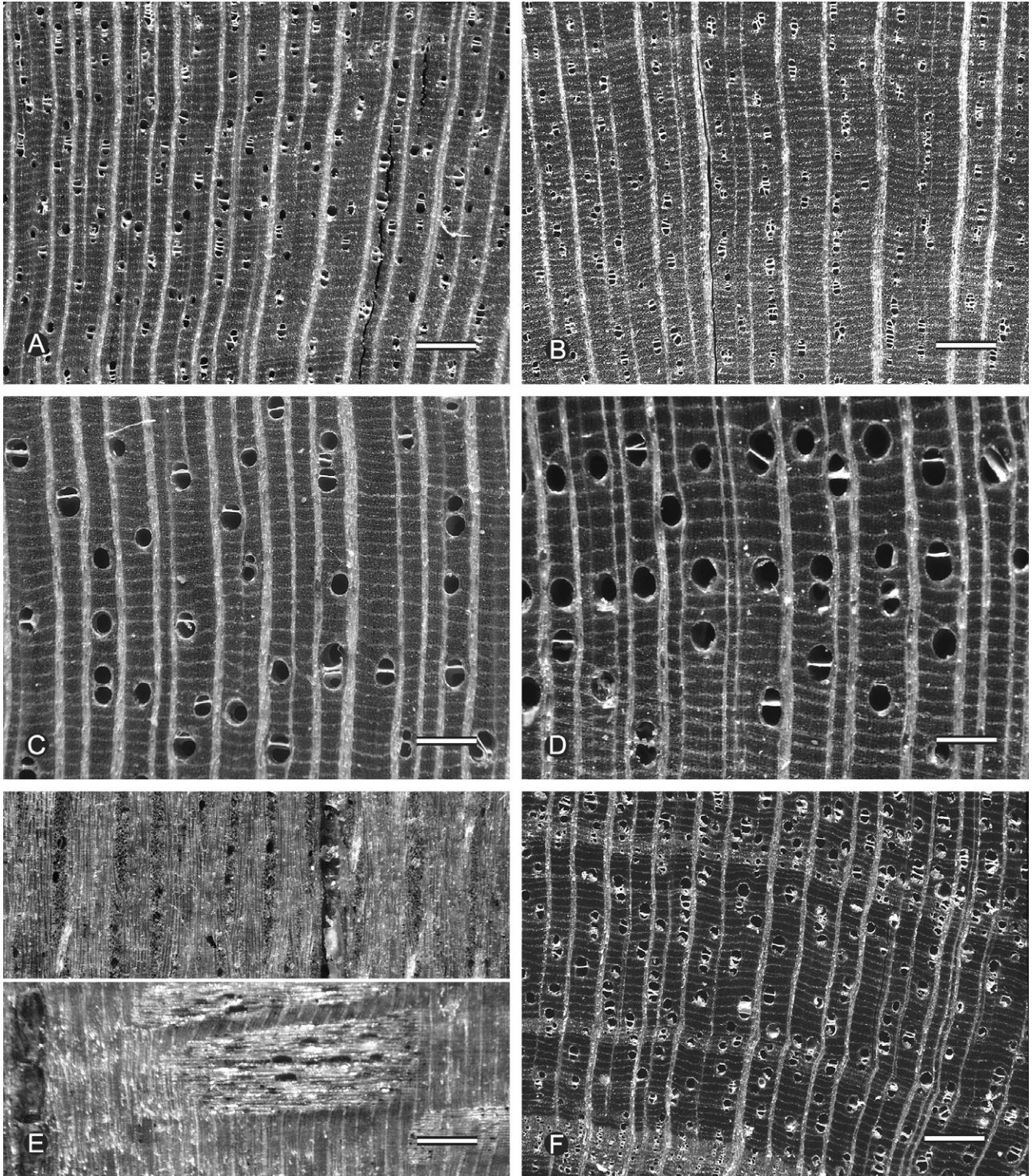
**Figure 22.** A–F, Duguetieae. A, *Duguetia echinophora* R.E.Fr., Uw 19482; B, *Duguetia eximia* Diels, Uw 29917; C, *Duguetia flagellaris* Huber, Uw 36736; D, *Duguetia furfuracea* (A.St.-Hil.) Saff., Uw 29402; E, *Duguetia granvilleana* Maas, Uw 29888; F, *Duguetia latifolia* R.E.Fr., Uw 7462.





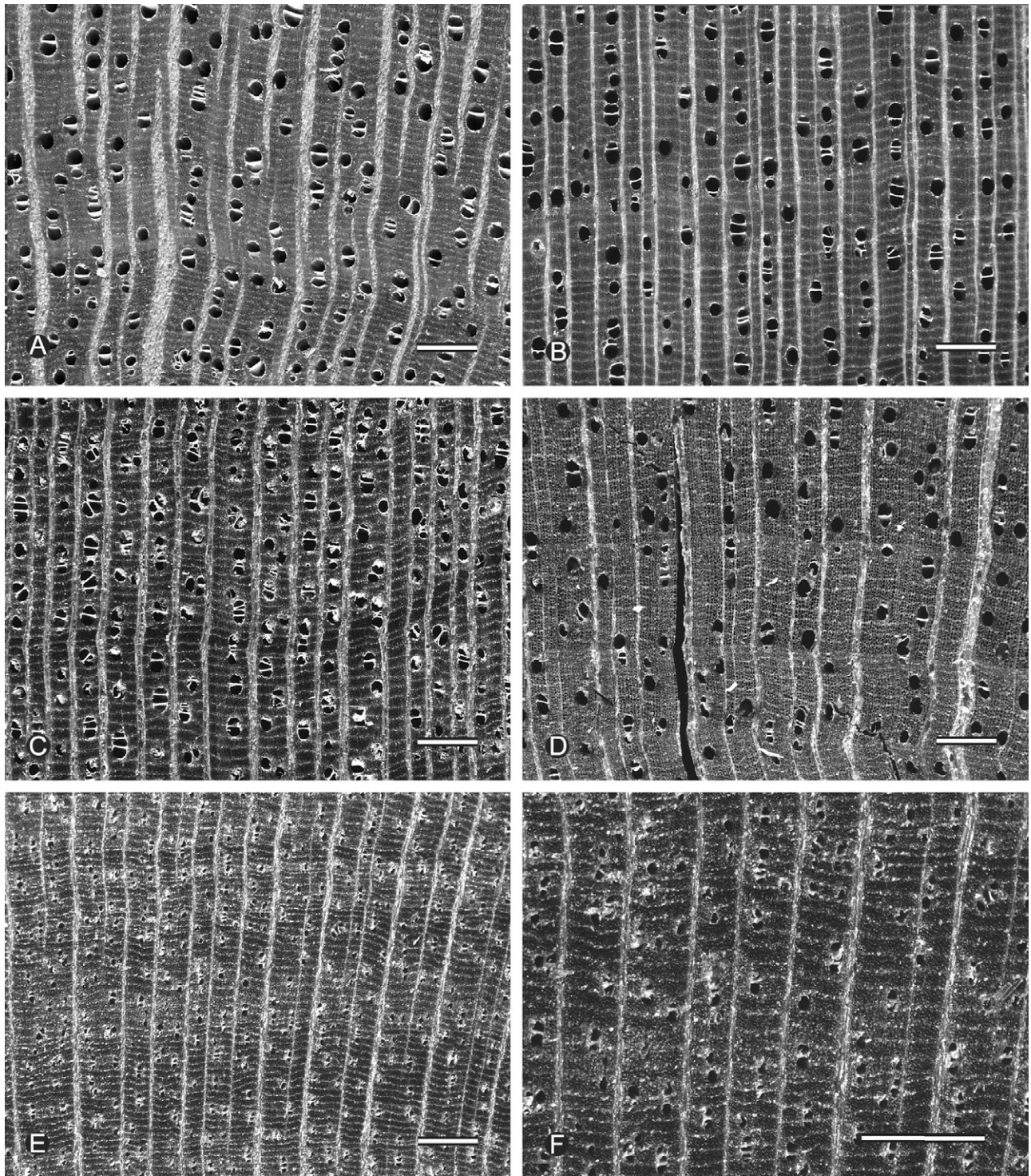
**Figure 23.** A–F, Duguetieae. A, *Duguetia neglecta* Sandw., Uw 26336; B, *Duguetia neglecta*, Uw 27370; C, *Duguetia odorata* (Diels) J.F.Macbr., Uw 19628; D, *Duguetia pauciflora* Rusby, Uw 762; E, *Duguetia pycnastera* Sandwith, Uw 11121; F, *Duguetia pycnastera*, Uw 30266.





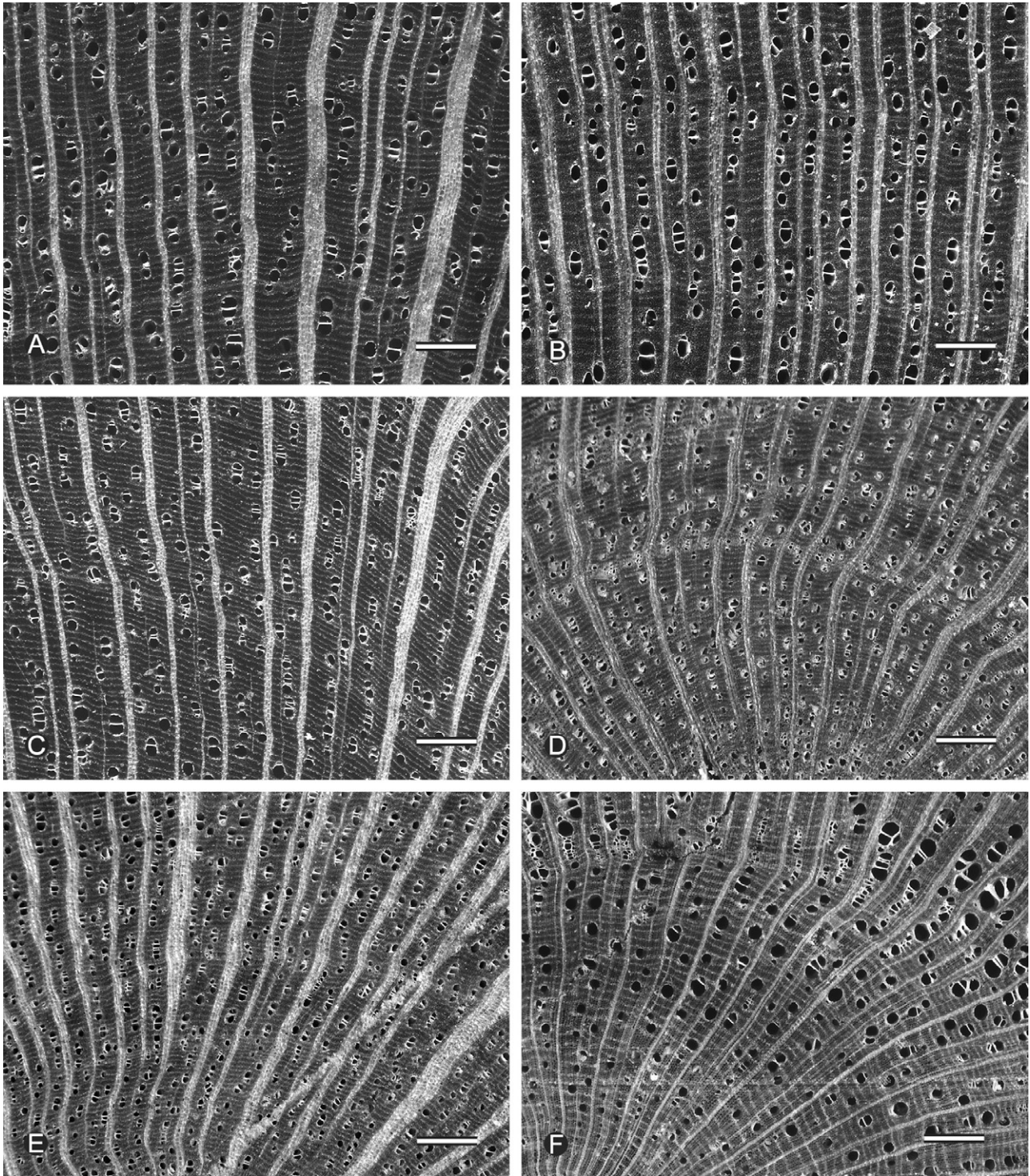
**Figure 24.** A–F, Duguetieae. A, *Duguetia quitarensis* Benth., Uw 30521; B, *Duguetia riparia* Huber, Uw 17969; C, *Duguetia staudtii* (Engl. & Diels) Chatrou, Uw 6562; D, *Duguetia staudtii*, Uw 29374; E, *Duguetia staudtii* (tangential and radial section), Uw 29374; F, *Duguetia stelechantha* (Diels)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





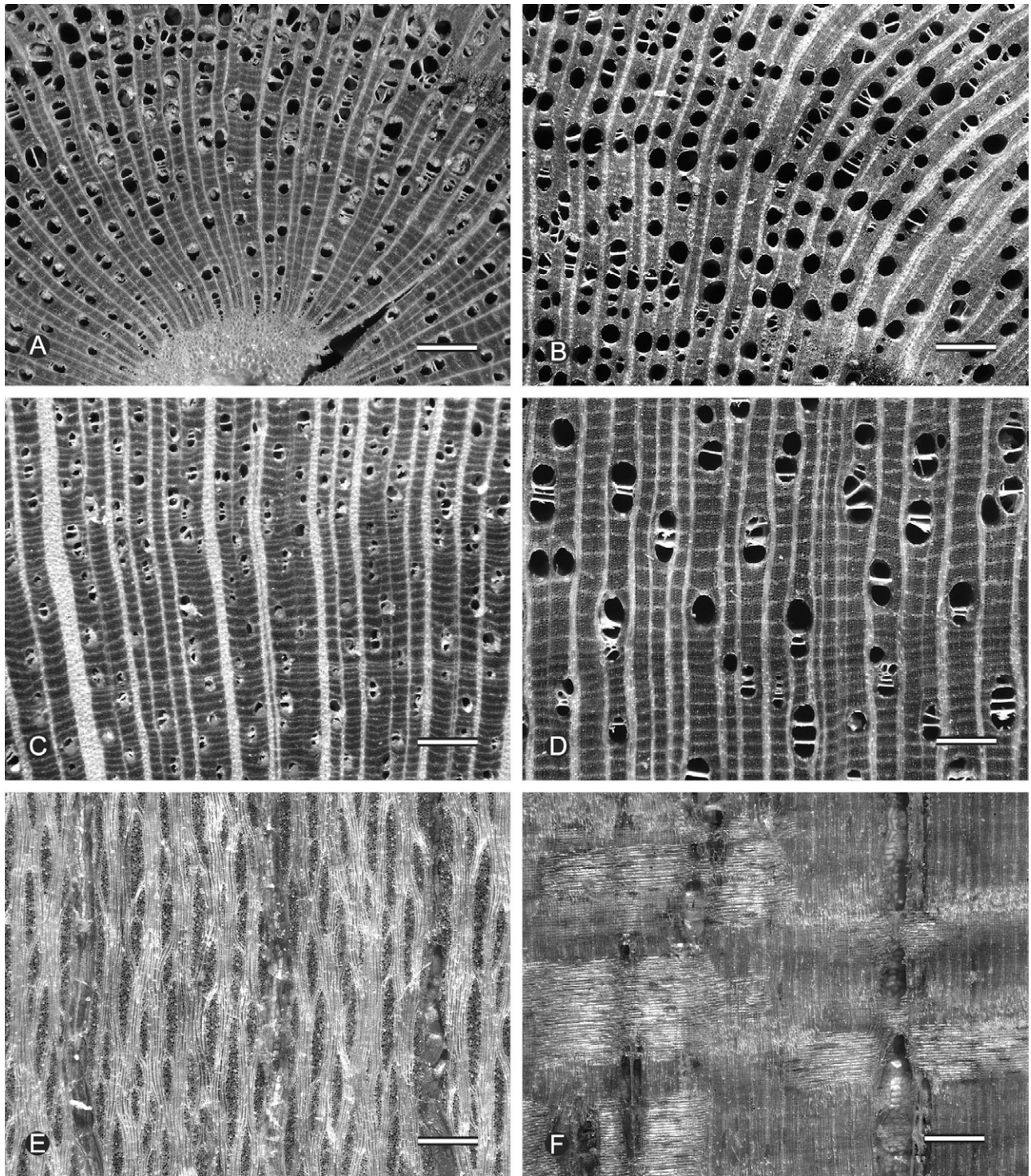
**Figure 25.** A–F, Duguetieae. A, *Duguetia stenantha* R.E.Fr., Uw 30330; B, *Duguetia surinamensis* R.E.Fr., Uw 7601; C, *Duguetia surinamensis*, Uw 15325; D, *Duguetia uniflora* (DC.) Mart., Uw 8276; E, *Duguetia yeshidan* Sandwith, Uw 36493; F, *Duguetia yeshidan*, Uw 36493.





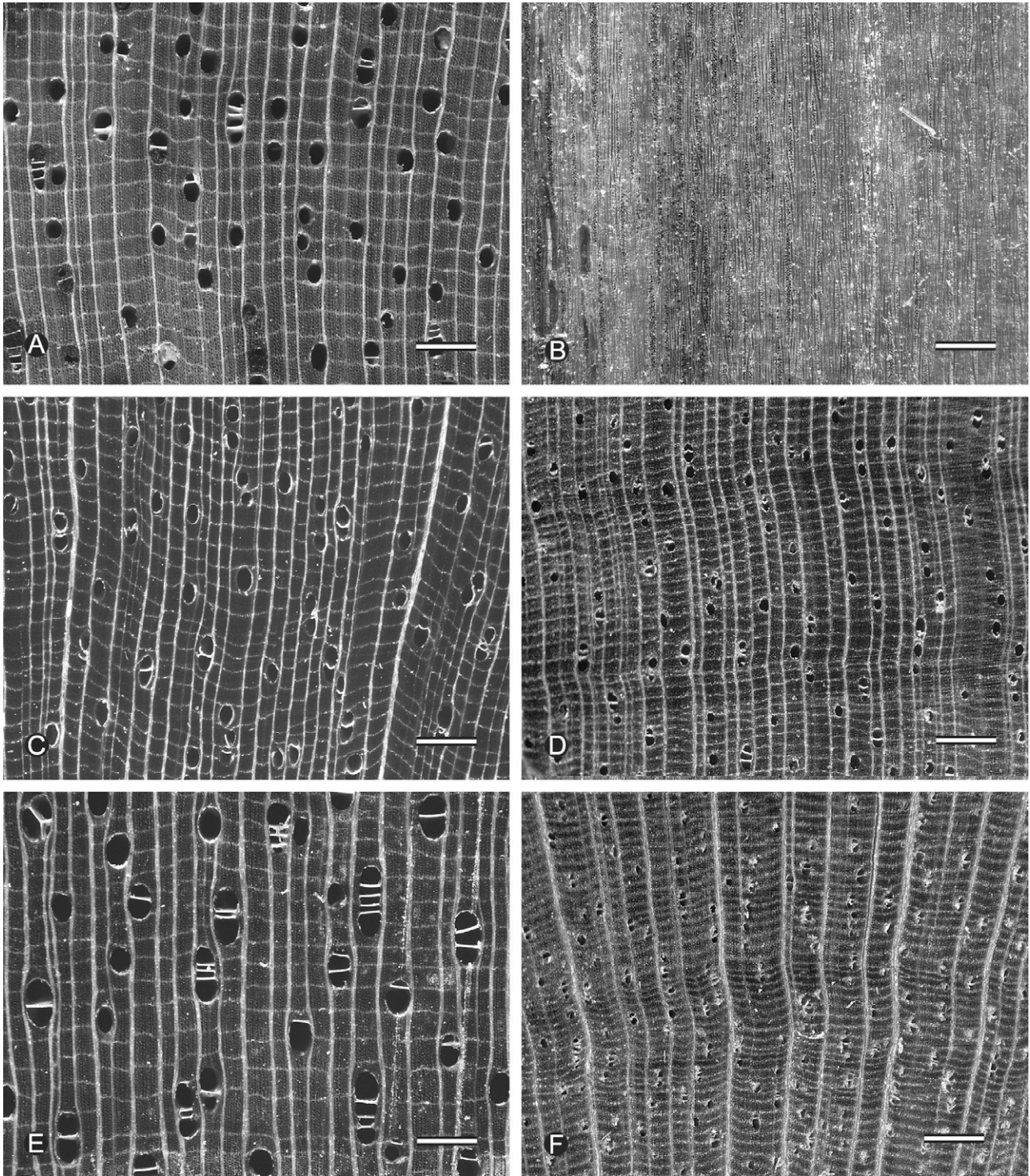
**Figure 26.** A–F, Duguetieae. A, *Fusaea longifolia* (Aubl.) Saff., Uw 4559; B, *Fusaea longifolia*, Uw 16133; C, *Fusaea longifolia*, Uw 30329; D, *Fusaea peruviana* R.E.Fr., Uw 35939; E, *Fusaea peruviana*, Uw 35940; F, *Pseudartabotrys letestui* Pellegr., Uw 35932.





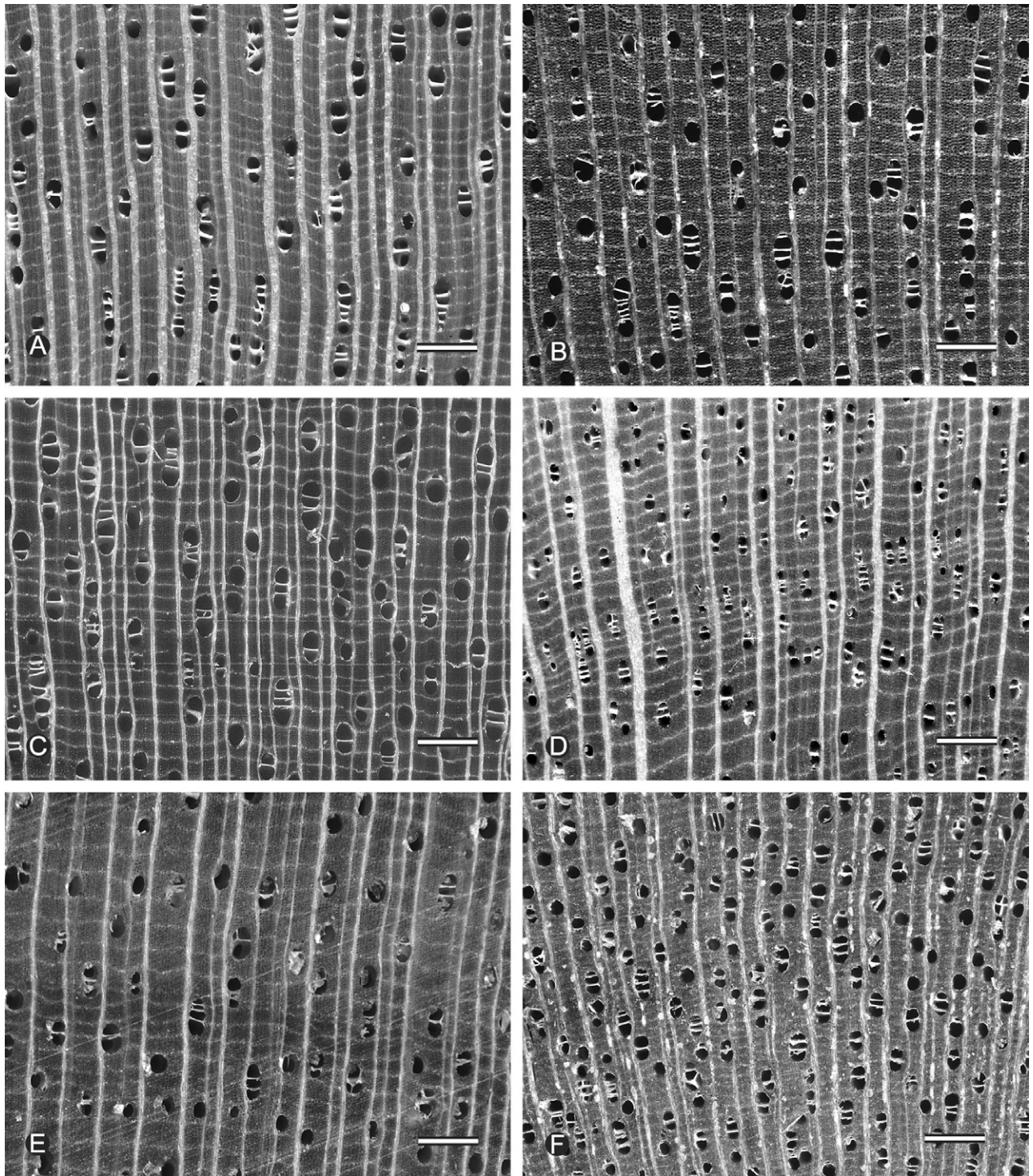
**Figure 27.** A, B, D–F, Xylopieae; C, Piptostigmataeae. A, *Artabotrys insignis* Engl. & Diels, Uw 29509; B, *Artabotrys oliganthus* Engl. & Diels, Uw 22118; C, *Greenwayodendron oliveri* (Engl.) Verdc., Uw 29490; D, *Xylopiya aethiopica* (Dunal) A.Rich., Uw 25875; E, *Xylopiya aethiopica* (tangential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





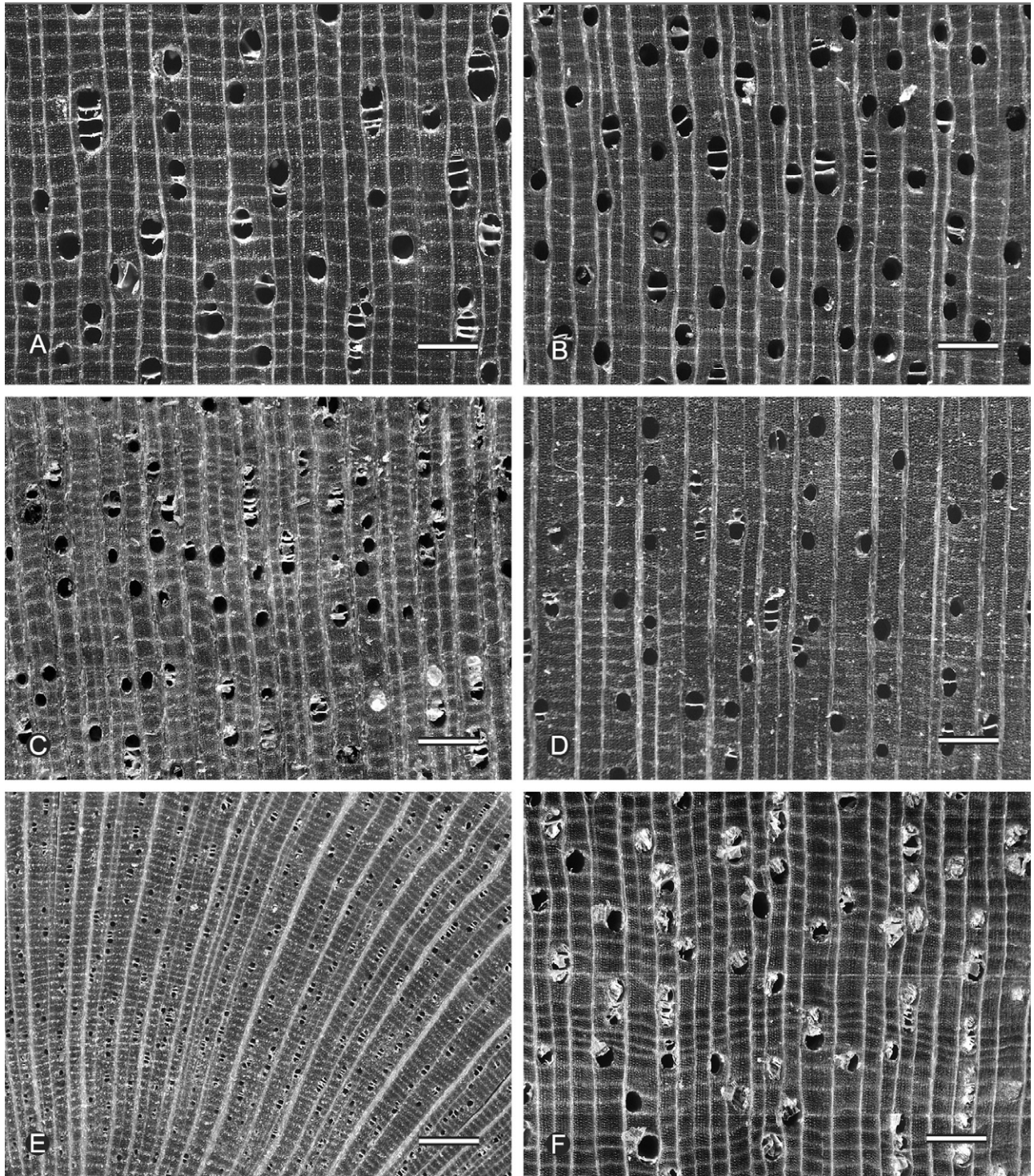
**Figure 28.** A–F, Xylopieae. A, *Xylopia aromatica* (Lam.) Mart., Uw 773; B, *Xylopia aromatica* (tangential section), Uw 7762; C, *Xylopia amazonica* R.E.Fr., Uw 2563; D, *Xylopia benthamii* R.E.Fr., Uw 9071; E, *Xylopia cayennensis* Maas, Uw 5703; F, *Xylopia cuspidata* Diels, Uw 30325.





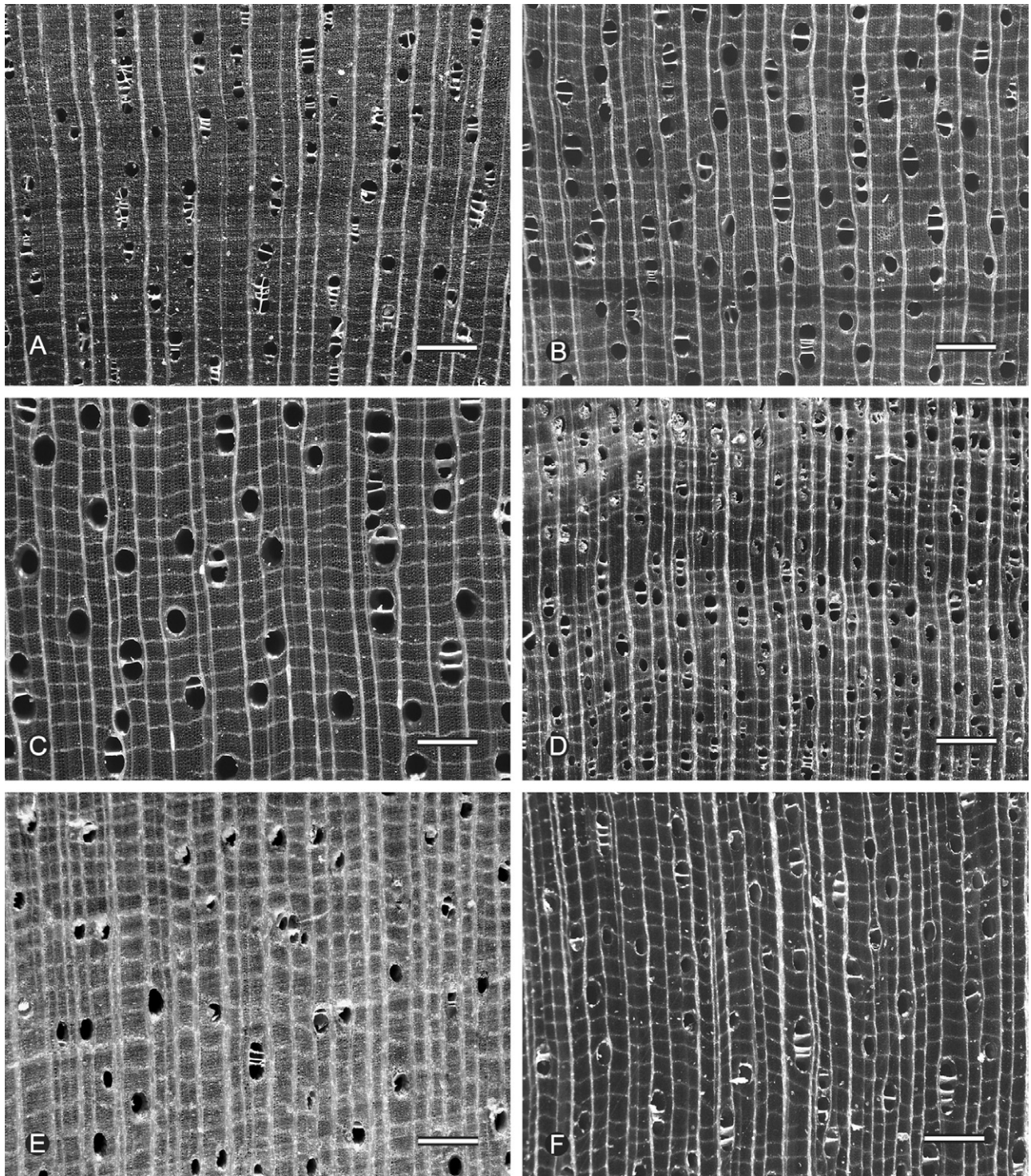
**Figure 29.** A–F. Xylopieae. A. *Xylopiea discreta* (L.f.) Sprague & Hutch., Uw 138a; B. *Xylopiea emarginata* Mart. var. *duckei* R.E.Fr., Uw 17208; C. *Xylopiea frutescens* Aubl., Uw 775; D. *Xylopiea holtzii* Engl., Uw 15600; E. *Xylopiea malayana* Hook.f. & Thomson, Uw 32066; F. *Xylopiea neglecta*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





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





**Figure 31.** A–F, Xylopieae. A, *Xylopiea pulcherrima* Sandwith, Uw 5020; B, *Xylopiea quintasii* Engl. & Diels, Uw 9501; C, *Xylopiea surinamensis* R.E.Fr., Uw 8875; D, *Xylopiea toussaintii* Boutique, Uw 24209; E, *Xylopiea trichostemon* R.E.Fr., Uw 20127; F, *Xylopiea 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) *Xylopi* 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 *Xylopi* 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 *Guatterrella* (Fig. 32E) and *Guatteriosis* (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.

#### *Bocageae* (Figs 36B–37A)

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

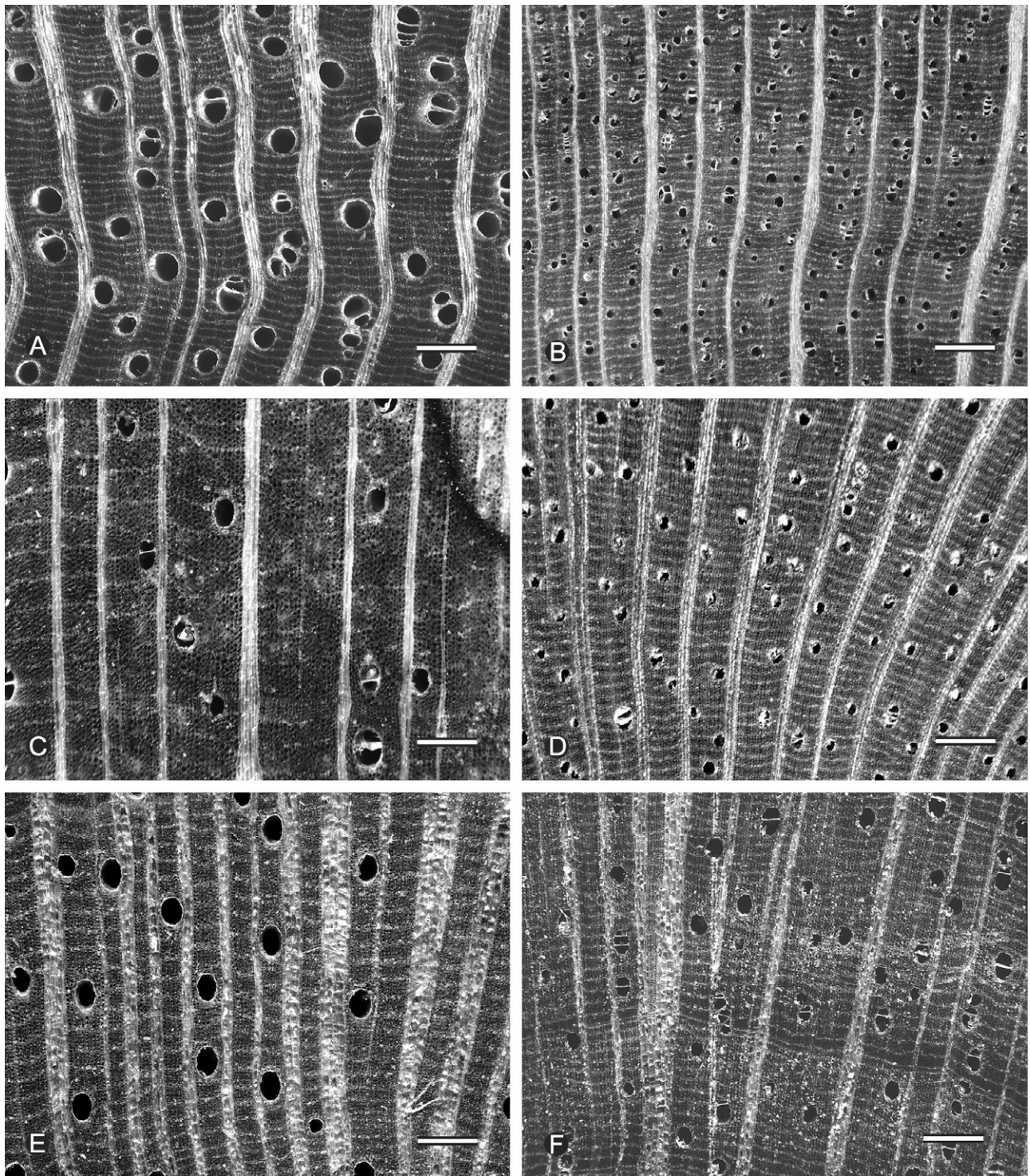
This early diverging clade varies in all features mentioned thus far: vessel number and diameter, ray number and width, and number of parenchyma bands. *Tetrameranthus duckei* R.E.Fr. (Fig. 38C) was studied by Ter Welle (1985). As the most notable features, he mentioned the wide and high (≤ 5000 µm) 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).

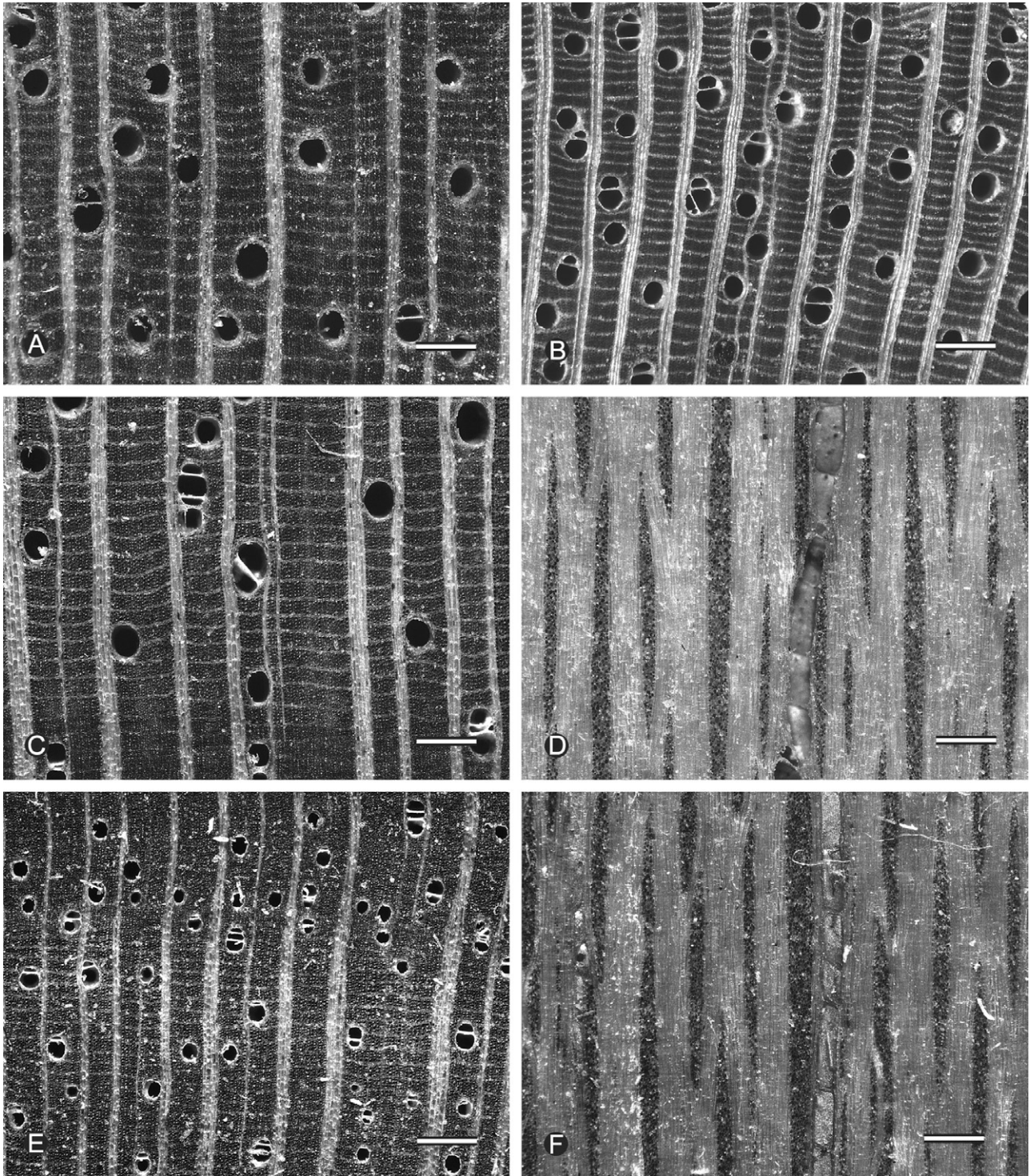
*Anaxagorea* is sister to all other Annonaceae (Richardson *et al.*, 2004; Chatrou *et al.*, 2012). The wood of *Anaxagorea* is rather uniform, characterized by the frequent presence of broad rays rather wide apart, and small vessels often in a radial arrangement, the multiples and groups consisting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





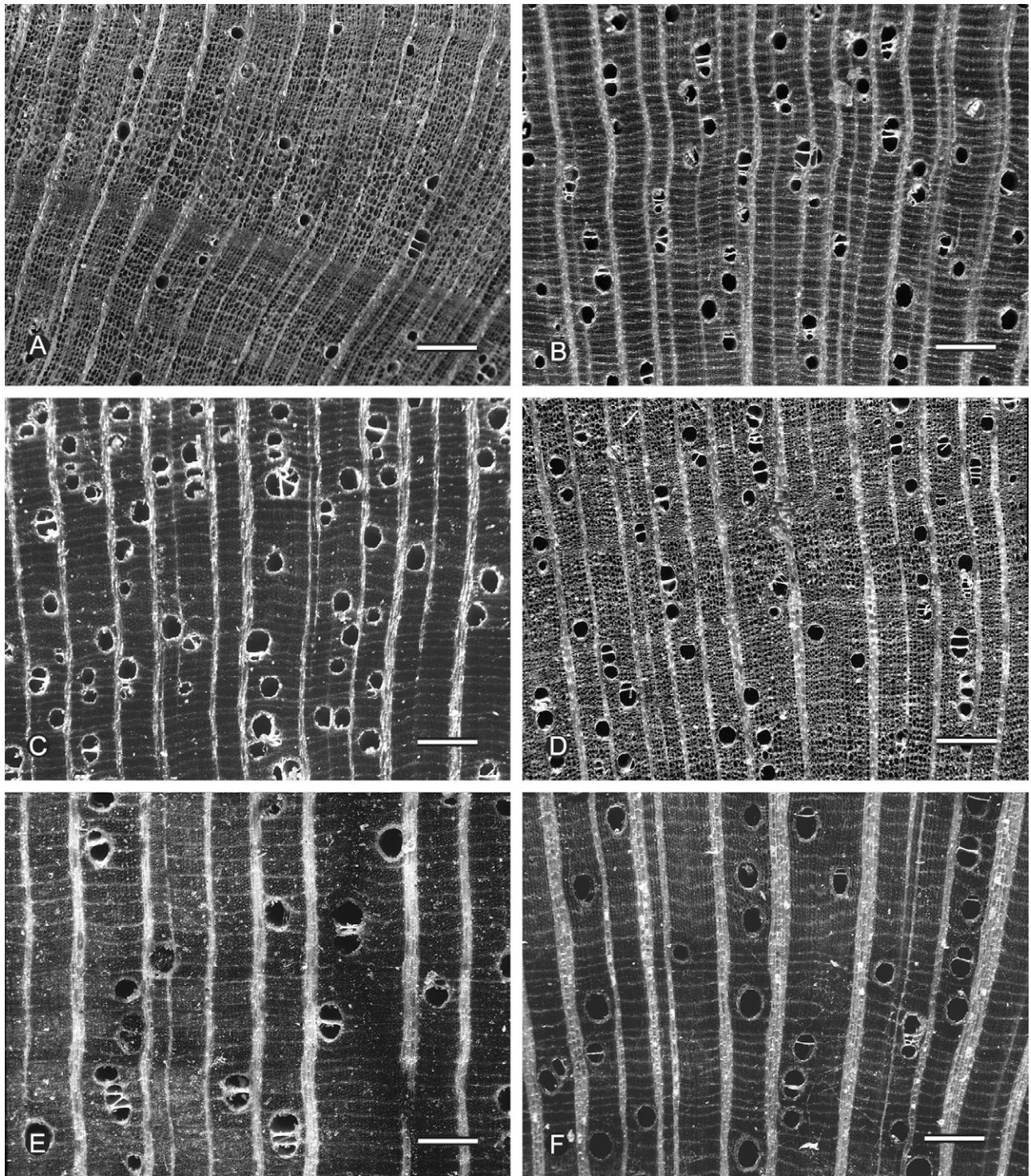
**Figure 32.** A–F, Guatterieae. A, *Guatteria alta* R.E.Fr., Uw 25132; B, *Guatteria anomala* R.E.Fr., Uw 36880; C, *Guatteria atra* Sandwith, Uw 34267; D, *Guatteria blainii* (Griseb.) Urb., Uw 29375; E, *Guatteria campinensis* (Morawetz & Maas) Erkens & Maas, Uw 29468; F, *Guatteria conspicua* R.E.Fr.,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





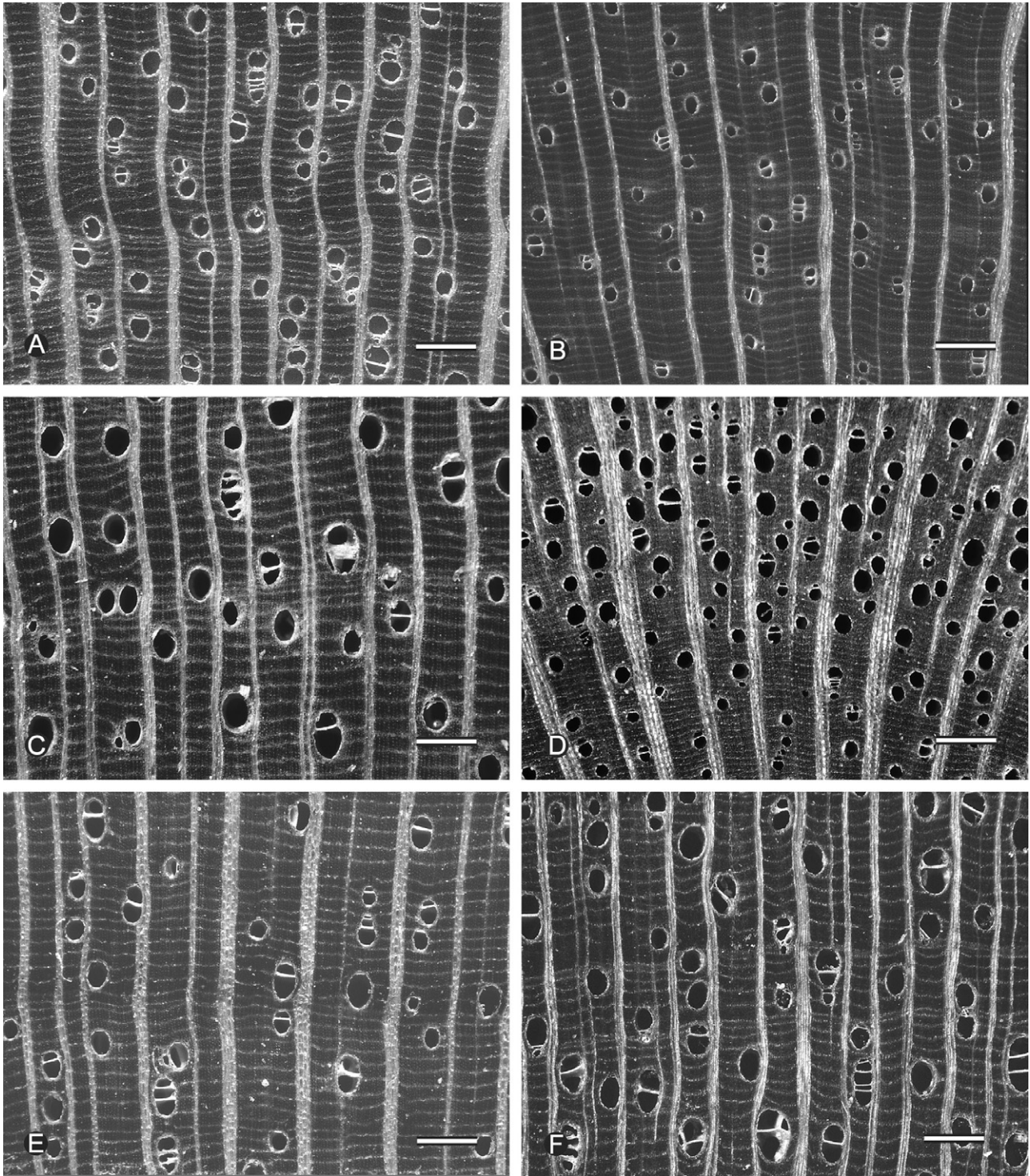
**Figure 33.** A–F, Guatterieae. A, *Guatteria curvipetala* R.E.Fr., Uw 7806; B, *Guatteria elegantissima* R.E.Fr., Uw 25071; C, *Guatteria discolor* R.E.Fr., Uw 8134; D, *Guatteria discolor* (tangential section), Uw 8134; E, *Guatteria dusenii* R.E.Fr., Uw 13675; F, *Guatteria dusenii* (tangential section),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





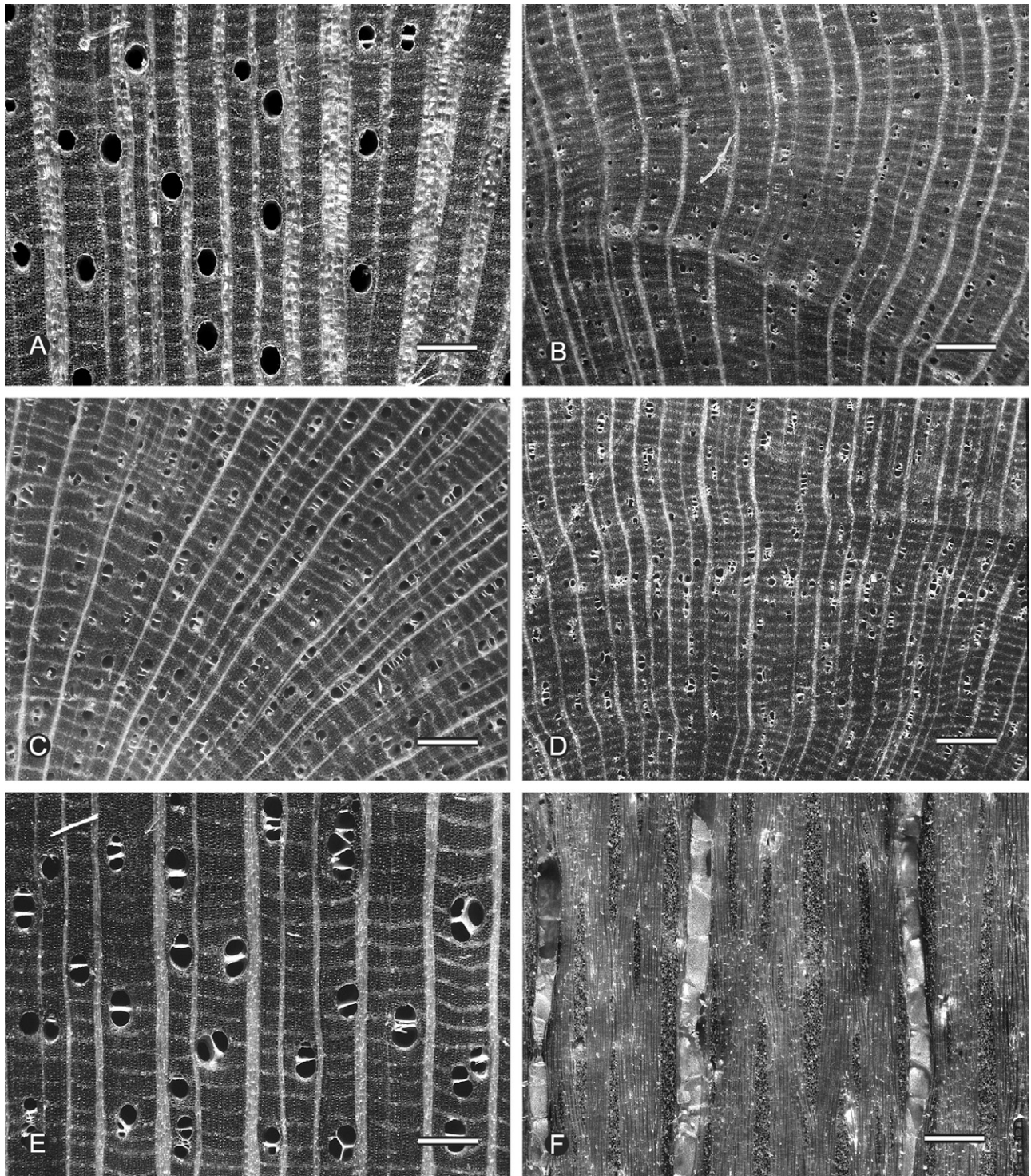
**Figure 34.** A–F, Guatterieae. A. *Guatteria heteropetala* Benth., Uw 33073; B. *Guatteria hispida* (R.E.Fr.) Erkens & Maas, Uw 29458; C. *Guatteria monticola* R.E.Fr., Uw 34268; D. *Guatteria obovata* R.E.Fr., Uw 29461; E. *Guatteria poeppigiana* Mart., Uw 17242; F. *Guatteria procera* R.E.Fr., Uw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





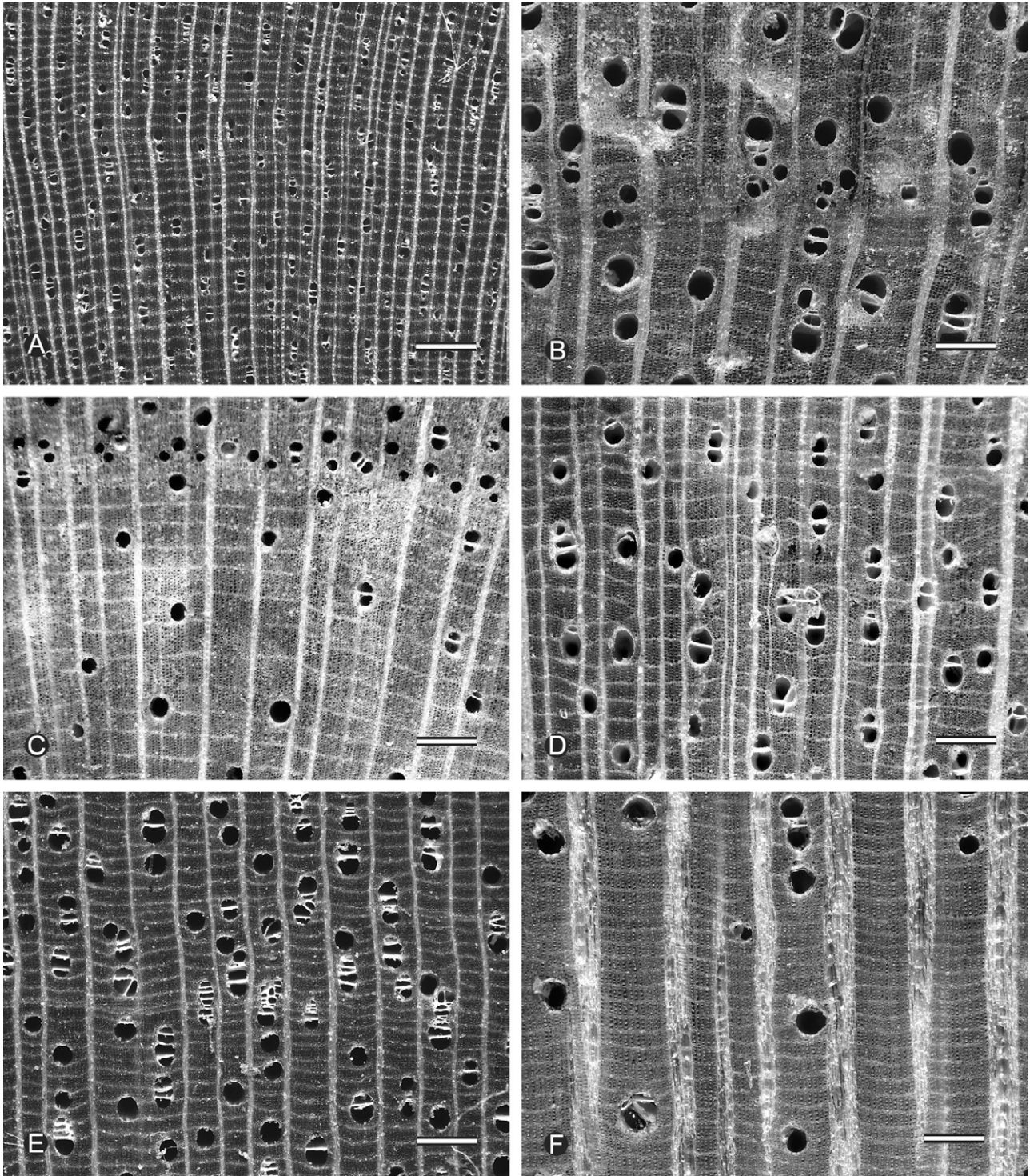
**Figure 35.** A–F, Guatterieae. A, *Guatteria punctata* (Aubl.) R.A.Howard, Uw 2565; B, *Guatteria punctata*, Uw 2566; C, *Guatteria rubrinervis* R.E.Fr., Uw 34270; D, *Guatteria scandens* Ducke, Uw 24786; E, *Guatteria schomburgkiana* Mart., Uw 254; F, *Guatteria schomburgkiana*, Uw 2568.





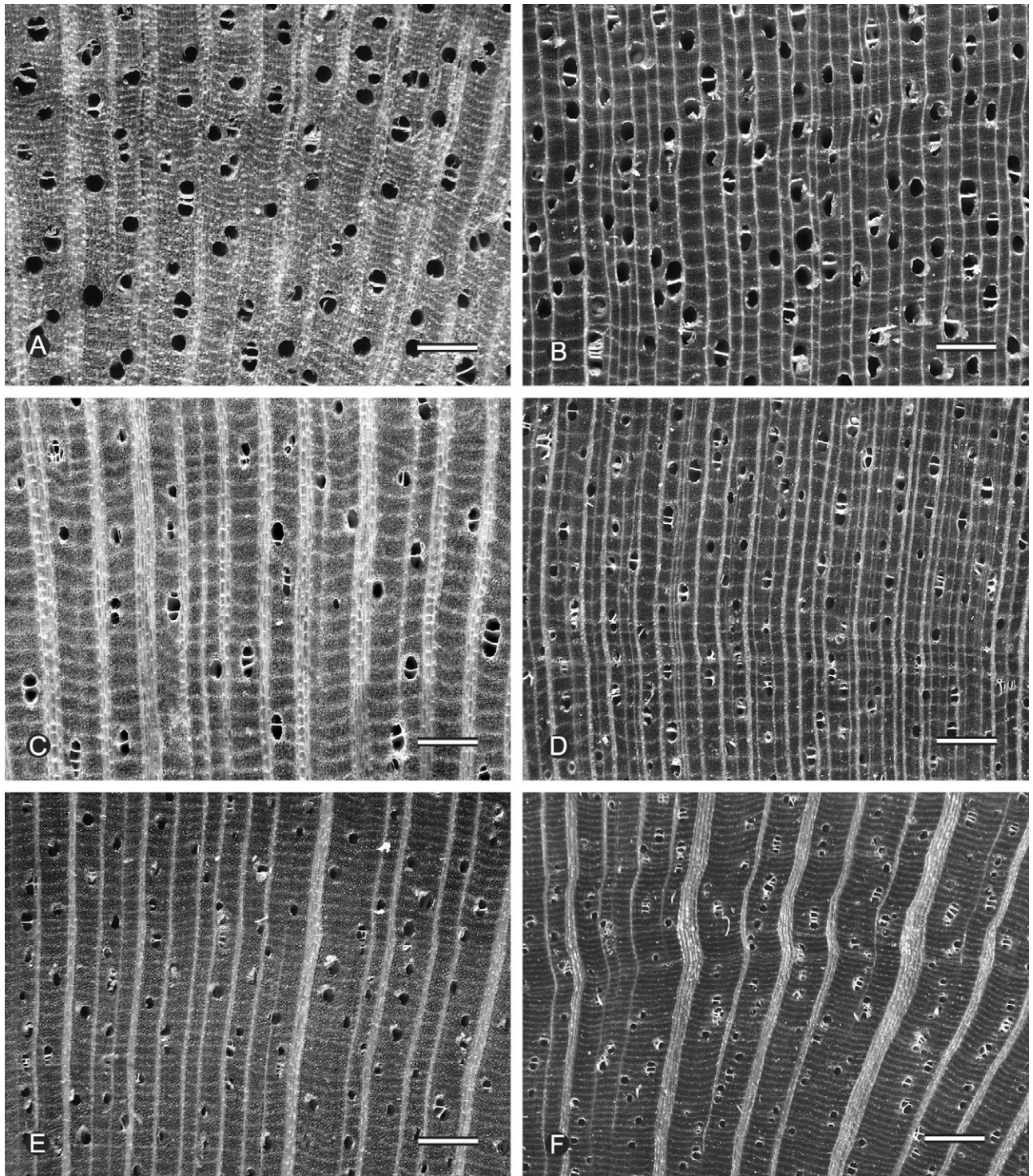
**Figure 36.** A, Guatterieae; B–F, Bocageae. A, *Guatteria trichostemon* R.E.Fr., Uw 16119; B, *Cymbopetalum brasiliense* (Vell.) Benth. ex Baill., Uw 8867; C, *Cymbopetalum schunkei* N. A. Murray, Uw 21087; D, *Froesiodendron surinamense* (R.E.Fr.) R.E.Fr., Uw 5015; E, *Porcelia ponderosa* (Rusby)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





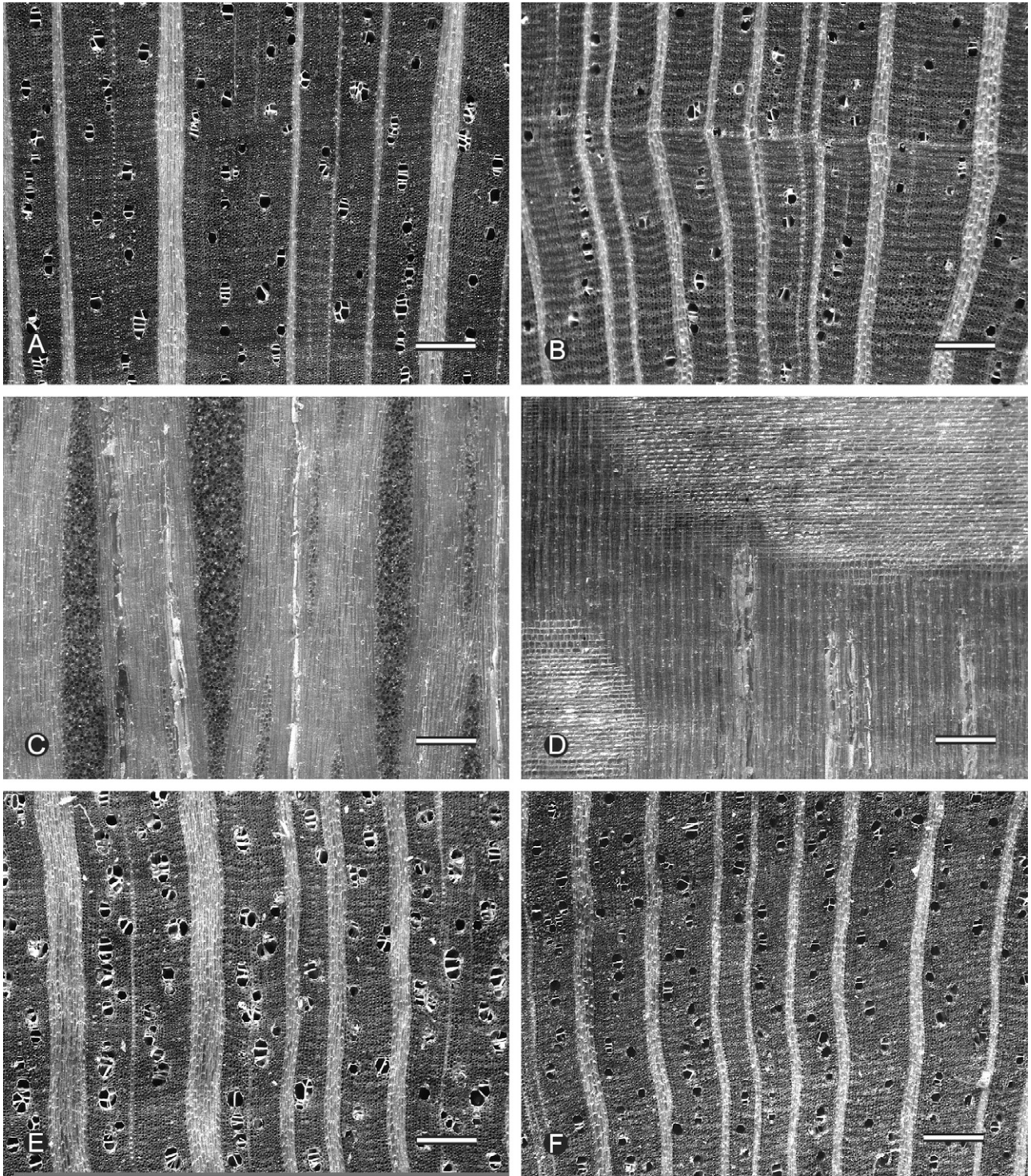
**Figure 37.** A, Bocageae; B–F, Ambavioideae. A, *Trigynaea caudata* (R.E.Fr.) R.E.Fr., Uw 764; B, *Cananga* sp., Uw s.n.; C, *Cleistopholis glauca* Pierre ex Engl. & Diels, Uw 29517; D, *Cyathocalyx bancanus* Boerl., Uw 26735; E, *Cyathocalyx subsessilis* Jovet-Ast, Uw 26736; F, *Mezzettia leptopoda*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





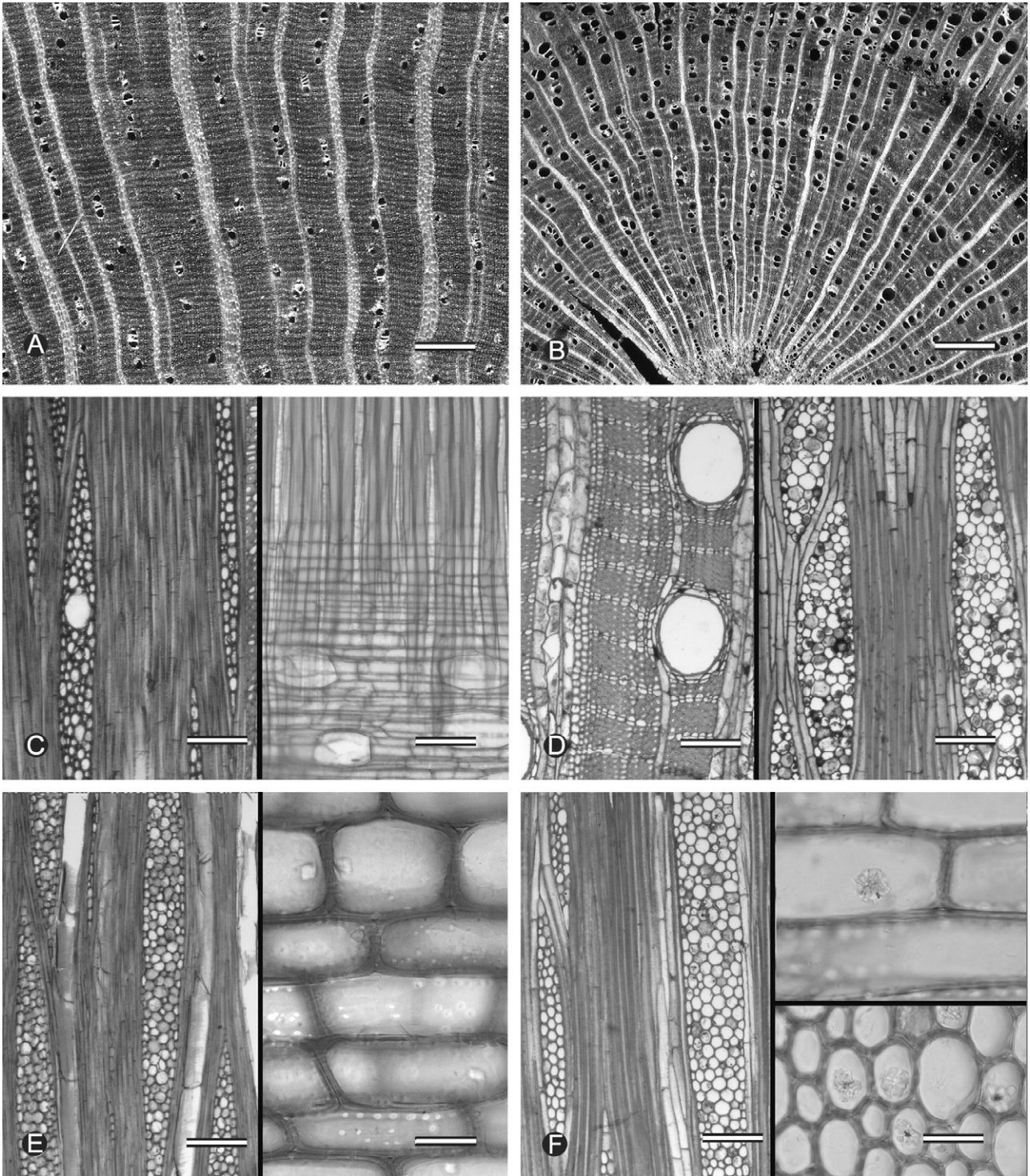
**Figure 38.** A–D, Ambavioideae; E, F, Anaxagoreoideae. A, *Mezzettia parviflora* Becc., Uw 32051; B, *Mezzettia umbellata* Becc., Uw 29513; C, *Tetrameranthus duckei* R.E.Fr., Uw 26746; D, *Meiocarpidium lepidotum* (Oliv.) Engl. & Diels, Uw 9544; E, *Anaxagorea acuminata* (Dunal) A.DC., Uw 19187; F, *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  $\mu$ m; right: radial section, bar = 85  $\mu$ m; D, *Guatteria maypurensis* Kunth, Uw 2679; left: transverse section, showing vasicentric and reticulate parenchyma, bar = 110  $\mu$ m; right: tangential section, showing multiseriate rays and axial parenchyma, bar = 110  $\mu$ m; E, *Fusaea*; left: *F. peruviana* R.E.Fr., Uw 35940, tangential section, bar = 110  $\mu$ m; right: *F. longifolia* (Aubl.) Saff., Uw 30329, radial section, showing small rhombic crystals in ray cells, bar = 20  $\mu$ m; F, *Anaxagorea dolichocarpa* Sprague & Sandwith; left: Uw 2564, tangential section, bar = 110  $\mu$ m; right: Uw 2031, radial section (above) and tangential section (below), showing druses in ray cells, bar = 20  $\mu$ m.



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



APPENDIX 1 *Continued*

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



APPENDIX 1 *Continued*

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



APPENDIX 1 *Continued*

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



APPENDIX 1 *Continued*

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