Bark anatomy of *Adansonia digitata* L. (Malvaceae)

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ABSTRACT
The bark structure of *Adansonia digitata* L. is described in detail. Characters of the bark that are shared with other Malvaceae include the presence of strongly dilating rays, mucilage cells and cavities, druses of calcium oxalate in the cells of cortical parenchyma and phloem rays, a storied arrangement of sieve tube members and axial parenchyma strands, the presence of secondary phloem fibers and their arrangement into tangential bands. The secondary phloem fibers are longer (2.8-8.6 mm) and more abundant than the libriform fibers (1.7-2.2 mm) in the wood of this species. The abundance of parenchyma in both axial and radial parts of the secondary phloem and in the pseudocortex is a noteworthy feature. Due to the complementarity of fibrous and parenchymatous tissues, the secondary phloem can provide substantial mechanical benefits and apparently play an important role in the biomechanical stability of the trunk. The meristematic capacity of dilated phloem rays and the pseudocortex allow for substantial bark dilatation with very limited abscission of the outer portions of the secondary phloem. Subsequent phellogen initiation in the outer part of the secondary phloem was not observed, not even in mature bark. Hence no rhytidome is present. The thin translucent phellem, formed by continuous phellogen arising in the subepidermal layer, allows for photosynthesis to potentially occur within the chloroplast-containing cells of phelloderm and pseudocortex, even when the plants are leafless, thus probably assisting them to survive harsh climatic conditions. The formation of sieve tube members by transverse anticlinal divisions from fusiform cambial initials in *A. digitata* is a first report for the Malvaceae *sensu lato*.

KEY WORDS
Bark anatomy, biomechanics, fibers, mucilage cells and cavities, translucent phellem.

RÉSUMÉ

*Anatomie de l'écorce d'*Adansonia digitata *(Malvaceae).*

La structure de l'écorce d'*Adansonia digitata* L. est décrite en détail. Les caractères communs avec les autres Malvaceae comprennent la présence de rayons fortement dilatés, ainsi que de cellules et de poches à mucilage, des cristaux d'oxalate de calcium en oursins contenus dans les cellules du parenchyme cortical et des rayons phloémiens, une disposition stratifiée des éléments conducteurs du phloème et des massifs de parenchyme axial, la présence de fibres associées au phloème secondaire et disposées en bandes tangentielles. Ces fibres sont plus longues (2,8-8,6 mm) et plus abondantes que les fibres libriformes (1,7-2,2 mm) reconnues dans le bois de cette espèce. L'importance du parenchyme, tant dans les sections axiales et radiales du phloème secondaire, que dans le pseudocortex, est un fait remarquable. En raison de la complémentarité des tissus fibreux et parenchymateux, le phloème secondaire peut participer efficacement au soutien et semble bien jouer un rôle important dans la stabilité biomécanique du tronc. L'activité méristématique des rayons phloémiens dilatés et du pseudocortex explique un épaississement significatif de l'écorce, pourtant associé à une très faible desquamation des zones superficielles du phloème secondaire. Dans ces dernières, comme d'ailleurs dans l'écorce âgée, la mise en place ultérieure d'un phellogène n'a pas été observée : il n'y a donc pas de rhytidome. Le suber mince et translucide, produit par le phellogène continu issu de l'assise sous-épidermique, permet la photosynthèse des cellules chlorophylliennes du phelloderme et du pseudocortex, même lorsque les individus sont défeuillés, contribuant probablement à leur survie dans des conditions climatiques sévères. Enfin, la formation d'éléments conducteurs phloémiens à partir d'initiales cambiales fusiformes par divisions transversales anticlines chez *A. digitata* est signalée pour la première fois dans les Malvaceae *sensu lato*.

MOTS CLÉS
Anatomie d'écorce, biomécanique, fibres, cellules et cavités à mucilage, suber translucide.

INTRODUCTION

The African baobab (*Adansonia digitata* L.) is a striking tree which attracts attention due to its extraordinary shape, grotesquely thickened trunk, enormous size and tolerance to harsh climatic conditions (high temperatures and low rainfall). Particularly noteworthy is the ability of the bark to recover after severe damage caused by elephants or bark harvesting by humans. It can be considered to be a "tree of life" because of the many uses to the inhabitants of the savannah (source of food, medicine, moisture and protection). The bast fibers of *A. digitata* have been (and continue to be) widely used by rural people for making ropes, cordage, harness straps, strings for musical instruments, baskets, bags, nets, snares, fishing lines, mats and cloth (Wickens 1982; Cunningham *et al.* 2014). *Adansonia digitata* is naturally distributed throughout semi-arid sub-Saharan Africa, extending from Angola, through southern Africa to East Africa, as far north as southern Sudan and Ethiopia (Wickens 1982; Baum 1995; Wickens & Lowe 2008). The genus consists of one species from mainland Africa (*A. digitata),* six from Madagascar and one (*A. gregorii* F.Muell) from north-western Australia (Wickens & Lowe 2008). However, Pettigrew *et al.* (2012) claimed that there is a second species in Africa (formally described as *A. kilima* Pettigrew, K.L.Bell, Bhagw., Grinan, Jillani, Jean Mey., Wabuyele & C.E.Vickers) but the status of this taxon is controversial and the subject of debate. Whereas one study has reported morphological support for the two entities (Dourie *et al.* 2015), another has considered the claimed diagnostic characters to be unreliable and *A. kilima* was formally reduced to synonymy with *A. digitata* (Cron *et al.* 2016). Historically the genus was accommodated in Bombacaceae but nowadays mostly in a broadened Malvaceae (which also includes Sterculiaceae and Tiliaceae), following an alternative phylogenetic classification (Alverson *et al.* 1999; Nyffeler & Baum 2000; Bayer & Kubitzki 2003). The genus is currently placed in the core Bombacoideae within Malvaceae (Baum *et al.* 2004).

The macromorphology of *A. digitata* is quite well known (Davis & Ghosh 1976; Wickens 1982; Baum 1995; Wickens & Lowe 2008; Sanchez *et al.* 2010; Pettigrew *et al.* 2012) but the anatomy is less well examined. The bark anatomy of *A. digitata* was briefly described by Moeller (1882); in addition, Metcalfe & Chalk (1950) provide some data on the structure of its juvenile bark and Den Outer (1986) examined the secondary phloem of this species. Very brief information about the bark anatomy of *A. digitata*, *A. grandidieri* Baill., *A. rubrostipa* Jum. & H.Perrier and *A. za* Baill. can also be found in Wickens & Lowe (2008). Descriptions of bark structure are also available for some other members of the Malvaceae *sensu lato* (Moeller 1882; Dumont 1887; Kuntze 1891; Metcalfe & Chalk 1950; Zahur 1959; Roth 1981; Den Outer 1983).

In contrast, more information is available on the wood structure of *Adansonia* (Fisher 1981; InsideWood 2004-onwards; Rajput 2004; Chapotin *et al.* 2006a). The abundance of parenchyma is a prominent feature of *Adansonia* wood (Rajput 2004; Chapotin *et al.* 2006c), commonly considered to have the main function of storing water and carbohydrates.

Results of ecophysiological studies (Chapotin *et al.* 2006b, c) indicated, however, only a limited use of stored water in baobab trees for physiological processes such as leaf flushing and buffering of daily water deficits, even during dry sea-

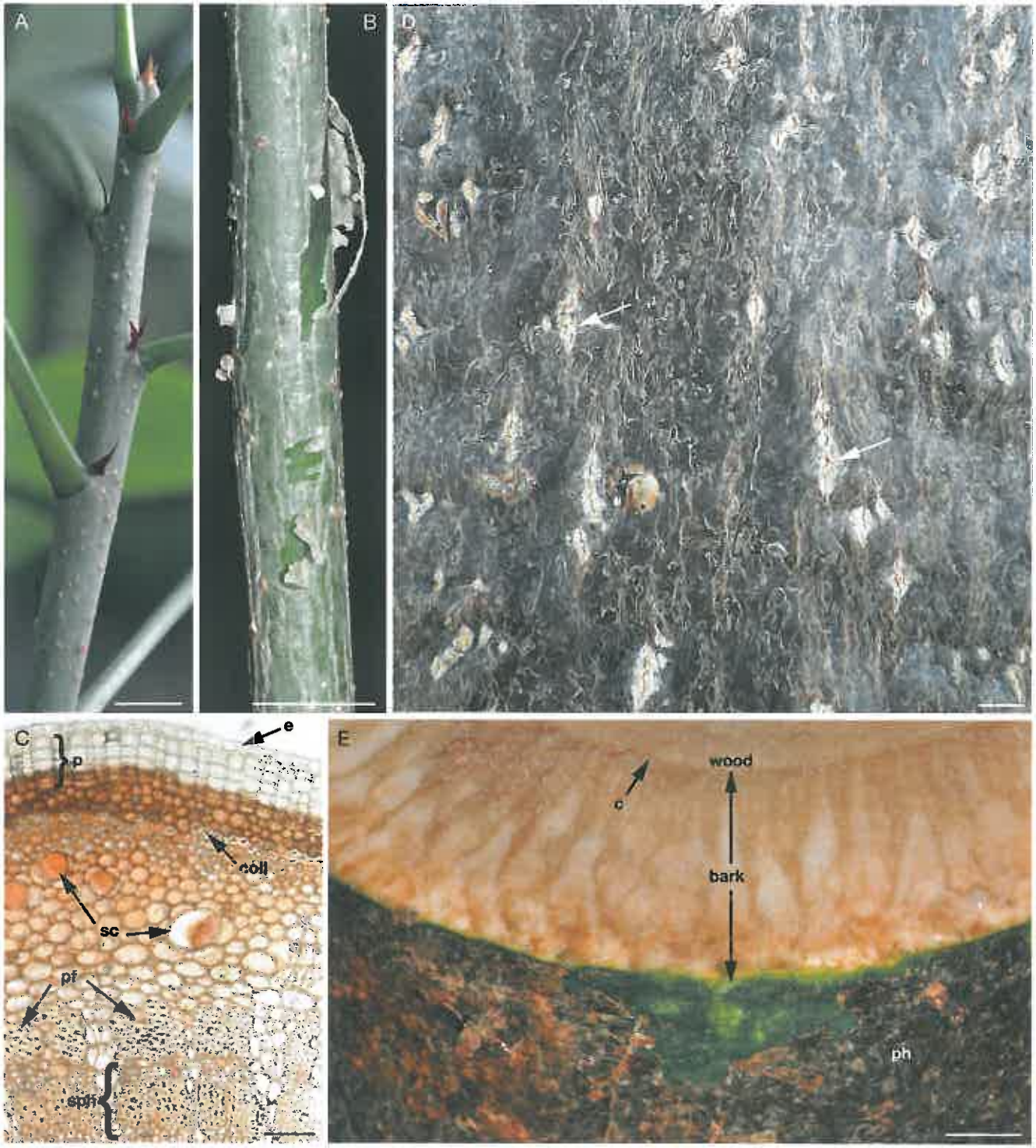

FIG. 1. — Appearance of bark: **A**, **B**, young stem: **A**, grayish white, waxy-like phellem and lenticels; **B**, translucent phellem; **C**, transverse section of young stem with periderm (**p**) under epidermis (**e**), collenchyma (**coll**) and secretory cavities (**sc**) in cortex, perivascular fibers (**pf**) and secondary phloem (**sph**); **D**, mature bark from the trunk with lenticels (**arrows**). Surface is covered with little flakes/scales; **E**, cut surface of mature branch: wood, bark and cambium (**c**) are visible. Green layers under phellem (**ph**). Scale bar: A, B, D, E, 10 mm; C, 100 µm.

sons. Indeed, abundant parenchyma also provides mechanical support for the baobab stem. A biomechanical analysis (Chapotin *et al.* 2006c) suggested that the stem of *Adansonia* could be considered to be a plant hydrostat, where the inner core of parenchyma tissue (i.e., parenchymatous wood) maintains a high water content and, through turgor pressure, stiffens (and maintains tension on) the outer strengthening ring of thick, fibrous bark. The structural traits responsible for the high strength and elasticity of baobab bark remain, however, obscure.

This study aims to present, for the first time, a detailed description of the bark anatomy of *A. digitata*. In addition, the data allows for some comparisons between the structure of bark and wood in *A. digitata* and in other Malvaceae.

MATERIAL AND METHODS

Samples of bark were collected near Tshipise in the Limpopo Province of South Africa (with the kind permission of the local Resort Manager, Mr Brian Brits). Voucher specimens and material preserved in FAA (formalin-acetic acid-alcohol) with labelling KK 90-14 are kept at the University of Johannesburg with the voucher specimens in JRAU (abbreviated according to Holmgren *et al.* 1990). For the bark investigation we collected parts of stems of different stages of development, from young tips of twigs to mature bark. The oldest bark sample (26 mm thick) came from the upper side of a branch (i.e., from the tension bark), elliptic in cross section and 175 × 120 mm in diameter. Some of the material was sectioned fresh (without fixation) and the rest was fixed in FAA (Johansen 1940).

Transverse and longitudinal sections (radial and tangential) of the bark were made with a freezing microtome (Ernst Leitz GMBH, Wetzlar, Germany). Sections from fresh unstained material were mounted in glycerol and immediately examined under a light microscope. Sections from fixed material were stained with a mixture of alcian blue/safranin and mounted in euparal. Maceration of secondary phloem was carried out in Jeffrey's solution for 24 hours before mounting the macerated material in glycerol. Digital images were taken using an Olympus ColorView Soft Imaging System and measurements were made with the Olympus Analysis Imaging Solutions (OASIS) programme.

The bark terminology used follows that of Angyalossy *et al.* (2016), Junikka (1994) and Trockenbrodt (1990). We also used the term 'pseudocortex' proposed by Whitmore (1962a, b) for a zone of living parenchymatous tissue to the outside of dilated secondary phloem. Unlike primary cortex, the pseudocortex is of mixed origin: its parenchyma can be derived both from cortical tissues and from phelloderm and/or secondary phloem parenchyma (the latter condition was reported by Whitmore (1962a, b) for some species of *Shorea* Roxb. ex C.F.Gaertn., but this was not observed in *Adansonia*).

RESULTS

The surface of the youngest stems is green and smooth, but the translucent grayish white, somewhat waxy phellem of periderm with white brown lenticels (Fig. 1A-C) appears very early during shoot development.

The epidermis is composed of a single layer (Fig. 1C) of thin-walled (in older portions of stems also evenly thick-walled) isodiametric to somewhat flattened cells covered by a thin cuticle (1-2 µm thick). The cortex consists of collenchyma and parenchyma (Fig. 1C). The outermost region of the cortex is bordered by two to five layers of nearly isodiametric, thin- to moderately thick-walled, parenchyma cells of 20-50 µm in tangential diameter with brownish content (as can be seen in unstained sections). Six to eight layers of laminar collenchyma are located beneath the outer parenchyma ring. Collenchyma cells are 8-24 µm in tangential diameter and are moderately thick-walled, (sometimes with sclerified walls). Ten to 30 layers of inner thin-walled parenchyma cells of 15-51 µm in tangential diameter are located under the collenchyma. Lysigenous mucilage cavities of 40-130 µm in tangential diameter, lined by a single layer of four to 12 cells, occur in the inner parenchyma (Fig. 1C). Some cells of the outer and inner parenchyma contain druses. Chloroplasts occur in the parenchyma and collenchyma cells throughout the cortex but are especially numerous in the outer parenchyma cells. Perivascular fibers occur in a continuous ring of six to 15 cells wide, which is interrupted by medullary rays (Fig. 1C). In older portions of stems the collenchyma cells are sclerified, forming a continuous ring. Dilatation in the cortex is effected by expansion and anticlinal divisions of parenchyma cells with the formation of long tangential strands of two to 20 cells. Mucilage-containing cavities are also expanded during dilatation but there is no obliteration of cortical tissues.

Initiation of the periderm is subepidermal (Fig. 1C). In young stems, phellem is composed of four to 10 or more layers of radially-flattened, thin-walled cells. Phelloderm forms two to six layers of isodiametric to radially-flattened, thin-walled cells containing chloroplasts. Sclereids are absent; crystals, presumably of calcium oxalate, are sometimes present. The surface of mature bark is smooth and waxy to the touch, grayish brown or reddish brown, sometimes with a greenish tint from the underlying tissues (Fig. 1D, E). The surface is covered with little flakes or scales of exfoliating phellem. Bark from old stems is thick and can be thicker than 25 mm (Fig. 2A). Formation of subsequent periderms and rhytidome was not observed (Fig. 2A, B) in the intact stem. Phellem (around 100 µm thick) is composed of 10 to 20 layers or more of thin-walled cells that are markedly flattened (Fig. 2C, D, E). Layers of cells with evenly sclerified walls rarely occur in the inner and middle portions of phellem (Fig. 2D, E). Reddish brown content occurs in some phellem cells. Phelloderm consists of 10 or more layers of thin-walled, isodiametric to radially-flattened cells. Phelloderm cells commonly contain chloroplasts, occasionally with druse crystals or with brown secretion that stains raspberry-red with safranin and alcian blue.

The pseudocortex persists during bark dilatation as a prominent parenchymatous zone, 3-4 mm in width, on the outside of the secondary phloem (Fig. 2A, B, D). This bulk of parenchyma is apparently derived from phelloderm, that is evident from the arrangement of phellem cells and parenchyma cells in the same radial files, and probably also from the inner cortical parenchyma. An initially regular radial pattern of phelloderm cells becomes completely disrupted in the pseudocortex due to anticlinal divisions of some cells (Fig. 2B, C, D). As a result, irregularly oriented (mostly radially to diagonally) dilatation meristems occur in the

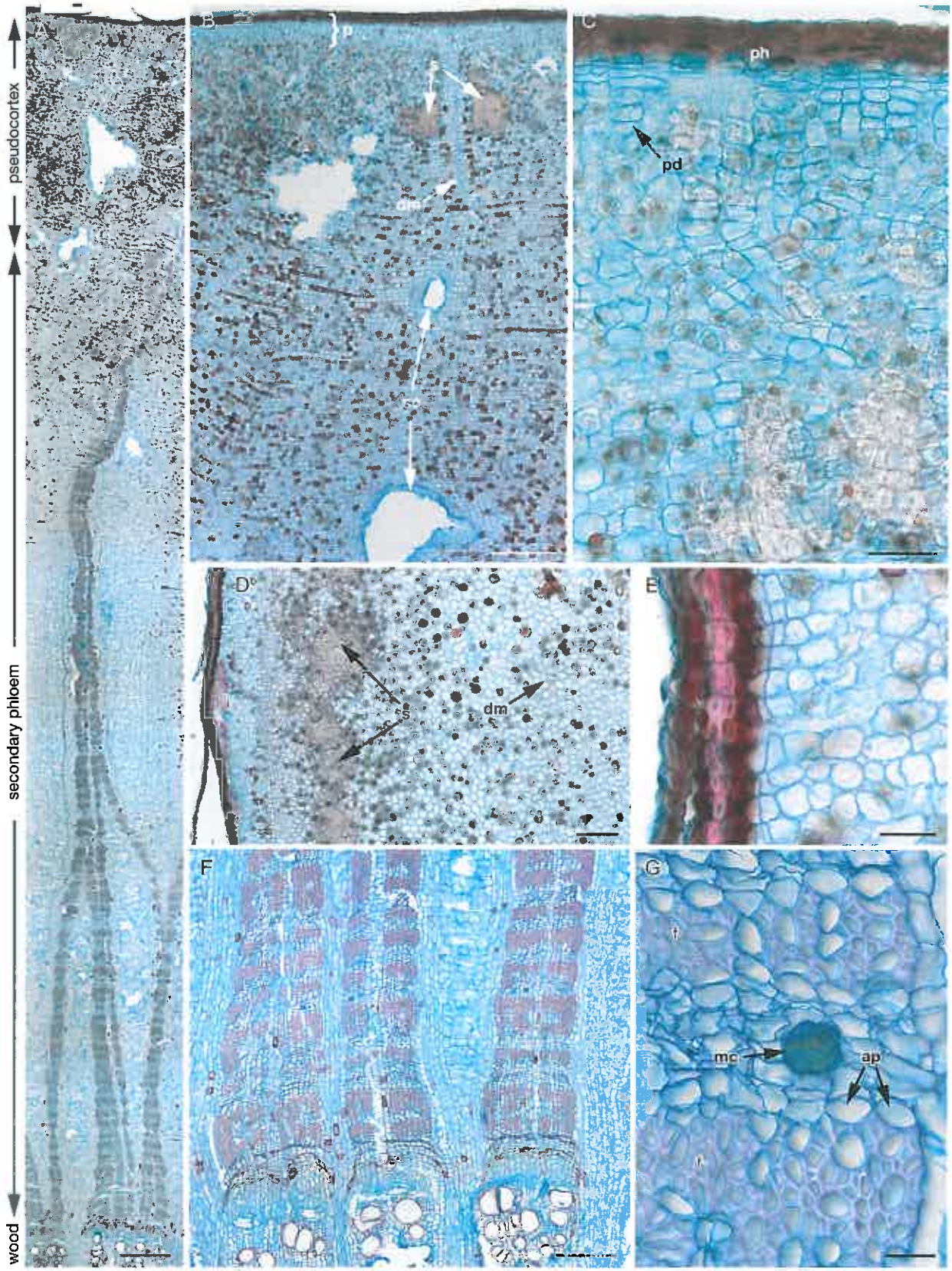

FIG. 2. — Microscopic structure of bark: **A-C, F, G**, transverse sections: **A**, general view of a mature stem bark (thickness 26 mm); **B**, pseudocortex under periderm (**p**) in mature stem, clusters of sclereids (**s**), dilatation meristem (**dm**), secretory cavities (**sc**); **C**, phellem (**ph**), regular pattern of phelloderm (**pd**) cells becomes disrupted in pseudocortex; **D, E**, radial longitudinal sections through periderm (**p**) and pseudocortex; **D**, clusters of sclereids (**s**), dilatation meristem (**dm**); **E**, phellem cells with sclerified walls; **F**, stratified secondary phloem; **G**, tangential bands of conductive elements accompanied by axial parenchyma (**ap**) with a single mucilage parenchyma cell (**mc**) alternate with bands of phloem fibers (**f**). Scale bars: A, 1 mm; B, F, 500 µm; C, 100 µm; D, 200 µm; E, G, 50 µm.

pseudocortex (Fig. 2B, D) forming tangential to diagonal (sometimes also radial or curved) files of isodiametric, thin-walled parenchyma cells. Some of them contain chloroplasts, druses or brown secretion that is stained raspberry-red by safranin and alcian blue. These parenchyma cells may be transformed into isodiametric sclereids aggregated into clusters (of nearly 50 cells) (Fig. 2B, D). Large mucilage-containing cavities of irregular shape (Fig. 2A, B) also occur in the pseudocortex.

The conducting secondary phloem (Fig. 2A, F) (i.e., the inner portion of secondary phloem showing no signs of collapse of sieve elements) is 3-6 mm wide, stratified in transverse section (Fig. 2F, G), i.e., it shows an alternation of four- to 10-seriate tangential bands of conductive elements accompanied by axial parenchyma with the two to 10(-15)-seriate tangential bands of phloem fibers. The volume of conducting secondary phloem is composed of 15-20% of phloem fibers, 20-25% of axial parenchyma, and 60% of phloem rays. Sieve tube members are 14-35 µm wide; their length varies from 174-385 µm (mean 270±9.6 µm). Sieve plates are simple, located on horizontal or slightly oblique cross walls. Axial parenchyma comprises thin-walled strands of 257-611 µm in length (mean 500±12.1 µm) that consist of 4-8 (up to 10) cells. Solitary mucilage-containing cells, distinguished by their large size and blue colour (in safranin and alcian blue), are visible in some of the axial parenchyma strands (Fig. 2G). No crystalliferous cells were observed in the axial parenchyma. Some axial parenchyma cells contain brown secretion that is stained raspberry-red by safranin and alcian blue. Secondary phloem fibers are very long (2423-8616 µm in length, mean 4162±204.3 µm), moderately thick to thick-walled and septate. Solitary thin-walled cells are scattered within the fibrous bands.

The storied arrangement of sieve tube members and axial parenchyma strands is distinctive in tangential sections of secondary phloem (Fig. 3A, B). The transition from conducting to non-conducting secondary phloem is gradual. Non-conducting secondary phloem differs from conducting phloem by the obliteration of conductive elements.

Secondary phloem rays are mostly multiseriate (up to 12-seriate) (Fig. 3A); uniseriate rays rarely occur and are present only in the youngest portions of secondary phloem adjacent to the vascular cambium. Uniseriate rays are composed mostly of square and upright cells. Multiseriate rays consist of procumbent, upright and square cells mixed throughout the ray body with square and upright cells, in one or three (up to six) marginal rows and rarely in incomplete sheaths. Some ray cells contain brown secretion that is stained raspberry-red in safranin and alcian blue. Druse crystals occur in ray cells. No sclerified ray cells were observed.

Dilatation of secondary phloem is effected by tangential expansion and multiple anticlinal divisions of ray cells (Fig. 3 C) with the formation of very wide wedge-shaped, goblet-shaped or funnel-shaped rays up to 5-8 mm in width. Zones of anticlinal cell divisions (dilatation meristems) occur in the central region of some rays (Fig. 3D).

DISCUSSION

Adansonia digitata shares some taxonomically important bark traits with other members of Malvaceae *sensu lato*. As is fairly commonly encountered in this family, *A. digitata* shows the presence of strongly dilating rays, mucilage cells and cavities in the cortex and mucilage cells in the axial parenchyma of secondary phloem, druses in the cells of cortical parenchyma and phloem rays, a storied arrangement of sieve tube members and axial parenchyma strands in secondary phloem, as well as the presence of secondary phloem fibers and their arrangement into tangential bands (Moeller 1882; Dumont 1887; Kuntze 1891; Metcalfe & Chalk 1950; Zahur 1959; Roth 1981; Den Outer 1983; Gregory & Baas 1989; Schweingruber *et al.* 2011). Unlike the majority of Malvaceae, the baobabs have very thick bark [up to 8 cm in thickness (Fischer, 1981; Wickens & Lowe, 2008)] that is an important adaptation for protection against fire in savanna (Wickens & Lowe 2008; Lawes *et al.* 2013; Pausas 2015). The bark thickness in *Adansonia* results mostly from formation of thick secondary phloem rather than of thick periderm, as occurs in most trees (Paine *et al.* 2010). In the sample of mature bark examined in this study (Fig. 2A), the secondary phloem occupies 75% of the bark volume; its share must be even higher in thicker bark from old trunks, that also consists mostly of this tissue (Kuntze 1891; Fisher 1981; Wickens & Lowe 2008). This prominent structural trait of baobab bark is seemingly related to its important biomechanical role rather than to the phylogenetic relationships of the genus. Following the hydrostatic model of baobab stem (Chapotin *et al.* 2006c), the thick, fibrous bark of this tree may not only serve as a protective layer, but also as a strengthening and elastic rind around the softer wood core.

In the secondary phloem of *Adansonia*, the fibers are arranged in tangential bands alternating with bands of sieve elements with companion cells and axial parenchyma, and interrupted by very large phloem rays. The wood fibers, however, are not arranged in regular bands: the libriform fibers are aggregated into short tangential lines or small clusters scattered in the axial parenchyma (Rajput 2004). Unlike the wood of *Adansonia* which contains 69-88% of parenchyma (Chapotin *et al.* 2006a), the volume of axial and radial parenchyma in secondary phloem is relatively low: it is *c.* 20-25% in conducting phloem of the sample under study. Bark, composed mostly of secondary phloem with phloem fibers arranged in regular tangential bands, has also been reported for other trees with very soft wood, such as *Carica papaya* L. and *Ochroma pyramidale* (Cav. ex Lam.) Urb. (Fisher 1980; Fisher & Mueller 1983; Kempe *et al.* 2014). As this pattern suggests, the secondary phloem of these trees can be considered as a composite material consisting of a reinforcing mesh of fibrous strands embedded in a parenchymatous elastic matrix. The strands of fibers, due to their composition, have higher tensile strength, whereas the parenchyma is stronger in resisting compression. Due to this complementarity of fibrous and parenchymatous tissues, the extensive secondary phloem of baobab can provide substantial mechanical

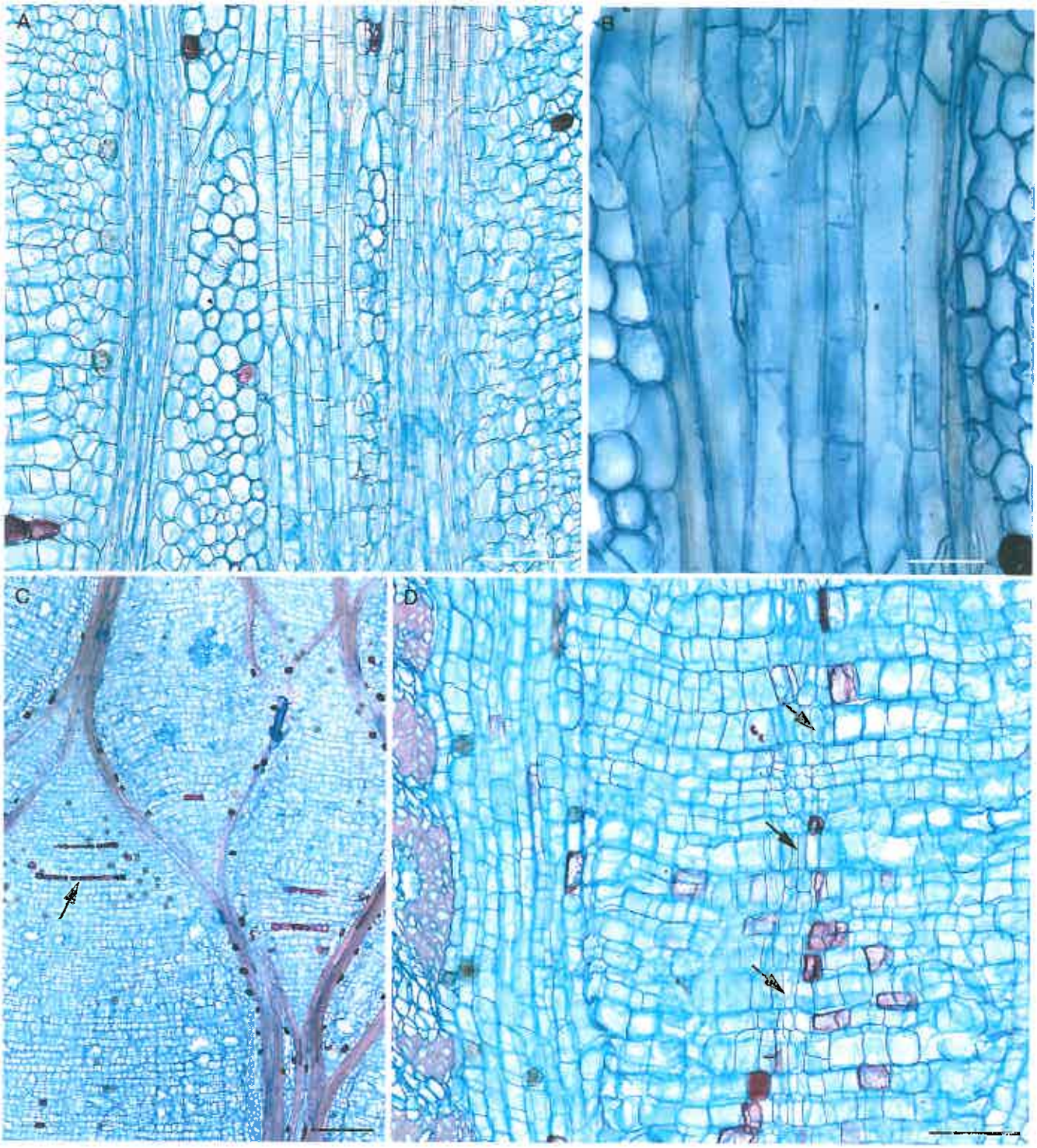

FIG. 3. — Secondary phloem: **A-D**, tangential longitudinal sections of secondary phloem; **A, B**, storied arrangement of sieve tube members and axial parenchyma in conductive secondary phloem; **C**, dilated rays with multiple anticlinal divisions of ray cells (**arrow**); **D**, dilatation meristem (**arrows**) in the central region of ray. Scale bars: A, D, 200 µm; B, 100 µm; C, 500 µm.

benefits even with a small total volume of fibers within the parenchyma (Niklas 1992).

It is noteworthy that the secondary phloem fibers of *A. digitata* are much longer (2.8-8.6 mm) than the libriform fibers in the wood of this species (1.7-2.2 mm) (Rajput 2004). These phloem fibers are formed by intrusive growth of cambial derivatives which are nearly equal in length to the axial parenchyma strands (0.2-0.6 mm). More than 12-fold intrusive elongation during fiber differentiation can result in considerable overlapping of fibers within the strands, thus providing greater strength to them. Longer phloem fibers can also confer higher elastic modulus of bark as compared to wood (Niklas 1992;

Donaldson 2008) – a feature reported for six *Adansonia* species from Madagascar by Chapotin *et al.* (2006a).

The abundance of parenchyma that may undergo further cell division even in older regions of the stem (some distance away from the cambium) is a prominent feature of the wood of *Adansonia* (Rajput 2004; Chapotin *et al.* 2006a), and provides the remarkable capacity of its bark and xylem for wound healing. On cuts of large branches of baobab, the pith, axial and ray parenchyma cells even in old wood portions (at least of 16-21 years old) contribute to forming a callus-like tissue that seals the transverse end of the exposed wood and produces periderm (Fisher 1981). Presumably, the same mechanism enables *Adansonia* to withstand ring-barking, a process that would kill most other trees (Wickens & Lowe 2008). The bark parenchyma of *A. digitata* also shows meristematic ability that can play a role in regeneration of damaged bark. Apparently, the abundant parenchyma (i.e., axial parenchyma and rays in the secondary phloem, including the large phloem rays that sharply expand in the course of dilatation, and the pseudocortex) contributes to the food/feed value of mature baobab bark that is stripped by elephants (Edkins *et al.* 2008; Kassa *et al.* 2013). The long and regularly arranged phloem fibers make it relatively easy to remove long axial strips (Malan & Van Wyk 1993).

The patterns of the cell division activity in dilated phloem rays and in the pseudocortex of *A. digitata,* as well as in "traumatic meristems" in axial parenchyma bands in its wood (Rajput 2004), resemble the meristematic zones that have been experimentally induced in the bark of *Melia azedarach* L. by mechanical pressure in combination with the application of auxin (NAA) or ethylene (Lev-Yadun & Aloni 1992). These experiments indicate an important role of dilatation stress and hormonal regulation in initiation of meristematic activity in bark parenchyma. Presumably, the meristematic capacity of the dilated phloem rays and the pseudocortex of *A. digitata* enable dilatation of the bark to occur with very limited abscission of its outer portions. A similar pattern of "expansion tissue" formation has been reported by Whitmore (1962a, b) in dilated bark of some *Shorea* species. As a result, the entire secondary phloem can persist in the course of dilatation and the loss of phloem fiber strands, conferring stiffness on the bark, is prevented. Even in mature bark, taken from a thick branch of the baobab tree, we did not observe any indication of subsequent phellogen initiation in the outer portions of the secondary phloem.

The thin translucent phellem of *A. digitata,* formed by continuous phellogen, allows for photosynthesis to potentially occur within the chloroplast-containing cells of phelloderm and pseudocortex. Similar translucent phellem has been reported in *Heteromorpha* Cham. & Schltdl. and *Polemannia* Eckl. & Zeyh., South African woody Apiaceae, that also show numerous chloroplasts in the phelloderm and parenchyma cells (Kotina *et al.* 2012). Some deciduous trees are known to have chloroplasts within the stem tissues underlying the phellem (e.g. Pearson & Lawrence 1958; Kauppi 1991). This ability of the stem to photosynthesize appears to be an adaptation to survive in arid climatic conditions during the dry season when the plants are leafless (Pearson & Lawrence 1958; Nilsen 1995; Chenusak & Cheesman 2015).

The sieve tube members in *A. digitata* (174-385 µm long) are much shorter than the axial parenchyma strands (257-611 µm long). Such a pronounced difference in length between these elements of secondary phloem can indicate the common occurrence of transverse to oblique anticlinal divisions of the cells derived from fusiform cambial initials in the course of differentiation of the sieve tube members. As a result, the mature sieve elements show distinctly reduced lengths compared with their mother cells whereas the axial parenchyma strands remain nearly equal in size to the fusiform initials. The occurrence of anticlinal transverse divisions in the formation of sieve tube members has been observed in many plant taxa (Esau & Cheadle 1955; Zahur 1959; Evert 1963; Ghouse & Yunus 1975; Khan & Siddiqui 2007; Kotina & Oskolski 2010), but it has not yet been reported for any species of the Malvaceae *sensu lato*.

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