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Bark structure in woody plants with herbaceous ancestry: a case of *Lobostemon* (Boraginaceae)

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ABSTRACT

The bark structure of *Lobostemon curvifolius* and *L. trigonus* (Lithospermeae, Boraginaceae), Cape-endemic shrubs derived from herbaceous ancestors, is described. *Lobostemon* shares several traits with *Echium* and other herbaceous relatives (uniseriate epidermis with trichomes, cortical parenchyma and endodermis, absence of sclerification in pericycle and phloem, continuous procambial ring). The evolutionary shift to a woody habit in *Lobostemon* mainly involved quantitative modifications of these bark features, while the development of a subsequent periderm in *L. trigonus* represents the most important qualitative change linked to shrub growth. Homogeneous secondary phloem appears as a continuation of primary phloem formed by the procambial ring, gradually transformed into vascular cambium. Periderm continuity during bark dilatation is maintained by tangential phellogen elongation, and in *L. trigonus* also by irregular phellem cracking with initiation of new periderms, but without outer bark abscission. The parenchyma-like phellem and phelloderm further reflect persistence of herbaceous traits in the woody stem.

Keywords: *Echium*, secondary woodiness, Cape Floristic Region, procambium, bark abscission, bark dilatation

РЕЗЮМЕ

Матшинга А., Оскольский А.А. Структура коры у вторично древесных растений на примере рода *Lobostemon* (Boraginaceae). Изучена структура коры *Lobostemon curvifolius* и *L. trigonus* (Lithospermeae, Boraginaceae), эндемичных кустарников Капского флористического региона, производных от травянистых предков. *Lobostemon* сходен с *Echium* и другими близкими травянистыми родами по наличию однорядной эпидермы с трихомами, кортикальной колленхимы, эндодермы, отсутствию склеренхимы в перицикле и флоэме, наличию непрерывного прокамбиального кольца. Эволюционный переход к кустарниковой жизненной форме у *Lobostemon* был сопряжен с количественными модификациями признаков коры у родственных травянистых групп; появление второй перидермы у *L. trigonus* представляет собой наиболее важное качественное новшество, сопряженное с древесностью. Гомогенная вторичная флоэма вероятно представляет собой продолжение круга первичной флоэмы, возникшее в результате постепенной трансформации кольца прокамбия в сосудистый камбий. Непрерывность перидермы у *Lobostemon* поддерживается путем тангентального увеличиения длины феллогена, а у *L. trigonus* также путем образования нерегулярных трещин в феллеме и формирования второй перидермы. Феллема и феллодерма напоминают паренхиму по своему строению, что тоже может рассматриваться как сохранение признаков травянистости в коре кустарникового стебля.

Ключевые слова: *Echium*, вторичная древесность, Капская флористическая область, прокамбий, сбрасывание коры, дилатация коры

The herbaceous habit has traditionally been regarded as derived from woody ancestors within flowering plants, yet substantial evidence indicates that the opposite trend is also widespread. A global analysis of habit evolution (Klimeš et al. 2022) shown that the transitions from herbs to shrubs and trees are even more common within the angiosperms that the evolutionary shifts from woody to herbaceous lineages. The structural background of the secondary woodiness, i.e. of transformations of herbaceous plants into shrubs and trees, remains, however, poorly understood.

Although the abundance and distribution of wood (secondary xylem) are insufficient to distinguish herbs, shrubs, and trees (e.g. Gatsuk 1976, Lens et al. 2012), most studies have focused on the wood structure in relation to habit shifts. Attempts to identify anatomical features that separate secondary woody plants from ancestrally woody lineages led to the theory of paedomorphosis in wood evolution (Carlquist 1962), which has been extensively revisited (e.g. Carlquist 2009, 2012, 2013, Dulin & Kirchoff 2010, Lens et al. 2013, Frankiewicz et al. 2020, Onyenedum & Pace 2021, Jones 2023, Frankiewicz & Oskolski 2023). According to this theory, juvenile or “paedomorphic” traits persist in the mature wood of secondarily woody plants. However, many such traits are instead linked to particular growth forms (e.g., rosette trees, stem succulents, slender-stemmed shrubs), regardless of whether their woodiness is derived or ancestral (Lens et al. 2013, Frankiewicz et al. 2020). Other wood traits, not necessarily juvenile, also correlate with plant habit (e.g. Arévalo et al. 2017). Current explanations of secondary woodiness therefore emphasize the interaction of ontogenetic trends, morphogenetic correlations, functional roles, and adaptive value of wood traits within specific evolutionary contexts. Nonetheless, it remains unlikely that universal anatomical criteria can reliably distinguish ancestral from secondary woodiness.

Shifts from herbaceous to woody forms affect not only the wood but also the bark, the tissues external to the vascular cambia. Unlike herbaceous stems, woody stems usually continue radial growth throughout their lifespan, requiring ongoing maintenance and regeneration of bark tissues. However, the bark anatomy of secondarily woody taxa remains poorly studied, and no investigations have directly addressed bark evolution in the context of habit transitions. This study aims to clarify structural changes in bark associated with the evolution of secondary woodiness, focusing on the shrubby genus *Lobostemon* Lehm., derived from herbaceous ancestors.

Lobostemon comprises 28 shrubby species endemic to the Cape Floristic Region (CFR) of South Africa (Buys 2011). Together with the small herbaceous genus *Echiostachys*, also endemic to the CFR (Manning & Goldblatt 2012, Velani et al. 2023), *Lobostemon* forms a clade sister to the largely herbaceous *Echium* of North America, Europe, and Macaronesia (Böhle et al. 1996, Chacón et al. 2016, 2019). Nested within the tribe *Lithospermeae* of the Boraginaceae family (Chacón et al. 2016, 2019), this clade is ancestrally herbaceous, and woody forms in *Lobostemon* and some *Echium* species appear to have evolved independently under similar climatic conditions.

Linder (2003) identified *Lobostemon* and *Echiostachys* among the 33 clades most strongly contributing to species richness and endemism in the CFR. Anatomical studies of these groups are therefore important to understanding structural evolution and adaptation to Mediterranean-type climates. Leaf and trichome diversity in *Lobostemon* has been investigated by Buys (2005, 2011), and wood anatomy has recently been studied by Frankiewicz et al. (2024). Bark anatomy of *Lobostemon*, however, remains virtually unstudied apart from a brief description of juvenile bark in *L. fruticosus* cuttings (Lodama et al. 2016).

In this study, we examine bark anatomy in young twigs and older stems of two *Lobostemon* species and compare these findings with available data on herbaceous stems in *Echium* and related *Lithospermeae* genera. Our aim is to identify anatomical features potentially associated with the evolution of secondary woodiness in this lineage.

MATERIAL AND METHODS

The sample of *Lobostemon curvifolius* [A. Oskolski # 368-19, abbreviated below as AO 368-19] used for the anatomical investigations was collected by the second author and Kamil Frankiewicz on 29.08.2019 from a shrub near road R43 near Worcester. Another sample of *L. curvifolius* [AO 834-25] was collected by the authors on 17.08.2025 in Grootbos Private Nature Reserve near Gansbaai, while the sample of *L. trigonus* [AO 806-25] was collected by them on 15.08.2025 near Mossel Bay. All these localities are found in the Western Cape province, South Africa. The pieces of twigs, branches and stems were stored and fixed in 70 % ethanol until use. A voucher specimens were deposited at the University of Johannesburg Herbarium (JRAU).

For anatomical examination, the samples were embedded in glycol methacrylate (GMA) according to a modification of the Feder & 'O'Brien (1968) method. Transverse, tangential, and radial sections of about 1 μm thick were cut using Leica Enuity ultramicrotome, then stained using the toluidine blue method and mounted in Entellan. All the sections were studied with a light microscope (Olympus CX41RF). Digital images were taken with a digital camera, an Olympus XC50, using an Olympus Stream Essentials 1.8 Imaging System. Descriptive terminology followed the recommendations of Angyalossy et al. (2016) for bark description.

RESULTS

Bark structure of *Lobostemon trigonus* (Thunb.) H. Buek

Examined sample: *L. trigonus* [A. Oskolski 806-25]

Surface of young leaf-bearing twigs (up to about 3–4 mm in diameter) smooth, glabrous, brownish green, pubescent (Figs 1A, B). Epidermis on these twigs is composed of a single layer of isodiametric (occasionally columnar) rectangular to rounded cells of 16–30 μm in tangential size with thin (3–4 μm thick) radial and inner tangential walls, and thicker (7–12 μm thick) outer walls covered by thin (1–2 μm thick) cuticle. Trichomes are abundant, non-glandular, two-cellular with small basal cell (40–50 μm in diameter) and very long terminal cell (Fig. 1C).

Cortex (Fig. 1C) consist of 1–3 layers of collenchyma (in 2–3 seriate clusters near stem ribs) and 14 – 18 layers of parenchyma, which can be subdivided into outer parenchyma and inner parenchyma/ and endodermis. Nearly all cells of cortical collenchyma and parenchyma are isodiametric and rounded, but their size and contents vary between its zones. Cells of collenchyma of 12–30 μm in tangential size, with dense stained contents, with unevenly thicker densely stained non-lignified cell walls (2–4 μm thick). without any traits of chloroplasts. Outer zone of cortical parenchyma (ca. 6–8 layers) consists of thin-walled cells of 12–35 μm in tangential size, with pale stained protoplasts. Inner zone of cortical parenchyma (8–10 layers) made of larger cells (15–50 μm in tangential size) both with non-stained protoplasts, and with pale stained protoplasts. Small to prominent intercellular spaces occur throughout the cortical parenchyma. Endodermis consists of isodiametric thin-walled cells of 20–40 μm in tangential size, without any visible contents. Crystals not found.

Pericycle consists of 1–3 layers of isodiametric rounded cells of 10–18 μm in tangential size with thicker cell walls (3–4 μm) with moderately stained protoplasts, without intercellular spaces. Pericyclic fibers and sclereids not found. Cambial (procambial?) zone is continuous, 2–4-seriate; the layer of cambial initials is hardly distinguishable.

Primary phloem is noticeable by solitary narrow (8–12 μm in tangential size) sieve tubes with companion cells, and groups of 2–3 sieve tubes scattered along inner cells of pericycle, without any association with arrangement of primary xylem. Primary xylem (metaxylem) in tangentially elongated to isodiametric clusters of 8–11 cell layers in radial dimensions, with radially arranged groups of 3-4 tracheary elements separated by 1–2-seriate radial bands of parenchyma cells. Protoxylem is hardly recognizable. Xylem clusters are separated from each other by 3–7-seriate medullary rays. Pith consists of large parenchyma cells (25–70 μm in diameter) with densely stained protoplasts and small intercellular spaces.

Bark on leafless parts of twigs (up to ca. 10–12 mm in diameter) is gray, smooth, glabrous, without cracks and lenticels (Figs 1A, B). Bark on thicker (> 12 mm in diameter) stems

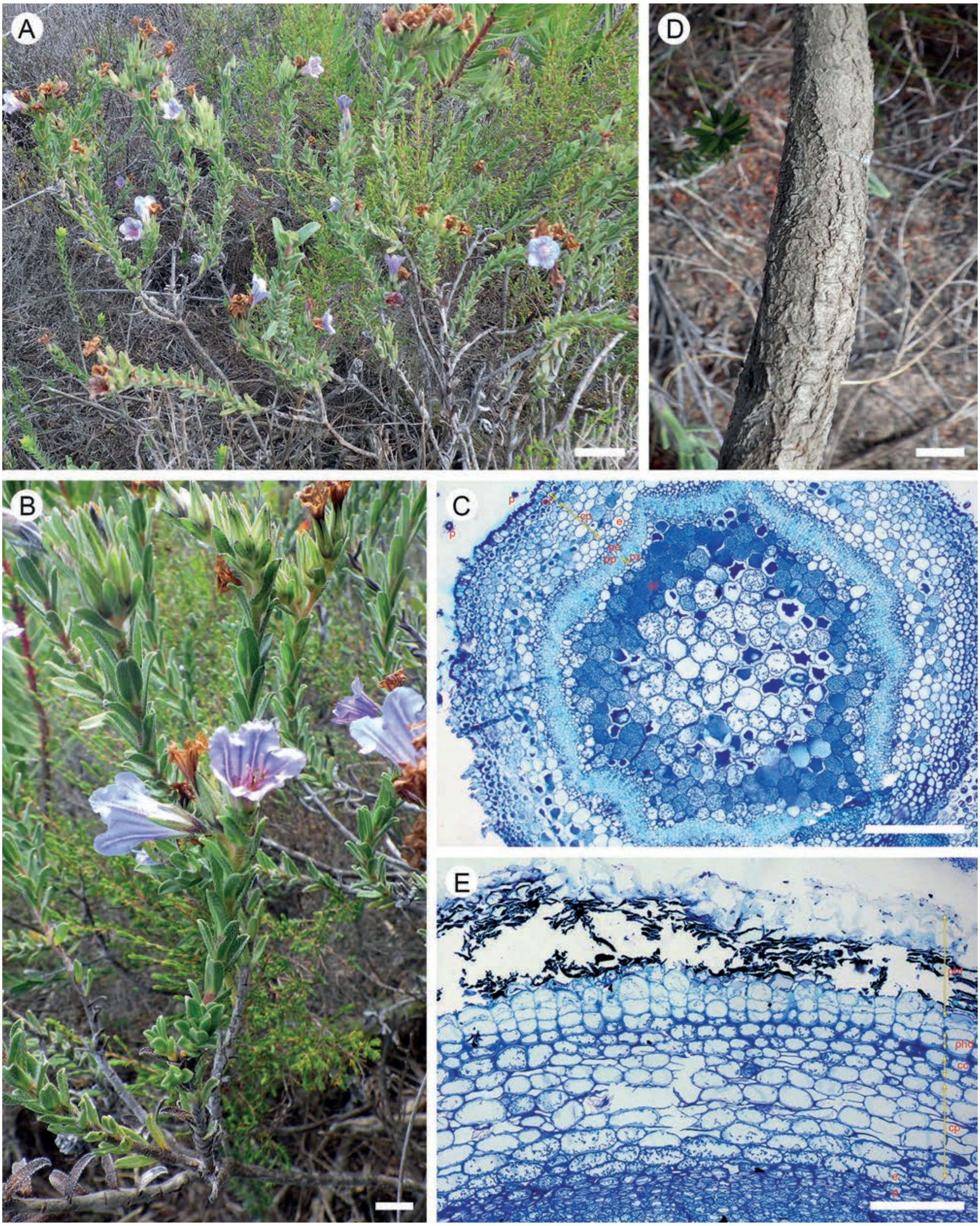

Figure 1 Macroscopic appearance and microstructure of the bark in *Lobostemon trigonus* (Thunb.) H. Buek. [AO 806-25] under light microscope (LM): A, B – appearance of the shrub, young twigs with leaf-bearing and leafless portions; C – transverse section (LM, TS) of juvenile stem, uniseriate epidermis, trichomes (t), cortical collenchyma (cc), cortical parenchyma (cp), endodermis (e), pericycle (pe), primary phloem (pp) and primary xylem (px) in nearly continuous rings, pith (pi); D– basal part of stem, rugose mature bark with fine cracks in reticulate pattern; E – TS of leafless twig (LM), phellem (phl) with collapsed and non-collapsed layers, phelloderm (phd), cortical collenchyma (cc), dilated cortical parenchyma (cp), endodermis (e) and pericycle (p). Scale bars = 20 mm (A), 10 mm (B, D), 100 µm (E), 50 µm (C)

dark gray, rugose, with fine horizontal and vertical cracks in reticulate pattern with cells of 4–7 mm in diameter, without lenticels, without any traits of sloughing (Fig. 1D). Chlorenchyma is present beneath the outer bark layer throughout.

Dilated cortex (Figs 1E, 2A) is narrow (6–8 cells wide), consists mostly of tangentially stretched parenchyma cells (about 25–85 μm in tangential size) and tangential strands of 2 parenchyma cells with unstained to moderately dense stained contents. Dilated pericycle (Fig. 2A) consists of clusters of isodiametric to tangentially stretched (17–38 μm in tangential size) vertically elongated to long fiber-like cells with moderately thick (2–7 μm) mostly non-lignified (occasionally with traits of poor lignification) walls. Radial files of 7–13 tangentially stretched parenchyma cells occur between the clusters of pericyclic cells.

First phellogen is initiated in outer region of cortex (Figs 1E, 2A). Phellem is composed of 6–16 layers of radially flattened (occasionally isodiametric) to obliterated cells, occasionally alternating with 2–3-seriate bands of non-obliterated cells (Fig. 1E) with thin non-suberized walls. Cracks are found in the phellem, but they do not reach the phellogen zone (Fig. 2A). Phelloderm comprises of 1–2 layers of radially flattened to isodiametric thin-walled cells, which are distinctive from cells of dilated cortex by thinner walls. No crystals found in the periderm. Initiation of the patches of subsequent periderm in the middle region of dilated cortex has been observed (Fig. 2B).

Secondary phloem (Figs 2A, C, D) consists of sieve tubes, companion cells and axial parenchyma. Sieve tubes are very narrow (13–23 μm wide), mostly in radial multiplies of 2–12, and in clusters of 4–9, or solitary. The sieve tube members are 100–217 μm (average 156.9 μm) in length. Sieve plates are simple, located on horizontal cross walls. Axial parenchyma consists of fusiform cells and strands of 2 cells, 15–25 μm in tangential size, with dense stained contents. Transition from conducting to non-conducting secondary phloem is sharp, distinguishable by obliteration of sieve tubes.

Secondary phloem rays are 1–6-seriate (Fig. 2E), composed of mostly upright (occasionally square) cells. Dilatations of secondary phloem are affected by tangential stretching and anticlinal divisions of phloem ray cells.

Sclereids, fibers, crystalliferous cells and secretory structures not found.

Bark structure of *Lobostemon curvifolius* H. Buek

Examined samples: *L. curvifolius* [A. Oskolski 368-19, 834-25]

Surface of young leaf-bearing twigs (up to about 8 mm in diameter) smooth, glabrous, green to brownish greens, pubescent with bristle-like white trichomes (Figs 3A, B, C). Epidermis on young parts of stems is composed of a single layer of isodiametric (occasionally columnar) rectangular to rounded cells of 14–30 μm in tangential size with thin (3–4 μm thick) radial and inner tangential walls, and thicker (6–8 μm thick) outer walls covered by thin (1–2 μm thick) cuticle. Trichomes are abundant, non-glandular, two-cellular with small basal cell (30–90 μm in diameter) and very long terminal cell (Fig. 3D).

Cortex consist of 1–2 layers of collenchyma and 14–20 layers of parenchyma, which can be subdivided into outer parenchyma, inner parenchyma, and endodermis. Nearly all cells of cortical collenchyma and parenchyma are isodiametric and rounded, but their size and contents vary between its zones. Cells of collenchyma of 20–40 μm in tangential size, with pale stained contents, with thicker densely stained cell walls. Outer zone of cortical parenchyma (ca. 9–12 layers) consists of thin-walled cells of 15–35 μm in tangential size, with pale stained protoplasts in 2–3 outermost layers, and with obliterated protoplasts in the deeper regions. Inner zone of cortical parenchyma made of larger cells (20–60 μm in tangential size) with slightly stained protoplasts. Small to prominent intercellular spaces occur throughout the cortical parenchyma. Endodermis consists of isodiametric thin-walled cells of 15–50 μm in tangential size, without any visible contents. Crystals not found (Figs 3D, E).

Pericycle (Fig. 3E) consists of 3–8 layers of isodiametric rounded cells of 10–25 μm in tangential size with thicker cell walls (3–5 μm) with moderately stained protoplasts, with small spaces. Pericyclic fibers and sclereids not found. Cambial (procambial?) zone is continuous, 2–4-seriate; the layer of cambial initials is hardly distinguishable.

Primary phloem (Fig. 3E) is noticeable by solitary narrow (7–12 μm in tangential size) sieve tubes with companion cells, and groups of 2–3 sieve tubes scattered along inner cells of pericycle, without any association with arrangement of primary xylem. Primary xylem (metaxylem) in tangentially elongated to isodiametric clusters of ca. 10 cell layers in radial dimensions, with radially arranged groups of 3–5 vessels separated by 2–3-seriate medullary rays. Protoxylem is hardly recognizable. Clusters are separated from each other by 2–5-seriate medullary rays.

Pith consists of large parenchyma cells (40–130 μm in diameter) with densely stained protoplasts and small intercellular spaces.

Bark on leafless parts of twigs (up to ca. 20 mm in diameter) is green to light gray, smooth, with bristle-like white trichomes, without cracks and lenticels (Fig. 3C). Bark on thicker (> 20 mm in diameter) stems light brown glabrous with gray patches bearing the bristle-like trichomes, smooth to slightly rugose, without cracks, lenticels, and any traits of sloughing (Fig. 3F). Chlorenchyma is present beneath the outer bark layer throughout.

Dilated cortex (Fig. 4A) is narrow (6–12 cells wide), consists mostly of tangentially stretched parenchyma cells (about 40–140 μm in tangential size) and tangential strands of 2–4 parenchyma cells with moderately dense stained contents. Dilated pericycle consists of clusters of isodiametric to tangentially stretched (20–50 μm in tangential size) vertically elongated to long fiber-like cells with moderately thick (2–6 μm) mostly non-lignified (occasionally with traits of poor lignification) walls. Radial files of 3–8 tangentially stretched parenchyma cells occur between the clusters of pericyclic cells.

First phellogen is initiated in outer region of cortex (Fig. 4A). Phellogen is hardly distinguishable as a continuous tangential layer of meristematic cells: periclinal divisions in meristematic zone co-occur with diagonal and anticlinal divisions in some derivative cells. Phellem is composed of 8–22 layers of mostly radially flattened (occasionally isodiametric) to obliterated cells with thin non-suberized walls. Cracks on the phellem surface were not observed (Fig. 2A). Phelloderm comprises of 1–2 layers of radially flattened to isodiametric thin-walled cells, which are distinctive from cells of dilated cortex by thinner walls and the lack of tangential stretching. Anticlinal and diagonal divisions occur in cells of phelloderm and adjacent layers of dilated cortical parenchyma. No crystals were found in the periderm. Initiation of subsequent not observed.

Secondary phloem (Figs 4A, B) consists of sieve tubes, companion cells and axial parenchyma. Sieve tubes are very narrow (10–20 μm wide), mostly in radial multiplies of 2–12, occasionally in clusters of 4–7, or solitary. The sieve tube members are 121 μm – 200 μm (average 146.7 μm) in length. Sieve plates are simple, located on horizontal cross walls. Axial parenchyma consists of fusiform cells and strands of 2 cells, 16–28 μm in tangential size, with dense stained contents. Transition from conducting to non-conducting secondary phloem is sharp, distinguishable by obliteration of sieve tubes.

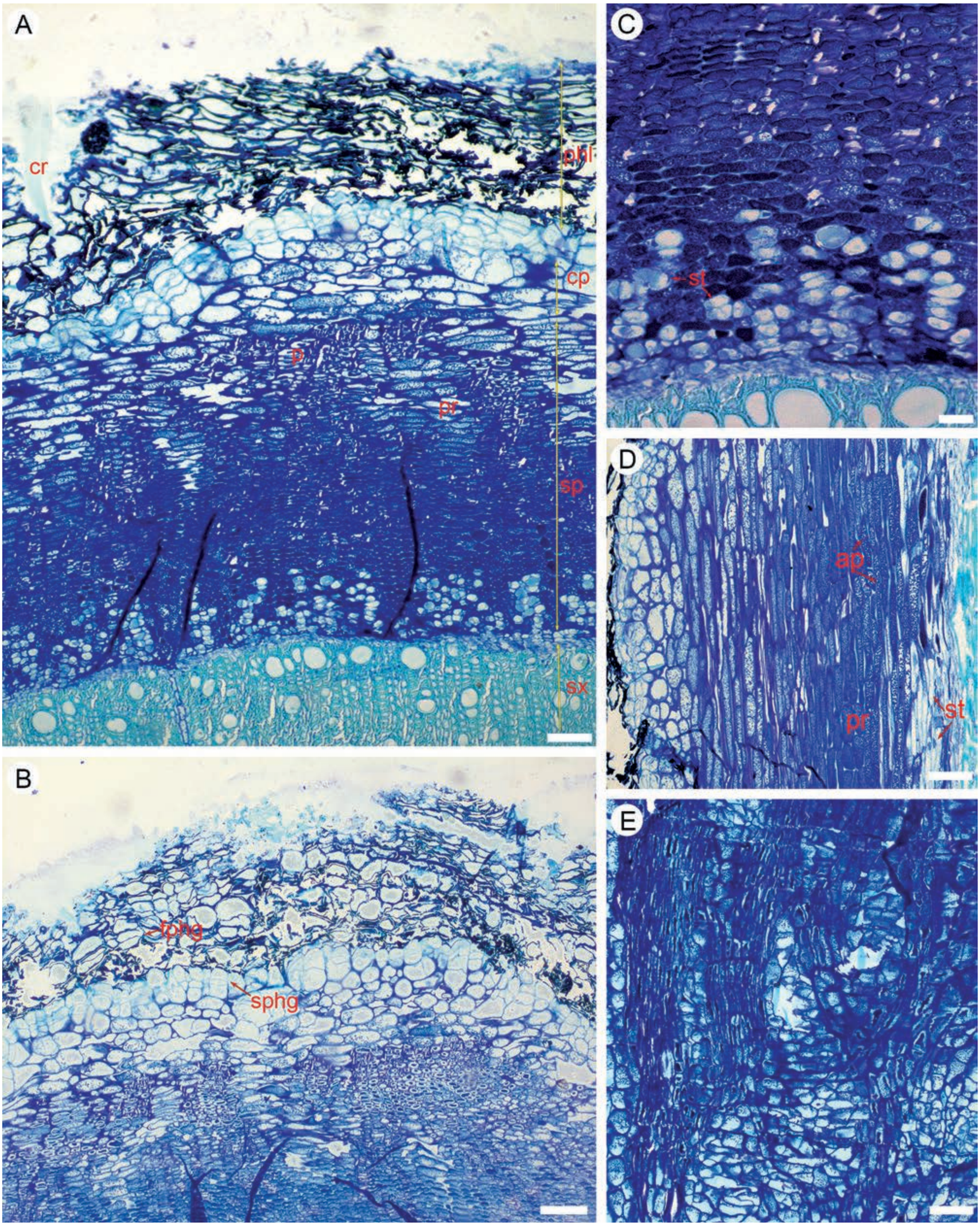

Figure 2 Microstructure of mature bark in *Lobostemon trigonus* (Thunb.) H. Buek. [AO 806-25] (LM): A – TS of mature bark with prominent periderm, thin-walled phellem cells (phl), crack in phellem (cr), phelloderm (phd), dilated cortical parenchyma (cp), dilated pericycle cells (p), secondary phloem (sph), dilated phloem rays (pr), secondary xylem (sx); B – TS of another portion of mature bark, first phellogen (fphg) and initiation of subsequent phellogen (sphg); C – TS of conductive secondary phloem, sieve tubes (st) with companion cells, axial parenchyma (TS); D – radial longitudinal section (RLS) of mature bark, sieve tube members (st) and axial parenchyma cells (ap) in conductive phloem, portion of phloem ray (pr), collapsed cells of pericycle (p), oblique and transverse cell divisions in the parenchyma cells of inner cortex (asterisks), periderm; E – tangential longitudinal section (TLS) of non-conductive phloem in mature bark, dilated rays. Scale bars = 100 µm (A, B, E), 50 µm (D), 20 µm (C)

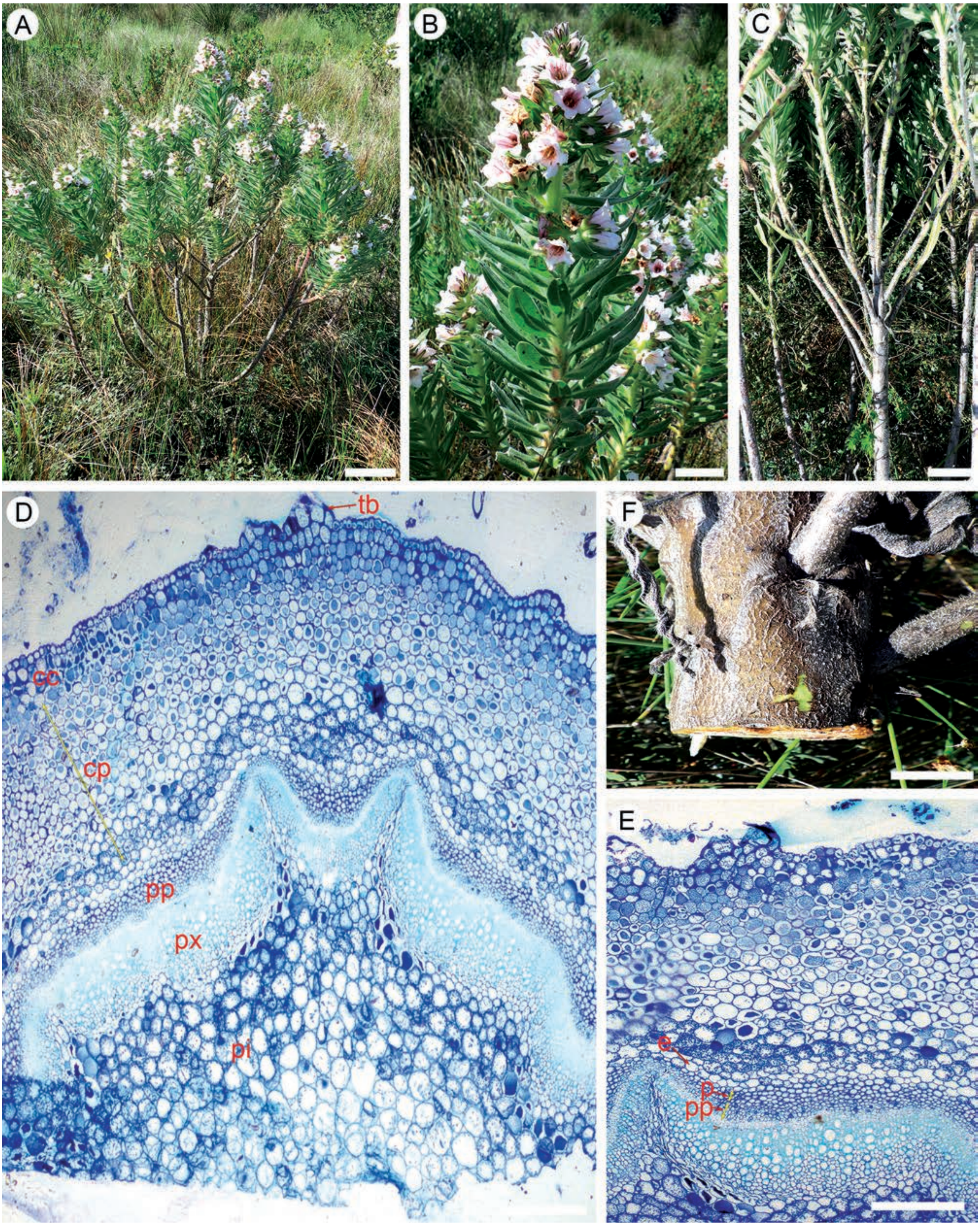

Figure 3 Macroscopic appearance and microstructure of the bark in *Lobostemon curvifolius* H. Buek [AO 834-25]: A – entire shrub; B – leaf-bearing part of twig with flowers; C – leafless parts of twigs and young stem, transition from green to gray surface, bristle-like trichomes; D, E – TS (LM) of juvenile stem; D - uniseriate epidermis, trichome base (tb), cortical collenchyma (cc), cortical parenchyma (cp), endodermis, pericycle, primary phloem, primary xylem (px) in tangentially elongated bands, pith (pi); E – details of endodermis (e), pericycle (p), and primary phloem (pp), sieve tubes with companion cells; F – basal part of stem, smooth brown mature bark with bristle-like trichomes on gray patches. Scale bars = 50 mm (A), 10 mm (B, C, F), 200 µm (D), 100 µm (E)

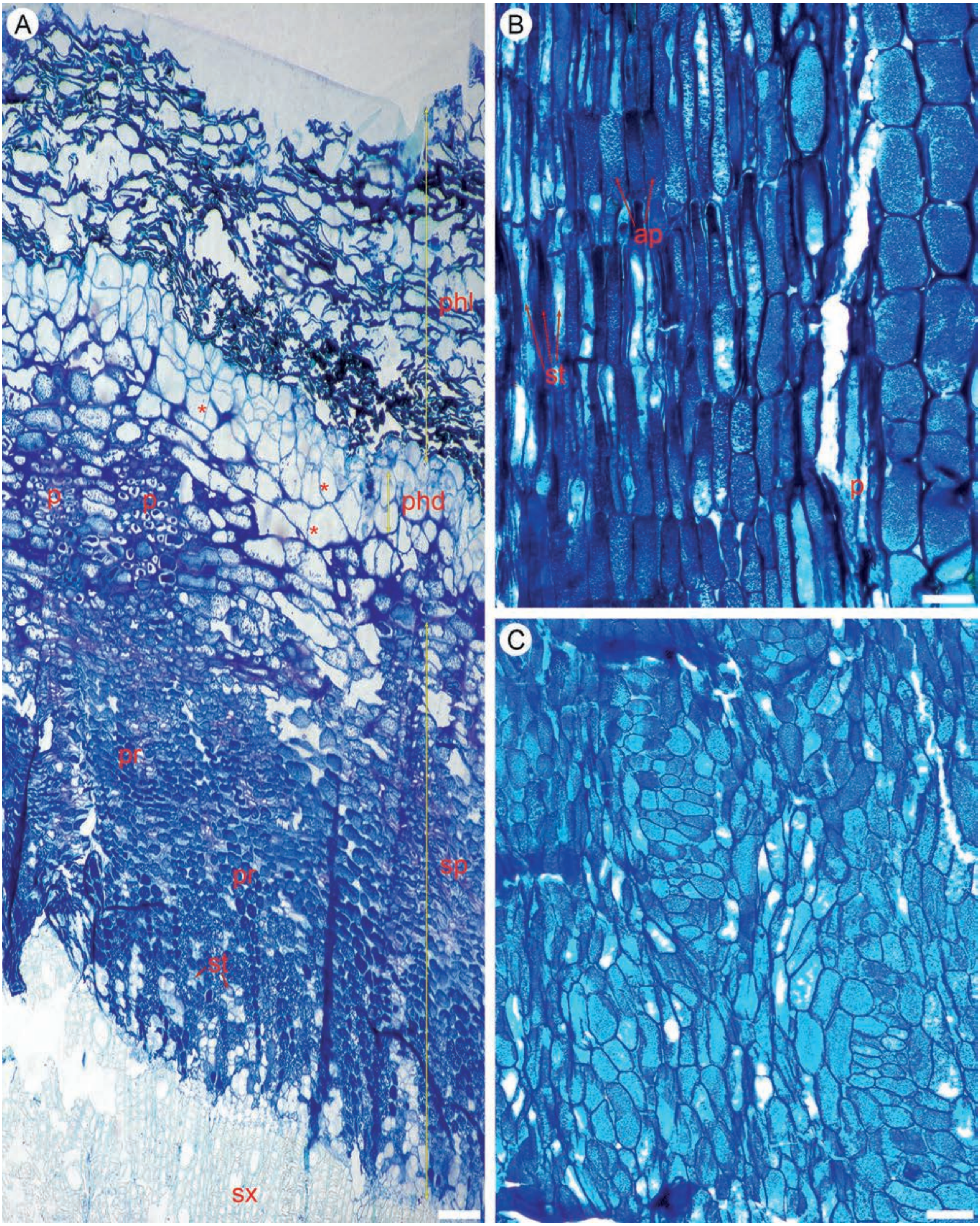

Figure 4 Microstructure (LM) of mature bark in *Lobostemon curvifolius* H. Buek: A – TS of mature bark (sample AO 834-25)with prominent periderm, thin-walled mostly collapsed phellem (phl) cells, phelloderm (phd) in 1-3 layers, anticlinal divisions in cells of phelloderm and cortex (asterisks); dilated pericycle cells (p), secondary phloem (sp) with sieve tubes (st), phloem rays (pr), secondary xylem (sx); B – RLS of mature bark(sample AO 368-19), sieve tube members (st) and axial parenchyma cells (ap) in conductive phloem, collapsed cells of pericycle (p); C – TLS of non-conductive phloem in mature bark, dilated rays (sample AO 368-19). Scale bars = 100 mm (A, C), 50 mm (B)

Secondary phloem rays are 1–6-seriate (Fig. 4C), composed of mostly upright (occasionally square) cells. Dilatation of secondary phloem is affected by tangential stretching and anticlinal divisions of phloem ray cells.

Sclereids, fibers, crystalliferous cells and secretory structures not found.

DISCUSSION

Our results, together with the observations of Lodama et al. (2016) on the young stem of *L. fruticosus*, show that stems of three *Lobostemon* species share several anatomical features: a uniseriate epidermis with trichomes, 1–3 layers of cortical parenchyma, a distinct endodermis, the absence of fibers and sclereids in both the pericycle and phloem, and the arrangement of primary xylem and phloem in tangentially expanded clusters rather than in separate collateral bundles. This suite of traits has also been reported (reviews: Metcalf & Chalk 1950, Schweingruber & Landolt 2010, Schweingruber et al. 2011) for other genera of the tribe *Lithospermeae* closely related to *Lobostemon* (Chacón et al. 2016), including *Echium* (Monti et al. 2003, Papp et al. 2011, Sava et al. 2019), *Onosma* (Akçin & Binzet 2010, 2019, Binzet & Akçin 2012, Daironas et al. 2014, Selvi et al. 2019, Ulcay 2023), *Arnebia* (Saad et al. 2007), *Moltkia* (Doğu et al. 2012), *Buglossoides* (Saeed & Saeed 2021), and *Lithospermum* (Starr 1912, Kováts 1973). Most of these taxa also share the absence of crystalliferous cells in the bark; druses have been reported only in the cortical parenchyma of *Buglossoides incrassatum* (Saeed & Saeed 2021). The similarity between shrubby *Lobostemon* and its mostly perennial or annual relatives suggests that the evolutionary transition from herbaceous to woody habit in this group involved mainly quantitative modifications of stem structure, without gains or losses of qualitative bark traits.

Compared with herbaceous genera of the tribe *Lithospermeae*, *Lobostemon* typically develops more cell layers in both the secondary phloem and cortex, a feature clearly associated with its thicker bark. Data from Akçin & Binzet (2019) further indicate that *Lobostemon* species possess wider sieve tubes than members of *Onosma*, probably as a compensatory adaptation to the higher hydraulic resistance of their taller stems (Liesche et al. 2017). The position of phellogen initiation, which is occurring in the outer or middle cortex in *Lobostemon* and *Arnebia*, but deeper near the pericycle in other taxa (Metcalf & Chalk 1950, Schweingruber & Landolt 2010, Akçin & Binzet 2019, Selvi et al. 2019), appears to be the only qualitative trait varying within this group. In addition, the occurrence of subsequent periderm in *L. trigonus* may represent an important feature associated with the transition to a woody habit.

In juvenile stems of *Lobostemon*, the primary xylem is arranged in tangentially expanded clusters, whereas the primary phloem forms a narrow band that is not directly associated with the xylem. This pattern of primary tissues, that has also been reported in *Onosma* (Selvi et al. 2019), *Lithospermum* (Kováts 1973), *Echium* (Sava et al. 2019) and *Moltkia* (Doğu et al. 2012), is commonly described in terms of collateral bundles, but in fact it likely originates from a continuous procambial ring. Although this condition is characteristic of the tribe *Lithospermeae*, it is not universal in Boraginaceae: in some members of this family (e.g. *Brunnera* and *Symphytum*), the primary tissues have a fascicular arrangement (Kotelnikova et al. 2011, Barykina & Alyonkin 2019), which can only arise from discrete procambial strands.

The transition from a procambial ring to a vascular cambium producing secondary phloem and xylem is gradual, and the stages are often difficult to distinguish (e.g. Oskolski et al. 2021). In *Lobostemon*, the homogeneous secondary phloem, composed solely of narrow sieve tubes with companion cells embedded in axial parenchyma and lacking sclereids, fibers, or idioblasts, closely resembles the primary phloem in both structure and cellular composition. Such a condition, also reported in many other Boraginaceae (Schweingruber & Landolt 2010, Schweingruber et al. 2011), may be interpreted as a continuation of primary patterns, formed by procambial ring, into the secondary phloem produced by vascular cambium. This continuity should not be surprising, as both procambium and vascular cambium rely on similar regulatory mechanisms (reviews: Tomescu & Groover 2019, Aloni 2021). The absence of rays in the secondary xylem documented in ten plant orders has likewise been attributed to the retention of metaxylem patterns in secondary xylem (Frankiewicz & Oskolski 2023). The phloem traits, however, have not yet been considered from this perspective.

Thus, the homogeneous secondary phloem in *Lobostemon* is probably the result of persistence, in thicker woody stems, of the morphogenetic mechanisms that regulate phloem development in thin herbaceous stems. This feature may be viewed among other “paedomorphic” traits sensu Carlquist (1962) associated with secondary woodiness. However, applying the concepts of paedomorphosis or other heterochronies (e.g. Onyenedum & Pace 2021, Frankiewicz & Oskolski 2023) seems unnecessary here, as the phloem of *Lobostemon* exhibits the same ontogenetic trends as of its herbaceous relatives. Nevertheless, our current knowledge of phloem structure in secondarily woody taxa remains too limited for broad generalizations, highlighting the need for further studies in this field.

The ability of the woody stem to increase in diameter and girth requires maintaining the continuity of its outer protective layer as it dilates. Like the members of *Echium*, *Onosma*, and *Arnebia*, *L. curvifolius* has a single periderm showing no evidence of rhytidome formation (Saad et al. 2007, Schweingruber & Landolt 2010, Akçin & Binzet 2019, Ulcay 2023). It is highly likely that its continuity of maintained by increase of phellogen perimeter by anticlinal divisions of its cells. Available data indicate that these genera possess a homogeneous phellem and phelloderm composed of thin-walled cells that usually resemble the parenchyma cells.

Unlike *L. curvifolius*, *L. trigonus* shows both the initiation of subsequent periderm and the cracks on the bark surface. The formation of irregular cracks in cork in response to dilatation coupled with capability of producing new deeper phellogens is a more specialized mode to mountain the continuity of protective tissues than *L. curvifolius* and herbaceous relatives show. At the same time, no separation layers enabling the regular abscission of outer cork portions (Shtein et al. 2023) have been found in *L. trigonus*. Instead, our observations suggest irregular stretching and collapse of outer phellem cells in both species of *Lobostemon*. These findings suggest that such homogeneous phellem and phelloderm, lacking separation layers, may represent ancestral herbaceous traits that have persisted in secondarily woody taxa like *Lobostemon*. Further research is required to test this hypothesis.

CONCLUSION

The evolutionary transition to a woody habit in *Lobostemon*, involving increases in plant size and stem diameter, was mostly accompanied by quantitative modifications of bark traits expressed in its closely related herbaceous genera *Echium*, *Onosma*, *Arnebia*, *Moltkia* and *Lithospermum* (*Lithospermeae*, Boraginaceae).

The homogeneous secondary phloem in *Lobostemon*, composed solely of narrow sieve tubes embedded in axial parenchyma closely resembles the primary phloem in its structure. Such a condition, also reported in many other Boraginaceae, may be interpreted as a continuation of primary phloem ring, formed by procambial ring gradually transformed into vascular cambium.

Continuity of periderm in the course of bark dilatation is maintained by tangential elongation of phellogen, occasionally with formation of irregular cracks in phellem coupled with initiation of subsequent periderm, but without regular abscission of outer bark layers.

Both the homogeneous secondary phloem in *Lobostemon*, and the periderm with parenchyma-like phellem and phelloderm are probably the result of persistence of herbaceous bark traits in thicker woody stems.

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LITERATURE CITED

Akcin, O.E. & R. Binzet 2010. The micromorphological and anatomical properties of *Onosma angustissimum* Bornm and *Onosma cassium* Boiss (Boraginaceae). *Bangladesh Journal of Plant Taxonomy* 17:1–8.

Akcin, O.E. & R. Binzet 2019. Anatomy of three *Onosma* species from Turkey. *Bangladesh Journal of Plant Taxonomy* 48(2):329–337.

Aloni, R. 2021. *Vascular differentiation and hormones*. Springer International, Cham.

Angyalossy, V., M.R. Pace, R.F. Evert, C.R. Marcati, A.A. Oskolski, T. Terrazas, E. Kotina, F. Lens, S.C. Mazzoni-Viveiros, ... & P. Bass 2016. IAWA List of microscopic bark features. *IAWA Journal* 37(4):517–615.

Arevalo, R., B.W. Van Ee, R. Riina, P.E. Berry & A.C. Wiedenenhoeft 2017. Force of habit: shrubs, trees and contingent evolution of wood anatomical diversity using *Croton* (Euphorbiaceae) as a model system. *Annals of Botany* 119:563–579.

Barykina, R.P. & V.Y. Alyonkin 2019. Propagation modes in Boraginaceae: Biomorphological and anatomical analyses. *Wulfenia* 26:155–174.

Binzet, R. & O.E. Akcin 2012. The anatomical properties of two *Onosma* L. (Boraginaceae) species from Turkey. *Journal of Medicinal Plants Research* 6:3288-3294.

Böhle, U.R., H.H. Hilger & W.F. Martin 1996. Island colonization and evolution of the insular woody habit in *Echium* L. (Boraginaceae). *Proceedings of the National Academy of Sciences* 93(21):11740–11745.

Buys, M.H. 2005. The systematic value of the leaf indumentum in *Lobostemon* (Boraginaceae). *Bothalia* 35(1):93–99.

Buys, M.H. 2011. Revision of *Lobostemon* (Boraginaceae). *Phytotaxa* 37(1):1–131.

Carlquist, S. 1962. A theory of paedomorphosis in dicotyledonous woods. *Phytomorphology* 12(1):30–45.

Carlquist, S. 2009. Xylem heterochrony: an unappreciated key to angiosperm origin and diversifications. *Botanical Journal of the Linnean Society* 161:26–65.

Carlquist, S. 2012. How wood evolves: a new synthesis. *Botany* 90:901–940.

Carlquist, S. 2013. More woodiness/less woodiness: evolutionary avenues, ontogenetic mechanisms. *International Journal of Plant Sciences* 174:964–991.

Chacón, J., F. Luebert, H.H. Hilger, S. Ovchinnikova, F. Selvi, L. Cecchi, C.M. Guilliams, K. Hasenstab-Lehman, K. Sutory, ... & M. Weigend 2016. The borage family (Boraginaceae s.str.): A revised infrafamilial classification based on new phylogenetic evidence, with emphasis on the placement of some enigmatic genera. *Taxon* 65:523–546.

Chacón, J., F. Luebert, F. Selvi, L. Cecchi & M. Weigend 2019. Phylogeny and historical biogeography of *Lithospermeae* (Boraginaceae): disentangling the possible causes of Miocene diversifications. *Molecular Phylogenetics and Evolution* 141:106626.

Daironas, J.V., F.K. Serebryanaya & I.N. Zilfikarov 2014. Comparative morphological and anatomical study of *Onosma caucasica* Levin. ex M. Pop. and *Onosma sericea* Willd (Boraginaceae Juss). *Pharmacognosy Journal* 6:22–28.

Doğu, S., M. Dinc & N.M. Pinar 2012. Anatomical and micromorphological differentiation in the genus *Moltika* Lehm in Turkey. *Pakistan Journal of Botany* 44(3):1083–1090.

Dulin, M.W. & B.K. Kirchoff 2010. Paedomorphosis, secondary woodiness, and insular woodiness in plants. *Botanical Review* 76:405–490.

Feder, N. & T.P. O'Brien 1978. Plant microtechnique: some principles and new methods. *American Journal of Botany* 55:123–142.

Frankiewcz, K., A.A. Oskolski, L. Banasiak, F. Fernandes, J.P. Reduron, J.A. Reyes-Betancort, L. Szczeparska, M. Alsarraf, J. Baczyński & K. Spalik 2020. Parallel evolution of arborescent carrots (*Daucus*) in Macaronesia. *American Journal of Botany* 107(3):1–19.

Frankiewcz, K. & A.A. Oskolski 2023. Raylessness and paedomorphosis: losses and gains of xylem rays en route from procambium to vascular cambium. *IAWA Journal* 44(3–4):516–530.

Frankiewcz, K., N. Velani, R. Manuel, T. Lyner, A.R. Magee, J.S. Boatwright, A.M. Musaya & A.A. Oskolski 2024. Secondaroily woody *Lobostemon* and *Echium* (Boraginaceae) from two Mediterranean-climate biodiversity hotspots share similar wood anatomies. *South African Journal of Botany* 174:116–124.

Gatsuk, L.E. 1976. The concept of herbs and the problem of their evolutionary position. In: *Problems of ecological plant morphology* (T.I. Serebryakova, ed.), pp. 55–130, Nauka, Moscow (in Russian). [Гатцук Λ.Е. 1976. Содержание понятия "травы" и проблема их эволюционного положения // Проблемы экологической морфологии растений / отв. ред. Т.И. Серебрякова. М.: Наука. С. 55–130]

Jones, C.S. 2023. Paedomorphosis and juvenility in secondary xylem: (not such) useful constructs. *IAWA Journal* 44(3):1–7.

Klimeš, A., I. Šímová, A. Zizka, A. Antonelli & T. Herben 2022. The ecological drivers of growth form evolution in flowering plants. *Journal of Ecology* 110:1525–1536.

Kotelnikova, K.V., D.J. Tretjakova & M.S. Nuraliev 2011. Shoot structure of *Symphytum officinale* L. (Boraginaceae) in relation to the nature of its axially shifted lateral branches. *Wulfenia* 18:63–67.

Kováts, D. 1973. Anatomical investigation on the vegetative system of *Lithospermum purpureo-coeruleun* L. *Annales Historico-Naturales Musei Nationalis Hungarici* 65:109–125.

Lens, F., S. Eeckhout, R. Zwartjes, E. Smets & S.B. Janssens 2012. The multiple fuzzy origins of woodiness within Balsaminaceae using an integrated approach, where do we draw the line. *Annals of Botany* 109(4):783–799.

Lens, F., N. Davin, E. Smets & M. del Arco 2013. Insular woodiness on the Canary Islands: a remarkable case of convergent evolution. *International Journal of Plant Sciences* 174:992–1013.

Liesche, J., M.R. Pace, Q. Xu, Y. Li & S. Chen 2017. Height-related scaling of phloem anatomy and the evolution of sieve elements end wall types in woody plants. *New Phytologist* 214:245–256.

Linder, H.P. 2003. The radiation of the Cape Flora. *Journal of Biogeography* 30(12):1721–1735.

Lodama, K.E., E.S. Du Toit, J.M. Steyn, H.T. Araya, G. Prinsloo, C.P. Du Plooy & P.J. Robbertse 2016. Improving rooting of *Lobostemon fructicosus* L. cuttings with delayed auxin treatment. *South African Journal of Botany* 105:111–115.

Manning, J.C. & P. Goldblatt 2012. Systematics of *Echiostachys*. *South African Journal of Botany* 78:25–40.

Metcalfe, C.R. & L. Chalk 1950. *Anatomy of the dicotyledons, vol. 2*. Clarendon Press, Oxford, UK.

Monti, C., M.C. Novoa & C.E. Vizcaíno 2003. Anatomía y etnobotánica de dos especies de Boraginaceae de la Provincia Pampeana (Argentina) usadas en medicina popular. *Latin American Journal of Pharmacy* 22(3):197–201.

Onyenedum, J.G. & M.R. Pace 2021. The role of ontogeny in wood diversity and evolution. *American Journal of Botany* 108(12):2331–2355.

Oskolski, A.A., N. Vuza & A. Shipunov 2021. Stem and leaf anatomy of *Aragoa* (Plantaginaceae): in search of lost rays. *Plants* 10(9):1773.

Papp, N., T. Bencsik, K. Németh, K. Gyergkák, A. Sulc & A. Farkas 2011. Histological study of some *Echium vulgare*, *Pulmonaria officinalis* and *Symphytum officinale* populations. *Natural Product Communications* 6(10):1475–1478.

Saad, H.E.A., H.A.E.F.A. El-Rahman, A.F. Ahmed & E.M.A. El-Karim 2007. Macro and micromorphology of *Arnebia hispidissima* (Lehm) DC growing in Egypt. *Mansoura Journal of Pharmaceutical Sciences* 23:138–167.

Saeed, N.A. & J.W. Saeed. 2012. Some diagnostic and anatomical characteristics of five taxa from Boraginaceae Juss. family, Erbil, Sulemania and Duhok-Iraq. ZANCO *Journal of Pure and Applied Sciences* 33(1):131–137

Sava, A.R., I. Boz & N. Costică 2019. Contribution to the knowledge of vegetative organs structure at *Echium russicum* J.F. Gmelin. *Analele Stiintifice ale Universitatii Al.I. Cuza din lasi* 65:44–54.

Schweingruber, F.H. & W. Landolt 2010. *The xylem database*. Swiss Federal Institute for Forest, Snow and Landscape Research. Available online: https://www.wsl.ch/dendropro/xylemdb/. Last accessed 21.09.2025.

Schweingruber, F.H., A. Börner & E.D. Schulze 2011. *Atlas of stem anatomy in herbs, shrubs and trees, vol. 2*. Berlin, Heidelberg, Germany, Springer, pp. 1–415.

Selvi, S., R. Polati, E.Y. Babacan, M.O. Rahman & U. Cakilcioğlu 2019. Micromorphological and anatomical investigation on six species of *Onosma* L. (Boraginaceae) from Turkey. *Bangladesh Journal of Plant Taxonomy* 26(1):69–81.

Shtein, I., J. Gričar, S. Lev Yadun, A.A. Oskolski, M.R. Pace, J.A. Rosell & A. Crivellaro 2023. Priorities for bark anatomical research: Study venues and open questions. *Plants* 12(10):1985.

Starr, A.M. 1912. Comparative anatomy of dune plants. *Botanical Gazette* 54(4):265–305.

Tomescu, A.M.F. & A.T. Groover 2019. Mosaic modularity: an updated perspective and research agenda for the evolution of vascular cambial growth. *New Phytologist* 222(4):1719–1735.

Ulcay, S. 2023. Research on the anatomical and ecological characteristics of *Onosma mollis* DC. (Boraginaceae). *Sakarya University Journal of Science* 27(4):813–821.

Velani, N., B.C. Boatwright, A.R. Magee & J.C. Manning 2023. Taxonomy of the small Southern African endemic genus *Echiostachys* Levyns (Boraginaceae). *South African Journal of Botany* 156:244–256.