FROM LIANAS TO TREES: THE IMPACT OF HABIT TRANSITION ON THE EVOLUTION OF WOOD AND BARK IN THE MALPIGHIACEAE (BUNCHOSIA CLADE)

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Premise of research. Shifts between climbing and self-supporting forms drive modifications in wood and bark anatomy, reflecting mechanical and physiological adaptations. The Bunchosia clade (Malpighiaceae) offers an ideal model to examine these changes, as evidence suggests independent transitions to self-supporting forms from a lianescent ancestor. This study examines how vascular traits differ between climbers and self-supporting species, explores their evolutionary history, and identifies the developmental mechanisms that have shaped these anatomical traits over time.

Methodology. We analyzed 24 Malpighiaceae species, including 19 from the Bunchosia clade, collecting stem samples for anatomical analysis. We examined 23 anatomical traits (18 discrete, five continuous), reconstructed their evolution using a calibrated phylogeny, estimated ancestral states, and tested correlations between habit and some vascular traits through stochastic mapping and phylogenetic comparative methods.

Pivotal results. The ancestral condition in the Bunchosia clade likely featured diffuse porous wood, vessel dimorphism, narrow rays, septate fibers, and biphasic development. In lianas, these traits were maintained but with further evolution of wider vessels, high vessel frequency, gelatinous fibers, and mixed heterocellular rays appearing. In contrast, self-supporting species lost biphasic development, reduced vessel frequency, and evolved narrower vessels with abundant axial parenchyma. Vessel dimorphism was maintained in most genera except the self-supporting *Bunchosia*. In bark, the sieve tube area decreased in self-supporting species and increased in lianas.

Conclusions. The study shows that the Bunchosia clade has anatomical differences between lianas and self-supporting species. These differences highlight adaptations to climbing or self-supporting habits, with anatomical evolution involving heterochronic (paedomorphic) and homeotic shifts, offering insight into vascular diversification in Malpighiaceae. These findings highlight the deep connection between plant developmental processes and the interaction between their morphological structures and the vascular system. Moreover, these mechanisms enable plants to adapt to environmental conditions, underscoring the importance of understanding their evolution in explaining their diversity and ability to thrive in various ecosystems.

Keywords: lianas, trees, wood anatomy, bark anatomy, Malpighiaceae, lianescent vascular syndrome.

Online enhancements: appendixes.

Introduction

The diversity of vascular system arrangements in plants with secondary growth is closely linked to habit and ecological strategies (Baas and Schweingruber 1987; Alves and Angyalossy-Alfonso 2000, 2002; Rowe and Speck 2005; Spicer and Groover 2010). Changes in habit, such as shifts between climbers and self-supporting forms, are often accompanied by modifications in wood and bark anatomy (Ewers and Fisher 1991; Angyalossy et al. 2015; Pace et al. 2015, 2022). These modifications reflect adaptations to different mechanical and physiological demands, shaping the evolutionary trajectories of plant lineages (Angyalossy et al. 2012, 2015).

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Climbing plants (lianas) and self-supporting plants (trees and shrubs) often differ considerably in the structure and organization of their vascular tissues (Ewers and Fisher 1991; Ewers et al. 1992; Angyalossy et al. 2015). Lianas typically display wider and less frequent vessels, vessel dimorphism, abundant axial parenchyma, and very tall and wide rays and often exhibit vascular variants (Angyalossy et al. 2015). In contrast, self-supporting plants are characterized by narrower and more frequent vessels, thicker fibers, and a lower proportion of axial parenchyma compared to climbers (Angyalossy et al. 2015). These anatomical differences reflect the selective pressures related to structural support and water transport efficiency in different growth forms (Baas and Carlquist 1985; Ewers et al. 1992). Additionally, the complexity observed in the vascular system of some lianas appears once they begin to climb (Caballé 1998; Isnard and Silk 2009).

The Malpighiaceae are ideal for studying these vascular differences, as they include both lianas and self-supporting species with a wide array of vascular modifications (Schenck 1893; Chodat and Vischer 1917; Obaton 1960; Caballé 1993; Cabanillas et al. 2017; Pace et al. 2018; Quintanar-Castillo et al. 2024). Malpighiaceae is composed of nearly 75 genera and 1300 species, distributed mainly in tropical and subtropical regions (Anderson et al. 2006–; Davis and Anderson 2010). The family shows a wide range of habits, from tiny herbs to shrubs, lianas, and trees (Anderson et al. 2006–). This range of habits reflects interesting adaptations to distinct ecological niches, contributing to the complexity of both morphology and ecology within the family. Many species exhibit specialized vascular traits associated with mechanical and hydraulic adaptations to their respective habits (Cabanillas et al. 2017; Pace et al. 2018; Quintanar-Castillo and Pace 2022). Within Malpighiaceae, the Bunchosia clade represents a well-defined lineage (Davis and Anderson 2010; Davis et al. 2014) that includes both climbers and self-supporting species (Quintanar-Castillo and Pace 2022), providing a unique opportunity to investigate whether habit shifts have influenced the vascular anatomy of the stem. The clade includes the genus *Bunchosia*, the largest genus in the group, with nearly 80 species of trees and shrubs (Anderson et al. 2006–); the genus *Echinopterys*, with only two species of shrubs and leaning shrubs (Anderson 2013); and the lianescent genera *Heladena* and *Henleophytum*, each with a single species (Anderson et al. 2006–), with *Henleophytum* being endemic to Cuba (Anderson 2013; Quintanar-Castillo et al. 2024). The genus *Thryallis* comprises five species, also described as leaning shrubs, while *Tristellateia* is the largest lianoid genus in the clade, with 21 species (Anderson et al. 2006–; Anderson 2013). All these genera are found mainly in continental America and the Caribbean, except for *Tristellateia*, which occurs in Africa and Asia (Davis and Anderson 2010).

Earlier studies have identified two independent transitions from a self-supporting to climbing habit in Malpighiaceae, with the self-supporting habit being the plesiomorphic state. These findings suggest that such shifts played a key role in the vascular organization of the family (Quintanar-Castillo and Pace 2022). Furthermore, although the derived state is the climber habit, multiple reversions to a self-supporting habit have occurred, many of them within lianescent clades (Quintanar-Castillo and Pace 2022). Recent studies suggest that in the Bunchosia clade, primarily composed of lianas, the shift to a self-supporting habit occurred twice independently (Quintanar-Castillo et al. 2025). Moreover, the evolution of different habits within the family has led to distinct developmental trajectories of the vascular system, resulting in distinct vascular configurations (Quintanar-Castillo et al. 2025). These shifts in habit have likely driven structural modifications in both wood and bark, influencing the mechanical and functional properties of the vascular system.

Recent studies on stem anatomy evolution in self-supporting Malpighiaceae clades have shown that wood and bark structure in the Byrsonimoid clade is highly conserved and with low variability, despite species occurring in different environments and exhibiting different habits (Bueno et al. 2025). In contrast, species in the Galphimioid clade show anatomical differences between trees and shrubs, with wood traits reflecting both habit and environmental influences (Sanches et al. 2025).

The Bunchosia clade, with its phylogenetic resolution and morphological diversity, offers a unique opportunity to investigate the evolutionary mechanisms underlying the anatomical divergence of vascular systems in climbing and self-supporting plants. By comparing wood and bark traits across different growth forms within this clade, it is possible to gain insights into the evolutionary pathways that have shaped anatomical diversity in the family within a well-resolved phylogenetic framework. We expect that lianescent members of the clade will show concordance in their anatomy, displaying characteristics of the lianescent vascular syndrome (Angyalossy et al. 2015), while the self-supporting members will lack these traits.

The present study aims to (1) describe the general wood and bark structure within the clade, (2) identify the anatomical differences between climbing and self-supporting members, and (3) determine how these anatomical features evolved throughout the history of the Bunchosia clade. By analyzing anatomical changes in the context of habit shifts, we seek to better understand the evolutionary pathways that have shaped the vascular system diversity in this clade.

Material and Methods

Taxon Sampling and Anatomical Procedures

We used the same species sampling as in Quintanar-Castillo et al. (2025), including 24 species of Malpighiaceae, 19 of which belong to the Bunchosia clade, representing all six genera that compose it. For lianas and leaning shrubs (e.g., *Thryallis*), we collected stem samples from mature specimens in their thickest portion. For trees, we obtained samples at chest height of the trunk using a hammer and chisel to extract a part containing wood, cambium, and bark.

Once the samples were collected, we immediately fixed them in FAA 70 (formalin, acetic acid, and 70% ethanol) and then transferred them to 70% ethanol for long-term preservation (Johansen 1940). Since Malpighiaceae possess very stiff wood, we softened the samples in a boiling water and glycerin solution (10 : 1) for a week, 8 h per day (Pace 2019). After softening, we embedded the samples in polyethylene glycol 1500 (Rupp 1964) to preserve both soft and stiff tissues. We sectioned the samples using a sliding microtome (Leica Hn40) and applied a polystyrene resin coat (Styrofoam dissolved in butyl acetate) to obtain complete stem sections and prevent tearing (Barbosa et al. 2010).

Table 1

Discrete Characters and Their States Used in the Ancestral State Reconstruction Analysis in the Bunchosia Clade

	Character	Character state
1	Biphasic development	Absent; present
2	Vessel dimorphism	Absent; present
3	Porosity	Diffuse; semiring porous
4	Vessel arrangement	Dendritic; diffuse; radial; tangential bands
5	Vessel grouping	Long radial multiples; solitary/short radial multiples
6	Apotracheal parenchyma	Absent; aggregate; diffuse
7	Paratracheal parenchyma	Confluent; scanty; vasicentric
8	Banded parenchyma	Absent; marginal; narrow bands; wide bands
9	Gelatinous fibers	Absent; present
10	Septate fibers	Absent; present
11	Interconnected rays	Absent; present
12	Ray width	Narrow rays; wide rays
13	Ray composition	Heterocellular with marginal rows of square and upright cells; heterocellular mixed rays
14	Prismatic crystals in the axial parenchyma	Absent; present
15	Prismatic crystals in ray parenchyma	Absent; crystals in all body ray; crystals only in marginal rows
16	Sieve tube distribution	Bands; clusters; radial rows
17	Druses position in phloem	Absent; druses in the axial parenchyma; druses in the axial and ray parenchyma
18	Sclereids arrangement	Absent; bands; clusters; diffuse

Sections were double stained in safranin and astra blue, in a proportion of 1 : 9 parts (Bukatsch 1972; modified by Kraus and Arduin 1997), and then mounted in either Canada balsam or synthetic resin to make permanent slides.

Character State Delimitation

We built a database including 23 characters: 18 discrete characters (table 1) and five continuous characters (table 2). We selected characters previously described or suggested as part of lianescent vascular syndrome, such as biphasic development, vessel dimorphism, vessel arrangement, and parenchyma proportion (Angyalossy et al. 2012, 2015; Luizon Dias Leme et al. 2021). Character states were scored based on our direct observations. The continuous characters correspond to anatomical traits of wood and secondary phloem. The anatomical trait delimitation followed the guidelines of the International Association of Wood Anatomists committee for wood and bark (Wheeler et al. 1989; Angyalossy et al. 2016) and Carlquist (2001).

Ancestral Character State Reconstruction

To reconstruct the evolution of the anatomical traits in the Bunchosia clade, we used the calibrated phylogeny of Malpighiaceae from Quintanar-Castillo and Pace (2022). This phylogeny

Table 2

Continuous Characters Used in Phylogenetic Analyses of the Bunchosia Clade Plus Outgroups

	Vessel frequency (mm^2)	Vessel width (μm)	Intervessel pit size (μm)	Parenchyma proportion (%)	Sieve tube area (μm^2)
Bunchosia glandulifera[a]	90 ± 17	55.89 ± 9.7	10.84 ± 1.01	22.76 ± 4.9	NA
Bunchosia maritima[a]	29 ± 11	67.16 ± 9.2	5.77 ± .8	25.66 ± 3.4	99.51 ± 18.03
Bunchosia montana[a]	73.5 ± 18	42.31 ± 8.8	3.6 ± .4	30.62 ± 6.5	114.94 ± 15.6
Bunchosia nitida[a]	35 ± 16	76.97 ± 13.9	4.36 ± .6	9.67 ± 3.2	NA
Bunchosia polystachia[a]	39 ± 17	71.89 ± 11.2	5.54 ± .5	34.1 ± 3.4	125.85 ± 16.7
Dicella nucifera	497 ± 80	135.95 ± 31.6	3.77 ± .5	2.53 ± .6	113.49 ± 18.4
Echinopterys eglandulosa[a]	365 ± 45	81.31 ± 13.4	5.57 ± .5	5.16 ± 1.1	169.90 ± 16.6
Echinopterys setosa[a]	298 ± 39	63.01 ± 10.9	5.37 ± .5	.67 ± .2	115.37 ± 19.6
Heladena multiflora[a]	1028 ± 114	91.78 ± 12.9	4.05 ± .7	5.56 ± 1.1	117.94 ± 11.7
Henleophytum echinatum[a]	631 ± 108	123.18 ± 31.8	4.68 ± .4	.98 ± .2	175.8 ± 42.2
Hiptage benghalensis	500 ± 58	157.84 ± 30.3	4.64 ± .6	17.38 ± 3.6	297.81 ± 49.9
Malpighia glabra	155 ± 36	41.1 ± 41.1	3.9 ± .4	8.03 ± 1.8	94.96 ± 17.01
Niedenzuella stannea	952 ± 100	88.6 ± 10.6	4.29 ± .5	1.86 ± .4	120 ± 27.3
Thryallis longifolia[a]	865 ± 85	89.67 ± 28.6	5.32 ± .5	.64 ± .1	170.86 ± 29.6
Tetrapterys schiedeana	838 ± 69	59.11 ± 6.2	3.58 ± .5	1.06 ± .3	63.86 ± 9.2
Tristellateia australasiae[a]	478 ± 104	95.85 ± 15.7	4.22 ± .5	2.01 ± .3	153.32 ± 39.3

Note. Mean and standard deviation for each character are shown. NA = not available.
[a] Belongs to the Bunchosia clade.

includes 154 species representing the main clades recognized in Malpighiaceae (Davis and Anderson 2010) and 13 taxa from Malpighiales and Saxifragales as the outgroup. We pruned the main tree to 16 tree tips, including all the members available of the Bunchosia clade (11 tips) and its sister clade (five tips) using the drop.tip function from the phytools R package (ver. 2.3-1; Revell 2024).

We estimated the character transition rates and selected the best-fit model (either equal rates or all rates different) for each character using a likelihood ratio test and the Akaike information criterion (fitMk function in phytools ver. 2.3-1; Revell 2024). Using the best-fit model (table A1 [tables A1–A3 are available online]), we reconstructed the evolutionary history of each character with a stochastic mapping approach (Bollback 2006). We ran 500 iterations using the make.simmap function and summarized the results (Revell 2024). Each character history was visualized on the pruned tree, with posterior probabilities at nodes displayed using the plotSimmap function in phytools (Revell 2024).

For continuous characters, we use the fastAnc function of phytools (ver. 2.3-1) with a maximum likelihood approach (Revell 2024) to estimate the ancestral states at nodes. We also calculate variance and 95% confidence intervals for each node. The contMap function was used to visualize the state reconstruction (Revell 2024).

Taking habit data from the Bunchosia clade from Quintanar-Castillo et al. (2025; table 3), we conducted a Pagel correlation test (Pagel 1994) to assess whether the habit of Bunchosia clade members evolved in correlation with biphasic wood development and vessel dimorphism. This analysis was performed using the fit.pagel function in phytools (Revell 2024; table A2). Additionally, we calculated phylogenetic signals for each continuous character in the pruned tree, using Pagel's λ (Pagel 1999) with the phylosig function in phytools (table A3; Revell 2024). All analyses were conducted in R (R Core Development Team 2021). The database and scripts are available at https://doi.org/10.5281/zenodo.16763921.

Results

Wood and Bark Evolution in the Bunchosia Clade

The anatomical characteristics shared by all the genera in the clade are growth rings delimited by radially flattened fibers (fig. 1*A*); oval and circular vessels (fig. 1*A*, 1*B*, 1*D*); a simple perforation plate (fig. 1*E*); intervascular pits alternate and vestured (fig. 1*F*); axial parenchyma diffuse, diffuse in aggregates, and scanty to vasicentric (fig. 1*D*) or banded and heterocellular rays, one to three cells wide (fig. 1*G*), with procumbent cells and one or two marginal rows of square to upright cells (fig. 1*H*); and prismatic crystals in axial or radial parenchyma of the wood (fig. 1*C*, 1*J*). In phloem, there are always druses, mainly in axial parenchyma (fig. 1*K*), except for *Heladena*, which has prismatic crystals instead of druses in phloem; sclerenchyma is composed of sclereids, mainly in clusters (fig. 1*L*, 1*M*). As for lianas, they present vessel dimorphism and biphasic development where vessels are arranged in radial multiples in the self-supporting or the initial phase and change their arrangement in the climbing phase; the rays are heterocellular mixed (fig. 1*I*).

Table 3

Species and Habit of the Bunchosia Clade Examined for Anatomical Descriptions

Species	Habit
Bunchosia argentea	Tree
Bunchosia armeniaca	Tree
Bunchosia elliptica	Tree
Bunchosia glandulifera[a]	Tree
Bunchosia linearifolia	Tree
Bunchosia macilenta[a]	Tree
Bunchosia maritima[a]	Tree
Bunchosia montana[a]	Tree
Bunchosia nitida[a]	Tree
Bunchosia polystachia[a]	Tree
Dicella nucifera[a]	Liana
Echinopterys eglandulosa[a]	Climbing shrub
Echinopterys setosa[a]	Shrub
Heladena multiflora[a]	Liana
Henleophytum echinatum[a]	Liana
Hiptage benghalensis[a]	Liana
Malpighia glabra[a]	Tree
Niedenzuella stannea[a]	Liana
Tetrapterys schiedeana[a]	Liana
Thryallis brachystachys	Climbing shrub
Thryallis longifolia[a]	Climbing shrub
Thryallis laburnum	Climbing shrub
Tristellateia australasiae[a]	Liana
Tristellateia greveana	Liana

[a] Used in phylogenetic comparative methods.

Biphasic development in wood. Wood development, particularly that of climbing plants, may be marked by a juvenile self-supporting phase with a change in wood arrangement in the adult stages. These differences in the development of wood identify it as biphasic wood (fig. 2*A*). The reconstruction of the biphasic development in wood shows that the presence of this trait is the most likely ancestral condition (fig. 2*C*), with a loss in the most recent common ancestor of the self-supporting genus *Bunchosia* (fig. 2*B*), and is maintained in the rest of the genera of the clade. Correlation analysis showed that biphasic wood development is related to habit ($P = 0.0786$; see table A2), whereas self-supporting species lack this condition (fig. 2*B*) and climbing species do manifest these changes in the development of wood.

Vessel dimorphism. Vessel dimorphism is a condition in wood where wider vessels are associated with narrower vessels (fig. 3*A*). Reconstruction for this trait shows that this condition was the most likely state in the ancestral node of the clade (fig. 3*C*), lost in only *Bunchosia*. Vessel dimorphism was maintained in all other genera of the clade. Correlation analysis between this character and the habit showed that there is no dependence between these traits ($P = 0.1351$; see table A2), that is, the presence of dimorphism in vessels is not related to a specific habit.

Porosity. Wood porosity within the Bunchosia clade can be diffuse or semiring porous (fig. 4*C*, 4*D*). Reconstruction for this trait shows that diffuse porosity was the most likely condition in the most recent common ancestor of the Bunchosia clade (fig. 4*A*), with two independent losses (fig. 4*A*). Semiring porosity is a derived state present in only *Echinopterys* and

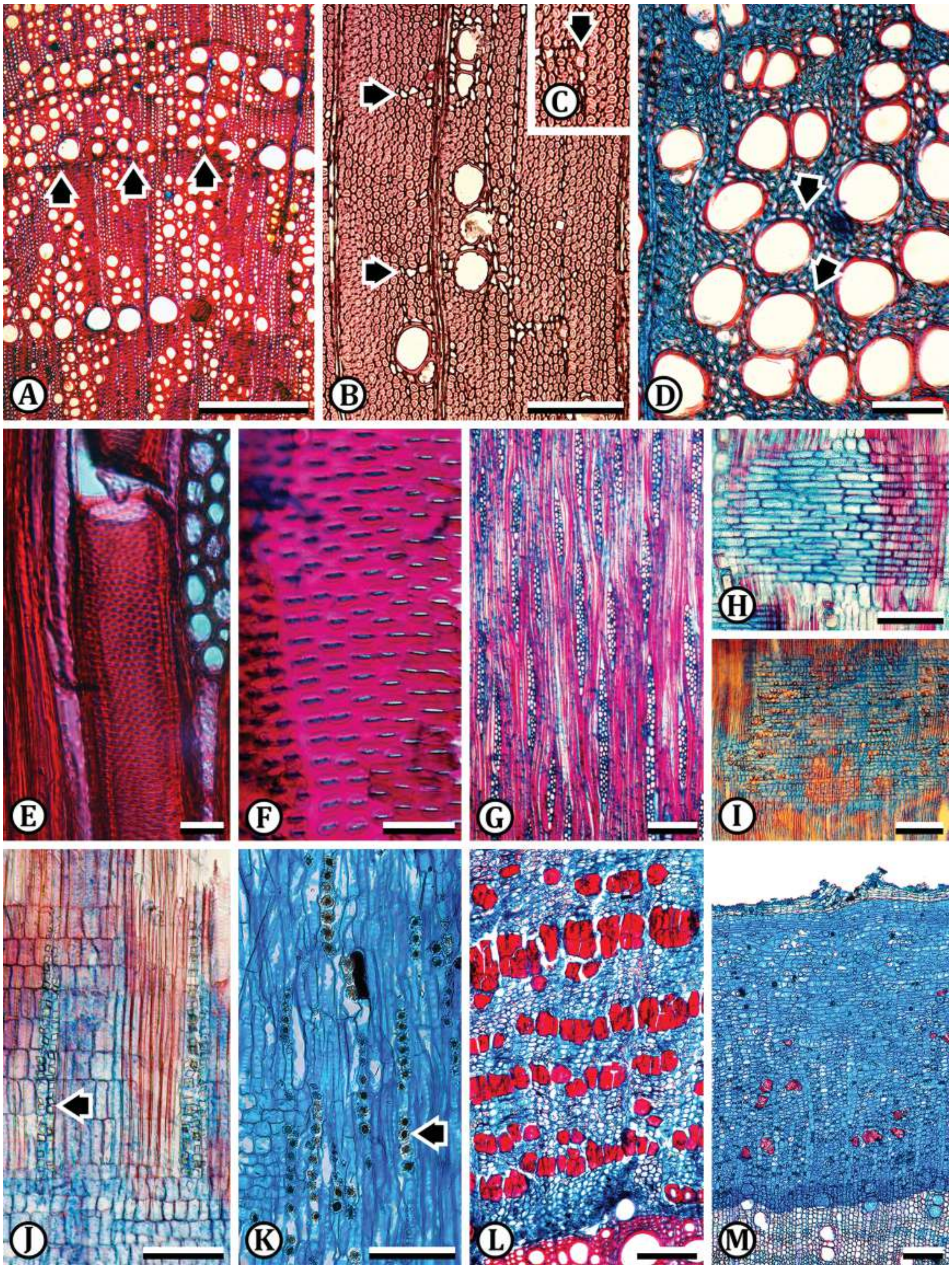

Fig. 1 General aspects of wood and bark in the Bunchosia clade. *A–D*, Transverse section. *A*, *Thryallis brachystachys*. Growth rings are delimited by radially flattened fibers (arrows) and, in this species, by semiring porosity. The vessels are round to oval. *B*, *C*, *Bunchosia nitida*. *B*, Diffuse to diffuse-in-aggregates apotracheal parenchyma (arrows). *C*, Detail of a prismatic crystal in ray parenchyma (arrow). *D*, *Tristellateia greveana*; scanty paratracheal parenchyma (arrows). *E–G*, Tangential section. *E*, *Bunchosia glandulifera*; simple perforation plate. *F*, *Henleophytum echinatum*; alternate, oval, and vestured intervascular pits. *G*, *Bunchosia argentea*; heterocellular rays, one to three cells wide. *H–K*, Radial section. *H*, *Bunchosia argentea*; rays with a body of procumbent cells and a marginal row of square to upright cells. *I*, *Echinopterys setosa*; rays with mixed procumbent, upright, and square cells. *J*, *Heladena multiflora*; prismatic crystals in the axial parenchyma of wood. *K*, *Bunchosia montana*; druses in the axial parenchyma of phloem. *L*, *M*, Transverse section. *L*, *Thryallis brachystachys*; sclereids are in clusters. *M*, *Bunchosia polystachia*; sclereids diffuse in small to large clusters, almost forming a stratified phloem. Scale bars = 500 μm in *A*; 200 μm in *B*, *C*, *F–H*, *K*, *L*; 100 μm in *I*, *J*; 50 μm in *D*; 25 μm in *E*.

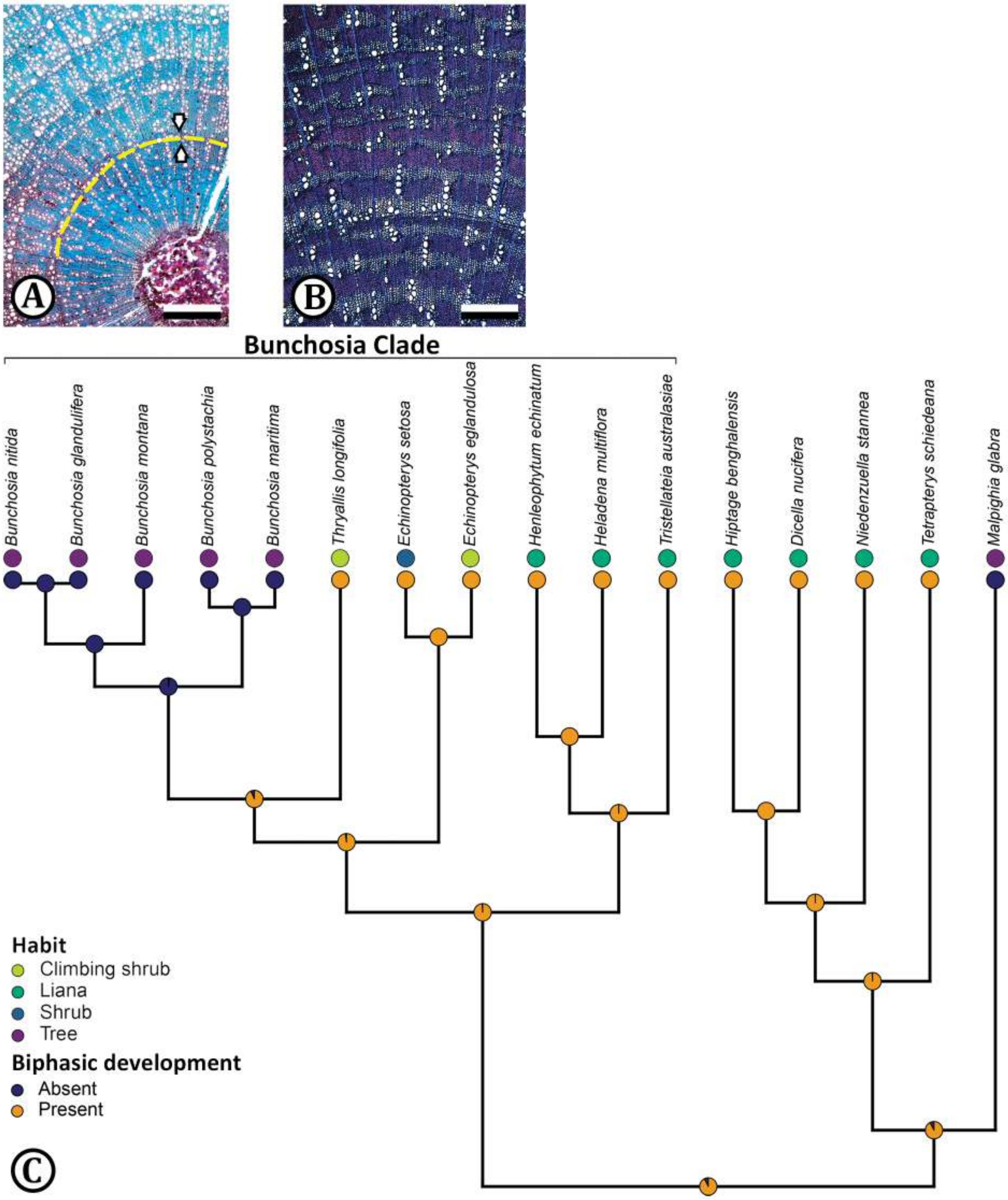

Fig. 2 Biphasic wood development in the Bunchosia clade. *A*, *B*, Transverse section. *A*, *Thryallis longifolia*. Wood with biphasic wood development. The yellow dotted line shows the change between the self-supporting phase and the climbing phase. In the self-supporting phase, the vessels have an arrangement in multiple long radials, while in the climbing phase, the arrangement of vessels changes to tangential bands or a dendritic pattern. *B*, *Bunchosia montana*; wood without biphasic growth. *C*, Ancestral character state reconstruction of biphasic wood development in the Bunchosia clade. Scale bars = 1 mm in *A*; 500 μm in *B*.

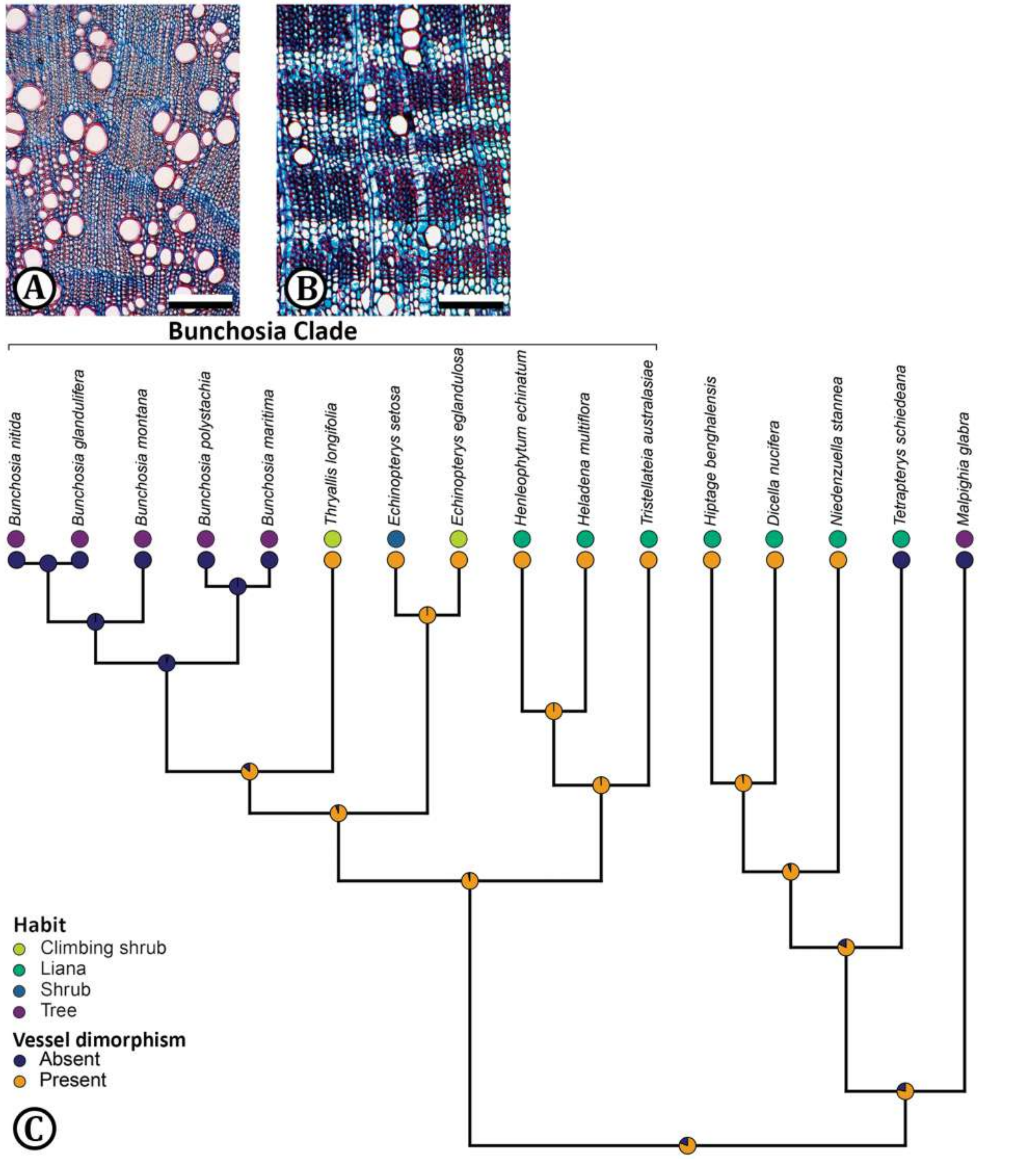

Fig. 3 The presence of vessel dimorphism in the Bunchosia clade. *A*, *B*, Transverse section. *A*, *Heladena multiflora*; wood with wide vessels accompanied by narrow vessels (vessel dimorphism). *B*, *Bunchosia maritima*; wood with nondimorphic vessels. *C*, Ancestral character state reconstruction of vessel dimorphism in the Bunchosia clade. Scale bars = 200 μm in *A*, *B*.

Thryallis (fig. 4*E*, 4*G*), but even the most recent ancestors of these genera had diffuse porosity (fig. 4*A*).

Vessel arrangement and grouping. There are four distinct types of vessel arrangements in the Bunchosia clade: vessels in a diffuse arrangement (fig. 4*C*), vessels with a dendritic tendency (fig. 4*D*), vessels in a radial pattern (fig. 4*E*), and vessels forming tangential bands (fig. 4*F*). The most likely ancestral condition is a diffuse pattern (fig. 4*B*), which independently changes to a dendritic pattern in the ancestral nodes of both subclades (fig. 4*B*). There are subsequent changes to a radial pattern in *Tristellateia*

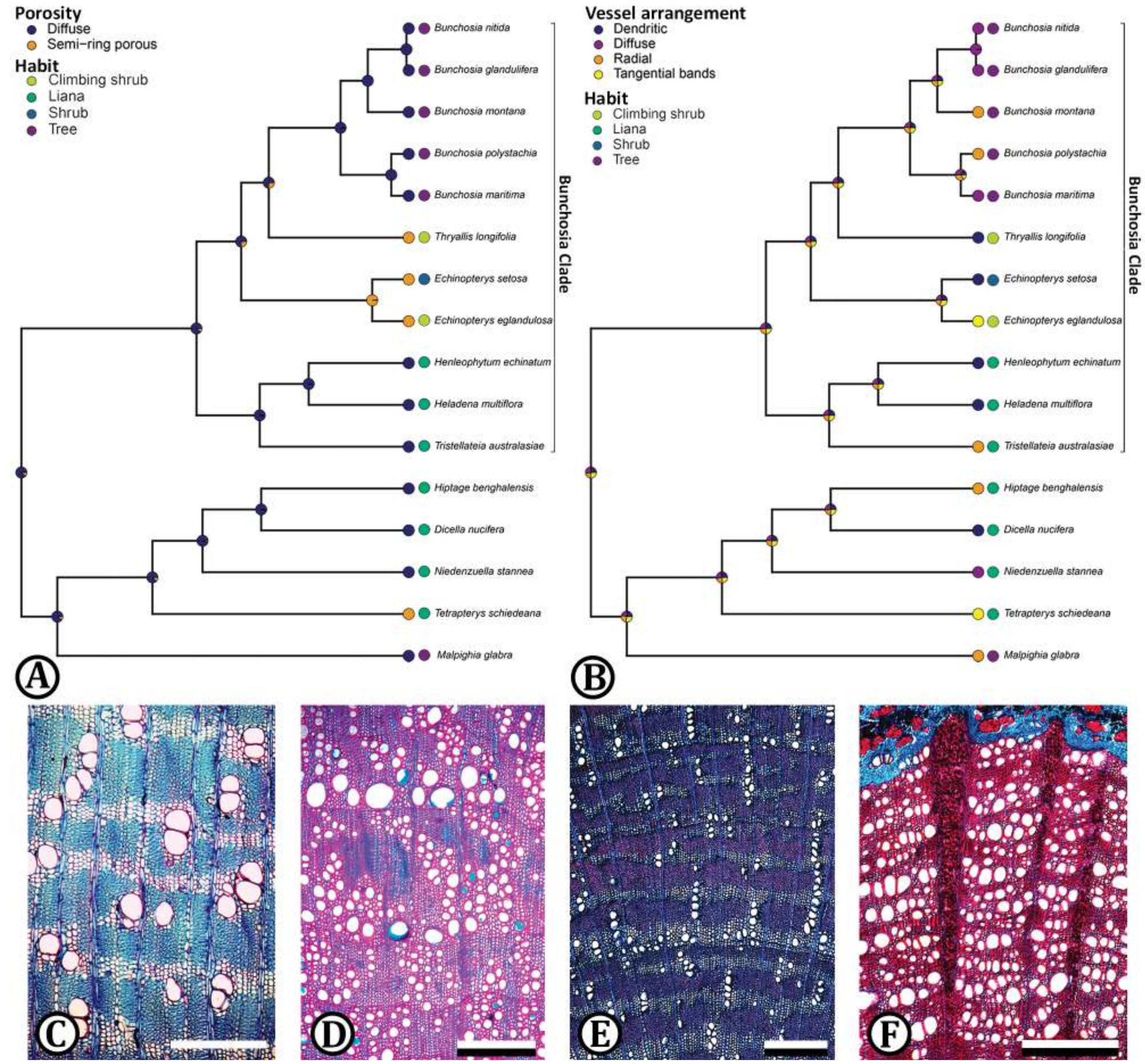

Fig. 4 Porosity and vessel arrangements in the Bunchosia clade. *A*, Ancestral character state reconstruction of porosity in the Bunchosia clade. *B*, Ancestral character state reconstruction of vessel arrangement. *C–F*, Transverse view. *C*, *Bunchosia argentea*; diffuse porosity and diffuse pattern of vessels. *D*, *Thryallis longifolia*; semiring porosity and vessels in a dendritic pattern. *E*, *Bunchosia montana*; vessels in long radial multiples. *F*, *Echinopterys eglandulosa*; vessels in tangential bands, interrupted by the rays. Scale bars = 500 μm in *C–F*.

and in *Bunchosia* and to only tangential bands in *Echinopterys eglandulosa*. The diffuse pattern appears independently in some species of *Bunchosia*.

The Bunchosia clade has two main types of vessel grouping: long radial multiples of greater than four vessels (fig. 5*C*) and solitary and short radial multiples of two or three vessels (fig. 5*D*, 5*E*). Long radial multiples are shown to be the most likely ancestral condition but with at least three subsequent changes to solitary and short radials multiples (fig. 5*A*). A change to solitary and short radial multiples occurred in the *Heladena*/*Henleophytum*/*Tristellateia* subclade, the latter being the only genus that maintained the plesiomorphic condition of radial multiples (fig. 5*A*). The other two changes occurred independently in *Echinopterys* and in the ancestral node of *Bunchosia* and *Thryallis*, with some *Bunchosia* species maintaining radial multiples (fig. 5*A*).

Regarding vessel frequency evolution, this trait varies throughout the evolution of the clade. In the *Heladena*/*Henleophytum*/*Tristellateia* subclade, there is an increase in vessel frequency (fig. 5*B*). On the other hand, in the *Bunchosia*/*Thryallis*/*Echinopterys* subclade, vessel frequency decreases in the self-supporting genera, particularly in *Bunchosia* (fig. 5*B*), and increases again only in the climbing genus *Thryallis*.

Vessel width in the Bunchosia clade varies among the habit types of its members, and vessels with a diameter less than 100 μm is the most likely ancestral condition for the clade

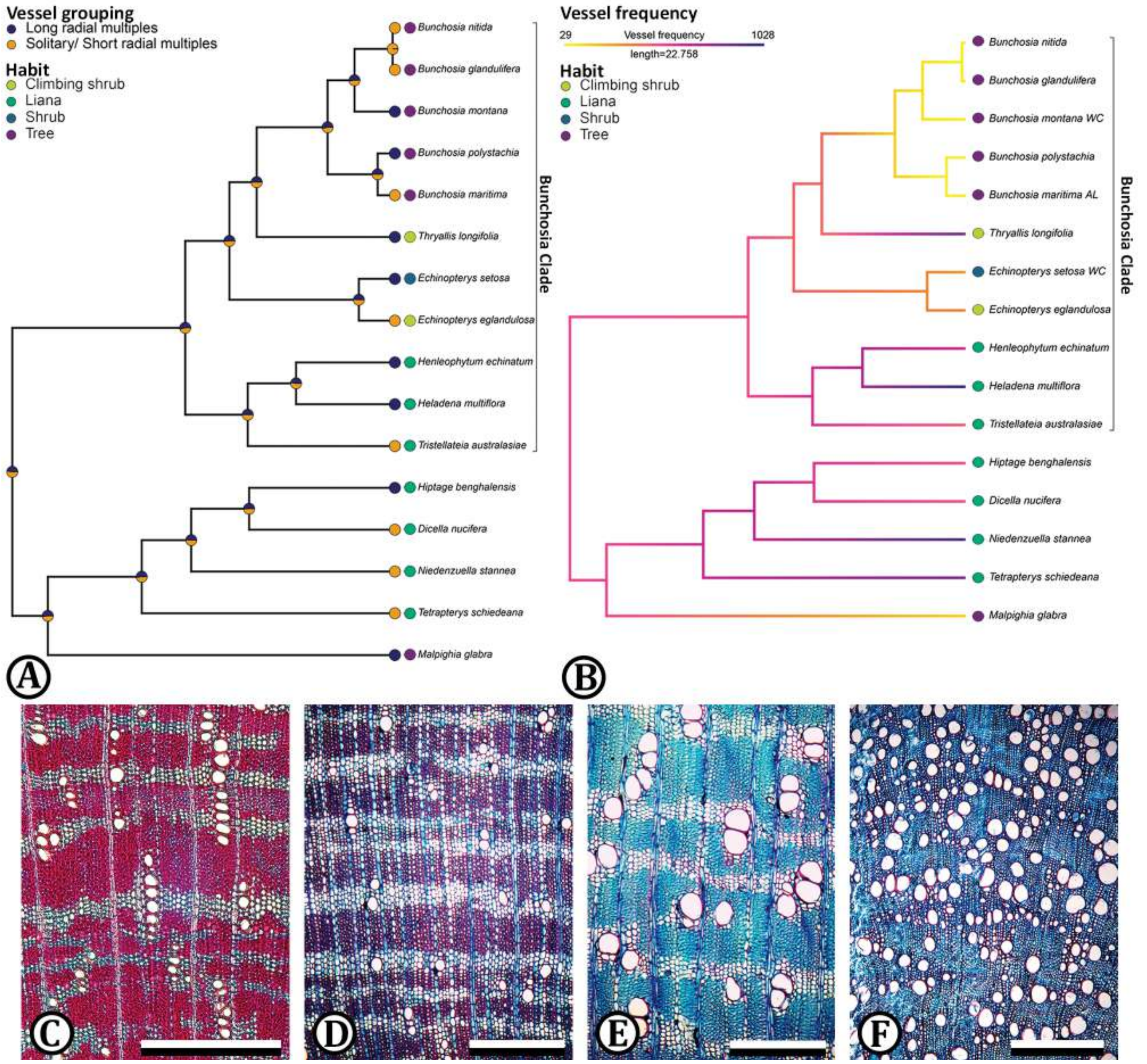

Fig. 5 Vessel grouping and frequency in the Bunchosia clade. *A*, Ancestral character state reconstruction of vessel grouping in the Bunchosia clade. *B*, Ancestral character state reconstruction of vessel frequency. *C–F*, Transverse view. *C*, *Thryallis longifolia*; vessels in long radial multiples. *D*, *Bunchosia maritima*; vessels are solitary or in short radials. *E*, *Bunchosia argentea*; low vessel frequency per millimeters squared. *F*, *Heladena multiflora*; higher vessel frequency per millimeters squared. Scale bars = 500 μm in *C–F*.

(fig. 6*A*). In the *Bunchosia*/*Thryallis*/*Echinopterys* subclade, the diameter reduces in *Bunchosia* (fig. 6*A*, 6*C*) and is maintained in *Thryallis* and in *Echinopterys*. In the *Heladena*/*Henleophytum*/*Tristellateia* subclade, there is an increase in vessel diameter (fig. 6*A*, 6*D*).

As for the intervessel pit diameter, Malpighiaceae typically have minute pits, and in the Bunchosia clade, this is the most likely ancestral condition (pits narrower than 5 μm; fig. 6*B*). This pit size is maintained in the *Heladena*/*Henleophytum*/*Tristellateia* subclade (fig. 6*B*, 6*F*), while in the *Bunchosia*/*Thryallis*/*Echinopterys* subclade, there is an increase in pit diameter, particularly in *Bunchosia* (fig. 6*B*, 6*E*).

Axial parenchyma. Apotracheal parenchyma in the Bunchosia clade may be absent, diffuse (fig. 7*C*), or diffuse-in-aggregates (fig. 7*D*). Diffuse axial parenchyma is the most likely ancestral condition in the clade (fig. 7*A*), a condition that is maintained in both subclades, but changes independently twice, once in *Henleophytum* and once in *Heladena*, being absent or in diffuse-in-aggregates, respectively. The second change occurs in *Bunchosia* and in *Thryallis*, where it also changes to being diffuse-in-aggregates or being absent, respectively.

Paratracheal parenchyma can be scanty (fig. 7*F*), vasicentric (fig. 7*E*, 7*F*), or confluent (fig. 7*E*). The analyses showed that the scanty parenchyma is the most likely ancestral condition

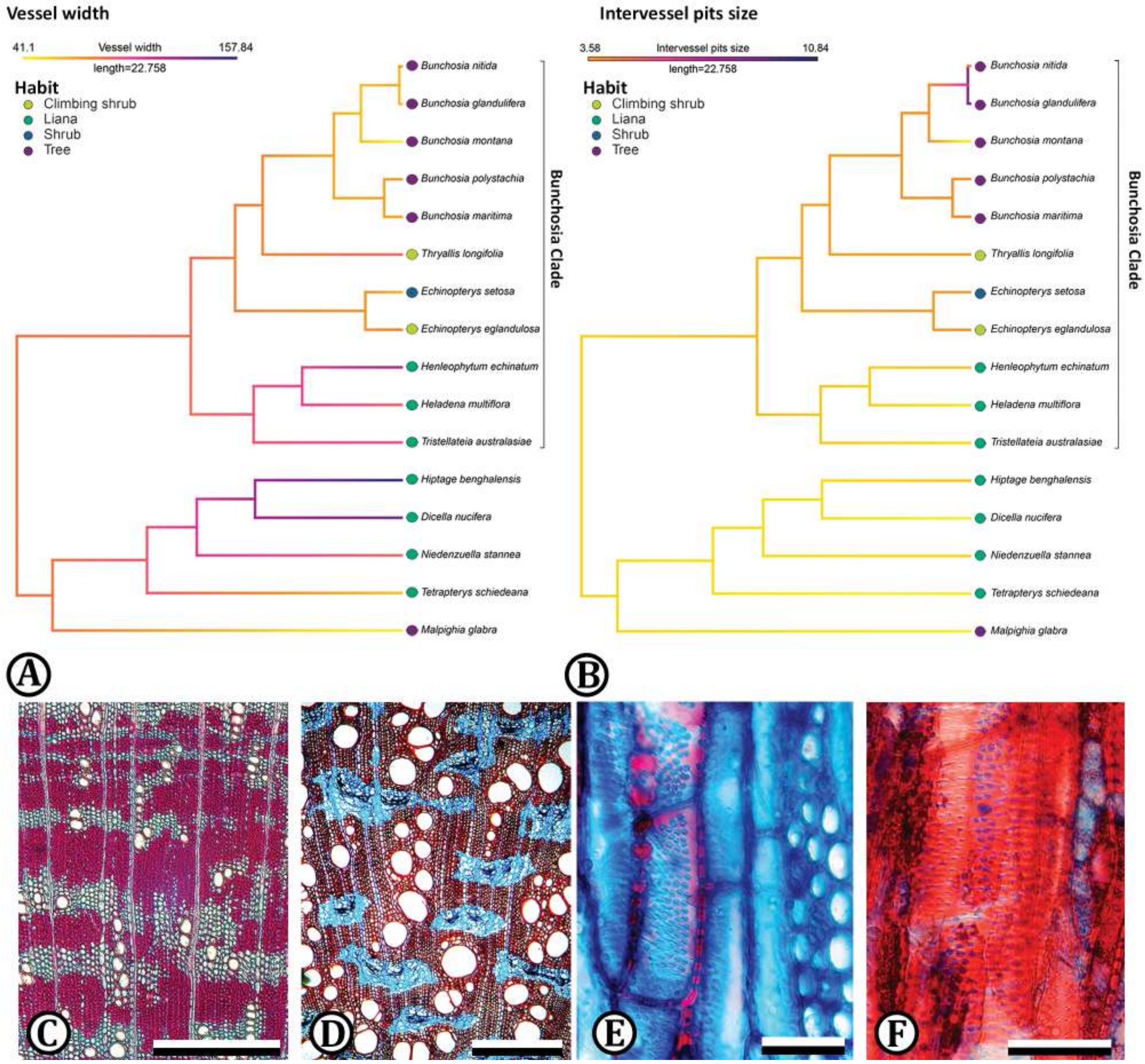

Fig. 6 Vessel width and intervessel pit size in the Bunchosia clade. *A*, Ancestral character state reconstruction of vessel width in the Bunchosia clade. *B*, Ancestral character state reconstruction of intervessel pit size. *C–D*, Transverse view. *C*, *Bunchosia montana*; vessels with narrow diameters. *D*, *Henleophytum echinatum*; vessels with a wide diameter. *E–F*, Tangential view. *E*, *Bunchosia argentea*; wide diameter pits. *F*, *Tristellateia australasiae*; narrow diameter pits. Scale bars = 500 μm in *C*, *D*; 50 μm in *E*, *F*.

(fig. 7*B*), maintained throughout the evolution of the clade. Three independent changes occurred in the group: two to a confluent arrangement in *Bunchosia* and in *Heladena* and one to a vasicentric distribution in *Tristellateia*.

In turn, banded parenchyma may be present in a marginal arrangement (fig. 8*D*), in narrow bands (fig. 8*E*), or in wide bands (fig. 8*F*) or may be absent. The absence of banded parenchyma appears to be the most likely ancestral condition (fig. 8*A*) and is maintained only in the *Heladena*/*Henleophytum*/*Tristellateia* subclade. The appearance of bands occurs independently in the *Bunchosia*/*Thryallis*/*Echinopterys* subclade and in *Heladena*.

Parenchyma proportion varies among the Bunchosia clade, with less than 10% of wood occupancy appearing to be the most likely ancestral condition (fig. 8*B*). This proportion is maintained in the lianescent of the *Heladena*/*Henleophytum*/*Tristellateia* subclade (fig. 8*B*) and increases in the *Bunchosia*/*Thryallis*/*Echinopterys* subclade, being more evident in the self-supporting genus *Bunchosia* (fig. 8*B*).

Fibers. Gelatinous fibers are a trait observed in a few climbing genera. The absence of gelatinous fibers is the most likely condition in the common ancestor of the clade (fig. 9*A*). Gelatinous fibers develop in the ancestral node of the *Henleophytum*/*Heladena*/*Tristellateia* subclade and are lost in *Heladena*. While

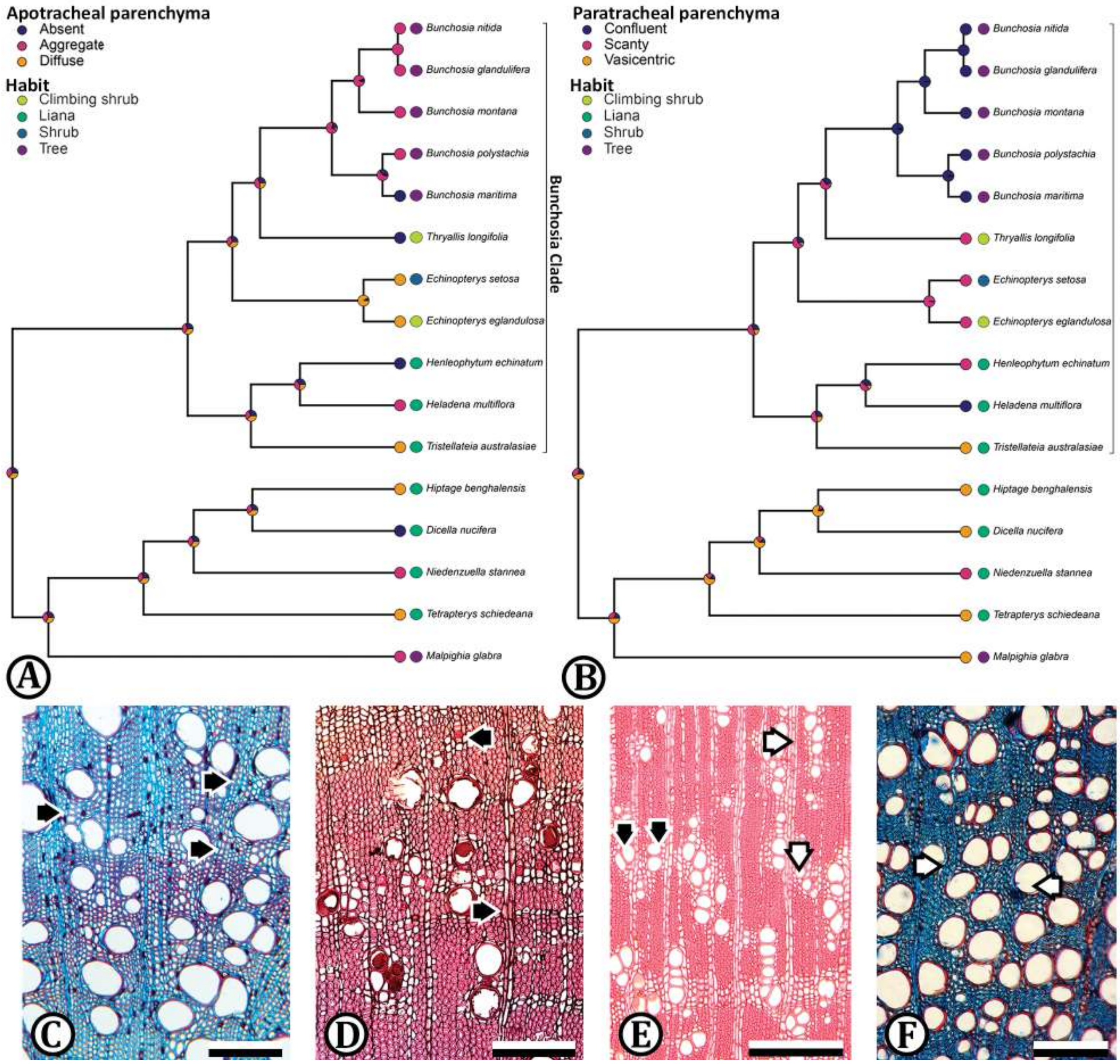

Fig. 7 Apotracheal and paratracheal parenchyma in the Bunchosia clade. *A*, Ancestral character state reconstruction for apotracheal parenchyma. *B*, Ancestral character state reconstruction for paratracheal parenchyma. *C–F*, Transverse view. *C*, *Tristellateia australasiae*; diffuse axial parenchyma (black arrows). Scanty axial parenchyma is associated with vessels. *D*, *Bunchosia nitida*; aggregate axial parenchyma (white arrows). *E*, *Bunchosia linearifolia*; vasicentric (white arrows) and vasicentric confluent (black arrows) axial parenchyma. *F*, *Tristellateia greveana*; scanty (white arrows) axial parenchyma. Scale bars = 200 μm in *C–F*.

in the *Bunchosia*/*Thryallis*/*Echinopterys* subclade, gelatinous fibers are absent (fig. 9*C*), and their presence seems to be a derived condition in *Echinopterys* (fig. 9*D*) and in *Thryallis*.

The presence of septate fibers (fig. 9*E*) is likely the ancestral condition in the clade (fig. 9*B*). This condition is maintained throughout the evolution of the group, being lost twice independently in the *Bunchosia* and *Echinopterys* genera.

Rays. Some genera in the Bunchosia clade have interconnected rays. The interconnected rays are characterized as multiseriate rays with long uniseriate marginal portions that interconnect with other rays (fig. 10*E*). The absence of interconnected rays is the most likely ancestral condition in the Bunchosia clade (fig. 10*A*). Its evolution occurred twice independently: once in the *Bunchosia*/*Thryallis*/*Echinopterys* subclade and another time in *Tristellateia* (fig. 10*A*).

In the Bunchosia clade, rays can be of two thickness types: those that are one to three cells wide (narrow rays; fig. 10*F*) and those that are more than four cells (fig. 10*G*) but fewer than 10 cells wide (wide rays). Narrow rays are the most likely ancestral condition in the clade (fig. 10*B*), and this is maintained at the ancestral nodes of each subclade. This condition is lost twice independently in *Echinopterys* and in *Thryallis*, where the ray width increases (fig. 10*B*).

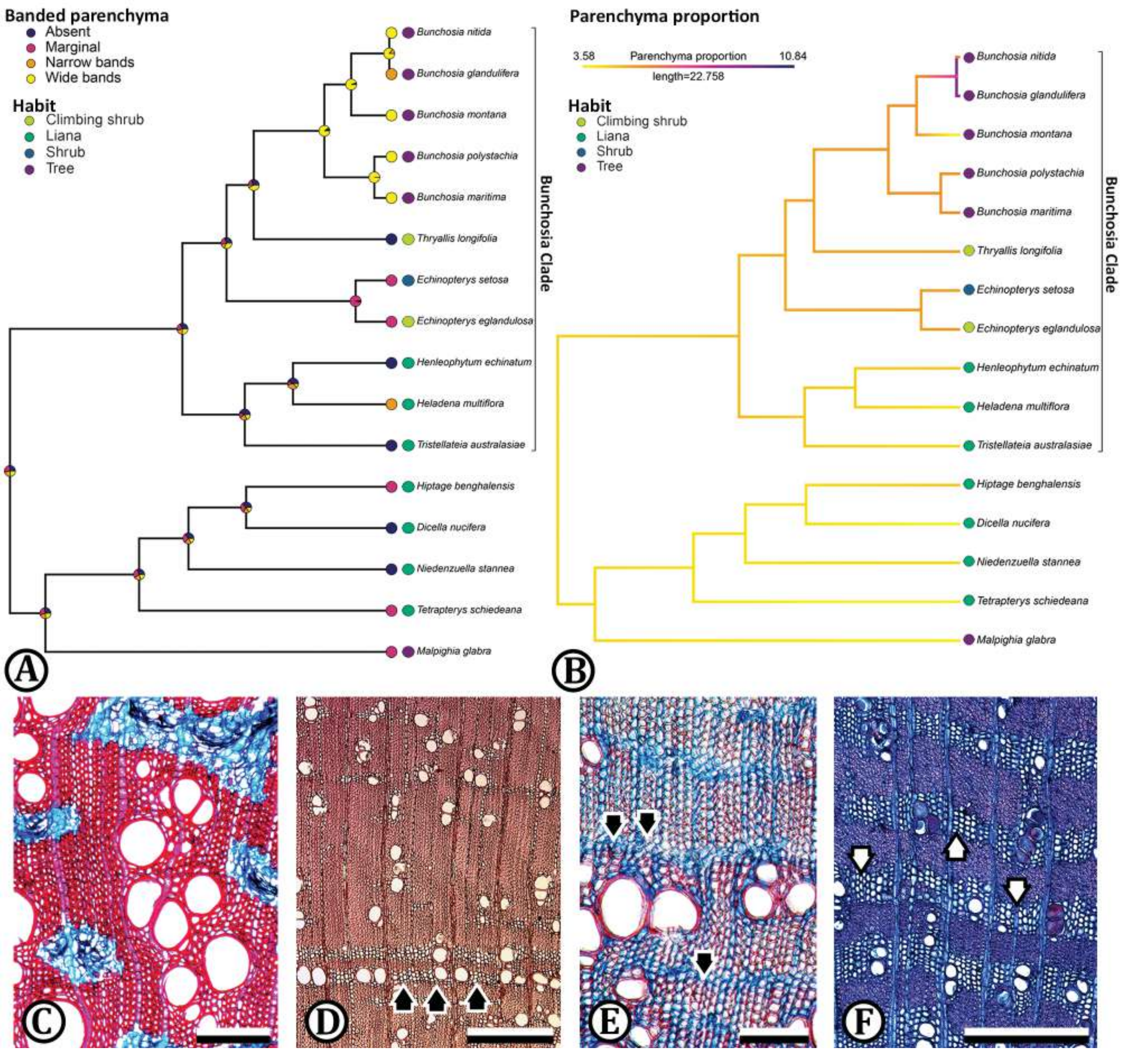

Fig. 8 Banded axial parenchyma and axial parenchyma proportions in the Bunchosia clade. *A*, Ancestral character state reconstruction of banded axial parenchyma. *B*, Ancestral character state reconstruction of parenchyma proportion. *C–F*, Transverse view. *C*, *Henleophytum echinatum*; banded parenchyma absent and low proportion of axial parenchyma. *D*, *Bunchosia nitida*; marginal parenchyma present (arrows). *E*, *Heladena multiflora*; narrow bands of axial parenchyma (arrows). *F*, *Bunchosia montana*; wide bands of axial parenchyma. Scale bars = 200 μm in *C*; 500 μm in *D*, *F*; 100 μm in *E*.

Furthermore, rays in the Bunchosia clade are heterocellular and may be composed of procumbent cells with one or more marginal rows of square to upright cells (fig. 10*H*) or mixed square, upright, and procumbent cells (fig. 10*I*). Heterocellular mixed rays are the most likely ancestral condition in the clade (fig. 10*C*), and it is maintained along the evolution of the clade. This state changes to heterocellular rays with body procumbent and square to upright marginal rows only in *Bunchosia*.

Mineral inclusions in wood. Prismatic crystals in the axial parenchyma of wood are common in the Bunchosia clade (fig. 11*C*). Their presence is the most likely ancestral condition within the group (fig. 11*A*), maintained throughout the evolutionary history of the group and lost three times independently, in *Echinopterys*, *Thryallis*, and *Tristellateia*.

Prismatic crystals in wood ray parenchyma may be absent (fig. 11*D*), may be throughout the ray body (fig. 11*E*), or may be in only the ray marginal rows (fig. 11*F*). The most likely ancestral condition in the Bunchosia clade is the presence of prismatic crystals throughout the ray body, a condition maintained in the ancestral nodes of both subclades (fig. 11*B*). In the *Henleophytum*/*Heladena*/*Tristellateia* subclade, this condition is lost once in the group formed by *Heladena* and *Henleophytum*. In *Bunchosia*,

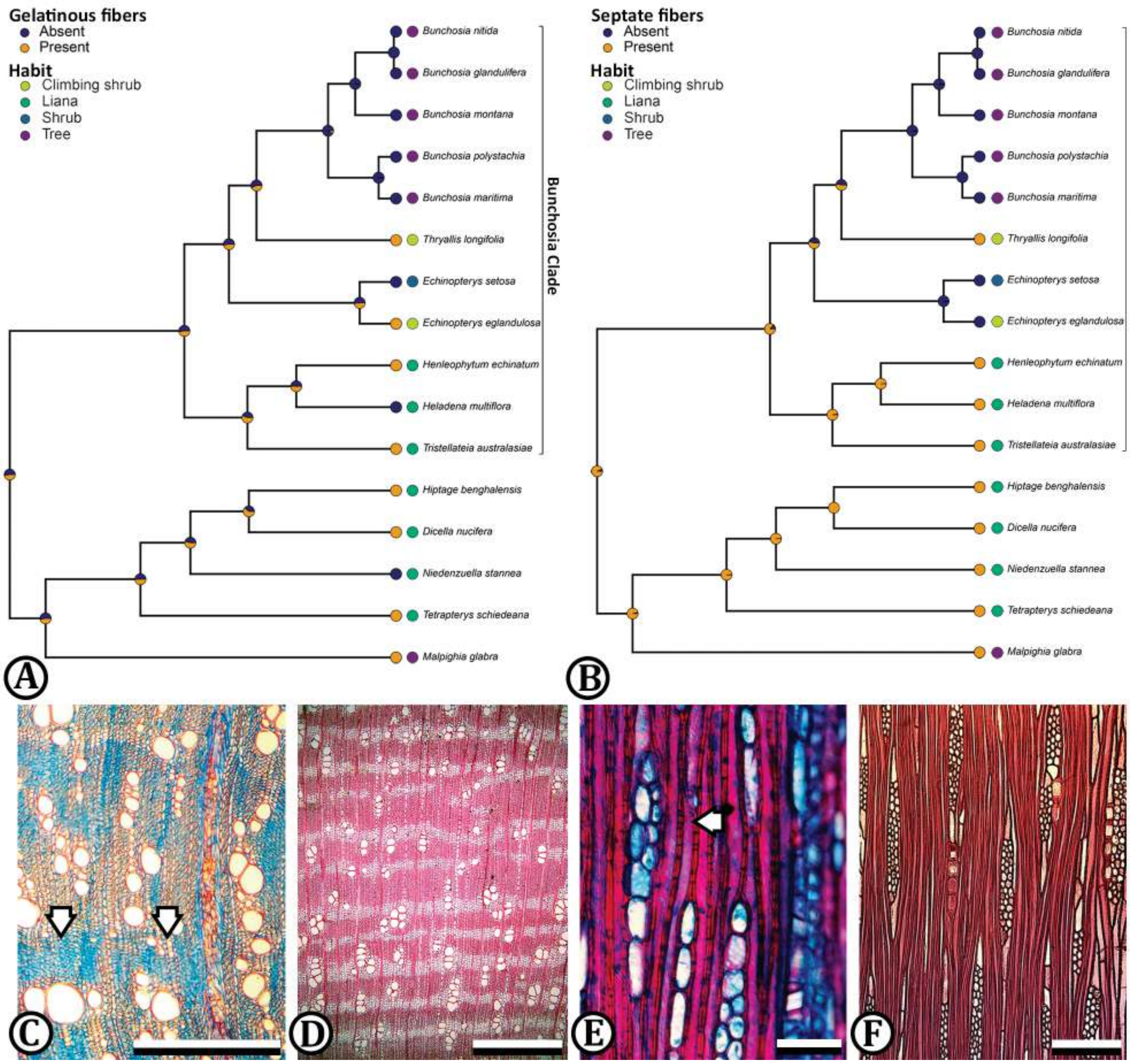

Fig. 9 Gelatinous and septate fibers in the Bunchosia clade. *A*, Ancestral character state reconstruction of gelatinous fibers in the Bunchosia clade. *B*, Ancestral character state reconstruction of septate fibers. *C*, *D*, Transverse view. *C*, *Echinopterys eglandulosa*; gelatinous fibers are present (arrows). *D*, *Bunchosia nitida*; gelatinous fibers are absent. *E*, *F*, Tangential view. *E*, *Henleophytum echinatum*; septate fibers present (arrow). *F*, *Bunchosia nitida*; septate fibers are absent. Scale bars = 500 μm in C, D; 50 μm in E; 200 μm in F.

this condition changes twice independently to crystals in only the ray marginal rows (fig. 11*B*) or is absent altogether.

Bark traits. Sieve tube distribution in the Bunchosia clade may be in clusters (fig. 12*C*, 12*D*) or radial rows (fig. 12*E*, 12*F*). The latter is the derived condition that arises three times independently in *Thryallis*, *Echinopterys*, and *Henleophytum*. While the cluster arrangement is the most likely ancestral state (fig. 12*A*), it is present in most clade members.

The sieve tube area is a variable trait within subclades. In the *Heladena*/*Henleophytum*/*Tristellateia* subclade, the sieve tube area seems to be maintained and to increase slightly (fig. 12*B*). On the other hand, in the *Bunchosia*/*Thryallis*/*Echinopterys* subclade, the sieve tube area decreases in the self-supporting genera, particularly in *Bunchosia* (fig. 12*B*), but increases in the climbing genus *Thryallis* and in *Echinopterys*.

In the Bunchosia clade, druses are a very common crystal type in the phloem, in both axial and ray parenchyma (fig. 13*E*), and may be occasionally restricted to axial parenchyma (fig. 13*D*) or may rarely be absent. Druses restricted to axial parenchyma are the most likely ancestral condition (fig. 13*A*) and are maintained only in *Henleophytum* and in some species of *Bunchosia*. Along with the evolution of the clade, druse distribution is extended to ray parenchyma in almost all extant genera and is lost in only *Heladena*, where prismatic crystals are present instead (fig. 13*C*).

Sclereids arrangement may be in bands (fig. 13*I*), clusters (fig. 13*H*), diffuse (fig. 13*G*), or absent (fig. 13*F*). The most likely

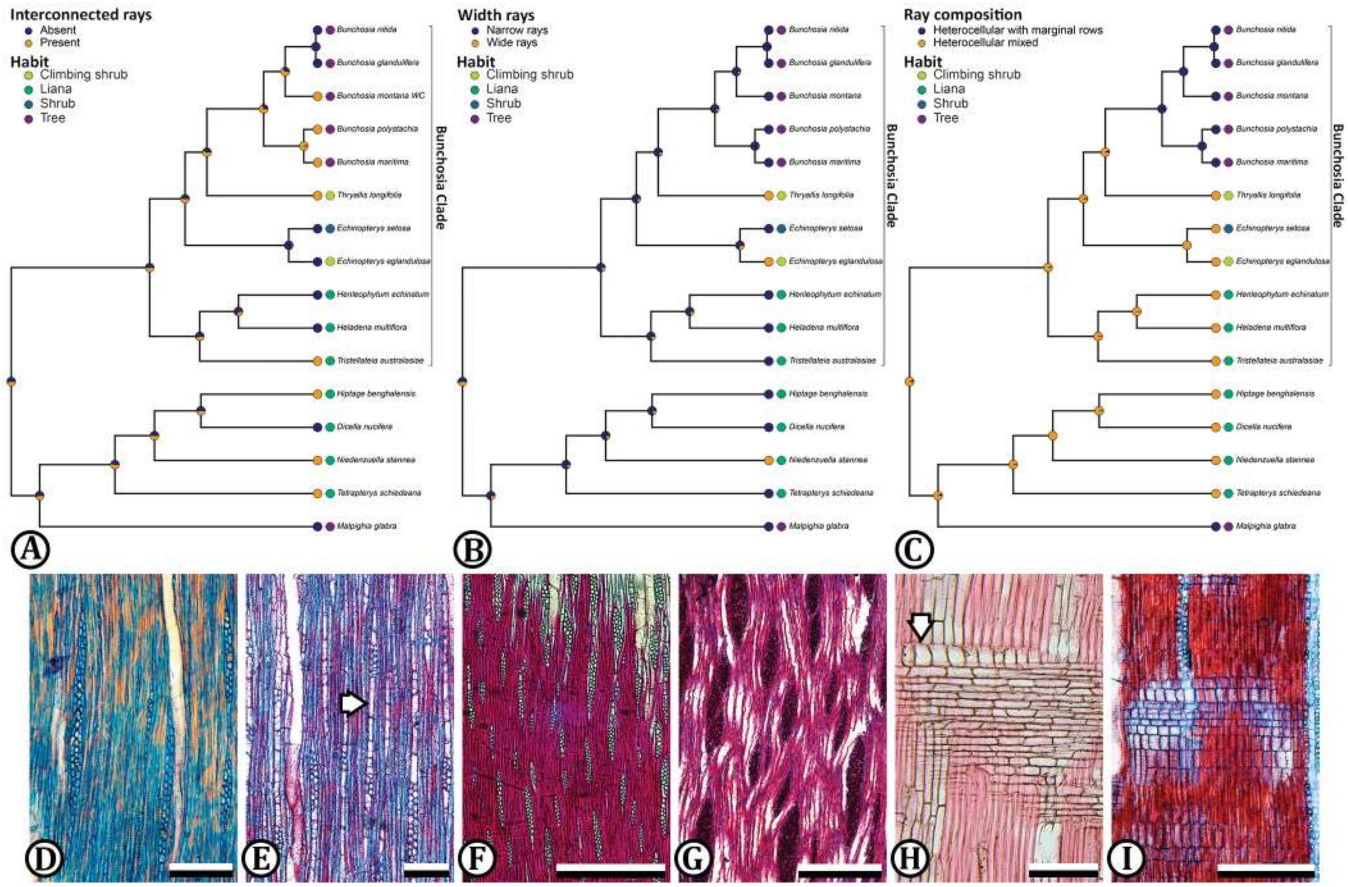

Fig. 10 Ray features in the Bunchosia clade. *A*, Ancestral character state reconstruction for interconnected rays in the Bunchosia clade. *B*, Ancestral state reconstruction of ray widths. *C*, Ancestral character state reconstruction of ray compositions. *D–G*, Tangential view. *D*, *Echinopterys setosa*; rays without connections. *E*, *Bunchosia polystachia*; interconnected rays present (arrow). *F*, *Bunchosia montana*; narrow rays. *G*, *Echinopterys eglandulosa*; multiseriate wide rays. *H*, *I*, Radial view. *H*, *Bunchosia glandulifera*; heterocellular ray with a marginal row of square cells. Arrow indicates the marginal row. *I*, *Henleophytum echinatum*; heterocellular ray mixed. Scale bars = 200 μm in *D*, *E*, *I*; 500 μm in *F*, *G*; 100 μm in *H*.

ancestral condition is sclereids arranged in clusters (fig. 13*B*, 13*I*), which changes to a diffuse arrangement at the ancestral nodes of both subclades and is maintained in most genera. Some species of *Bunchosia* and *Echinopterys* changed to a banded arrangement, whereas *Henleophytum* maintained sclereids in clusters, and only *Heladena* has no sclereids as a derived condition.

Discussion

Wood and Bark Characterization in the Bunchosia Clade

In general, the anatomical traits of the Bunchosia clade align with characteristics previously described for the Malpighiaceae. These include narrower vessels in self-supporting forms and wider vessels in lianas and vessels in short radial multiples (two or three vessels) or forming a conspicuous radial pattern (as in some *Bunchosia* species) with groups of more than five radially oriented cells. Additional traits include simple perforation plates; minute vestured intervascular pits; axial parenchyma that is scanty to vasicentric, banded, or sometimes diffuse; and prismatic crystals in axial and ray parenchyma, frequently in chambers. The rays are typically one to three cells wide, usually biseriate, and heterocellular. Fibers are frequently septate, and gelatinous fibers are not uncommon (Solereder 1908; Record and Hess 1949; Metcalfe and Chalk 1950; León and Williams 2006; Guimarães et al. 2016; Amorim et al. 2017; Cabanillas et al. 2017; Pace et al. 2018; Nagamine-Pinheiro et al. 2021; Quintanar-Castillo et al. 2024; Bueno et al. 2025; Sanches et al. 2025).

Although little is known about the phloem in Malpighiaceae, certain characteristics are notable, including simple and slightly inclined to transverse sieve plates, one or two companion cells per sieve tube element, and rays similar in composition and height to those of the xylem. Rays undergo dilation by both cell expansion and cell division. Additionally, sclereids in the nonconducting phloem and abundant druses in both the conducting and nonconducting phloem have been reported in species of *Banisteriopsis*, *Byrsonima*, *Callaeum*, *Mcvaughia*, and *Stigmaphyllon* (Cabanillas et al. 2017; Pace et al. 2018; Almeida et al. 2019; Bueno et al. 2025).

As previous studies have indicated (Metcalfe and Chalk 1950; Guimarães et al. 2016; Cabanillas et al. 2017; Pace et al. 2018; Bueno et al. 2025; Sanches et al. 2025), two patterns in the distribution of crystal shape are typical in the Malpighiaceae: (1) the Byrsonimoids, a lineage of self-supporting plants that are sister to all other Malpighiaceae (here called core Malpighiaceae),

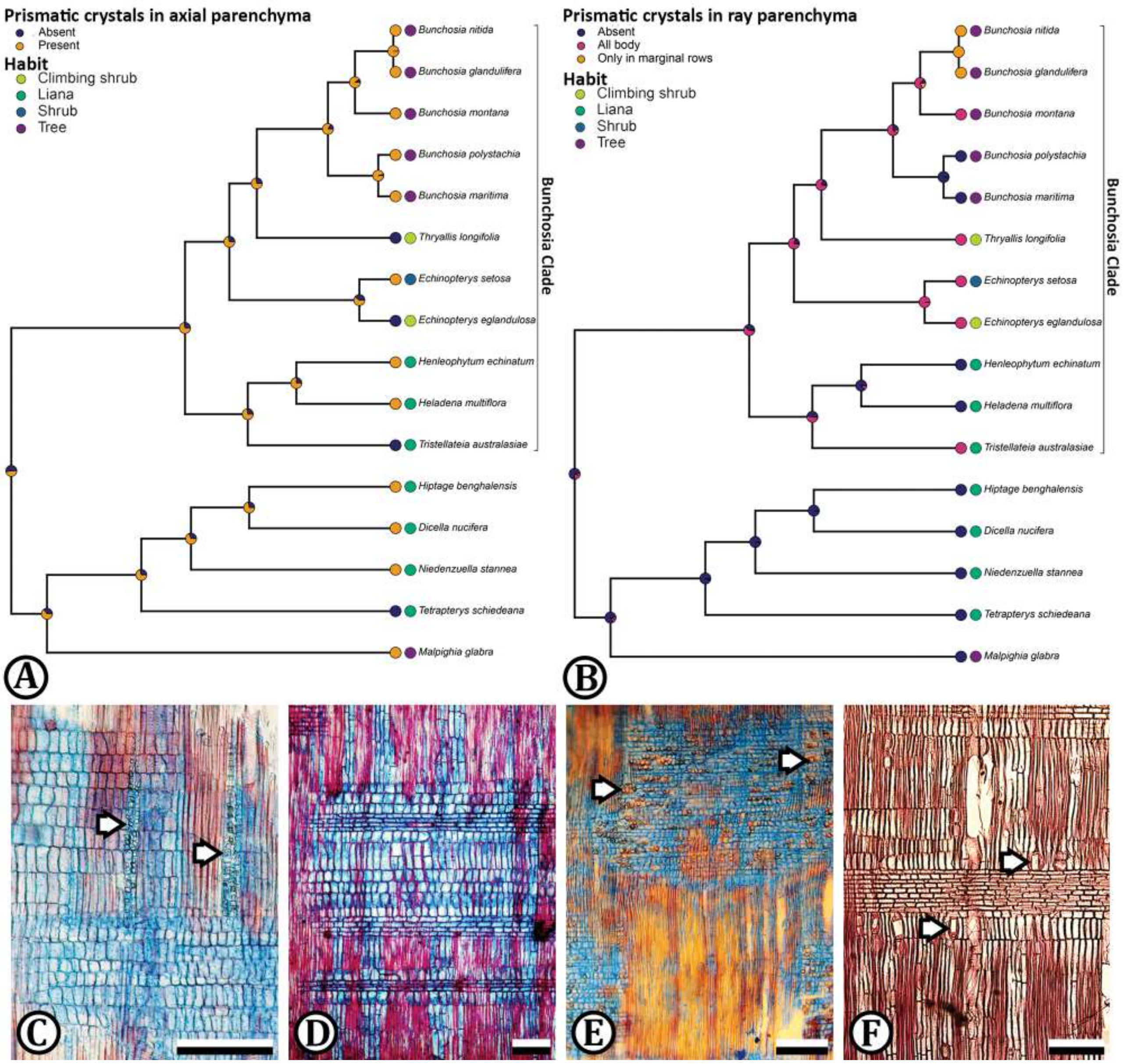

Fig. 11 Prismatic crystals distribution in the Bunchosia clade. *A*, Ancestral character state reconstruction of prismatic crystals in axial parenchyma. *B*, Ancestral character state reconstruction of prismatic crystals in radial parenchyma. *C*, *Heladena multiflora*; prismatic crystals in axial parenchyma series. *D*, *Bunchosia maritima*; prismatic crystals are absent in axial and ray parenchyma. *E*, *Echinopterys setosa*; prismatic crystals are present throughout the ray body. *F*, *Bunchosia nitida*; prismatic crystals are present in only the ray margins. Scale bars = 200 μm in *C*, *E*; 500 μm in *D*, *F*.

contain prismatic crystals in both secondary phloem and xylem (Bueno et al. 2025); in contrast, (2) core Malpighiaceae exhibit prismatic crystals confined exclusively to the axial and ray parenchyma of the wood, while the phloem has only druses. Notably, the presence of prismatic crystals in the phloem of *Heladena* appears to be unique within the core Malpighiaceae and may constitute a synapomorphy for this genus.

Regarding biphasic wood, vessel dimorphism, mixed heterocellular rays, and prismatic crystals throughout the ray body, these traits are characteristic of lianas in the clade and align with the so-called lianescent vascular syndrome (Pace and Angyalossy 2013; Angyalossy et al. 2015). Although abundant axial parenchyma is also considered part of this syndrome, the lianas in the Bunchosia clade do not exhibit this trait prominently. Only *Heladena* and *Henleophytum* have nonlignified axial parenchyma. As Metcalfe and Chalk (1950) described, low axial parenchyma abundance is characteristic of many members in the family, regardless of their habit.

While gelatinous fibers are not listed as part of the lianescent vascular syndrome, they have been associated with stems that tend to twist, such as those of lianas (Bowling and Vaughn 2009; Chery et al. 2022). This characteristic has also been reported in

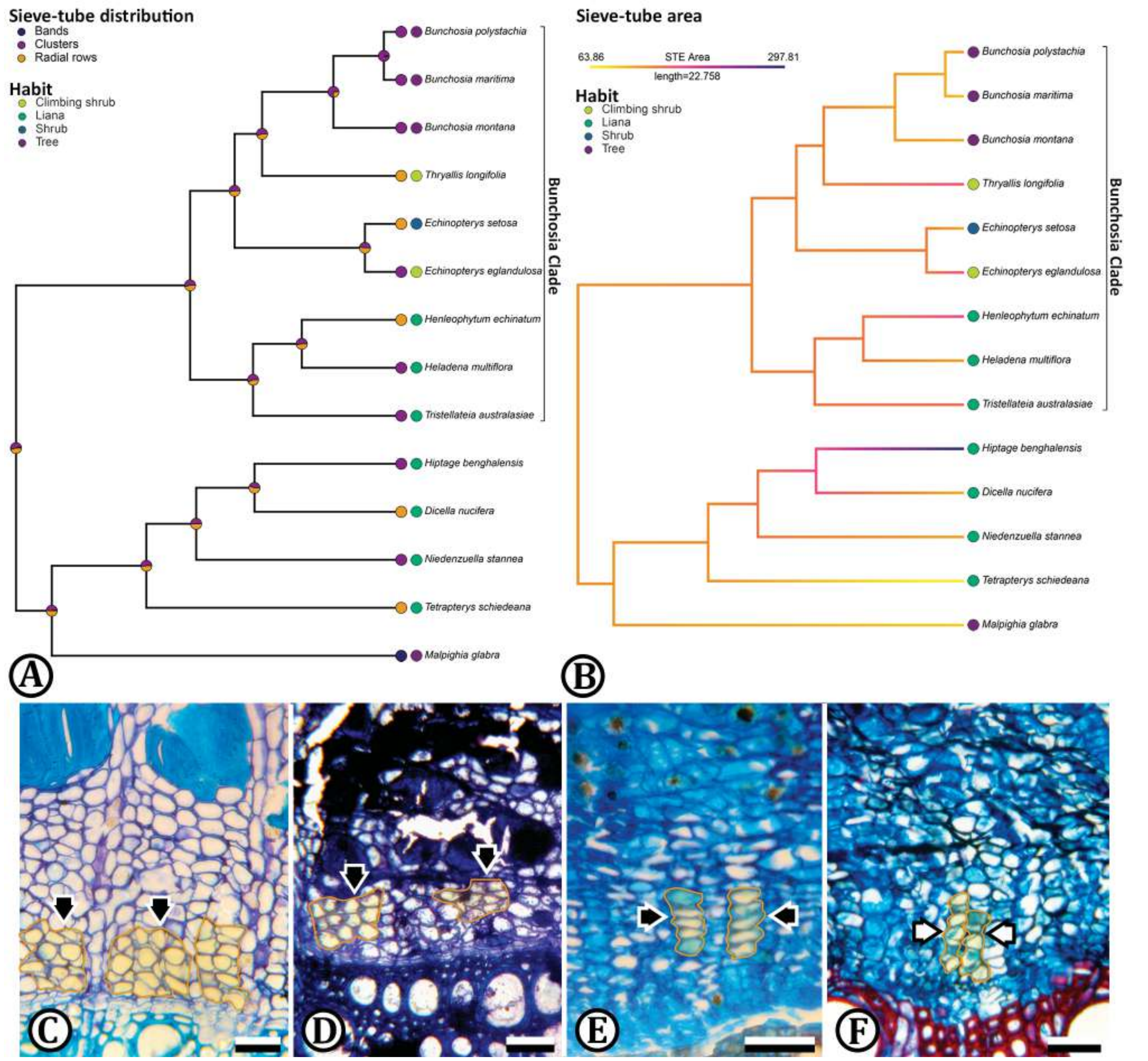

Fig. 12 Sieve tube distribution and sieve tube area in the Bunchosia clade. *A*, Ancestral character state reconstruction of sieve tube arrangement. *B*, Ancestral character state reconstruction of sieve tube areas. *C–F*, Transverse view. *C*, *Bunchosia montana*; sieve tubes in bands (arrows). *D*, *Echinopterys eglandulosa*; sieve tubes in clusters (arrows). *E*, *Echinopterys setosa*; sieve tubes in radial rows (arrows). *F*, *Henleophytum echinatum*; sieve tubes in radial rows (arrows). Scale bars = 50 μm in *C–F*.

Banisteriopsis, *Diplopterys* (Nagamine-Pinheiro et al. 2021), *Callaeum* (Cabanillas et al. 2017), *Heteropterys* (Amorim et al. 2017), and *Stigmaphyllon* (Guimarães et al. 2016).

Ancestral Anatomical Conditions in the Bunchosia Clade

From our results we infer that the ancestral condition of the anatomy stem includes biphasic wood, vessel dimorphism, and diffuse porosity and includes vessels in long radial multiples, scanty and diffuse axial parenchyma, septate and gelatinous fibers, mixed heterocellular rays, and prismatic crystals in axial and radial parenchyma. Several of these traits are characteristic features of the lianescent vascular syndrome as defined by Angyalossy et al. (2015). Meanwhile, the ancestral phloem condition most likely included sieve elements in clusters, druses confined to the axial parenchyma, and sclereids in large clusters.

Vessel System: Efficiency, Safety, and Developmental Shifts

Biphasic wood is common in the lianas of the clade, with correlation analyses showing an association between climbing habit and biphasic wood. This biphasic pattern reflects differences in xylem arrangement between the self-supporting and climbing phases. Generally, the self-supporting phase has vessels in radial

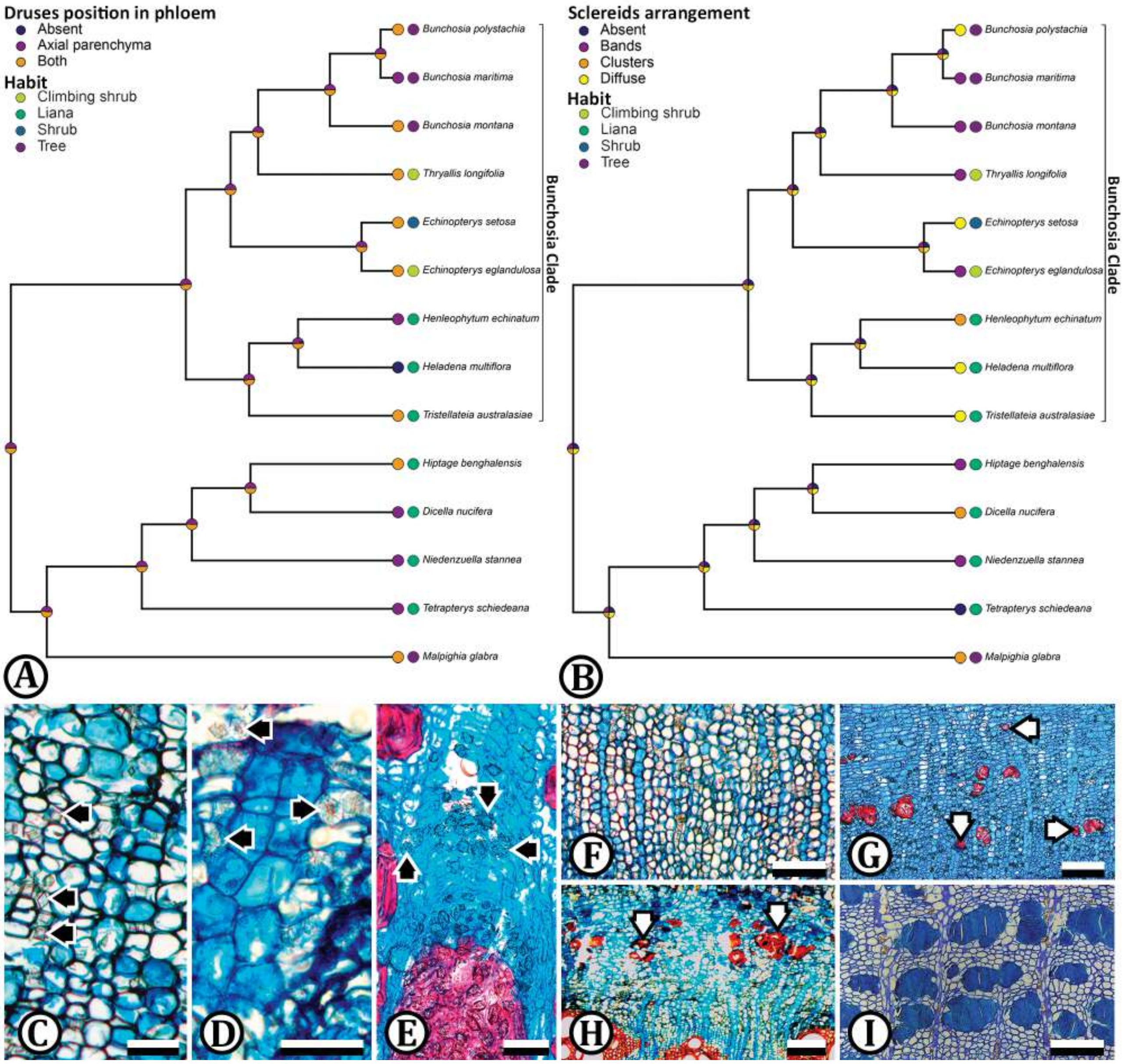

Fig. 13 Druses and sclereids distribution in the phloem of the Bunchosia clade. *A*, Ancestral character state reconstruction of druse position in the phloem. *B*, Ancestral character state reconstruction of sclereids arrangement reconstruction. *C–I*, Transverse view. *C*, *Heladena multiflora*; prismatic crystals in the axial parenchyma of phloem. *D*, *Henleophytum echinatum*; druses are restricted to the axial parenchyma of phloem. *E*, *Echinopterys eglandulosa*; druses in both axial and radial parenchyma. *F*, *Heladena multiflora*; bark with no sclerenchyma. *G*, *Bunchosia polystachya*; sclereids with a diffuse distribution. *H*, *Henleophytum echinatum*; sclereids are in clusters without a specific arrangement. *I*, *Bunchosia montana*; sclereids in clusters, forming bands only interrupted by radial parenchyma. Scale bars = 50 μm in *C–E*; 200 μm in *F–I*.

multiples, narrow vessels, less axial parenchyma, and abundant fibers. In contrast, during the climbing phase, vessels are frequently solitary, larger in diameter, and with fewer fibers and more axial parenchyma (Fisher and Ewers 1992; Angyalossy et al. 2015). Interestingly, this biphasic condition is also observed in *Echinopterys setosa*, a self-supporting species, suggesting that it may represent a retained anatomical trait from the lianescent ancestor inferred for the clade (Quintanar-Castillo et al. 2025). Among the genera analyzed, *Bunchosia* is the only genus lacking biphasic wood. Throughout *Bunchosia*'s wood development, the vascular system remains self-supporting, and its vessel arrangement resembles the early developmental stages of lianas in the clade. This is compelling evidence of a truncated ontogeny, denoting a case of heterochrony due to paedomorphosis (Onyenedum and Pace 2021), where the wood permanently retains the characteristics of the self-supporting phase of the common ancestors in the clade.

Vessel dimorphism is the most likely ancestral condition in the Bunchosia clade, with correlation analyses showing no dependence on habit within the group. Although this trait is typically associated with the climbing habit (Angyalossy et al. 2015), vessel dimorphism functionally enhances conduction safety and efficiency by allowing narrow vessels to maintain water flow when larger vessels suffer embolism (Carlquist 1985; Ewers et al. 1992; Rosell and Olson 2014; Carvalho et al. 2015; Olson et al. 2023).

Regarding vessel grouping and arrangement, the most likely ancestral state is a diffuse pattern with long radial multiples. This condition independently shifted to a dendritic pattern, tangential bands, or radial multiples. The radial and diffuse arrangement observed in only self-supporting species may be related to vessel diameter, as self-supporting species within the clade have smaller vessels. A similar vessel pattern has been described in Byrsonimoid and Galphimioid woods, where all their members are trees or shrubs (Bueno et al. 2025; Sanches et al. 2025). Additionally, some shrubby *Galphimia* species found in tropical dry forests exhibit semiring porosity (Sanches et al. 2025). However, lianescent members within the clade, such as *Tristellateia*, also exhibit a radial pattern. Nagamine-Pinheiro et al. (2021) noted that radial vessel patterns occur only in narrow vessels, while larger vessels remain solitary in *Banisteriopsis muricata* and *Diplopterys pubipetala*, despite radial arrangement being common in the family (Metcalfe and Chalk 1950). Radial vessel arrangement has been suggested to enhance water conduction by maintaining the water column during cavitation events (Hacke et al. 2006).

Vessel frequency in the Bunchosia clade varies between subclades. Lianescent species exhibit increased vessel frequency, whereas self-supporting members (e.g., *Bunchosia*) exhibit low frequency. A similar pattern is observed for vessel diameter: in lianas, vessel diameter increases, while in Bunchosia species, it decreases. Narrow vessels and low density have also been reported in other arboreal and arborescent species, such as Byrsonimoids and Galphimioids (Bueno et al. 2025; Sanches et al. 2025). Narrow vessels appear to be a common feature in Malpighiaceae, particularly in self-supporting species (Metcalfe and Chalk 1950; León and Williams 2006; Amorim et al. 2017; Nagamine-Pinheiro et al. 2021). In Byrsonimoids, narrow vessels have been identified as the ancestral condition for the clade (Bueno et al. 2025), suggesting that narrow vessel diameter is a conserved trait in self-supporting clades, while in lianescent clades, it represents a reversion in self-supporting species nested within these groups. A high density of narrow vessels has also been described for shrubby Galphimioids (Sanches et al. 2025). Vessels in high density have been associated with improved hydraulic safety, particularly in drier environments, whereas wider vessels prevail in humid environments (Hacke et al. 2022; Olson et al. 2023).

Minute intervessel pits are characteristic of Malpighiaceae (Metcalfe and Chalk 1950). However, in the Bunchosia clade, self-supporting species (*Bunchosia* and *Echinopterys*) exhibit an increase in intervessel pit diameter, whereas lianas retain smaller pits. Since the lianescent vascular syndrome predicts that lianas evolve toward more efficient conducting systems, this result goes against the expectations, as narrower pits let less water flow but they also confer greater resistance to cavitation (Hacke et al. 2006).

Parenchyma, Rays, and Flexibility-Related Features

Axial parenchyma distribution is one of the most informative traits in Malpighiaceae (Amorim et al. 2017). For instance, in *Banisteriopsis*, *Byrsonima*, and some Galphimioids, the axial parenchyma is typically scanty (León and Williams 2006; Bueno et al. 2025; Sanches et al. 2025). In *Heteropterys* species, axial parenchyma varies from scanty to vasicentric or aliform (Amorim et al. 2017), while in *Bunchosia*, it is generally abundant and arranged in bands (Metcalfe and Chalk 1950; León and Williams 2006). Reconstruction analyses suggest that banded axial parenchyma is a novelty in the Bunchosia clade. This trait evolved independently in the clade comprising *Bunchosia*, *Thryallis*, and *Echinopterys* and in *Heladena*, where the banded parenchyma is nonlignified. Marginal parenchyma, found in only *Echinopterys*, has also been described in *Heteropterys* (Amorim et al. 2017), *Mcvaughia* (Almeida et al. 2019), and *Acridocarpus*. This feature has been described as the ancestral condition for the Byrsonimoid clade (Bueno et al. 2025).

Regarding axial parenchyma abundance, a low proportion is maintained throughout evolution, increasing in only *Bunchosia*, where most self-supporting species are found (except *Echinopterys setosa*), exhibiting both banded and marginal parenchyma. *Bunchosia* is possibly the genus with the highest proportion of parenchyma in Malpighiaceae. A decrease in axial parenchyma in lianas and an increase in self-supporting species have also been documented in Bignoniaceae (Pace and Angyalossy 2013; Pace et al. 2015) and in some Sapindales (Anacardiaceae and Sapindaceae; Pace et al. 2022). Although most lianas tend to have more parenchyma than their self-supporting counterparts (Morris et al. 2016), this pattern does not encompass the full diversity of plants. We hypothesize that in lianescent lineages where conspicuous vascular variants develop (as in the abovementioned families), the variants assume the role of increasing flexibility, leading to a reduction in axial parenchyma. This hypothesis requires phylogenetic correlation testing in a broader study encompassing multiple families.

Nonlignified axial parenchyma is a common characteristic in lianas and succulents (Carlquist 2001; Angyalossy et al. 2015). In the Bunchosia clade, it is present in only *Heladena* and *Henleophytum*, although it has also been reported in other Malpighiaceae genera such as *Heteropterys* and *Stigmaphyllon*, where its presence is associated with phloem wedges or other kinds of vascular variants (Pace 2015; Nagamine-Pinheiro et al. 2021; Quintanar-Castillo and Pace 2022; Quintanar-Castillo et al. 2024). Nonlignified parenchyma has been linked to an increase in flexibility, storage, wound repair, retaining meristematic capacity, and allowing parenchyma dedifferentiation and the formation of new cell types, including new cambia (Fisher and Ewers 1992; Angyalossy et al. 2015; Pace et al. 2018).

Parenchyma abundance is generally associated with flexibility, wound repair, and storage capacity in lianas (Dobbins and Fisher 1986; Carlquist 2001; Pace et al. 2009; Angyalossy et al. 2015). However, in the Bunchosia clade, lianas lack this abundance, suggesting that other stem tissues, such as secondary phloem (if vascular variants are present) or septate fibers, may fulfill these functions. The replacement of one cell type by another can be considered a case of homeosis, where a character is spatially replaced by another (Sattler 1988; Onyenedum and Pace 2021). Alternatively, the reduction in parenchyma proportion can be seen as heterometry, reflecting a quantitative change in a trait from ancestor to descendant (Onyenedum and Pace 2021). In the Bunchosia clade, there is a shift to an increased proportion of parenchyma in the self-supporting genus *Bunchosia*.

Support and Storage Tissues: Fibers, Crystals, and Sclerenchyma

Septate fibers are present in almost all climbing species of the clade, while reconstruction analyses indicate that this condition was lost in self-supporting species. Their presence may be related to water storage and the deposition of carbohydrates, oils, resins, and crystals and the prevention and repair of embolisms (Butterfield and Meylan 1976; Carlquist 2001; Angyalossy et al. 2015; Pace et al. 2022; Plavcová et al. 2023). Septate fibers are common in Malpighiaceae; while they are only reported here for lianescent species, they are also found in self-supporting genera such as *Byrsonima*, *Galphimia*, and *Mcvaughia* (Record and Hess 1949; Metcalfe and Chalk 1950; León and Williams 2006; Almeida et al. 2019; Bueno et al. 2025; Sanches et al. 2025).

Reconstruction analyses indicate that narrow rays are the likely ancestral condition in the clade, maintained in almost all genera but lost in *Echinopterys* and in *Thryallis*. Wide rays are a common feature in lianas and form part of the lianescent vascular syndrome (Lev-Yadun and Aloni 1995; Angyalossy et al. 2015). Although ray height was not considered here, available literature indicates that wide and tall rays can increase stem flexibility (Carlquist 1992; Angyalossy et al. 2015).

Mixed heterocellular rays are the most likely ancestral condition in the clade and are maintained in all climbing groups. Only in *Bunchosia* does the ray composition change. Mixed heterocellular rays are common in Malpighiaceae and are more prevalent in lianas than trees or shrubs (Amorim et al. 2017; Cabanillas et al. 2017; Pace et al. 2018; Almeida et al. 2019). They are also listed as part of lianescent vascular syndrome (Angyalossy et al. 2015). In some shrubby Galphimioids species, these rays are considered characteristic of this habit and a potential synapomorphy (Sanches et al. 2025). Rays composed of a procumbent body with square to upright marginal cells are typical of self-supporting species. However, in this clade, this condition is derived, whereas in other arboreal or shrubby groups, it is inferred as the ancestral condition (Bueno et al. 2025; Sanches et al. 2025).

According to the reconstruction analyses, interconnected rays represent a derived condition in the clade and were observed in *Bunchosia*, *Thryallis*, and *Tristellateia*. Carlquist (2001) described interconnected rays as multiseriate rays with uniseriate portions that join with other rays. A more comprehensive study, involving additional family members, is needed to clarify the evolutionary pattern of this feature. Interconnected rays can appear in lianas, where they likely enhance stem flexibility in self-supporting lineages derived from lianas where their presence could be interpreted as retention due to common ancestry, but also in self-supporting lineages without a lianescent ancestor (e.g., *Byrsonima*; Bueno et al. 2025).

Aggregated rays were observed in only *Echinopterys* and *Tristellateia*, suggesting a derived condition linked to the presence of limiting rays (see Quintanar-Castillo and Pace 2022). Although the Malpighiaceae have no prior records of aggregated rays, their occurrence in these species may reflect a strategy to increase extension in thickness and height, as wider and taller rays are known to enhance flexibility in lianas (Angyalossy et al. 2015).

Prismatic crystals in the axial parenchyma of wood are a common trait in the clade and were reconstructed as the most likely ancestral condition. However, *Echinopterys*, *Thryallis*, and *Tristellateia* do not present crystals in axial parenchyma, although they can be found in ray parenchyma. The distribution of prismatic crystals in ray parenchyma is variable, and the general presence throughout the ray body was reconstructed as the most likely ancestral condition. A reduction in crystal quantity and distribution appears as a derived condition, manifesting as a restriction to marginal rows in some self-supporting species or a complete absence in some climbing groups. Previous studies on mineral inclusions in the core Malpighiaceae suggest differences in crystal composition between secondary xylem and phloem; prismatic crystals are common in the former, whereas druses predominate in the latter (Pace 2015; Amorim et al. 2017; Cabanillas et al. 2017; Pace et al. 2018; Almeida et al. 2019; Quintanar-Castillo et al. 2024). Only in *Heladena* were exclusively small prismatic crystals found in phloem parenchyma, a trait that may represent a potential synapomorphy for the genus. Except for *Heladena*, this topological distinction can help elucidate the nature of the tissues (xylem vs. phloem), particularly in nonlignified parenchyma (Pace 2015). Previous reports describe both prismatic crystals and druses in the phloem of *Banisteriopsis* but never exclusively (Pace et al. 2018). In Byrsonimoids, prismatic crystals in the axial parenchyma of the nonconductive phloem appear to represent a synapomorphy of the group (Bueno et al. 2025). Crystals have been associated with mechanical support, protection against herbivory, and a calcium reservoir for metabolic processes or as a strategy to eliminate excess calcium (Franceschi and Nakata 2005; Evert 2006; Paiva 2019, 2021).

Sclerenchyma in the Bunchosia clade consists exclusively of sclereids, occupying mainly the nonconducting area, a pattern that was also found in other Malpighiaceae (Cabanillas et al. 2017). While sclereid arrangement varies within the group, no clear pattern distinguishes between lianescent and self-supporting species. In *Callaeum* and *Stigmaphyllon*, sclereids occur in clusters, mostly in the nonconducting phloem (Amorim et al. 2017; Cabanillas et al. 2017), although they have also been described in conducting regions (Pace et al. 2018). In exclusive self-supporting clades such as Byrsnonimoids, sclerenchyma is more diverse, ranging from true fibers to fiber sclereids to sclereids (Bueno et al. 2025).

Secondary Phloem Evolution and Anatomical Variation

Relatively few studies have addressed the diversity of secondary phloem in Malpighiaceae (Metcalfe and Chalk 1950; Cabanillas et al. 2017; Pace et al. 2018; Almeida et al. 2019; Quintanar-Castillo and Pace 2022; Quintanar-Castillo et al. 2024). In the Bunchosia clade, lianescent species exhibit larger sieve tube elements, a trait also reported for other lianas in the family (such as *Callaeum*; Cabanillas et al. 2017) and that has also been defined as a common trait in lianas in general (Carlquist 1992; Angyalossy et al. 2012, 2015). However, the differences in sieve tube element size between self-supporting and lianescent species in the clade were not particularly pronounced. The arrangement of sieve tubes also varies; a cluster arrangement is common, whereas an arrangement in radial rows represents a derived condition found only in lianas of the group. In *Mcvaughia sergipana*, sieve tubes are arranged in radial multiples or diffuse patterns (Almeida et al. 2019), while in Byrsonimid species, both radial and clustered arrangements occur (Bueno et al. 2025). Since self-supporting taxa can also have sieve tube elements in radial rows, no specific arrangement appears exclusive to either lianas or self-supporting species.

The vascular system diversity in the Bunchosia clade is shaped by both developmental processes (Quintanar-Castillo et al. 2025) and habit. The results presented here highlight the anatomical shifts that plants experience during habit transitions and illustrate the conservatism observed in the shift from climbing to self-supporting forms. As previous works suggest (Quintanar-Castillo et al. 2025), the common ancestor of the Bunchosia clade was reconstructed as a climbing plant (liana) with regular secondary growth. We propose that this ancestor exhibited anatomical traits consistent with the lianescent vascular syndrome, an ensemble of traits commonly found in lianas across diverse lineages. Among these are dimorphic vessels, septate and gelatinous fibers, mixed heterocellular rays, and prismatic crystals distributed throughout the ray body. Interestingly, although abundant axial parenchyma is a hallmark of the syndrome, its scarcity in this group mirrors patterns described for other members of Malpighiaceae. Some wood and bark traits appear to reflect distinct developmental trajectories: for instance, the presence of septate fibers and scanty parenchyma may be explained by homeosis, whereas conspicuous wide rays could represent a case of heterometry. Overall, the vascular system traits align with prior findings for Malpighiaceae; however, the presence and topology of mineral inclusions appear more diverse than previously reported. Studying the anatomy of the vascular system within an evolutionary framework can provide insight into the processes underlying structural variation.

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