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Bark anatomy of lianescent Bignoniaceae: a generic synopsis

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ABSTRACT

Species with lianescent habit account for half of the diversity of Bignoniaceae. Recent molecular phylogenetic studies have provided the basis for new circumscriptions of entire liana lineages within tribes Bignonieae and Tecomeae *s.s.*, where only monophyletic taxa are recognized. However, some clades remain without good morphological synapomorphies. In search of features of taxonomic potential, we collected, sectioned, and analyzed the bark of 83 lianescent species of the Bignoniaceae, covering all 20 genera from tribe Bignonieae currently recognized, plus three of the most widely cultivated lianas of Tecomeae *s.s.* Detailed bark descriptions are given to major lineages within both tribes, following their most recent phylogenetic hypotheses and classifications. Our anatomical studies allowed us to identify 19 potential synapomorphies for large clades or specific genera of lianas, such as the fibrous phloem found in members of the *Fridericia* Mart. emend L.G.Lohmann and allies clade, the exclusive presence of sclereids in the regular phloem of *Pleonotoma* Miers, and the presence of radially elongated fibers in *Manaosella* J.C.Gomes, among others. Using a combination of features, we were able to produce the first bark key to identify genera of lianescent Bignoniaceae. Our work reinforces the importance of bark features for a deeper understanding of taxonomic and phylogenetic relationships among taxa.

RÉSUMÉ
Anatomie de l'écorce des Bignoniaceae lianescentes : synopsis générique.
La moitié des Bignoniaceae sont des espèces à port lianescent. Des travaux récents ont proposé de nouveaux découpages dans les groupes entièrement lianescents, notamment pour les tribus des Bignonieae et des Tecomeae s.s. Nus avons ici rassemblé, sectionné et analysé les tiges de 83 Bignoniaceae grimpantes, comprenant tous les genres de Bignonieae et trois autres de Tecomeae s.s. largement cultivées, afin de trouver des caractères d'intérêt taxonomique permettant de décrire précisément la diversité anatomique de leurs écorces, en rapport avec les dernières phylogénies. Nous avons pu reconnaître 19 synapomorphies potentielles de la tige et de l'écorce à l'échelle de clades ou de genres lianescents, telles que – entre autres – le phloème fibreux des *Fridericia* Mart. emend L.G.Lohmann et alliés, la présence exclusive de sclérites dans le phloème régulier de *Pleonotoma* Miers, ainsi que de fibres étirées radialement chez *Manaosella* J.C.Gomes. La combinaison de ces caractères nous a permis de construire une première clé d'identification des écorces pour la détermination générique des Bignoniaceae lianescentes, même en l'absence de toute autre donnée morphologique. Nos résultats confirment l'importance de l'anatomie de l'écorce dans la compréhension de la taxonomie et de la phylogénie, et donc de la diversification.

MOTS CLÉS
Bignoniaceae,
cellules compagnes du phloème,
fibres phloémiennes,
lignification,
périderme,
phloème tertiaire,
rayon limitant,
sclérites phloémiennes.

INTRODUCTION

Bark is defined as all the tissues outside of the vascular cambium, encompassing two of the broadest and externalmost plant tissues: the secondary phloem (inner bark) and the periderm (outer bark) (Evert 2006; Angyalossy *et al.* 2016; Shtein *et al.* 2023). Both the phloem and the periderm are complex tissues, formed by more than one cell type, resulting from the activity of lateral meristems, the cambium, and the phellogen, respectively (Evert 2006). The periderm includes the phelloderm, the phellogen, and the phellem; while the secondary phloem typically includes sieve elements, axial parenchyma, rays, and sclerenchyma (either fibers, sclereids or both) (Esau 1969; Roth 1981; Angyalossy *et al.* 2016; Shtein *et al.* 2023). Differences in cell type, abundance, morphology, and configuration within these two broad tissues constitute rich sources of characters for phylogenetic studies (Rosell & Olson 2014). These tissues are fundamental to understand the adaptations of plants to their environments (Rosell & Olson 2014; Rosell *et al.* 2015, 2017), and likely impacted plant diversification patterns (Pace *et al.* 2015a).

The few bark studies published to date have shown that the bark can be diverse (*Eucalyptus* L'Hér, Myrtaceae; Chattaway 1953; Lauraceae; Richter 1981, 1985) or conserved (Combretaceae; Angyalossy-Alfonso & Richter 1991) within lineages. This duality has also been shown by Zahur (1959) and Roth (1981), authors of the largest treatments on bark anatomy to date. More importantly, features that are prone to the delimitation of a number of taxa within a clade, such as the type of dilatation tissue in the Dipterocarpaceae (Whitmore 1962) and Leguminosae (Costa *et al.* 1997), may be homogeneous within other groups (*Meryta* J.R.Forst. & G.Forst., Araliaceae; Oskolski *et al.* 2007). Therefore, additional studies of bark anatomy are fundamental to better understand the diversity of this tissue and to help characterize phylogenetic groups that are frequently delimited solely based on molecular characters or a few morphological features. Here, we characterize

the bark of lianescent members of two Bignoniaceae tribes, Bignonieae and Tecomeae *s.s.* (sensu Olmstead *et al.* 2009).

The Bignoniaceae are a pantropical family of trees, shrubs, and lianas (Gentry 1980; Olmstead *et al.* 2009), centered in tropical South America (Lohmann 2004; Fischer *et al.* 2004; Olmstead *et al.* 2009). The family includes many species of economical importance, especially due to their high-quality wood used for timber (e.g., *Paratecoma peroba* (Record) Kuhlm., several *Handroanthus* Mattos; Record & Hess 1972) and their ornamental value (e.g., *Tecoma stans* Juss., *Campsis radicans* (L.) Seem.; Lohmann 2004; Heywood *et al.* 2007; Pace *et al.* 2021). The bark of Bignoniaceae has been increasingly studied by Roth (1981) and Pace *et al.* (2011, 2015a, 2021). The former described rather similar bark types in two species of *Jacaranda* and three species of *Tabebuia* Gomes ex DC. (currently placed in *Handroanthus* (Grose & Olmstead 2007b). Namely, the bark of the studied taxa included concentric rings of fiber bands (stratified phloem *sensu* Angyalossy *et al.* 2016) alternating with sieve tubes and phloem parenchyma, interrupted by regular phloem rays that suffer little or no dilatation towards the nonconducting phloem. A different distribution of these fibers, scattered in the phloem instead of stratified, served as a basis to support the inclusion of *Astianthus* D.Don. within Tecomeae *s.s.*, and its position as sister to *Campsis* Lour., a taxon that shows identical fiber distribution (Pace *et al.* 2021; also explored here for *Campsis*). In turn, Pace *et al.* (2011, 2015a, 2021) studied differences between the regular and variant secondary phloem in lianas and explored how some variable key cell types evolved within Bignonieae, the largest Bignoniaceae tribe.

The Bignoniaceae are a large plant family, with *c.* 827 species in 87 genera (Olmstead *et al.* 2009). Despite the availability of those bark anatomical studies, a lot remains to be explored. The Bignoniaceae have undergone substantial taxonomic changes in the last decades (e.g., Spangler & Olmstead 1999; Zjhra *et al.* 2004; Grose & Olmstead 2007a; Olmstead *et al.* 2009; Lohmann & Taylor 2014;

TABLE 1. — Past and present taxonomic circumscription of the genera in Bignonieae according to Lohmann (2006). *, Species segregated from *Tanaecium* to a monophyletic *Bignonia*; **, species segregrated from *Pyrostegia* to a monophyletic *Cuspidaria*.

Clade num.	Clade in Phylogeny (Lohmann 2006; Fig. 1)	Presently accepted genus name (Lohmann & Taylor 2014), with updates from Fonseca & Lohmann 2019	Genera according to the previous classification (Fischer *et al.* 2004)
I	Perianthomega	*Perianthomega* Bureau ex Baill.	*Perianthomega*
II	Stizophyllum	*Stizophyllum* Miers	*Stizophyllum*
III	Martinella	*Martinella* Baill.	*Martinella*
IV	Pleonotoma	*Pleonotoma* Miers	*Pleonotoma*
V	Manaosella	*Manaosella* J.C.Gomes	*Manaosella*
VI	Leucocalantha	*Pachyptera* DC. ex Meisn.	*Leucocalantha*, Part of *Mansoa* (2 species), *Pachyptera*
VII	Arrabidaea and allies clade; Lundia	*Lundia* DC.	*Lundia*
VIII	Arrabidaea and allies clade; Cuspidaria s.l. clade	*Cuspidaria* DC.	Part of Arrabidaea (4 species), *Cuspidaria*, *Pyrostegia cinerea***, *Saldanhaea*
	Arrabidaea and allies clade; Tynanthus	*Tynanthus* Miers	*Tynanthus*
IX	Arrabidaea and allies clade; True Arrabiaea clade	*Fridericia* Mart. emend L.G.Lohmann	Most *Arrabidaea* (more than 50 species), *Fridericia*, *Piriadacus*, *Sampaiella*
	Arrabidaea and allies clade; Xylophragma s.l. clade	*Xylophragma* Sprague	Part of *Arrabidaea* (2 species), *Xylophragma*
X	Arrabidaea and allies clade; Bromeliad clade	*Tanaecium* Sw. emend L.G.Lohmann	Part of *Arrabidaea* (4 species), *Ceratophytum*, *Pseudocatalpa*, *Spathicalyx*, *Sphingiphila*, *Paragonia*, *Periarrabidaea*
X	Incertae sedis; Sphingiphila	*Tanaecium* Sw. emend L.G.Lohmann	*Sphingiphila*
XI	Callichlamys	*Callichlamys* Miq.	*Callichlamys*
XII	core Multiples of four clade; Anemopaegma	*Anemopaegma* Mart. ex Meisn.	*Anemopaegma*
	core Multiples of four clade; Mansoa	*Mansoa* DC.	*Mansoa* (excluding 2 species now placed in *Pachyptera*)
	core Multiples of four clade; Pyrostegia	*Pyrostegia* C.Presl	*Pyrostegia* (excluding 1 species now placed in *Cuspidaria*)
	core Multiples of four clade; Mimetic clade	*Bignonia* L.	*Bignonia*, *Cydista*, *Clytostoma*, *Macranthisiphon*, *Mussatia*, *Phryganocydia*, *Potamoganos*, *Saritaea*, *Roentgenia*, *Tanaecium nocturnum**
XIII	Multiples of four clade; Pithecoctenieae clade	*Amphilophium* Kunth emend L.G.Lohmann	*Amphilophium*, *Distictella*, *Distictis*, *Glaziova*, *Haplolophium*, *Pithecoctenium*
XIV	Cat's claw clade	*Dolichandra* Cham. emend L.G.Lohmann	*Dolichandra*, *Macfadyena*, *Melloa*, *Parabignonia*
XV	SMANG clade; Gardnerodoxa-Neojobertia	*Adenocalymma* Mart. ex Meisn. emend L.G. Lohmann	*Gardnerodoxa*, *Neojobertia*
XV	SMANG clade; Volcano gland clade	*Adenocalymma* Mart. ex Meisn. emend L.G.Lohmann	*Adenocalymma*, *Memora*

Callmander *et al.* 2016; Ragsac *et al.* 2019, 2021; Calió *et al.* 2022; Fonseca *et al.* 2023). The recent taxonomic treatments based on molecular phylogenetic data provide an important framework for comparative morpho-anatomical studies within this group, allowing us to explore previously neglected characters of taxonomic importance and study their evolutionary history. Tribe Bignonieae currently encompasses 20 genera (Lohmann & Taylor 2014; Fonseca & Lohmann 2018), instead of the 47 genera formerly recognized (Fischer *et al.* 2004; Table 1). Under the current circumscription (Lohmann & Taylor 2014) it also includes *Perianthomega* Bureau ex Baill., a genus previously treated within Tecomeae *s.l.* (Gentry 1992; Fischer *et al.* 2004). It is among the largest groups of lianas in the Neotropics (Gentry 1991; Lohmann 2006), including substantial variation in flower traits (Alcantara & Lohmann 2010, 2011), extra-floral nectaries (Nogueira *et al.* 2012, 2013, 2016), tendril morphology (Sousa-Baena *et al.* 2014), and wood anatomical traits (Pace *et al.* 2009, 2015a, b, 2016; Pace &

Angyalossy 2013; Gerolamo & Angyalossy 2017; Gerolamo *et al.* 2020). Stems of members of Bignonieae have been the focus of anatomical studies since the XIXth and XXth centuries (Schenck 1893; Solereder 1908; Chodat & Vischer 1917). The attention devoted to the wood anatomy of Bignonieae is largely due to the variant secondary growth, with the alteration of four to multiple of four portions of the cambium that produce less xylem and more phloem, giving the stems a typical architecture of a "Malta Cross" when sectioned (Dobbins 1971, 1981). Characters from stem and wood anatomy (Dos Santos 1995) support clades within this tribe (Lohmann 2003, 2006). The importance of wood anatomy in systematic studies of the Bignoniaceae has grown substantially during the past three decades (Dos Santos & Miller 1992, 1997; Dos Santos 1995; Pace & Angyalossy 2013; Pace *et al.* 2015b), contributing important information for an improved circumscription of enigmatic genera within the family (Pace *et al.* 2016, 2021) and allowing to place fossil wood at the generic rank (Moya & Brea
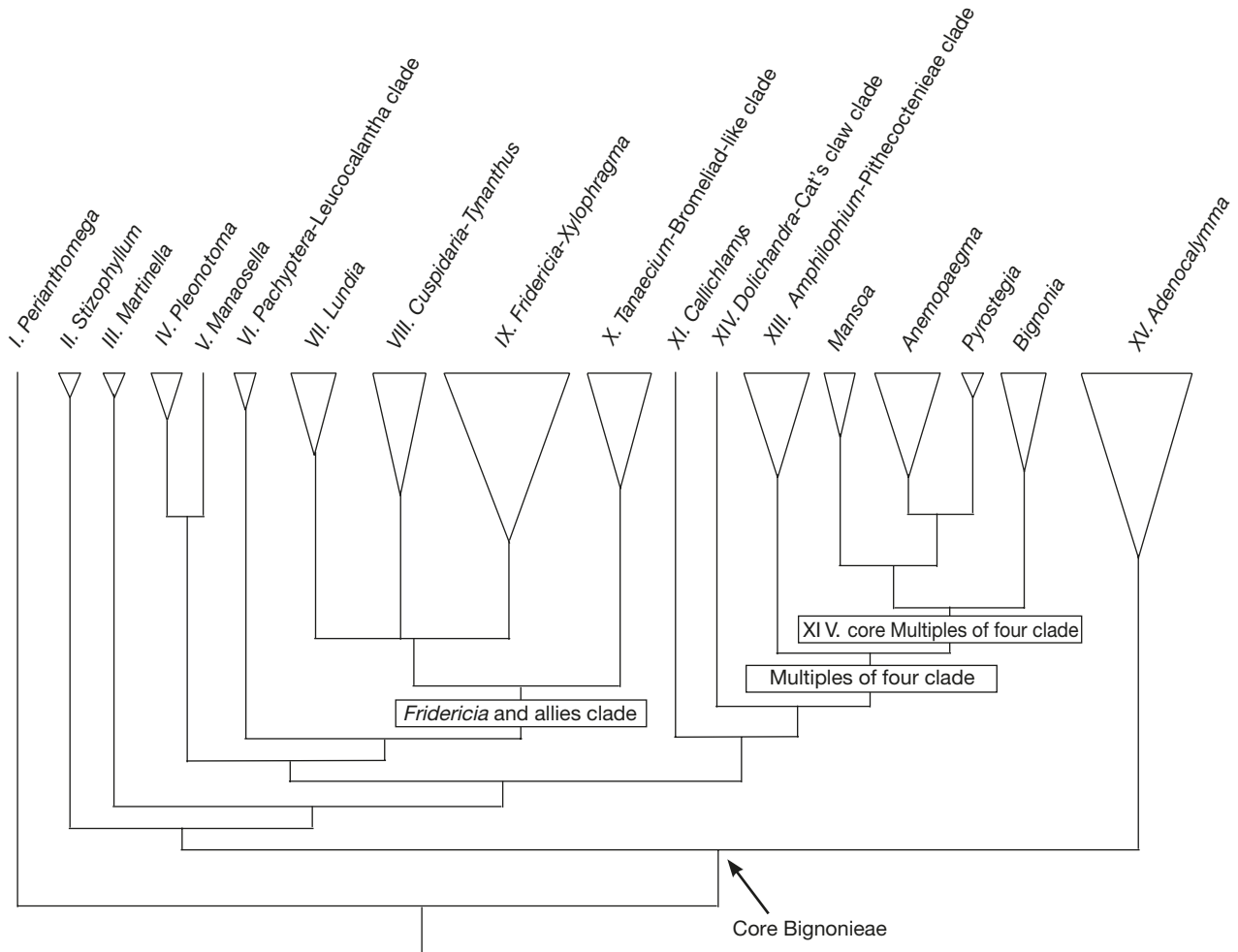
Fig. 1. — Phylogeny of tribe Bignonieae (modified from Lohmann 2006) indicating the fifteen clades delimited based on bark morphology.

2018; Franco *et al.* 2021). Here we aim to: i) describe the phloem and periderm anatomy of all 20 genera currently recognized within tribe Bignonieae, plus the three most cultivated lianescent genera of Tecomeae s.s. (i.e., *Campsis*, *Pandorea* Spach, and *Podranea* Sprague); ii) search for potential phloem characters that could represent anatomical synapomorphies for specific clades within both Bignonieae and Tecomeae *s.s.*; and iii) produce a key to identify genera within those lineages using phloem features.

MATERIAL AND METHODS

Taxon sampling and anatomical procedures
Eighty (80) species representing all 20 genera currently recognized in tribe Bignonieae (Lohmann & Taylor 2014; Fonseca & Lohmann 2018) plus the three of the most widely cultivated ornamental lianas of Tecomeae *s.s.*, i.e., *Campsis radicans*, *Pandorea jasminoides* (Lindl.) K.Schum., and *Podranea ricasoliana* Sprague, were sampled either in the field or from living collections, with some additional samples obtained from wood collections (Appendix 1,

including authorities for the species names). Because stems with similar diameters represent better proxies for the multiple qualities of the stems than their absolute age (Pace *et al.* 2009), we selected stems with a diameter of *c.* 2 cm for our analyses; this diameter represents the most frequent diameter encountered for lianas in tropical forests (Gerwing *et al.* 2006). Whenever possible, stems of wider diameters were also sampled to ensure that no extreme differences would be missed with aging. All samples were immediately fixed in the field, either with 70% formalin acetic-acid ethanol (FAA 70; Berlyn & Miksche 1976) or Karnovsky's (1965) solution, to guarantee that the soft fragile tissues of the bark were preserved. After one week, all samples were transferred to a solution of 70% ethanol.

Since the bark is generally characterized by the presence of lignified sclerenchymatic stiff tissues occurring together with soft primary-walled cells, we followed the techniques described by Barbosa *et al.* (2010, 2018) to obtain good transverse, longitudinal radial, and longitudinal tangential sections. The sections were double stained either in Astrablue and safranin (Bukatsch 1972) or in lacmoid and acid-ferric chloride (Cheadle *et al.* 1953) and mounted either in syn-

TABLE 2. — Description of the periderm of the lianas of Bignoniaceae.

| Species | Rhytidome | Phellem | | | | | Phelloderm | | | | | Lenticel's filling tissue (when observed) | | |
| | | Non-stratified | | Stratified | | | | | | Stratified | | Non-stratified | | |
		Evenly thin walled	Evenly thick walled	Thick and thin walled cells alternating	Cells with dark contents alternating with other cells	Presence of crystals	Thin: with less than 3 layers of cells	Thick: with over 3 layers of cells	Non-stratified	Thick and thin walled cells alternating	Cells with dark contents alternating with regular cells	Filling cells unlignified	Filling cell lignified	Stratified: with closing layer lignified
Adenocalymma alboaurantiacum	–	+	–	–	–	–	–	+	+	–	–	?	?	?
Adenocalymma bracteatum	–	+	–	–	–	–	–	+	+	–	–	?	?	?
Adenocalymma comosum	–	–	+	–	–	–	+	–	+	–	–	+	+	+
Adenocalymma divaricatum	–	–	+	–	–	–	–	+	+	–	–	–	+	–
Adenocalymma flaviflorum	+	+	–	–	–	–	–	+	+	–	–	+	–	–
Adenocalymma mirabile	–	–	–	+	–	–	–	+	+	–	–	?	?	?
Adenocalymma peregrinum	–	+	–	–	–	–	+	–	+	–	–	+	+	+
Adenocalymma salmoneum	–	+	–	–	–	–	–	+	+	–	–	+	+	+
Adenocalymma validum 1	–	–	–	+	–	–	–	+	+	–	–	?	?	?
Adenocalymma validum 2	–	–	–	+	+	–	–	+	+	–	–	+	+	+
Amphilophium crucigerum	–	–	–	+	–	+	–	+	+	–	–	+	+	+
Amphilophium elongatum	–	+	–	–	–	–	+	–	+	–	–	+	–	–
Amphilophium magnoliifolium	–	+	–	–	–	–	–	+	–	–	+	+	–	–
Amphilophium paniculatum	–	+	–	–	–	–	–	+	–	–	+	+	–	–
Anemopaegma chamberlaynii	–	+	–	–	–	–	+	–	+	–	–	+	–	–
Anemopaegma laeve	–	–	+	–	–	–	+	–	+	–	–	?	?	?
Anemopaegma robustum	–	+	–	–	+	–	–	+	+	–	–	?	?	?
Bignonia binata	–	+	–	–	–	–	–	+	+	–	–	?	?	?
Bignonia campanulata	–	+	–	–	–	–	–	+	+	–	–	+	–	–
Bignonia capreolata	–	–	–	+	–	–	–	+	+	–	–	?	?	?
Bignonia magnifica	–	+	–	–	–	–	–	+	+	–	–	+	–	–
Bignonia sciuripabula	–	–	–	+	–	–	–	+	+	–	–	+	–	–
Callichlamys latifolia	–	+	–	–	–	–	–	+	+	+	–	+	–	–
Campsis radicans	+	+	–	–	–	–	+	–	+	–	–	?	?	?
Cuspidaria convoluta	–	–	–	+	–	–	–	+	+	–	–	+	+	+
Cuspidaria pulchra	–	+	–	–	–	–	–	+	+	–	–	+	–	–
Dolichandra quadrivalvis	–	–	–	+	–	–	+	–	+	–	–	?	?	?
Dolichandra unguiculata	–	–	–	+	–	–	+	–	+	–	–	?	?	?
Dolichandra unguis–cati	–	–	–	+	–	–	+	–	+	–	–	?	?	?
Fridericia chica	+	+	–	–	–	–	–	+	+	–	–	?	?	?
Fridericia conjugata	+	+	–	–	–	–	–	+	+	–	–	?	?	?
Fridericia nigrescens	–	–	–	+	–	–	–	+	+	–	–	?	?	?
Fridericia platyphylla	–	–	+	–	–	–	–	+	–	+	–	?	?	?
Fridericia samydoides	–	+	–	–	–	–	–	+	–	+	–	+	+	+
Fridericia speciosa	–	–	+	–	–	–	–	+	+	–	–	+	–	–
Fridericia triplinervia	–	–	+	–	–	–	–	+	+	–	–	?	?	?
Lundia corymbifera	–	+	–	–	–	–	–	+	+	–	–	+	–	–
Lundia longa	–	–	–	+	–	–	–	+	+	–	–	?	?	?
Lundia virginalis	–	+	–	–	–	–	–	+	+	–	–	+	–	–
Manaosella cordifolia	–	–	–	+	–	–	+	–	–	–	–	+	–	–
Mansoa difficilis	–	+	–	–	–	–	–	+	+	–	–	+	–	–
Mansoa onohualcoides	–	+	–	–	–	–	–	+	+	–	–	?	?	?
Pachyptera aromatica	–	–	+	–	–	–	–	+	+	–	–	?	?	?
Pachyptera kerere	–	–	+	–	–	–	–	+	+	–	–	?	?	?
Pandorea jasminoides	–	+	–	–	–	–	–	+	+	–	–	–	+	–
Perianthomega vellozoi	–	+	–	–	–	–	–	+	+	–	–	–	+	–
Pleonotoma tetraquetra	–	–	–	+	–	–	–	+	+	–	–	?	?	?
Podranea ricasoliana	+	+	–	–	–	–	+	–	+	–	–	?	?	?
Pyrostegia venusta	–	–	–	+	–	–	–	+	+	–	–	?	?	?
Stizophyllum riparium	–	–	–	+	–	–	–	+	+	–	–	?	?	?
Tanaecium bilabiatum	–	+	–	–	–	–	–	+	+	–	–	?	?	?
Tanaecium pyramidatum	–	–	–	+	–	–	–	+	+	–	–	–	+	–
Tanaecium tetramerum	–	–	–	+	–	–	–	+	+	–	–	?	?	?
Tynanthus cognatus	–	–	–	+	–	–	–	+	+	–	–	+	–	–
Tynanthus elegans	–	–	–	+	–	–	–	+	+	–	–	+	–	–
Xylophragma myrianthum	–	+	–	–	–	–	–	+	+	–	–	+	–	–

thetic resin or Canada balsam to produce permanent slides. For details in the phloem, some samples were imbedded in methacrylate copolymers (HistoResin – Leica, Germany), sectioned with the aid of a rotary microtome, and stained with 0.05% toluidine blue (O'Brien *et al.* 1964).

Anatomical analysis and terminology adopted
Samples were analyzed qualitatively for their phloem anatomy, taking into consideration the transverse, longitudinal radial, and tangential sections. The terminology adopted here follows Trockenbrodt (1990), Angyalossy-Alfonso & Richter (1991), Richter *et al.* (1996), and the IAWA Bark List (Angyalossy *et al.* 2016), except for the cases described below.

Phloem wedges and interwedges (regular and variant phloem)
According to the terminology proposed by Ozório-Filho (2002), Pace *et al.* (2009), and Lima *et al.* (2010) for Bignoniaceae, phloem wedges correspond to the four to multiples of four regions of the stem where more phloem than xylem is produced, conferring the aspect of a "Malta Cross" in the adult stems. In turn, the interwedges correspond to the regions between the phloem wedges, where the cambium maintains a regular activity. Hence, the variant phloem is located within the phloem wedges, whereas the regular phloem is located in the interwedges.

Limiting rays
In all plants with phloem wedges, the formation of wide and multiseriate rays at both sides, flanking the wedges (Angyalossy *et al.* 2015), is common. These wide rays were first noticed by Schenck (1893), who named them "begrenzenden Markstrahlen," referring to limiting rays, in German. We here abide to this same nomenclature, which has been used in all subsequent literature of the family (Dobbins 1969, 1970, 1971, 1990; Pace *et al.* 2009, 2015a).

Fibrous, semi-fibrous, and non-fibrous phloem
Fibers are present in the variant phloem of all species of Bignonieae, where they show three different arrangements: i) Non-fibrous, with clear fiber bands alternating with more than 10 rows of phloem parenchyma and sieve tubes between them; ii) Semi-fibrous, with fiber bands more closely arranged, tending to form a wavy pattern intermingling all other axial cell types and showing less than 10 rows of phloem and ray parenchyma among them; and iii) Fibrous, with fibers forming the ground tissue where all other cell types are inserted.

Assemblages
Assemblage is the name given for a group of sieve elements, companion cells, and axial parenchyma cells that are derived from the same fusiform cambial derivative and which can be recognized as such thanks to the fact that together they present the same size and outline of a neighboring parenchyma cell.

RESULTS

The results from this work are presented in five sections, as follows:
Section 1: Periderm diversity in Bignoniaceae lianas;
Section 2: Stems and cambial variants of Bignoniaceae lianas;
Section 3: Bark anatomical features shared among Bignonieae lianas;
Section 4: Bark description of major Bignonieae and Tecomeae s.s. clades;
Section 5: Key for the identification of liana Bignoniaceae genera using bark anatomy.

Section 1: Periderm diversity in Bignoniaceae lianas
Because the periderm of the liana Bignoniaceae studied here was shown to be extremely variable, even within genera, we chose to summarize and illustrate the overall periderm diversity encountered within this section. Complete periderm descriptions for each taxon can be found in Table 2. A generic description of the periderm per genus is given in section 3 and illustrated when something unique to that genus was found.

All species studied here have a periderm originated in the outer cortical layers under the epidermis (Fig. 2A). Most commonly, species have just one periderm formed during their entire life span (Table 2), even if with a conspicuous phellem (Fig. 2B). A few species within *Adenocalymma* Mart. ex Meisn. emend L.G.Lohmann and *Fridericia* Mart. emend L.G.Lohmann (tribe Bignonieae), and *Podranea* (tribe Tecomeae *s.s.*), form sequent periderms, i.e., a rhytidome (Fig. 2C, D) that is always reticulate, with one periderm at some point merging with another (Fig. 2D). The phellem constitutes the most diverse periderm tissue, either forming evenly thick-walled and lignified cells (Fig. 2E) or evenly forming thin-walled cells (Fig. 2F). The phellem was often stratified, marked by the alternation of thin and thick-walled cells (Fig. 2H-J) or cells with and without dark contents (Table 2). The phelloderm was either thin, formed by three or fewer cell layers (Fig. 2F, H) or, more commonly (Table 2), thick, with three cell layers or more (Fig. 2G, I, J). Only rarely the phelloderm showed dark contents (Fig. 2G) or a lignified layer (Table 2). Prismatic crystals were common only in the phellem of *Amphilophium crucigerum* (L.) L.G.Lohmann (Fig. 15A, B).

Lenticels were not always found, often lacking in species with rhytidomes and stratified phellem (Table 2). When present, lenticels were of three types according to their filling tissue: (i) Non-stratified, with only unlignified cells (Fig. 2K), (ii) Non-stratified, with mostly lignified phellem cells (Fig. 2L), or (iii) Mostly unlignified, except for the closure layers (Fig. 2M).

Section 2: Stems and cambial variants of Bignoniaceae lianas
Overall stem anatomical architecture
One of the most conspicuous features of numerous lianescent Bignoniaceae is the presence of a cambial variant known as xylem furrowed by phloem wedges. This feature has been extensively explored in previous works (see introduction). Below we describe how the shape and number of phloem
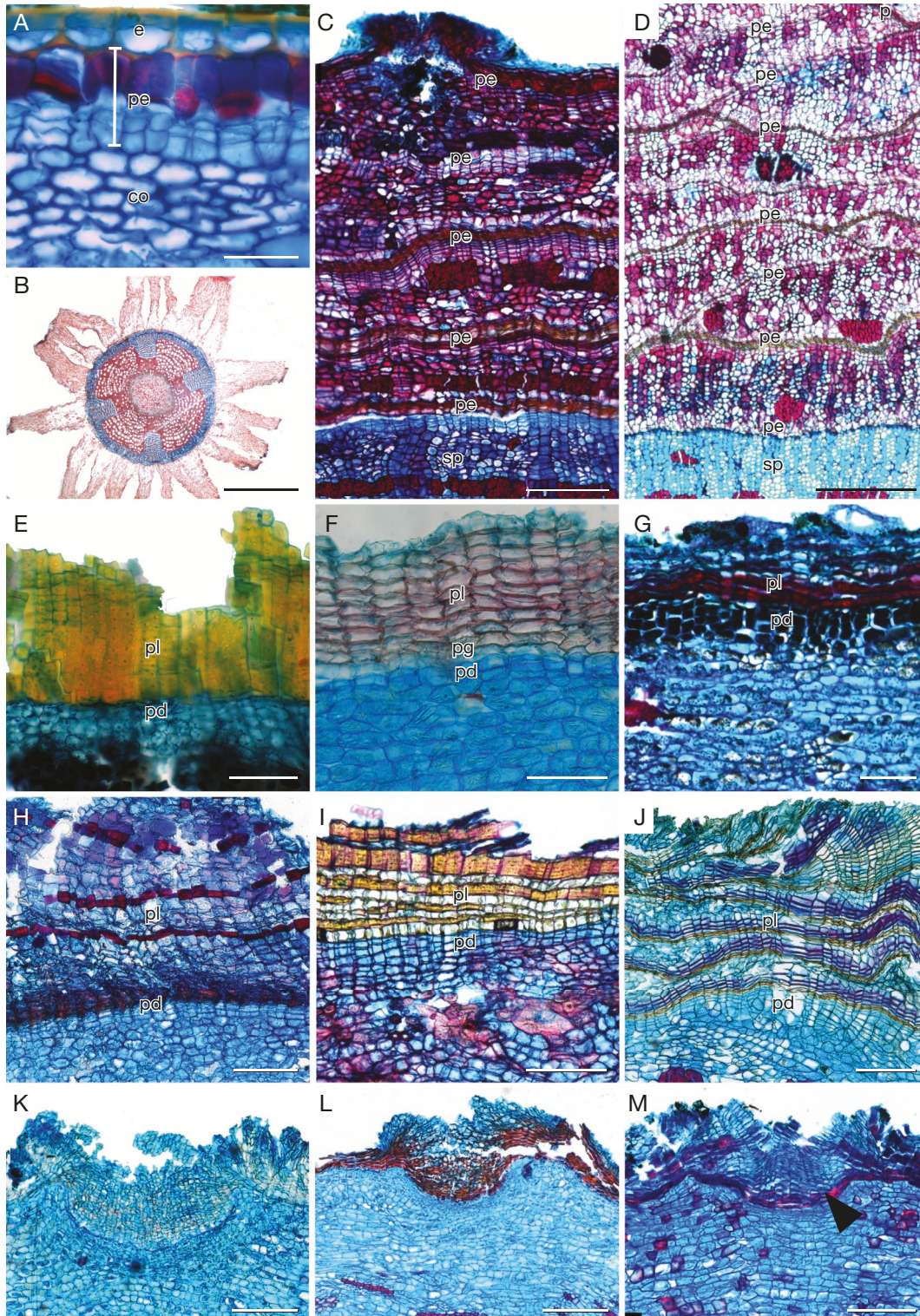
FIG. 2. — Transverse sections: **A**, cortical periderm origin, *Anemopaegma chamberlaynii*; **B**, single periderm, with a very thick phellem, *Adenocalymma alboaurantiacum*; **C**, rhytidomes (sequent periderms) in *Fridericia chica*; **D**, rhytidome with reticulate periderms conspicuous, *Podranea ricasoliana*; **E**, phellem with evenly thick-walled, lignified cells, and phelloderm thin, *Pachyptera aromatica*; **F**, phellem with evenly thin-walled cells, phelloderm thin, *Perianthomega vellozoi*; **G**, stratified phellem, with alternating thick walled, lignified cells, and thin walled, unlignified cells, phelloderm with dark contents, *Mansoa onohualcoides*; **H**, stratified phellem, with many layers of thin-walled cells alternating with thick walled, lignified cells, phelloderm thick, *Lundia longa*; **I**, stratified phellem, with alternating layers of thin walled and thick walled, lignified cells, phelloderm thick, *Fridericia nigrescens*; **J**, stratified phellem, with some layers of thin-walled cells alternating with thin walled, lignified cells, phelloderm thick, *Pleonotoma tetraquetra*; **K**, lenticel non-stratified, with filling tissue homogeneous, non-lignified, *Lundia corymbifera*; **L**, lenticel non-stratified, with filling tissue homogeneous, lignified, *Mansoa difficilis*; **M**, lenticel stratified, with most of the filling tissue non-lignified, except for the closing layer (arrowhead, *Adenocalymma comosum*). Abbreviations: **co**, cortex; **e**, epidermis; **pd**, phelloderm; **pe**, periderm; **pg**, phellogen; **pl**, phellem; **sp**, secondary phloem. Scale bars: A, 50 µm; B, 8 mm; C, H-L, 200 µm; D, 500 µm; E-G, M, 100 µm.

Intraxylary phloem | Wavy cambium | Wavy cambium

A | B | C

Type 1: Phloem arcs | Type 2: Four phloem wedges | Type 3: Four phloem arcs in shrubs

D | E | F

Type 4: Multiples of four phloem wedges | Type 5: Multidissected phloem wedges | Type 6: Included phloem wedges
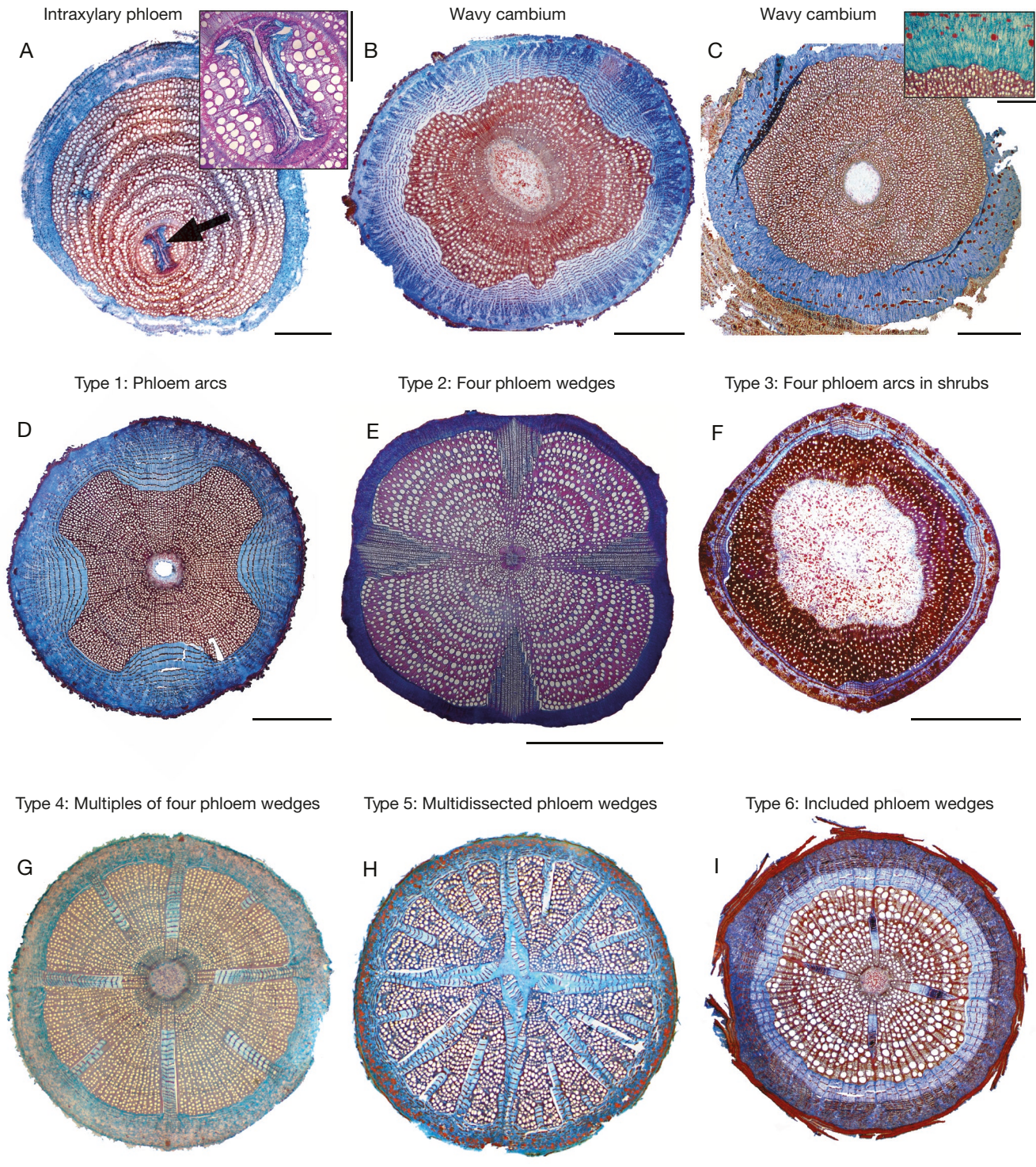
G | H | I

FIG. 3. — Stem cross-sections illustrating the diversity of stem architectures in Bignoniaceae lianas: **A**, *Campsis radicans*, transverse section (**TS**). Phloem wedges absent. Intraxylary secondary phloem and xylem present, note center of the pith totally occupied in the insert, giving a dumbbell shape to the pith; **B**, *Pandorea jasminoides*, TS, irregular, wavy cambium, forming irregular shallow arcs; **C**, *Podranea ricasoliana*, TS, irregular, wavy cambium. Insert: narrow waves of the cambium; **D**, *Perianthomega vellozoi*, TS, Type 1, four wide phloem arcs; **E**, *Tynanthus cognatus*, TS, Type 2, four phloem wedges; **F**, *Adenocalymma nodosum*, TS, Type 3, four phloem arcs, variant cambium without anticlinal divisions; **G**, *Mansoa onohualcoides*, TS, Type 4, multiple of four phloem wedges; **H**, *Dolichandra unguis-cati*, TS, Type 5, multiple dissected phloem wedges; **I**, *Amphilophium crucigerum*, TS, Type 6, included phloem wedges. Scale bars: 0.5 cm. Scale bars in inserts: 2 mm.

wedges can help to sort genera in the family. A xylem furrowed by phloem wedges is a feature exclusive of tribe Bignonieae, lacking in the lianas belonging to other Bignoniaceae tribes, such as the three lianas from Tecomeae *s.s.* treated here: *Campsis radicans* (Fig. 3A), *Pandorea jasminoides* (Fig. 3B), and *Podranea ricasoliana* (Fig. 3C). In turn, these three lia-
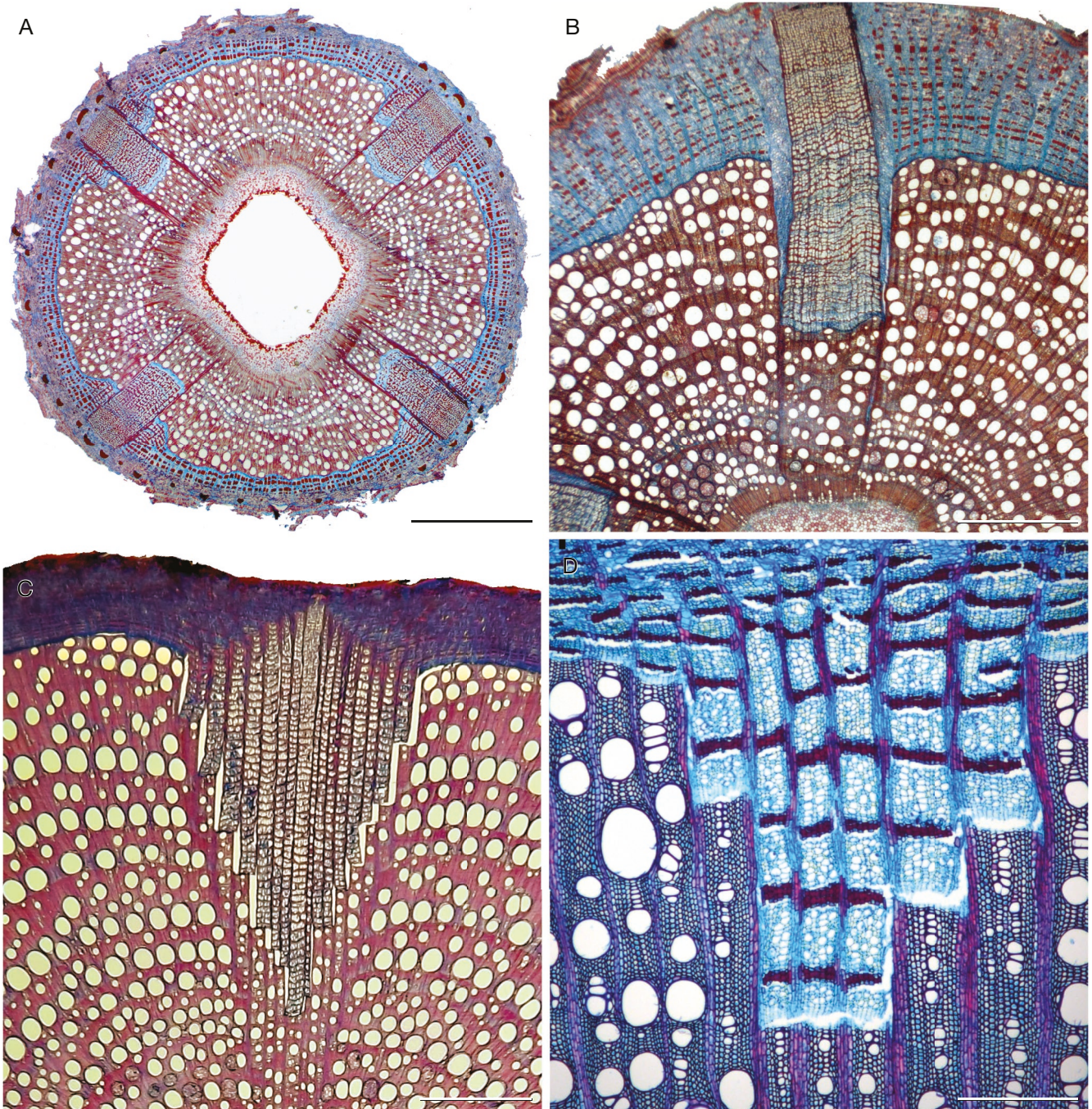
Fɪɢ. 4. — Overall stem architecture of Bignoniaceae lianas: **A**, *Stizophyllum riparium*, transverse section (**TS**), stem with four phloem wedges. Hollow stem. Note phloem wedge with lateral steps; **B**, *Tanaecium pyramidatum*, TS, Phloem wedge devoid of lateral steps. Extremely wide rays limit the phloem wedges; **C**, *Tynanthus cognatus*, TS, Narrow lateral steps forming an almost perfect V pattern; **D**, *Mansoa difficilis*, wide steps, not forming a perfect V pattern. Scale bars: A, 0.5 cm; B, 1 mm; C, 400 µm; D, 200 µm.

nas show other conspicuous features. *Campsis radicans* is the only species with intraxylary secondary phloem and xylem (Fig. 3A), which can be perceived as darker areas in the pith periphery (Fig. 3A insert). The secondary growth in the pith progresses until all the space has been occupied, leaving a conspicuous shape of a dumbbell (Fig. 3A). *Pandorea jasminoides* (Fig. 3B) and *Podranea ricasoliana* (Fig. 3C) both display a wavy cambium. In *Pandorea* the cambium gives the impression of phloem wedges or arcs in some portions (Fig. 3B). In *Podranea* the waviness of the cambium happens in narrower cambial portions (see insert in Fig. 3C), never resembling phloem wedges (Fig. 3C).

Within tribe Bignonieae, cambial variants are present in all species studied so far, except for the very unusual South American Chaco-endemic treelet *Tanaecium tetramerum* (A.H.Gentry) Zuntini & L.G.Lohmann (see further details under *Tanaecium* Sw. emend L.G.Lohmann). Six homologous main anatomical types have been established (see Pace *et al.*

2009) and are followed here. Two types are marked by the presence of four phloem arcs: *Perianthomega* (named Type 1; Fig. 3D), and the shrubby *Anemopaegma* Mart. ex Meisn., *Cuspidaria* DC., and *Fridericia* (named Type 3; Fig. 3F). These are described as two different types, because shrubs are considered an underdeveloped phenomenon of Type 2 (Fig. 3E; described below), a typical feature of the self-supporting habit. The extent of the phloem arcs in *Perianthomega* is much wider, being easily distinguishable from the shrubs, which have almost unnoticeable phloem arcs.

The most common type in tribe Bignonieae is Type 2 (Fig. 3E), which is marked by four deep phloem wedges, formed during early stages of stem ontogeny and maintained throughout the plant's life span. This type is found in most *Adenocalymma*, all *Cuspidaria*, the species-rich *Fridericia* (which reunite most of the former *Arrabidaea* DC.), *Manaosella* J.C.Gomes, *Martinella* Baill., *Pachyptera* DC., *Pleonotoma* Miers, *Stizophyllum* Miers, *Tanaecium*, *Tynanthus* Miers, and *Xylophragma* Sprague.

The second most common type, named Type 4, is marked by the presence of multiples of four phloem wedges (Fig. 3G), which are formed between the first four phloem wedges, progressing with the formation of 8, 16, 32, and 64 phloem wedges, exponentially. This feature is characteristic of the mature stems of some *Adenocalymma*, all *Lundia* DC., and all species included in the multiples of four clade: *Anemopaegma*, *Bignonia* L., *Mansoa* DC., and *Pyrostegia* C.Presl. (Fig. 1).

The two remaining types found in Bignonieae are restricted to individual genera. Type 5 is typical of *Dolichandra* Cham. emend L.G.Lohmann and marked by the presence of multiple-dissected phloem wedges (Fig. 3H). Type 5 resembles Type 4 (multiples of four phloem wedges; Fig. 3G), but because *Dolichandra* is the only genus in the family with non-lignified wood axial and ray parenchyma, this parenchyma undergoes divisions dissecting the wood, with portions of the phloem merging with the pith (Fig. 3H). The last type, Type 6, is exclusive of members of *Amphilophium* Kunth emend L.G.Lohmann and is marked by the inclusion of four to multiples of four phloem wedges within the wood (Fig. 3I), a type of interxylary phloem that is restricted to this genus. Four to multiples of four phloem wedges are originally formed, but then the cambium seals the wedges at the flanks, producing wood on top of these wedges, and including these portions of phloem in the wood (Fig. 3I).

It is worth mentioning that, for the species with phloem wedges, the formation of lateral steps while the stem increases in girth is common (Fig. 4A, C, D). These steps correspond to flanking areas that switch from a regular to a variant activity. The only known exception to this pattern is *Tanaecium* (Fig. 4B), which lacks these lateral steps, even in very thick stems. For all other genera, lateral steps are formed, but some form very narrow steps, almost perfectly symmetrical on each side, forming a distinctive V pattern outward (Fig. 4C); this pattern is most conspicuous within the clade formed by *Cuspidaria* and *Tynanthus* (Fig. 1; 4C). All other species form much wider, more asymmetrical steps, that rarely form a perfect V pattern (Fig. 4D). *Stizophyllum* belongs to this group and can also be recognized by the hollow stems (Fig. 4A).

SECTION 3: BARK ANATOMICAL FEATURES SHARED AMONG BIGNONIEAE LIANAS

Given the presence of variant secondary growth, the Bignonieae lianas form regular phloem between the phloem wedges and variant phloem within the phloem wedges (Fig. 6A). We first describe common features in each phloem type. We then explore clade by clade and describe the features that characterize each lineage.

Regular phloem

For all Bignonieae, the secondary phloem of the interwedges is rather homogeneous, with many features that are identical among taxa. Here we provide a description of features that are shared among all genera. Only two characters were variable, the arrangement of sieve-tube elements, which often appear in assemblages (Fig. 5A insert) and the thickness of fiber bands, which vary from thin (three or fewer rows of fibers per fiber band) or thick (more than three rows of fibers per fiber band) (Fig. 5B); these characters will be treated in detail in each genus or clade. The full description of the features that are common among genera is provided below.

Conducting phloem. The conducting phloem consists of sieve-tube elements associated with their companion cells on the corner of the elements and phloem axial parenchyma alternating with fiber bands, interrupted only by the rays (Fig. 5A, B). Rays are generally multiseriate (Fig. 5A-C) and are higher than 1 mm, as seen in tangential section (Fig. 5C). Fibers are absent only in *Pleonotoma*, where sclereids are found instead (further treated in genus *Pleonotoma*). The sieve-tube elements are generally found in multiples of 2-4, rarely solitary. The sieve-tube elements are scattered in a matrix of phloem parenchyma, forming radially organized rows (Fig. 5A), only interrupted by the sieve-elements. Sieve-tubes are always smaller than 500 μm, as seen in longitudinal section (Fig. 5C).

Nonconducting phloem. The cessation of function of sieve-elements starts right after the first fiber band and is marked by the accumulation of definitive callose at the sieve-plates (Fig. 5D), expansion of the phloem parenchyma cells and ray dilatation (Fig. 5E), immediately followed by the total collapse of the sieve-tubes (Fig. 5D). Dilatation meristems are found in many species (Fig. 5E). Dilatation growth largely involves the phloem axial and ray parenchyma cells, some of which undergo belated sclerosis (Fig. 5F).

Variant phloem portion

The variant phloem is located in the phloem arcs/wedges (Fig. 6A). Unlike the regular phloem, the variant phloem in Bignonieae displays much diversity, with remarkable differences in phloem characters among genera, and sometimes even within a single genus. In this section, we treat the features that are common to all genera.

Conducting phloem. The sieve elements on the conducting phloem are generally arranged in multiples, sometimes soli-
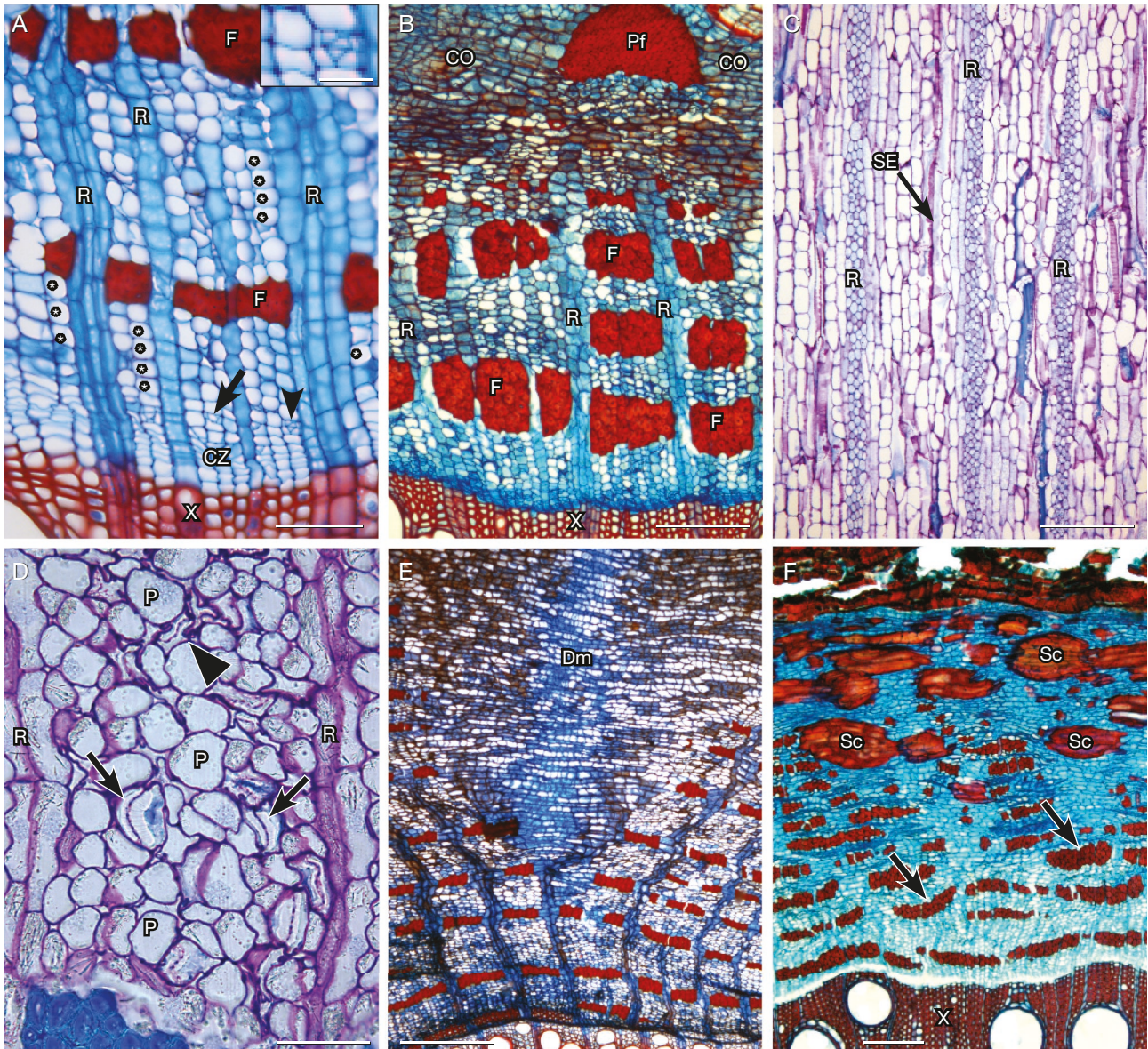
FɪG. 5. — General features of the regular phloem; **A**, *Tanaecium pyramidatum* transverse section (**TS**), very narrow sieve elements (**arrow**), sometimes arranged in assemblages (**arrowhead**). Note that the entire assemblage shows the same dimentions of a single axial parenchyma cell (insert). Rays are generally multisseriate. Axial parenchyma (*) is abundant and form radial rows among the sieve tubes. Fiber bands varying from thin (≤ 3 rows of fibers) to thick (≥ 3 rows of fibers); **B**, *Stizophyllum riparium*, TS, thick fiber bands interrupted by phloem rays. Cortex still present along with the primary phloem and pericyclic fibers; **C**, *Amphilophium crucigerum* longitudinal tangential section (**LT**), rays are multiseriate and taller than 1 mm; **D**, *Perianthomega vellozoi*, TS, sieve tubes with callose deposition (**arrows**), indicating loss of function and subsequent collapse (**arrowhead**); **E**, *Perianthomega vellozoi*, TS, dilatation meristem in the nonconducting phloem; **F**, *Dolichandra unguiculata*, TS, phloem fibers originated from the cambium (**arrows**) and belated formation of sclereids from expanded axial parenchyma cells at the level of the nonconducting phloem. Scale bars: A-C, F, 200 µm; D, 120 µm; E, 2 mm. Insert in A, 30 µm.

tary (Fig. 6A-C). The sieve elements have generally more than 500 µm in length, as seen in longitudinal section (Fig. 6D). The P-protein can be frequently found at the sieve plates forming a slime plug (Fig. 6B, D). Within wedges, the rays are always uniseriate to biseriate and shorter than 1 mm in tangential section (Fig. 6D, E, H). When a ray is bordering a group of sieve elements, their companion cells tend to be located next to the ray cells (Fig. 6B). The fibers located within fiber bands are usually thicker than the xylem fibers (Fig. 6C). The variation found in all other characters of the variant phloem is described in section 4.

Nonconducting phloem. The cessation of function in the variant phloem starts at approximately 8-12 sieve tubes away from the cambium. The first sign of function loss is seen by the accumulation of definitive callose at the sieve plates (Fig. 6F) and/or the expansion of the axial and ray parenchyma cells (Fig. 6G, H), which compress the sieve tubes leading to collapse (Fig. 6G). The companion cells appear empty, and the same pattern is soon observed on the sieve elements. Ray dilatation is rare; whenever present, it is found in the outmost part of the wedge (arrows in Fig. 6A). Higher accumulation of crystals and starch is sometimes recorded for this zone
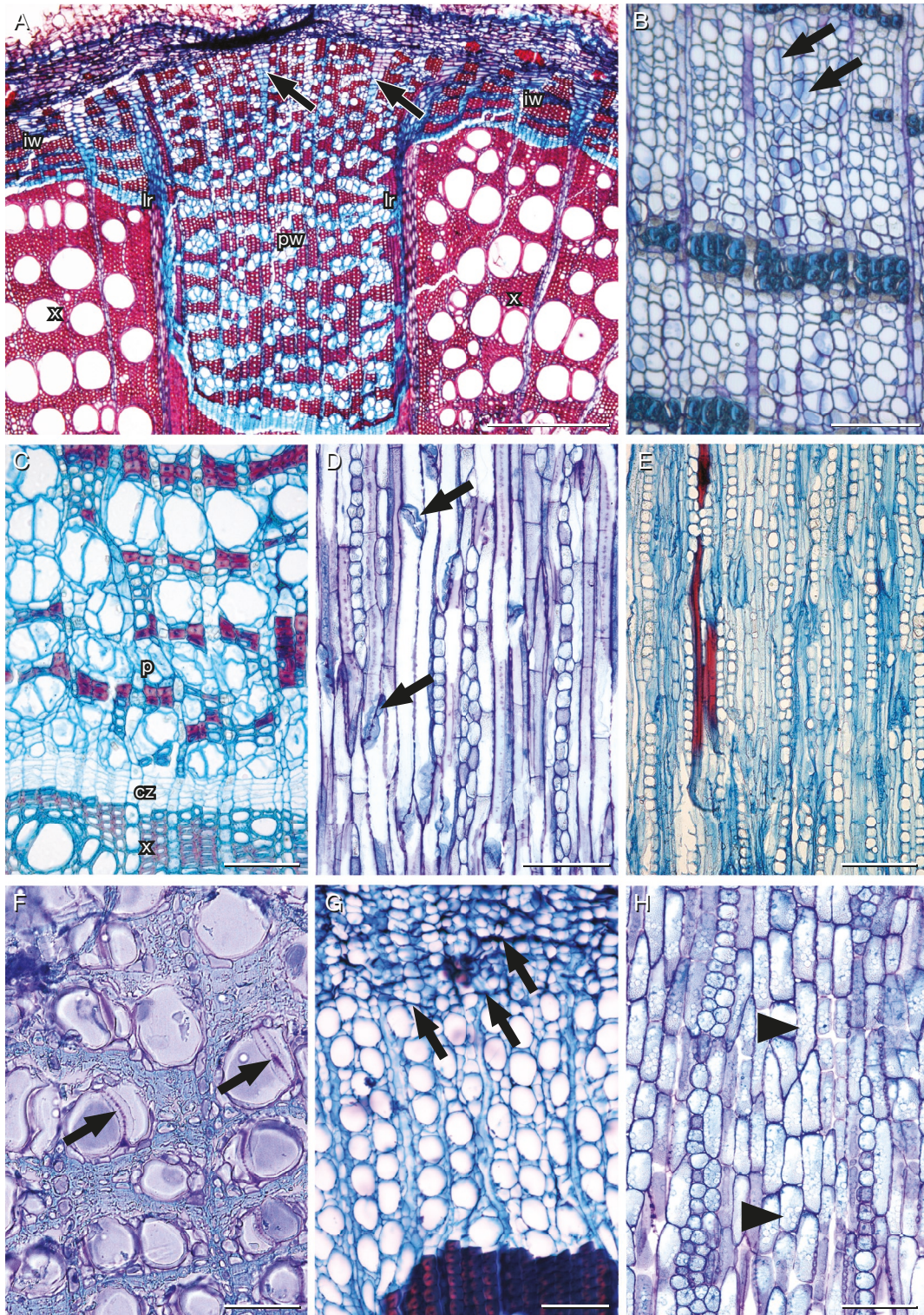
Fɪɢ. 6. — General features of the variant phloem; **A**, *Adenocalymma alboaurantiacum* transverse section (**TS**), variant phloem located in the phloem wedges (**Pw**), and regular phloem located in the interwedges (**Iw**). Fibrous phloem, sieve tubes generally in multiples, sometimes solitary. Ray dilatation occur very soon in the regular phloem, while it only occurs in the outermost parts of the phloem wedge (**arrows**); **B**, *Bignonia magnifica*, TS, non-fibrous phloem, with a series of concentric fiber bands, alternating with a large amount of sieve tubes and axial parenchyma cells. Thin fiber bands, up to 3 cells in width, surrounded by acicular crystals (seen as beige deposits). Sieve elements solitary or in multiples, p-protein visible at sieve plates (**arrows**), one companion cell per sieve tube. Whenever a sieve tube is lying next to a ray, its companion cell faces it; **C**, *Pleonotoma tetraquetra*, TS, fibrous phloem, sieve tubes solitary or in multiples of 2, sieve-tube centric axial parenchyma, fibers square to rectangular; **D**, *Bignonia magnifica* longitudinal tangential section (**LS**), sieve tubes longer than 500 µm, with p-protein accumulated at the sieve plates. Rays uni to biseriate. Axial parenchyma with 3-4 cells per strand; **E**, *Callichlamys latifolia*, LS, rays uni to biseriate, non-storied; **F**, *Callichlamys latifolia*, TS, definitive callose deposited in the sieve plates (**arrows**). No collapse of cells in fibrous phloems; **G**, *Pachyptera aromatica*, TS, sieve tubes eventually collapse in non-fibrous phloems (**arrows**); **H**, *Bignonia magnifica*, LS, starch accumulation greatly increases in nonconducting phloem. Scale bars: A, 500 µm; B, E, 200 µm; C, D, G, H, 100 µm; F, 50 µm.

(Fig. 6H). In species where the fibers are abundant (fibrous phloem), no collapse is observed, neither for the sieve elements nor the phloem parenchyma (Fig. 6A, F). On the other hand, for species with non-fibrous to semi-fibrous phloem, total or partial collapse is common in this zone (Fig. 6G).

SECTION 4: BARK DESCRIPTION OF MAJOR BIGNONIEAE AND TECOMEAE S.S. CLADES

A detailed description of the conducting secondary phloem of genera in Bignonieae is given following their phylogenetic arrangement (Fig. 1), excluding the general characters described above. When closely related genera sharing the same morphology form a monophyletic group, a single description of the most inclusive clade is provided. Thus, from the 20 genera studied, 15 clades are described and numbered using Roman numerals, following the phylogenetic order provided in Fig. 1. Recent taxonomic changes are mentioned within each description and summarized in Table 2.

I. *Perianthomega* clade

TAXONOMIC INFORMATION. — This clade contains a single genus, *Perianthomega*, with four phloem arcs in transversal section (Fig. 3D). The genus was placed previously in Tecomeae *s.l.* (Gentry 1992; Fischer *et al.* 2004; Table 1), but subsequently transferred into Bignonieae (Lohmann & Taylor 2014).

TOTAL NUMBER OF SPECIES IN THIS CLADE. — One species (Lohmann & Taylor 2014).

STUDIED SPECIES. — One species, *Perianthomega vellozoi* Bureau.

Regular phloem
Thin to thick fiber bands (Fig. 7A), without assemblages.

Variant phloem
General configuration. Non-fibrous, stratified, with approximately 12-18 rows of sieve tubes and phloem parenchyma cells between fiber bands (Fig. 7B). A tendency to a storied structure is evident in the cambial zone (Fig. 7D) and secondary xylem, less so in the secondary phloem (Fig. 7E).

Sieve tube elements. As seen in transverse section, each sieve element is associated with one companion cell (Fig. 7C), sometimes two, one at each opposite corner of the sieve element. Sieve tubes are solitary or radial and composed of 2-3 cells (Fig. 7B, C). As seen in longitudinal section, the sieve elements are short (< 500 µm) (Fig. 7E) and their end walls are transverse to slightly inclined (Fig. 7D, E), bearing simple sieve plates (Fig. 7E).

Axial parenchyma. The phloem parenchyma forms a matrix where sieve elements and fiber bands are embedded (Fig. 7B, C). Long radial rows of phloem parenchyma, sometimes with more than 10 cells, are present. Furthermore, a crystalliferous parenchyma is found surrounding the fiber bands (Fig. 7C).

Fibers. The fiber bands are composed of 4-6 rows of cells (Fig. 7B).

Rays. Limiting rays are not present in *Perianthomega*. The rays are non-lignified, not even when crossing the fiber bands (Fig. 7B).

Crystals. Acicular crystals are present and more abundant in the crystalliferous parenchyma, although also found in all other cells of the phloem and ray parenchyma (Fig. 7C).

Periderm
Only one periderm is formed (Fig. 7F). The phellem is composed of evenly thin-walled cells. The phelloderm is thin, with less than three layers of cells (Fig. 7F).

II. *Stizophyllum* clade

TAXONOMIC INFORMATION. — This clade contains a single genus, *Stizophyllum*, with four phloem wedges in transversal section (Fig. 4A).

TOTAL NUMBER OF SPECIES IN THIS CLADE. — Three species (Lohmann & Taylor 2014).

STUDIED SPECIES. — Three species, *Stizophyllum inaequilaterum* Bureau & K.Schum., *S. perforatum* (Cham.) Miers, and *S. riparium* (Kunth) Sandwith.

Regular phloem
Thick fiber bands (Fig. 8B), assemblages present (Fig. 8C).

Variant phloem
General configuration. Fibrous phloem (Fig. 8A, D), with some non-fibrous, parenchyma bands in alternation (Fig. 8A, D). Axial elements with either a tangential (Fig. 8A) or a radial arrangement (Fig. 8D).

Sieve tube elements. As seen in transverse section, each sieve element is associated with 1-3 companion cells (Fig. 8E), lying on the same corner of the sieve tube (Fig. 8E). The sieve elements are generally arranged in multiples of 2-3 in a radial or tangential disposition, sometimes in clusters (Fig. 8E). Sieve tubes of narrower radial diameter can be found associated with a parenchyma band (Fig. 8D). Such sieve tubes are found in radial multiples of 2-4 cells. As seen in longitudinal section, the sieve elements are thinner than 1 mm, with end walls inclined, bearing sieve plates with 6-10 sieve areas (Fig. 8F). Ray sieve-tube elements are common (Fig. 8F).

Axial parenchyma. The phloem parenchyma is sieve-tube-centric incomplete (Fig. 8D, E), not surrounding the entire sieve tube or sieve tube group, and commonly lignified (Fig. 8E). A parenchyma band of 3-4 rows of cells is present (Fig. 8A, D) associated with narrower sieve elements. In addition, radial rows of axial parenchyma cells are present in some places, sometimes entirely lignified
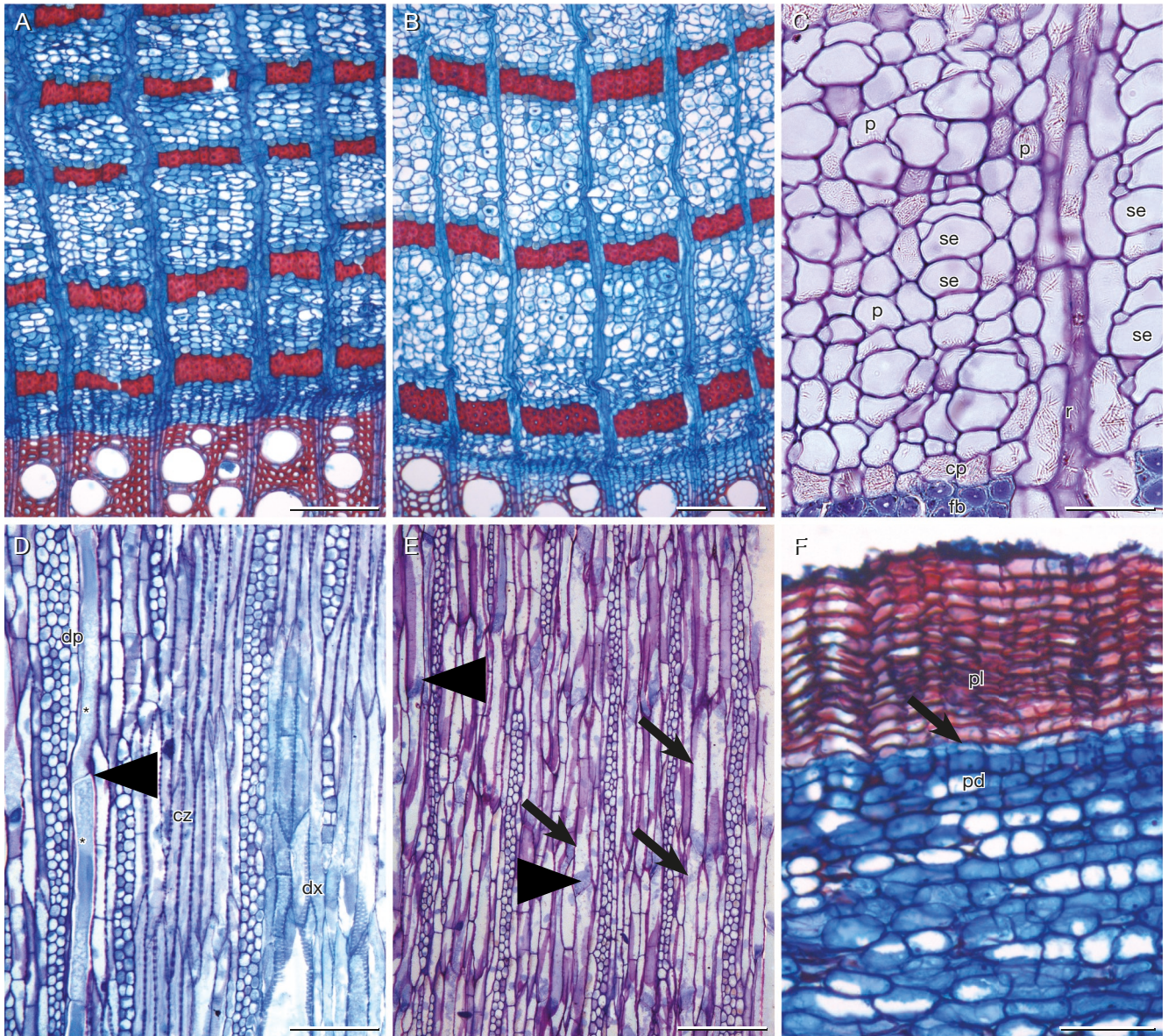
Fig. 7. — Secondary phloem of *Perianthomega vellozoi*: **A**, regular phloem, transverse section (**TS**). Stratified phloem, with thin to thick fiber bands, interrupted only by rays, and alternating with axial parenchyma and sieve tubes. Rays not lignified, not even when crossing the fiber bands; **B**, Variant phloem, TS, non-fibrous, stratified phloem, with mostly thick fiber bands, interrupted only by rays, and alternating with axial parenchyma and sieve tubes. Rays not lignified, not even when crossing the fiber bands; **C**, detail of the secondary phloem, TS, Sieve tubes solitary or in multiples of two-three, with one companion cell lying on the corner. Crystalliferous parenchyma with acicular crystals around the fibers. Acicular crystals also present in other axial and ray parenchyma cells. When sieve tubes touch a ray, their companion cells stay next to the ray; **D**, portion of the cambium showing a storying tendency for the fusiform initials, longitudinal tangential section (**LS**). Part of the developing xylem showing two maturing sieve tube elements (*), and the developing xylem, with some cells with pits already; **E**, secondary phloem, LS, sieve tubes smaller than 500 µm (**arrows**). P-protein accumulated in their sieve plates. Rays very tall, higher than 1 mm. Storied tendency not lost; **F**, periderm, TS, phellogen (**arrow**) produces a thin phelloderm and evenly thin walled phellem cells. Abbreviations: **se**, sieve element; **cp**, crystalliferous parenchyma; **cz**, cambial zone; **dp**, developing phloem; **dx**, developing xylem; **p**, axial parenchyma; **pd**, periderm; **pl**, phellem; **r**, rays. Scale bars: A, B, E, 200 µm; C, 50 µm; D, 150 µm; F, 100 µm.

Fibers. Fibers form a matrix where all other cells can be found (Fig. 8A, D, E).

Rays. The limiting rays are lignified to both xylem and phloem sides, with a radial row of non-lignified cells between them (Fig. 8A). The wedge rays have randomly alternating portions that can be lignified or non-lignified (Fig. 8D, E).

Crystals. Acicular crystals are present in most of the phloem and ray parenchyma cells.

Periderm
Only one periderm is present. The phellem is stratified, composed of thin and thick-walled cells disposed in alternation. The phelloderm is thick, with more than three layers of cells, non-stratified (Table 2).
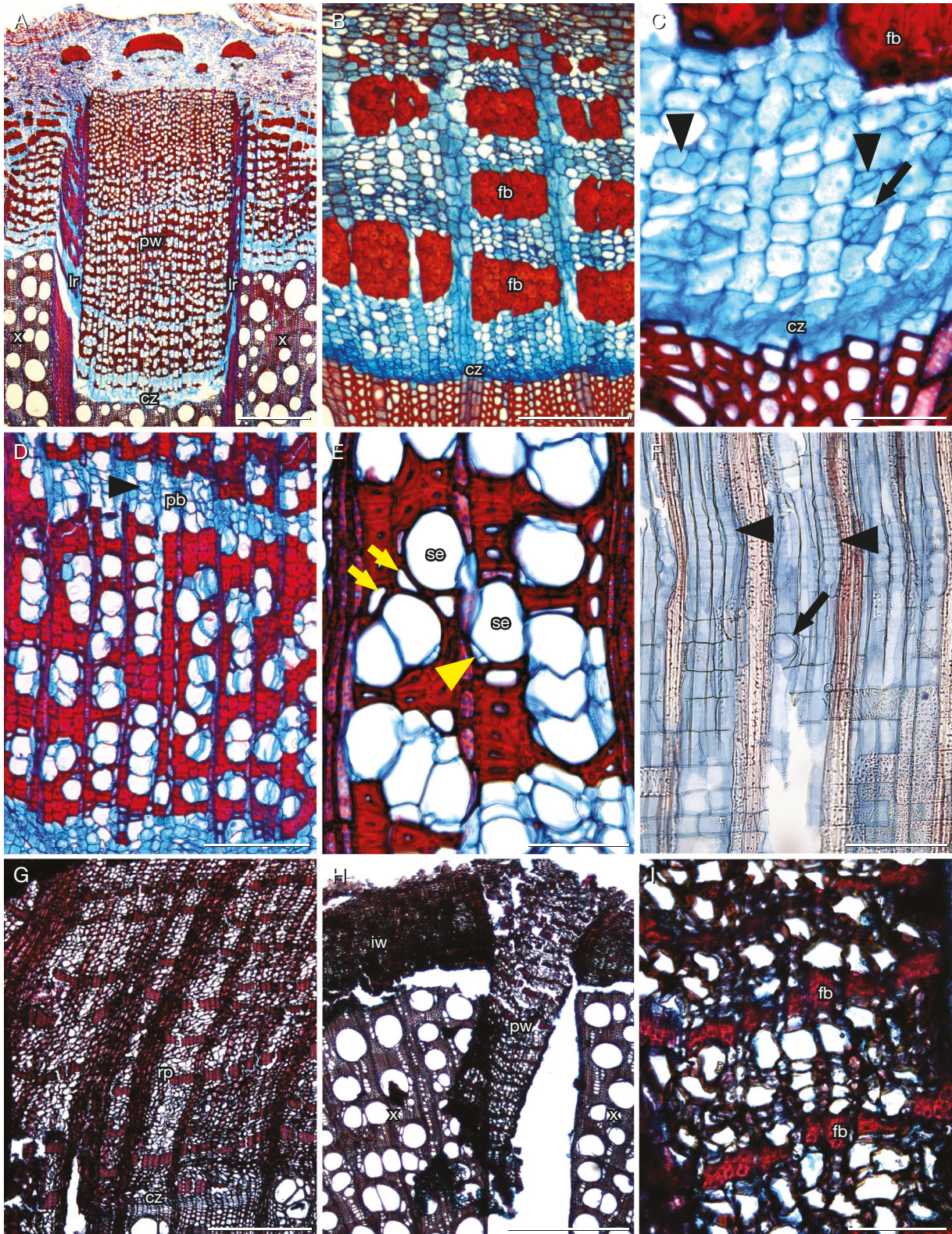
Fig. 8. — Secondary phloem of *Stizophyllum* and *Martinella*: **A**-**E**, **G**-**I**, transverse sections: **F**, longitudinal radial section; **A**-**F**, *Stizophyllum riparium*; **A**, overall view of the phloem wedge, with a fibrous phloem, with alternating parenchymatic bands; **B**, regular phloem. Thick fiber bands, multisseriate rays; **C**, detail of the regular conducting phloem, showing narrow sieve tubes (**arrowheads**) and assemblages (**arrow**); **D**, variant phloem, fibrous, with sieve tubes solitary or in radial multiples, parenchyma band present; **E**, detail of the variant phloem. Sieve tubes with one to three companion cells, lying on the same side of the sieve tube (**yellow arrowhead**). Axial parenchyma sieve-tube-centric incomplete; **F**, heterocellular mixed rays, sieve tubes with compound sieve plates (**arrowheads**), radial sieve element present (**arrow**); **G**-**I**, *Martinella obovata*; **G**, regular phloem. Thin fiber bands, multisseriate rays; **H**, overall view of the phloem wedge, non-fibrous phloem; **I**, detail of the variant phloem. Sieve tubes solitary or in radial multiples. Fiber bands thin. Abbreviations: **cz**, cambial zone; **fb**, fiber bands; **iw**, interwedge; **lr**, limiting ray; **pw**, phloem wegde; **rp**, regular phloem; **se**, sieve element; **x**, secondary xylem. Scale bars: A, H, 1 mm; B, D, 200 µm; C, E, 50 µm; F, I, 100 µm; G, 500 µm.

III. *Martinella* clade

TAXONOMIC INFORMATION. — This clade contains a single genus, *Martinella*, with four phloem wedges in transversal section.

TOTAL NUMBER OF SPECIES IN THIS CLADE. — Five species (Kataoka & Lohmann 2021).

STUDIED SPECIES. — One species, *Martinella obovata* (Kunth) Bureau & K.Schum.

Regular phloem
Thin fiber bands (Fig. 8G), assemblages absent.

Variant phloem
General configuration. Non-fibrous (Fig. 8H), with approximately 10 rows of sieve tubes and phloem parenchyma cells between fiber bands. The axial elements are arranged radially (Fig. 8I).

Sieve tube elements. As seen in transverse section, each sieve element is associated with one companion cell, sometimes two, one at each corner of the sieve element. Sieve tubes occur in radial multiples of 2-3 cells (Fig. 8I).

Axial parenchyma. The phloem parenchyma forms a matrix where sieve elements and fiber bands are embedded (Fig. 8I). Sometimes radial rows of phloem parenchyma are also detected between sieve elements.

Fibers. Fiber bands are present, composed by 2-3 rows of cells (Fig. 8I).

Rays. The limiting rays are lignified only to the xylem side.

Crystals. Not observed.

Periderm
Not observed.

IV. *Pleonotoma* clade

TAXONOMIC INFORMATION. — This clade contains a single genus, *Pleonotoma*, with four phloem wedges in transversal section.

TOTAL NUMBER OF SPECIES IN THIS CLADE. — 16 species (Lohmann & Taylor 2014; Gomes *et al.* 2020).

STUDIED SPECIES. — Five species, *Pleonotoma dendrotricha* Sandwith, *P. melioides* (S.Moore) A.H.Gentry, *P. orientalis* Sandwith, *P. tetraquetra* (Cham.) Bureau, and *P. stichadenia* K.Schum.

Regular phloem
Fibers are absent, with sclereids found otherwise (Fig. 9A). Sclereids are arranged in clusters, differentiating close to the cambial zone (Fig. 9A, C). Because these sclereids have tapering ends, they are considered fibersclereids (Fig. 9C). Assemblages present (Fig. 9B arrowhead).

Variant phloem
General configuration. Fibrous (Fig. 9D) to semi-fibrous (Fig. 9E), typically with one tangential row of sieve tubes surrounded by phloem parenchyma and fibers (Fig. 9E), presenting, therefore, a tangential arrangement (Fig. 9E).

Sieve-tube elements. As seen in transverse section, each sieve element is associated with 1-3 companion cells (Fig. 9E, F). The sieve elements are generally in multiples of two, ranging from solitary to multiples of 4-5 in a tangential arrangement (Fig. 9E), sometimes in clusters. Sieve elements of two distinct diameters can be found adjacent to each other (Fig. 9E). Sieve elements of narrower radial diameter can be, moreover, found associated with a parenchyma band. As seen in longitudinal section, the sieve elements are long (> 1 mm) and their end walls are inclined, bearing sieve plates with more than 30 sieve areas.

Axial parenchyma. The phloem parenchyma is sieve-tube-centric to sieve-tube-centric incomplete (Fig. 9E, F). A parenchyma band of 3-4 rows of cells is associated with narrower sieve elements. In addition, radial rows of phloem parenchyma cells are often present, sometimes lignified (Fig. 9E).

Fibers. Present as either fiber bands of 2-3 rows of cells (Fig. 9E) or as the fibers constituting the ground tissue where all other cells are embedded (Fig. 9D).

Rays. The limiting rays are lignified only to the xylem face (Fig. 9E). The wedge rays are non-lignified, even when crossing the fiber bands (Fig. 9E, F).

Crystals. Prismatic crystals are abundant, both in the phloem and ray parenchyma (Fig. 9F), and even more common in the ray cells. The number of crystals per cells is variable, ranging from a single crystal per cell that occupies almost the entire cell lumen, to many (*c.* eight), but much smaller crystals per cell (Fig. 9F).

Periderm
A single periderm formed. The phellem is stratified, composed of thin and thick-walled cells in alternation. The phelloderm is thick, with over three cell layers, non-stratified (Table 2).

V. *Manaosella* clade

TAXONOMIC INFORMATION. — This clade contains a single genus, *Manaosella*, with four phloem wedges in transversal section.

TOTAL NUMBER OF SPECIES IN THIS CLADE. — One species.

STUDIED SPECIES. — One species, *Manaosella cordifolia* (DC.) A.H. Gentry.

Regular phloem
Thin to thick fiber bands, fibers tangentially elongated in some portions, assemblages absent.

Variant phloem
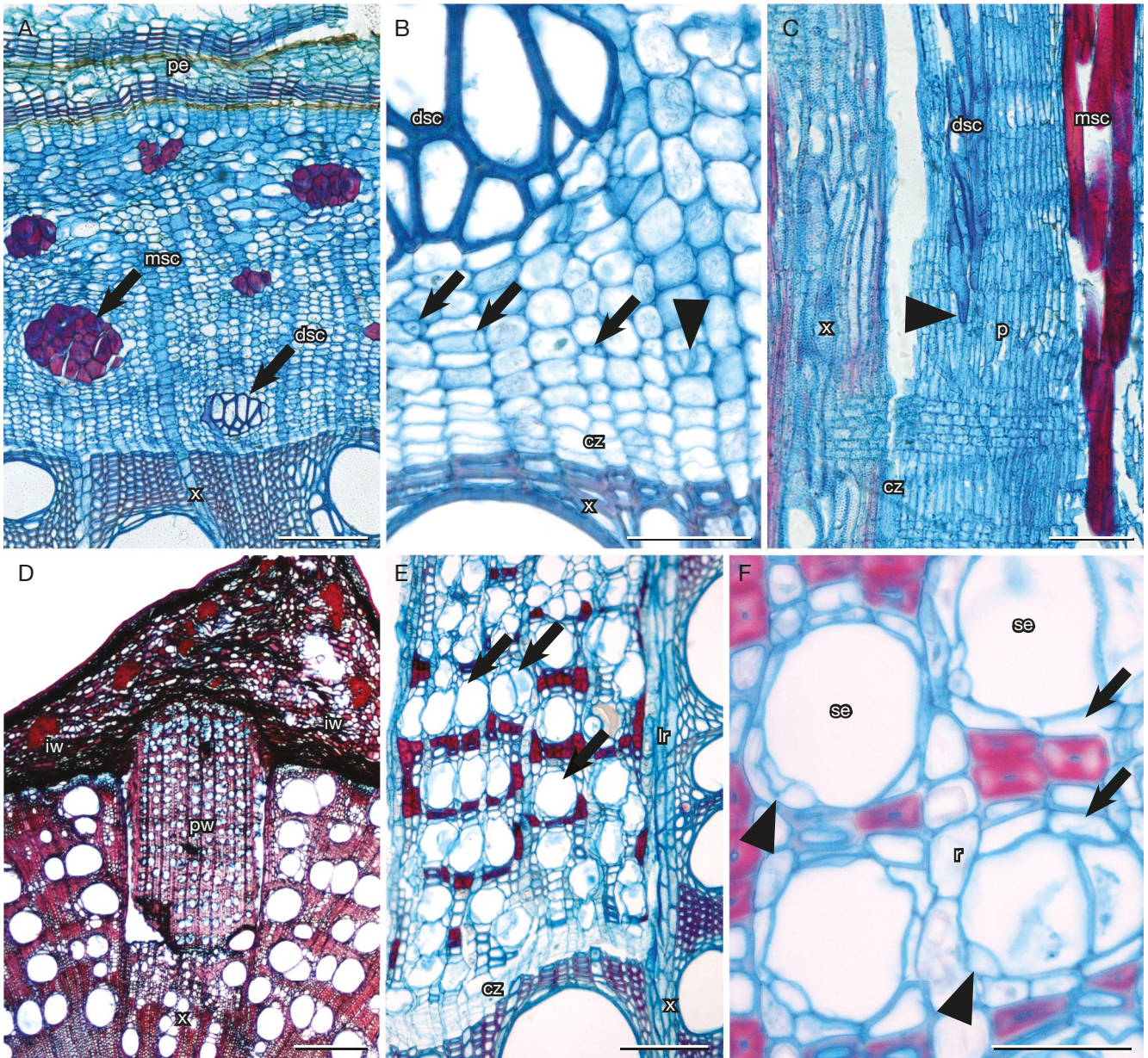**General configuration.** Non-fibrous (Fig. 10A), with approximately 14-16 rows of sieve tubes and phloem parenchyma

FIG. 9. — Secondary phloem of *Pleonotoma*: **A**, **B**, **D-F**, transverse sections; **C**, longitudinal radial section; **A-C**, **E**, **F**, *Pleonotoma tetraquetra*; **D**, *Pleonotoma melioides*; **A**, overall view of the regular phloem. Sclerenchyma formed exclusively by sclereids, differentiating next to the cambial zone, in the conducting phloem; **B**, detail of the conducting phloem, sieve tubes are very narrow. Sclereids differentiating. Acicular crystals present in axial and ray parenchyma; **C**, heterocellular rays. Sclereids differentiating from axial parenchyma cells, close to the cambium. Mature sclereids also present; **D**, overall view of the phloem wedge, fibrous phloem; **E**, variant phloem marked by rectangular fibers, sieve tubes solitary or in radial and tangential multiples of 2-3, parenchyma sieve-tube-centric; **F**, detail of variant phloem. Sieve tubes with one or two companion cells lying on the same side of the sieve tube. Axial parenchyma sieve-tube-centric. Prismatic crystals present in both axial and ray parenchyma cells. Scale bars: A, C, 200 µm; B, F, 50 µm; D, 500 µm; E, 100 µm.

cells between fiber bands. The axial elements present a diffuse arrangement, sometimes with a radial tendency (Fig. 10A-C).

Sieve-tube elements. As seen in transverse section, each sieve element is associated with one companion cell (Fig. 10C). Sieve tubes of two distinct diameters occur adjacent to one another and are predominantly solitary (Fig. 10B, C), occasionally radially disposed and arranged in multiples of 2-3. As seen in longitudinal section, the sieve elements are thinner than 1 mm and their end walls are inclined, bearing sieve plates with 7-15 sieve areas.

Axial parenchyma. The phloem parenchyma forms a matrix in which sieve elements and fiber bands are embedded (Fig. 10A-C). Sometimes radial rows of phloem parenchyma can be also detected between or next to sieve elements (Fig. 10B, C).

Fibers. The fiber bands in *Manaosella* bear cells that are conspicuously radially elongated (Fig. 10B), a feature not found in any other Bignonieae genus. The fiber bands are composed of 2-3 rows of cells, with the cells located in the center or upper portions of the band radially elongated.
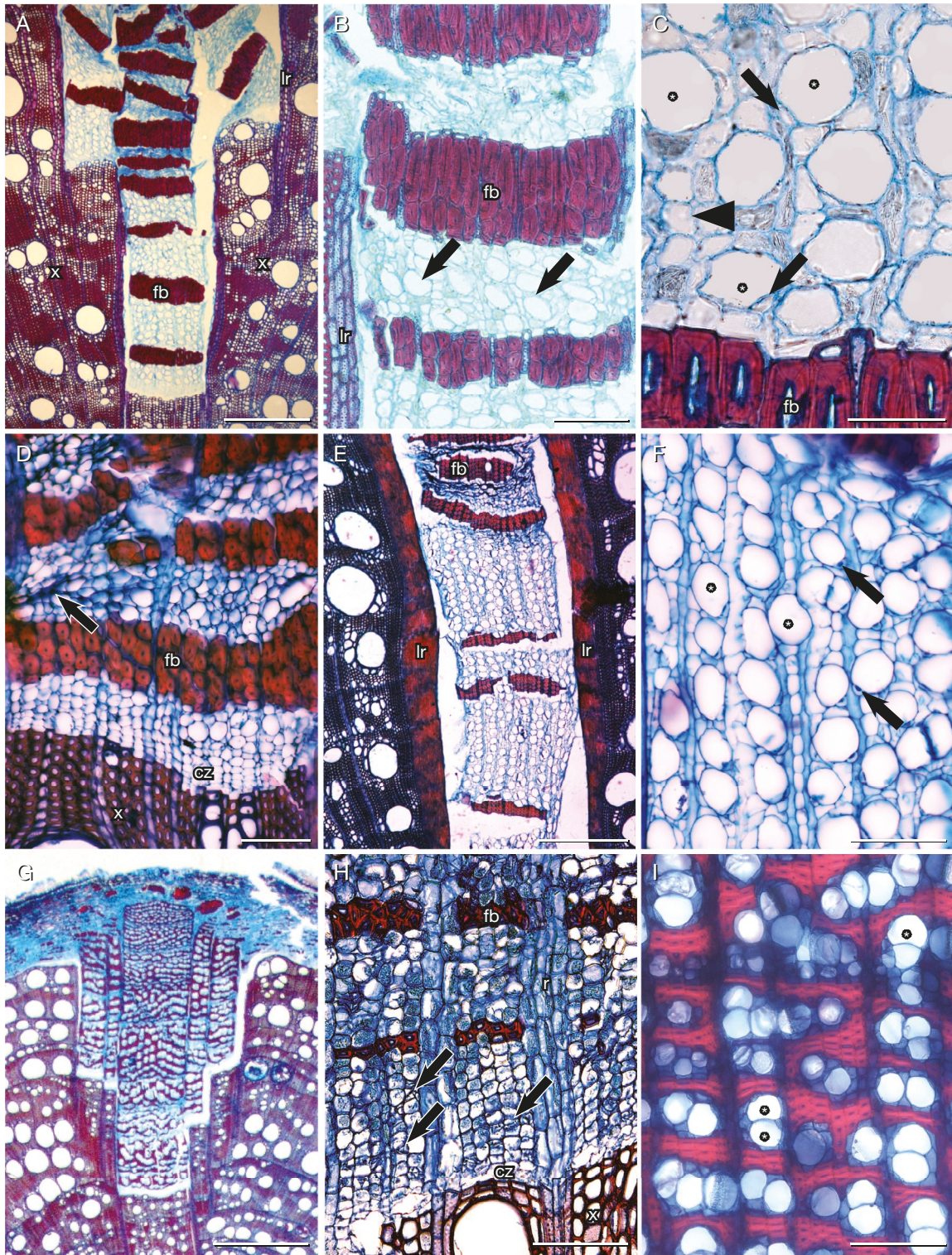
Fɪɢ. 10. — Secondary phloem of *Manaosella*, *Pachyptera*, and *Lundia*. Transverse sections: **A**-**C**, *Manaosella cordifolia*; **A**, overall view of the phloem wedge and the variant phloem of *Manaosella*. Stratified, non-fibrous phloem; **B**, fiber bands of generally three cells, some of which are tangentially very long. Rays lignify when crossing the fiber bands. Sieve tubes (**arrows**) diffuse; **C**, Sieve tubes (*****) with one companion cell (**arrows**) lying at one corner of the sieve tube. Axial parenchyma forms the background tissue. Acicular crystals common in axial and ray parenchyma; **D**-**F**, *Pachyptera aromatica*; **D**, overall view of the regular phloem, with fiber bands formed by 3-4 polygonal fibers. Axial parenchyma forms the background tissue. Nonconducting phloem evident after the first fiber band, with collapse of sieve tubes (**arrow**) and dilatation of axial and ray parenchyma; **E**, overall view of the phloem wedge and variant phloem. Stratified, non-fibrous. Sieve tubes in radial arrangement. Axial parenchyma as the background tissue. Rays lignified when crossing the fiber bands. Fiber bands thin to thick; **F**, detail of the variant phloem. Sieve tubes (*****) solitary or in multiples. One to two companion cells (**arrows**) lying to the same side of the sieve tube; **G**-**I**, *Lundia*; **G**, *Lundia glazioviana*. Overall view of the phloem wedge, variant and regular phloem. Fibrous phloem. Sieve tubes arranged tangentially or in clusters; **H**, *Lundia damazioi*. Regular phloem. Thin fiber bands. Axial parenchyma forms the background tissue. Tiny sieve tubes (**arrows**); **I**, *Lundia damazioi.* Variant phloem. Wide sieve tubes (*****) solitary or in multiples. Axial parenchyma sieve-tube-centric. One to two companion cells per sieve tube, lying at the same corner of the sieve tube. Abbreviations: **cz**, cambial zone; **fb**, fiber band; **lr**, limiting rays; **x**, secondary xylem. Scale bars: A, E, 500 µm; B, D, F, I, 100 µm; C, 50 µm; G, 400 µm.

Rays. The limiting rays are lignified only to the xylem face (Fig. 10A, B). The wedge rays are non-lignified, except when crossing the fiber bands (Fig. 10B, C).

Crystals. Acicular crystals are very abundant and are found in most cells of the phloem and ray parenchyma (Fig. 10C).

Periderm
A single periderm formed. The phellem is stratified, composed of thin and thick-walled cells in alternation. The phelloderm is thin, with less than three layers of cells, non-stratified (Table 2). Lenticels non-stratified, unlignified.

VI. *Pachyptera* clade

TAXONOMIC INFORMATION. — This clade contains a single genus, *Pachyptera*, with four phloem wedges in transversal section. *Pachyptera* currently includes species from three previously recognized genera (see Fischer *et al.* 2004; Table 1), *Leucocalantha* Barb. Rodr., *Mansoa*, and *Pachyptera*.

TOTAL NUMBER OF SPECIES IN THIS CLADE. — Five species (Francisco & Lohmann 2018).

STUDIED SPECIES. — Two species, *Pachyptera aromatica* (Barb. Rodr.) L.G. Lohmann, and *P. kerere* (Aubl.) Sandwith.

Regular phloem
Thin to thick fiber bands (Fig. 10D), assemblages absent.

Variant phloem
General configuration. Non-fibrous (Fig. 10D), with approximately 8-18 rows of sieve tubes and phloem parenchyma cells between fiber bands (Fig. 10E). Axial elements present a diffuse to radial arrangement (Fig. 10E, F).

Sieve-tube elements. As seen in transverse section, each sieve element is associated with one companion cell (Fig. 10F). The sieve elements occur either solitary or in multiples (Fig. 10F), sometimes in short groups of 2-3 cells either in tangential or radial arrangement (Fig. 10F). As seen in transverse section, the sieve elements are thinner than 1 mm and their end walls are inclined, bearing compound sieve plates with 6-7 sieve areas.

Axial parenchyma. The phloem parenchyma intermingles all other cells (Fig. 10E, F). Crystalliferous parenchyma is, moreover, found surrounding the fiber bands.

Fibers. Fiber bands are present, composed by 2-4 rows of cells (Fig. 10E).

Rays. The limiting rays are lignified only to the xylem face (Fig. 10E). The wedge rays are non-lignified, except when crossing the fiber bands.

Crystals. Acicular crystals are present in the phloem and ray parenchyma. The crystalliferous parenchyma bears prismatic crystals.

Periderm
A single periderm formed. The phellem is non-stratified, composed of evenly thick-walled cells. The phelloderm is thick, with more than three cell layers, non-stratified (Table 2).

VII. *Lundia* clade

TAXONOMIC INFORMATION. — This clade contains a single genus, *Lundia*, with multiple of four phloem wedges in transversal section.

TOTAL NUMBER OF SPECIES IN THIS CLADE. — 13 species (Lohmann & Taylor 2014; Kaehler & Lohmann 2021a).

STUDIED SPECIES. — Five species, *Lundia longa* (Vahl) DC., *L. damazioi* C.DC., *L.* densiflora DC., *L. virginalis* DC.*,* and *L. nitidula* DC.

Regular phloem
Thin fiber bands (Fig. 10H) and assemblages present.

Variant phloem
General configuration. Fibrous (Fig. 10G, I), with axial elements in a tangential to diagonal arrangement (Fig. 10G, I).

Sieve-tube elements. As seen in transverse section, each sieve element is associated with one companion cell, rarely two (Fig. 10I). The sieve elements may be solitary to multiples of 2-3 (Fig. 10I). Narrower sieve elements with just one companion cell may be found in a parenchyma band present in all species studied. As seen in longitudinal section, the sieve elements are long (over 1 mm) and their end walls are inclined, bearing sieve plates with 12-15 sieve areas.

Axial parenchyma. The phloem parenchyma is sieve-tube-centric to sieve-tube-centric incomplete, therefore surrounding or partially surrounding the groups of sieve elements (Fig. 10I). Furthermore, a parenchyma band composed of 2-3 cells of phloem parenchyma is associated with sieve elements of narrower diameter. The phloem parenchyma tends to form radial rows of 4-6 cells in some places.

Fibers. Fibers form the background tissue where all other cells are embedded (Fig. 10G, I).

Rays. The limiting rays are only lignified to the xylem face (10G). The wedge rays have randomly alternating portions lignified and non-lignified.

Crystals. Acicular crystals are present in the phloem and ray parenchyma across the entire phloem wedge (absent in *Lundia longa*).

Periderm
A single periderm formed. The phellem is non-stratified, composed of evenly thin-walled cells in *Lundia corymbifera* and *L. virginalis*. The phellem is stratified in *Lundia longa*, with alternating thin and thick-walled cells. The phelloderm is thick, with over three layers of cells, non-stratified (Table 2). The lenticels are non-stratified, with unlignified filling tissue (Table 2).

VIII. *Cuspidaria-Tynanthus* clade

TAXONOMIC INFORMATION. — This clade contains two genera, *Cuspidaria* and *Tynanthus*, both with four phloem wedges in transversal section. While the circumscription of *Tynanthus* has remained constant in different classification systems, *Cuspidaria* currently includes species from three previously recognized genera (see Fischer *et al.* 2004; Table 1), *Cuspidaria*, *Arrabidaea*, and *Pyrostegia*.

TOTAL NUMBER OF SPECIES IN THIS CLADE. — 35 species belonging to *Cuspidaria* (21) and *Tynanthus* (14) (Lohmann & Taylor 2014; Medeiros & Lohmann 2015; Kaehler *et al.* 2019).

STUDIED SPECIES. — Four species, *Cuspidaria convoluta* (Vell.) A.H.Gentry, *C. pulchra* (Cham.) L.G.Lohmann, *Tynanthus cognatus* (Cham.) Miers, and *T. elegans* (Vell.) L.G.Lohmann.

Regular phloem
Thin to thick fiber bands, assemblages present (Fig. 11D). Mostly thin fiber bands in *T. cognatus* (Fig. 11D).

Variant phloem
General configuration. Fibrous (Fig. 11A-C, E, F), with axial elements in a tangential arrangement of one row of sieve tubes, surrounded by a sieve-tube-centric phloem parenchyma (Fig. 11A-C). A band of parenchyma sometimes present (Fig. 11F).

Sieve-tube elements. As seen in transverse section, each sieve element is associated with 2-3 (sometimes over 4) companion cells that occur at the same side of the sieve element (Fig. 11B, E). The sieve elements generally occur in multiples of 2-3 (up to 5) radially elongated cells (Fig. 11B). Solitary sieve elements are also present in *Cuspidaria* (Fig. 11F). As seen in transverse section, the sieve elements are of variable length, from 400 μm to approximately 1 mm and their end walls are inclined, bearing compound sieve plates with 12-30 sieve areas (Fig. 11G).

Axial parenchyma. The phloem parenchyma is typically sieve-tube-centric, surrounding the groups of sieve elements (Fig. 11B, C, E, F). In *Cuspidaria convoluta*, lignified lines of phloem parenchyma cross the entire phloem wedge (Fig. 11C yellow arrows); some non-lignified lines are also found occasionally in this species (Fig. 11F).

Fibers. Fibers are very abundant, forming background tissue (Fig. 11A-C, F).

Rays. The limiting rays are lignified to both xylem and phloem faces (Fig. 11A), with a radial row non-lignified between them. The wedge rays have randomly alternating portions lignified and non-lignified. The lignified portions never bear crystals and are differentiated very close to the cambium.

Crystals. Acicular and navicular crystals are present solely on the non-lignified portions of the phloem and ray parenchyma.

Periderm
A single periderm is formed. The phellem is stratified, composed of thin and thick-walled cells in alternation. The phelloderm is thick, with over three cell layers, non-stratified (Table 2). In *Tynanthus* the lenticels are non-stratified, with unlignified filling tissue (Table 2). In *Cuspidaria* the lenticels are stratified, with a closing layer of lignified cells (Table 2).

IX. *Fridericia-Xylophragma* clade

TAXONOMIC INFORMATION. — This clade includes species from two genera, *Fridericia* and *Xylophragma*, both with four phloem wedges in transversal section. *Fridericia* currently includes species from four previously recognized genera (Table 1), *Arrabidaea*, *Fridericia*, *Piriadacus* Pichon, and *Sampaiella* J.C.Gomes. In turn, *Xylophragma* includes species previously included in *Arrabidaea* and *Xylophragma*.

TOTAL NUMBER OF SPECIES IN THIS CLADE. — 67 species belonging to *Fridericia* (60) and *Xylophragma* (7) (Lohmann & Taylor 2014; Kaehler *et al.* 2019; Kaehler & Lohmann 2021b, 2022).

STUDIED SPECIES. — 12 species, *Fridericia chica* (Bonpl.) L.G.Lohmann, *F. cinnamomea* (DC.) L.G.Lohmann, *F. conjugata* (Vell.) L.G.Lohmann, *F. nigrescens* (Sandwith) L.G.Lohmann, *F. ornithophila* (A.H.Gentry) L.G.Lohmann, *F. patellifera* (Schltdl.) L.G.Lohmann, *F. platyphylla* (Cham.) L.G.Lohmann, *F. samydoides* (Cham.) L.G.Lohmann, *F. speciosa* Mart*., F. triplinervia* (Mart. ex DC.) L.G.Lohmann, *Xylophragma myrianthum* (Cham.) Sprague, and *X. platyphyllum* (DC.) L.G.Lohmann.

Regular phloem
Thick fiber bands, assemblages present.

Variant phloem
General configuration. Semi-fibrous (Fig. 12B) to fibrous (Fig. 12A, C), with semi-fibrous species (*Fridericia chica*, *F. conjugata*, and *F. speciosa*) (Fig. 12B), and fibrous species (*Fridericia chica*, *F. ornithophila*, *F. patellifera*, *F. platyphylla*, *F. samydoides*, *Xylophragma myrianthum*, and *X. platyphylla*) showing a matrix of fibers that intermingle all other cells (Fig. 12C, D). Interestingly, in *Fridericia chica* we found specimens with both a semi-fibrous and a fibrous configuration. The sieve tubes and associated phloem parenchyma exhibit a tangential arrangement (Fig. 12A-D).

Sieve-tube elements. As seen in transverse section, each sieve element is associated with one or two companion cells (Fig. 12B), rarely three, at the same side of the sieve element (Fig. 12B). The sieve elements may be solitary to multiples of 2-3 (Fig. 12B-D), in a diffuse to tangential arrangement (Fig. 12A-D). Such arrangement results from the way that the multiple sieve elements are organized, forming short radial groups in some places, and short tangential groups in others; while some groups form clusters of 3-4 cells, most groups exhibit a tangential tendency (Fig. 12B-D). Narrower sieve elements with just one companion cell may be found in a parenchyma band in most species (except *Fridericia platyphylla* and *F. speciosa*). As seen in longitudinal section, the sieve elements are long (over 500 μm) and their end walls
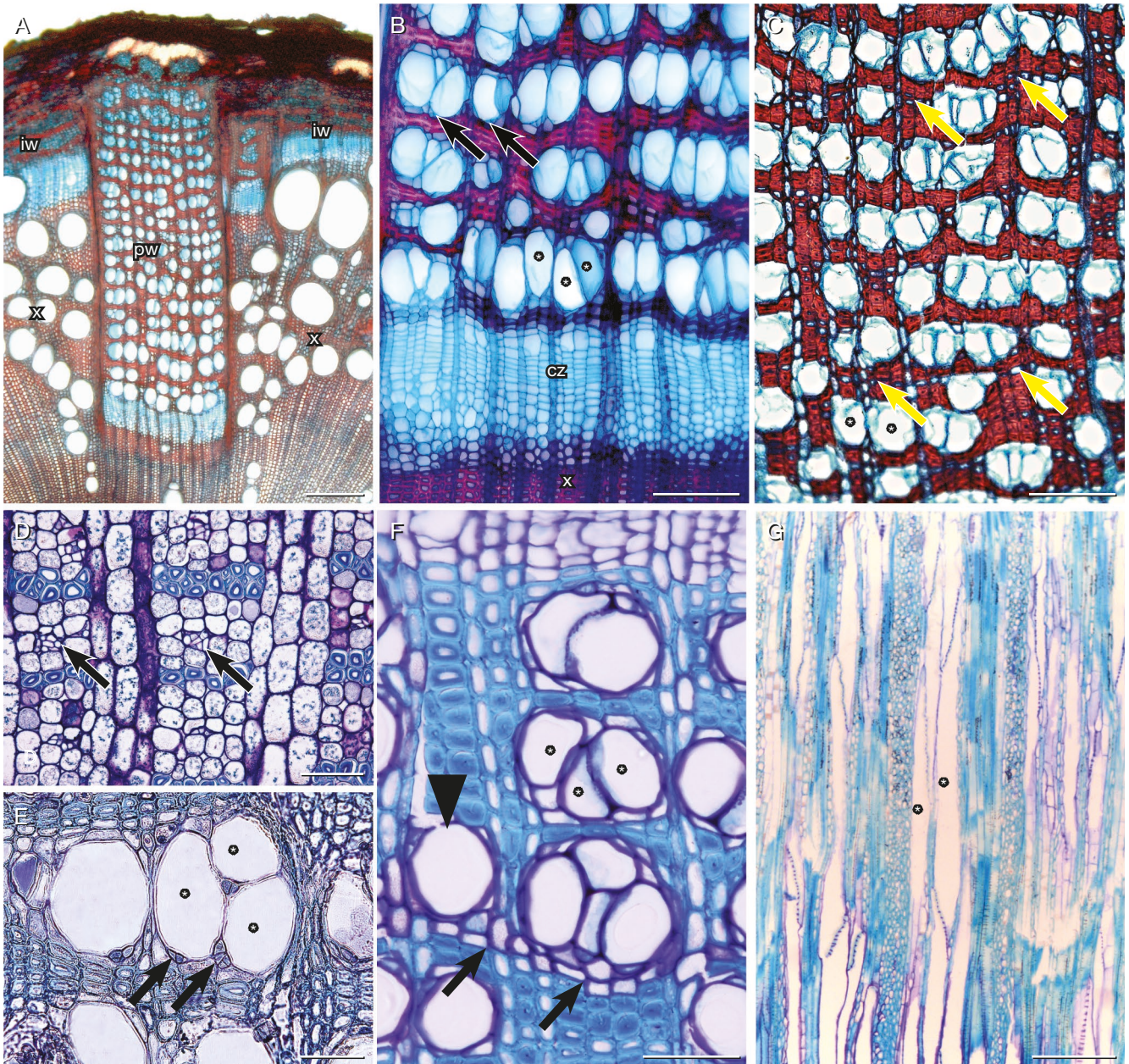
Fig. 11. — Secondary phloem of the *Cuspidaria-Tynanthus* clade: **A-F**, transverse sections; **G**, longitudinal tangential section; **A**, overall view of the phloem at the wedge and interwedges. Fibrous variant phloem, *Tynanthus cognatus*; **B**, detail of the variant phloem. Sieve tubes radially elongated (*), generally in tangential multiples, surrounded by sieve-tube-centric parenchyma, all embedded in a matrix of fibers. Two to four companion cells per sieve tube, lying on their corner (**arrows**), *Tynanthus cognatus*; **C**, Fibrous phloem. Sieve tubes (*) solitary or in tangential multiples. Sieve-tube centric parenchyma, *Cuspidaria convoluta*; **D-F**, comparison of the sieve tube dimensions on regular and variant portion of *Tynanthus cognatus*; **D**, regular phloem with thin fiber bands and assemblages (**arrows**); **E**, variant phloem. Sieve tubes with two to four (or more) companion cells, lying at the same corner of the sieve tube; **F**, Variant phloem of *Cuspidaria convoluta.* Sieve tubes (*) solitary or in multiples. Parenchyma band present (**arrows**); **G**, sieve tubes are lower than 1 mm, with inclined, compound sieve plates. Rays varying from 2 to 8-seriate. Scale bars: A, G, 200 µm; B, C, 100 µm; D-F, 50 µm.

are inclined, bearing sieve plates with more than 20 sieve areas (Fig. 12E, F).

Axial parenchyma. The phloem parenchyma is typically sieve-tube-centric, surrounding the groups of sieve elements (Fig. 12B-D). Furthermore, in most species (except *Fridericia platyphylla* and *F. samydoides*) a parenchyma band of 2-3 cells of phloem parenchyma is associated with sieve elements of radial narrower diameter (Fig. 12C arrows).

Fibers. In semi-fibrous species the fiber bands are waved (Fig. 12B), with borders displaying 5-6 cells and the middle portion displaying 1-2 cells. In fibrous species, on the other hand, the fibers intermingle all other cells with no distinct arrangement (Fig. 12C, D).

Rays. The limiting rays are lignified to both xylem and phloem faces, with a radial row non-lignified between them (Fig. 12A). The wedge rays have randomly alter-
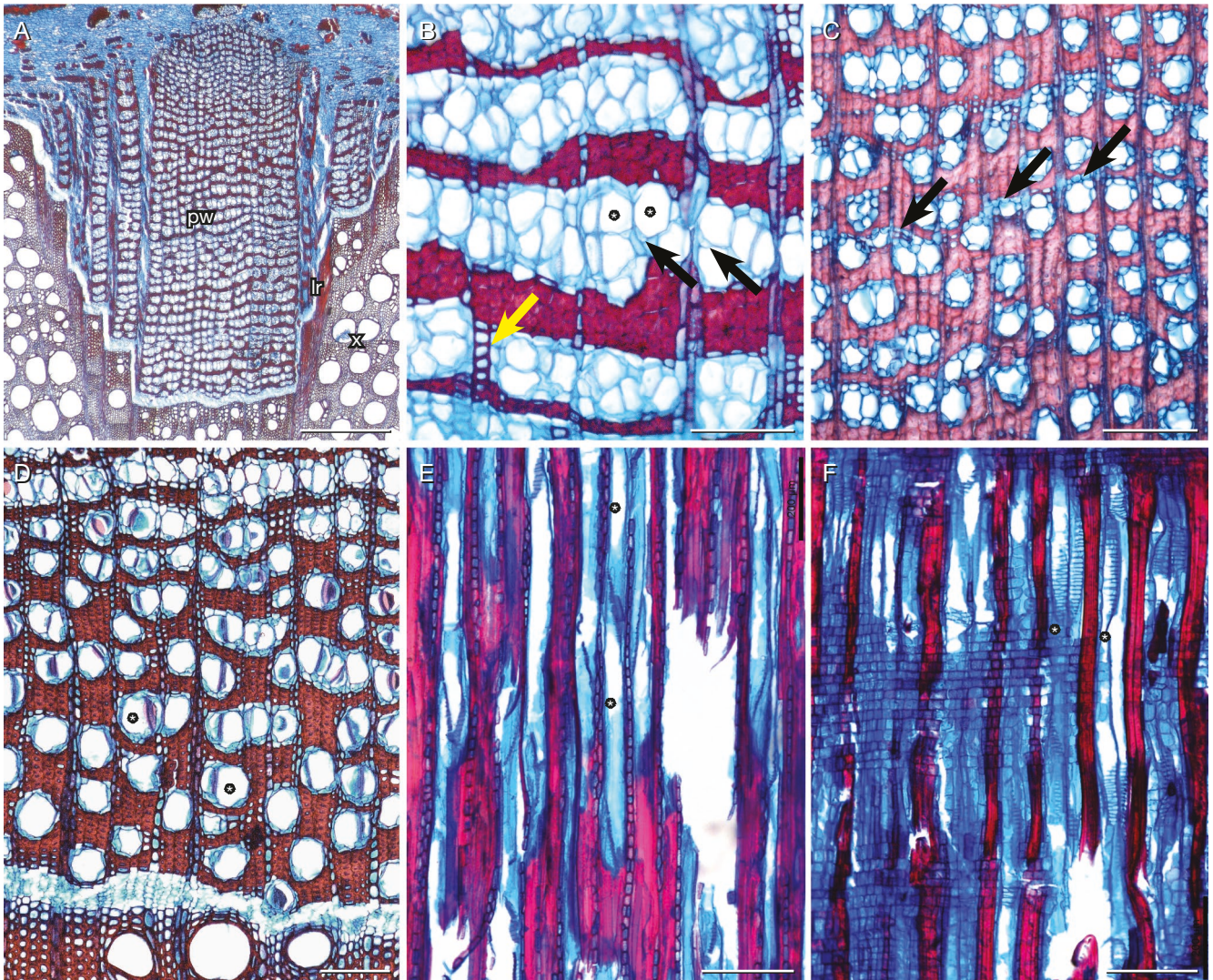
FIG. 12. — Secondary phloem of the *Fridericia-Xylophragma* clade: **A-D**, transverse sections; **A**, *Fridericia samydoides*, overall view of the phloem wedge, with fibrous phloem, and sieve tubes with a tangential arrangement; **B**, *Fridericia chica* variant phloem. Semi-fibrous phloem, with U-shaped fiber bands. Sieve tubes (*) with one or more companion cells lying at the same side of the sieve tube. Rays lignified or not in different portions across the phloem. Radial rows of axial parenchyma sometimes lignify (**yellow arrow**); **C**, *Fridericia nigrescens* variant phloem. Fibrous phloem, sieve tubes in tangential arrangement. Sieve-tube centric axial parenchyma. Axial parenchyma can also form narrows bands across the variant phloem (**arrows**); **D**, *Xylophragma myrianthum* variant phloem. Fibrous phloem. Sieve tubes (*) in tangential arrangement. Sieve-tube-centric axial parenchyma; **E**, *Xylophragma myrianthum* tangential section of variant phloem. Uniseriate rays. Sieve tube element (*) with inclined compound sieve plates; **F**, *Fridericia chica* radial section of variant phloem. Heterocellular rays, with upright, square, and procumbent cells mixed. Sieve tubes (*) with compound sieve plates with many areas. Scale bars: A, 1 mm; B, D, 100 µm; C, E, F, 200 µm.

nating portions lignified and non-lignified (Fig. 12B). In *Fridericia conjugata* the rays are only lignified when crossing the fibers.

Crystals. Acicular and navicular crystals are present in the phloem and ray parenchyma, both in lignified and non-lignified cells, across the entire phloem wedge.

Periderm
A single periderm is formed in *Fridericia nigrescens*, *F. platyphylla*, *F. speciosa*, *F. triplinervia*, and *Xylophragma myrianthum* (Table 2). Sequent periderms (rhytidome) are formed in *Fridericia chica*, *F. conjugata*, and *F. samydoides*

(Table 2). The phellem is non-stratified, evenly thin-walled in *Fridericia chica*, *F. conjugata, F. samydoides*, and *Xylophragma myrianthum* (Table 2). The phellem is non-stratified, evenly thick-walled in *Fridericia platyphylla*, *F. speciosa*, and *F. triplinervia*. The phellem is stratified in *Fridericia nigrescens.* The phelloderm is thick, non-stratified in *Fridericia chica*, *F. conjugata*, *F. nigrescens*, *F. speciosa*, *F. triplinervia*, and *Xylophragma myrianthum* (Table 2). The phelloderm is stratified in *Fridericia platyphylla* and *F. samydoides* (Table 2). Lenticels are non-stratified in *Fridericia speciosa* and *Xylophragma myrianthum*; stratified in *F. samydoides* (Table 2). Lenticels were not observed in the remaining species.
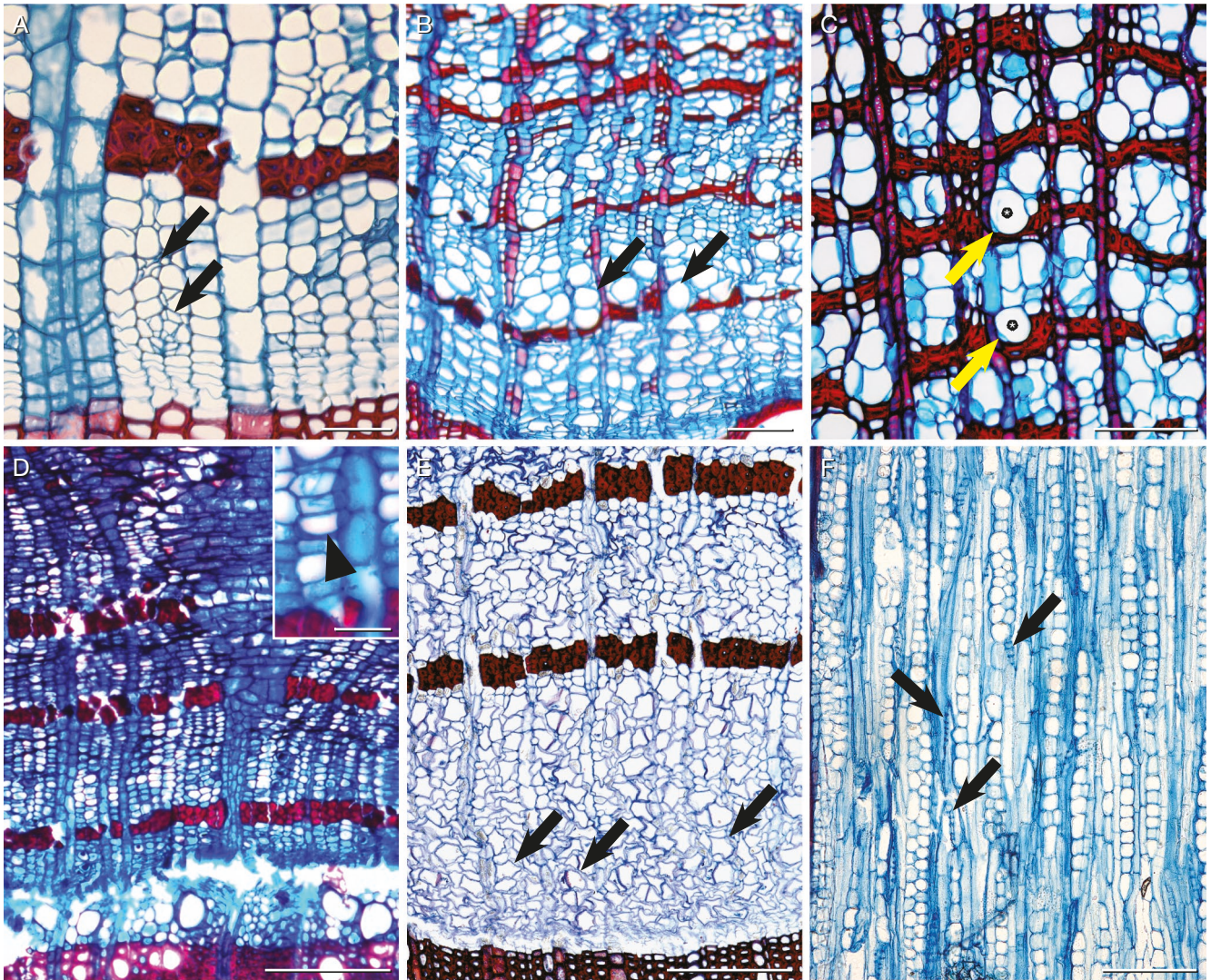
Fig. 13. — Secondary phloem of *Tanaecium* and *Callichlamys*: **A-E**, transverse sections: **A-C**, *Tanaecium pyramidatum*; **A**, regular phloem. Tiny sieve tubes (**arrows**) mostly in assemblages with parenchyma cells. Thin fiber band of up to 3 cells; **B**, variant phloem to the same scale as the previous photo. Semi-fibrous phloem. Note sieve tubes (**arrows**) much wider. Rays lignified or not in random portions; **C**, detail of the variant phloem. Sieve tubes (*) with one to two companion cells (**yellow arrows**) lying in the same corner of the sieve tube. Sieve-tube-centric axial parenchyma; **D**, *Tanaecium tetramerum*, thin fiber bands. Sieve tubes with one companion cell each (insert); **E**, **F**, *Callichlamys latifolia*; **E**, variant phloem. Sieve tubes (**arrows**) solitary or in short multiples. Non-fibrous phloem. Fiber bands thin; **F**, longitudinal tangential section. Sieve tubes (**arrows**) with inclined, compound sieve plates. Rays uni- to biseriate. Scale bars: A-C 100 μm; D-F, 200 μm; insert, 25 μm.

X. *Tanaecium* clade

TAXONOMIC INFORMATION. — This clade contains a single genus, *Tanaecium*, with four phloem wedges in transversal section and a single species, *Tanaecium tetramerum* (A.H.Gentry) Zuntini & L.G.Lohmann, that lacks phloem wedges and only shows a regular phloem. *Tanaecium* currently includes species from seven previously recognized genera (Table 1), *Arrabidaea*, *Ceratophytum* Pittier, *Pseudocatalpa* A.H.Gentry, *Spathicalyx* J.C.Gomes, *Sphingiphila* A.H.Gentry, *Paragonia* Bureau, and *Periarrabidaea* A.Samp.

TOTAL NUMBER OF SPECIES IN THIS CLADE. — 21 species (Frazão & Lohmann 2019).

STUDIED SPECIES. — Three species, *Tanaecium bilabiatum* (Sprague) L.G.Lohmann, *T. pyramidatum* (Rich.) L.G.Lohmann, and *T. tetramerum* (A.H. Gentry) Zuntini & L.G.Lohmann.

Regular phloem
Thin to thick fiber bands, assemblages generally present (Fig. 13A), but absent in *T. tetramerum*. Exclusively thin fiber bands occur in *Tanaecium bilabiatum* and *T. tetramerum* (Fig. 13D).

Variant phloem
General configuration. Semi-fibrous (Fig. 13B, C) to fibrous, with semi-fibrous species (*Tanaecium pyramidatum*) exhibiting fiber bands alternating with 4-8 rows of sieve elements and phloem parenchyma (Fig. 13B, C), and fibrous species (*Tanaecium bilabiatum*) showing a matrix of fibers that intermingle all other cells. The axial elements exhibit a diffuse to tangential arrangement (Fig. 13B, C).

Sieve-tube elements. As seen in transversal section, each sieve element is associated with 1-2 companion cells (Fig. 13C). The sieve elements are generally solitary or in multiples of 2-3 cells (Fig. 13C). As seen in tangential section, the sieve elements are short (< 1 mm) and their end walls are inclined, bearing compound sieve plates with 16-18 sieve areas.

Axial parenchyma. The phloem parenchyma is sieve-tube-centric incomplete. In *Tanaecium pyramidatum*, the phloem parenchyma is much more abundant, also forming radial rows (Fig. 13B, C) that may be lignified in some portions (Fig. 13B, C), completely lignified in the nonconducting phloem. In *T. bilabiatum*, incomplete tangential rows may be found near the sieve elements.

Fibers. In *T. pyramidatum* the fiber band has 1-2 rows of cells (Fig. 13B, C), while in *T. bilabiatum* the fibers form a matrix that intermingle all other cells.

Rays. The limiting rays are lignified to both xylem and phloem faces, with a radial row non-lignified between them. The wedge rays have randomly alternating portions lignified and non-lignified (Fig. 13B).

Crystals. Absent.

Periderm
A single periderm is formed. The phellem is stratified in *Tanaecium pyramidatum* and *T. tetramerum*, non-stratified and thin-walled in *T. bilabiatum* (Table 2). The phelloderm is thick, with over three layers of cells, non-stratified. Lenticels were only observed in *T. pyramidatum*, non-stratified, with lignified filling cells (Table 2).

XI. *Callichamys* clade

TAXONOMIC INFORMATION. — This clade contains a single genus, *Callichlamys* Miq., with four phloem wedges in transversal section.

TOTAL NUMBER OF SPECIES IN THIS CLADE. — One species (Lohmann & Taylor 2014).

STUDIED SPECIES. — One, *Callichlamys latifolia* (Rich.) K.Schum.

Regular phloem
Thin fiber bands, assemblages present.

Variant phloem
General configuration. Non-fibrous (Fig. 13E), with approximately 9-18 rows of sieve tubes and phloem parenchyma cells between fiber bands. The axial elements show a diffuse arrangement (Fig. 13E).

Sieve-tube elements. As seen in transverse section, each sieve element is associated with one companion cell, seldom two. Sieve tubes of two distinct diameters occur together and are predominantly solitary, occasionally in radial or tangential

multiples of 2-3. As seen in longitudinal section, the sieve elements are short (< 1 mm) with inclined end walls, bearing sieve plates with 6-7 sieve areas (Fig. 13F).

Axial parenchyma. The phloem parenchyma forms a matrix where sieve elements and fiber bands are embedded (Fig. 13E), with cells that may be as wide as the sieve tubes. Sometimes radial rows of 3-4 cells of phloem parenchyma may be found between sieve elements. A crystalliferous parenchyma surrounds the fiber bands.

Fibers. The fiber bands in *Calliclamys* are composed of 3-4 cell rows (Fig. 13E).

Rays. The limiting rays are lignified only to the xylem face. The wedge rays are non-lignified, even when crossing the fiber bands (Fig. 13E).

Crystals. Acicular crystals are predominate in the crystalliferous parenchyma, but can be also found in other cells of the phloem and ray parenchyma.

Periderm
A single periderm formed. The phellem is non-stratified, and evenly thin-walled (Table 2). The phelloderm is thick, with over three layers of cells, stratified. Lenticels are non-stratified, with unlignified filling cells (Table 2).

XII. Multiples of four clade

TAXONOMIC INFORMATION. — This clade contains four genera, *Anemopaegma*, *Bignonia*, *Mansoa*, and *Pyrostegia*, with multiples of four phloem wedges in transversal section. While the circumscription of *Anemopaegma* has remained constant in different classification systems, *Bignonia* currently includes species from eight previously recognized genera (Fischer *et al.* 2004; Table 1), *Cydista* Miers, *Clytostoma* Miers ex Bureau, *Macranthisiphon* Bureau ex K.Schum., *Mussatia* Bureau ex Baill., *Phryganocydia* Mart. ex Bureau, *Potamoganos* Sandwith, *Roentgenia* Urb., and *Saritaea* Dugand, plus *Tanaecium nocturnum* (Barb. Rodr.) Bureau & K.Schum.

TOTAL NUMBER OF SPECIES IN THIS CLADE. — 96 species, belonging to *Anemopaegma* (45), *Bignonia* (31), *Mansoa* (18), and *Pyrostegia* (2) (Lohmann & Taylor 2014; Zuntini *et al.* 2015; Silva-Castro & Queiroz 2016).

STUDIED SPECIES. — 16 species, *Anemopaegma chamberlaynii* (Sims.) Bureau & K.Schum., *A. chrysoleucum* (Kunth) Sandwith, *A. leave* DC*., A. longidens* Mart. ex DC., *A. oligoneuron* (Sprague & Sandwith) A.H.Gentry, *A. robustum* Bureau & K.Schum., *Bignonia binata* Thunb., *B. campanulata* Cham., *B. corymbosa* (Vent.) L.G.Lohmann, *B. magnifica* W.Bull., *B. prieurei* DC., *B. sciuripabulum* (K.Schum.) L.G.Lohmann, *Mansoa difficilis* (Cham.) Bureau & K.Schum., *M. onohualcoides* A.H.Gentry, *M. standleyi* (Steyerm.) A.H.Gentry, and *Pyrostegia venusta* (Ker. Gawl.) Miers.

Regular phloem
Thin fiber bands (Fig. 14D) and assemblages absent or present (Fig. 14D) (present in *Anemopaegma laeve*, *Bignonia binata*, *B. campanulata*, *Mansoa difficilis*, and *Pyrostegia venusta*).
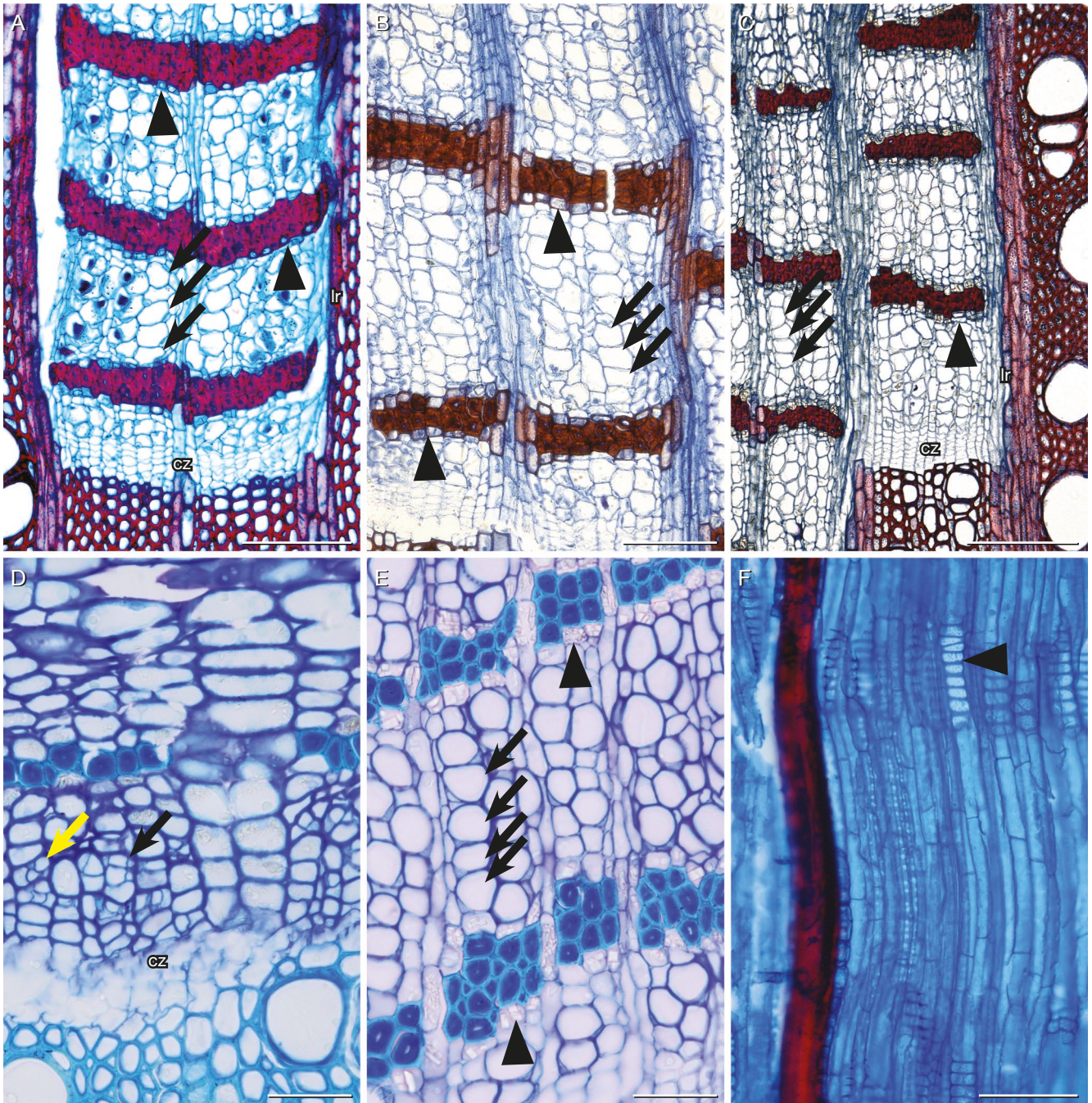
Fɪɢ. 14. — Secondary phloem of the Multiples of four clade: **A-E**, transverse sections: **A-C**, **E**, variant phloem. Non-fibrous, sieve tubes (**arrows**) in radial multiples. Axial parenchyma also forming radial rows. Crystalliferous parenchyma around fiber bands (**arrowheads**), prismatic crystals present. In **E** some styloid crystals along the prismatic crystals. Limiting rays (**lr**) lignified only to the xylem face. Rays lignify only when crossing the fiber bands in **A**, **B**, never lignifying in **C**; **E**, fiber bands thin, with two-three layers of cells; **A**, *Bignonia sciuripabulum*; **B**, *Mansoa difficilis*; **C**, *Pyrostegia venusta*; **D**, *Anemopaegma laeve* regular phloem; **E**, *Anemopaegma laeve*. Sieve tubes (**arrows**) narrow. Sometimes in assemblages (**yellow arrow**); **F**, *Mansoa difficilis* radial section. Sieve tubes with compound sieve plates (**arrowhead**) and over a millimeter. Abbreviations: **cz**, cambial zone; **lr**, limiting ray. Scale bars: A, B, F, 100 µm; C, 200 µm; D, E, 50 µm.

Variant phloem

General configuration. Non-fibrous (Fig. 14A-C, E), with approximately 8-14 rows of sieve tubes and phloem parenchyma cells between fiber bands (Fig. 14A-C, E). The axial elements occur in radial rows of sieve tubes intercalating radial rows of phloem parenchyma in an alternated fashion (Fig. 14A-C, E).

Sieve-tube elements. As seen in transverse section, each sieve element is associated with one companion cell (Fig. 14A, E). The sieve tubes occur in radial multiples, sometimes in short groups of 2-3 cells and sometimes in long groups of 9-12 sieve tubes in the same plant (Fig. 14A-C, E). Moreover, the sieve tube rows are often interrupted by 1-2 phloem parenchyma cells (Fig. 14B, E). In *Anemopaegma*, only short

radial rows of sieve tubes have been encountered. As seen in longitudinal section, the sieve elements are long (> 1 mm) and their end walls are inclined, with most sieve elements bearing compound sieve plates with 4-12 sieve areas (Fig. 14F), although simple sieve plates are occasionally encountered.

Axial parenchyma. Radial rows of phloem parenchyma are distinctive, composed of 4-6 cells that are sometimes interrupted by sieve tubes (Fig. 14A-C, E). Crystalliferous parenchyma is, moreover, found surrounding the fiber bands (Fig. 14A-C, E).

Fibers. The fiber bands have 2-3 cell rows (Fig. 14A-C, E).

Rays. The limiting rays are only lignified to the xylem face (Fig. 14A-C). The rays are non-lignified, except when crossing the fiber bands and when located in the nonconducting phloem area (Fig. 14A, B). In some species the rays do not lignify, not even when crossing the fiber bands (Fig. 14E).

Crystals. The crystalliferous parenchyma bears acicular crystals in *Bignonia magnifica*, prismatic crystals in *Anemopaegma laeve* (Fig. 14E), *Bignonia binata, B. sciuripabula* (Fig. 14A), *Mansoa* (Fig. 14B), and *Pyrostegia* (Fig. 14C), and styloid crystals in *Bignonia campanulata*. Styloid crystals may also be found in the crystalliferous parenchyma of *Anemopaegma laeve* (Fig. 14E) and *Mansoa standleyi*. Prismatic and styloid crystals are found scattered among the phloem and ray parenchyma cells of *Anemopaegma oligoneuron* and *A. robustum*.

Periderm
A single periderm is formed. The phellem is non-stratified in *Anemopaegma, Bignonia binata, B. campanulata, B. magnifica*, and *Mansoa* (Table 2). The non-stratifed phellem of *Anemopaegma chamberlaynii, A. robustum, Bignonia binata, B. campanulata, B. magnifica,* and *Mansoa* is evenly thin-walled. In *Anemopaegma laeve* the phellem is evenly thick-walled (Table 2). The phellem is stratified in *Bignonia sciuripabula, B. capreolata,* and *Pyrostegia venusta,* with alternating lignified and non-lignified cells. The phelloderm is non-stratified, thin and with less than three cell layers in *Anemopaegma chamberlaynii* and *A. leave,* but thick, with more than three layers of cells in *Anemopaegma robustum, Bignonia binata, B. campanulata, B. magnifica, B. sciuripabula, B. capreolata, Mansoa difficilis, M. onohualcoides,* and *Pyrostegia venusta* (Table 2). Lenticels are non-stratified, with unlignified filling tissue in *Anemopaegma chamberlaynii, Bignonia campanulata, B. magnifica, B. sciuripabula,* and *Mansoa difficilis* (Table 2).

XIII. *Amphilophium* clade

TAXONOMIC INFORMATION. — This clade contains a single genus, *Amphilophium*, with multiples of four phloem wedges in transversal section. *Amphilophium* currently includes species from six previously recognized genera (see Fischer *et al.* 2004; Table 1), *Amphilophium, Distictella* Kuntze, *Distictis* Mart. ex Meisn, *Glaziova* Bureau, *Haplolophium* Cham., and *Pithecoctenium* Mart. ex Meisn.

TOTAL NUMBER OF SPECIES IN THIS CLADE. — 47 species (Lohmann & Taylor 2014).

STUDIED SPECIES. — Seven species, *Amphilophium bracteatum* (Cham.) L.G.Lohmann, *A. crucigerum* (L.) L.G.Lohmann, *A. dolichoides* (Cham.) L.G. Lohmann, *A. elongatum* (Vahl.) L.G. Lohmann, *A. magnoliifolium* (Kunth) L.G. Lohmann, *A. paniculatum* (L.) Kunth, and *A. pulverulentum* (Sandwith) L.G. Lohmann.

Regular phloem
Thin to thick fiber bands (Fig. 15D), assemblages absent.

Variant phloem
General configuration. Non-fibrous (Fig. 15C), with 20-30 rows of sieve tubes and phloem parenchyma cells between fiber bands (Fig. 15C). The axial elements tend to be diffuse, sometimes forming short radial and tangential groups (Fig. 15C, F). As seen in tangential section, the axial parenchyma is storied (Fig. 15G).

Sieve-tube elements. As seen in transverse section, each sieve element is associated with one companion cell (Fig. 15F). The sieve tubes are generally solitary or in multiples of two, showing no distinct arrangement (Fig. 15F), often scattered among the phloem parenchyma cells or forming radial or tangential rows of two or three cells (Fig. 15F). In *A. crucigerum* and *A. elongatum* sieve tubes of two distinct diameters are present (Fig. 15F). In *A. crucigerum* the large and narrow sieve elements occur adjacent to one another in the phloem (Fig. 15F), while in *A. elongatum* they are organized radially from wide (70 μm in average) to narrow (35 μm in average), gradually decreasing in diameter. As seen in longitudinal section, the sieve elements are rather short (< 1 mm) and their end walls are transverse to inclined, with most sieve elements bearing simple sieve plates (Fig. 15E). Compound sieve plates with 2-3 sieve areas are sometimes encountered.

Axial parenchyma. The phloem parenchyma tends to intermingle all the cells (Fig. 15F), although at some portions they can be recognized as forming radial rows of 3-4 cells (Fig. 15F). Crystalliferous parenchyma surrounds the fiber bands (Fig. 15E), except for *A. magnoliifolium* and *A. pulverulentum* where parenchyma cells surround the fiber bands, but crystals are lacking.

Fibers. Fiber bands occur at considerable distances (more than 20 cells) from one another in *Amphilophium* (Fig. 15C), the Bignonieae genus with the most distant fiber bands. The fiber bands possess 2-3 rows of cells and are discontinuous between two limiting rays, i.e., they never occupy the entire space between two rays (Fig. 15C).

Rays. The limiting rays are only lignified to the xylem face (Fig. 15C). The wedge rays are non-lignified, not even when crossing the fiber bands.

Crystals. The crystalliferous parenchyma bears styloid crystals in *Amphilophium elongatum*, prismatic crystals in *A. crucigerum* (Fig. 15E), and *A. paniculatum*; crystals are lacking in *A. magnoliifolium*. Most, if not all of the axial and ray parenchyma cells contain acicular and navicular crystals.
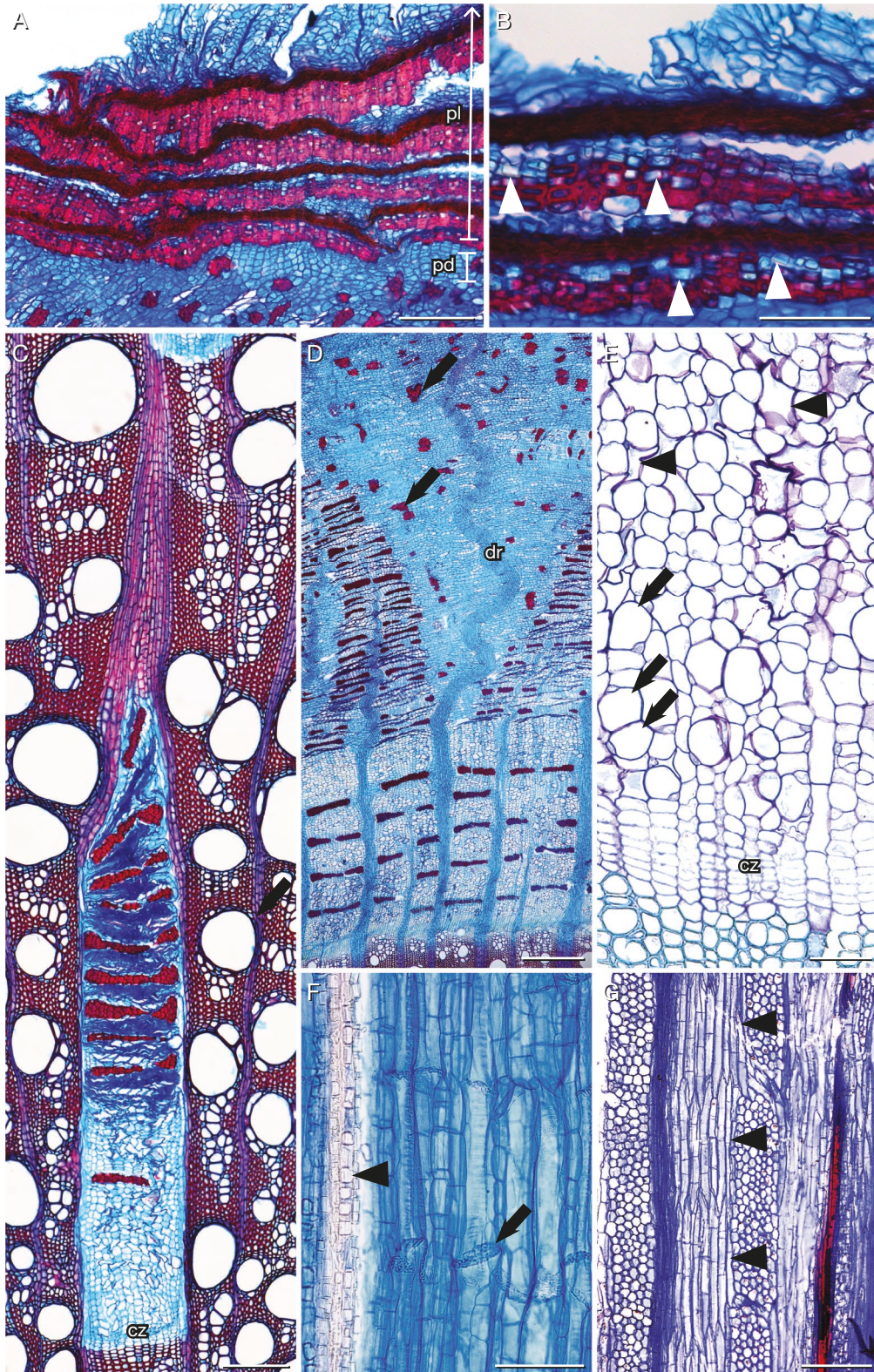
Fig. 15. — Secondary phloem of *Amphilophium*: **A-G**, *Amphilophium crucigerum*; **A-E**, transverse sections; **A**, periderm with a stratified phellem, with an alternation of thick-walled lignified cells, and thin-walled, non-lignified cells. Phelloderm thick; **B**, prismatic crystals abundant in the phellem (**arrowheads**); **C**, included phloem wedge forms interxylary phloem in the genus. The cambium remains active and produce phloem in the enclosed wedgde, causing a conspicuous collapse of the nonconducting phloem; **D**, regular phloem with thin to thick fiber bands. A large portion of the nonconducting undergoes extensive collapse. Some of the rays greatly dilate by division of the ray margins, forming wedge shaped rays. Some ray cells undergo belated sclerosis forming sclereids (**arrows**); **E**, detail of the secondary phloem, showing turgid sieve tubes (**arrows**) with one companion cell lying on its corner. Loss of conductivity happens a few layers away from the cambium, with collapse of the sieve tubes (**arrowheads**); **F**, longitudinal radial section. Wide sieve tubes with simple sieve plates. Crystalliferous parenchyma bearing prismatic crystals around fiber band; **G**, longitudinal tangential section, regular phloem. Axial parenchyma storied, rays wide, with over 5 cells in width. Abbreviations: **cz**, cambial zone. Scale bars: A, C, G, 200 µm; B, F, 100 µm; D, 600 µm; E, 50 µm.
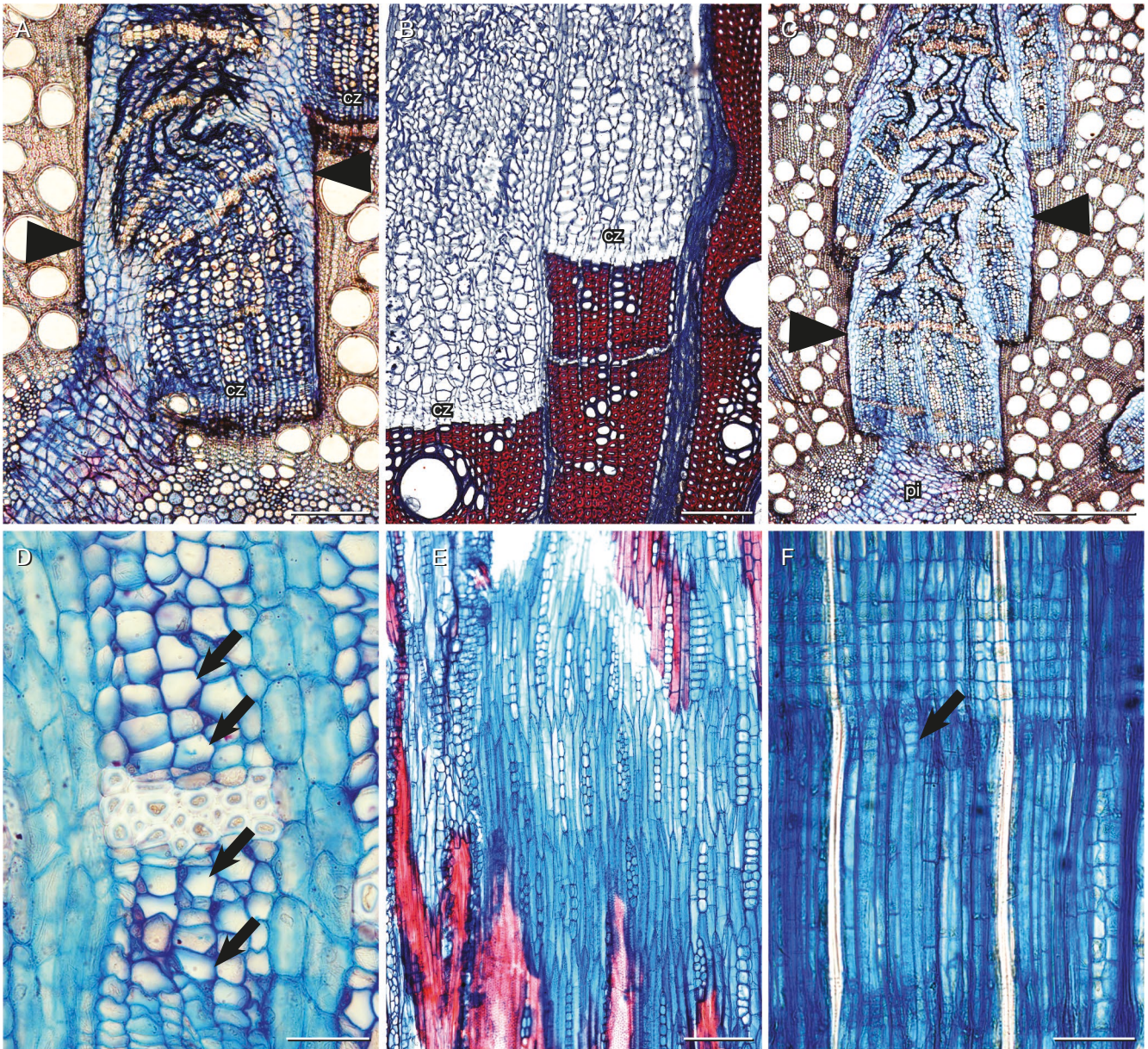
FIG. 16. — Secondary phloem of *Dolichandra*: **A-D**, transverse sections; **B**, *Dolichandra unguiculata*. All other photos are from *Dolichandra unguis-cati*; **A**, limiting rays non-lignified, tend to expand and divide (**arrows**), non-fibrous phloem. Thin fiber bands; **B**, non-fibrous phloem, sieve tubes in short radial multiples. Limiting rays non-lignified; **C**, pith also undergo divisions, uniting to divisions at the limiting rays (**arrowheads**). Nonconducting phloem collapsed; **D**, detail of the conducting variant phloem. Sieve tubes (**arrows**) with one or two companion cells. Acicular crystals abundant; **E**, tangential section. Storied structure in both axial and ray cells; **F**, radial section. Sieve tube elements with compound sieve plates (**arrow**). Abbreviations: **cz**, cambial zone; **pi**, pith. Scale bars: A, 200 µm; B, E, 150 µm; C, 500 µm; D, 50 µm; F, 100 µm.

Periderm

A single periderm is formed (Fig. 15A). The phellem is non-stratified, with evenly thin-walled cells in *Amphilophium elongatum*, *A. magnoliifolium*, and *A. paniculatum*; stratified, with alternating thin and thick-walled cells in *A. crucigerum* (Fig. 15A, B). Prismatic crystals are found in the phellem of *Amphilophium crucigerum* (Fig. 15B). The phelloderm is thin in *Amphilophium elongatum* and thick in *A. crucigerum* and *A. magnoliifolium*, with more than three cell layers (Table 1). Stratified lenticels are found in *Amphilophium crucigerum*.

XIV. *Dolichandra* clade

TAXONOMIC INFORMATION. — This clade contains a single genus, *Dolichandra*, with multiple dissected phloem wedges in transversal section. *Dolichandra* currently includes species from four previously recognized genera (see Fischer *et al.* 2004; Table 2), *Dolichandra*, *Macfadyena* A.DC., *Melloa* Bureau, and *Parabignonia* Bureau ex K.Schum.

TOTAL NUMBER OF SPECIES IN THIS CLADE. — 9 species (Fonseca *et al.* 2017).

STUDIED SPECIES. — Three species, *Dolichandra quadrivalvis* (Jacq.) L.G.Lohmann, *Dolichandra unguiculata* (Vell.) L.G.Lohmann, and *Dolichandra unguis-cati* (L.) L.G. Lohmann.
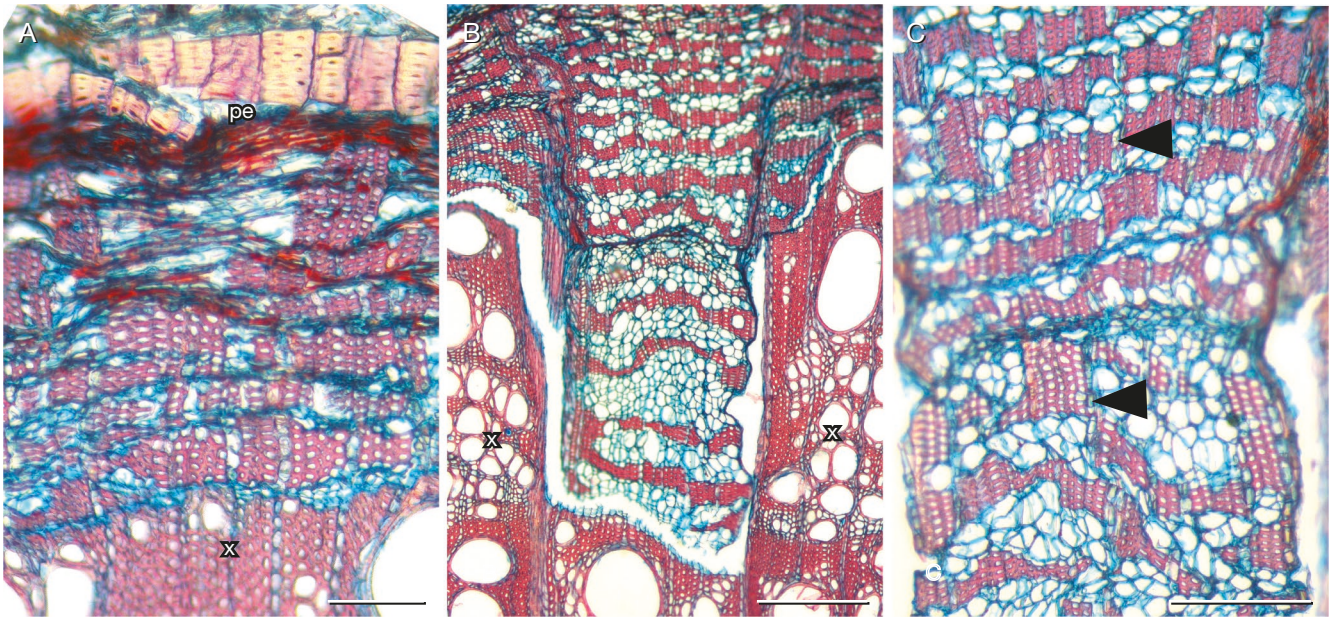
Fig. 17. — Secondary phloem of *Adenocalymma mirabile*: **A**-**C**, *Adenocalymma mirabile* transverse-sections; **A**, regular phloem. Thin to thick fiber bands. Periderm with stratified phellem, with alternating thin and thick-walled, lignified cells. Phelloderm thick, with over 3 cell layers; **B**, overall view of the variant phloem. Non-fibrous to semi-fibrous phloem. Fiber bands thin to thick, U-shaped in several portions. Limiting ray lignified to both xylem and phloem face; **C**, detail of the variant phloem. Rays alternate in being lignified or not. Prismatic crystals present in rays (**arrowheads**). Sieve tubes in short radial or tangential multiples. Abbreviations: **pe**, periderm; **x**, secondary xylem. Scale bars: A, C, 200 µm; B, 300 µm.

Regular phloem
Thin to thick fiber bands, without assemblages.

Variant phloem
The variant phloem of *Dolichandra* is nearly identical to that of the Multiples of four s.s. clade. In fact, the sieve tubes and phloem parenchyma arrangement, the sieve plate type, the presence of crystals, and the number of cells between fiber bands is alike in both clades (Fig. 16A-C). The presence of sieve elements of two distinct diameters (40 µm and 15 µm in average) tending to gradually go from wide to narrow diameter in subsequent bands (Fig. 16D) is similar to that found in *Amphilophium*. Another similarity with *Amphilophium* is the storied structure (Fig. 16E); however, the storied structure in *Dolichandra* is found both for axial and radial elements (Fig. 16E). A further remarkable difference from the Multiples of four s.s. clade is the non-lignification of the limiting rays (Fig. 16A-C), that tend to divide, compress, and dissect the phloem wedges (Fig. 16A, C). The crystalliferous parenchyma in *Dolichandra* bears acicular crystals, which are also found in the rays (Fig. 16D, F).

Periderm
A single periderm is formed. The phellem is stratified, with alternating thin and thick-walled cells. The phelloderm is non-stratified, thin, with less than three cell layers. Lenticels were not observed.

XV. *Adenocalymma* clade

TAXONOMIC INFORMATION. — This clade contains a single genus, *Adenocalymma*, with four to multiples of four phloem wedges in transversal section. In the most recent circumscription of the genus (Fonseca & Lohmann 2019), *Adenocalymma* houses four genera recognized in previous classification systems (see Fischer *et al.* 2004; Table 1), *Adenocalymma*, *Gardnerodoxa* Sandwith, *Memora*, and *Neojobertia* Baill.

TOTAL NUMBER OF SPECIES IN THIS CLADE. — 76 species (Fonseca & Lohmann 2019).

STUDIED SPECIES. — 13 species, *Adenocalymma adenophorum* (Sandwith) L.G.Lohmann, *A. alboaurantiacum* (Faria & Proença) L.H.Fonseca & L.G. Lohmann, *A. bracteatum* (Cham.) DC., *A. acutissimum* (Cham.) Miers., *A. divaricatum* Miers., *A. flaviflorum* (Miq.) L.G.Lohmann, *A. longilineum* (A. Samp.) L.G.Lohmann, *A. mirabilis* (Sandiwth) L.H.Fonseca & L.G.Lohmann, *A. nodosum* (Silva Manso) L.G.Lohmann, *A. peregrinum* (Miers.) L.G.Lohmann, *A. salmoneum* J.C.Gomes, *A. tanaeciicarpum* (A.H.Gentry) L.G.Lohmann, and *A. validum* (K.Schum.) L.G.Lohmann.

Regular phloem
Thin to thick fiber bands (Fig. 17A, 18A), assemblages absent or present (present in *Adenocalymma bracteatum*, *A. divaricatum*, *A. salmoneum*, and *A. validum*).

Variant phloem
The variant phloem of *Adenocalymma* is by far the most diverse in Bignonieae. In fact, besides from the wedge number, either four or in multiples of four, *Adenocalymma* species can range from non-fibrous, semi-fibrous (Fig. 17B) to fibrous, with axial elements ranging from radially to tangentially arranged, sometimes with radial groups of 2-3 sieve tiubes (Fig. 17B), sometimes in clusters. Given the high diversity of the secondary phloem of *Adenocalymma*, we here divide them in three distinct groups based on their phloem structures.

Group 1: Non-fibrous Adenocalymma
Six of the analyzed species were included in this group: *Adenocalymma adenophorum*, *A. bracteatum*, *A. flaviflorum*, *A. longilineum*, *A. nodosum*, and *A. peregrinum*.

General configuration. Non-fibrous (Fig. 18B), with approximately 7-13 rows of sieve tubes and phloem parenchyma between fiber bands. The axial elements present a radial to diffuse arrangement.

Sieve-tube elements. As seen in transverse section, each sieve element is associated with 2 companion cells, one at each corner of the sieve element (Fig. 18C). The sieve elements are generally in multiples of 2-3, sometimes solitary (Fig. 18C). Sieve tubes of narrower radial diameter are present in *A. nodosum* associated with a tangential parenchyma band. As seen in longitudinal section, the sieve elements are short (< 1 mm) and their end walls are inclined, bearing sieve plates with 7-14 sieve areas.

Axial parenchyma. The phloem parenchyma intermingles all other cells (Fig. 18B, C), and form radial rows of 3-5 cells at certain portions. A tangential band is also present in *Adenocalymma nodosum*.

Fibers. Fiber bands of 2-5 rows of cells are present (Fig. 18B).

Rays. The limiting rays are lignified only to the xylem face. The wedge rays are non-lignified, except when crossing the fiber bands (Fig. 18B) and except in *A. longilineum*, which present portions of the rays lignified even when not touching the fiber bands.

Crystals. Crystals are absent in *Adenocalymma peregrinum*. Prismatic crystals are present in *A. adenophorum*, *A. flaviflorum*, *A. longilineum* and *A. nodosum*, being restricted to the ray cells crossing the fiber bands in *A. adenophorum* and *A. flaviflorum* and being scattered and rare in phloem and ray parenchyma cells of *A. nodosum*.

Group 2: Semi-fibrous Adenocalymma
Three of the analyzed species were included in this group: *Adenocalymma comosum*, *A. mirabilis*, and *A. salmoneum*.

General configuration. Semi-fibrous (Fig. 17B, C, 18E), exhibiting wavy fiber bands (Fig. 17B, 18E). The axial elements show a tangential arrangement (Fig. 18E).

Sieve-tube elements. As seen in transverse section, each sieve element is associated with one companion cell. The sieve elements are generally in multiples of 2-3 (Fig. 17B), rarely solitary, with sieve elements in both radial and tangential rows, sometimes in clusters (Fig. 18E). As seen in longitudinal section, the sieve elements are short (< 1 mm) and their end walls are inclined, bearing sieve plates with 7-12 sieve areas.

Axial parenchyma. The phloem parenchyma forms the background tissue (Fig. 17B), it is complete in *A. salmoneum*, and without this arrangement in *A. comosum*. In addition, radial rows of 4-7 cells of phloem parenchyma are present in some places.

Fibers. Fiber bands wavy, in some portions thicker than in others (Fig. 17B, C, 18E).

Rays. The limiting rays are lignified only to the xylem face. The wedge rays can be non-lignified or lignified, especially when crossing the fiber bands (Fig. 17B, C, 18E).

Crystals. Crystals are very abundant, being styloid and acicular in *A. comosum*, prismatic to styloid in *A. mirabile* (Fig. 17C), prismatic in *A. salmoneum*, and prismatic and acicular in *A. validum*.

Group 3: Fibrous Adenocalymma
Three of the analyzed species were included in this group: *Adenocalymma alboaurantiacum*, *A. divaricatum*, and *A. validum*.

General configuration. Fibrous (Fig. 18D, F, G), presenting a matrix of fibers in which all other cells are embedded (Fig. 18D, F, G). The axial elements show a tangential arrangement (Fig. 18D, F).

Sieve-tube elements. As seen in transverse section, each sieve element is associated with one companion cell, sometimes two in *A. validum*, one in each corner of the sieve element. The sieve elements occur in multiples of 2-3, sometimes solitary (Fig. 18F). As seen in longitudinal section, the sieve elements are short (< 1 mm) and their end walls are inclined, bearing sieve plates with 7-10 sieve areas. Reticulated sieve plates are present in *A. divaricatum*.

Axial parenchyma. The phloem parenchyma is sieve-tube-centric incomplete in *A. validum*, complete in *A. alboaurantiacum* (Fig. 18F), and *A. divaricatum*. Radial rows of phloem parenchyma can be also detected alternating with sieve elements and near the ray cells.

Fibers. A matrix of fibers is present (Fig. 18D, F, G). Fibers are more abundant in *A. divaricatum* (Fig. 18D) than in the other species studied.

Rays. The limiting rays are lignified only to the xylem face, but with some portions lignified also to the phloem face (Fig. 18D). The wedge rays have randomly alternating portions lignified and non-lignified (Fig. 18D).

Crystals. All species in this group present crystals in the ray cells (Fig. 18F, G). They are prismatic in *A. divaricatum*, prismatic in *A. salmoneum*, and prismatic and acicular in *A. validum* (Fig. 18F, G).

Periderm
A single periderm is formed (Fig. 17A) in all species, except for *Adenocalymma flaviflorum*, which also forms a rhytidome.
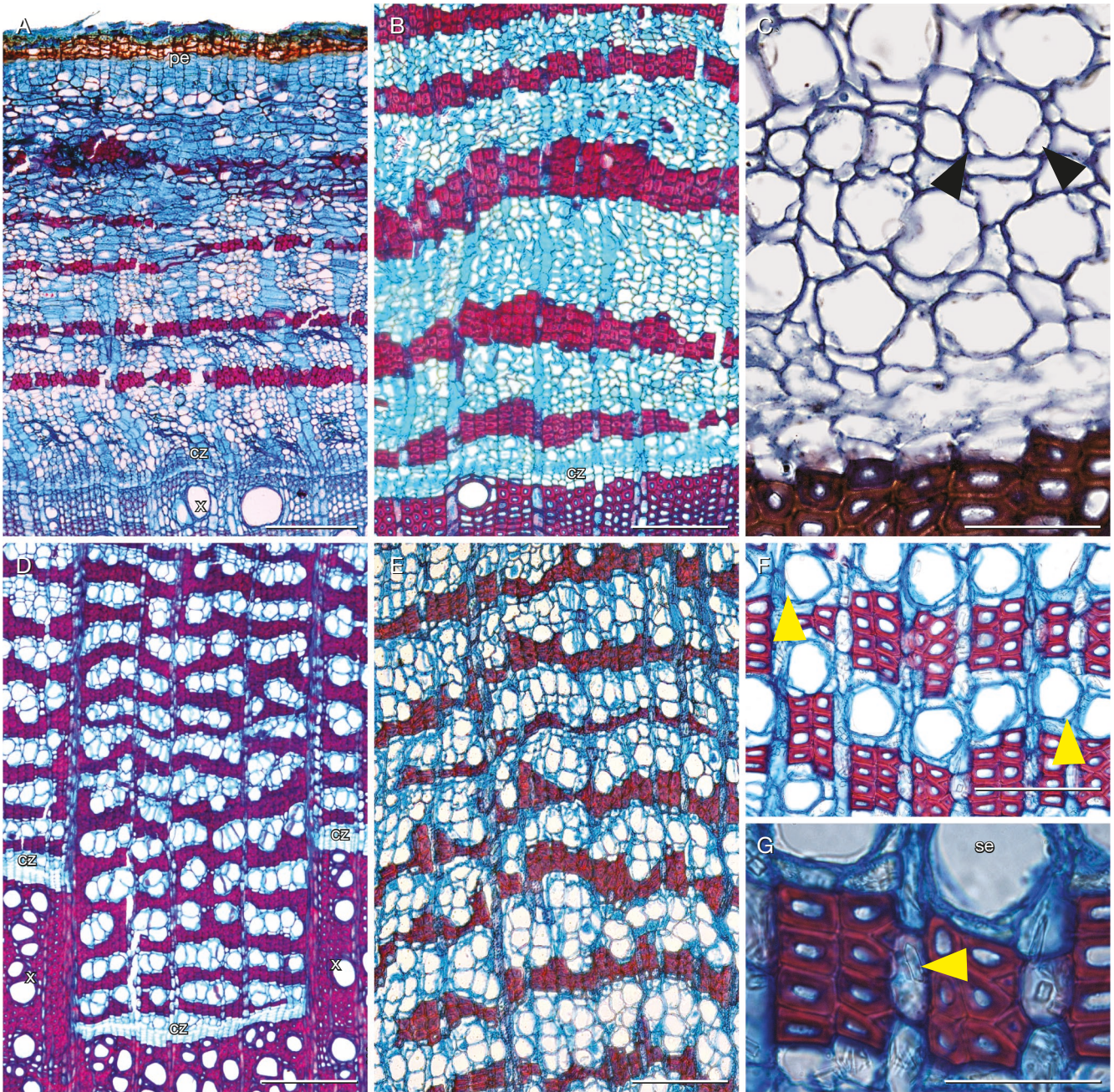
Fɪɢ. 18. — Secondary phloem of *Adenocalymma*: **A**-**G**, transverse sections; **A**, *Adenocalymma bracteatum*, thin fiber bands. Single periderm with a thin-walled phellem, and a thick-walled phelloderm; **B**, *Adenocalymma flaviflorum* variant phloem. Non-fibrous, sieve tubes in radial multiples of 2 till 5 cells. Rays lignify when crossing the fiber bands; **C**, Detail of the variant phloem of *Adenocalymma flaviflorum*. Sieve tubes typically with two companion cells, each lying on a different corner. Axial parenchyma as the background tissue; **D**, *Adenocalymma divaricatum* variant phloem. Fibrous-phloem. Sieve tubes in tangential arrangement. Rays with portions lignified and non-lignified; **E**, *Adenocalymma comosum* variant phloem. Semi-fibrous phloem. U-shaped fiber bands. Sieve tubes in radial multiples of two to three cells, rarely solitary; **F**, **G**, *Adenocalymma alboaurantiacum* variant phloem. Fibrous-phloem. Sieve tubes with a tangential arrangement. Rays sometimes lignify when crossing the fiber bands. Axial parenchyma sieve-tube-centric. Crystals abundant; **G**, detail of the styloid crystals in rays (**arrowhead**). Prismatic crystals also present. Abbreviations: **cz**, cambial zone; **pe**, periderm; **x**, secondary xylem. Scale bars: A, D, 200 µm; B, E, 150 µm; C, G, 50 µm; F, 100 µm.

The phellem can be non-stratified and evenly thin-walled in *A. bracteatum* and *A. flaviflorum* or non-stratified and evenly thick-walled in *A. comosum, A. divaricatum, A. peregrinum,* and *A. salmoneum* (Table 2). The phellem is stratified in *A. mirabile* and *A. validum*, with alternating thin and thick-walled cells (Fig. 17A). In *Adenocalymma validum*, there is also an alternation of cells with dark content and cells without any conspicuous content. The phelloderm is non-stratified (Fig. 17A), thin in *A. comosum* and *A. peregrinum*, or thick-walled, in *A. bracteatum, A. divaricatum, A. flaviflorum, A. mirabile, A. salmoneum,* and *A. validum* (Table 2). Lenticels are stratified in *Adenocalymma comosum, A. peregrinum, A. salmoneum,* and *A. validum* and non-stratified, with unlignified filling tissue in *A. flaviflorum* (Table 2). Lenticels were not observed in *A. mirabile*.
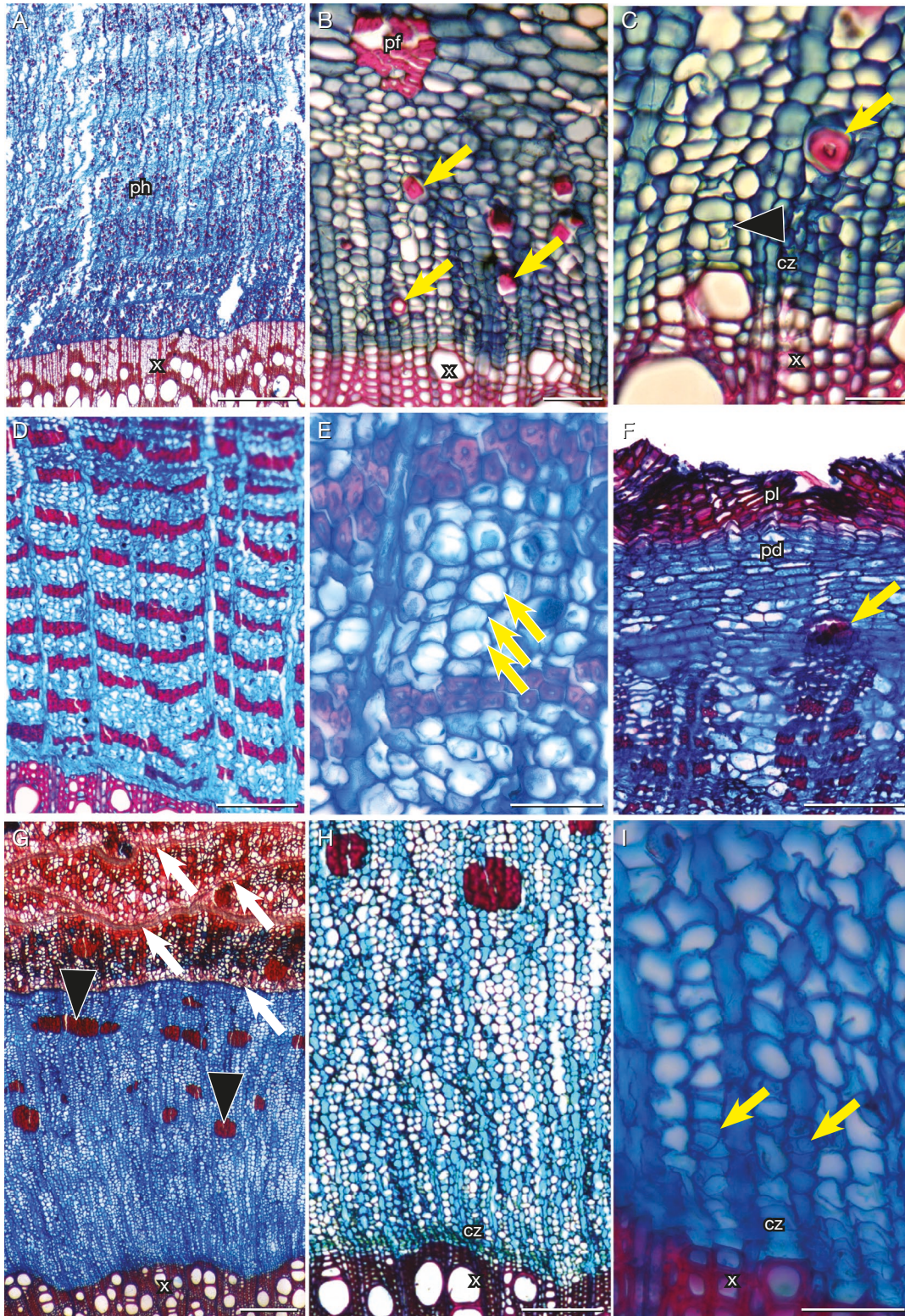
FIG. 19. — Secondary phloem of lianas of Tecomeae s.s: **A-I**, transverse sections: **A-C**, *Campsis radicans*; **A**, Overall view of the secondary phloem. Non-stratified, with scattered individual fibers; **B**, Detail of the secondary phloem showing individual fibers (**arrows**); **C**, detail of the secondary phloem showing the sieve tubes (**arrowhead**) solitary or in radial multiples of two, with one companion cell. Note the individual fiber (**yellow arrow**); **D-F**, *Pandorea jasminoides*; **D**, stratified phloem, with fibers bands alternating with sieve tubes and axial parenchyma, interrupted by the rays that do not lignify, not even when crossing the fiber bands; **E**, detail of the secondary phloem, with sive tubes in radial multiples (**arrows**), with one companion cell on their corner; **F**, detail of the single periderm, showing an evenly thin-walled phellem, thick phelloderm. Note the pericyclic fiber strand (**arrow**); **G-I**, *Podranea ricasoliana*; **G**, overall view of the bark. Rhytidome present, with sequent periderms (**arrows**) reticulate. Secondary phloem non-fibrous, devoid of fibers, with fibersclereids present in clusters (**arrowheads**). Course of rays straight; **H**, detail of the secondary phloem showing the axial parenchyma as the matrix where other cell types are found. Detail of the fibersclereid cluster (**arrowhead**); **I**, detail showing the sieve tubes in short radial multiples, with one companion cell lying on their corner (**arrows**). Abbreviations: **cz**, cambial zone; **pd**, phelloderm; **pf**, pericyclic fibers; **ph**, phloem; **pl**, phellem; **x**, secondary xylem. Scale bars: A, 1 mm; B, E, I, 50 μm; C, 25 μm; D, F-H, 200 μm. Fig. 19B and C by courtesy of Kishore Rajput.

Lianescent Tecomeae
Campsis radicans
Non-stratified phloem (Fig. 19A), marked by scattered fibers (Fig. 19A-C). The conducting phloem has sieve tubes solitary or in multiples of 2-4 (Fig. 19C). One companion cell lying on the corner of the sieve tube (Fig. 19C). The sieve plates are simple in transverse walls, or with 2-4 sieve areas per sieve plate in a slightly inclined wall. The axial parenchyma constitutes the background tissue (Fig. 19B, C), with parenchyma strands with 3-4 cells. Rays straight (Fig. 19A), 2-3-seriate, heterocellular, with body of procumbent cells and two square to upright marginal cells, lacking dilatation (Fig. 19A). Sclerenchyma composed of scattered fibers (Fig. 19A), either solitary (Fig. 19B, C) or in multiples of two, with an angular outline (Fig. 19B). Non-storied. Nonconducting phloem marked by empty sieve elements and companion cells, collapsed. Cell expansion is the main dilatation phenomenon recorded, with no further sclerification.

Pandorea jasminoides
Stratified phloem (Fig. 19D), marked by the alternation of fiber bands, interrupted only by the rays, with areas of sieve tubes and axial parenchyma (Fig. 19D). Conducting phloem composed of sieve tubes solitary or in multiple of 2-3 (Fig. 19E), intermingled by axial parenchyma cells (Fig. 19E). Sieve plates varying from almost transverse end walls and simple sieve plates, to inclined with 4-5 sieve areas. One companion cell lying on the corner of the sieve tube (Fig. 19E) or two companion cells, each on opposite sides of the sieve tube (Fig. 19E). Companion cells in strands of 2-4 cells. Axial parenchyma diffuse (Fig. 19D, E), abundant, in strands of four cells. Course of rays straight (Fig. 19D). Rays bi- to triseriate, heterocellular mixed, with procumbent, square and upright cells intermixed across the entire ray. Rays taller than 1 mm,

as seen in tangential section. Rays slightly dilated in the outermost portions of the nonconducting phloem. Rays do not sclerify, not even when touching the fiber bands (Fig. 19D, E). Sclerenchyma composed of fibers, polygonal to rectangular in shape (Fig. 19D, E). Fibers in tangential bands of 2-3 cells, interrupted by the rays (Fig. 19D, E). Non-storied. Nonconducting phloem marked by empty sieve elements and companion cells, collapsed. Cell expansion common, dilatation of rays, no further sclerification seen. Pericyclic fibers forming a ring of discrete strands before a remaining cortex. Single periderm, phellem non-stratified, with evenly thin-walled cells, phelloderm non-stratified, thick, with three or more cell layers (Fig. 19F).

Podranea ricasoliana
Non-stratified phloem (Fig. 19G, H). Sieve tubes solitary or in multiples of 2-3 (Fig. 19I). Most sieve plates simple, on a transverse to slightly inclined wall. One or two companion cell per sieve-tube element (Fig. 19I), lying on opposite sides of the sieve tube. Companion cells in strands of two cells. Axial parenchyma constitutes the ground tissue (Fig. 19H, I), two cells per parenchyma strand, sometimes up to four. Course of rays straight (Fig. 19G). Ray dilatation seemingly absent (Fig. 19G). Rays bi-triseriate, heterocellular mixed, with procumbent, square and upright cells intermixed across the entire ray. Rays smaller than 1 mm, except when two or more rays merge. Rays do not sclerify, not even when touching the fibersclereid clusters (Fig. 19G, H). Sclerenchyma composed of fibersclereids only, differentiated in the nonconducting phloem in discrete, evenly distributed clusters. Non-storied. In young stems, pericyclic fibers forming a ring of discrete strands. Multiple periderms (rhytidome), reticulate (Fig. 19G). The phellem and phelloderm are thin walled, non-stratified (Fig. 19G). The phelloderm is thin, with less than three cell layers (Fig. 19G).

SECTION 5. KEY FOR THE IDENTIFICATION OF LIANA BIGNONIACEAE GENERA USING BARK ANATOMY

This key is designed for cases when only the stem is available for identification. We recommend using additional identification keys based on vegetative or reproductive characters when additional material is available.

DISCUSSION

In this study we provide the first detailed description of the bark anatomy of 83 species of Bignoniaceae, including all 20 genera presently recognized in tribe Bignonieae plus the three widely cultivated species of lianas belonging to tribe Tecomeae *s.s.* We were able to i) characterize and illustrate all major clades of lianescent Bignoniaceae; ii) identify 19 potential synapomorphies (Table 3; Fig. 20); and iii) provide the first bark identification key that can be used in the absence of vegetative or reproductive features.

The first study aiming to describe Bignoniaceae bark structure is that of Roth (1981), where the phloem is described as extremely homogeneous, marked by a stratified structure, with an alternation of fiber bands. Subsequent works, on the other hand, have disputed this statement, showing that although a stratified phloem is prevalent, some genera show a non-stratified phloem, with either scattered fibers (e.g., Rajput *et al.* 2017; Pace *et al.* 2021), or fibers forming the entire background tissue (Pace *et al.* 2015a). Here we confirm that although the bark tends to be homogeneous within some clades, it is not homogeneous in the family as a whole and can be extremely informative in sorting genera. The bark diversity in Bignoniaceae becomes especially important in the lianas, since liana wood anatomy converges to a very similar pattern regardless of their taxonomic position, a well-known case of convergent evolution to the climbing habit which homogenizes lianescent woods (Schenck 1893; Carlquist 1985, 2001). This phenomenon has been coined as the "lianescent vascular syndrome" and includes both qualitative (Angyalossy

et al. 2012, 2015) and quantitative attributes (Luizon Dias Leme *et al.* 2021). Lianescent wood is typically marked by wide vessels associated with narrow ones, more abundant parenchyma at the expense of fibers, wide and tall heterocellular rays (Carlquist 1985; Angyalossy *et al.* 2016). In fact, works that incorporated the wood of lianas in their sampling saw a reduction in phylogenetic signal, only restored when the lianas were eliminated from the analyses (Lens *et al.* 2008 for Icacinaceae). The bark can, therefore, be a rich source of characters for phylogenetic inference, constituting anatomical synapomorphies to various liana clades.

STEM ARCHITECTURE SHAPED BY CAMBIAL VARIANTS

Two of the lianas studied here lack a cambial variant, *Pandorea jasminoides* and *Podranea ricasoliana*, only showing a wavy cambium. All other lianas have cambial variants. A single genus has hollow stems and branches, *Stizophyllum*, where ant domatia are sometimes formed (Lohmann & Taylor 2014).

The genus *Campsis* has been long known for having intraxylary phloem, something unique in the family (Fig. 20), derived initially from bicollateral bundles (Sanio 1864; Handa 1935), and then increased by the formation of a medullary cambium, producing secondary xylem towards the protoxylem and secondary phloem towards the pith (Handa 1935; Rajput *et al.* 2017). This medullary secondary growth occurs in two facing sides of the pith, which coincide with the position of the opposite leaves typical of the family (Handa 1935). The growth is so intense that it compresses all the parenchyma of the pith, forming a dumbbell-shaped area of collapsed pith parenchyma in the center (Sanio 1864; Handa
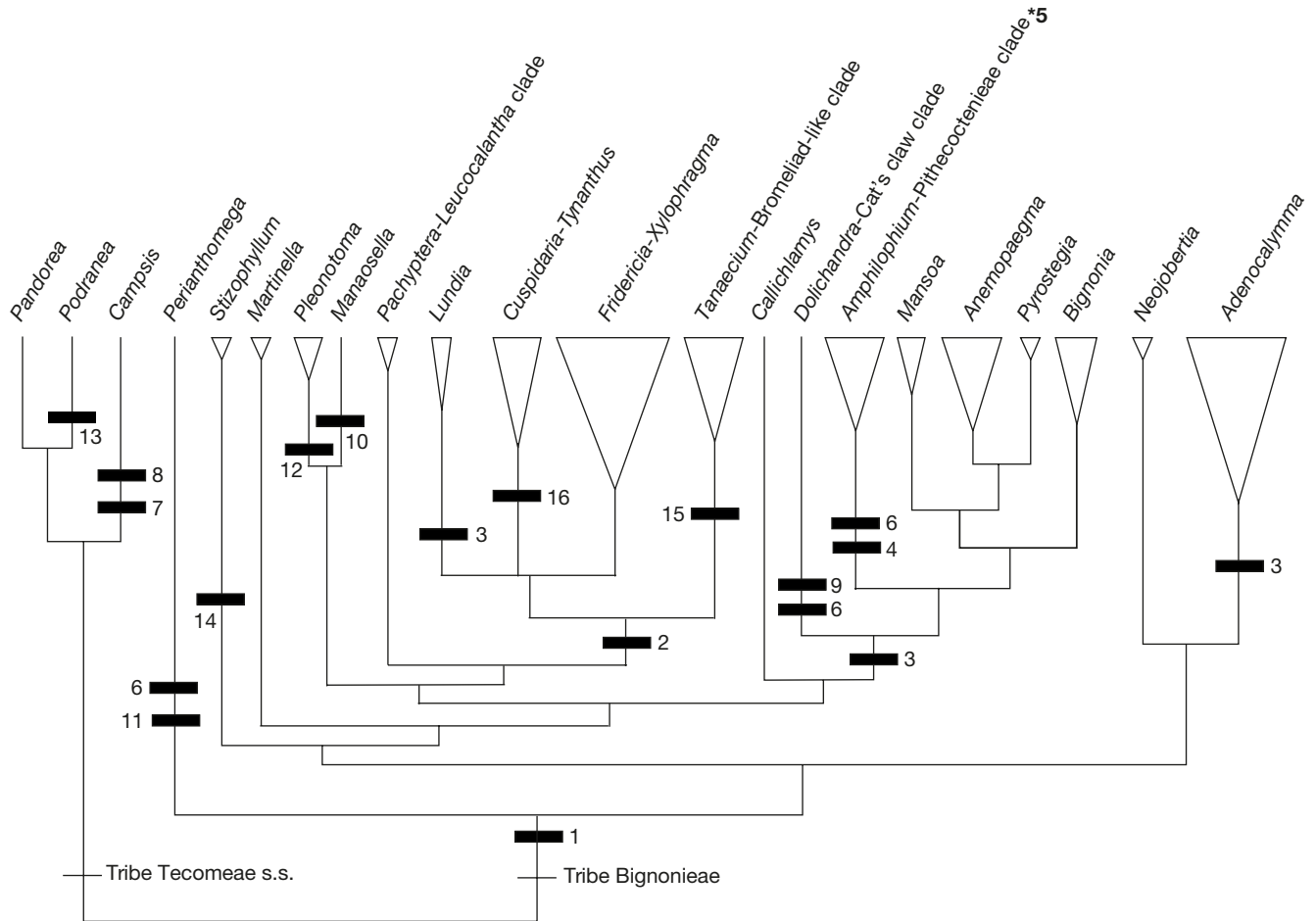
FIG. 20. — Phylogenetic mapping of the synapomorphies delimited in this study: **1**, xylem furrowed by phloem wedges; **2**, fibrous or semi-fibrous phloem; **3**, multiple of four phloem wedges; **5**, prismatic crystals in the phellem (*), found only in *Amphilophium crucigerum*; **6**, storied structure; **7**, interxylary phloem; **8**, fibers scattered in the phloem; **9**, multiple dissected phloem wedges, non-lignified parenchyma in wood; **10**, phloem fibers tangentially elongated; **11**, four conspicuous phloem arcs; **12**, fibers absent in the regular phloem, sclereids found instead; **13**, fibers absent in the phloem, sclereids found instead; **14**, hollow stems; **15**, limiting rays without lateral steps; **16**, symmetrical lateral steps on both sides of the phloem wedges.

TABLE 3. — Unique traits (potential synapomorphies) for Bignoniaceae liana lineages. *, trait is present in many, but not all species analyzed and needs more sampling to determine its distribution.

Number in Fig. 20	Feature	Clade
1	Phloem wedges	Tribe Bignonieae
2	Fibrous or semi-fibrous phloem	Fridericia and allies clade
3	Multiple of four phloem wedges	Multiples of four clade, *Lundia*, *Adenocalymma**
4	Included phloem wedges	*Amphilophium* (Pithecoctenieae clade)
5	Prismatic crystals in the phellem	*Amphilophium crucigerum*
6	Storied structure	*Amphilophium*, *Dolichandra*, *Perianthomega*
7	Intraxylary phloem	*Campsis*
8	Scattered fibers in the phloem	*Campsis*
9	Multiple dissected phloem wegdes, non-lignified parenchyma in wood	*Dolichandra* (Cat's claw clade)
10	Phloem fibers tangentially elongated	*Manaosella*
11	Four conspicuous phloem arcs	*Perianthomega*
12	Fibers absent in the regular phloem, sclereids found instead	*Pleonotoma*
13	Fibers absent in the phloem, sclereids found instead	*Podranea*
14	Hollow stem	*Stizophyllum*
15	Limiting rays without lateral steps	*Tanaecium* (Bromeliad-like clade)
16	Symmetrical lateral steps on both sides of the phloem wedges	*Tynanthus-Cuspidaria* clade

1935; Rajput *et al.* 2017). The genus *Campsis* is disjunct between North America and Asia, and intraxylary phloem has been found in species from both populations (United States and China; Sanio 1864; Handa 1935), representing a synapomorphy of the genus.

Much more common than intraxylary phloem is the presence of xylem interrupted by phloem wedges, a well-established synapomorphy for tribe Bignonieae (Lohmann 2006; Lohmann & Taylor 2014; Fig. 20). This cambial variant has been known and studied in detail since the XIXth century, with constant new discoveries (Schenck 1893; Solereder 1908; Dos Santos 1995; Dobbins 1971, 1981; Gasson & Dobbins 1991; Pace *et al.* 2009; Gerolamo & Angyalossy 2017; Gerolamo *et al.* 2020). *Perianthomega* used to be part of Tecomeae *s.l.* (Gentry 1992; Fischer *et al.* 2004), but the presence of four phloem arcs supported its inclusion in Bignonieae (Lohmann 2006; Pace *et al.* 2009). The presence of four phloem wedges is by far the most common feature in the tribe, with three independent origins of genera with multiple of four phloem wedges, once in the Multiple of four clade, once in *Lundia*, and at least once in *Adenocalymma* (Fig. 20). More studies with a broader sampling of *Adenocalymma* species are necessary to unravel if the phloem wedges have evolved once or multiple times in this genus, given that many *Adenocalymma* have only four phloem wedges, even in stems thicker than 5 cm (Pace *personal observation*).

A single evolution of included phloem wedges occurred in *Amphilophium*, and a single evolution of multiple dissected phloem wedges in *Dolichandra* (Table 3, Fig. 20; Pace *et al.* 2009). The case of *Amphilophium* is especially interesting, because the genus is quite variable morphologically, and the most recent classification of the genus (Lohmann & Taylor 2014) merged six previously recognized genera (Table 1), i.e., *Amphilophium, Distictella, Distictis, Glaziova, Haplolophium*, and *Pithecoctenium* (Lohmann & Taylor 2014). Detailed morphological comparative studies of seeds and pollen have delimited features that support clades within *Amphilophium* (Burelo-Ramos *et al.* 2009, 2012). However, stability of classification depends on the principle that there are only rarely reasons for dividing a genus into two or more monophyletic genera if its own monophyletic status remains questioned, even if smaller monophyletic genera can be recognized by morphological synapomorphies (Stevens 2001 onwards). Here we found included phloem wedges supporting a merged *Amphilophium*, although more studies are needed to understand the evolution of this subtype of cambial variant within the genus.

Dolichandra, which reunites four genera of the previous classification with a cat's claw tendril, i.e., *Dolichandra, Macfadyena, Melloa*, and *Parabignonia* (Lohmann & Taylor 2014; Fonseca & Lohmann 2015; Table 1) is the only genus with non-lignified axial and ray parenchyma in the wood (Pace *et al.* 2009). This parenchyma undergoes cell division, dissecting the wood into many pieces (Dos Santos 1995; Pace *et al.* 2009). This is a potential synapomorphy of this genus (Fig. 20).

Within Bignonieae, the shrubs and treelets tend to have a paedomorphic reduction of the phloem wedges (e.g., in shrubby *Adenocalymma, Anemopaegma*, and *Fridericia*; Pace *et al.* 2009; see Onyenedum & Pace 2021 for use of the term), with total suppression encountered in *Tanaecium tetramerum* (Pace *et al.* 2016), a treelet species from the Andean chaco (Gentry 1990).

The shape of the phloem wedges is also informative. Phloem wedges typically form lateral steps, that result from the conversion of a regular cambial activity to a variant activity of the cambial regions adjacent to the wedges. This pattern is also present in other lineages with phloem wedges, such as in the Paleotropical genus *Tristellateia* Thouars of Malpighiaceae (Quintanar-Castillo & Pace 2022). These lateral steps summed to the wide limiting rays track stem girth increase. Lateral steps are only lacking in *Tanaecium*, which reunites seven genera of the previous classification, part of *Arrabidaea, Ceratophytum, Pseudocatalpa, Spathicalyx, Sphingiphila, Paragonia*, and *Periarrabidaea* (Lohmann & Taylor 2014; Frazão & Lohmann 2019; Table 3), likely representing a synapomorphy of this genus. *Tanaecium* is the genus with the widest limiting rays (check Fig. 4B), reinforcing the suggestion that lateral steps act in stem accommodation to girth increase. In their absence, the limiting rays widen up even more.

All other genera have lateral steps. *Tynanthus* and *Cuspidaria*, which together form a clade, are the only ones with almost symmetrical steps on both sides, which is likely a synapomorphy of this clade. *Tynanthus* has not underwent modifications in its circumscriptions, while *Cuspidaria*, as presently understood (Lohmann & Taylor 2014), reunites species belonging to four genera previously recognized, *Arrabidaea, Cuspidaria, Pyrostegia*, and *Saldanhaea* (Table 1).

DIFFERENT PHLOEM CELL TYPES MAY EVOLVE IN A CORRELATED FASHION

Many features of the phloem vary in a correlated fashion (Pace *et al.* 2015a) and should be scored as a single character in phylogenetic analyses to prevent biased phylogenetic estimates (Maddison 1990). This is the case of sieve-tube plate type, number of sieve areas per sieve plate, and sieve-tube and axial parenchyma arrangements. The main driver commanding these correlated evolutions was shown to be fiber arrangement and abundance (Pace *et al.* 2015a). Our findings corroborate this statement. In species with stratified phloem, the presence of parenchyma around the fiber bands is ubiquitous, most sieve tubes are shorter and with one to a few sieve areas per sieve plate. In species where the fibers form a background matrix, the axial parenchyma is sieve-tube-centric, the sieve plates are compound with many sieve areas, and the sieve-tube elements are long. The genus with the lowest amount of phloem fibers is *Amphilophium*, where simple sieve plates are the most common and the sieve-tube elements are the shortest (Pace *et al.* 2015a). The genera with fibrous phloem are those with compound sieve plates with more than 10 sieve areas and longer sieve-tube elements (taller than 1 mm). More studies of fiber abundance

in the phloem are needed to determine if the correlations recovered represent a general pattern in phloem evolution. Studies including the type of phloem sclerenchyma, i.e., fibers or fiber-sclereids, found no correlation between the mechanical tissue type and the sieve-tube-element's morphology (Liesche *et al.* 2017). However, sieve plate type and number of sieve-areas per sieve plate were shown to scale positively with both sieve-tube length and stem length (Liesche *et al.* 2017). Given the correlated evolution between both the sieve tube and axial parenchyma with the sclerenchyma, we focus our discussions on the mechanical tissues.

Rays are narrow and heterocellular within the phloem wedges, and wide and heterocellular in the regular phloem; the constancy of this trait leads to low taxonomic value within Bignoniaceae lianas. Rays are continuous between the secondary xylem and phloem. The selective pressure for the wood of lianas to be flexible (Angyalossy *et al.* 2015) likely constrains the diversification of other ray morphological traits in the phloem of lianas.

BARK ANATOMICAL SYNAPOMORPHIES
OF LIANESCENT BIGNONIACEAE

The periderm of Bignoniaceae is quite varied, even within different species of the same genus. A single periderm is more common than multiple ones (i.e., a rhytidome). Rhytidome is characteristic of *Campsis*, *Podranea*, some *Adenocalymma*, and some *Fridericia*. Sampling of thicker stems are needed to confirm if just one periderm is indeed formed in the species where we did not find sequent periderms. The only unique feature delimited for the periderm here is the phellem with prismatic crystals, exclusively present in *Amphilophium crucigerum*, an autapomorphy for the species. Calcium oxalate crystals are common in the phloem of Bignoniaceae, and vary in shape and abundance, being more abundant around fibers, but also present in other cells. In the periderm, calcium oxalate crystals are generally lacking. Their presence in *Amphilophium crucigerum*, a broadly distributed species throughout the Neotropics (Lohmann & Taylor 2014), may act as an additional protective layer against herbivores. Calcium oxalate crystals may have a function of storage, protection or simply excretion (Franceschi & Nakata 2005). However, putative functions for calcium oxalate need rigorous experiments to be confirmed (Paiva 2019, 2021). Crystals in the phellem, which is dead and suberized at maturity, cannot be mobilized. Therefore, crystals may act either as a defense mechanism or as a mean for excretion (Paiva 2019, 2021). Their common presence in phellems of some trees have generally been related to excretion (Roth 1981; Paiva 2019).

A higher number of putative synapomorphies were recovered within the secondary phloem. As predicted by Esau (1969) and Roth (1981), the sclerenchyma is one of the most informative phloematic features taxonomically. Indeed, five of the 19 potential synapomorphies identified are located in this tissue.

Podranea, a liana native to Africa and largely planted as ornamental, is marked by the absence of fibers and presence of sclereids instead. This is the first record of this phloem type in Bignoniaceae. Phloem with scattered fibers is unique to *Campsis* and shared with the Central and North American tree *Astianthus viminalis* (Pace *et al.* 2021; Ragsac *et al.* 2021), its sister lineage. Most species of Bignonieae have a non-fibrous, stratified phloem with alternating fiber bands. This type is the most common throughout the Bignoniaceae (Roth 1981). The species-rich clade *Fridericia* and allies (Lohmann 2006), where all species display a fibrous phloem, with fibers forming the background tissue where other cells are embedded, represents an exception to this pattern. As we mentioned before, many characters evolved in correlation with these abundant fibers, such as the tangential arrangement of sieve-tubes, sieve-tube-centric axial parenchyma, and long sieve-tubes with compound sieve plates with many sieve areas.

A unique morphology was found within *Pleonotoma*. The regular phloem lacks fibers and sclereids are found instead, a synapomorphy for this genus (Fig. 20), providing additional support to the hypothesis of an uncoupled diversification of the regular and variant phloem (Pace *et al.* 2011). The variant phloem of *Pleonotoma* bears semi-fibrous to fibrous phloem. In this genus, sclereids differentiate in the conducting phloem, although sclereids generally differentiate in the nonconducting phloem (Holdheide 1951; Angyalossy *et al.* 2016). Whenever slereids differentiate in the conducting phloem, their shape is sufficient to identify them as sclereids (Evert 2006; Angyalossy *et al.* 2016). Another synapomorphy derived from the mechanical tissue is found in *Manaosella*, the only genus with radially elongated fibers in the fiber bands, as seen in transversal section (Fig. 20).

The presence of a storied structure in *Amphilophium*, *Dolichandra*, and *Perianthomega*, is also worth noting and might represent synapomorphies of the individual genera (Fig. 20). Storying is more evident closer to the cambium, becoming blurred by intrusive growth and cell expansion further away from the cambium. While no hypotheses have attempted to explain the evolution of storied structures, those features are more common in lower latitudes and tropical areas (Alves & Angyalossy-Alfonso 2000; Wheeler & Baas 2018). Furthermore, storied structures are generally correlated to shorter cambial initials (Wheeler & Baas 2018), although there are exceptions to this pattern (see Meliaceae *in* Pace *et al.* 2022). Storied structures have evolved in parallel in at least three neotropical Bignoniaceae lineages: tribe Bignonieae, Tecomeae s.s., and the *Tabebuia* and allies clade (Pace & Angyalossy 2013; Pace *et al.* 2015b).

In sum, this work illustrates the enormous diversity of barks found within lianescent Bignoniaceae. Aspects of the entire stem, such as cambial variant details and the sclerenchyma, were among the most informative features. When features are combined, entire lineages can be characterized, allowing individual lineages to be identified using bark anatomy exclusively (see Section 4). Despite all the advances made here, studies of the bark anatomy of additional Bignoniaceae members are still needed to understand broad scale patterns of phloem evolution within the family as a whole.

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APPENDIX 1. — Taxa, collectors, and localities. Vouchers for all specimens were deposited at the SPF herbarium, unless specified otherwise after the voucher information.

Adenocalymma

Adenocalymma adenophorum (Sandwith) L.G.Lohmann, *El Ottra 38*, Adolfo Ducke Forest Reserve, Amazonas, Brazil.

Adenocalymma albiflorum (Salzm. ex DC.) B.M. Gomes & L.H. Fonseca, *Pace 78*, Adolfo Ducke Forest Reserve, Amazonas, Brazil.

Adenocalymma alboaurantiacum (Faria & Proença) L.H. Fonseca & L.G.Lohmann*, Zuntini 18*, Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil.

Adenocalymma bracteatum (Cham.) DC., *Castanho 153*, *Lohmann 861*, Rio Negro, Amazonas, Brazil.

Adenocalymma comosum (Cham.) DC., *Pace 53*, Livings collection Plantarum Institute, Nova Odessa, São Paulo, Brazil.

Adenocalymma divaricatum Miers, *Udulutsch 2808*, Lençóis, Bahia, Brazil.

Adenocalymma flaviflorum (Miq.) L.G. Lohmann, *Sousa-Baena 2*, Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil.

Adenocalymma longilineum (A.Samp.) L.G.Lohmann, *Pace 62*, Adolfo Ducke Forest Reserve, Amazonas, Brazil.

Adenocalymma mirabile (Sandwith) Fonseca & L.G. Lohmann, *Dos Santos 48*, Buriticupu Forest Reserve, Maranhão, Brazil, vouchers in MAD, MO, and MG.

Adenocalymma nodosum (Silva Manso) L.G. Lohmann, *Pace 20*, Uberlândia, Minas Gerais, Brazil.

Adenocalymma peregrinum (Miers) L.G. Lohmann, *Pace 26*, Livings collection Plantarum Institute, Nova Odessa, São Paulo, Brazil.

Adenocalymma salmoneum J.C. Gomes, *Lohmann 658*, Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil.

Adenocalymma tanaeciicarpum (A.H. Gentry) L.G. Lohmann, *Dos Santos 263*, Porto de Moz, Pará, Brazil, vouchers in MAD, MO and MG.

Adenocalymma validum (K. Schum.) L.G. Lohmann, *Zuntini 23*, Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil; *Pace 65*, Adolfo Ducke Forest Reserve, Amazonas, Brazil.

Amphilophium

Amphilophium bracteatum (Cham.) L.G. Lohmann, *Ozório-Filho 8*, São Paulo, São Paulo, Brazil.

Amphilophium crucigerum (L.) L.G. Lohmann, *Pace 1*, *Pace 2*, *Pace 3*, *Pace 34*, São Paulo, São Paulo, Brazil; *Pace 148a*, Botucatu, São Paulo, Brazil.

Amphilophium dolichoides (Cham.) L.G. Lohmann, *Ozório-Filho 9*, São Paulo, São Paulo, Brazil,

Amphilophium elongatum (Vahl) L.G. Lohmann, *Pace 45*, Livings collection Plantarum Institute, Nova Odessa, São Paulo, Brazil; *Pace 170*, Alto da Serra de Paranapiacaba Biological Reserve, São Paulo, Brazil.

Amphilophium magnoliifolium (Kunth) L.G. Lohmann, *Lohmann 851*, Rio Negro, Amazonas, Brazil; *Dos Santos 272*, Porto de Moz, Pará, Brazil, vouchers in MAD, MO, and MG.

Amphilophium paniculatum (L.) Kunth, *Pace 46*, Livings collection Plantarum Institute, Nova Odessa, São Paulo, Brazil.

Amphilophium pulverulentum (Sandwith) L.G.Lohmann, *Pace 61*, Adolfo Ducke Forest Reserve, Amazonas, Brazil.

Anemopaegma

Anemopaegma chamberlaynii (Sims) Bureau & K. Schum., *Zuntini 15*, Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil; *Pace 166*, Alto da Serra de Paranapiacaba Biological Reserve, São Paulo, Brazil.

Anemopaegma chrysoleucum (Kunth) Sandwith, *Dos Santos 144*, Marabá, Pará, Brazil, vouchers in MAD, MO and MG.

Anemopaegma leave DC., *Pace 388*, Boa Nova, Bahia, Brazil.

Anemopaegma longidens Mart. ex DC., *Dos Santos 394*, Parauapebas, Pará, Brazil, vouchers in MAD, MO and MG.

Anemopaegma oligoneuron (Sprague & Sandwith) A.H.Gentry, *Lohmann 76*, Adolfo Ducke Forest Reserve, Amazonas, Brazil.

Anemopaegma robustum Bureau & K.Schum., *Pace 74*, Adolfo Ducke Forest Reserve, Amazonas, Brazil.

Bignonia

Bignonia binata Thunb, *Galvanese 22*, Rio Negro, Amazonas, Brazil.

Bignonia campanulata Cham., *Pace 39*, Livings collection Plantarum Institute, Nova Odessa, São Paulo, Brazil.

Bignonia corymbosa (Vent.) L.G. Lohmann, *Zuntini 2*, *Zuntini 17*, Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil.

Bignonia magnifica W. Bull, *Pace 51*, Livings collection Plantarum Institute, Nova Odessa, São Paulo, Brazil.

Bignonia prieurei DC., *Zuntini 13*, Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil; *Pace 71*, Adolfo Ducke Forest Reserve, Amazonas, Brazil.

Bignonia sciuripabulum (K. Schum.) L.G. Lohmann, *Zuntini 8*, Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil**.**

Callichlamys

Callichlamys latifolia (Rich.) K. Schum, *Zuntini 175*, Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil.; *Pace 42*, Livings collection Plantarum Institute, Nova Odessa, São Paulo, Brazil; *Pace 63*, Adolfo Ducke Forest Reserve, Amazonas, Brazil.

Campsis

Campsis radicans (L.) Seems, *Hicock 841*, Connecticut, USA, vouchers in Y; *Pond 448*, Camden County, Dismal Swamp, North Carolina, USA, vouchers in MAD.

Cuspidaria

Cuspidaria convoluta (Vell.) A.H. Gentry, *Pace 48* Livings collection Plantarum Institute, Nova Odessa, São Paulo, Brazil. *Cuspidaria pulchra* (Cham.) L.G. Lohmann, *Pace 24*, *Pace 25*, Uberlândia, Minas Gerais, Brazil.

APPENDIX 1. — Continuation.

Dolichandra

Dolichandra quadrivalvis (Jacq.) L.G.Lohmann, *Pace 103, Pace 104, Pace 105*, Corumbá, Mato Grosso do Sul, Brazil.

Dolichandra unguiculata (Vell.) L.G. Lohmann, *Zuntini 176*, Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil.

Dolichandra unguis-cati (L.) L.G. Lohmann, *Ceccantini 2687*, Matozinhos, Minas Gerais, Brazil; *Groppo 322*, São Paulo, São Paulo, Brazil.

Fridericia

Fridericia chica (Bonpl.) L.G. Lohmann, *Pace 50*, Livings collection Plantarum Institute, Nova Odessa, São Paulo, Brazil.

Fridericia cinnamonea (DC.) L.G.Lohmann, *Pace 70*, Adolfo Ducke Forest Reserve, Amazonas, Brazil.

Fridericia conjugata (Vell.) L.G. Lohmann, *Pace 44*, Livings collection Plantarum Institute, Nova Odessa, São Paulo, Brazil.

Fridericia leucopogon (Cham.) L.G.Lohmann, *Pace 183*, São Sebastião, São Paulo, Brazil.

Fridericia nigrescens (Sandwith) L.G.Lohmann, *El Ottra 37*, Adolfo Ducke Forest Reserve, Amazonas, Brazil.

Fridericia ornithophila (A. H. Gentry) L.G. Lohmann, *Dos Santos 61*, Buriticupu Forest Reserve, Maranhão, Brazil, vouchers in MAD, MO and MG.

Fridericia patellifera (Schltdl.) L.G.Lohmann, *Dos Santos 96*, Marabá, Pará, Brazil, analyzed at the MAD wood collection, vouchers in MAD, MO and MG.

Fridericia platyphylla (Cham.) L.G. Lohmann, *Pace 22, Pace 23*, Uberlândia, Minas Gerais, Brazil.

Fridericia samydoides (Cham.) L.G. Lohmann, *Pace 49*, Livings collection Plantarum Institute, Nova Odessa, São Paulo, Brazil.

Fridericia speciosa Mart., *Pace 40*, Livings collection Plantarum Institute, Nova Odessa, São Paulo, Brazil.

Fridericia triplinervia (Mart. ex DC.) L.G.Lohmann, *El Ottra 39*, Adolfo Ducke Forest Reserve, Amazonas, Brazil.

Lundia

Lundia damazioi C. DC., *Pace 55, Pace 56*, Mata da CUASO, São Paulo, São Paulo, Brazil.

Lundia densiflora DC., *Nogueira* s.n.

Lundia glazioviana Kraenzl., *Zuntini 126*, Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil.

Lundia longa (Vell.) DC., *Zuntini 1*, Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil.

Lundia nitidula DC., *Nogueira 139*, Oliveiras, Minas Gerais, Brazil.

Lundia virginalis DC., *El Ottra 21*, São Paulo, São Paulo, Brazil.

Manaosella

Manaosella cordifolia (DC.) A.H. Gentry, *Pace 41*, Brazil, Livings collection Plantarum Institute, Nova Odessa, São Paulo, Brazil.

Mansoa

Mansoa difficilis (Cham.) Bureau & K. Schum., *Pace 35*, São Paulo, São Paulo, Brazil; *Zuntini 4*, Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil.

Mansoa onohualcoides A.H. Gentry, *Zuntini 276*, Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil.

Mansoa standleyi (Steyerm.) A.H. Gentry, *Pace 43*, Livings collection Plantarum Institute, Nova Odessa, São Paulo, Brazil.

Martinella

Martinella obovata (Kunth) Bureau & K. Schum., *Zuntini 7*, Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil; *Dos Santos 237*, Porto de Moz, Pará, Brazil, vouchers in MAD; *Dos Santos 317*, Gurupa, Pará, Brazil, vouchers in MAD.

Pachyptera

Pachyptera aromatica (Barb. Rodr.) L.G. Lohmann, *Gerolamo 9*, Adolfo Ducke Forest Reserve, Amazonas, Brazil.

Pachyptera kerere (Aubl.) Sandwith, *Castanho 143*, *Lohmann 834*, Rio Negro, Amazonas, Brazil.

Pandorea

Pandorea jasminoides (Lindl.) K.Schum., *Pace 18, 19*, Campus da Unicamp, Campinas, São Paulo, Brazil.

Perianthomega

Perianthomega vellozoi Bureau, *Pace 10, Pace 15*, Viçosa, Minas Gerais, Brazil; *Pace 28, Pace 29*, Santa Cruz de la Sierra, Santa Cruz, Bolivia.

Pleonotoma

Pleonotoma dendrotricha Sandwith, *Dos Santos 173*, Parauapebas, Pará, Brazil, vouchers in MAD, MO and MG.

Pleonotoma melioides (S. Moore) A.H. Gentry, *Dos Santos 298*, Senador José Pontifírio, Pará, Brazil, vouchers in MAD, MO, and MG.

Pleonotoma orientalis Sandwith, *Dos Santos 160*, Parauapebas, Pará, Brazil, vouchers in MAD, MO and MG.

Pleonotoma tetraquetra (Cham.) Bureau, *Ozório-Filho 11*, São Paulo, São Paulo, Brazil.

Pleonotoma stichadenia K. Schum., *Zuntini 7*, Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil; *Dos Santos 187*, Parauapebas, Pará, Brazil, vouchers in MAD, MO and MG.

Podranea

Podranea ricasoliana (Tanfani) Sprague, *Pace 11*, Instituto Butantá, São Paulo, São Paulo, Brazil.

Pyrostegia

Pyrostegia venusta (Ker Gawl.) Miers, *Pace 17*, Campinas, São Paulo, Brazil; *Pace 36*, Campus da USP, São Paulo, São Paulo, Brazil.

APPENDIX 1. — Continuation.

Stizophyllum

Stizophyllum inaequilaterum Bureau & K.Schum., *Dos Santos 178*, Serra dos Carajás Biological Reserve, Pará, Brazil, vouchers in MAD, MO and MG.

Stizophyllum perforatum (Cham.) Miers, *Dos Santos 350*, Peixe-Boi, Pará, Brazil, vouchers in MAD, MO and MG.

Stizophyllum riparium (Kunth) Sandwith, *Pace 16*, *Pace 33*, São Paulo, São Paulo, Brazil; *Zuntini 9*, Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil.

Tanaecium

Tanaecium bilabiatum (Sprague) L.G. Lohmann, *Lohmann 850*, Rio Negro Amazonas, Brazil.

Tanaecium pyramidatum (Rich.) L.G. Lohmann, *Pace 14*, *Pace 35*, Mata da CUASO, São Paulo, São Paulo, Brazil.

Tanaecium pyramidatum (A. H. Gentry) Zuntini & L.G. Lohmann, *Pace 31*, *Pace 32*, Valle Grande, Santa Cruz, Bolivia.

Tynanthus

Tynanthus cognatus (Cham.) Miers: *Pace 9a*, *Pace 9b*, Mata da CUASO, São Paulo, São Paulo, Brazil.

Tynanthus elegans Miers, *Zuntini 147*, Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil.

Xylophragma

Xylophragma myrianthum (Cham. ex Steud.) Sprague, *Zuntini 230*, Vale do Rio Doce Forest Reserve, Espírito Santo, Brazil.

Xylophragma platyphyllum (DC.) L.G.Lohmann, *Dos Santos 6*, Buriticupu Forest Reserve, Maranhão, Brazil, vouchers in MAD, MO and MG; *Dos Santos 188*, Serra dos Carajás Biological Reserve, Pará, Brazil, vouchers in MAD, MO and MG.