



# Bark anatomy of *Polylepis* (Rosaceae): a loose stratified phellem instead of the lenticels?

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## ABSTRACT

Bark structure of *Polylepis incana* (*Sanguisorbeae*, Rosaceae) is described and compared with that in related genera *Cliffortia* and *Leucosidea*. Tribe *Sanguisorbeae* shows an extraordinary diversity of bark abscission patterns. The outermost bark portions are peeling off along the non-conducting secondary phloem (*Leucosidea*, *Cliffortia ruscifolia*), or along the periderm (*C. strobilifera*). The protective function is performed by phellem (*Leucosidea*), or by sclerified secondary phloem (*Cliffortia*). In *Polylepis*, the separation layers occur in phellem and non-sclerified phloem, while a prominent protective layer is absent: its function is performed by multiple uniseriate layers of suberized phellem cells. Such pattern of peeling bark has not been reported yet elsewhere. Lenticels lack in *Polylepis*, but its phellem is similar in its structure (probably, also in some functions) to stratified filling lenticular tissue. Smooth surface of *Polylepis* bark is maintained by permanent abscission of thin layers representing an extreme case of the peeling type of bark architecture.

**Keywords:** *Cliffortia*, *Leucosidea*, *Sanguisorbeae*, secondary phloem, periderm, phellem, bark abscission, dilatation

## РЕЗЮМЕ

**Оскольский А.А., Мтембу А., Шипунов А.Б., Котина Е.Л. Анатомия коры *Polylepis* (Rosaceae): рыхлая стратифицированная феллема вместо чечевичек?** В работе описана структура коры *Polylepis incana* (*Sanguisorbeae*, Rosaceae). Сравнение структуры коры у представителей близких родов *Polylepis*, *Cliffortia* и *Leucosidea* показывает необычно высокое разнообразие паттернов сбрасывания коры среди *Sanguisorbeae*. Наружные слои коры могут отделяться вдоль непроводящего луба (*Leucosidea*, *Cliffortia ruscifolia*) или вдоль перидермы (*C. strobilifera*). Защитную функцию у *Leucosidea* выполняет феллема, у *Cliffortia* – склерифицированный луб. У *Polylepis* и феллема, и непроводящий луб служат как отделительные слои, а выраженный защитный слой отсутствует: по-видимому, его функцию выполняют многочисленные однорядные слои танниносных клеток феллемы с суберинизированными стенками. Такой паттерн сбрасывания коры пока неизвестен в других группах растений. Чечевички у *Polylepis* отсутствуют, но по своей структуре (и, вероятно, по некоторым функциям) его феллема сходна со стратифицированной выполняющей тканью чечевичек. Гладкая поверхность коры *Polylepis* поддерживается благодаря постоянному сбрасыванию тонких наружных слоёв, что представляет собой предельное выражение отслаивающейся (peeling) коры как особого архитектурного типа.

**Ключевые слова:** *Cliffortia*, *Leucosidea*, *Sanguisorbeae*, вторичная флоэма, перидерма, феллема, сбрасывание коры, дилатация

The genus *Polylepis* Ruiz & Pavón belonging to the tribe *Sanguisorbeae* DC. (Rosaceae) comprises 45 species of shrubs or trees native to the mid- and high-elevation tropical Andes from northern Argentina to Colombia and western Venezuela. Some species of this genus form forests growing well above normal treeline at elevations over 4800 m. Thus, *Polylepis* appears to be the highest natural occurring arborescent angiosperm genus in the Western Hemisphere, and probably in the world (Simpson 1979, Boza Espinoza & Kessler 2022).

The name of this genus, that is derived from Greek words πολλά (many) and λέπις (scale), refers to distinctive appearance of its bark. All species of *Polylepis* share brown scaly bark which consists of numerous thin peeling layers. The bark can be made up of more than 100 such layers (Miyagawa 1975, Kessler 1995) and may be up to 3 cm thick. The thickness and appearance of bark have certain systematic value: the sections *Sericeae* and *Reticulatae* share thinner

bark that flacks off in relatively thick scales comparing with other sections of this genus (Boza Espinoza & Kessler 2022). Simpson (1979) suggested that thick loose bark of *Polylepis* can serve as an insulation from severe diurnal variations of temperature and irradiation in tropical highlands; this hypothesis has not been experimentally tested, however. The anatomy of *Polylepis* bark has been studied by Miyagawa (1975) and Lotova & Timonin (2005), but the structure and formation of peeling periderm in this genus have not been properly examined to date.

The multilayered peeling barks are characteristic not only for *Polylepis*, but also for other woody genera of the tribe *Sanguisorbeae* (Lotova & Timonin 2005). Kotina et al. (2017) revealed some significant differences in bark structure between *Leucosidea* Eckl. & Zeyh. and *Cliffortia* L., two genera of this tribe from the southern Africa. Particularly, *Leucosidea* has been found as distinctive from other Rosaceae in having storied structure of the secondary phloem as well as

the stratification of this tissue with conductive elements and crystalliferous axial parenchyma arranged into alternating bands. The examination of bark structure in other woody genera of *Sanguisorbeae*, including *Polylepis*, is required to clarify the evolution of these interesting traits within this lineage.

Resently, Shetin et al. (2023) presented a classification of four major architectural bark types (termed as *stretched*, *exfoliating*, *furrowed* and *peeling* barks) distinguished as possible combinations of binary states of two functional features: (1) by the ability or disability of the outermost layers of bark to maintain its continuity in the course of tangential expansion (dilatation), and (2) by the presence or absence of separation layers, i.e., the layers of fragile tissues enabling a regular abscission of outer portions of bark. This classification was proposed as a conceptual framework to clarify relationships between external bark appearance and its microscopic structure. A comparative study of bark structure in *Polylepis*, *Leucosidea* and *Cliffortia* could elucidate diversity of peeling barks (recognized by the disability to maintain continuity coupled with the presence of separation layers) distinguishing between different anatomical variants for this type of bark architecture.

In the present study, we examine the bark structure of *Polylepis* and re-examine it for *Leucosidea* and *Cliffortia* in order to elucidate the evolutionary pathways of selected traits as well as the diversity of anatomical variants of peeling barks within the tribe *Sanguisorbeae*.

This study has been inspired by Alexey Shipunov, the third co-author of this paper, who met an untimely end on 4th of December 2022. In August 2016 Alexey visited South Africa, where he was stunned by many local plants. Large trees of *Leucosidea sericea* in the Walter Sisulu Botanical Garden made a great impression for Alexey. In the eyes of him, a botanist with holarctic background, these trees appear like bizarre giant potentillas (albeit belonging to another tribe than *Potentilla*). Then Alexey took an interest in the woody *Sanguisorbeae*. In November 2018, he collected an anatomical sample of *Polylepis incana* Kunth during his field trip in Ecuador. Alexey was a driver of the present study; unfortunately, he did not look at the final version of its manuscript.

## MATERIAL AND METHODS

An anatomical sample of *Polylepis incana* (a piece of branch of ca. 3 cm in diameter with smaller twigs and juvenile shoots) has been collected by the third author on 03.11.2018 in the vicinity of Quito (0.296917°S 78.245778°W) in Ecuador at the altitude 3629 m. The sample has been fixed in 70 % ethanol. We also re-examined the bark sections of *Cliffortia ruscifolia* L. [E. Kotina & B.-E. Van Wyk 95-14], *C. strobilifera* L. [E. Kotina & B.-E. Van Wyk 96-14] and *Leucosidea sericea* Eckl. & Zeyh. [E. Kotina & B.-E. Van Wyk 85-14] on the microslides that had been described by Kotina et al. (2017). The bark samples and microslides are deposited at the Department of Botany and Plant Biotechnology, University of Johannesburg, South Africa,

The pieces of mature bark were embedded in polyethylene glycol 1500 and sectioned with the aid of a rotary microtome with the use of a polystyrene resin, as described in Barbosa et al. (2010). Sections were double stained in saf-

ranin and alcian blue (Jansen et al. 2004), and mounted in Entellan. For anatomical examination of juvenile stems and, the samples were also 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 by using a Porter Blum MT-1 98 ultramicrotome, then stained with toluidine blue, and mounted in Entellan. Length of sieve tube members was measured on the small fragments of secondary phloem macerated using Jeffrey's solution (Johansen 1940). Sudan IV test was used for detection of suberized cell walls (Johansen 1940).

Descriptive terminology followed the recommendations of Angyalossy et al. (2016). It is important to stress, however, that the definition of periderm as “secondary protective tissue” recommended by Angyalossy et al. (2016: p. 576) is not necessarily relevant for the plants with peeling bark (*sensu* Shtein et al. 2023), including *Polylepis* and related genera. In the barks of such architectural type, the periderm commonly serves only as a separation layer while the protective function is confined to sclerified secondary phloem (Frankiewicz et al. 2021, 2023).

In the present study, we used the terms “separation layer” for a layer of fragile tissues enabling a regular abscission of outer portions of bark, and “protection layer” for a continuous layer or zone of thick-walled cells (usually with suberized or lignified cell walls) and/or of tanniferous cells in periderm, non-conducting secondary phloem, or any other tissues located in the outer regions of bark that could protect the conducting phloem and vascular cambium.

## RESULTS

### Bark structure of *Polylepis incana*

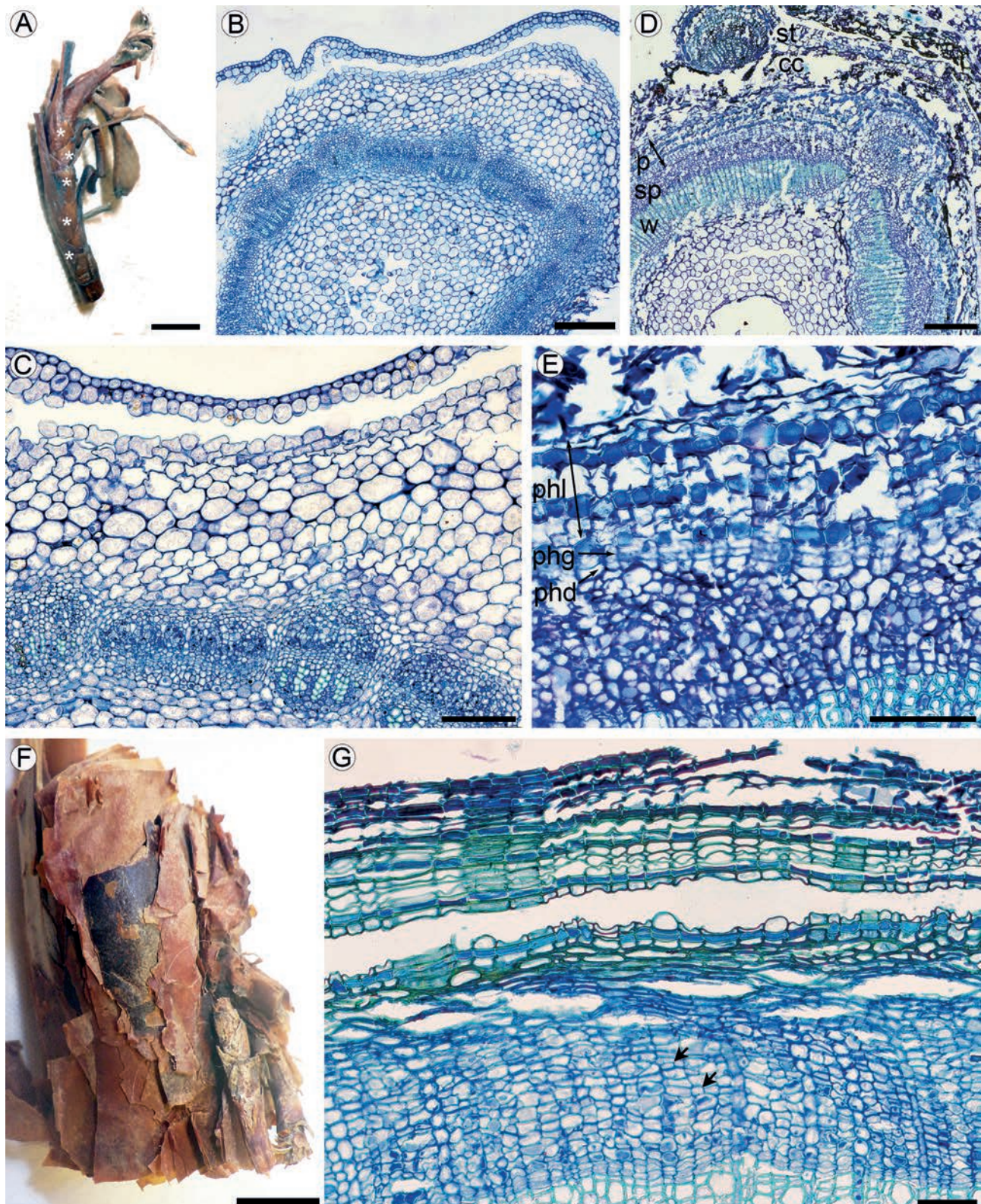
**Examined sample:** *Polylepis incana* [A. Shipunov s.n.]

The surface of young stems is smooth and mostly covered by stipule sheaths (Fig. 1A). The epidermis on young stems is composed of a single layer of small (10–20 µm in tangential size) isodiametric thin-walled cells; the cuticle is unobservable under light microscope (Figs 1B, C)

The cortex consists of 10–14 layers of thin-walled parenchyma cells of 15–35 µm in tangential size (up to 50 µm in the middle zone of cortex). Druses were observed only in a few parenchyma cells; no chloroplasts were found. Dilatation of the cortical tissue is effected mostly by tangential stretching of cells and their breaking with the formation of schizo-rhexogenous intercellular cavities (Figs 1B, D). Primary phloem and primary xylem are arranged into nearly continuous ring; pericyclic fibres not observed (Fig. 1C).

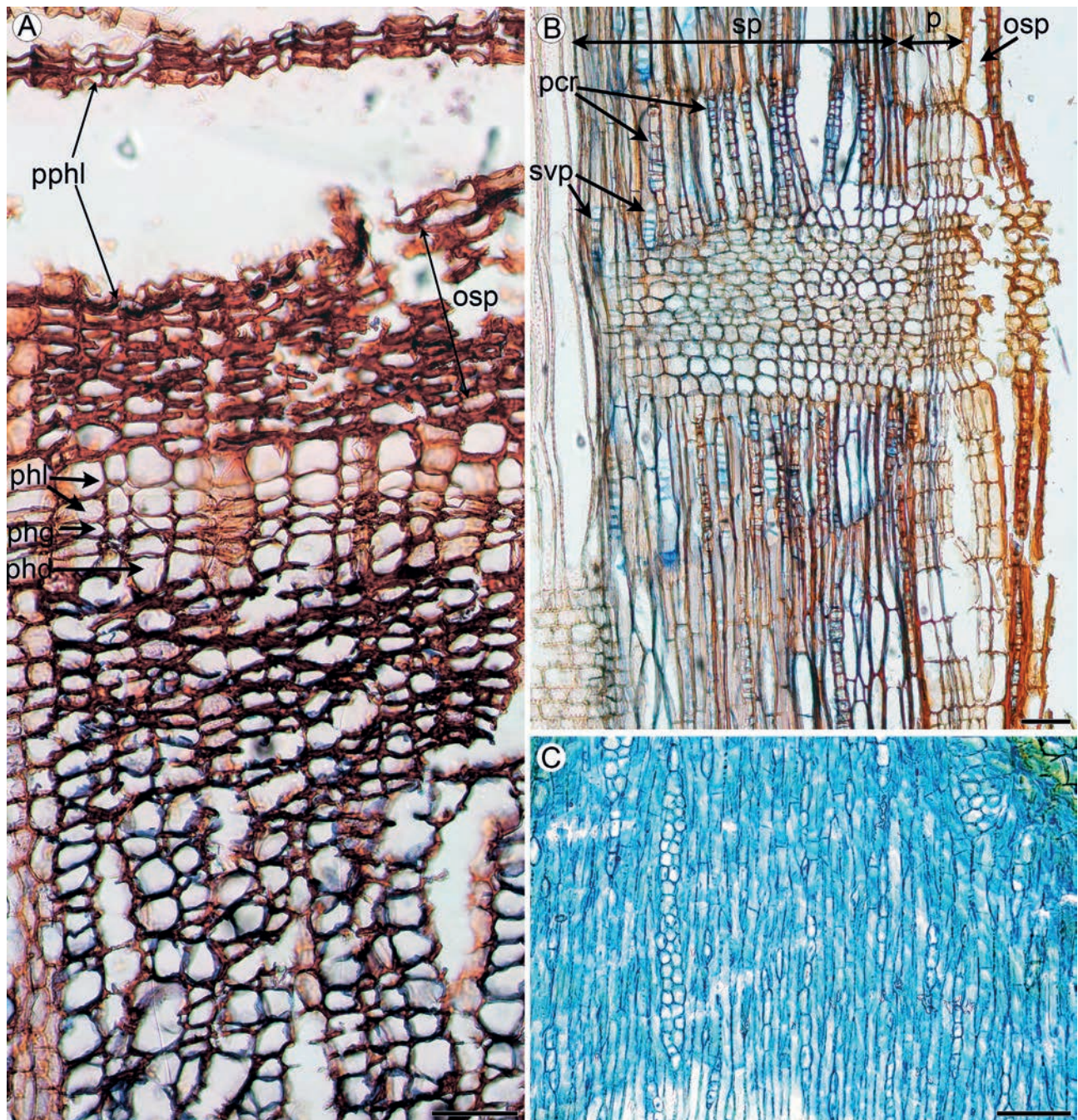
The mature bark is yellow-brownish, peeling with thin papery stringy scales, without lenticels (Fig. 1F). The initiation of first-formed periderm occurs in the deeper layers of the cortex in very young stems (Fig. 1D). Phellem is stratified, more than 10 cell layers in width, made of 1–2(3)-seriate bands of radially-flattened phelloid cells with thin non-suberized walls alternating with uniseriate lines of radially-flattened cells with thin suberized walls and dark content showing negative reaction to tannin (Figs 1D, F, 2A). The phelloderm comprises 1–2 layers of isodiametric to radially-flattened, thin-walled cells (Figs 1E, 2A). Subsequent periderms are initiated as concentric rings in non-





**Figure 1** Macroscopic appearance and microstructure of the bark in *Polylepis incana* Kunth [A. Shipunov, s.n.]: A – young twig with persistent sheaths (white asterisks) formed by pairs of fused stipules; B, C – juvenile stem prior to initiation of lateral meristems, light microscopy (LM), transverse section (TS): B – epidermis without trichomes, schizo-rhexigenous cavities in cortex, nearly continuous ring of primary vascular tissues, C – very thin cuticle on epidermal cells, cortical parenchyma (the lack of collenchyma), pericyclic fibers absent; D, E – young stem after initiation of vascular cambium and phellogen (LM, TS): D – stipule sheaths (st), collapsed cortex (cc), first periderm (p), secondary phloem (sp), wood (w), pith, E – first phellogen (phg), pheloderm (phd), phellem (phl) with uniseriate lines of cells with dark content, secondary phloem, initiation of first phellogen in the depth of cortex (radial files of peridermal cells are not collinear to the files of secondary phloem elements); F – branch with mature peeling bark without lenticels; G – bark with prominent first periderm from a small branch (ca. 5 mm in diameter), conducting secondary phloem with anticlinal divisions in some axial parenchyma cells (black arrows), stratified phellem with alternating layers of phelloid and lines of the cells with dark content, abscission along the phelloid layer (LM, TS). Scale bars = 10 mm (F), 5 mm (A), 200  $\mu$ m (B, D), 100  $\mu$ m (C), 50  $\mu$ m (E, G)





**Figure 2** Structure of mature bark in *Polylepis incana* [A. Shipunov, s.n.] (LM): A – non-conducting secondary phloem, initiation of new periderm (1–2-seriate phellogen (phl), phellogen (phg), phellogen derivatives (phd)), obliterated secondary phloem (osp), peeled layers of phellogen (pphl) (TS); B – secondary phloem (sp), sieve tube members with compound sieve plates (svp), strands of axial parenchyma with prismatic crystals (pcr) in chambered cells, secondary phloem rays made mostly of square cells with few upright and procumbent cells; initiation of subsequent periderm (p); obliterated secondary phloem (osp), radial longitudinal section (RLS); C – uni- and 2–3-seriate rays in secondary phloem, no storied arrangement of phloem elements, tangential longitudinal section (TLS). Scale bars = 100  $\mu$ m (C), 50  $\mu$ m (A, B)

conducting secondary phloem (Figs 2A, B, 3A); their cells are arranged into radial rows which are collinear to the radial files of phloem cells. Crystalliferous cells and sclereids were not observed in periderm.

The secondary phloem shows no distinctive patterns in the arrangement of its conductive elements and/or axial parenchyma (Figs 2A, B). Sieve tube members are 15–27  $\mu$ m wide; their length varies within 190–590  $\mu$ m (average 367.3  $\mu$ m). Sieve plates are compound with 3 to 9 sieve areas, located on vertical or slightly oblique cross walls (Fig. 2B).

Axial parenchyma consists of fusiform cells and strands of 2–4 cells scattered between the conductive elements. The axial parenchyma strands with prismatic crystals in chambered cells commonly occur. Anticlinal division of axial parenchyma cells occur in some strands (Fig. 1G). The transition from conducting to non-conducting secondary phloem is gradual. Non-conducting secondary phloem differs from conducting secondary phloem by flattening of axial parenchyma cells and obliteration of sieve tubes. No sclereids found in the secondary phloem.



Secondary phloem rays (Figs 2B, C) are uniseriate and 2–3-seriate (rarely 4-seriate). Uniseriate rays are composed of square and upright cells while multiseriate rays can have also procumbent cells in their central portions. The height of the multiseriate rays is 120–430 µm. Crystalliferous and/or sclerified ray cells not found. Storied arrangement is not found for any elements of the secondary phloem (Fig. 2C).

Dilatation of secondary phloem is weak, effected by tangential expansion of the cells of axial and radial parenchyma as well as by anticlinal divisions of axial parenchyma cells. The outermost portions of bark are peeling off along the layers of phelloid cells in phellem (forming 3–4-seriate scales), and along non-conducting secondary phloem. No prominent protective layer has been observed (Fig. 1G, 2A, B).

### Phellem structure and patterns of bark abscission in *Leucosidea* and *Cliffortia*

**Examined samples:** *Cliffortia ruscifolia* [E. Kotina & B.-E. Van Wyk 95-14], *C. strobilifera* [E. Kotina & B.-E. Van Wyk 96-14], and *Leucosidea sericea* [E. Kotina & B.-E. Van Wyk 85-14].

Re-examination of the bark sections of *Leucosidea sericea*, *Cliffortia ruscifolia* and *C. strobilifera* showed that the uniseriate lines of radially-flattened thin-walled cells with dark content occur in phellem of these species (Figs 3A, B). This feature has not been mentioned in previous descriptions of these samples (Kotina et al. 2017). Subsequent periderms in *Leucosidea* and *Cliffortia* are initiated as concentric rings in non-conducting secondary phloem.

In both species of *Cliffortia* (Fig. 3), the phellem is of 3–4(6) cells in width, consisting mostly of thin-walled (probably phelloid) cells, with one or two lines of the cells containing dark deposits. The outermost portions of bark are stripped along the deeper layers of non-conducting phloem in *C. ruscifolia* (Fig. 3A) or along phellem bands in *C. strobilifera* (Fig. 3B) which function as separation layers. The initiation of subsequent periderm in *C. strobilifera* is seemingly associated with the formation of continuous 2–8-seriate bands of sclereids and the cells with dark content in the adjacent region of non-conducting secondary phloem flanked the periderm from the inside (Fig. 3B). These bands of sclereids much increase in width in the outermost parts of non-conducting phloem located to the outside from the last initiated periderm. Unlike *C. strobilifera*, the sclereids in *C. ruscifolia* are scattered within the non-conducting phloem forming no continuous bands on the inside to newly initiated subsequent periderms. The non-conducting phloem of this species shows, however, nearly solid sclerification to the outside of these periderms: its sclereids are arranged into large aggregations interrupted only by dilated non-sclerified phloem rays (Fig. 3A). These bands and aggregations of sclereids found in non-conducting phloem of *Cliffortia* seemingly function as protective layers.

The phellem of *L. sericea* is stratified (Fig. 4A), 7–16 cells in width, made of 2–5(6)-seriate bands of radially flattened cells with moderately thick (mostly sclerified) walls alternating with the uniseriate lines of thin-walled cells. Dark deposits regularly present in these thin-walled cells, and occasionally occur in moderately thick-walled cells too. Solitary sclereids occur in non-conducting phloem of this

species, but those are not arranged into continuous bands (Fig. 4B). The outermost portions of bark are peeling off along the layers of non-conducting secondary phloem, while the phellem bands persist as protective layers (Fig. 4B).

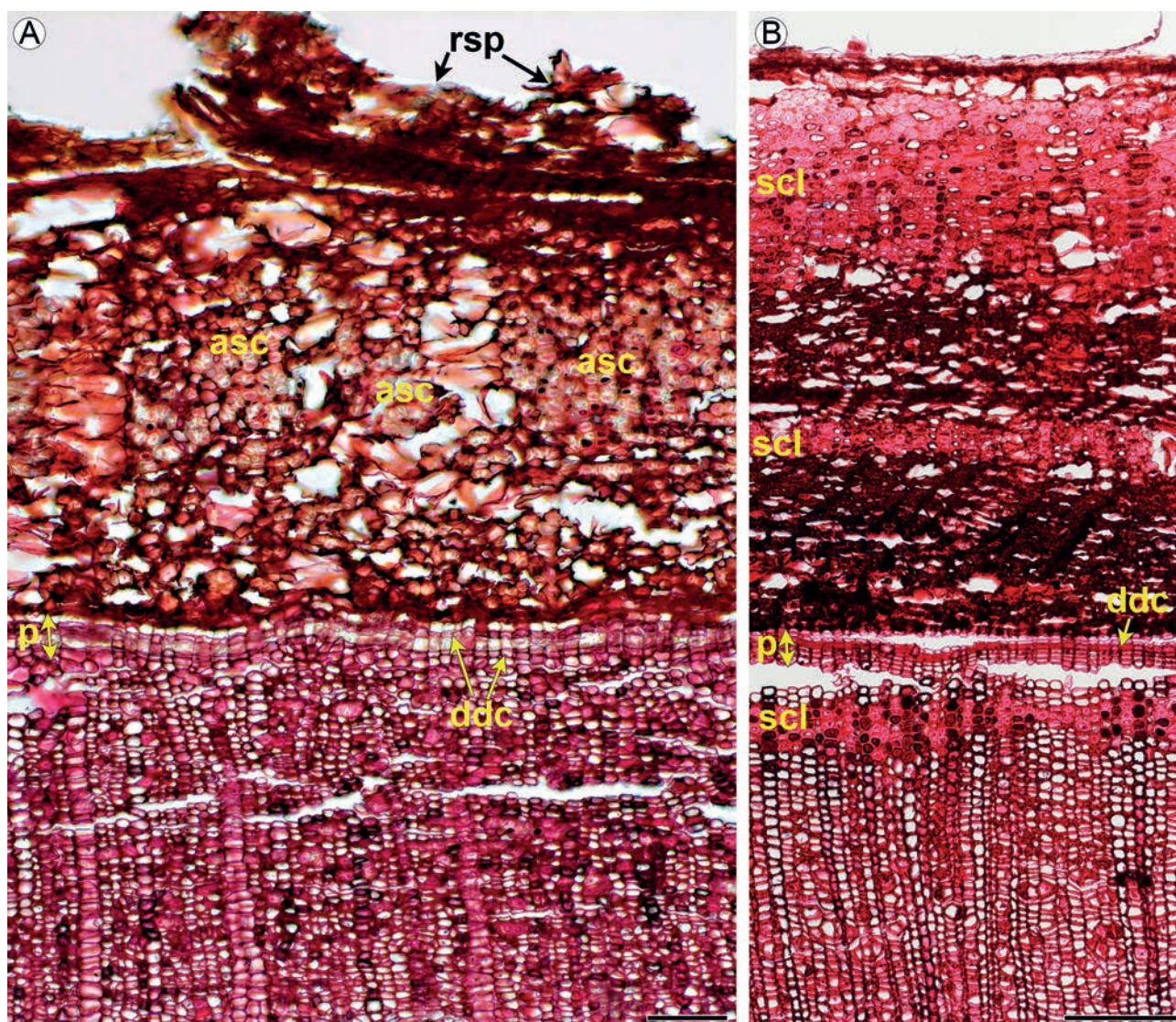
## DISCUSSION

Our observations on the *Polylepis* bark structure are mostly consistent with the data of other authors (Miyagawa 1975, Lotova & Timonin 2005). *Polylepis incana* is similar in most bark anatomical traits to *Cliffortia* and *Leucosidea*, two other genera of the tribe *Sanguisorbeae* whose bark structure has been studied to date (Lotova & Timonin 2005, Kotina et al. 2017). All these genera share the presence of schizorhexigenous intercellular spaces in dilated cortex, initiation of first periderm in deep layers of the cortex, the presence of seemingly tanniniferous phellem cells in uniseriate lines or narrow bands, the anticlinal divisions of the cells of axial parenchyma in secondary phloem, and the occurrence of prismatic crystals in chambered axial parenchyma cells phloem. Among these two genera, *Polylepis* shows greater overall similarity to *Cliffortia*, whereas *Leucosidea* is distinctive from the studied species as well as from other Rosaceae in having storied and stratified secondary phloem with regular alternation of the lines of conductive elements and crystalliferous axial parenchyma (Kotina et al. 2017). Such pattern of (dis)similarities is consistent with their phylogenetic relationships between these genera: while *Polylepis* and *Cliffortia* are closely related to each other being placed to the same subtribe *Sanguisorbinae* Torr. & A. Gray, *Leucosidea* belongs to another subclade within *Sanguisorbeae* which is considered as the subtribe *Agrimoniinae* J. Presl (Potter et al. 2007). The bark anatomical examination of *Hagenia* J.E. Gmel., another woody genus of *Agrimoniinae*, would be of great interest to clarify the origin and evolution of storied cambium and stratified secondary phloem within Rosaceae.

The juvenile stems of *P. incana* are distinctive from those in *Cliffortia* and *Leucosidea* by the lack of trichomes, very thin cuticle on epidermal cells, and the absence of collenchyma and chlorenchyma in the cortex. Obviously, this suite of traits is associated with such characteristic feature of *Polylepis* as the presence of the sheaths around the stem formed by pairs of fused stipules. These sheaths are shaped like tubes nested inside each other near the branch tips completely covering the juvenile shoots (Boza Espinoza & Kessler 2022). Presumably, these multilayered coverings can protect them in severe highland climate and provide them mechanical support making trichomes, cuticle and collenchyma redundant.

Miyagawa (1975) reported the lack of phelloderm in the periderm of *Polylepis*. Our observations do not confirm this suggestion: the phellogen of *P. incana* is flanked by a distinctive 1–2-seriate phelloderm (Figs 1E, 2A). The lack of phelloderm would imply a shift of cork cambium activity from bifacial to unifacial mode, but such cases are unknown. Recently, Frankiewicz et al. (2021) did not recognize phelloderm in the periderm of peeling bark in some species of *Buddleja* L. (Scrophulariaceae), but this layer has been found in its periderm after careful examination (Frankiewicz et al. 2023).





**Figure 3** Structure of mature bark in *Cliffortia* (LM, TS): A – *C. ruscifolia* L. [E. Kotina & B.-E. Van Wyk 95-14]: conducting and obliterated secondary phloem, initiation of subsequent periderm (p) with uniseriate line of thin-walled cells with dark content (ddc) in phellem, aggregates of sclereids (asc) in secondary phloem; remnants of secondary phloem on bark surface (rsp). B – *C. strobilifera* L. [E. Kotina & B.-E. Van Wyk 96-14]: conducting and obliterated secondary phloem, initiation of subsequent periderm (p) with uniseriate line of thin-walled cells with dark content (ddc) in phellem, bands of sclereids (scl) in secondary phloem, periderm on the bark surface. Scale bars = 100  $\mu$ m

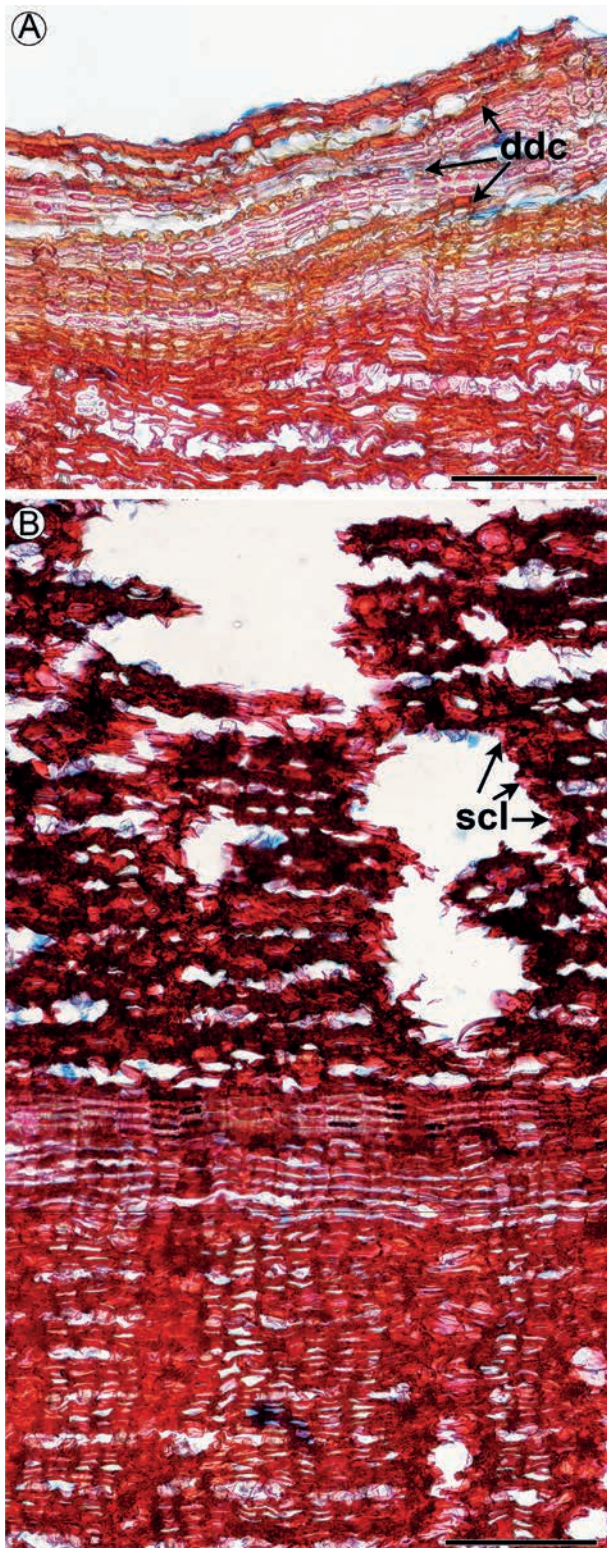
Noteworthy, that tribe Sanguisorbeae shows an extraordinary diversity of the patterns of bark abscission which has not been reported yet in other plant lineages of similar magnitude.

In *Cliffortia strobilifera* (Fig. 3B), the periderm (phellem) acting as separation layer combined with protective secondary phloem subjected to nearly solid sclerification in its outermost regions. This pattern is the most common among the taxa with peeling barks: it has been found, for instance, in species of *Eucalyptus* L'Hér. with stringy barks (Chattaway 1955), in *Melaleuca* L. (Chiang & Wang 1984, Crivellaro & Schweingruber 2013), *Lonicera* L. (Eremin & Kopanina 2012, Schweingruber et al., 2019) and *Buddleja* (Frankiewicz et al. 2021, 2023). Unlike *C. strobilifera*, *C. ruscifolia* (Fig. 3A) has separation layer in the innermost region of non-conductive phloem which is adjacent to the underlying phellem, but the outer phloem region in this species is also protective. In *Leucosidea*, the bark scales are separated in secondary phloem while the periderm is responsible for pro-

tection (Figs 4A, B). Such pattern has been reported in *Vitis* L. (Eremin & Kopanina 2012, Schweingruber et al. 2019) and in some *Clematis* L. (mentioned as *Atragene* by Eremin & Kopanina (2012)). Unlike *Leucosidea* and *Cliffortia*, the separation of outer bark portions in *Polylepis* occurs both in phellem, and in non-conducting phloem. At the same time, a prominent protective layer is absent in this genus: its function is seemingly performed by multiple uniseriate lines of phellem cells with suberized walls and dark contents. Such allocation of separation and protective structures in a peeling bark is very uncommon. We did not find other examples for it: all aforementioned taxa with peeling bark except *Polylepis* have prominent protective layers.

The lack of solid protective bands in the peeling bark of *Polylepis* is thought to be compensated by formation of thicker phellem that can reach 1 cm (rarely up to 3 cm) in thickness having more than 100 lines of suberized cells associated with phelloid (Miyagawa 1975, Kessler 1995).





**Figure 4** Mature bark of *Leucosidea sericea* Eckl. & Zeyh. [E. Kotina & B.-E. Van Wyk 85-14] (LM, TS): A – Periderm: stratified phellem made of bands of the cells with moderately thick sclerified walls alternating with uniseriate lines of thin-walled cells containing dark deposits (ddc); B – Mature bark: fractured obliterated secondary phloem on the bark surface with underlying solid layer of phellem; sclereids (scl) scattered in non-conducting secondary phloem. Scale bars = 100 μm

Simpson (1979) suggested that such thick and loose bark can serve as an insulation from both the nightly frosts and the intense diurnal irradiation in tropical highlands. It is worth noting, however, that the *Polylepis* phellem is very similar in its structure to stratified filling tissue of the lenticels found in some other Rosaceae (e.g. *Prunus* L.) as well as in several other families. Both these tissues composed of alternating layers of loose nonsuberized tissues and compact, suberized layers (Angyalossy et al. 2016, Rosner & Morris 2022). Such similarity suggests that the stratified phellem of *Polylepis* may perform some functions of lenticels that are absent in its bark. Apart from gas exchange, this phellem could be involved in accumulation of fog or rain water and/or in recovery of xylem vessels from embolisation after seasonal drought by evaporative enhancement due to bark transpiration (Rosner & Morris 2022). Supposedly, these functions can be the most important for the trees growing in high elevations with significant variations of temperature and rainfall. Eco-physiological studies are required, however, to clarify functional value of peeling stratified phellem in *Polylepis*.

*Polylepis incana* has relatively smooth bark, but such condition is attained by another way than the smoothness of exfoliating barks (e.g. in *Platanus* L.). The latter type of bark architecture is characterized by the ability of conspicuous expansion without superficial disruptions (Shtein et al. 2023). Unlike that, the *Polylepis* bark does not show any traits of such expansion: instead, its smoothness is maintained by permanent regular abscission of its outermost layers and their regeneration. Thus, the bark of *Polylepis* must be considered as an extreme case of the peeling bark. Obviously, the occurrence of lenticels, which is typical for stretched and exfoliating barks, is hardly compatible with such type of bark architecture.

In our study, we examined only the structure of relatively thin bark of *P. incana* found on a branch of ca. 3 cm in diameter. The anatomical features of thick mature bark of this species remain unknown. The species from different section of the genus *Polylepis* showing prominent difference in thickness and appearance of their bark (Boza Espinoza & Kessler 2022) were also out of scope of the present research. A comparative anatomical study of the bark diversity and development in *Polylepis* would be of great interest for clarification of the origin and adaptive value of such an uncommon bark structure.

## CONCLUSIONS

*Polylepis* is similar to *Cliffortia*, *Leucosidea*, and other genera of the tribe *Sanguisorbeae* (Rosaceae) is the presence of schizo-rhexigenous intercellular spaces in dilated cortex, initiation of first periderm in deep layers of the cortex, the presence of phellem cells with dark content in uniseriate lines or narrow bands, the anticlinal divisions of the cells of axial parenchyma in secondary phloem, and the occurrence of prismatic crystals in chambered axial parenchyma cells.

*Polylepis* shows greater overall similarity to *Cliffortia*, whereas *Leucosidea* is distinctive from them in having storied and stratified secondary phloem with regular alternation of the lines of conductive elements and crystalliferous axial

parenchyma. Such pattern of (dis)similarities is consistent with their phylogenetic relationships between these genera.

The juvenile stems of *Polylepis* are distinctive from those in *Cliffortia* and *Leucosidea* by the lack of trichomes, very thin cuticle on epidermal cells, and the absence of chlorenchyma and collenchyma in the cortex. These traits are associated with the presence of the stipule sheaths covering the juvenile shoots in *Polylepis*.

Despite Miyagawa's (1975) report, the phelloderm is present in the periderm of *Polylepis*.

The tribe *Sanguisorbeae* shows an extraordinary diversity of the bark abscission patterns that has not been reported yet in other plant lineages of similar magnitude.

The outermost portions of bark are stripped along the deeper layers of non-conducting phloem in *C. ruscifolia*, or along phellem bands in *C. strobilifera* which function as separation layers. In both *Cliffortia* species, the protection is performed by sclerified outer regions of non-conducting secondary phloem. Unlike *Cliffortia*, the sclerified phellem in *Leucosidea* serves as protective layer.

Unlike *Cliffortia* and *Leucosidea*, the separation of outer bark portions in *Polylepis* occurs both in phellem, and in non-conducting phloem while the prominent hard protective layer is absent in this genus: its function is seemingly performed by multiple uniseriate lines of phellem cells with suberized walls and dark content. Such allocation of separation and protective structures in peeling bark has not been reported yet in other plant groups.

The loose stratified phellem of *Polylepis* is very similar in its structure to stratified filling tissue of lenticels. Such similarity suggests that this phellem may perform some functions of the absent lenticels, such as gas exchange, accumulation of fog or rain water and/or in recovery of xylem vessels from embolisation after seasonal drought by evaporative enhancement.

The *Polylepis* bark does not show an ability to continuous tangential expansion without superficial disruptions: its smoothness is maintained by permanent regular abscission of thin outer layers and their regeneration. Such combination of traits must be considered as an extreme case of the peeling type of bark architecture.

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