

Original Article

Bark wings are related to the primary vascular system: the case of *Piptadenia gonoacantha* (Leguminosae)

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ABSTRACT

Bark wings are projections commonly interpreted as plant protective structures against herbivory. Their location in stems has been typically thought to be random, something that here we dispute, using *Piptadenia gonoacantha* as a case study. We collected stem samples from several specimens in different developmental stages from natural populations in the Brazilian Atlantic rainforest. These stems were studied in detail under light microscopy to determine the formation of bark wings and their possible correlation with other anatomical features. Stems of *P. gonoacantha* are deeply lobed during primary growth, with each lobe containing a large vascular bundle, alternating with smaller vascular bundles in the interlobes. On top of these lobes, prickles develop, being composed of epidermal tissue and the cortex beneath. Some of the eight lobes merge and a phellogen is installed on top of them, which starts to produce a large sheath of phellem, which will become the conspicuous bark wings of *Piptadenia*. The phellogen switches on and off, leaving marks resembling growth rings. The bark wings in *Piptadenia* have very specific positioning, always in the front of five to eight major vascular bundles, indicating that bark wings appear always in very precise locations.

Keywords: bark wings; development; ontogeny; periderm; prickles

INTRODUCTION

The bark is the externalmost tissue of the plant body, representing 9–15% of the stem volume (Harkin and Rowe 1971). Bark has a complex anatomical structure, derived from a combination of tissues of different origins, typically at least the vascular cambium and phellogen, in addition to remnants of the primary plant body, such as the cortex and pericyclic fibres (Roth 1981, Angyalossy *et al.* 2016, Shtein *et al.* 2023). Bark has two major roles, that of protection of stems and roots as the first barrier to the external environment, and that of conduction of food and signalling molecules (Niklas 1999, Rosell *et al.* 2007, Angyalossy *et al.* 2016, Shtein *et al.* 2023). With regard to protective structures, cuspidal structures are frequently present in bark tissues (Roth 1981, Evert 2006, Angyalossy *et al.* 2016). These structures are generally spiny, hard, dry and nonphotosynthetic, and

represent either projections from the bark, which are named prickles, or modified organs (leaves, branches, stipules, and even roots), known as spines or thorns (Tomlinson 1990, Lorenzi and Gonçalves 2011, Kaplan and Specht 2022). Both spines and prickles have been shown to act as major defence structures, reducing predation by herbivores (Roth 1981, Hanley *et al.* 2007).

Within this group of bark outgrowth structures are wings or ribs, which are longitudinally longer projections of the bark, usually covering the entire extension of an internode (Gregory 1888a, b, c, Mcnair 1930, Smithson 1954, Bowen 1963, Angyalossy *et al.* 2016). Many plants are known for their presence of bark wings, such as *Acer campestre* L. (Sapindaceae), *Euonymus alatus* (Thunb.) Siebold (Celastraceae), *Liquidambar styraciflua* L. (Altingiaceae), *Quercus macrocarpa* Lapeyr. (Fagaceae), and *Ulmus × hollandica* Mill. (Ulmaceae) (Table 1).

Table 1. Summary of the studies on bark wings

Study	Species and family	Number of bark wings	Presence is related to:	Originated from:
Gregory 1888	<i>Euonymus alatus</i> (Celastraceae)	4	Where the stomata were and between the angles	Early development: no mention Later development: no mention
Gregory 1888	<i>Acer campestre</i> (Sapindaceae)	6	No mention	Early development: cortex Later development: no mention
Gregory 1888	<i>Quercus macrocarpa</i> (Fagaceae)	5	Strongly developed leaf-traces	Early development: epidermis + cortex Later development: Pphellogen
Gregory 1888	<i>Liquidambar styraciflua</i> (Altingiaceae)	3–4	Run through the leaves and originates from lenticels	Early development: cortex Later development: phellogen
McNair 1930	<i>Euonymus alatus</i> (Celastraceae)	4	Primary vascular system	Early development: epidermis Later development: no mention
Smithson 1952	<i>Acer campestre</i> (Sapindaceae)	6	Rupture of the bark due to radial growth, position of leaf-traces and vascular bundles	Early development: no mention Later development: phellogen
Smithson 1952	<i>Ulmus × hollandica</i> (Ulmaceae)	4–8	Where the vascular bundles are larger	Early development: no mention Later development: phellogen

A few species appear to have wings of random growth, resulting from a periderm or rhytidome that grows considerably and eventually breaks up to form wings, generally by disruption of this rhytidome or periderm (Gregory 1888a, c). However, in most cases, bark wings are not randomly distributed in stems, something that has been explored (Gregory 1888a, b, c, Smithson 1952, 1954), but is not detailed in current botany teaching. Commonly, bark wings are related to one aspect of the primary plant body, either the distribution of vascular bundles within the vascular system, stomata, or the position of leaf orthostichies (Gregory 1888a, b, c, McNair 1930, Smithson 1954, Bowen 1963). For instance, in *Quercus macrocarpa*, the stem is five-angled and with one wing in each angle, and these wings are directly related to strongly developed leaf-traces (=vascular bundles; Gregory 1888a, b). In *Acer campestre*, the stem is hexangular, with six wings always arranged in relation to both the leaf and bundle traits, which are also very regular, and in a vertical direction alternating from one internode to the next (Smithson 1952). In *Liquidambar styraciflua* (Altingiaceae), the wings originate in the lenticels (Gregory 1888a, b), and this species also develops annual growth rings in the phellem synchronized with annual growth rings in the xylem (Gregory 1888a, b). These and other examples are summarized in Table 1.

As we can see from the previous examples, the presence of bark wings in very distantly related families suggests enormous diversity. However, knowledge, particularly regarding the structural development of bark wings, remains limited. In addition, previous studies have focused on plants from temperate areas of the Northern Hemisphere. However, bark wings are also common in plants from the tropics. Within this enormous diversity is an iconic neotropical tree, *Piptadenia gonoacantha* J.F.Macbr (Leguminosae, Mimosoid clade), with wide bark wings covering the whole stem in a wavy pattern (Fig. 1A–F). It has brownish-brown, greyish-white branches, and visibly striated, erect spikes, arranged in longitudinal series on branch wings or ribs (Carvalho 2014). Given the common presence of these wings, it is widely known in its native range in Brazil under

the popular name alligator-wood ('pau-jacaré', in Portuguese), given the bark's resemblance to the rough skin of an alligator. Accidental impacts with the tree can cause immediate bruising, since the wings are quite sharp and have prickles on their surface.

The genus *Piptadenia* contains about 24 species distributed in 10 countries (Hernández *et al.* 2020), with many displaying some sort of bark wings [e.g. *Piptadenia retusa* (Jacq.) P.G.Ribeiro, Seigler & Ebinger; M.R.P., personal observation]. The Brazilian state of Minas Gerais is the richest in number of species of *Piptadenia*, accounting for ~29% of the diversity of this genus in Brazil (Moura *et al.* 2017), with specimens growing both in the Atlantic Forest and cerrado domains (Oliveira Filho, 2006). Only *P. gonoacantha* and *P. viridiflora* (Benth) Kunth. [currently *Lachesiodendron viridiflorum* (Kunth) P.G. Ribeiro, L.P. Queiroz & Luckow] occur in other South American countries (Moura *et al.* 2017). The present study species, *P. gonoacantha*, occurs in both primary and secondary forests (Longui *et al.* 2009, Damásio *et al.* 2013), and ranges from 3 to 20 m in height (Carvalho 2014; Fig. 1G). Despite being an emblematic species of the Brazilian Atlantic rainforest, nothing is known about how its wings are formed or their origin. Therefore, the aim of this study was to unravel the structural development of the bark wings in *P. gonoacantha* and possible relationships with its anatomy, both in primary and in secondary growth. Given previous studies on bark wings (Table 1), we hypothesize that the development of these bark wings is not random, but directly related to other anatomical features of the primary plant body, probably the vascular system.

MATERIAL AND METHODS

Thirteen stem samples of *P. gonoacantha* were collected from three different specimens, growing in natural populations at the University of São Paulo Forest Reserve with vouchers deposited in the National Herbarium of Mexico (MEXU) and the Herbarium of the National Museum of Natural History of the Smithsonian Institution (USA). Samples included apical regions containing parts in primary growth, and sampled all the way to

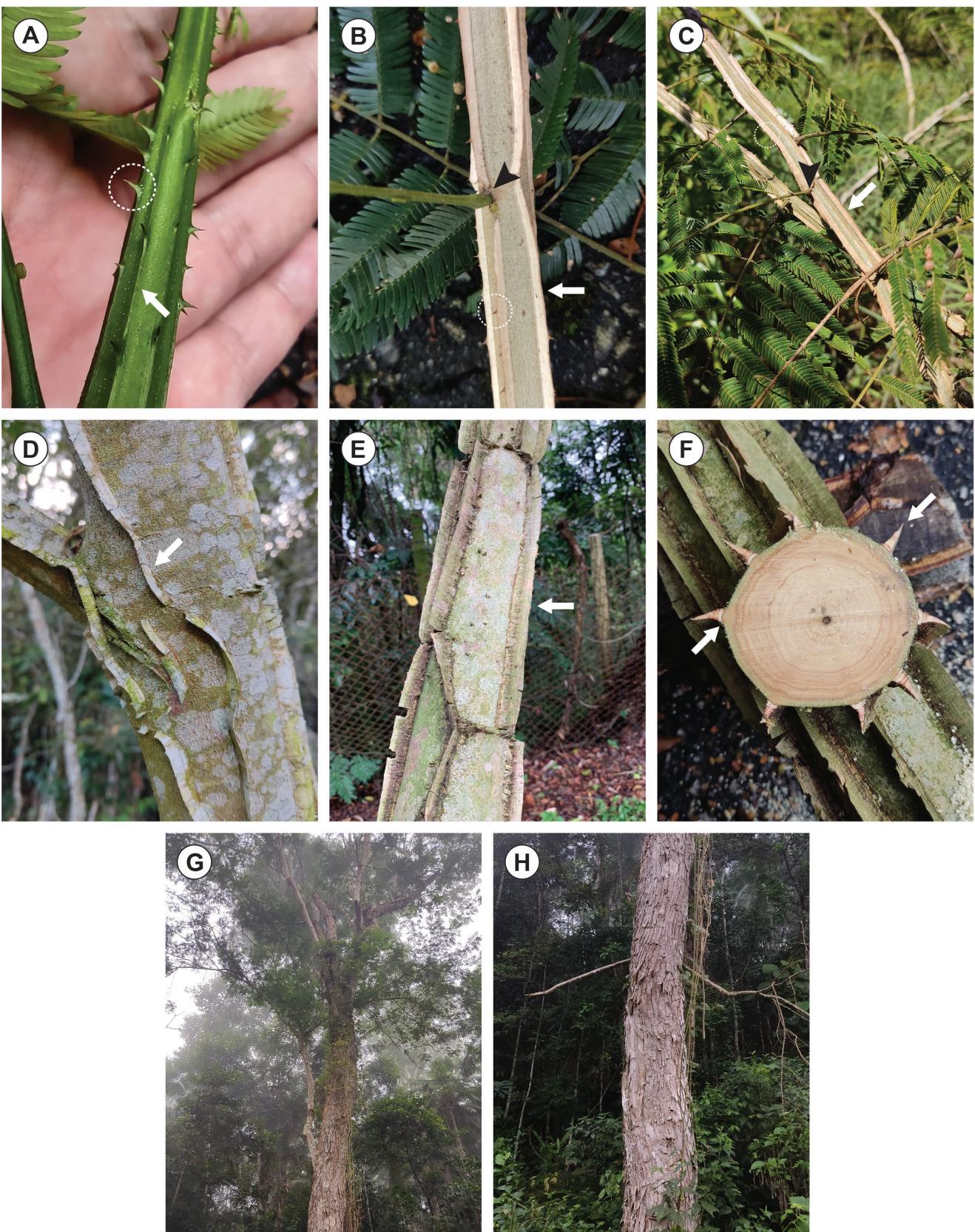


Figure 1. Stem morphology of *Piptadenia gonoacantha* (Leguminosae). In A–F white arrows point to wings in the stems. A, stem in primary growth, with lobes and prickles, the latter developing upon the lobes (white dotted circle). B, C, leaves and branches originate at the same level as the wings (black arrowhead). Note prickles (white dotted circles). C, arrangement of branches on the stem. D, E, wings in older portions of the stem. F, transverse section of the stem, with eight well-developed wings. G, a 20-m-tall tree. H, in fully mature trunks, the bark wings wear-off and rough bark that detaches as plates is found instead.

the main trunk, in advanced secondary growth. The samples were fixed in FAA (formaldehyde, glacial acetic acid, and 50% ethanol; Johansen 1940), for 24 h, placed in a vacuum chamber within a fume hood. After this, the samples were preserved in 70% alcohol. For all samples, we applied the technique of Rupp (1964), which allows anatomical cuts of large portions of the stem, for a general visualization of the tissues. The technique consists of placing the samples in a highly diluted solution of water and polyethylene glycol 1500 (PEG-1500) in a large jar, placing this jar within an oven at 60°C for, on average, 1–2 weeks, until total evaporation of the water from the PEG solution and automatic self-inclusion of the sample in pure PEG. Moulds of folded paper were prepared and each sample was positioned inside the mould and filled with pure PEG-1500 until the samples were covered, leaving them at room temperature until the PEG-1500 solidified, which typically took <1 h. Subsequently, sections 10–25 µm thick were produced in a slide microtome, with permanent steel blades sharpened with sandpaper (Barbosa *et al.* 2018), using a polystyrene resin (Styrofoam) dissolved in butyl acetate and applied to the samples to keep them firm and without tissue rupture (Barbosa *et al.* 2010). Sections were made in transverse, tangential and radial directions.

Being water soluble, PEG-1500 dissolved immediately when placed in water after sectioning, but not the polystyrene resin coat. Subsequently, the sections were dehydrated in an alcohol series of 10, 20, 30, 40 and 50%, stained with safrablau [a mixture of 1:9 parts 1% safranine and 1% astra blue dissolved in 50% ethanol (Kraus and Arduin 1997)], and continuing the alcohol series of 60, 70, 80, 90 and 100%. The samples were then washed in butyl acetate to dissolve the polystyrene resin, and placed on permanent slides containing a small amount of Canada balsam, covered with coverslips and placed in an oven at 50°C for resin solidification, with a weight over each coverslip to apply pressure and eliminate air bubbles and obtain an optimal final result.

An optical microscope was used for qualitative analysis of each sample, verifying the characteristics of tissues and cells such as pith, xylem, and phloem (primary and secondary), cambium, pericycle, endodermis, cortex, epidermis, and periderm. Photographic records were made using a Leica DMLB microscope with a Leica DFC 310FX camera at the Plant Anatomy Laboratory of the Institute of Biology of the University of São Paulo.

RESULTS

Transverse sections of the stem are noncylindrical since its primary growth is distinctively lobed, typically with eight lobes (Fig. 2A, B). Each lobe has a large vascular bundle, while minute vascular bundles are present in the interlobular region of the concavities (Fig. 2A, B, D inset). At this stage, the pericycle is multilayered and parenchymatous, and the endodermis is evident with more enlarged cells (Fig. 2C). Prickles develop on the lobes and are composed of the epidermis externally and cortex internally (Fig. 2D, E). The lobular region is distinctive also by having more, bulkier cortical cells than the interlobular regions (Fig. 2C). While the stems are still in primary growth, the pericyclic cells differentiate into fibres (Figs 2E, 3C, E).

Secondary growth starts in the first internodes, with initiation of the vascular cambium producing secondary xylem inwards

and secondary phloem outwards (Fig. 3A, B). Two or three lobes typically merge into a single one, reducing the number of lobes from eight (Fig. 2A, B) to five to seven (Fig. 3), while the stems start losing their initial lobulation. This merging is evidenced by the distribution of the vascular bundles, which become side by side (Fig. 3A, C), given the activity of the cambium. In these regions (fascicular) the secondary xylem initially has more vessels than the interfascicular regions (Fig. 3D, E), and there is an initially greater production of secondary phloem in these areas compared with adjacent areas (Fig. 3C–F). The multilayered pericycle completes its differentiation into fibres in the outermost vascular regions (Fig. 3E–G).

Where the lobes merged, and sometimes where a prickle was present, a phellogen is formed (Fig. 3E). An epidermal rupture occurs, derived from the production of phellem outwards, and the consequent suberization of the external cortex and epidermis, which continues to correspond to the position of the larger vascular bundles (Fig. 3D–F). This is how the wings start to develop. Pith cells begin to expand and extend (Fig. 3D). The wings are the result of intense formation of phellem outwards at five to seven locations (Fig. 3D, H). These locations correspond to the major vascular bundles that were present during primary growth (Fig. 3D, H). Because the phellogen shows more intense activity in the lobes than the adjacent regions, wings are very conspicuous throughout the stems (Fig. 1B–F), even when secondary growth is advanced (Figs 1D–F, 3G, H). The wings disappear only in very mature stems (Fig. 1G, H).

The phellem has marks that indicate arrest and resumption of phellogen activity (Fig. 3H, I). The number of phellem rings corresponds to the number of growth rings in the secondary xylem (wood) (Fig. 3H).

DISCUSSION

Bark projections are common in plants, and have usually been directly related to protection (Roth 1981, Bazely *et al.* 1991, Raven and Johnson 2001, Hanley *et al.* 2007). These projections can be spines, thorns, prickles, wings, or a combination of them. However, except for spines and thorns, which are modified organs, there is a widespread tendency to assume that wings and prickles are of random distribution and can be found anywhere in a plant (Simpson 2006). By studying *P. gonoacantha* and looking at the specialized literature, we were able to see that this is rarely the case. For instance, in *P. gonoacantha* we have shown how the conspicuous wings are directly related to the primary vascular system and the lobulation of the stem during primary growth. More specifically, each lobe of the young stem corresponds to a large vascular bundle, immediately beneath a leaf or a newly formed branch. On top of these lobes, a periderm is installed and its phellogen produces a long, bristle phellem wing. These results agree with observations in other distantly related taxa with conspicuous wings, such as *Euonymus alatus* (Celastraceae; McNair 1930, Bowen 1963), *Acer campestre* (Sapindaceae; Smithson 1952b), *Liquidambar styraciflua* (Altingiaceae; Gregory 1888b), and *Ulmus × hollandica* (Ulmaceae; Smithson 1952a). This indicates that bark wings are not randomly distributed. Very bulky prickles, similarly to wings, can also be composed entirely of phellem, as in *Ceiba* Mill. (Malvaceae; Guía-Ramírez *et al.* 2021).

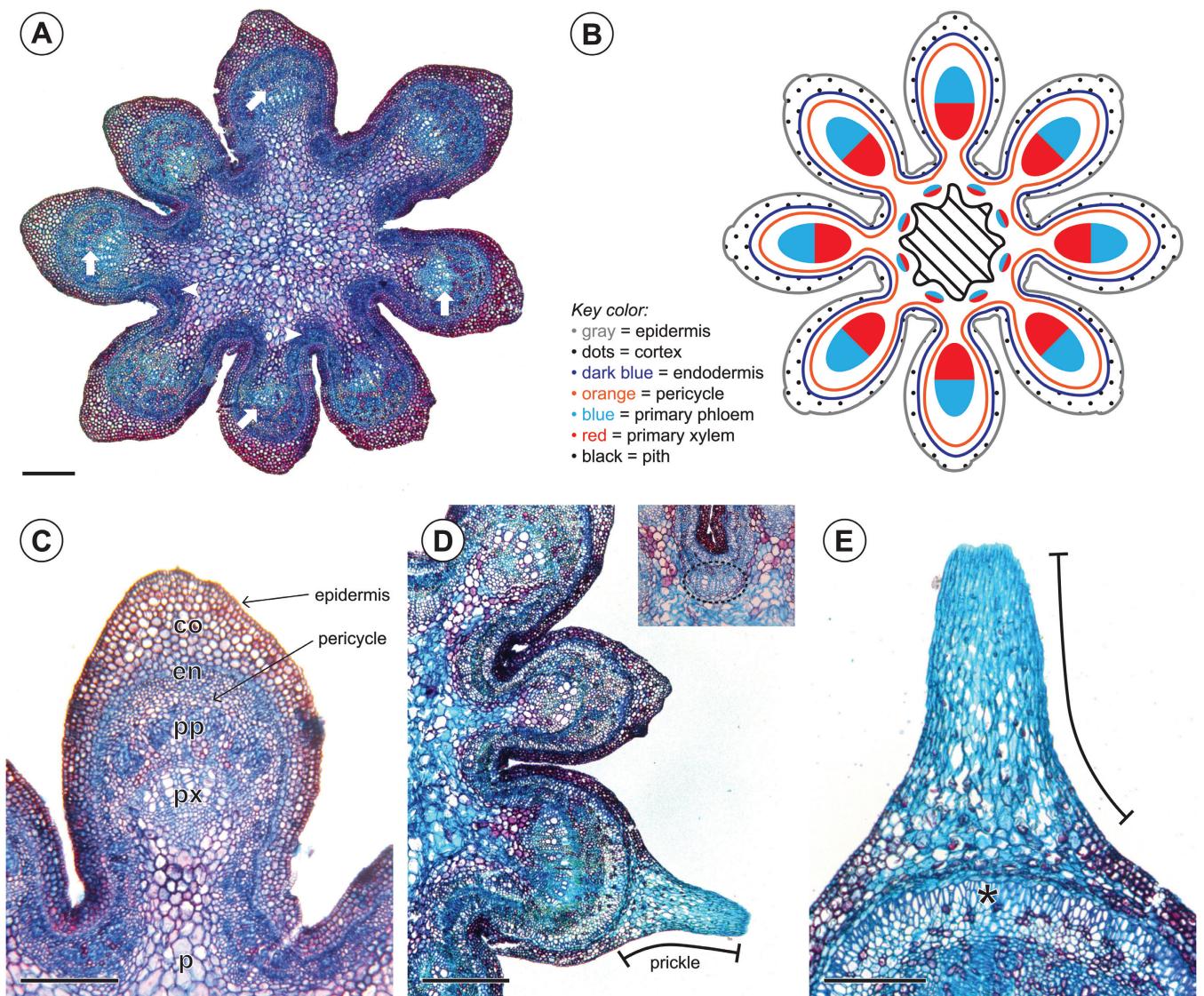


Figure 2. Development of bark wings in young stems of *Piptadenia gonoacantha* (Leguminosae). A, stem in primary growth. Eight lobes are visible, each with a large vascular bundle (white arrow). Small vascular bundles are present in the interlobe areas (white arrowhead). B, schematic representation of bark wing structures. C, lobe with epidermis, a parenchymatic cortex (co), endodermis (en), a multilayered pericycle, primary phloem (pp), primary xylem (px), and pith (p). D, E, prickles forming (indicated by the black line) immediately over the edge of the lobes. Inset: smaller vascular bundle present in the interlobe. Note in E pericycle differentiating into fibres. Scale bars: A, C and E = 200 µm, D = 500 µm.

It is not clear why two or more aspects of the primary and secondary plant body that appear to be selectively uncoupled, such as the vascular system, the stem shape, and the presence of bark projections, may be directly correlated. The concept of ontogenetic enablers appears to offer the most plausible explanation. It is common in morpho-anatomical evolution to find certain morphologies that favour the evolution of other forms. In fact, this is not the first time that the stem shape during primary growth has been hypothesized to favour the evolution of a specific, more complex stem anatomy (i.e. to act as an ontogenetic enabler). In lianas of the tribe Paullinieae (Sapindaceae), the triangular shape of the stem during primary growth was suggested to favour the evolution of complex vascular variants (Chery *et al.* 2020), which gives rise to some of the more complex stem structures in nature (Schenk 1893, Angyalossy *et al.* 2012, Cunha

Neto 2023). In the Malvacean genus *Bytneria* s.s., adult stems have conspicuous lobulation, and this lobulation can be traced back to the primary body, with each lobe also corresponding to one of the major vascular bundles (Luna-Márquez *et al.* 2021), similar to in the wings of *P. gonoacantha* found here. What is different in *Bytneria* is that when secondary growth starts, it is the vascular cambium which keeps and increases the lobes (Luna-Márquez *et al.* 2021), while in *P. gonoacantha*, the lobes disappear, but the periderm forms enormous wings in front of the major vascular bundles.

In addition, on top of each lobe and all of the wings, we found spiny structures. Here we were able to identify them as prickles, given that they are not vascularized and are composed solely of an epidermis and the cortex beneath. The evolution of spiny structures on top of lobes seems also to be favoured by

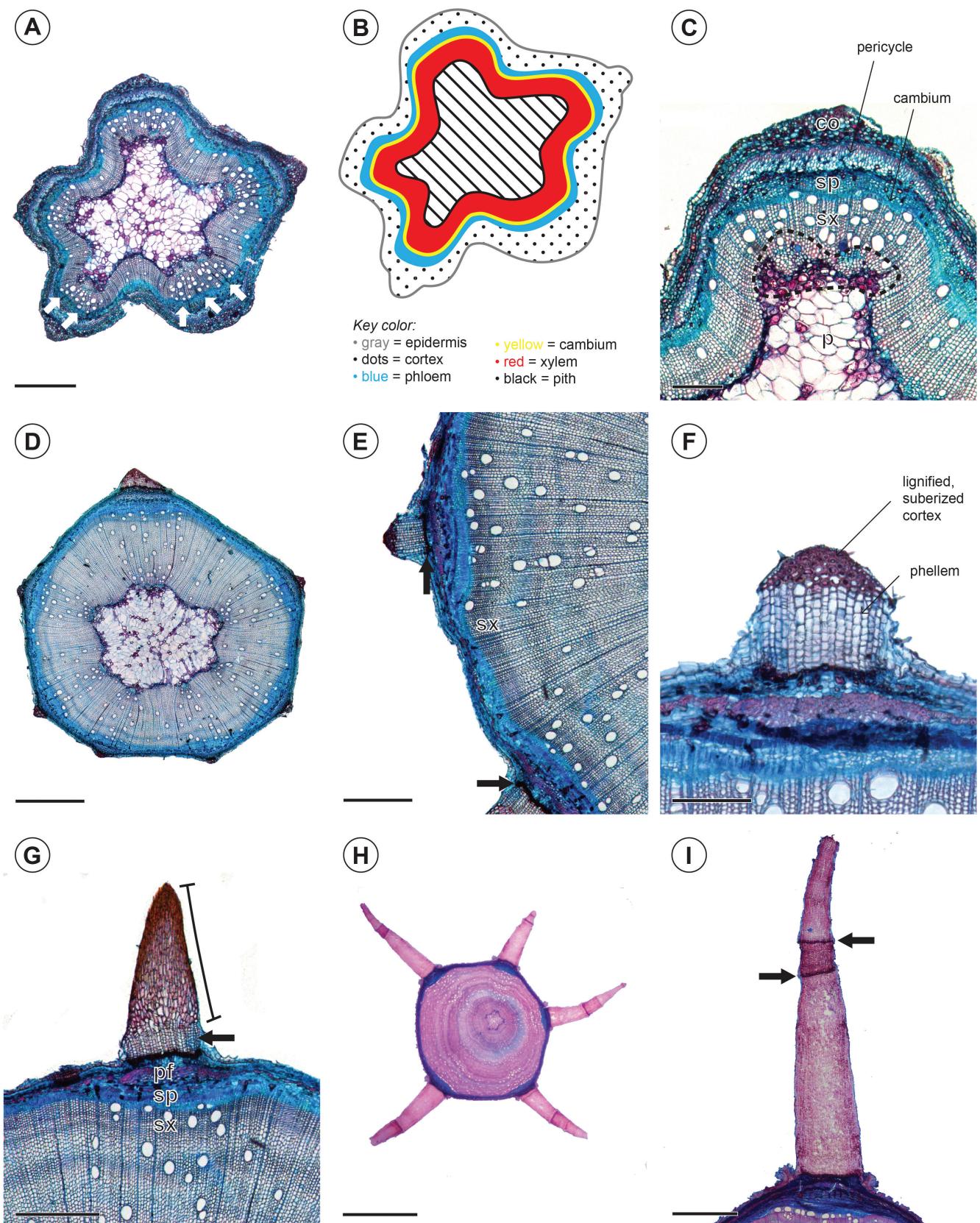


Figure 3. Development of mature bark wings, with stem in secondary growth. A, B, some of the lobes present in primary growth merge, resulting in five wings at this stage (indicated by the white arrows). C, detail of A showing primary xylem (pointed black lines), secondary xylem (sx), secondary phloem (sp), pericycle with external portion differentiated into fibres (note stronger red colour), cortex (co), and epidermis. D, more advanced stage of secondary growth, with wings entering their secondary stage of formation. Note their brown colour. E, phellogen formation (black arrows). F, detail of E showing cortex and phellem. G, a wing in development where a prickle was present previously (black line). Note the portion composed of phellem (black arrow). Abbreviations: pf = pericyclic fibres, sp = secondary phloem, sx = secondary xylem. H, entire stem cross-section, displaying five well-developed bark wings. I, marks of cessation of phellogen activity and its resumption are evident in older wings (black arrows). Scale bars: A, E, and G = 500 µm; C and F = 200 µm, D = 800 µm, H = 5000 µm, and I = 1250 µm.

stem shape, as the prickles of lobed *Bytneria* (Luna-Márquez *et al.* 2021), and with the spines (modified leaves) in lobed cacti (Soffiatti and Rowe 2020). Unlike other species, such as in *Ceiba* (Guía-Ramírez *et al.* 2021), where the prickles are formed by the phellogen, producing a large phellem prickle that is sometimes stratified, the prickles of *P. gonoacantha* are purely cortex and epidermis, which later become suberized.

Activity of the phellogen is much earlier in the lobes than in the interlobes, creating the conspicuous wings. More importantly, the phellogen producing the rings seem to switch on and off, leaving conspicuous marks in the phellem. The fact that the number of phellogen arrest marks corresponds exactly to the number of growth rings in the wood suggests strongly that both might be seasonal, and follow the same environmental triggers as the wood. Periderm growth rings are common (Serra *et al.* 2022). Periodic sampling studies are needed to confirm or rebut their seasonality in *P. gonoacantha*.

CONCLUSIONS

With the present ontogenetic analysis, we have shown that the bark wings in *P. gonoacantha* are directly related to the primary vascular system. Each bark wing is formed in front of a major vascular bundle, demonstrating that their development is not random, something that is probably true for most of the other species with bark wings.

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