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Leaf anatomy of four endemic species of the *Cladocolea-Struthanthus* complex (Loranthaceae) from Guerrero, Mexico

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Abstract

The *Cladocolea-Struthanthus* complex was established by Kuijt (1975) due to the morphological similarities between both genera. This study analyzed the leaf anatomy of four endemic species of this complex from Guerrero, Mexico. The aim was to identify anatomical features to support taxonomic studies within the species studied. Leaf anatomy of *Cladocolea kuijtii*, *C. molotensis, C. spathiflora* and *S. racemosus* was compared from transverse leaf sections. The cuticle is generally smooth and fimbriate. The epidermis is one-layered, occasionally with trichomes in *C. kuijtii* and *C. molotensis*. All analyzed species are amphistomatic and isobilateral, consisting of palisade parenchyma. The sclerenchyma is represented by brachysclereids, cristarque cells and astrosclereids. Crystals such as prism and druses were observed. In *Cladocolea spathiflora*, crystal sand is reported for the first time in Loranthaceae. A dichotomous key was constructed using anatomical characters to assist recognition of endemic *Cladocolea* and *Struthanthus* species. The taxonomic importance of these characters is discussed for the complex and for the family.

Key words: cristarque cells, crystal sand, polyphenolic compounds, sclereids, trichomes

Introduction

The family Loranthaceae comprises 76 genera and over 1,000 species that are distributed in tropical regions of the Old and New World (Nickrent 2020). In Mexico, Loranthaceae is represented by 55 species in five genera (Villaseñor 2016): *Cladocolea* Tiegh. (1895: 166), *Oryctanthus* (Griseb.) Eichler (1868: 87), *Phthirusa* Mart. (1830: 110), *Psittacanthus* Mart. (1830: 106), and *Struthanthus* Mart. (1830: 102). The genus *Cladocolea* in Mexico comprises about 20 species (Galván-González 2016, Martínez-Ambriz 2020), of which 16 occur in Guerrero (Martínez-Ambriz 2014, Galván-González 2016). *Struthanthus* includes about 15 species (Maldonado-Borja 2021; Maldonado-Borja *et al*. 2023), of which six are found in Guerrero. Both genera were established as a complex by Kuijt (1975), due to morphological similarities, such as being aerial parasitic shrubs with erect stems, occasionally possessing epicortical roots. The leaves are entire, alternate, opposite to subopposite, glabrous or pubescent without stipules. The inflorescences in *Cladocolea* are a determinate triad, spike or raceme with single ebracteolate flowers, which are sessile or rarely pedicellate (Kuijt 1981). The flowers are unisexual, occasionally bisexual (<1 cm), yellow, green, whitish, or yellowish (Kuijt 1975, Galván-González 2016, Martínez-Ambriz 2020). The inflorescences in *Struthanthus* are indeterminate, spike, raceme or clusters of pedunculate or sessile paired triads, bracteate and/or bracteolate; the flowers are sessile or pedicellate, unisexual (<1 cm) or bisexual, whitish, yellowish-whitish, whitish-greenish or yellowish-green (Martínez-Ambriz 2020, Maldonado-Borja 2021, Maldonado-Borja *et al.* 2024).

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Some studies in Loranthaceae have examined epidermal derivates such as stomata (Hauenstein *et al*. 1990) and trichomes (Ibrahim *et al*. 2015, Ohikhena *et al*. 2017). On the other hand, Kuijt & Lye (2005) described the sclerenchyma within the subtribe Psittacanthinae and introduced the term cristarque cells for crystalliferous sclereids. These are similar in shape and distribution to brachysclereids, but contain a single solitary crystal. Additionally, Rueda (2015) recorded cristarque cells along vascular bundles for Mexican species of *Cladocolea*. Caires & Leitão (2015) also observed cristarque cells in *Oryctina* Tiegh. (1895: 168), assessing their taxonomic value.

In addition, prism crystals have been registered in Loranthaceae (Shavvon *et al*. 2012), such as *Loranthus* L. (1753: 331), Chilean Loranthaceae (Hauenstein *et al*. 1990) and Mexican species of *Psittacanthus* (Gómez-Sánchez *et al*. 2011). Moreover, epidermal crystals were recorded in *Cladocolea molotensis* Martínez-Ambr. and Lozada-Pérez (2016:153) (Martínez-Ambriz & Lozada-Pérez 2016). Sclerenchyma and idioblasts were also compared in *Cladocolea* and *Struthanthus* from Amazonian species (Guimarães *et al*. 2007). Currently, there are no anatomical studies on endemic species of the *Cladocolea-Struthanthus* complex from Mexico. This survey seeks to identify features that could support taxonomical studies and serve as a complementary tool for the identification of species within this genus.

Materials and methods

Plant samples were obtained from healthy and mature leaves collected in or near the type localities in the state of Guerrero (Table 1), and vouchers were deposited in the HUMO herbarium. Sections of 5 mm^2 were taken from the middle region of the blade and fixed in FPA (Ruzin 1999). Transverse sections of the leaf blade were dehydrated in a progressive alcohol series (30%, 50%, 70%, 80%, 95%, 100%) and then placed in xylene. Subsequently, they were embedded in paraffin blocks and sectioned (10 μm thick) using a LEICA RM2125 rotary microtome. The samples were mounted on slides using Haupt adhesive and 4% formalin, and allowed to dry for two days in an oven. Slides were then stained with alcoholic safranin, mounted with 2–4 drops of Cytoseal® (Fisher Scientific), and then dried in an oven at 45 °C for 72 hours (Cutler *et al.* 2008). Photomicrographs were captured using a Nikon 80i microscope with a Nikon DS-Ri2 camera and calibrated using Macnification v. 2.05 software (Schols and Lorson 2008). For the anatomical descriptions, specialized literature was consulted (Payne 1978, Metcalfe & Chalk, 1983, Kuijt & Lye 2005, Azcárraga *et al*. 2010).

TABLE 1. List of the *Cladocolea-Struthanthus* complex voucher samples examined in this study. Taxa sampled are deposited in herbarium HUMO.

Taxa	Voucher	Locality
Cladocolea kuijtii Martínez-Ambr. and Cruz Durán	Galván-González *et al*., 414, 415	La Guitarra, 10 km E of Puerto la Gallina, General Heliodoro Castillo, Guerrero
C. kuijtii Martínez-Ambr. and Cruz Durán	Galván-González *et al*., 397, 501	Ejido el Molote, 11 km N of Nueva Delhi, Atoyac de Álvarez, Guerrero
C. kuijtii Martínez-Ambr. and Cruz Durán	Galván-González *et al*., 505	Ejido el Molote, 115 km N of Nueva Delhi, Atoyac de Álvarez, Guerrero
C. molotensis Martínez-Ambr. and Lozada-Pérez	Galván-González *et al*., 393, 396	Ejido el Molote, 95 km N of Nueva Delhi, Atoyac de Álvarez, Guerrero
C. molotensis Martínez-Ambr. and Lozada-Pérez	Galván-González *et al*., 404	25 km E of Omiltemi, Chilpancingo de los Bravo, Guerrero
C. molotensis Martínez-Ambr. and Lozada-Pérez	Galván-González *et al*., 502, 503	Ejido el Molote, 11 km N of Nueva Delhi, Atoyac de Álvarez, Guerrero
C. spathiflora Galv.-González, Cerros, Espejo and López-Ferr.	Galván-González *et al*., 418, 423	Colonia el Renacimiento, 10 km SW of Chilpancinguito, General Heliodoro Castillo, Guerrero

.....continued on the next page

TABLE 1. (Continued)

Taxa	Voucher	Locality
Struthanthus racemosus (Kuijt) Galv.-González	Galván-González *et al*., 429	4 km NW of Tlaxco, Xalpatlahuac, Guerrero
S. racemosus (Kuijt) Galv.-González	Galván-González *et al*., 432	Tlaxco, 200 m W of Telesecundaria Tierra y Libertad, Xalpatlahuac, Guerrero
S. racemosus (Kuijt) Galv.-González	Galván-González *et al*., 492	16 km NW of Tlaxco, Xalpatlahuac, Guerrero
S. racemosus (Kuijt) Galv.-González	Galván-González *et al*., 493	32 km NW of Tlaxco, Xalpatlahuac, Guerrero

Results

The cuticle is of variable thickness (1.41–2.87 μm), fimbriated (Fig. 1A), and occasionally smooth (Fig. 1B). The epidermis is one-layered and has four types of unicellular trichomes observed in *C. kuijtii* and *C. molotensis*: clavate (Fig. 1C), falcate (Fig. 1D), filiform (Fig. 1E) and subulate (Fig. 1F); *C. spathiflora* and *S. racemosus* lack trichomes. Polyphenolic compounds are only present in the epidermis of *C. spathiflora* (Fig. 1A). The leaf blades are amphistomatic and isobilateral, with palisade parenchyma of several cell sizes (47.75–98.05 μm) (Fig. 1G–J). These parenchyma cells may contain polyphenolic compounds (*C. spathiflora* and *S. racemosus*) (Fig. 1I). The sclerenchyma is represented by cristarque cells (Fig. 2A–B), and astroesclereids (Fig. 2C–D). Sclereids are scattered in the mesophyll and associated with veins. Cristarque cells are solitary or organized in clusters, often with one or more prism crystals (Fig. 2A), druses (Fig. 2B), as well as crystal sand (*C. spathiflora*) (Fig. 2E), and are distributed in the mesophyll and associated to midrib. Astrosclereids are irregular in shape and size (Fig. 2C), scattered in the mesophyll (Fig. 1G–I), as well in the first layer of palisade parenchyma and the epidermis (rarely in *S. racemosus*). The vascular bundles in the midrib range from two to eight caps, partitioned by primary medullary rays. In the four species, there is a collenchymatous sheath associated with the xylem and phloem in the midrib (Fig. 2J–L). *Cladocolea spathiflora* exhibits crystalline forms not previously described within the genus or family (Fig. 2A–H).

Identification key to endemic species of the *Cladocolea-Struthanthus* complex from Guerrero, Mexico, based on leaf anatomy

1. Trichomes absent 2
- Trichomes filiform, clavate, falcate or subulate 3
2. Parenchyma two- to three-layered, polyphenolic compounds in the epidermal cells only ..... *Struthanthus racemosus*
- Parenchyma three-layered, polyphenolic compounds in epidermal and mesophyll cells ..... *Cladocolea spathiflora*
3. Abaxial cristarque cells in midrib, trichomes with smooth and fimbriated cell walls ..... *Cladocolea kuijtii*
- Abaxial and adaxial cristarque cells in midrib, trichomes with smooth cell walls ..... *Cladocolea molotensis*

Discussion

The findings obtained in this study had not been previously documented in other Loranthaceae genera. These characters could be used for taxonomic purposes, thereby enhancing the understanding of the *Cladocolea-Struthanthus* complex from an anatomical perspective. The leaf anatomy of *Cladocolea kuijtii* Martínez-Ambr. & Cruz-Durán (2015: 75), *C. molotensis* Martínez-Ambr. & Lozada-Pérez (2016: 153), *C. spathiflora* Galv.-González, Cerros, Espejo & López-Ferr. (2017: 295) and *Struthanthus racemosus* (Kuijt) Galv.-González (2024: 408) is described.

Leaf anatomy of six *Cladocolea* species studied by Rueda (2015) showed variation in cuticle thickness and agree with results obtained in this work. The cuticle thickening is a response to the ecological environments in which plants develop (Cutler *et al*. 2008). Therefore, anatomical, and ecological studies could support the taxonomic value of cuticle within *Cladocolea*. The one-layered epidermis within the Loranthaceae family has been documented previously (Gómez-Sánchez *et al*. 2011, Metcalfe & Chalk 1983, Ibrahim *et al.* 2015), as observed in the species examined in

this study. However, hypodermis has been reported in some Loranthaceae species (Ibrahim *et al.* 2015), this was not observed in the analyzed species in this study.

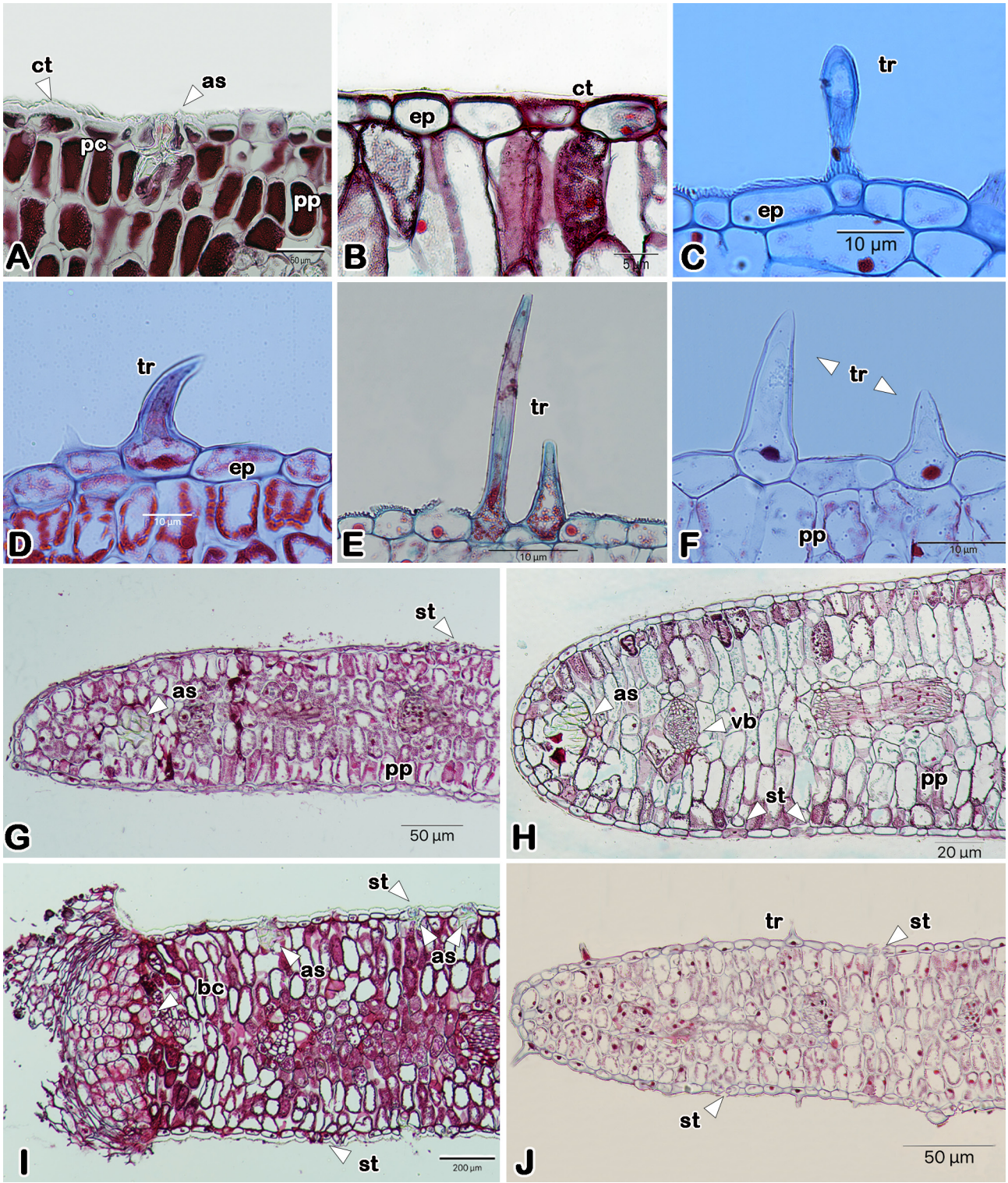

FIGURE 1. Leaf blade in transversal sections of four species of the *Cladocolea-Struthanthus* complex. A. Epidermis and polyphenolic compounds, B. Smooth cuticle, C. Clavate trichome, D. Falcate trichome, E. Filiform trichome, F. Subulate trichome, G. Mesophyll and astrosclereids, H. Mesophyll, I Astrosclereids near epidermal cells, J. Mesophyll with astrosclereids. as= astrosclereids, ct= cuticle, ep= epidermis, pc= polyphenolic compounds, pp= palisade parenchyma, st= stomata, tr= trichomes. Photos Hernández-Salazar M.

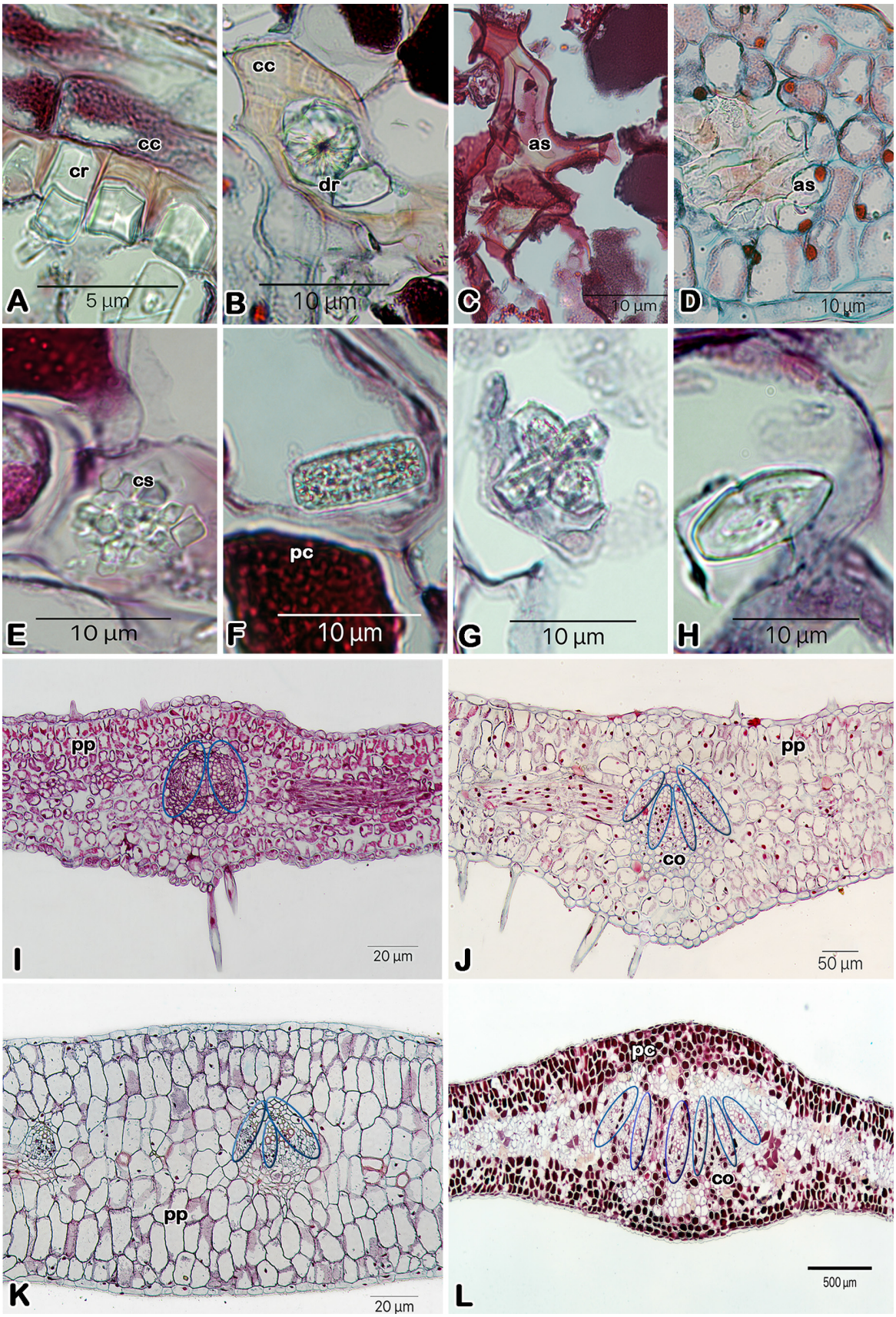

FIGURE 2. Crystals and midrib of four endemic species of the *Cladocolea-Struthanthus* complex. A. Cristarque cell, B. Cristarque cell and druse, C-D. Astrosclereids, E. Crystal sand, F. Prism with inclusions, G. Star-shaped prism, H. Elongated oval-shaped prism. Midrib vascular bundles (blue ellipse indicate xylem and phloem caps), I. *C. kuijtii*, J. *S. racemosus*, K. *C. molotensis*, L. *C. spathiflora*. cc= cristarque cells, co= collenchyma, cr= prism crystals, cs= crystal sand, pc= polyphenolic compounds, pp= palisade parenchyma. Photos Hernández-Salazar M.

Leaf blades are amphistomatic and agree with prior findings of Loranthaceae or Santalaceae (Metcalfe & Chalk 1983, Gómez-Sánchez *et al*. 2011, Carmona-Gallego *et al*. 2018). Moreover, Metcalfe & Chalk (1983) suggested absence of sunken stomata in certain Loranthaceae species, but both *C. spathiflora* and *S. racemosus* showed stomata are semi-sunken in both epidermises, which is in agreement with Rueda (2015). Therefore, stomata should be considered as a character to facilitate *Cladocolea-Struthanthus* species recognition among other Loranthaceae genera.

Diverse trichomes have been documented in Loranthaceae, including simple, dendritic, candelabrum-like, and stellate with intracellular crystals (Metcalfe and Chalk 1983, Huaenstein *et al.* 1990, Ohikhena *et al*. 2017) and intraspecific variation has been confirmed (Ibrahim *et al*. 2015, Ohikhena *et al*. 2017). For Mexican Loranthaceae, simple and filiform trichomes have been recorded (Gómez-Sánchez e*t al*. 2011). Trichomes in *Cladocolea* occur in both leaf surfaces as suggested by Rueda (2015). According to Payne's (1978) terminology, filiform, falcate, subulate, and clavate trichomes occur in *Cladocolea kuijtii* and *C. molotensis*. Hence, trichomes hold potential for species identification in *Cladocolea* as for other flowering plants (Cutler *et al*. 2008). Suberized leaf margins in *C. spathiflora* are unique and allow to distinguish this species, as reported previously by Galván-González *et al.* (2017).

Dorsiventral mesophyll is registered in the family (Caires & Leit*ão* 2015, Gómez-Sánchez *et al*. 2011, Guimarães *et al*. 2007, Metcalfe & Chalk 1983). However, in the analyzed species in this study, only isobilateral mesophyll was observed. In addition, wavy cell walls in the mesophyll cells of *C. spathiflora* were also observed in *Englerina gabonensis* (Engl.) Balle (1956: 168) (Ibrahim *et al*. 2015).

Polyphenolic compounds are a mechanism developed in plants to avoid foliar desiccation and herbivory (Fahn 2000). These compounds have been reported in other Santalales, e.g. *Loranthus* (Metcalfe & Chalk 1983), *Struthanthus vulgaris* (Salatino *et al*. 1993), *Phoradendron* Nutt. (1848: 185–186), *Psittacanthus* (Gómez-Sánchez *et al*. 2011), and *Tripodanthus belmirensis* F.J. Roldán and Kuijt (2005: 207–209) (Carmona-Gallego *et al*. 2018). Rueda (2015) registered polyphenolic compounds in some Mexican *Cladocolea* species; however, in this study these compounds are reported for the first time in epidermal cells. Therefore, histochemical analyses are required to determine phenolic compounds to know whether these characters allow to differentiate between *Cladocolea-Struthanthus* complex species.

According to Esau (1977) and Crang *et al*. (2018), sclereids are structural support cells, that include astrosclereids, cristarque cells and fibers. In addition, sclereids were observed in both mesophyll and epidermal cells in *C. kuijtii*, *C. molotensis*, and *C. spathiflora*, except for *S. racemosus*, where they were observed only in the mesophyll. Therefore, this is a distinctive trait between both genera. Branched sclereids were also recorded in *C. spathiflora*, as described by Varela *et al*. (2008) and Ibrahim *et al*. (2015).

Cristarque cells are diagnostic because they occur in few flowering plant families such as Huaceae A.Chev. (Bass 1972), Lecythidaceae A.Rich. (Achille 1825), Melastomataceae Juss. (1789), Moraceae Gaudich. (Gaudich. 1835), Ochnaceae DC. (1811), and Loranthaceae genera (Dickinson 2000, Kuijt & Lye 2005, Caires & Leitão 2015). Prism crystals are common in cristarque cells. On the other hand, Kuijt & Lye (2005) registered cristarque cells only in *C. coriacea* Kuijt (1987: 449), but in this study, they were observed in the four species. In addition, cristarque cells and fibers were associated with vascular bundles in the analyzed species. In addition, Rueda (2015) examined 18 species of *Cladocolea*, of which *C. cupulata* and *S. racemosus* lack cristarque cells. This differs from our findings, particularly in the latter, because these cells are only observed in the adaxial side of veins. Therefore, presence or absence, distribution, arrangement and crystal shape allowed recognition in the *Cladocolea-Struthanthus* complex, particularly at the species level, as in other flowering families studied (Chantarasuwan *et al*. 2014).

Vascular bundles are collateral in the four species studied, as mentioned for the family (Metcalfe & Chalk 1983). The vascular bundle variation in the midvein could contribute to differentiate *Cladocolea* and *Struthanthus* endemic species (Table 2). According to Aloni (2015), parasitic plants and their host form a continuous system of vessel opening, favoring the rapid absorption of water and nutrients by parasitic plants. In addition, the number and size of vascular bundles depend on the ecological conditions in which plants live (Castellanos-Ramírez *et al.* 2023). In this context, a similarity analysis is suggested to determine if vascular bundles are related to such conditions.

Collenchyma and fiber bundles in the midvein allowed differentiation among *Tripodanthus* Tiegh. (1895: 178) species (Loranthaceae) (Carmona-Gallego *et al.* 2018). Likewise, vascular bundle size and collenchyma have been taxonomically significant in Loranthaceae (Waly 2013). In the species studied, such as *C. spathiflora*, larger vascular bundles are recorded in the midvein. Therefore, this character has taxonomic value, as suggested by Galván-González *et al.* (2024).

TABLE 2. Comparison of anatomical characters of four endemic species of the *Cladocolea-Struthanthus* complex from Mexico.

Character	*C. kuijtii*	*C. molotensis*	*C. spathiflora*	*S. racemosus*
Cuticle	Smooth and thin, occasionally fimbriated	Slightly thickened, fimbriated on the midrib and margins	Thickened and fimbriated	Fimbriated and thin
Stomata	Same level of epidermal cells and occasionally semi-sunken	Same level of epidermal cells and occasionally semi-sunken	Same level of epidermal cells and semi-sunken	Same level of epidermal cells and semi-sunken
Trichomes	Unicellular and uniseriate, subulate, clavate, falcate and filiform type with smooth walls	Unicellular and uniseriate, filiform, clavate, falcate and subulate type with striated walls	Absent	Absent
Mesophyll (palisade parenchyma)	One or two layers	One or two layers	Three layers	Two to three layers
Polyphenolic compounds	Absent	Absent	In epidermis and mesophyll	In mesophyll
Midrib	Composed of two separate bundles	Composed of two to four separate bundles	Composed of four separate bundles	Composed of two to three separate bundles
Collenchyma	Associated with xylem and phloem of vascular bundle	Associated with xylem and phloem of vascular bundle	Associated with xylem and phloem of vascular bundle	Associated with xylem and phloem of vascular bundle
Cristarque cells	Phloem	Xylem, occasionally in phloem	Xylem and phloem	Phloem, occasionally in xylem
Astrosclereids	Epidermis and mesophyll	Epidermis and mesophyll	Epidermis and mesophyll	Mesophyll
Crystals	Prism	Prism, druses and sand crystals	Prism, druses and sand crystals	Prism

Although druse occurrence and distribution have been studied in Loranthaceae (Varela *et al.* 2008, Gómez-Sánchez *et al*. 2011, Ibrahim *et al.* 2015), in the present study, druses and crystal sand were registered for the first time in cristarque cells. Prism and cubic-shaped crystals were observed in the studied species, and this is consistent in Loranthaceae (Caires & Leitão 2015, Shavvon *et al.* 2012). Nevertheless, druses with dark nuclei were observed in *C. spathiflora*, as previously reported in Mexican *Psittacanthus* species (Gómez-Sánchez *et al*. 2011). Among the analyzed species, prism crystals in *C. molotensis* were rare, and when present, they were associated to sclerenchyma. No crystals were seen in *C. molotensis* epidermis, as suggested by Martínez-Ambriz & Lozada-Pérez (2016). Also, unique crystals shapes were found in *C. spathiflora*, and they have not been previously reported in the Loranthaceae family. According to Cody & Horner (1983) and Franceschi & Nakata (2005), crystal morphology is a combination of genetic and environmental factors. Thus, crystals in these species may be related to specific ecosystems and host plants. Therefore, a comprehensive analysis of crystal morphology and chemical composition is warranted to assess their taxonomic significance. Also, this will show whether crystal types are exclusive to the *Cladocolea-Struthanthus* complex, or they are shared with other Loranthaceae genera.

Conclusions

Endemic species studied are part of a comprehensive study on the leaf anatomy of Mexican species of the *Cladocolea-Struthanthus* complex (Hernández-Salazar 2024). The characters that allowed to differentiate the four taxa are cuticle type, polyphenolic compounds in epidermal and mesophyll cells, trichome types, cristarque cells, as well as crystal

shape and distribution. Additionally, collenchyma distribution in the midrib, and whether astrosclereids are scattered in the mesophyll. The findings obtained in this study demonstrate variation among these species while other characters remain constant. It is important to highlight that *C. spathiflora* shows unique characters not shared with other species in the complex. Thus, its taxonomic position remains uncertain, as suggested by Galván-González *et al.* (2024). Furthermore, the leaf anatomy characters had not been previously reported in the family, and some are of taxonomic value. An identification key was also provided. Finally, this study contributes to the anatomical knowledge of Mexican species of the *Cladocolea-Struthanthus* complex.

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Supplementary material

Anatomical descriptions of endemic species of *Cladocolea-Struthanthus* complex

Cladocolea kuijtii Martínez-Ambr. & Cruz-Durán
Cuticle: Fimbriate, occasionally smooth (0.60–1.30 μm), with possible intrusions. Epidermis: Uniseriate and one-layered, composed of oblong, quadrangular, and rounded cells with thin, convex walls. The cells in the midrib smaller and rounded than those in the epidermis. Occasionally, papillose cells present. Stomata: Amphistomatic, stomata at epidermis level, occasionally semi-sunken. Trichomes: Four types, all unicellular and uniseriate: clavate with smooth walls and no adjacent epidermal cells (4.28 × 16.06–6.6 × 16.36 μm), subulate (3.35 × 24.54–9.82 × 27.88 μm), filiform with smooth and slightly thickened walls (3.77 × 34.81–7.08 × 36.62 μm), and falcate with thickened walls (2.91 × 16.17–4.67 × 16.70 μm). Trichomes distributed throughout the leaf blade and abundant on the adaxial epidermis of the midrib. Occasionally, trichomes with striated walls and serrated ornamentation on one side. Mesophyll: Isobilateral (41.56–98.05 μm), consisting of two layers of palisade parenchyma with irregular, thin-walled, smooth cells. First layer contains smaller, rounded cells, a second layer consists of slightly elongated cells with tangentially extended periclinal walls. Midrib region up to three parenchyma layers. Collateral vascular bundles in the middle of the leaf blade. The midrib comprises two to seven xylem and phloem caps separated by medullary parenchyma and surrounded by an annular collenchyma arc. Occasionally, crystal-bearing idioblasts (cristarque cells) are present on adaxial and abaxial side of midrib. Sclerenchyma: Astrosclereids scattered in the mesophyll, epidermis, and trichome bases. Cristarque cells with prism, cubic or rectangular crystals, either grouped or solitary.

Cladocolea molotensis Martínez-Ambr. & Lozada-Pérez

Cuticle: Thin (1.11–1.86 μm) and fimbriate, with some smooth sections. Epidermis: Uniseriate and one-layered, composed of irregular rectangular and quadrangular cells, rarely rounded, with generally convex and smooth periclinal walls. Stomata: Amphistomatic, stomata at epidermis level, occasionally semi-sunken, and rarely sunken. Trichomes: Four types, all unicellular and uniseriate: falcate (2.91 × 16.17–4.14 × 21.90 μm), subulate (3.84 × 16.89–4.31 × 28.37 μm) with slightly thickened and striated walls, clavate (3.35 × 24.54–9.82 × 27.88 μm), and filiform (3.77 × 24.81–5.88 × 57.70 μm). Trichomes distributed across the entire leaf blade, abundant near the adaxial and abaxial midrib. Mesophyll: Isobilateral (34.27–96.20 μm), consisting of two to three layers of irregular palisade parenchyma cells. First layer with smaller cells, the second has tangentially elongated periclinal cells. All cells thin, with smooth walls and containing polyphenols. In the midrib region, cells are enlarged and rounded. Collateral vascular bundles arranged in rows in the midrib region, with all vascular bundles in the middle. The midrib divided into two to four xylem and phloem caps, separated by medullary parenchyma. Annular collenchyma arc surrounds the vascular bundles, with cristarque cells associated with the adaxial side collenchyma. Sclerenchyma: Cristarque cells associated with the vascular bundles, with aggregated prism crystals and crystal sand. Astrosclereids are present in the mesophyll and epidermis, usually fragmented when in the mesophyll. Crystals: Prism crystals, generally associated with brachysclereids (rarely found in the mesophyll), rectangular, cubic, and quadrangular shapes. Druses infrequent, and crystal sand associated with sclereids.

Cladocolea spathiflora Galv.-González, Cerros, Espejo & López-Ferr.

Cuticle: Thickened with fimbriate ornamentations (3.34–7.80 μm). Cuticular intrusions throughout the leaf blade. Epidermis: Uniseriate, composed of small, generally oblong cells with thin, convex walls. Marginal and midrib cells are rounded, smaller, and contain suberized tissue. Polyphenolic compounds present. Abundant star-shaped crystals, with one or more per cell. Stomata: Amphistomatic leaf blade, stomata at the epidermal level or semi-sunken. Adjacent cells larger than other epidermal cells. Mesophyll: Isobilateral (104.08–110.14 μm), consisting of three layers of palisade parenchyma. Adaxial cells are generally isodiametric and tangentially elongated along periclinal walls, while abaxial cells are occasionally tangentially elongated, with smooth, thin cell walls, rarely thickened. Midrib cells rounded and smaller. Abundant polyphenolic compounds. Collateral vascular bundles, midrib consists of up to four caps of xylem and phloem separated by medullary parenchyma. Vascular bundles in the midrib are in the middle of the leaf blade, with vessel elements arranged in rows. Annular collenchyma associated with vascular bundles, and cristarque cells near to the vascular tissues. Fibers associated with collenchyma, xylem, and phloem in the midrib. Sclerenchyma:

astrosclereids in the palisade parenchyma, occasionally the epidermis. Crystals in the cristarque cells vary in shape and size, either solitary or grouped.

Struthanthus racemosus (Kuijt) Galv.-González

Cuticle: Thin and fimbriate (0.62–0.95 μm), occasionally smooth, with possible intrusions. Epidermis: Uniseriate, oblong, rounded, and quadrangular cells of varying sizes, with thin and convex walls. Stomata: Amphistomatic, stomata at the epidermal level, rarely semi-sunken. Mesophyll: Isobilateral (46.52–109.27 μm), with two to three layers of palisade parenchyma. The first layer is composed of smaller, slightly widened cells, while the second layer consists of isodiametric and tangentially elongated cells along the periclinal wall, with smooth walls and undulated ornamentation. Polyphenolic compounds. Collateral vascular bundles, all in the middle of the leaf blade, the midrib being the largest, divided into two to three caps of xylem and phloem, surrounded by an annular collenchyma arc with cristarque cells on adaxial and abaxial side, and a few fibers in the adaxial collenchyma. Sclerenchyma: Astrosclereids in the mesophyll, rarely in the epidermis. Cristarque cells with druses and crystalline sand. Crystals: star-shaped and oval-shaped prism crystals not previously recorded in the genus or family.