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**Acta Botanica
Mexicana**

Leaf architecture and anatomy of Asteraceae species in a xerophytic scrub in Mexico City, Mexico

Arquitectura y anatomía foliar de especies de Asteraceae en un matorral xerófilo de la Ciudad de México, México

Patricia Rivera^{1,2,3} , Teresa Terrazas¹ , Alicia Rojas-Leal¹ , José Luis Villaseñor¹

Abstract:

Background and Aims: Leaf architecture and anatomy in the Asteraceae family are extremely diverse and have been studied from ecological, physiological and evolutionary perspectives. The aims of this study are to describe in detail leaf architecture and anatomy for 61 species belonging to 13 tribes of Asteraceae inhabiting a xerophytic scrub in Mexico City, Mexico and to discuss characters common to these tribes.

Methods: Mature and undamaged leaves of 61 species of Asteraceae were collected in southwestern Mexico City in the “Reserva Ecológica del Pedregal de San Ángel” (REPSA). Standard anatomical techniques were used to obtain permanent slides of cleared leaves and transverse and paradermal sections. The permanent slides were analyzed to describe leaf architecture and anatomy by tribe following the standard terminologies.

Key results: The results show a significant variation in leaf architecture although pinnate venation, brochidodromous secondary venation, areoles moderately developed and looped ultimate marginal venation predominate in the material studied. For anatomy, the most common traits are the striate cuticle, occurrence of trichomes and glands, as well as collateral vascular bundles with a parenchymatous sheath with girders in the Asteraceae present in this xerophytic scrub. There are no unique combinations of leaf characters for the family or any tribe.

Conclusions: Leaf diversity in the family and within each tribe is consistent with some previous reports. Anatomical descriptions are a fundamental piece of the evolutionary, ecological and physiological studies in Asteraceae. The results of this descriptive study will allow testing hypotheses about the factors causing leaf diversity in this plant lineage. More leaf anatomical studies of the family are necessary to confirm the patterns proposed for the tribes and the family.

Key words: Asteroideae, Compositae, Heliantheae, leaf anatomy, midvein, vascular bundle sheath, venation pattern.

Resumen:

Antecedentes y Objetivos: La arquitectura y anatomía foliar en la familia Asteraceae son extremadamente diversas y han sido estudiadas desde distintas perspectivas, como la ecológica, fisiológica y evolutiva. Los objetivos de este estudio son describir detalladamente la arquitectura y anatomía foliar de 61 especies incluidas en 13 tribus de la familia Asteraceae que habitan un matorral xerófilo en la Ciudad de México, México y discutir los caracteres comunes de las tribus.

Métodos: Se colectaron hojas maduras y sanas de 61 especies de Asteraceae al sureste de la Ciudad de México en la “Reserva Ecológica del Pedregal de San Ángel” (REPSA). Se usaron técnicas anatómicas estandarizadas para obtener hojas aclaradas y secciones transversales y paradermales. Estas preparaciones permanentes se analizaron para describir la arquitectura y anatomía foliar por tribu con base en la terminología convencional.

Resultados clave: Los resultados muestran una variación significativa en la arquitectura foliar, aunque predominan la venación pinnada, venación secundaria broquidódroma, areolas moderadamente desarrolladas y márgenes en bucles. En la anatomía los atributos más comunes son la cutícula estriada, la presencia de tricomas y glándulas, así como haces vasculares colaterales con una vaina parenquimatosa con extensiones en las Asteráceas presentes en este matorral xerófilo. No hay una combinación única de caracteres foliares para la familia o las tribus.

Conclusiones: La diversidad foliar dentro de la familia y al interior de cada tribu corresponde con reportes previos. Las descripciones anatómicas son una pieza fundamental de los estudios evolutivos, ecológicos y fisiológicos en Asteraceae. Los resultados de este estudio descriptivo permitirán probar hipótesis acerca de los factores que causan la diversidad foliar en este linaje de plantas. Se necesitan más estudios anatómicos foliares en Asteraceae para confirmar los patrones propuestos para las tribus y la familia.

Palabras clave: anatomía foliar, Asteroideae, Compositae, Heliantheae, patrón de venación, vaina del haz vascular, vena media.

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Introduction

As pointed out by Endress et al. (2000) the backbone of plant systematics is the comparative study of plant structure, morphology and anatomy. The information obtained through comparative morpho-anatomical studies is necessary for ecological, phylogenetic and evolutionary studies. For example, anatomical characters, especially of leaves, have been extensively used in the systematics of several plant families, including Bromeliaceae (De Faria et al., 2012), Myrtaceae (Al-Edany and Al-Saadi, 2012), Amaryllidaceae (Lin and Tan, 2015), Malpighiaceae (Araújo et al., 2010) and Asteraceae (Castro et al., 1997; Milan et al., 2006; Adedeji and Jewoola, 2008; Bombo et al., 2012; Akin-nubi et al., 2014; Rojas-Leal et al., 2017; Lusa et al., 2018). Particularly in Asteraceae, leaf architecture and anatomical characters are extremely diverse (Bombo et al., 2012; Rojas-Leal et al., 2014, 2018) and have been studied from an ecological (Bercu et al., 2012; Moroney et al., 2013; Rivera et al., 2017; Ferraro and Scremin-Dias, 2018), physiological (Bondarev et al., 2003; McKown and Dengler, 2007; Santiago and Kim, 2009), and medical perspective (Cambi et al., 2006; Hulley et al., 2010; García-Sánchez et al., 2012).

Asteraceae is one of the largest families of angiosperms. While cosmopolitan, it is usually dominant in arid and temperate vegetation. Evidence suggests that North America, particularly Mexico, has been important for diversification in some of the most diverse lineages of the family (Noyes and Rieseberg, 1999; Suárez-Mota and Villaseñor, 2011; Villaseñor, 2018). Leaf diversity in the family has been associated to variable environmental conditions such as drought (Ferraro and Scremin-Dias, 2018), saline soils (Grigore and Toma, 2006; Bercu et al., 2012) and light conditions (Rossatto and Kolb, 2010). However, the environment alone does not explain the variation in leaf anatomical characters, because some of these as well as most leaf architectural characters can be constrained by the phylogenetic history, the growth form or the ploidy level of the species (Rivera et al., 2017).

In this paper, we describe the leaf architecture and anatomy of 61 species belonging to 13 tribes of the Asteraceae growing in a xerophytic scrub natural reserve within the central campus of the Universidad Nacional Autónoma de México. This area represents the remnants of the native

flora of Mexico City before the extensive urbanization and it is one of the best-studied protected areas in Mexico in terms of its biodiversity (Lot and Cano-Santana, 2009; Céspedes et al., 2018). The aims of this work are to present a detailed description of the diversity in the leaf architecture and anatomy of Asteraceae occurring in a xerophytic scrub and to discuss characters common to the tribes present.

Materials and Methods

Site description

Plant samples were collected in the “Reserva Ecológica del Pedregal de San Ángel” (REPSA). The REPSA is located in southwestern Mexico City, between coordinates 19°18'21" - 19°20'11"N, 99°10'15" - 99°12'4"W and from 2200 to 2310 m a.s.l. The REPSA has a total area of 237.3 hm (UNAM, 2006). The average annual temperature is 15.6 °C and the total annual rainfall 833 mm. The climate type in the area is temperate subhumid (Cb(w1)w), with a distinctive rain season from June to October and a dry season from November to May. The substratum is volcanic rock from the Xitle volcano eruption, and the soil is scarce and shallow.

Sampling

Samples of mature and healthy leaves of 61 species were collected from August 2008 to December 2009, during two rainy seasons. Leaves were fixed with a formaldehyde-glacial acetic acid-ethyl alcohol solution (Ruzin, 1999) for 24 hours; then rinsed with tap water and stored in a glycerin-ethyl-alcohol-water solution (GAA 1:1:1) until sectioning. All the leaves were scanned with an HP Photosmart Plus scanner (Hewlett-Packard Development Company, Palo Alto, USA), with the highest resolution (2400 dpi) before sectioning. Leaf area was determined using an image analyzer according to the procedure described by Garnier et al. (2001). At least three leaves per species were cleared following Martínez-Cabrera et al. (2007). Three to six leaves per species were dehydrated in increasing concentrations of ter-butanol (10-100%) with an automatic tissue processor (TP1020 Leica, Westlar, Germany) remaining for 24 hours in each concentration. The tissues were embedded in paraffin and transverse and paradermal sections of 10 to 12 µm in thickness were cut with a rotatory microtome (RM2125 Leica, Westlar, Germany).

The sections were stained with safranin-fast green (Ruzin, 1999) and mounted on synthetic resin. Photographs and measurements were obtained through a microscope (BX-51 Olympus, Tokio, Japan) attached to an image analyzer (Image Pro, 2019).

Descriptions were made from cleared leaves and transverse and paradermal sections of three leaves per species. Voucher specimens are at the Herbario Nacional de México (MEXU) of the Instituto de Biología, Universidad Nacional Autónoma de México. Details of the voucher specimens as collector and collection number are given in Appendix. Leaf architecture follows Ellis et al. (2009). Leaf lamina and midvein descriptions follow Metcalfe and Chalk (1979), Dickson (2000) and Koch et al. (2009). Quantitative characters for each species are available in Rivera et al. (2017) and tribe classification follows Anderberg et al. (2007).

Results

The leaf architecture and foliar anatomy are summarized and illustrated (Figs. 1-15) by tribe. When the taxon name is given for a character state means that the character state occurs only in it.

Asteraceae

Tribe Anthemideae

Two species: *Artemisia ludoviciana* Nutt. and *Cotula australis* (Sieber ex Spreng.) Hook. f. (Figs. 1, 2).

Leaves sessile, alternate, simple (*Artemisia* L.), pinnatisect or bipinnatisect (*Cotula* L., Fig. 1A); lamina size microphyll, lamina shape linear to lanceolate, margin entire, revolute (*Artemisia*), apex acuminate, base truncate (*Artemisia*) or concave (*Cotula*); primary vein framework pinnate, primary vein straight or slightly undulate, secondary venation brochidodromous, areole development moderate (*Artemisia*) or lacking (*Cotula*), veinlets simple, straight, unbranched, marginal ultimate venation looped (*Artemisia*) or incomplete (*Cotula*); teeth absent; leaves hypostomatic; in surface view, cells tetragonal-elongated with S-undulate anticlines (Figs. 2A, B), adaxial epidermis glabrate, abaxial epidermis subglabrous (*Cotula*) to tomentose (*Artemisia*), with multicellular trichomes and anomocytic stomata (Fig.

2A), in transverse view, cuticle striate and thin (<0.44 µm), epidermises uniseriate with conical or rectangular cells and thicker outer periclinal walls, adaxial epidermis thicker than the abaxial (*Artemisia*) or both epidermises equally thick (*Cotula*), stomata at the same level as the epidermal cells (*Cotula*) or above (*Artemisia*); mesophyll homogenous or heterogeneous (Figs. 2C, D), palisade parenchyma generally occupying 50% of the mesophyll (*Artemisia*, Fig. 2C); vascular bundles collateral with a parenchymatous bundle sheath, canals associated with vascular bundles (Fig. 2E); midvein contour gently protruded in both surfaces (Fig. 2F) or flat adaxially and projected abaxially (Fig. 2G), cuticle conspicuously striate and thicker than in the lamina, epidermises uniseriate with narrow convex cells and thicker outer periclinal and anticlinal walls, beneath the epidermis, annular collenchyma and towards the vascular bundle parenchyma, a single central collateral vascular bundle, within the bundle, xylem with radial rows of three to five vessels, phloem formed by three to five rows of cells, a cap of sclereids (three to four layers) external to xylem.

Tribe Astereae

Six species: *Baccharis pteronioides* DC., *B. salicifolia* (Ruiz & Pav.) Pers., *Conyza bonariensis* (L.) Cronquist, *C. canadensis* (L.) Cronquist, *C. coronopifolia* Kunth and *Laennecia sophiifolia* (Kunth) G.L. Nesom (Figs. 1, 3).

Leaves sessile or petiolate, alternate, simple (Fig. 1B) or pinnately lobed (*Laennecia* Cass., *C. coronopifolia*); lamina size microphyll to notophyll, lamina shape linear-lanceolate to linear-oblong, margin entire (*C. bonariensis*, *Laennecia*), dentate to serrate (*Baccharis* L., *C. canadensis*, *C. coronopifolia*), margin revolute (*C. bonariensis*), apex acuminate to convex, base cuneate (*Baccharis*), truncate or lobate (*C. bonariensis*, *C. canadensis*, *Laennecia*) to cordate (*C. coronopifolia*); primary vein framework pinnate (*B. salicifolia*, *Laennecia*) or palmate (*B. pteronioides*, *Conyza* Less.), primary vein straight, secondary venation brochidodromous or actinodromous (*B. pteronioides*, *Conyza*), areole development moderate, veinlets simple, curved, unbranched or one-branched (*C. coronopifolia*), marginal ultimate venation looped; teeth lacking principal vein, with accessory vein straight (*Baccharis*, *Conyza*) or absent



Figure 1: Leaf morphology. A. *Cotula australis* (Sieber ex Spreng.) Hook. f.; B. *Baccharis pteronioides* DC.; C. *Schkuhria pinnata* (Lam.) Kuntze ex Thell.; D. *Helminthotheca echioides* (L.) Holub.; E. *Sonchus oleraceus* L.; F. *Taraxacum officinale* F.H. Wigg.; G. *Bidens pilosa* L.; H. *Dahlia coccinea* Cav.; I. *Piqueria trinervia* Cav.; J. *Pseudognaphalium viscosum* (Kunth) Anderb.; K. *Ambrosia cumanensis* Kunth; L. *Montanoa tomentosa* Cerv.; M. *Tithonia tubiformis* (Jacq.) Cass.; N. *Galinsoga parviflora* Cav.; O. *Barkleyanthus salicifolius* (Kunth) H. Rob. & Brettell; P. *Pittocaulon praecox* (Cav.) H. Rob. & Brettell; Q. *Dyssodia papposa* (Vent.) Hitchc.; R. *Tagetes micrantha* Cav. Scale is 0.5 cm in A, C; 1 cm in B, D-R.

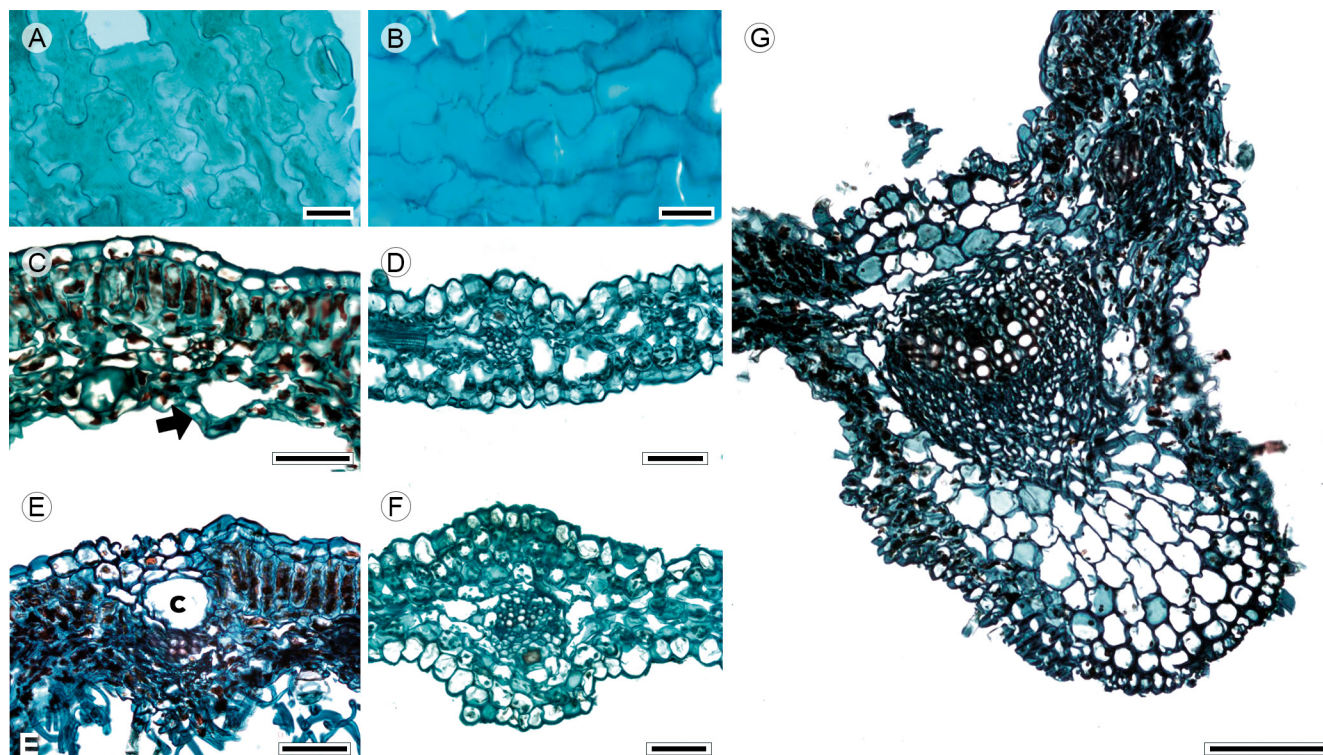


Figure 2: Lamina and midvein in Anthemideae. A, D, F. *Cotula australis* (Sieber ex Spreng.) Hook. f.; B, C, E, G. *Artemisia ludoviciana* Nutt. Scale is 20 µm in A, B; 50 µm in C-F, 100 µm in G. c=canal.

(*Laennecia*); leaves amphistomatic; in surface view, cells tetragonal or polygonal-elongated with straight anticlines (*Baccharis*, Fig. 3A, *C. canadensis*) or tetragonal to tetragonal-elongated with S-undulated to V-undulated anticlines (*C. bonariensis*, *C. coronopifolia*, Fig. 3B, *Laennecia*), adaxial and abaxial surfaces pubescent, with multicellular trichomes and glands and anomocytic or cyclocytic stomata (*Baccharis*, Fig. 3A), in transverse view, cuticle conspicuously striate and thickness between 0.28 and 0.57 µm, epidermises uniseriate with square or cupola cells (Figs. 3C-E) and thicker outer periclinal walls, both epidermis with the same width, stomata at the same level as epidermal cells; mesophyll heterogeneous (Figs. 3C, D) or homogeneous (*Laennecia*, Fig. 3E), palisade parenchyma occupying 33 to 41% of the mesophyll, except for *Laennecia*, paraveinal mesophyll between the vascular bundles; collateral vascular bundles with a parenchymatous bundle sheath, extensions of the sheath (girders) (Fig. 3E), except in *C. bonariensis* and *C. canadensis*, girders across the leaf (*C. coronopifolia*, *Laennecia*) or linked to either adaxial or abaxial surface (*Baccharis*), canals generally associated with vascular bun-

dles (Fig. 3D); midvein contour with a slight central depression adaxially and flat abaxially (Fig. 3F) or flat adaxially and round and protruding abaxially (Fig. 3G), cuticle thicker than in the lamina, epidermises uniseriate with narrow convex cells and thicker outer periclinal walls, annular collenchyma below the epidermises mostly in the central region of the midrib (*Baccharis*) and parenchyma towards the vascular tissue, with palisade parenchyma towards the center of the midvein, a single central collateral vascular bundle (Figs. 3F, G) or three bundles, within the bundle, xylem with radial rows of two to six vessels separated by one or two rows of parenchyma, phloem formed by three to five rows of cells, a cap of sclereids associated with phloem and xylem, more conspicuous in the larger bundle.

Tribe Bahieae

Two species: *Florestina pedata* (Cav.) Cass. and *Schkuhria pinnata* (Lam.) Kuntze ex Thell. (Figs. 1, 4, 5).

Leaves petiolate, opposite at the base and alternate near the apex, pinnatisect or bipinnatisect (*Schkuhria* Roth,

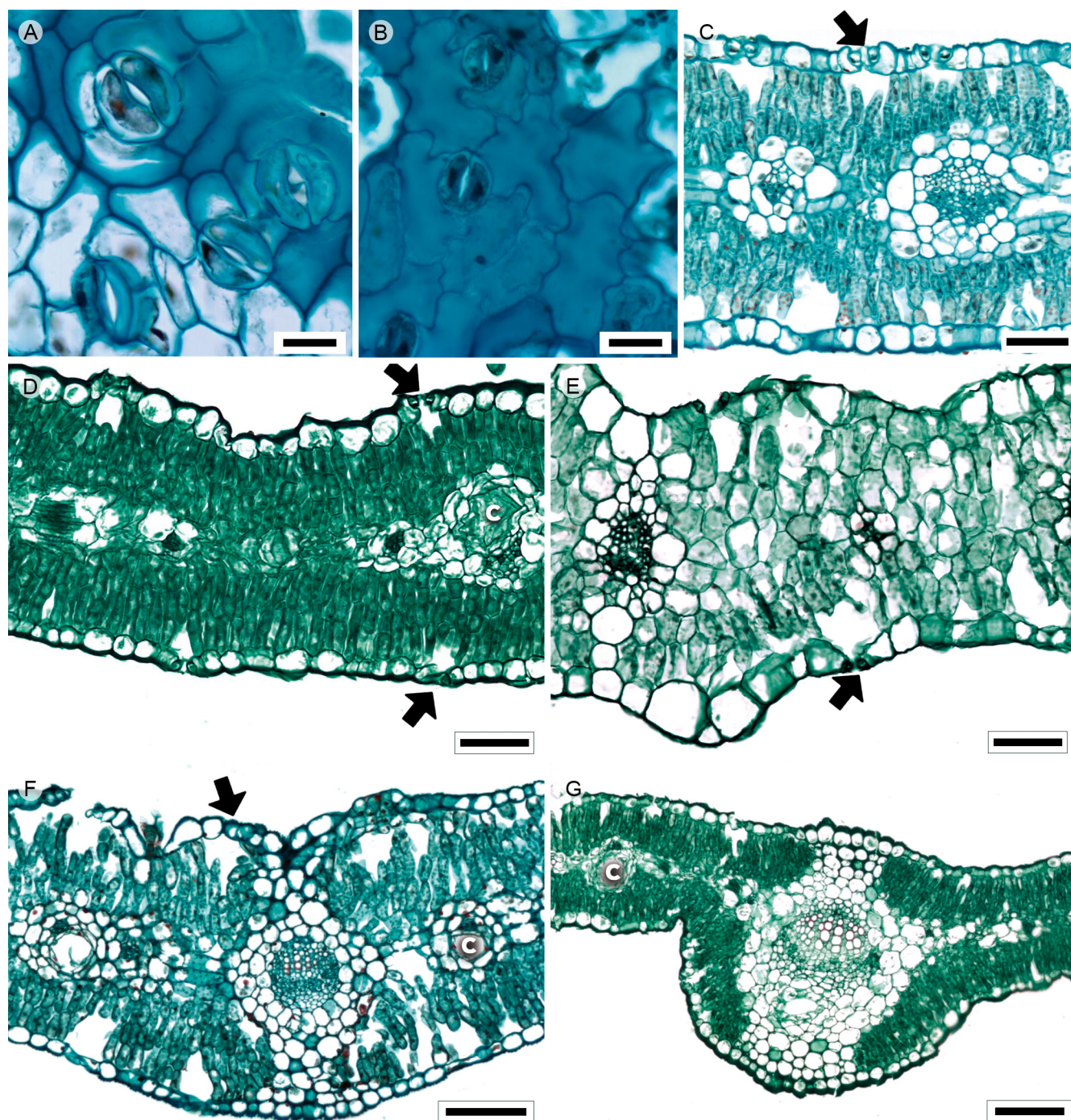


Figure 3: Lamina and midvein in Astereae. A, C. *Baccharis salicifolia* (Ruiz & Pav.) Pers.; B. *Conyza bonariensis* (L.) Cronquist; D, G. *Conyza canadensis* (L.) Cronquist; E. *Laennecia sophiifolia* (Kunth) G.L. Nesom; F. *Baccharis pteronioides* DC. Scale is 20 μ m in A, B; 50 μ m in C-E, 100 μ m in F, G. c=canal.

Fig. 1C) or palmatisect (*Florestina* Cass.); lamina size microphyll, lamina shape linear (*Schkuhria*) or elliptic (*Florestina*), margin entire, apex straight, base concave or cuneate; primary vein framework pinnate (Fig. 4A), primary vein undulate (*Florestina*), weak, secondary venation brochidodromous, areole development moderate, veinlets sim-

ple, straight, unbranched (*Florestina*) or absent (*Schkuhria*), marginal ultimate venation looped; teeth absent; leaves amphistomatic; in surface view, cells tetragonal or polygonal elongated with S-undulated and U-undulated anticlines (Figs. 5A, B), both surfaces subglabrous, with short glandular trichomes and anomocytic stomata (*Florestina*,

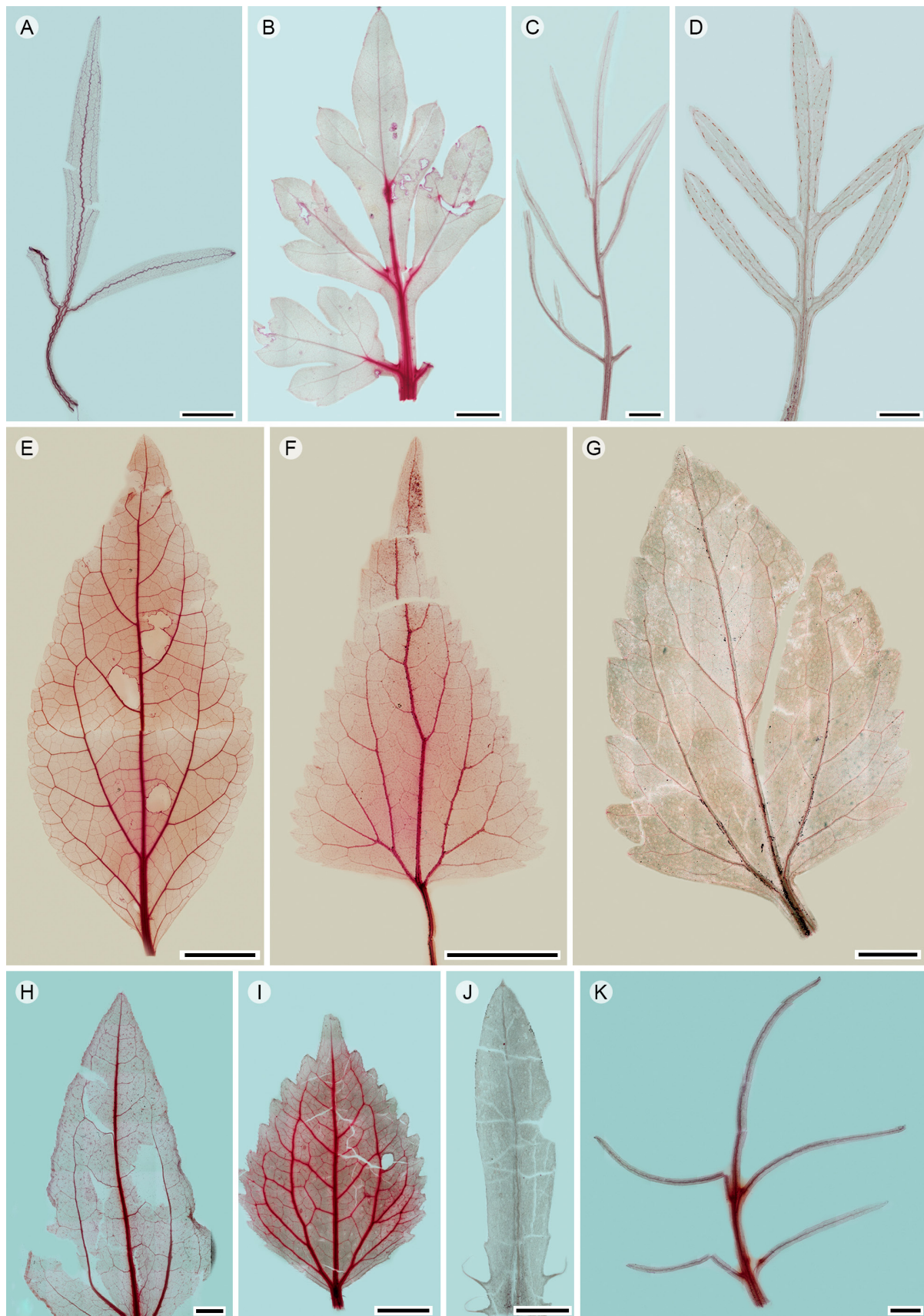


Figure 4: Cleared leaves. A. *Florestina pedata* (Cav.) Cass.; B. *Bidens odorata* Cav.; C. *Cosmos bipinnatus* Cav.; D. *Heterosperma pinnatum* Cav.; E. *Brickellia secundiflora* (Lag.) A. Gray; F. *Fleischmannia pycnocephala* (Less.) R.M. King & H. Rob.; G. *Stevia micrantha* Lag.; H. *Zinnia peruviana* (L.) L.; I. *Galinsoga parviflora* Cav.; J. *Pectis prostrata* Cav.; K. *Tagetes micrantha* Cav. Scale is 2 mm in A-D, G, H, J; 1 cm in E, F; 5 mm in I, 21 mm in K.

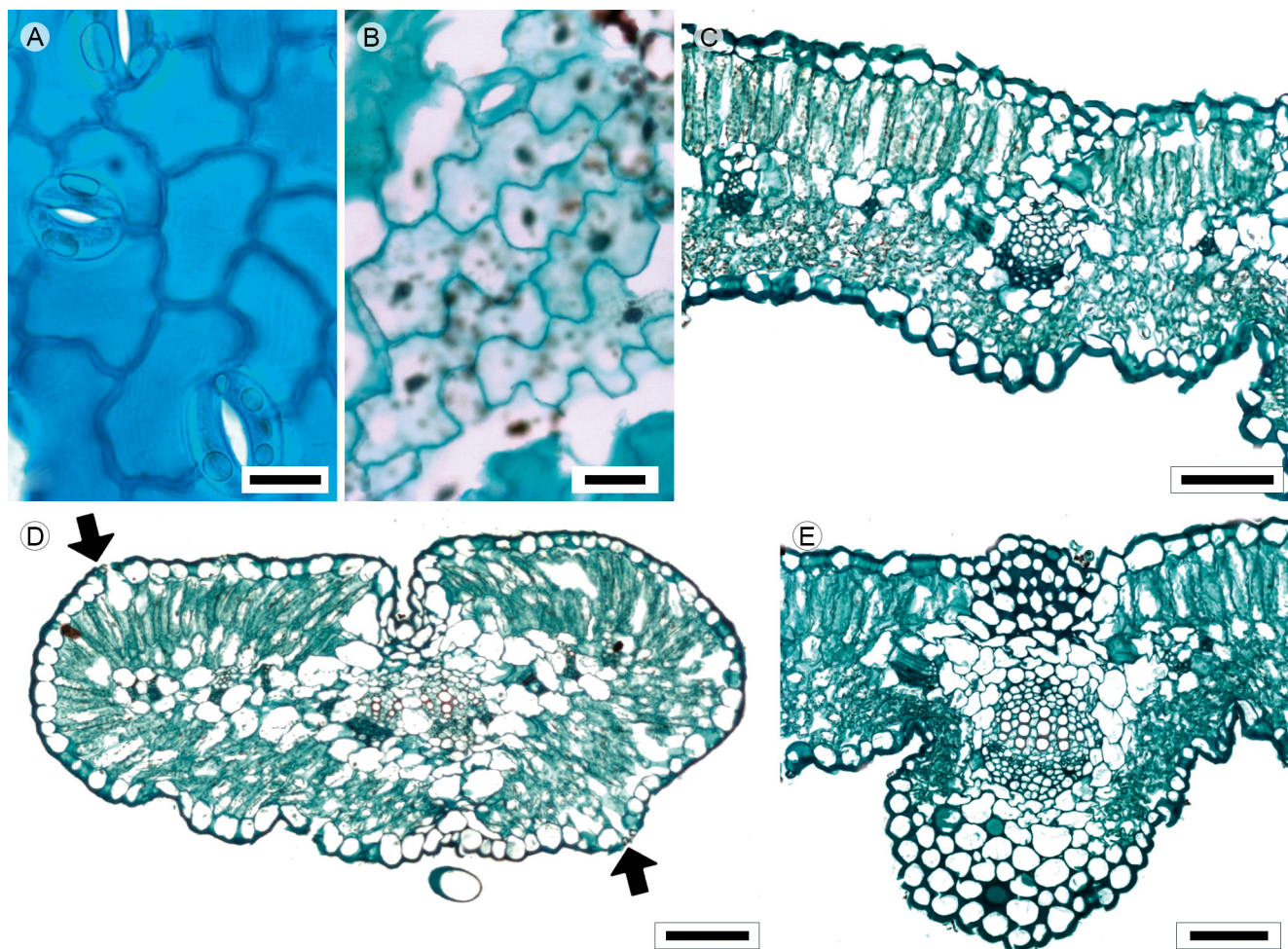


Figure 5: Lamina and midvein in Bahieae. A, C, E. *Florestina pedata* (Cav.) Cass.; B, D. *Schkuhria pinnata* (Lam.) Kuntze ex Thell. Scale is 20 μm in A, B; 100 μm in C-E.

Schkuhria) or anisocytic (*Schkuhria*), in transverse view, cuticle striate with a thickness between 0.33 to 0.38 μm , epidermises uniseriate, with rectangular to hemispherical cells and thicker outer periclinal walls (Figs. 5C, D), adaxial epidermis wider than abaxial (*Florestina*) or both epidermises the same width (*Schkuhria*), stomata at the same level as the epidermal cells; mesophyll heterogeneous (*Florestina*, Fig. 5C) or homogeneous (*Schkuhria*, Fig. 5D), palisade parenchyma occupying 54% of the leaf in *Florestina*; collateral vascular bundles with a parenchymatous bundle sheath, sheath extensions rare (Fig. 5C), canals associated with vascular bundles; midvein contour with a slight central depression adaxially and flat abaxially in *Schkuhria* (Fig. 5D), round and slightly projected adaxially and round and protruding abaxially in *Florestina* (Fig. 5E), cuticle similar to lamina, epidermises uniseriate, with cupola cells and

thicker outer periclinal walls, immediately beneath the epidermises, four rows of annular collenchyma (*Schkuhria*) or two to four rows of angular collenchyma (*Florestina*) and parenchyma towards the vascular tissue, with palisade one third towards the abaxial surface, a single central collateral vascular bundle (Fig. 5E) or two bundles, within the bundle, xylem with radial rows of three to four vessels separated by one or two rows of parenchyma, phloem formed by three to five rows of cells, caps of sclereids with thin walls associated to xylem and phloem.

Tribe Cardueae

One species: *Cirsium vulgare* (Savi) Ten. (Fig. 6).

Leaves sessile, alternate, pinnately lobed; lamina size mesophyll, lamina shape triangular, margin toothed

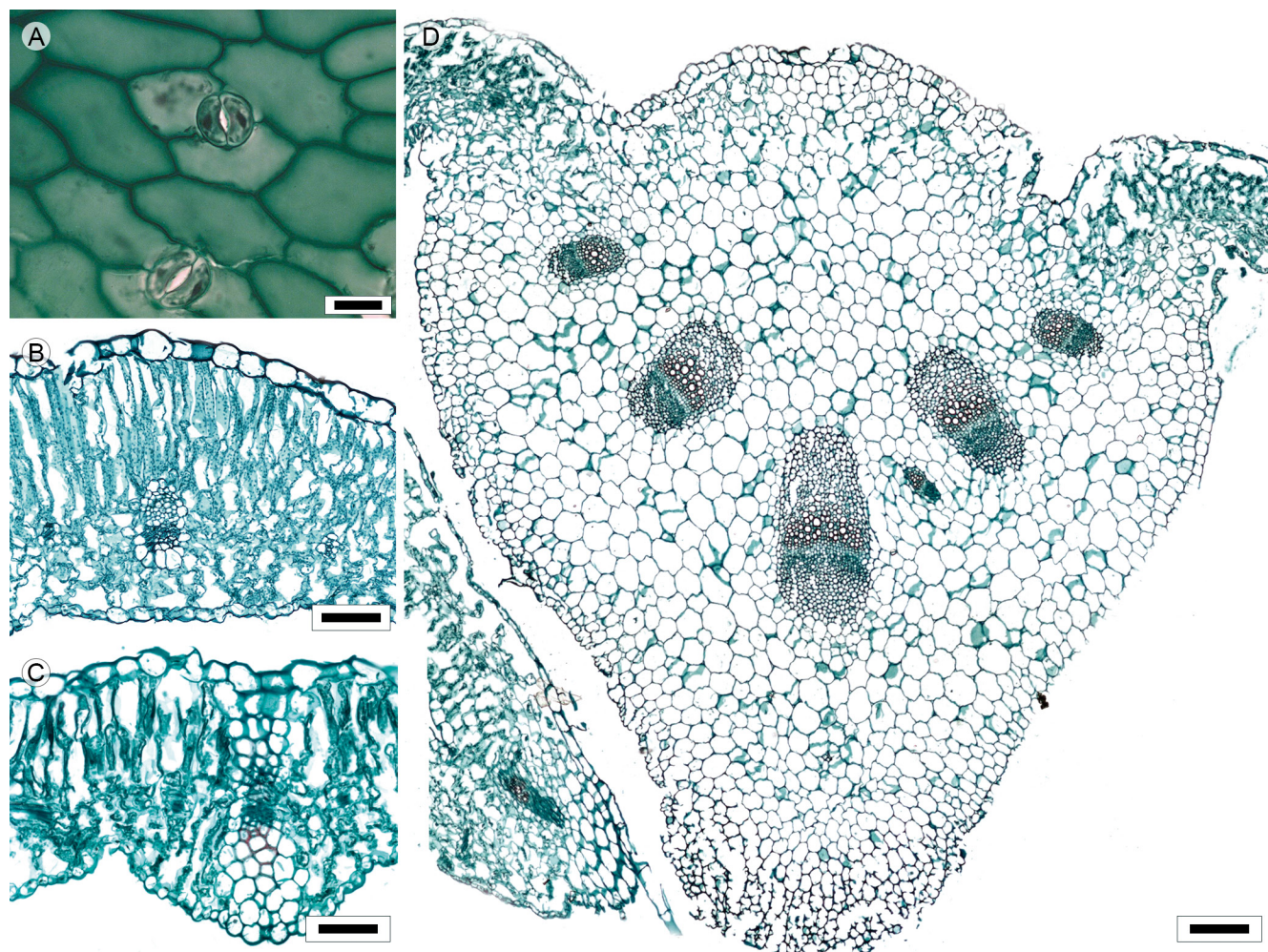


Figure 6: Lamina and midvein in Cardueae. A-D. *Cirsium vulgare* (Savi) Ten. Scale is 20 µm in A; 100 µm in B, C; 300 µm in D.

and ending in spines, apex acuminate and base cordate to amplexicaul; primary vein framework pinnate, primary vein straight, prominent, secondary venation brochidodromous, areole development moderate, veinlets simple, curved, unbranched, marginal ultimate venation looped; teeth lacking principal vein, with accessory vein straight, spinose; leaves amphistomatic; in surface view, cells elongated polygonal with straight anticlines (Fig. 6A), abaxial and adaxial surfaces pubescent, with multicellular trichomes and stiff hairs stomata anomocytic or anisocytic in the same plant, in transverse view, cuticle striate and 0.3 µm in thickness, epidermises uniseriate, with rectangular cells and thicker cells and outer periclinal walls, adaxial epidermis wider than abaxial epidermis, stomata at the same level as epidermal cells; mesophyll heterogeneous with two or three rows of palisade

parenchyma (Fig. 6B), occupying 54% of the mesophyll; collateral vascular bundles with a parenchymatous bundle sheath, girders seldom in secondary veins, with some lignified cells (Fig. 6C), canals absent; midvein contour protruded adaxially and sharply projected abaxially triangular (Fig. 6D), cuticle similar to lamina, epidermises uniseriate, with squared cells, immediately beneath the abaxial epidermis annular collenchyma (1-3 layers) and abundant parenchyma towards the vascular tissue, no palisade in the midvein, five to six collateral vascular bundles, the smaller ones towards the adaxial surface (Fig. 6D), within the bundles, xylem in clusters of two to nine vessels or radial rows of three to five vessels and parenchyma, phloem abundant and formed by five to seven rows of cells, caps of sclereids wide (10-12 layers) on each side of the vascular tissue.

Tribe Cichorieae

Four species: *Helminthotheca echioides* (L.) Holub, *Lactuca serriola* L., *Sonchus oleraceus* L. and *Taraxacum officinale* F.H. Wigg. (Figs. 1, 7).

Leaves sessile, although at the lamina base narrow looking like a petiole, leaves opposite or alternate, simple (*Helminthotheca* Vaill., *Lactuca* L., Fig. 1D) to pinnately lobed (*Sonchus* L., *Taraxacum* F.H. Wigg., Figs. 1E, F); lamina size mesophyll to macrophyll, lamina shape variable, generally elliptic to obovate, margin dentate or serrate, frequently combining both characteristics, edge of the leaf blade appear sinuous (*Helminthotheca*), apex straight, base truncate or lobate to cordate; primary vein framework pinnate or palmate (*Sonchus*), primary vein straight, prominent, secondary venation brochidodromous (*Helminthotheca*, *Lactuca*, *Taraxacum*) or basal actinodromous (*Sonchus*), areole development moderate, veinlets simple, straight (*Lactuca*, *Taraxacum*) or once-branched (*Helminthotheca*, *Sonchus*), marginal ultimate venation looped (*Lactuca*, *Sonchus*, *Taraxacum*) or incomplete (*Helminthotheca*); teeth principal vein terminating in a tooth apex (*Helminthotheca*, *Taraxacum*) or accessory veins straight (*Sonchus*); leaves amphistomatic or hypostomatic (*Sonchus*); in surface view, cells tetragonal or tetragonal elongated with S-undulate or U-undulate anticlines (Figs. 7A-C), both surfaces glabrous (*Sonchus*, *Taraxacum*) or bristly and glandular (*Helminthotheca*) and anomocytic stomata, in transverse view, cuticle smooth and thickness between 0.31 and 0.45 µm, epidermises uniseriate, with conical cells and thicker outer periclinal walls, adaxial epidermis wider than the abaxial (*Sonchus*, *Taraxacum*), stomata at the same level as epidermal cells; mesophyll heterogeneous (*Helminthotheca*, *Sonchus*, Figs. 7D, E) or homogeneous (*Lactuca*, *Taraxacum*, Fig. 7F), palisade occupying 36 to 46% of the mesophyll, collateral vascular bundles with a parenchymatous bundle sheath (Figs. 7D-F), girders present in all species and running across the mesophyll, canals absent; midvein contour ample flat adaxially and round sharply projected abaxially (Fig. 7G) or protruded in both surfaces with a large lysogenic area in *Taraxacum* (Fig. 7H), cuticle similar to lamina, epidermises uniseriate, with squared cells, immediately below a hypodermis (single layer) and parenchyma towards the

vascular tissue, with palisade parenchyma abaxially in *Taraxacum*, three to five collateral vascular bundles, within the bundles, xylem in radial rows of three to eight vessels separated by one or two rows of parenchyma, phloem formed by five to ten rows of cells, caps of sclereids (four to six layers) associated with xylem and phloem.

Tribe Coreopsideae

Six species: *Bidens odorata* Cav., *B. pilosa* L., *Cosmos bipinnatus* Cav., *C. parviflorus* (Jacq.) Pers., *Dahlia coccinea* Cav. and *Heterosperma pinnatum* Cav. (Figs. 1, 4, 8).

Leaves petiolate, rarely sessile (*C. bipinnatus*), opposite, generally pinnatisect or bipinnatisect; lamina size microphyll to mesophyll, lamina shape linear (*Cosmos* Cav., *Heterosperma* Cav.) or ovate to elliptic (*Bidens* L., *Dahlia* Cav., Figs. 1G, H), margin serrate (*Bidens*, *Dahlia*) or entire (*Cosmos*, *Heterosperma*), apex acuminate or straight, base truncate or concave; primary vein framework pinnate (Figs. 4B-D), primary vein straight or undulate (*Heterosperma*), prominent or weak (*Heterosperma*), secondary venation brochidodromous, areole development moderate (*Bidens*, *Dahlia*), poor (*Cosmos*) or lacking (*Heterosperma*), veinlets simple, curved (*Bidens*, *Heterosperma*), straight (*C. bipinnatus*) or once branched (*C. parviflorus*, *Dahlia*), marginal ultimate venation looped; teeth with principal vein and two accessory veins straight (*Bidens*), accessory veins convex (*Dahlia*) or absent (*Cosmos*, *Heterosperma*); leaves amphistomatic, in surface view, cells tetragonal elongated or polygonal elongated with straight (*Dahlia*) or S-undulated to U-undulated anticlines (Figs. 8A-C), both epidermises glabrous or glabrate (*Cosmos*, *Heterosperma*), with multicellular trichomes and glands (*Bidens*, *Dahlia*) and stomata anomocytic or anisocytic (*Dahlia*, *Heterosperma*), in transverse view, cuticle striate in all species except *C. parviflorus* and thickness between 0.23 and 0.42 µm, epidermises uniseriate, with cupola or conical cells and thicker outer periclinal walls, tannins occluding cell lumina in *Cosmos* (Fig. 8E), stomata at the same level as epidermal cells; mesophyll homogeneous in *C. bipinnatus* (Fig. 8D) and heterogeneous in *C. parviflorus* (Fig. 8E) and the rest of the species (Fig. 8F), palisade occupying 41 to 53% of the mesophyll; collateral vascular bundles with a parenchyma

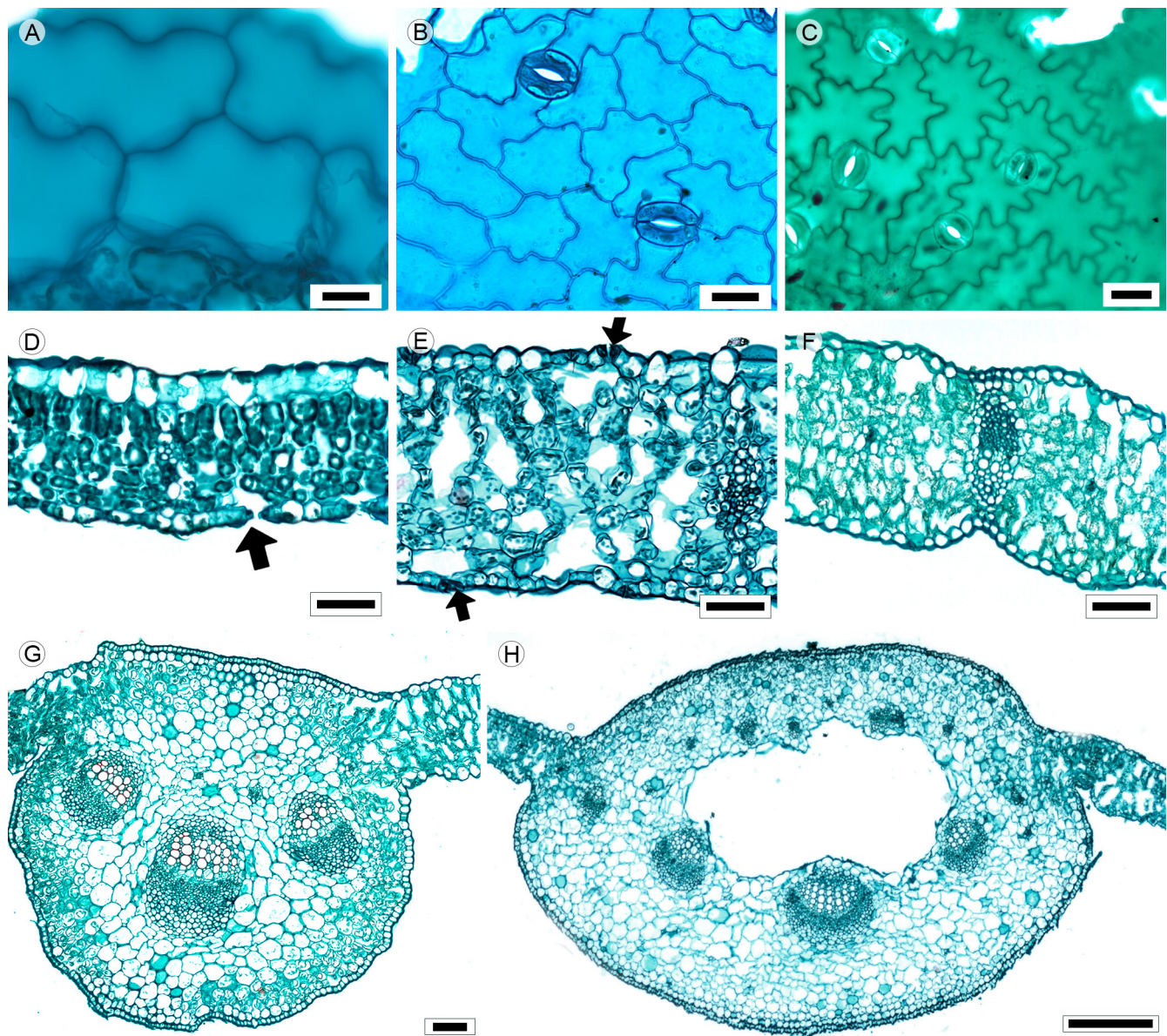


Figure 7: Lamina and midvein in Cichorieae. A, D. *Sonchus oleraceus* L.; B, E, H. *Taraxacum officinale* F.H. Wigg., C. *Lactuca serriola* L.; F, G. *Helminthotheca echioides* (L.) Holub. Scale is 20 µm in A-C; 50 µm in D, E, 100 µm in F, G; 300 µm in H.

matous bundle sheath (Figs. 8E, F), girders in *Dahlia* and *Heterosperma*, canals associated with vascular bundles or in the mesophyll (Fig. 8F); midvein contour projection on the adaxial surface and round and slightly protruding on the abaxial (*Bidens*, *Dahlia*, Fig. 8G) or convex adaxially and round abaxially (*Cosmos*, *Heterosperma* Figs. 8H, I), cuticle similar to lamina. epidermises uniseriate, with convex cells and thick-walled cells, below the adaxial epidermis one-three layers of annular collenchyma and palisade parenchyma and abaxially two layers of angular collenchyma, vascular tissue surrounded by parenchyma or a sheath (Fig.

8H), a single central collateral vascular bundle (*Cosmos*, *Heterosperma*) or three bundles (*Bidens*, *Dahlia*, Fig. 8G), within the bundles, xylem in radial rows of three to five vessels, phloem formed by three to five rows of cells, a cap of sclereids (three to four layers) external to xylem in *Bidens*.

Tribe Eupatorieae

Fourteen species: *Ageratina adenophora* (Spreng.) R.M. King & H. Rob., *A. choricephala* (B.L. Rob.) R.M. King & H. Rob., *A. cylindrica* (McVaugh) R.M. King & H. Rob., *A. deltoidea* (Jacq.) R.M. King & H. Rob., *Brickellia secundiflora*

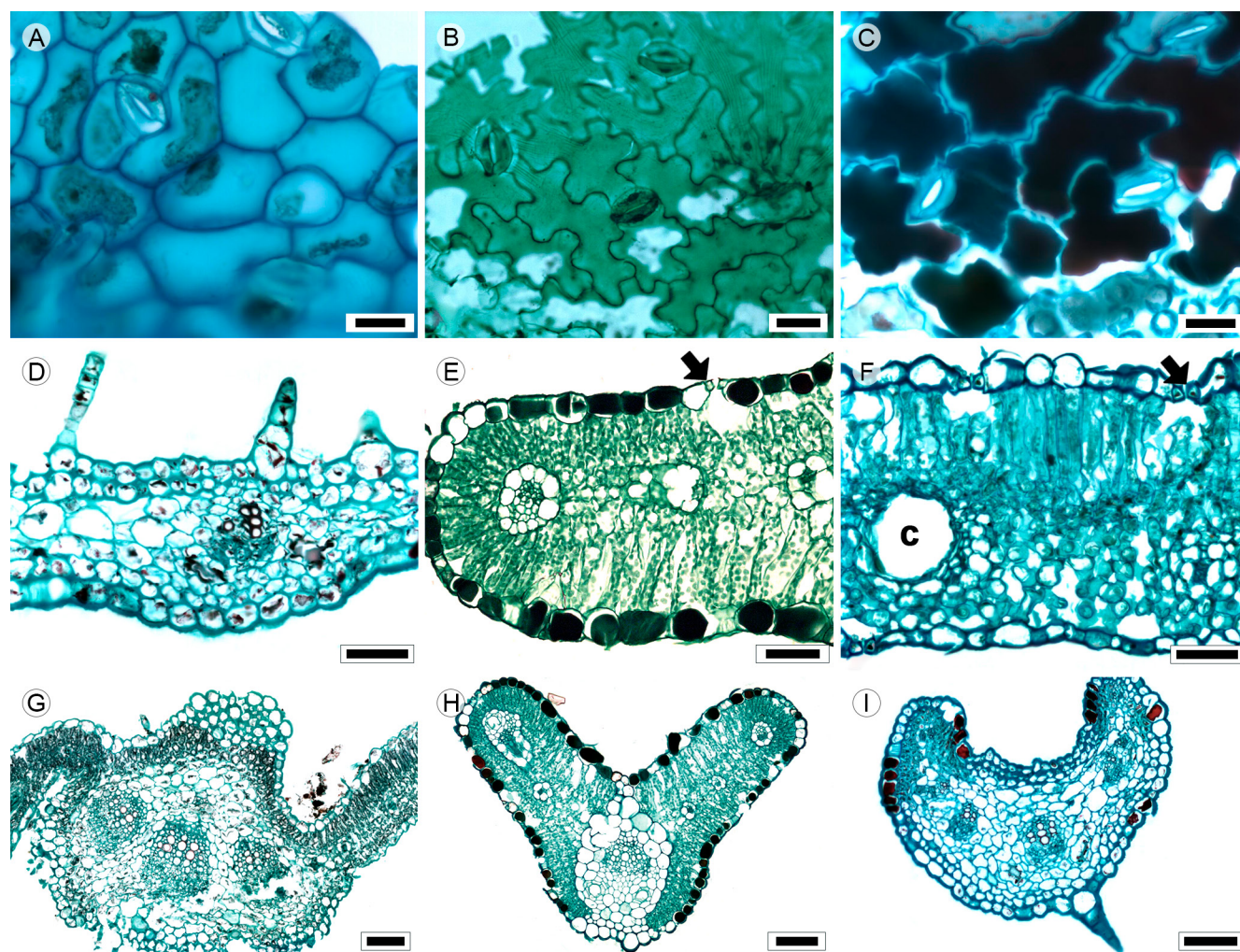


Figure 8: Lamina and midvein in Coreopsideae. A, F. *Dahlia coccinea* Cav.; B. *Bidens odorata* Cav.; C, E, G. *Cosmos parviflorus* (Jacq.) Pers.; D, I. *Cosmos bipinnatus* Cav.; H. *Cosmos parviflorus* (Jacq.) Pers. Scale is 20 μ m in A-C; 50 μ m in D-F, 100 μ m in G-I. c=canal.

(Lag.) A. Gray, *B. veronicifolia* (Kunth) A. Gray, *Chromolaena pulchella* (Kunth) R.M. King & H. Rob., *Fleischmannia pycnocephala* (Less.) R.M. King & H. Rob., *Piqueria trinervia* Cav., *Stevia micrantha* Lag., *S. origanoides* Kunth, *S. salicifolia* Cav., *S. subpubescens* Lag. and *S. tomentosa* Kunth (Figs. 1, 4, 9).

Leaves petiolate rarely sessile (*S. salicifolia*), opposite, simple (Fig. 11); lamina size variable from microphyll (*B. veronicifolia*) to macrophyll (*A. deltoidea*), lamina shape ovate to elliptic, linear (*S. salicifolia*) or triangular (*A. deltoidea*), margin crenate to serrate, sometimes both (*Stevia* Cav.), apex straight to rounded, base highly variable: truncate, concave, concavo-convex, cuneate or cordate; primary vein framework pinnate or palmate, primary vein

straight, prominent or weak (*Ageratina* Spach, *Stevia*), secondary venation brochidodromous or actinodromous basal (*Fleischmannia* Sch. Bip., *Stevia*, Figs. 4F, G), areole development moderate or poor (*Brickellia* Elliott), veinlets simple, curved, linear (*Ageratina*) or once-branched (*Chromolaena* DC., *S. tomentosa*), marginal ultimate venation looped; teeth with accessory veins and simple or lacking teeth (*Chromolaena*); leaves hypostomatic in most species, just four species amphistomatic (*A. cylindrica*, *P. trinervia*, *S. origanoides*, *S. salicifolia*); in surface view, cells tetragonal-elongated or polygonal with straight, V-undulated, U-undulated or S-undulated anticlines (Figs. 9A-C), both surfaces tomentose, rarely glabrous (*Piqueria*), with multicellular trichomes and stomata anomocytic, anisocytic (*S. origanoides*) or staurocytic (*A. cylindrica*, *P. trinervia*, *S.*

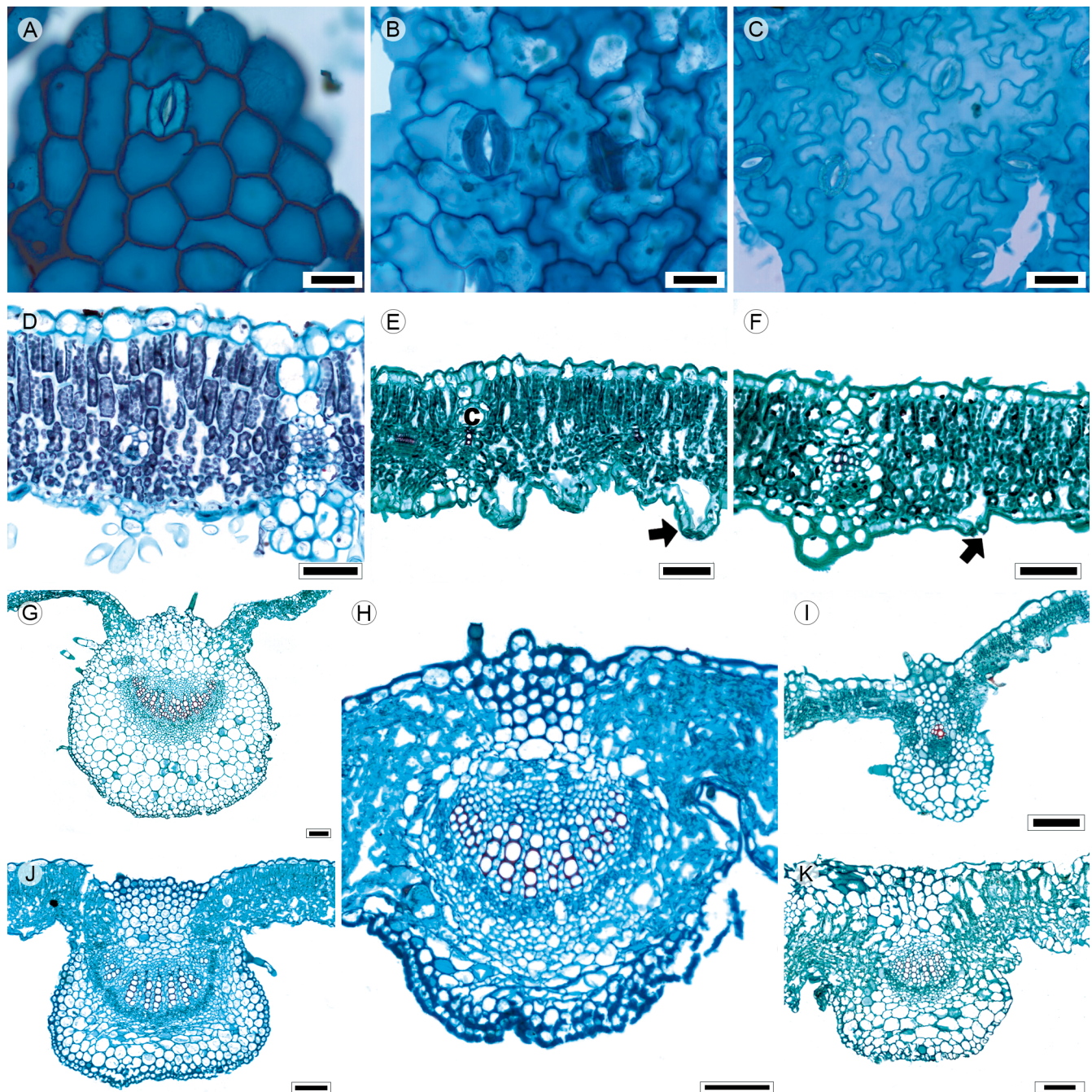


Figure 9: Lamina and midvein in Eupatorieae. A, K. *Stevia organoides* Kunth; B. *Stevia salicifolia* Cav.; C, D. *Stevia tomentosa* Kunth, E. *Brickellia veronicifolia* (Kunth) A. Gray; F. *Fleischmannia pycnocephala* (Less.) R.M. King & H. Rob.; G. *Ageratina deltoidea* (Jacq.) R.M. King & H. Rob.; H. *Piqueria trinervia* Cav.; I. *Brickellia secundiflora* (Lag.) A. Gray; J. *Ageratina choricephala* (B.L. Rob.) R.M. King & H. Rob. Scale is 20 μm in A-C; 50 μm in D-F, 100 μm in H-K; 300 μm in G.

salicifolia); in transversal view, cuticle striate and 0.21 to 0.60 μm in thickness, epidermises uniseriate, with rectangular or convex cells and thicker outer periclinal walls (Figs. 9D-F), adaxial epidermis sometimes wider than the abaxial (*A. cylindrica*, *A. deltoidea*, *Brickellia*, *Chromolaena*, *Fleischmannia*, *Stevia*), stomata at the same level or above the

epidermal cells (*A. deltoidea*, *Brickellia*, *C. pulchella*, *Fleischmannia*, *S. micrantha*, *S. organoides*, Figs. 9E, F); mesophyll heterogeneous (Figs. 9D-F), except in *Piqueria*, homogeneous, palisade occupying 45 to 56% of the mesophyll, collateral vascular bundles with a parenchymatous bundle sheath or sclerenchyma (*S. salicifolia*), girders in secondary

veins (Fig. 9F), canals associated with vascular bundles or in the mesophyll; midvein contour flat or slightly projected adaxially and abaxially round or square protruded or highly protruded (Figs. 9G-K), cuticle conspicuously striate, epidermises uniseriate, with square and convex cells and thicker outer periclinal walls, below both epidermises, angular collenchyma (1 to 3 layers) limited by the mesophyll (*Piqueria*) or exclusively parenchyma (Fig. 9K), a central collateral vascular bundle forming an open arc, within the bundle, xylem in clusters of three to ten vessels or radial rows of three to five vessels separated by radial rows of parenchyma, phloem formed by one to five rows of cells, caps of parenchyma or sclerenchyma (three to seven layers) associated to xylem and phloem (Fig. 9H).

Tribe Gnaphalieae

Three species: *Pseudognaphalium canescens* (DC.) Anderb., *P. semilanatum* (DC.) Anderb. and *P. viscosum* (Kunth) Anderb. (Figs. 1, 10).

Leaves sessile, alternate, simple (Fig. 1J); lamina size microphyll, lamina shape elliptic to oblong, margin entire, revolute (*P. viscosum*), apex straight to acuminate, base truncate, sometimes cordate to sagittate (*P. viscosum*); primary vein framework pinnate, primary vein straight, weak, secondary venation brochidodromous, areole development moderate, veinlets simple, curved, marginal ultimate venation looped; teeth absent; leaves hypostomatic (*P. canescens*, *P. semilanatum*) or amphistomatic (*P. viscosum*); in surface view, cells tetragonal or elongated tetragonal with U-undulated to V-undulated anticlines (Figs. 10A-C), adaxial surface hirsute, abaxially densely tomentose, with glandular trichomes and anomocytic stomata, in transverse view, cuticle apparently smooth and between 0.20 and 0.42 µm in thickness, epidermises uniseriate, with rectangular and conical cells (Figs. 10D, E), adaxial epidermis wider than abaxial, stomata at the same level as epidermal cells; mesophyll heterogeneous with one to two rows of palisade parenchyma, palisade occupying 41 to 46% of the mesophyll; vascular bundles collateral with a parenchymatous bundle sheath in *P. canescens* and *P. semilanatum*, with girders (Figs. 10D, E), canals absent; midvein contour flat or slightly convex adaxially and abaxially round and protruded (Figs.

10F-H), cuticle similar to lamina, epidermises uniseriate with convex cells and thick outer periclinal walls, immediately beneath the abaxial epidermis a layer of angular collenchyma and mesophyll extending to most of the abaxial faces, abundant parenchyma surrounding the vascular tissue, a single central collateral vascular bundle, within the bundle, xylem in radial rows of two to five vessels, phloem formed by three to four rows of cells, a cap of parenchyma (two or three layers) associated with phloem.

Tribe Heliantheae

Eleven species: *Acmella repens* (Walter) Rich., *Aldama buddleiiformis* (DC.) E.E. Schill. & Panero, *A. excelsa* (Willd.) E.E. Schill. & Panero, *Ambrosia cumanaensis* Kunth, *Lagascea rigida* (Cav.) Stuessy, *Montanoa grandiflora* Alamán ex DC., *M. tomentosa* Cerv., *Simsia amplexicaulis* (Cav.) Pers., *Tithonia tubiformis* (Jacq.) Cass., *Verbesina virgata* Cav. and *Zinnia peruviana* (L.) L. (Figs. 1, 4, 11).

Leaves petiolate or sessile, opposite, sometimes alternate near the apex, simple or pinnately lobed (*Ambrosia* L., Fig. 1K; *M. grandiflora*, *Simsia* Pers.); lamina size microphyll to megaphyll, lamina shape ovate to elliptic, margin entire (*Acmella* Rich. ex Pers., *Aldama* La Llave, *Zinnia* L.), crenate to serrate (*M. grandiflora*), dentate (*V. virgata*) and erose (*Simsia*), apex straight to acuminate, base truncate, concave, cuneate or cordate (Figs. 1L, M); primary vein framework pinnate or palmate, primary vein straight (Fig. 4H), prominent (*Lagascea* Cav.), secondary venation brochidodromous or actinodromous basal (*Aldama*, *M. tomentosa*, *Tithonia* Desf. ex Juss., *Zinnia*, Fig. 4H), areole development moderate or good (*Lagascea*), veinlets once-branched (*Acmella*, *M. tomentosa*), simple, straight (*Aldama*, *Ambrosia*, *Lagascea*, *Tithonia*, *Zinnia*) or simple curved in the other taxa, marginal ultimate venation looped or incomplete (*Simsia*, *Verbesina* L.); teeth with primary and accessory veins straight (*Ambrosia*), only accessory veins curved (*Acmella*, *Simsia*, *Tithonia*, *Verbesina*) or absent (*Aldama*, *Lagascea*, *Zinnia*); leaves amphistomatic, rarely hypostomatic; in surface view, cells tetragonal, tetragonal-elongated or polygonal with straight to S-undulate anticlines (Figs. 11A-C), both epidermises hispid to tomentose, with glands and unicellular or multicellular trichomes and

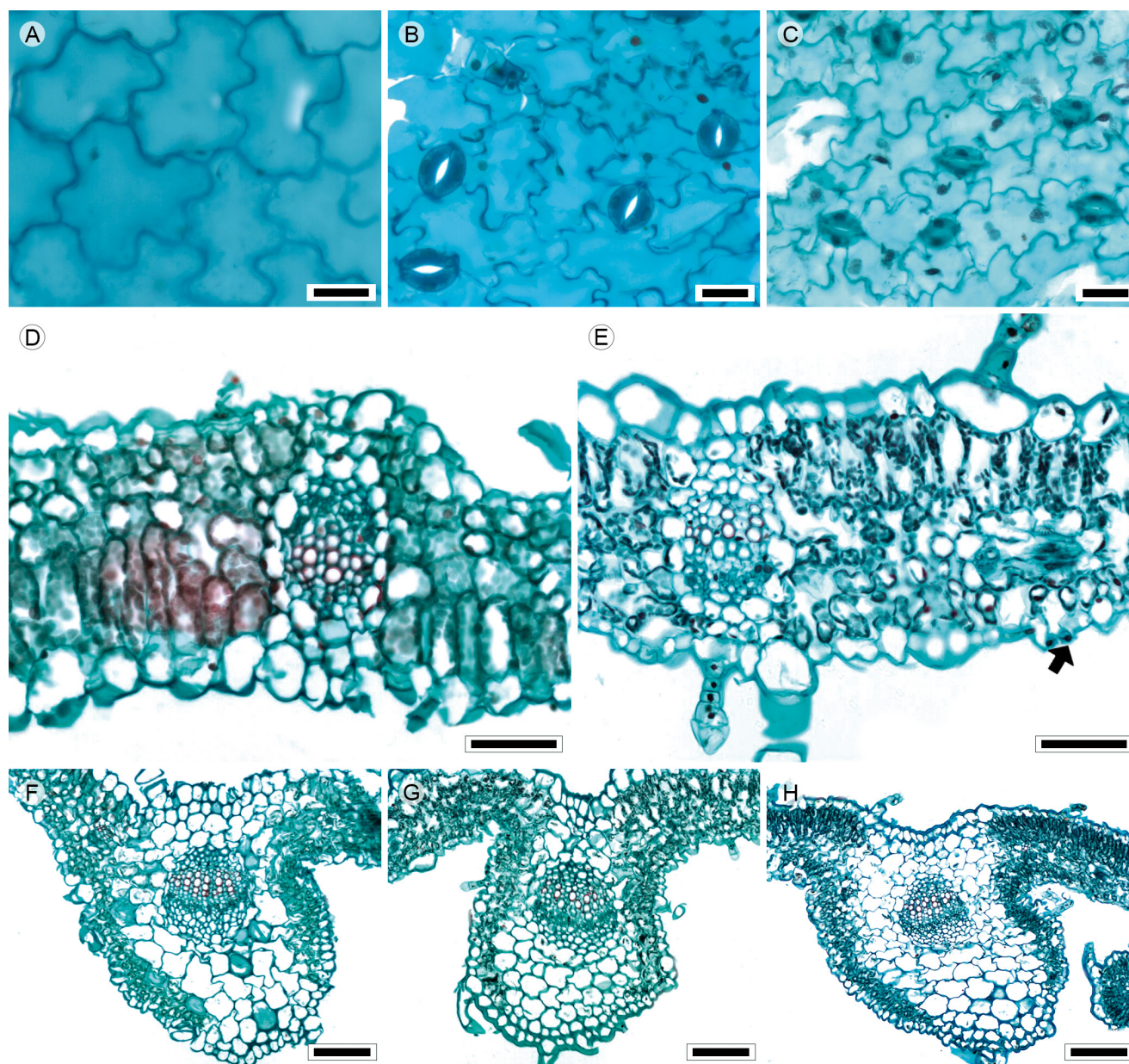


Figure 10: Lamina and midvein in Gnaphalieae. A, D, F. *Pseudognaphalium canescens* (DC.) Anderb.; B, E, G. *Pseudognaphalium semilanatum* (DC.) Anderb.; C, H. *Pseudognaphalium viscosum* (Kunth) Anderb. Scale is 20 μm in A-C; 50 μm in D, E, 100 μm in F-H.

stomata anomocytic, anisocytic or staurocytic (*Lagascea*), in transverse view, cuticle striate and between 0.21 and 1.15 μm in thickness, epidermises uniseriate, with cupola or rectangular cells and thicker outer periclinal walls, adaxial epidermis is wider than abaxial in most species or both are equally wide (*Acmella*, *Lagascea*, *Verbesina*), stomata at the same level as other epidermal cells or above (Fig. 11G); mesophyll heterogeneous (Figs. 11D-G), palisade occupying from 32 to 100% of the mesophyll (*Aldama*, *Lagascea*, *Simsia*); collateral vascular bundles with a parenchy-

matous bundle sheath, girders of parenchyma (Figs. 11D, E) or sclerenchyma (*Aldama*, *Lagascea*, Fig. 11F), secondary veins with angular collenchyma toward both surfaces, canals associated with vascular bundles; midvein contour flat or protruded on the adaxial surface and abaxially round and protruding (Figs. 11H-J) or a crest toward both surfaces (*Ambrosia*, Fig. 11G), cuticle similar to lamina, epidermises uniseriate with cupola cells and thicker outer periclinal walls, immediately beneath the epidermises, parenchyma (Fig. 11H) or annular or angular collenchyma, frequently

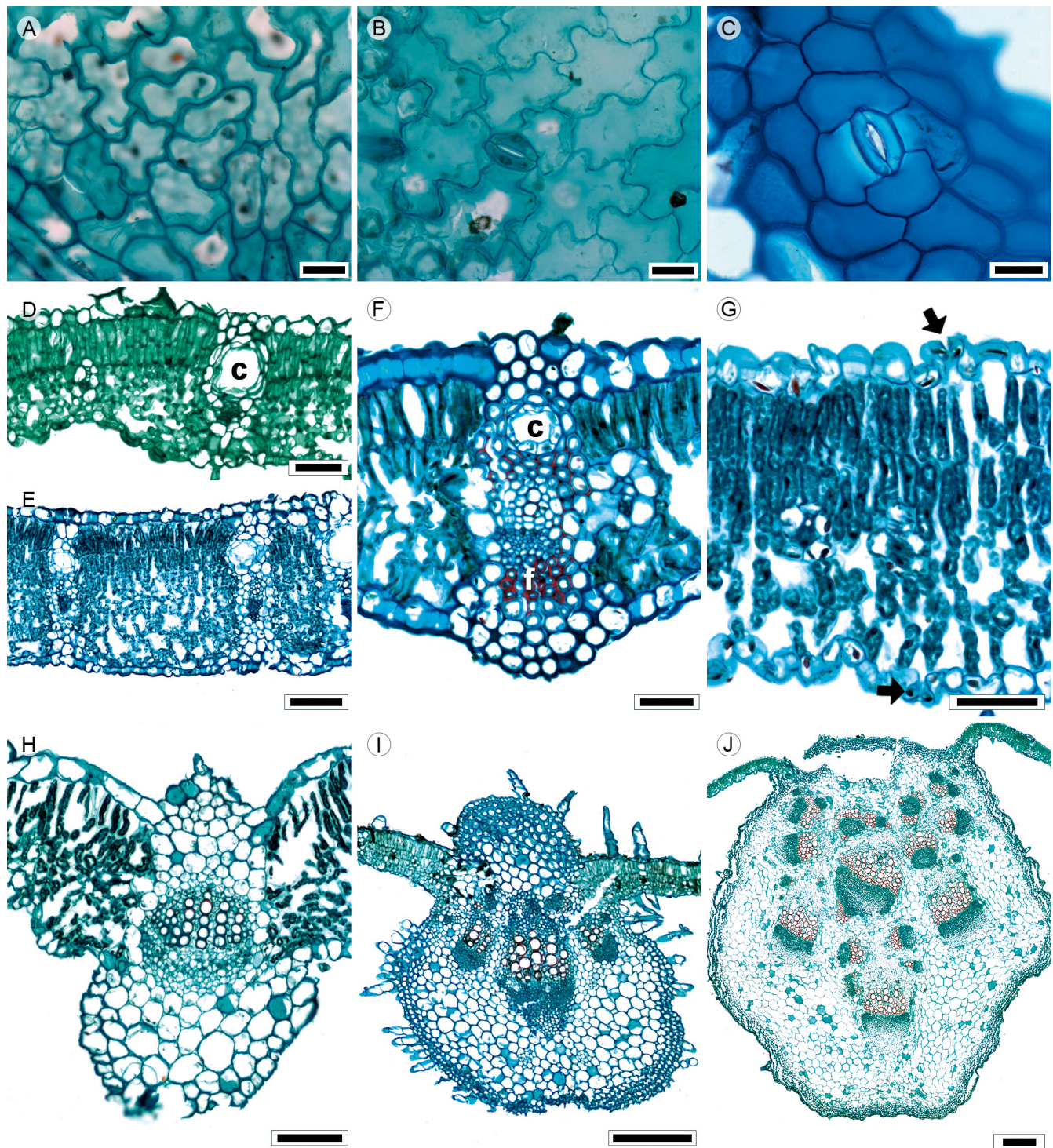


Figure 11: Lamina and midvein in Heliantheae. A, D. *Montanoa tomentosa* Cerv., B, J. *Montanoa grandiflora* Alamán ex DC.; C, F. *Lagascea rigida* (Cav.) Stuessy, E. *Verbesina virgata* Cav.; G. *Ambrosia cumanensis* Kunth, H. *Zinnia peruviana* (L.) L.; I. *Tithonia tubiformis* (Jacq.) Cass. Scale is 20 µm in A-C; 50 µm in D, F, G, 100 µm in E, H; 300 µm in I, J. c=canal.

continuous (four to five layers, Figs. 11I, J) or discontinuous (two to five layers), mesophyll or parenchyma towards the vascular tissue, a single central collateral vascular bundle or more than ten bundles (Figs. 11H-J), within the bundles,

xylem in radial rows of two to ten vessels or in clusters of three to fifteen or more vessels, phloem formed by five to ten rows of cells, caps of parenchyma (*Simsia*, *Zinnia*) or sclerenchyma associated with xylem and phloem.

Tribe Millerieae

Four species: *Galinsoga parviflora* Cav., *Jaegeria hirta* (Lag.) Less., *Melampodium longifolium* Cerv. ex Cav. and *M. perforiatum* (Cav.) Kunth (Figs. 1, 4, 12).

Leaves sessile (*Jaegeria* Kunth) or petiolate (*Galinsoga* Ruiz & Pav., *Melampodium* L.), opposite and simple; lamina size notophyll to mesophyll, lamina shape elliptic, obovate or ovate, margin crenate to serrate (Fig. 1N), apex acuminate to straight, base cuneate to rounded, sometimes concave (*Galinsoga*) or sagittate (*Melampodium*); primary vein framework palmate (Fig. 4I), primary veins straight, prominent, secondary venation actinodromous basal, areole development moderate, veinlets simple, curved (*Galinsoga*), straight (*Jaegeria*) or once-branched (*Melampodium*), marginal ultimate venation looped (*Jaegeria*, *Galinsoga*) or incomplete (*Melampodium*), teeth with accessory veins straight; leaves amphistomatic; in surface view, cells tetragonal-elongated with S-undulated, U-undulated or V-undulated anticlines (Figs. 12A-C), both epidermis strigose to hirsute, with multicellular trichomes and stomata anomocytic, in transverse view, the cuticle apparently smooth and between 0.23 and 0.24 µm in thickness, epidermises uniseriate, with cupola or rectangular cells and thicker outer periclinal walls, adaxial epidermis wider than the abaxial, stomata at the same level as the epidermal cells; mesophyll heterogeneous (Figs. 12C, D), palisade occupying 25 to 39% of the mesophyll, in *Jaegeria* most of the mesophyll occupied by aerenchyma (Fig. 12C); collateral vascular bundles with a parenchymatous bundle sheath and girders (*Galinsoga* and *Melampodium*), canals associated with vascular bundles; midvein contour with a projection on the adaxial surface and abaxially wide slightly protruding (*Jaegeria*) or round and protruding (Figs. 12G-I), cuticle similar to lamina, epidermises uniseriate, rectangular or convex cells with thicker outer periclinal walls, immediately beneath the epidermises parenchyma or annular collenchyma, one to three layers, restricted to the projections and parenchyma towards vascular tissue, a central arc of vascular tissue (Figs. 12G, I) and in *Galinsoga* opposite to the main arc phloem and some vessels evident (Fig. 12H), within the bundle, xylem in radial rows of two to five vessels or clusters of five to

ten vessels, phloem formed by one to four rows of cells, caps associated to vascular tissue absent.

Tribe Nassauvieae

One species: *Acourtia cordata* (Cerv.) B.L. Turner (Fig. 13).

Leaves sessile, alternate and simple; lamina size macrophyll, lamina shape elliptic to oblong, margin dentate, apex convex, base cordate; primary vein framework pinnate, primary vein straight, prominent, secondary venation brochidodromous, areole development moderate, veinlets simple, curved, marginal ultimate venation looped; teeth more than one central plus two accessories straight; leaves amphistomatic; in superficial view, cells tetragonal-elongated with S-undulate anticlines (Fig. 13A), both surfaces pubescent, with multicellular trichomes and stomata anomocytic or anisocytic, in transverse view, the cuticle smooth and less than 0.06 µm in thickness, epidermises uniseriate, with convex cells and thicker outer periclinal walls, both epidermis of the same width, stomata at the same level as epidermal cells; mesophyll heterogeneous with one row of palisade parenchyma, occupying 26% of the mesophyll (Fig. 13B); collateral vascular bundles with a parenchymatous sheath, girders present in secondary veins and usually composed of sclerenchyma associated to phloem (Fig. 13C), canals absent; midvein contour adaxially flat and abaxially protruded triangular (Fig. 13D), cuticle similar to lamina, epidermises uniseriate with narrow convex cells and thick outer periclinal walls, immediately beneath the epidermises, angular collenchyma of one or two layers and parenchyma towards the vascular tissue, three collateral vascular bundles, within the bundles, xylem with more than twelve vessels, separated by parenchyma, phloem formed by six to ten rows of cells, caps of abundant sclerenchyma associated with xylem and phloem (Fig. 13D).

Tribe Senecioneae

Three species: *Barkleyanthus salicifolius* (Kunth) H. Rob. & Brettell, *Pittocaulon praecox* (Cav.) H. Rob. & Brettell and *Roldana lobata* La Llave (Figs. 1, 14).

Leaves petiolate, alternate and simple; lamina size mesophyll to macrophyll, lamina shape ovate-elliptic (*Pit-*

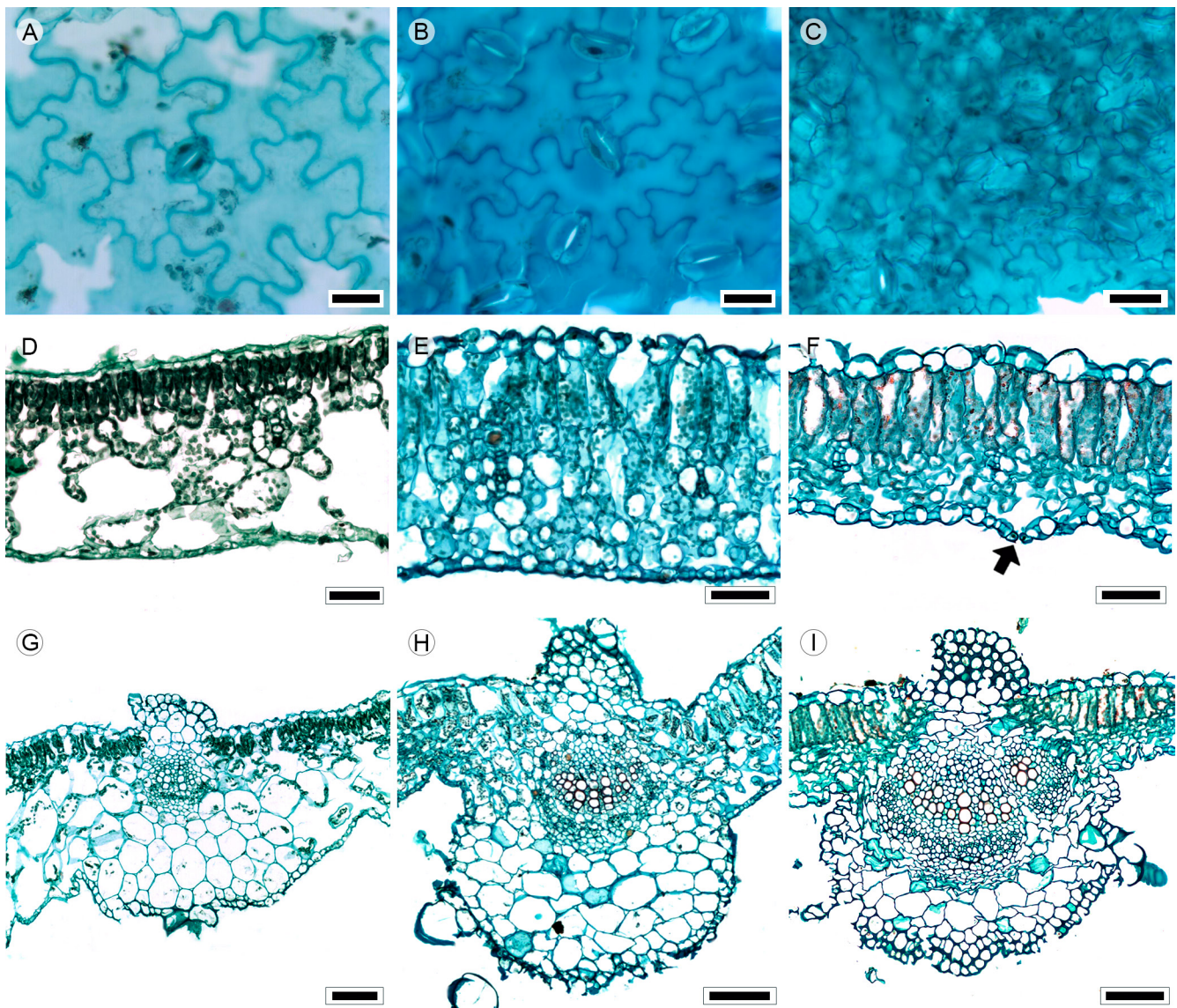


Figure 12: Lamina and midvein in Millerieae. A, D, G. *Jaegeria hirta* (Lag.) Less.; B, E, H. *Galinsoga parviflora* Cav.; C. *Melampodium longifolium* Cerv. ex Cav.; F, I. *Melampodium perfoliatum* (Cav.) Kunth. Scale is 20 μ m in A-C; 50 μ m in D-F, 100 μ m in G-I.

tocaulon H. Rob. & Brettell) or linear-elliptic (*Barkleyanthus* H. Rob. & Brettell, *Roldana* La Llave), margin entire, serrate or dentate, apex acuminate acute (*Barkleyanthus*, Fig. 10; *Pittocaulon*, *Roldana*), base lobate (*Pittocaulon*, Fig. 1P), rounded to truncate (*Roldana*) or cuneate (*Barkleyanthus*); primary vein framework pinnate or actinodromous, primary vein straight, prominent, secondary venation is parallelodromous (*Barkleyanthus*), actinodromous suprabasal (*Pittocaulon*) or mixed craspedrodromous (*Roldana*), areole development moderate (*Barkleyanthus*, *Pittocaulon*) or good (*Roldana*), veinlets once-branched (*Barkleyanthus*, *Pittocaulon*) or absent (*Roldana*), marginal ultimate vena-

tion looped; teeth with accessory veins (*Barkleyanthus*, *Roldana*) or absent (*Pittocaulon*); leaves amphistomatic or hypostomatic, in surface view, cells polygonal-elongated with straight anticlines (Figs. 14A-C), both epidermises glabrous or glabrate and stomata anomocytic, in transverse view, the cuticle striate and between 0.36 and 0.46 μ m in thickness, epidermises uniseriate, with rectangular or conical cells and thicker outer periclinal walls, both epidermis equally in width, stomata at the same level as the epidermal cells; mesophyll heterogeneous (Fig. 14D) or homogeneous (*Pittocaulon*, *Roldana*, Figs. 14E, F), palisade occupying 53% of the mesophyll (*Barkleyanthus*); collater-

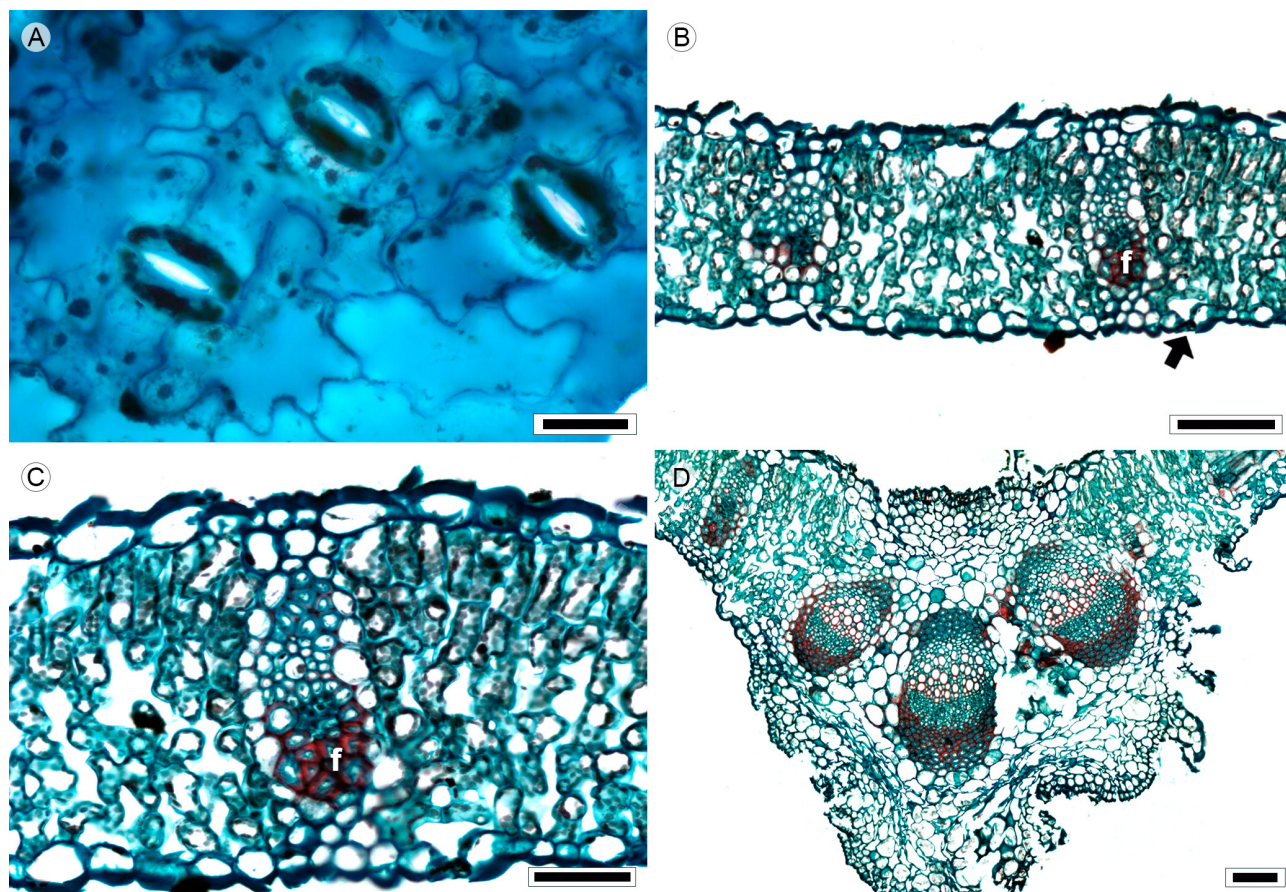


Figure 13: Lamina and midvein in Nassauvieae. A-D. *Acourtia cordata* (Cerv.) B.L. Turner. Scale is 20 μm in A; 100 μm in B, D; 50 μm in C. f=fibers.

al vascular bundles with a parenchymatous bundle sheath, girders in secondary veins, canals associated with vascular bundles or in the mesophyll (*Barkleyanthus*); midvein contour slightly convex or protruded adaxially and abaxially round and protruded (Figs. 14G, I) or gently protruded in both surfaces (Fig. 14H), cuticle similar to lamina, epidermises uniseriate with convex cells and thicker outer periclinal walls, immediately beneath the epidermis angular collenchyma, one to three layers surrounding almost all the midrib (*Pittocaulon*), restricted to a small region in either surface (*Barkleyanthus*) or lacking (*Roldana*), a single central collateral vascular bundle or three bundles forming an arc (Fig. 14E), within the bundle, xylem in radial rows of two to ten vessels, phloem formed by two to five rows of cells, cap of sclerenchyma associated with xylem.

Tribe Tageteae

Four species: *Dyssodia papposa* (Vent.) Hitchc., *Pectis prostrata* Cav., *Tagetes micrantha* Cav. and *T. tenuifolia* Cav. (Figs. 1, 4, 15).

Leaves sessile, opposite, simple (*Pectis* L.) or pinnatisect (*Dyssodia* Cav., *Tagetes* L., Figs. 1Q, R); lamina size nanophyll to mesophyll, lamina shape linear-elliptic to obovate, margin entire (*P. prostrata*, *T. micrantha*), toothed (*Dyssodia*) or serrate (*T. tenuifolia*), apex straight or acuminate, base cuneate or truncated; primary vein framework pinnate (Figs. 4J, K), primary vein straight, prominent, secondary venation brochidodromous, areole development moderate (*T. tenuifolia*), poor (*Dyssodia*, *Pectis*) or lacking (*T. micrantha*), veinlets simple, curved (*Dyssodia*, *Tagetes*), straight (*Pectis*) or absent (*Pectis*), marginal ultimate venation looped (*Pectis*, *Tagetes*) or incomplete (*Dyssodia*); teeth with primary and accessory veins straight, primary vein termination at the apex of tooth; leaves amphistomatic; in surface view, cells tetragonal, tetragonal-elongated or polygonal with straight to S-undulate anticlines (Figs. 15A-C), glabrate in both surfaces and stomata anomocytic or anisocytic, in transverse view, the cuticle striated or smooth and between 0.19 and 0.44 μm in thickness, epidermises uniseriate, with square

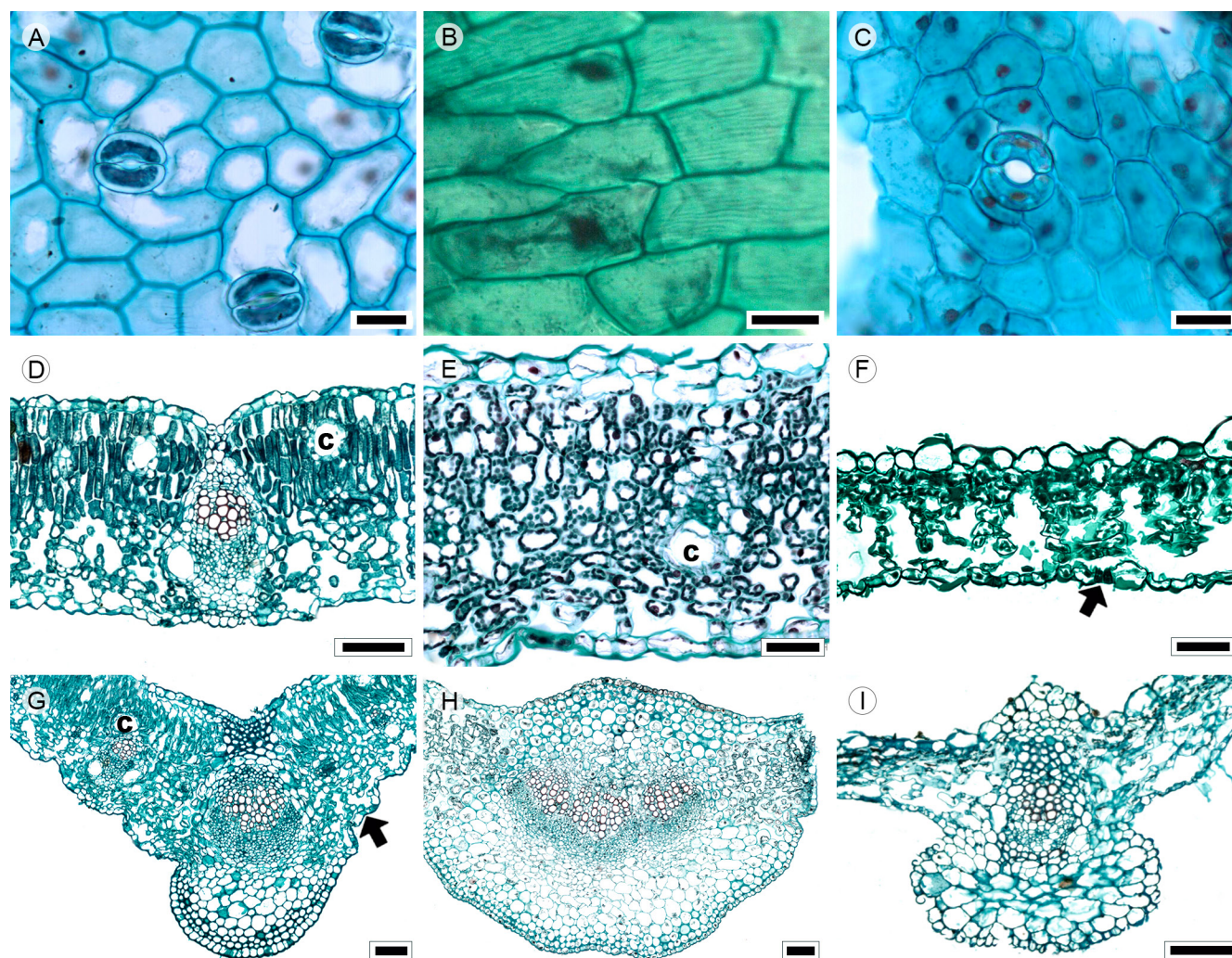


Figure 14: Lamina and midvein in Senecioneae. A, D, G. *Barkleyanthus salicifolius* (Kunth) H. Rob. & Brettell; B, E, H. *Pittocaulon praecox* (Cav.) H. Rob. & Brettell; C, F, I. *Roldana lobata* La Llave. Scale is 20 μ m in A-C; 50 μ m in E, F; 100 μ m in D, G-I; 300 μ m in I, J. c=canal.

or convex cells and thicker outer periclinal walls, both epidermises equal in width, tannins occluding cell lumina in *Dyssodia*, stomata at the same level as the epidermal cells; mesophyll heterogeneous (Figs. 15D-F), palisade occupying 27 to 42% of the mesophyll; collateral vascular bundles with a parenchymatous bundle sheath, paraveinal mesophyll between vascular bundles (Fig. 15D), canals associated with vascular bundles or in the mesophyll (Fig. 15E); midvein contour adaxially flat and abaxially gently protruded (*Pectis*, (Fig. 15H, *T. micrantha*) or adaxially flat and abaxially protruded round (*T. tenuifolia*) or triangular (*Dyssodia*) (Figs. 15G, I), cuticle conspicuously striate and thicker than the lamina, epidermises uniseriate with convex cells and thicker outer periclinal walls, immediately beneath the epidermises, a layer of annular collenchyma and parenchyma towards

the vascular tissue, a single central collateral vascular bundle or three bundles (Fig. 15H), within the bundles, xylem in grouped in radial rows of two to four vessels, phloem formed of two to three rows of cells, caps of sclerenchyma (one to three layers) associated with phloem and mainly xylem.

Discussion

We find that most of the studied species are petiolate (61%), simple (68%) and microphyll (29%). The laminar shape is most often ovate (45%) with some type of vascularized margin projections in 62% of the species. The brochidodromous venation pattern predominates (62%), followed by actinodromous (33%); areole development is moderate in 86% of the species and the freely ending veinlets are simple and curved in 53% of these; 90% of the species have looped

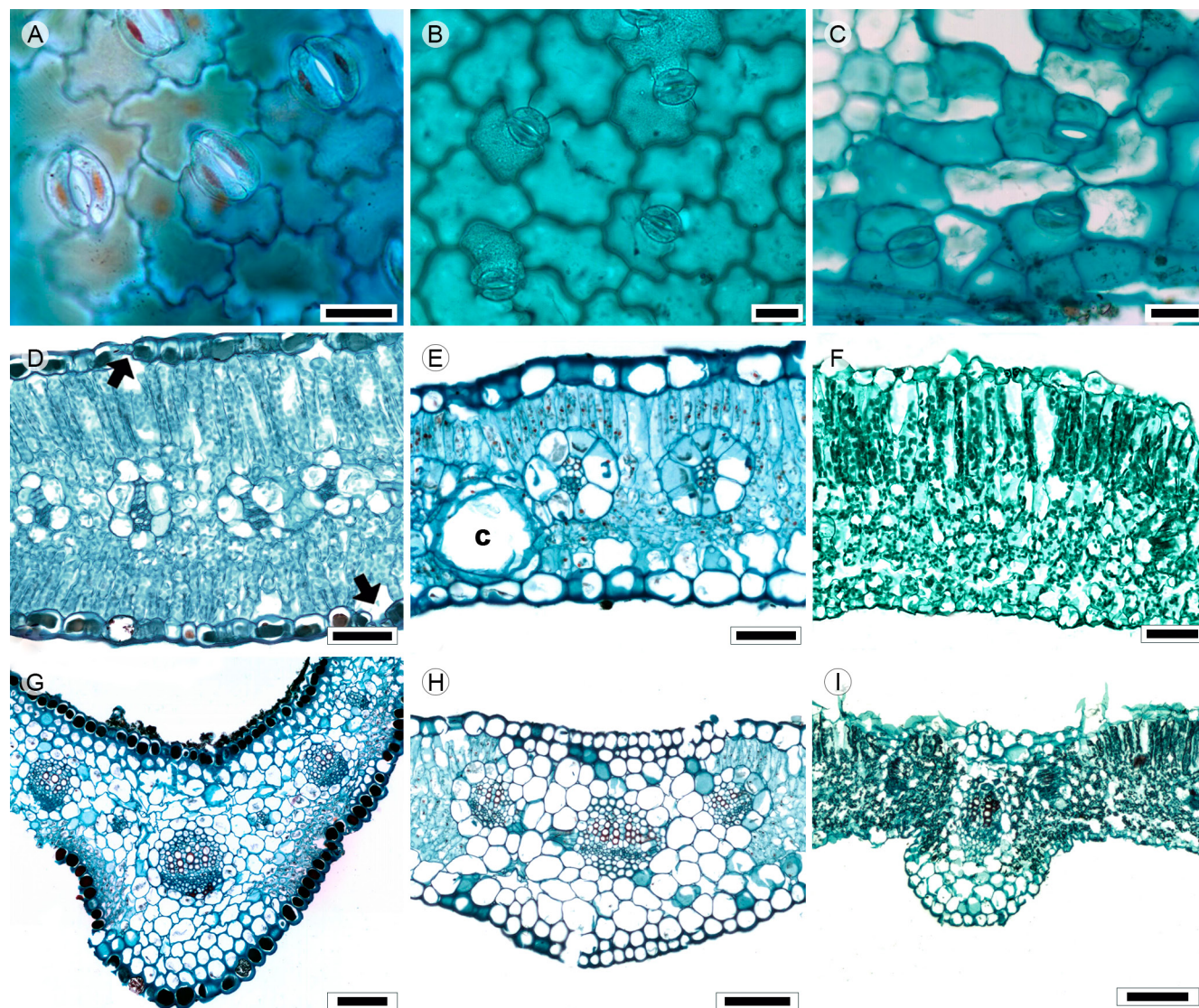


Figure 15: Lamina and midvein in Tageteae. A, D, G. *Dyssodia papposa* (Vent.) Hitchc.; B, E, H. *Pectis prostrata* Cav.; C. *Tagetes micrantha* Cav.; F, I. *Tagetes tenuifolia* Cav. Scale is 20 μ m in A-C; 50 μ m in D-F, 100 μ m in G-I.

marginal ultimate venation. The leaves are amphistomatic (66%) with anomocytic stomata (62%). Seventy four percent of the species have striate cuticle. The surface of 75% of the species is pubescent. The stomata of 77% of the species are at the same level as the rest of the epidermal cells. Epidermal cells in superficial view are tetragonal-elongated with S-undulated anticlines (63%). Almost all species (98%) have a vascular bundle sheath, but only in 73% of these there are sheath extensions, whereas sclerified cells associated with bundle sheaths are rare in the species studied, as in other members of the family (Aytas-Akcin and Akcin, 2017). Bundle sheaths have also been recorded for other taxa of Asteraceae (Bombo et al., 2012; Chwil et al., 2015;

Mendes et al., 2016; De Sousa et al., 2018; Lusa et al., 2018) and they appear to be one of the most common traits in the family.

Although we did not find a unique combination of characters for any of the tribes, some patterns exist. For instance, the brochidodromous venation pattern appears to be the most common trait in most tribes, except in Senecioneae which has three different types (parallelodromous, actinodromous suprabasal and mixed craspedrodromous); this is consistent with Rojas-Leal et al. (2018), who found four venation patterns for the Mexican genera of the Senecioneae tribe. Stomata raised above epidermal cells appear to be a trait more common in the Eupatorieae as well as a

particular type of midvein contour (adaxially flat or slightly projected and abaxially round or square protruded or highly protruded). This combination of characters has been recorded in other members of this tribe (Milan et al., 2006; Santos et al., 2016). The presence of paraveinal mesophyll and bundle sheaths without girders are common in the Tageteae tribe whereas the presence of bundle sheaths with extensions and canals associated with them is a common feature in the Heliantheae as recorded for other members (Bombo et al., 2012). The occurrence of abundant sclerified cells associated with vascular bundles in the lamina and the midvein in *A. cordata* is a distinctive feature of the Nassauvieae compared to the other tribes studied. The midvein contour which is flat or slightly convex adaxially and round and protruded abaxially, is a common trait of the *Pseudognaphalium* species studied (Gnaphalieae). In the Millerieae, the midvein contour (adaxially projected and abaxially slightly protruding or round and conspicuously protruded) is common to the three species studied, which also represent three genera. Sampling more species of all tribes of Asteraceae will allow improving not only the tribal descriptions, but also confirm the traits just mentioned for some tribes or find additional ones.

In the Asteraceae tribes studied there is a predominance of small leaf size, serrate margins, poorly developed areole development and the presence of bundle sheath extensions. This combination of characters has been related to efficiency in leaf hydraulic conductance (Sack and Scoffoni, 2013; Sack et al., 2015), light absorption (Nikolopoulos et al., 2002) and biomechanical support (Read and Stokes, 2006). Rivera et al. (2017) tried to explain leaf variation in this xerophytic scrub associating it with different drought-resistance strategies (Ferraro and Scremin-Dias, 2018). However, their results showed that leaf variation could not be solely explained by dry conditions promoted by the volcanic outcrop rocks. Rivera et al. (2017) suggest that characters as plant lifespan, growth form, genome size and species biogeographic history help explain the leaf variation since this attributes have been found related to different extents with anatomical characters in different plant species (Press, 1999; Santiago and Wright, 2007). Detailed anatomical and architectural descriptions are the first steps for any exhaustive study on the causes of leaf variation.

Conclusions

Here we present leaf characters occurring in the thirteen tribes of the Asteraceae present in the REPSA. There is significant variation in leaf architecture and anatomy in this area. The variation observed is consistent with the diversity reported for other authors for the family and for some Mexican tribes. The results of this descriptive study will allow testing evolutionary and ecological hypotheses about the effect of intrinsic and extrinsic factors of the species on the leaf diversity in this area. We suggest future avenues of research on the leaf anatomy of Asteraceae following the format and the terms used in our descriptions of the tribes. We consider that this model will allow standardization of leaf descriptions without losing useful information. Anatomical descriptions are a fundamental piece of the evolutionary, ecological and physiological study of the leaves in Asteraceae.

Author contributions

PR, TT and JLV designed the study. PR carried out the laboratory work and drafted the manuscript. TT and ARL revised and corrected the descriptions and discussion. JLV reviewed and approved the manuscript. All authors read and approved the final manuscript.

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Appendix: Collectors and collection numbers of vouchers of the species studied of Asteraceae. All species are deposited in the Herbario Nacional de México (MEXU) Instituto de Biología, Universidad Nacional Autónoma de México.

Asteraceae

Tribe Anthemideae

Artemisia ludoviciana Nutt., L. Céspedes 443

Cotula australis (Sieber ex Spreng.) Hook. f., L. Céspedes 476

Tribe Astereae

Baccharis pteronioides DC., O. Hinojosa 565

Baccharis salicifolia (Ruiz & Pav.) Pers., L. Céspedes 438

Conyza bonariensis (L.) Cronquist; F. Soto 71, L. Céspedes 477

Conyza canadensis (L.) Cronquist, O. Hinojosa 464

Conyza coronopifolia Kunth, O. Hinojosa 467

Laennecia sophiifolia (Kunth) G.L. Nesom, O. Hinojosa 583

Tribe Bahieae

Florestina pedata (Cav.) Cass., L. Céspedes 223, 470

Schkuhria pinnata (Lam.) Kuntze ex Thell., L. Céspedes 124

Tribe Cardueae

Cirsium vulgare (Savi) Ten., O. Hinojosa 506

Tribe Cichorieae

Helminthotheca echinoides (L.) Holub., L. Céspedes 478

Lactuca serriola L., F. Soto 91

Sonchus oleraceus L., L. Céspedes 456

Taraxacum officinale F.H. Wigg., O. Hinojosa 525

Tribe Coreopsidaeae

Bidens odorata Cav., O. Hinojosa 518

Bidens pilosa L., O. Hinojosa 550

Cosmos bipinnatus Cav., L. Céspedes 440

Cosmos parviflorus (Jacq.) Pers., L. Céspedes 439

Dahlia coccinea Cav., O. Hinojosa 585

Heterosperma pinnatum Cav., O. Hinojosa 515

Tribe Eupatorieae

Ageratina adenophora (Spreng.) R.M. King & H. Rob., O. Hinojosa 563

Ageratina choricephala (B.L. Rob.) R.M. King & H. Rob., L. Céspedes 623

Ageratina cylindrica (McVaugh) R.M. King & H. Rob., L. Céspedes 280

Ageratina deltoidea (Jacq.) R.M. King & H. Rob., O. Hinojosa 549

Brickellia secundiflora (Lag.) A. Gray, O. Hinojosa 555

Brickellia veronicifolia (Kunth) A. Gray, O. Hinojosa 497

Chromolaena pulchella (Kunth) R.M. King & H. Rob., O. Hinojosa 559

Fleischmannia pycnocephala (Less.) R.M. King & H. Rob., O. Hinojosa 554

Piqueria trinervia Cav., O. Hinojosa 522

Stevia micrantha Lag., F. Soto 153

Stevia organoides Kunth, L. Céspedes 668, O. Hinojosa 523

Stevia salicifolia Cav., L. Céspedes 638, O. Hinojosa 498

Stevia subpubescens Lag., O. Hinojosa 561

Stevia tomentosa Kunth, L. Céspedes 433

Tribe Gnaphalieae

Pseudognaphalium canescens (DC.) Anderb., L. Céspedes 484

Pseudognaphalium semilanatum (DC.) Anderb., L. Céspedes 516

Pseudognaphalium viscosum (Kunth) Anderb., O. Hinojosa 504

Tribe Heliantheae

Acmeilla repens (Walter) Rich., O. Hinojosa 519

Aldama buddleiiformis (DC.) E.E. Schill. & Panero, L. Céspedes 441

Aldama excelsa (Willd.) E.E. Schill. & Panero, L. Céspedes 370

Ambrosia cumanaensis Kunth, O. Hinojosa 507

Lagascea rigida (Cav.) Stuessy, L. Céspedes 483

Montanoa grandiflora Alamán ex DC., L. Céspedes 436, 607

Montanoa tomentosa Cerv., L. Céspedes 369, F. Soto 15

Simsia amplexicaulis (Cav.) Pers., L. Céspedes 473

Tithonia tubiformis (Jacq.) Cass., L. Céspedes 444

Verbesina virgata Cav., L. Céspedes 437

Zinnia peruviana (L.) L., O. Hinojosa 508

Tribe Millerieae

Galinsoga parviflora Cav., L. Céspedes 475

Jaegeria hirta (Lag.) Less., L. Céspedes 372, F. Soto 176

Melampodium longifolium Cerv. ex Cav., F. Soto 14

Melampodium perfoliatum (Cav.) Kunth, F. Soto 19

Tribe Nassauvieae

Acourtia cordata (Cerv.) B.L. Turner, L. Céspedes 442

Tribe Senecioneae

Barkleyanthus salicifolius (Kunth) H. Rob. & Brettell, L. Céspedes 559, F. Soto 85

Pittocaulon praecox (Cav.) H. Rob. & Brettell, O. Hinojosa 505

Roldana lobata La Llave, L. Céspedes 448

Tribe Tageteae

Dyssodia papposa (Vent.) Hitchc., L. Céspedes 206, 471

Pectis prostrata Cav., O. Hinojosa 524

Tagetes micrantha Cav., L. Céspedes 434

Tagetes tenuifolia Cav., L. Céspedes 474