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Morphoanatomical and histochemical characterization of the vegetative organs of *Hypseocharis pimpinellifolia* (Geraniaceae)

Caracterización morfoanatómica e histoquímica de los órganos vegetativos de *Hypseocharis pimpinellifolia* (Geraniaceae)

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Abstract

Hypseocharis pimpinellifolia (Geraniaceae), locally known as "soldaque", is a perennial hemicryptophytic herb, endemic to the high Andes of northwestern Argentina. The tuberous roots of the soldaque represent a compelling area of study, as they have been used by local inhabitants for both nutritional and medicinal proposes since ancient times. The objective of the present work was to investigate the morphology, anatomy, and histochemistry of the vegetative organs of *H. pimpinellifolia,* in order to identify diagnostic botanical traits and determine the sites of synthesis and accumulation of secondary metabolites with medicinal or nutritional potential. The samples were analyzed using conventional anatomical and histochemical techniques. Soldaque presented leaves with anomocytic stomata, unicellular non-glandular trichomes, and multicellular biseriate capitate glandular trichomes that accumulate lipids and phenolic compounds.

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The brachyblast and rhizomes exhibited similar structures with incipient secondary growth. The tuberous roots showed high polymorphism, and atypical growth with abundant starch-storing parenchyma, idioblasts containing calcium oxalate crystals, and an internal meristem forming a central wedge with phenolic compounds, lipids, and pectins. This study provides the first morpho-histological and histochemical description of the vegetative organs of *H. pimpinellifolia* representing the first report for the genus *Hypseocharis.*

Keywords: Geraniaceae; glandular trichomes; soldaque; tuberous roots.

Resumen

Hypseocharis pimpinellifolia (Geraniaceae), conocida localmente como «soldaque», es una hierba hemicriptófita perenne, endémica de los altos Andes del noroeste de Argentina. Las raíces tuberosas de esta planta representan una perspectiva interesante, ya que han sido utilizadas desde la antigüedad, como alimento y medicina por los habitantes locales. El objetivo del presente trabajo fue investigar la morfología, anatomía e histoquímica de los órganos vegetativos de *H. pimpinellifolia* para identificar rasgos botánicos diagnósticos y determinar los sitios de síntesis y acumulación de metabolitos secundarios con potencial medicinal o alimenticio. Las muestras se analizaron utilizando técnicas convencionales de anatomía e histoquímica. Soldaque presentó hojas con estomas anomocíticos, tricomas unicelulares no glandulares y tricomas glandulares capitados multicelulares biseriados, que acumulan lípidos y compuestos fenólicos. Los braquiblastos y los rizomas mostraron estructuras similares, con un crecimiento secundario incipiente. Raíces tuberosas con gran polimorfismo, crecimiento inusual con abundante parénquima amilífero de reserva, idioblastos con cristales de oxalato de calcio y un meristema interno que forma una cuña central con compuestos fenólicos, lípidos y pectinas. Este estudio proporciona la primera descripción morfo-histológica e histoquímica de los órganos vegetativos de *H. pimpinellifolia* y representa el primer informe sobre el género *Hypseocharis*.

Palabras clave: Geraniaceae; tricomas glandulares; soldaque; raíces tuberosas.

INTRODUCTION

The genus *Hypseocharis* J. Rémy (Geraniaceae) is restricted to the Andean region of South America, distributed from northern of Peru (Ancash Department) to northwestern Argentina (Southern limit in La Rioja Province) at elevations ranging from 2000 to 4200 m asl (Slanis & Grau, 2001). The genus comprises around nine species, two of them, *Hypseocharis tridentata* Griseb. and *H. pimpinellifolia* J. Remy, are found in Argentina (Barboza, 1996; Zuloaga *et al.*, 2019).

Although the genus is currently placed within the family Geraniaceae, its classification has been subject to ongoing debate (Lozada *et al*., 2020). Based on gynoecial characteristics, Weddell (1857) proposed the segregation of the genus into its own family, Hypseocharitaceae Wedd. Subsequently, based on both morphology (Bentham & Hooker, 1862; Knuth, 1908, 1930; Cronquist, 1981; Boesewinkel, 1988) and chloroplast DNA sequences (rbcL gene) (Price & Palmer, 1993), other authors have alternately assigned *Hypseocharis* to either Oxalidaceae or Geraniaceae (Slanis & Grau, 2001; Lozada *et al*., 2020). Based on floral structure and molecular phylogenetic analyses, Devi (1991) and Palazzesi *et al*. (2012) identified *Hypseocharis* as a sister core to the Geraniaceae, proposing the reinstatement of the independent family Hypseocharitaceae. However, this proposal has not yet been formally adopted by the Argentinean Flora (Barboza, 1996; Zuloaga *et al*., 2019), in which the genus is still placed within Geraniaceae, a criterion followed in the present work.

Hypseocharis pimpinellifolia, commonly known as "soldaque" or "solda-solda", is a perennial hemicryptophytic herb endemic to the high Andes of northwestern Argentina. It inhabits the Prepuna and Puna environments in the provinces of Jujuy, Salta, Tucumán, Catamarca, and La Rioja (Slanis & Grau, 2001), occurring at elevations between 2500 and 4200 m asl. Although it is present in fog grasslands, the species shows greater affinity for semi-arid environments with sandy, clayey, or rocky soils, and appears to have a low tolerance to saline conditions (Barboza, 1996; Zuloaga *et al*., 2019).

The Prepuna and Puna ecoregions are characterized by a cold, arid climate with mean annual precipitation ranging from 150 to 230 mm, concentrated during summer months (Aagesen *et al*., 2009). These high-altitude environments exhibit pronounced daily and seasonal thermal amplitudes, with summer temperatures averaging 16-18°C, and winter temperatures averaging 6°C, frequently accompanied by frost events, snowfall, and extreme low temperatures reaching -20°C (Matteucci, 2018). Additional stressors include intense solar radiation (Suárez *et al*., 2018) and poorly developed, skeletal soils with low organic matter content (occasionally saline) (Cabrera, 1968). In response to these extreme conditions, the native flora displays specialized adaptive and plastic strategies (Cabrera, 1968; Matteucci, 2018; Arana *et al*., 2021).

Hypseocharis pimpinellifolia exhibits polymorphism across contrasting high- mountain environments, occupying a range of habitats from arid Prepuna valleys to the extreme Puna plateaus. This phenotypic variation reflects its remarkable ecological plasticity in response to diverse microclimatic and edaphic conditions (Slanis & Grau, 2001).

Archaeological evidence suggests that soldaque roots may have constituted a relevant component of the human diet during the Pleistocene era and subsequent civilizations. Root remains, aged between 7000-10000 years old, have been found in sedimentary deposits at archaeological sites in several Andean provinces, including Jujuy (Aschero, 1984; Yaccobaccio, 1990), Tucumán (Oliszewski & Arreguez, 2015), and Catamarca (Babot *et al.*, 2009).

Currently, Andean communities in the Argentine Puna consume *H. pimpinellifolia* roots both as an emergency food source and as a medicinal resource. The roots are traditionally used for their anti-inflammatory properties to treat lumbar pain and to promote wound healing (Slanis & Grau, 2001). According to Aschero (1984), ethnohistorical records also document its use as a stimulant to alleviate the symptoms of altitude sickness (known as *mal de altura* or *puna sickness*). Additionally, this species has forage value, as its leaves are regularly consumed by cattle (Slanis & Grau, 2001; Califano, 2020).

Morphological, anatomical, and histochemical studies of the plants provide valuable information for identifying diagnostic traits for quality control of derived products, as well as to guide research towards the isolation and chemical characterization of bioactive compounds. However, current knowledge of *H. pimpinellifolia* in these fields remains limited. Although the floral anatomy (particularly nectaries and floral architecture) of the genus (Devi, 1991; Jeiter *et al.*, 2017) and the reproductive and vegetative morphological features of the species (including leaf morphology, the number of stamens and the fruit type, among others features) (Slanis & Grau, 2001; Lozada *et al.*, 2020) have been investigated, the anatomy and histochemistry of the vegetative organs of *Hypseocharis* species are still completely unexplored.

Therefore, this work aimed to characterize the morphology, anatomy, and histochemistry of the vegetative organs of *H. pimpinellifolia* in order to identify diagnostic traits for the accurate botanical identification of the species. Also, to identify the site of synthesis and accumulation of specialized metabolites with medicinal or nutritional potential.

MATERIALS AND METHODS

Plant material

Hypseocharis pimpinellifolia individuals were collected at 3050 m asl from Abra del Infiernillo (26°44'14"S, 67°47'01"W) in Tafí del Valle Department, Tucumán province, Argentina, in April 2017. A voucher specimen was deposited at LIL (accession LIL 617276), Tucumán, Argentina. The botanical identification was performed by Dr. Ana Soledad Cuello (INBIOFIV, CONICET-UNT).

Light microscopy

Samples of leaves, stems (aerial stem or brachyblast and rhizome), and tuberous roots of five individuals were analyzed. A portion of the material was fixed in FAA (formalin, acetic acid, 50% ethanol, 5:5:90 v/v/v) and stored for one week before processing.

The middle leaflets, the rachis (proximal, middle, and distal regions relative to the petiole), the petiole (proximal, middle, and distal regions relative to the stem), the brachyblast (at the middle region), the rhizome (proximal, middle and distal portions relative to the brachyblast) and the tuberous root (proximal, middle and distal regions relative to the rhizome) were analyzed.

Portions of approximately 2 mm^2 of each organ, previously fixed in FAA, were placed between dental wax supports and sectioned at 10-35 μm thickness with a rotary microtome (Microm HM 315) (Mercado & Ponessa, 2021), subsequently clarified with 50 % NaClO solution, washed with distilled water, and stained with astra blue-safranin and then mounted in 50% glycerol (D'Ambrogio de Argüeso, 1986; Zarlavsky, 2014).

For epidermis and foliar venation studies, diaphanized of apical and median leaflets were made according to Dizeo de Strittmater's (1973) technique. For the description of leaf venation, the terminology proposed by Hickey (1974, 1979) and Ellis *et al*. (2009) was applied, and for the classification of stomata, the terminology proposed by Dilcher (1974) was used.

Stomatal density and stomatal dimensions were quantified in the median region of the lamina of the terminal leaflet. Measurements were taken from 10 microscopic fields per leaflet, using material from three individuals.

Sections and diaphanized epidermis were visualized with a Zeiss Axiolaboptic microscope equipped with a polarized light filter and a Zeiss Axiocam ERc 5s digital camera. Measurements were made using AxioVision software version 4.8.2 (Carl Zeiss Ltd, Herts, UK).

Histochemistry

The main classes of chemical compounds of different plant organs were investigated in transverse microtome sections of fresh material made following the previously mentioned technique proposed by Mercado & Ponessa (2021).

Ferric chloride (10%) in methanol (Zarlavsky, 2014) and Neu's reagent (2-aminoethyl-diphenylborinate, Sigma) 10% in absolute methanol (Neu, 1957), were used to visualize flavonoids and other hydroxycinnamic acids. Vainillin–HCl (Gardner, 1975) was used to visualize tannins. Cresyl blue was used for the detection of mucilage, and picric acid for protein identification (Zarlavsky, 2014).

Some of the sections were treated with 50% NaClO solution and washed with distilled water, prior to dyeing with Sudan IV for the detection of lipids (D'Ambrogio de Argüeso, 1986; Zarlavsky, 2014) and ruthenium red for pectins (Johansen, 1940; Zarlavsky, 2014). Lugol reagent, iodine potassium iodide (IKI) (Johansen, 1940), and observation under polarized light were employed for the detection of starch.

Unstained sections served as a control and were simultaneously observed under light and UV microscopes.

Sections stained with Neu's reagent and unstained control sections were examined under an epifluorescence microscope (Olympus BX43 U-TVO 5xc-3) with UV light (filter UV-1A: 365 nm excitation filter, 400 nm barrier filter). Under these conditions, flavonoids and hydroxycinnamic acids were detected through their differential fluorescence (Merck, 1980; Mondolot-Cosson *et al*., 1997). Photographs were taken with a digital Nikon Coolpix 4500 camera.

RESULTS

Hypseocharis pimpinellifolia exhibited an herbaceous habit with characteristic tuberous, pivoting, napiform roots (7-20 x 2-6 cm), covered by a reddish-brown scaly bark. Occasionally, there was a wedge-shaped area of brownish-dark tissue in the central region (Fig. 1A, 8A- B). The rhizome, lacking visible nodes or cataphylls and covered by an exfoliating rhytidome-like periderm, measured 5-8 cm in length and 1-1.5 cm in diameter. This was followed by a short brachyblast of 1-2 cm in length by 1-1.5 cm in diameter, where the leaves and flowers were inserted in a compressed spiral pattern. The pinnately compound leaves (6-21 cm in length), exhibited marked foliar polymorphism between individuals. The leaves were arranged in a rosette with broad petiole bases, intermixed with leaf debris and petioles from previous years, enveloping the brachyblast (Fig. 1A-C). The leaflets (15-21) were alternate to subopposite, measuring10-30 mm in length, sessile or subsessile, elliptical or obovate, irregularly pinnately lobed, often with 5-11 lobes, and had smooth to crenate margins and an acute to lobed apex. The terminal leaflets showed the same size as the others or were slightly larger (Fig. 1B-C).

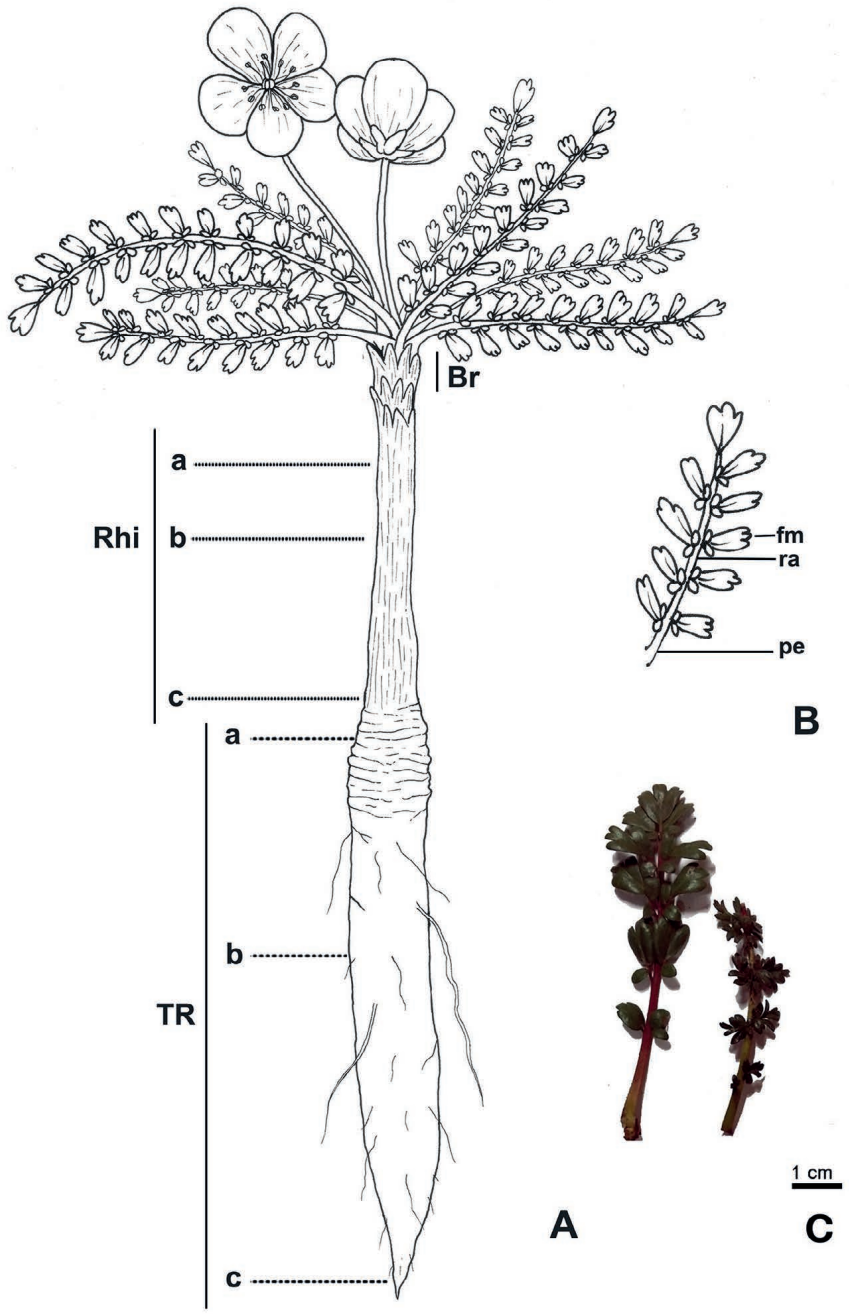

Fig. 1. Morphology of *Hypseocharis pimpinellifolia*. A) General aspect of the plant. B) Pinnate leaf. C) Representative leaves illustrating foliar polymorphism among individuals at the same developmental stage. Abbreviations: Tr, tuberous root (proximal (a), middle (b), and distal (c) sections, with respect to the rhizome); Rhi, rhizome (proximal (a), middle (b), and distal (c) sections, with respect to the brachyblast); Br, brachyblast; pe, petiole; ra, rachis; ml, middle leaflets in their middle portion. (Illustration by Lic. Mariana Leal, INBIOFIV–CONICE-UNT).

Fig. 1. Morfología de *Hypseocharis pimpinellifolia*. A) Aspecto general de la planta. B) Hoja pinnada. C) Diferentes hojas que ilustran el polimorfismo foliar de distintos individuos en la misma etapa de madurez. Abreviaturas: Tr, raíz tuberosa (sección proximal (a), media (b) y distal (c), respecto al rizoma); Rhi, rizoma (sección proximal (a), media (b) y distal (c) respecto al braquiblasto); Br, braquiblasto; pe, pecíolo; ra, raquis; ml, folíolos medios en su porción media. (Ilustración: Lic. Mariana Leal, INBIOFIV–CONICE-UNT).

Leaf venation is pinnate. Each leaflet exhibited a pinnate eucamptodromous venation pattern, with a moderately thick primary vein that was straight to slightly curved and unbranched (Fig. 2A). Secondary epimedial costal veins were arranged alternately to sub-oppositely, with decurrent uniform acute divergence angles, and following a straight to slightly curved path toward the apex of each lobe (Fig. 2B). Tertiary veins were alternate to sub-opposite, originating at acute angles from the admedial and exmedial region of the secondary veins, following a percurrent model forming prominent arches that connected adjacent tertiary veins. Quaternary veins, constituted the highest venation order, formed areolas with imperfect development, irregular shapes, and a random arrangement. They were sometimes devoid of venules or presented simple or branched venules that were divided two to three times (Fig. 2C). The marginal venation was incompletely looped and occasionally bore simple or branched venules (Fig. 2C).

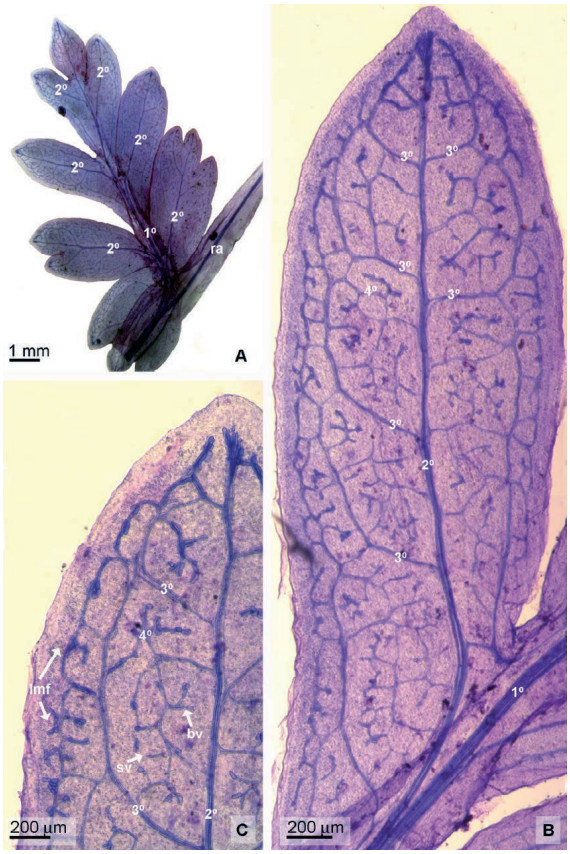

Fig. 2. *Hypseocharis pimpinellifolia* leaflet architecture. A) Middle leaflets. B) Middle lobe of the leaflet. C) Lobe margin and apex detail. Abbreviations: 1º, primary veins; 2º, secondary veins; 3º, tertiary veins; 4º, quaternary veins; bv, branched venule; ra, rachis; lmf, ultimate marginal venation; sv, simple venule.

Fig. 2. Arquitectura del folíolo de *Hypseocharis pimpinellifolia*. A) Folíolos medios. B) Lóbulo medio del folíolo. C) Detalle del margen y ápice del lóbulo. Abreviaturas: 1º, venas primarias; 2º, venas secundarias; 3º, venas terciarias; 4º, venas cuaternarias; bv, vénula ramificada; ra, raquis; lmf, venación marginal final; sv, vénula simple.

In superficial view, the leaves were amphistomatic, with a smooth to slightly striated cuticle surrounding the trichomes. Epidermal cells were polygonal, with slightly to strongly curved anticlinal walls on the adaxial and abaxial epidermis, respectively. Anomocytic stomata (occlusive cells of 32.07 ± 2.68 μm length by 27.68 ± 0.74 μm width) were observed at densities of 68.09 ± 18.01 stomata/mm^2 on the adaxial epidermis and 143.12 ± 13.04 stomata/mm^2 on the abaxial epidermis (Fig. 3A-B). On the veins, along inner margins (towards the base of the leaf) of the basal lobes, and less frequently on the outer margins (towards the apex of the leaf) of the middle and upper lobes, unicellular, sting-like non glandular trichomes (NGT) (45.2 ± 4.42 μm length) were observed (Fig. 3C). On both epidermal surfaces (being more frequently on the abaxial side) pluricellular glandular trichomes (GT) (61.34 ± 5.91 in length x 36.01 ± 6.21 μm in diameter at head level) were also observed. These glandular trichomes consist of a pair of foot cells, one or two pairs of stalk cells, and a pluricellular head composed of two pairs of cells (Fig. 3D).

Histochemical analyses using Sudan IV revealed the presence of lipid droplets in the heads and stalks cells of the GT. Phenolic compounds were detected with ferric chloride and Neu's reagent in both the stalk and head cells of the GT; the characteristic blue fluorescence observed indicated they likely correspond to caffeic and/or chlorogenic acid derivatives (Fig. 3D-G, Table 1).

The transverse section of the leaflets showed isobilateral mesophyll (233.67 ± 12.83 μm thick). The one-layered epidermis had a thick cuticle (11.38 ± 1.11 μm on the adaxial surface and 12.85 ± 1.83 μm on the abaxial surface), and quadrangular cells (18.0 ± 3.25 μm) interrupted by stomata, which were either slightly elevated or level with the epidermal surface. The mesophyll consisted of two adaxial layers of palisade cells (123.45 ± 9.66 μm), followed by two to three layers of compact spongy parenchyma (37.15 ± 1.6 μm, interrupted by collateral vascular bundles surrounded by parenchymatic sheaths) and a single layer of shorter abaxial palisade cells (64.74 ± 9.19 μm) (Fig. 4A and B). Sections of the secondary veins at the leaflet lamina, showed vascular bundles with collenchymatous phloem cap and parenchymatous sheaths that extended towards the abaxial epidermis forming a beam, occasionally reinforced with collenchyma (Fig. 4A and D). The leaflet margin lacked structural reinforcement tissues (Fig. 4C). Calcium oxalate crystals and dispersed lipid droplets were observed in the mesophyll and palisade cells, respectively (Fig. 4D-E, Table 1). The transverse section of the primary vein of the leaflet exhibited a subcircular shape, with a one-layered epidermis interrupted by stomata, GT, and NGT, similar to those described for the lamina. At the midvein, a single layer of subepidermal laminar collenchyma was evident, followed by loosely arranged ground parenchyma containing idioblasts with druses.

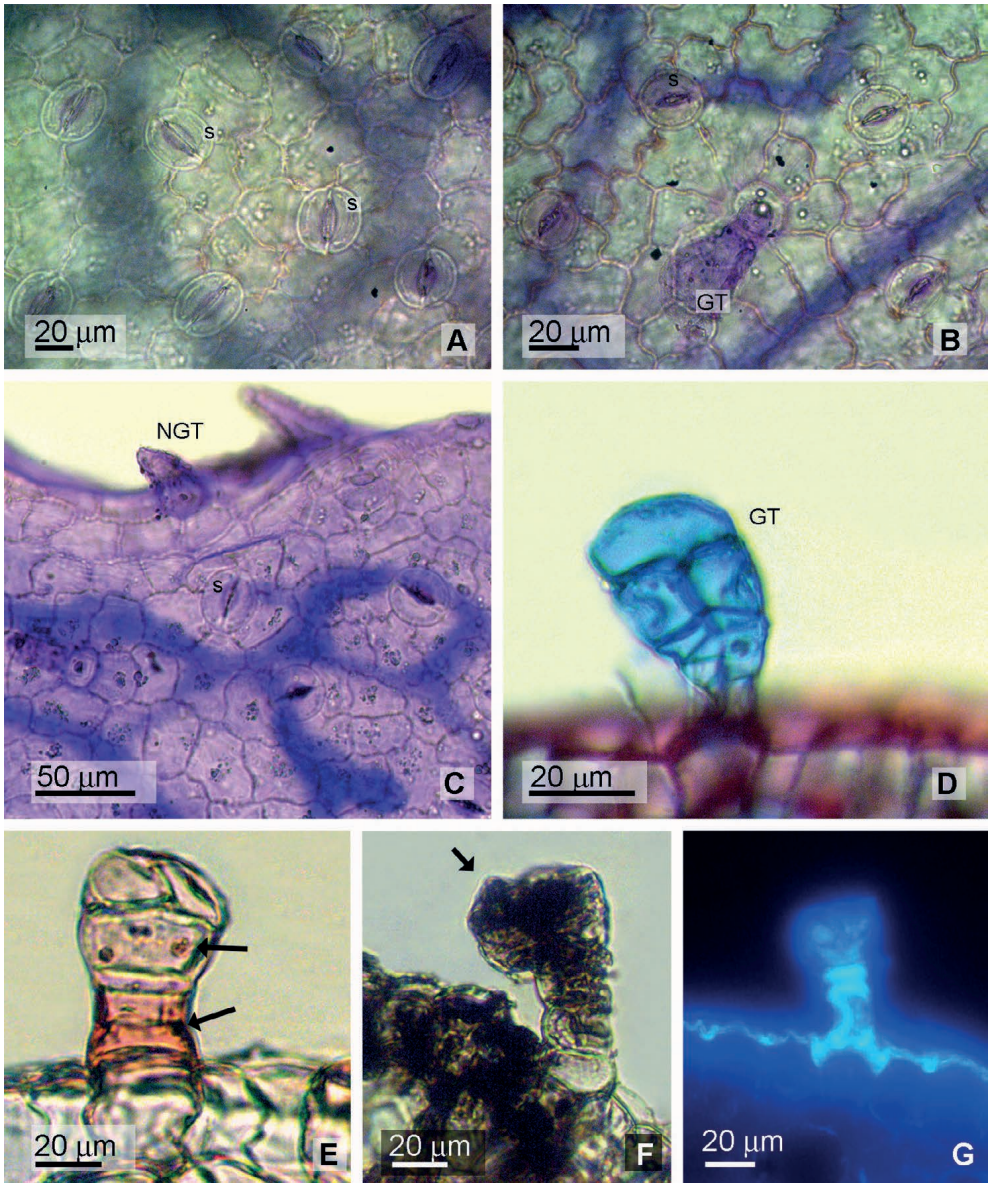

Fig. 3. *Hypseocharis pimpinellifolia.* Middle leaflet epidermis, surface view. A) Adaxial epidermis. B) Abaxial epidermis. C) Non-glandular trichome. D-G) Glandular trichome. E) Positive staining with Sudan IV for lipids (arrows). F) Ferric chloride, positive for phenols (arrow). G) Positive staining with Neu's reagent for phenols indicated by bright blue fluorescence. Abbreviations: s, stomata; GT, glandular trichome; NGT, non-glandular trichome.

Fig. 3. *Hypseocharis pimpinellifolia*. Epidermis del folíolo medio, vista superficial. A) Epidermis adaxial. B) Epidermis abaxial. C) Tricoma no glandular. D-G) Tricoma glandular. E. Tinción positiva con Sudan IV para lípidos (flechas). F. Cloruro férrico, positivo para fenoles (flecha). G. fluorescencia azul brillante con Reactivo de Neu para fenoles. Abreviaturas: s, estomas; GT, tricoma glandular; NGT, tricoma no glandular.

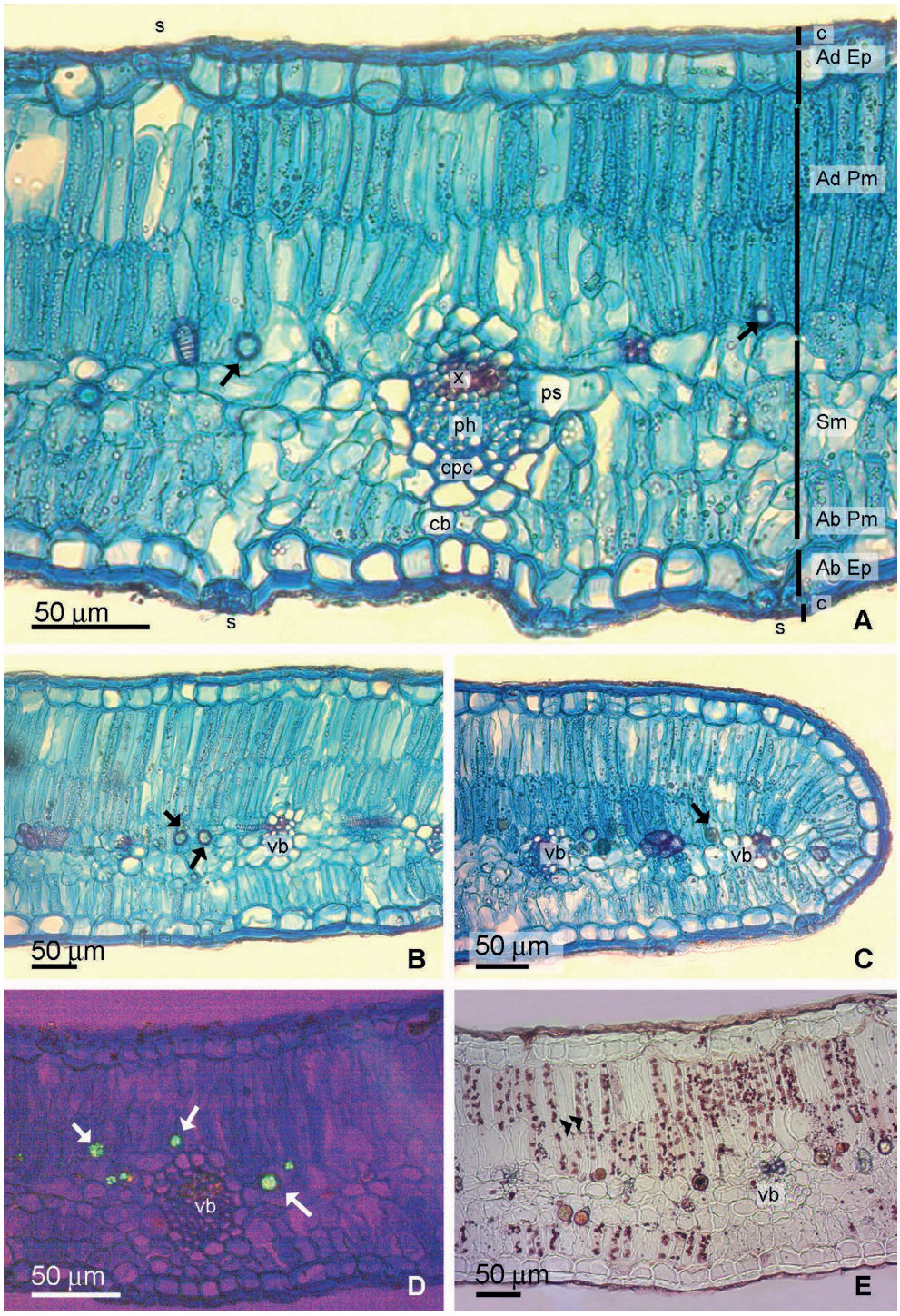

Fig. 4. *Hypseocharis pimpinellifolia*. Leaf anatomy, leaflets transverse section. A) Secondary vein. B) Tertiary vein. C) Leaf margin. D) Polarized light reveals the presence of calcium oxalate druses (arrow). E) Sudan IV positive staining for lipids. Abbreviations: Ab Ep, abaxial epidermis; Ab Pm, abaxial palisade mesophyll; Ad Ep, adaxial epidermis; Ad Pm, adaxial palisade mesophyll; arrowhead, lipid droplets in the palisade mesophyll cells; arrow, calcium oxalate druses; c, cuticle; cb, collenchyma beam; cpc, collenchyma phloem cap; ph, phloem; ps, parenchyma sheath; s, stomata; Sm, spongy mesophyll; vb, vascular bundle; x, xylem.

Fig. 4. *Hypseocharis pimpinellifolia*. Anatomía de la hoja, sección transversal de los folíolos. A) Vena secundaria. B) Vena terciaria. C) Margen de la hoja. D) Luz polarizada revela

presencia de drusas de oxalato de calcio (flecha). E) Tinción positiva con Sudan IV para lípidos. Abreviaturas: Ab Ep, epidermis abaxial; Ab Pm, mesófilo en empalizada abaxial; Ad Ep, epidermis adaxial; Ad Pm, mesófilo en empalizada adaxial; gotas lipídicas en las células del mesófilo en empalizada (punta de flecha); drusas de oxalato de calcio (flecha); c, cutícula; cb, haz de colénquima; cpc, casquete floemático de colénquima; ph, floema; ps, vaina parenquimática; s, estomas; Sm, mesófilo esponjoso; vb, haz vascular; x, xilema.

Table 1. Histochemical characterization of *H. pimpinellifolia* vegetative organs.
Tabla 1. Caracterización histoquímica de órganos vegetativos de *H. pimpinellifolia*.

Reagents	Components	Leaflet	Root	GT	Brachyblast
Ruthenium red	Pectins		+		
Lugol reagent (IK)	Starch		+		
Sudan IV	Lipids -suber	+	+	+	
Picric acid	Proteins		+		
Ferric chloride	Phenolic compounds		+	+	+
Neu's reagent	Flavonoids and hydroxycinnamic acids		+	+	
Vainillin – HCl	Tannins		+		

(+) Indicates the presence of the chemical group, GT, glandular trichome.
(+) Indica la presencia del grupo químico, GT, tricoma glandular.

The vascular system consisted of a collateral vascular bundle with a collenchymatous phloem cap (occasionally extended as a sheath) and three to four inverted collateral minor bundles, each with collenchymatous phloem caps (Fig. 5A-B). When present, the petiolule of the leaflets had a similar structure to that previously described for the primary vein. It had a subtriangular outline, slightly canaliculate on the adaxial side, and a vascular system consisting of one to three collateral vascular bundles accompanied by one or two smaller inverted collateral bundles (Fig. 5C).

In superficial view, the epidermis of the rachis, presented a slightly striated cuticle and polygonal epidermal cells with a longitudinal axis that was parallel to the longitudinal axis of the organ, straight anticlinal walls and both GT and NGT. Anomocytic stomata were also observed (45.74 ± 2.45 μm length x 30.18 ± 2.65 μm width) (Fig. 5D) which were identical to those observed in the lamina. Transverse sections of the distal and middle zones of the rachis presented a subcircular shape. The proximal region showed a semicircular outline with a small concavity towards the adaxial face (Fig. 5E-G). One-layered epidermis with stomata, GT and NGT distributed mainly over the adaxial epidermis, one-layered subepidermal collenchyma, loosely arranged ground parenchyma, and two to four collateral vascular bundles with collenchyma or sclerenchyma phloem caps and two to five inverted minor bundles. The number of bundles in the vascular system increases from the proximal to the distal section (Fig. 5E-G).

The petiole in its distal and middle portions, close to the rachis, presented an identical structure to the distal zone of the rachis (Fig. 5H). The proximal section showed a subcircular plane-convex shape with short wings that sheathed the brachyblast.

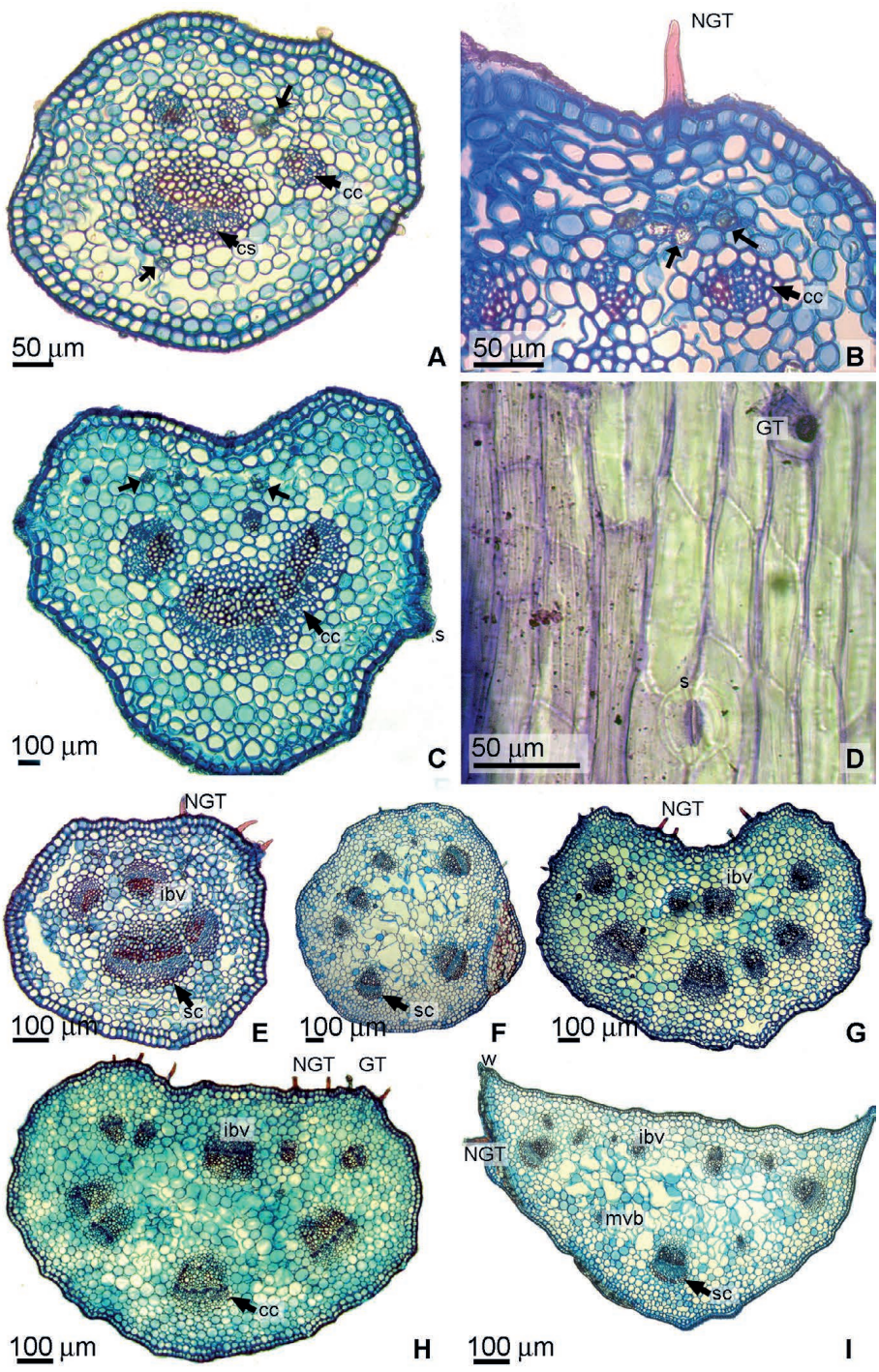

Fig. 5. *Hypseocharis pimpinellifolia*. Leaf anatomy. A-B) Transversal section of the mid vein at the leaflet. C) Petiolule transversal section. D) Superficial view of rachis epidermis. E-G) Rachis transversal section. E) Distal region. F) Middle region. G) Proximal region in relation to the petiole. H-I) Petiole transversal section. H. Middle region. I. Proximal region in relation to the stem. Abbreviations: arrow, druses; cc, collenchyma cap; cs, collenchyma sheath; GT, glandular trichome; ibv, inverted vascular bundles; mbv, minor vascular bundle; NGT, non-glandular trichome; s, stomata; sc, sclerenchyma cap; w, wing.

Fig. 5. *Hypseocharis pimpinellifolia*. Anatomía de la hoja. A-B) Sección transversal de la vena media en el folíolo. C) Sección transversal del peciólulo. D) Vista superficial de la epidermis del raquis. E-G) Sección transversal del raquis. E. Región distal. F. Región me- ➤

dia. G. Región proximal en relación con el pecíolo. H-I) Sección transversal del pecíolo. H. Región media. I. Región proximal en relación con el tallo. Abreviaturas: drusas (flecha); cc, casquete de colénquima; cs, vaina de colénquima; GT, tricoma glandular; ibv, haces vasculares invertidos; mbv, haz vascular menor; NGT, tricoma no glandular; s, estomas; sc, casquete de esclerénquima; w, ala.

The vascular system consisted of three to four collateral vascular bundles with interspersed minor bundles and four to six inverted collateral bundles (Fig. 5I). Occasionally, the central ground parenchyma of the rachis and petiole exhibited loosely arranged parenchyma cells, that resembled aerenchyma (Fig. 5F and I).

In transverse section, the brachyblast showed a circular shape. The epidermal tissue was replaced early by a periderm originating from the external layers of the cortical parenchyma (Fig. 6A and B). The cortex consisted of 17-23 layers of compact parenchyma containing crystalliferous idioblasts with calcium oxalate rhomboidal crystals and druses (Fig. 6B). The vascular system formed an eustele with an early onset of secondary growth, in which the bundles retained partial individuality. A broad pith was also observed.

The proximal transverse section of the rhizome exhibited the same basic structure as the brachyblast, except for the presence of cauline buds which would give rise to new brachyblast branches or foliar traces (Fig. 6C). In the middle and proximal sections of the rhizome, secondary growth became evident, with a more developed vascular cylinder and a reduced pith that appeared either centric or markedly eccentric (Fig. 6D-E). The secondary xylem presented broad parenchyma rays (Fig. 6F). Phenolic compounds were revealed with ferric chloride in idioblasts of the periderm, cortex, and xylem parenchyma (Fig. 6G, Table 1).

The napiform tuberous root measured 7-20 cm in length and 2-6 cm in diameter at its widest point exhibiting considerable polymorphism (Fig. 7A). Mature roots occasionally showed a wedge-shaped region with brownish-red deposits, formed by one or several concentric tissue layers in cross section (Fig. 7B), resembling heartwood. These deposits became evident toward the end of the first third of the root and extend approximately to the end of the distal third, without reaching the organ tip.

In the proximal section, near to the rhizome, the root showed a well-developed periderm, eight to nine layers of cortical parenchyma, and a vascular cylinder with secondary growth, phloem and xylem formed continuous rings with wide parenchyma rays, occasionally exhibited crystalliferous idioblast with calcium oxalate crystals in the form of druses and prisms (Fig. 7C).

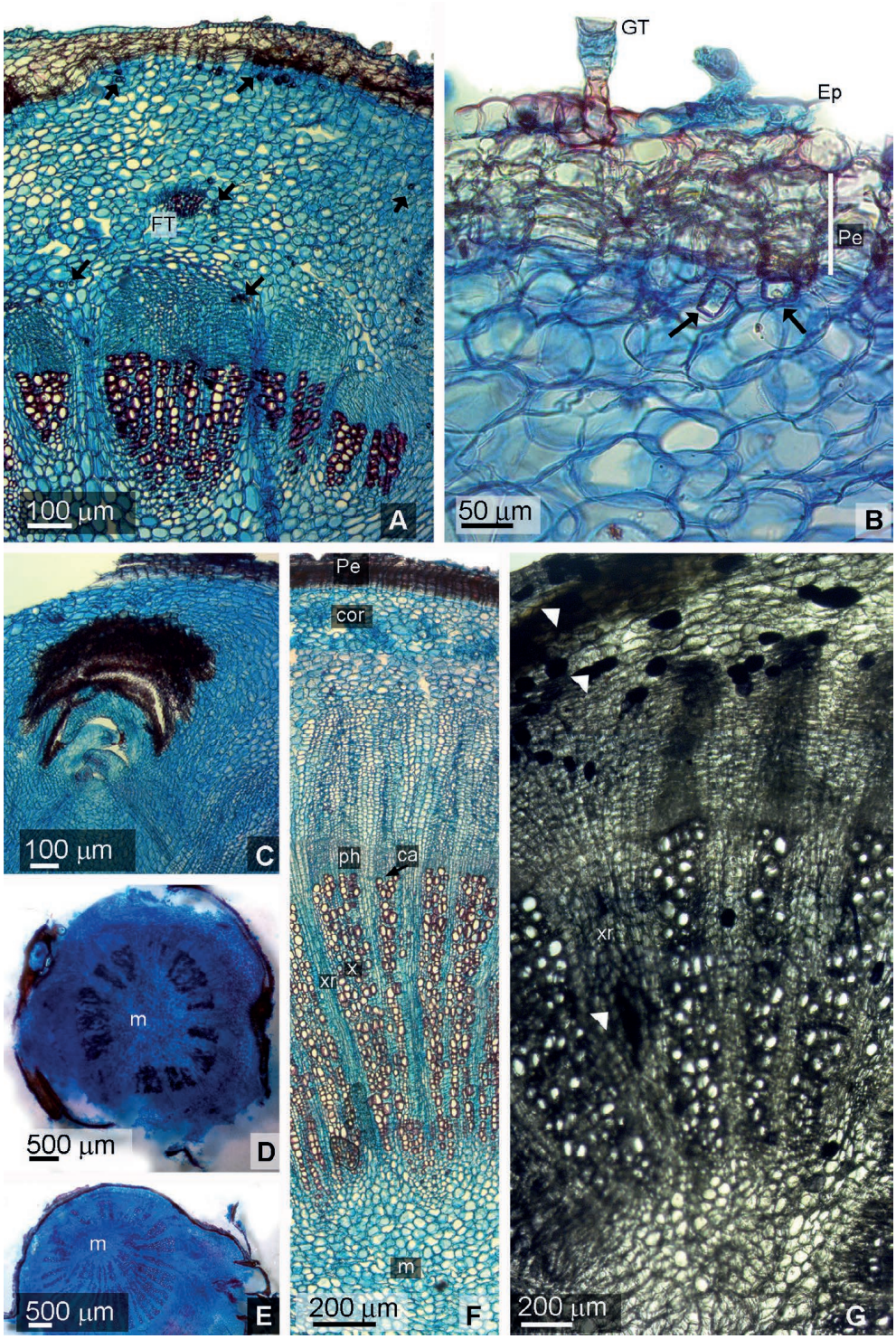

Fig. 6. *Hypseocharis pimpinellifolia.* Caulinar anatomy, transversal section. A-B) Brachyblast. B. Periderm formation from sub-epidermal cortex layers. C-G) Rhizome. C. Caulinar bud in the cortical parenchyma of the proximal section of the rhizome. D. Rhizome with central medulla. E. Rhizome with eccentric reduced medulla. F. Rhizome section at the middle region of the organ. G. Ferric chloride positive staining, cells containing phenolic compounds in the periderm, cortex, and xylem rays (arrowhead). Abbreviations: arrow, calcium oxalate crystals and druses; FT, foliar trace; Ep, epidermis; ca, cambium; Pe, periderm; GT, glandular trichome; m, medulla; xr, xylem ray; x, xylem; ph, phloem; cor, cortex.

Fig. 6. *Hypseocharis pimpinellifolia.* Anatomía caulinar, sección transversal. A-B) Braquiblasto. B. Formación de peridermis a partir de capas subepidérmicas del córtex. C-G) Rizoma. C. Yema caulinar en el parénquima cortical de la sección proximal del rizoma. D. Rizoma con médula central. E. Rizoma con médula reducida excéntrica. F. Sección de rizoma en la región media del órgano. G. Tinción positiva con cloruro férrico, células que contienen compuestos fenólicos en la peridermis, el córtex y los radios xilemáticos (punta de flecha). Abreviaturas: cristales de oxalato de calcio y drusas (flecha); FT, traza foliar; Ep, epidermis; ca, cambium; Pe, peridermis; GT, tricoma glandular; m, médula, xr, radio xilemático; x, xilema; ph, floema; cor, córtex.

The mid and distal zones of the root exhibited unusual secondary growth, with a periderm formed by suber or phellem, two to three layers of phellogen, and one or two layers of phelloderm (Fig. 7D and E). The cortex consisted of 15-26 layers of parenchyma, and the vascular system showed abundant amylaceous parenchyma, derived from both phloematic and xylem parenchyma (Fig. 7D). The phloem was arranged in strands and occasionally accompanied by isolated peri phloematic fibers (Fig. 7F), while the xylem vessels appeared dispersed arranged in lines or in small groups between the abundant parenchyma (Fig. 7D and F). Within the pith, the development of internal concentric meristems, similar to phellem, was evidenced by the presence of concentric tissue layers resembling a periderm, referred to as internal periderm (Fig. 7D and G). This structure corresponded to the wedge-shaped region, where the concentric periderm layers and the disorganized xylem vessels were intercalated. In fresh unstained sections, this region was characterized by an amber colored content (Fig. 8A), which tested positive for phenolic compounds (Fig. 8B, Table 1). When treated with various histochemical reagents and stains, the internal periderm and secondary xylem vessels walls in this region revealed the presence of phenolic compounds related to chlorogenic and/or caffeic acid (Fig. 8C), pectates (Fig. 8D), lipids possibly suberin, and tannins (Fig. 8E-F, Table 1).

In the distal region, a section of a root where the central wedge was not developed allowed the observation of the proto and metaxylem vessels, indicating that the root is derived from a diarch pattern (Fig. 9A-B). Emerging lateral roots presented periderm, 8-10 layers of cortical parenchyma, and isolated fibers or groups of fibers delimiting the vascular cylinder (Fig. 9C). Fresh sections of untreated root revealed cortical idioblasts with amber coloration (Fig. 10A), which gave positive reaction for phenolic compounds (Fig. 10B, Table 1). Other histochemical assays revealed the presence of suberin, pectin, tannins, and phenolic compounds in the periderm (Fig. 10C-F, Table 1). Starch, calcium oxalate crystals, and proteins were also observed in the storage parenchyma of the cortex and medullary rays (Fig. 10G-J, Table 1).

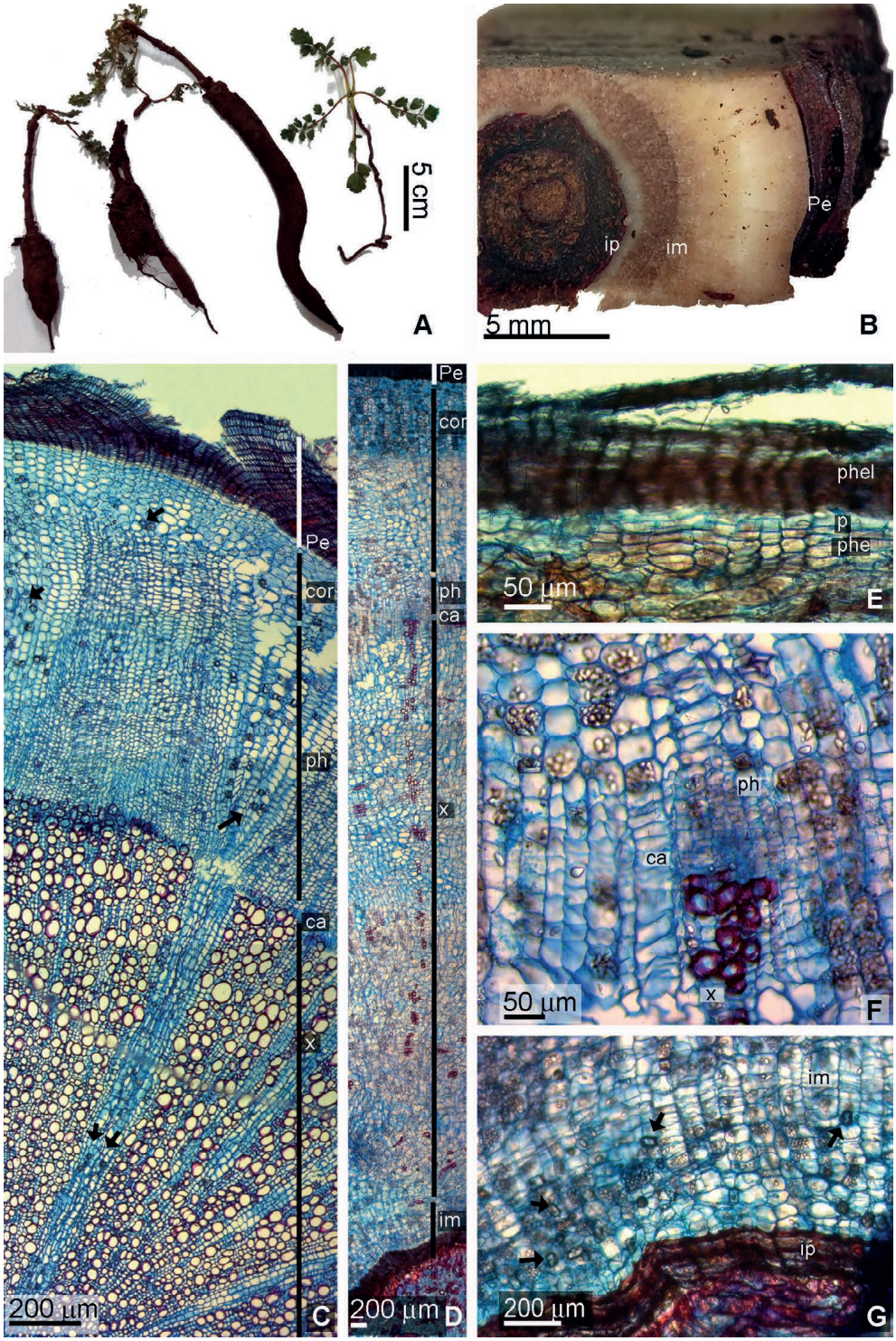

Fig. 7. *Hypseocharis pimpinellifolia*. Tuberous roots. A) Polymorphism in tuberous roots. B-F) Tuberous roots transversal section at the proximal and middle regions in relation to the rhizome. B. Root with concentric layers of tissue in the central wedge. C. Proximal region. D. Middle region. E. Periderm detail. F. Vascular system detail. G) Detail of the periderm delimiting the central wedge. Abbreviations: p, phellogen; phel, phellem; phe, phelloderm; ip, internal periderm; im, internal meristem; ca, cambium; arrow, calcium oxalate crystals and druses; Pe, periderm; x, xylem; ph, phloem; cor, cortex.

Fig. 7. *Hypseocharis pimpinellifolia.* Raíces tuberosas. A) Polimorfismo en raíces tuberosas. B-F) Sección transversal de raíces tuberosas en las regiones proximal y media en relación

con el rizoma. B. Raíz con capas concéntricas de tejidos en la cuña central. C. Región proximal. D. Región media. E. Detalle de la peridermis. F. Detalle del sistema vascular. G) Detalle de la peridermis delimitando la cuña central. Abreviaturas: p, felógeno; phel, felema; phe, felodermis; ip, peridermis interna; im, meristema interno; ca, cambium; cristales de oxalato de calcio y drusas (flecha); Pe, peridermis; x, xilema; ph, floema; cor, córtex.

DISCUSSION AND CONCLUSION

A morpho-anatomical description is considered the first and preferred method of botanical characterization, emphasizing diagnostic features which may be useful in distinguishing between similar species. Although, individual structural elements may be common within the same organs of related plant taxa, the unique organization of these elements within a specific species constitutes its characteristic "fingerprint" (Upton *et al*., 2011). In this context, the detailed morpho-anatomical characterization of the vegetative organs of *H. pimpinellifolia* provides a valuable framework for future taxonomic studies and establishes reliable diagnostic criteria for quality control, particularly in comparison with closely related species such as *H. tridentata*, which remains unexplored. This information could be particularly relevant if the species is found to be suitable for future commercial or pharmacobotanical use.

Following the works of Metcalfe & Chalk (1950), which today serve as standard references in plant anatomy, the use of anatomical characters often offers important diagnostic characters for taxonomic identification and quality control of whole and powdered herbal drugs (Alamgir *et al*., 2017). Thus, a good knowledge of plant anatomy and histology is essential for plant species recognition. Trichomes and stomatal types, transverse sections outlines, the organization of the vascular system in different organs (particularly in the midrib), mesophyll structure, the presence/ distribution/ characteristics of crystalliferous idioblasts, and secondary metabolites have been demonstrated to hold diagnostic value in different taxa, including species.

This study presented the first morpho-histological and histochemical characterization of *H. pimpinellifolia* vegetative organs, representing the first contribution to the anatomical study of vegetative organs within the genus. Traits that could be considered of diagnostic value for soldaque include leaves and brachyblasts with anomocytic stomata, unicellular non-glandular trichomes (NGT) and biseriated multicellular glandular trichomes (GT) that accumulate lipids and phenolic compounds, tuberous root with unusual growth with abundant amylaceous parenchyma, idioblast with calcium oxalate crystals, and an internal meristem which originates a central wedge with deposition of phenolic compounds, lipids and pectin.

The glandular trichomes and the internal meristem of the tuberous roots could be responsible for the synthesis of compounds related to the anti-inflammatory and wound-healing medicinal properties attributed to

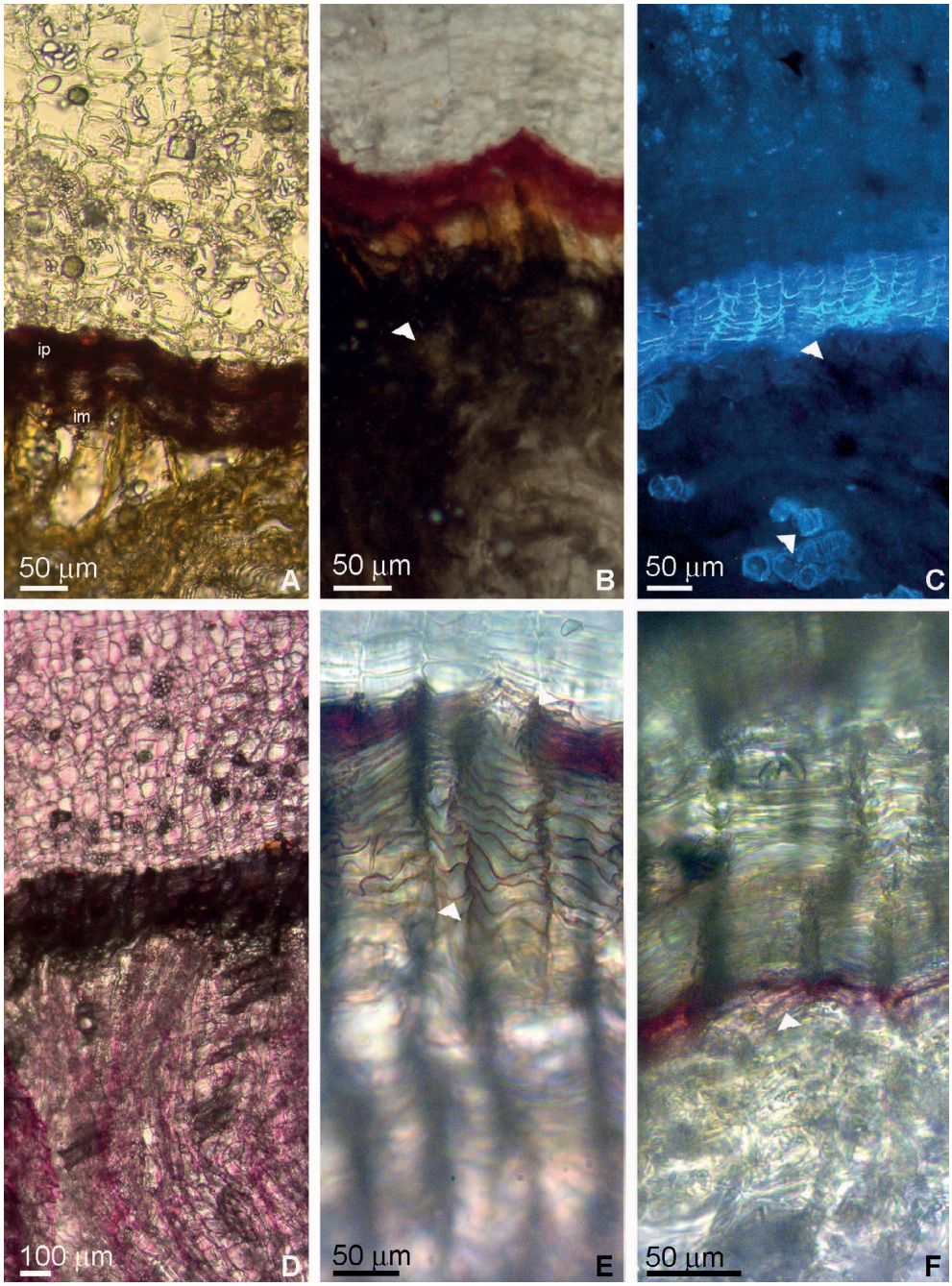

Fig. 8. *Hypseocharis pimpinellifolia*. Tuberous roots, histochemistry of internal meristem and periderm at the proximal and middle regions in relation to the rhizome. A) Unstained internal meristem and periderm. B) Ferric chloride positive staining for phenolic compounds (arrowhead). C) Neu's reagent positive staining for phenols indicated by bright blue fluorescence at the internal periderm and lignified walls of xylem vessels (arrow head). D) Pectins in primary cell walls of the reserve parenchyma and central parenchyma stained with ruthenium red. E) Sudan IV positive reaction (arrowhead) for lipids, cutin and, suberin (arrowhead). F) Vanillin-HCl positive staining for tannins (arrowhead) at the internal meristem. Abbreviations: ip, internal periderm; im, internal meristem.

Fig. 8. *Hypseocharis pimpinellifolia*. Raíces tuberosas, histoquímica del meristema interno y de la peridermis en las regiones proximal y media en relación con el rizoma. A) Meristema interno y peridermis sin teñir. B) Tinción positiva con cloruro férrico para compuestos fenólicos (punta de flecha). C) Reactivo de Neu positivo para fenoles reveló fluorescencia

azul brillante en la peridermis interna y en las paredes lignificadas de los vasos del xilema (punta de flecha). D) Pectinas en las paredes celulares primarias del parénquima de reserva y del parénquima central, teñidas con rojo de rutenio. E) Reacción positiva con Sudán IV para lípidos, cutina y suberina (punta de flecha). F) Tinción positiva con vainillin-HCl para taninos (punta de flecha) en el meristema interno. Abreviaturas: ip, peridermis interna; im, meristema interno.

the vegetative parts of soldaque. Histochemical studies of the root indicate that, like other Andean roots and *Hypseocharis* species such as *H. bilobata* Killip (Ayala Tineo, 2010), soldaque contains high levels of phenolic compounds, particularly hydroxycinnamic acids such as chlorogenic and caffeic acids (Jiménez-Sammán, 2014; Doroteo *et al*., 2013; Silva de Lima *et al*., 2017; Gabilondo, 2015; Wang *et al*., 2016). These compounds also act as antioxidants, playing a key role in defense against pathogenic organisms and other abiotic stress factors (Kumar *et al*., 2020) and may be responsible for the bioactivity attributed to *H. pimpinellifolia*. Studies of this nature are relevant for the quality control of products derived from this species and will also support future research aimed at the isolation and identification of metabolites of pharmacological and functional interest.

In addition, the presence of proteins, lipids, and starch indicates that the root of *H. pimpinellifolia* has great nutritional potential. Similarly, as noted by Grigore & Toma (2008), the occurrence of calcium oxalate crystals and phenolic compounds may be associated with osmoregulatory mechanisms related to abiotic stress conditions in which plants develop. *Hypseocharis pimpinellifolia*, a species with the ability to tolerate stress factors such as drought, extreme cold temperatures, and ultraviolet radiation of the Puna environment, would therefore represent a promising source of unconventional food (Ortega-Cabello *et al*., 2018). However, further studies are required to assess its potential nutritional and pharmaceutical value.

Regarding the systematic position of *Hypseocharis*, Slanis & Grau (2001) and Lozada *et al*. (2020) described the alternating correspondence of the genus between Oxalidaceae and Geraniaceae families. Its morpho-anatomical characteristics such as the presence of simple unbranched NGT, capitate GT, anomocytic stomata, stem and petiole in transverse section exhibiting a circle of separate vascular bundles, oxalate crystals, stem modifications as brachyblasts and rhizomes, and the development of tuberous roots responds to the general structural pattern described for some members of the Oxalidaceae, but can also be ascribed to certain Geraniaceae (Metcalfe & Chalk, 1950). Seed and floral morphology, as well as phylogenetic evidence from chloroplast rbcL and trnL–F sequences, show that *Hypseocharis* is a sister group or diverged early within Geraniaceae (Fiz *et al*., 2008; APG IV, 2016); thus, the observed morpho-anatomical similarities are best interpreted as homoplastic adaptations to extreme environments. Broader sampling across multiple *Hypseocharis* species, including reproductive organs, in future analyses will be essential to expand the available data within the genus.

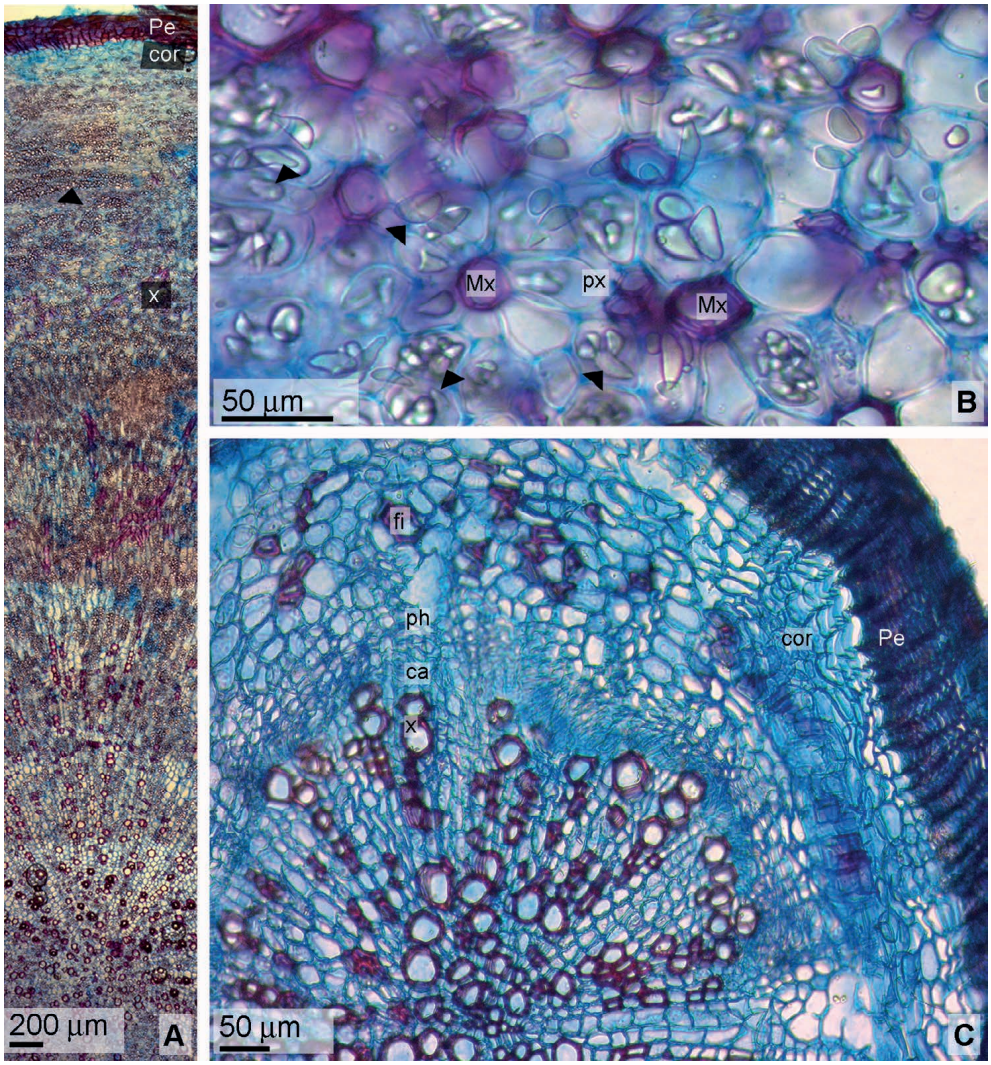

Fig. 9. *Hypseocharis pimpinellifolia*. Tuberous roots. Transversal section at the distal region in relation to the rhizome. A) Distal section without central wedge. B) Metaxylem and protoxylem vessels of a diarch root. C) Lateral root transection. Abbreviations: Mx, metaxylem; px, protoxylem; Pe, periderm; co, cortex; fi, fibers; ph, phloem; ca, cambium; x, xylem; arrowhead, starch grains.

Fig. 9. *Hypseocharis pimpinellifolia.* Raíces tuberosas. Sección transversal en la región distal en relación con el rizoma. A) Sección distal sin cuña central. B) Se evidencian vasos de metaxilema y protoxilema de una raíz diarca. C) Sección transversal de raíz lateral. Abreviaturas: Mx, metaxilema; px, protoxilema; Pe, peridermo; co, corteza; fi, fibras; ph, floema; ca, cámbium; x, xilema; punta de flecha, granos de almidón.

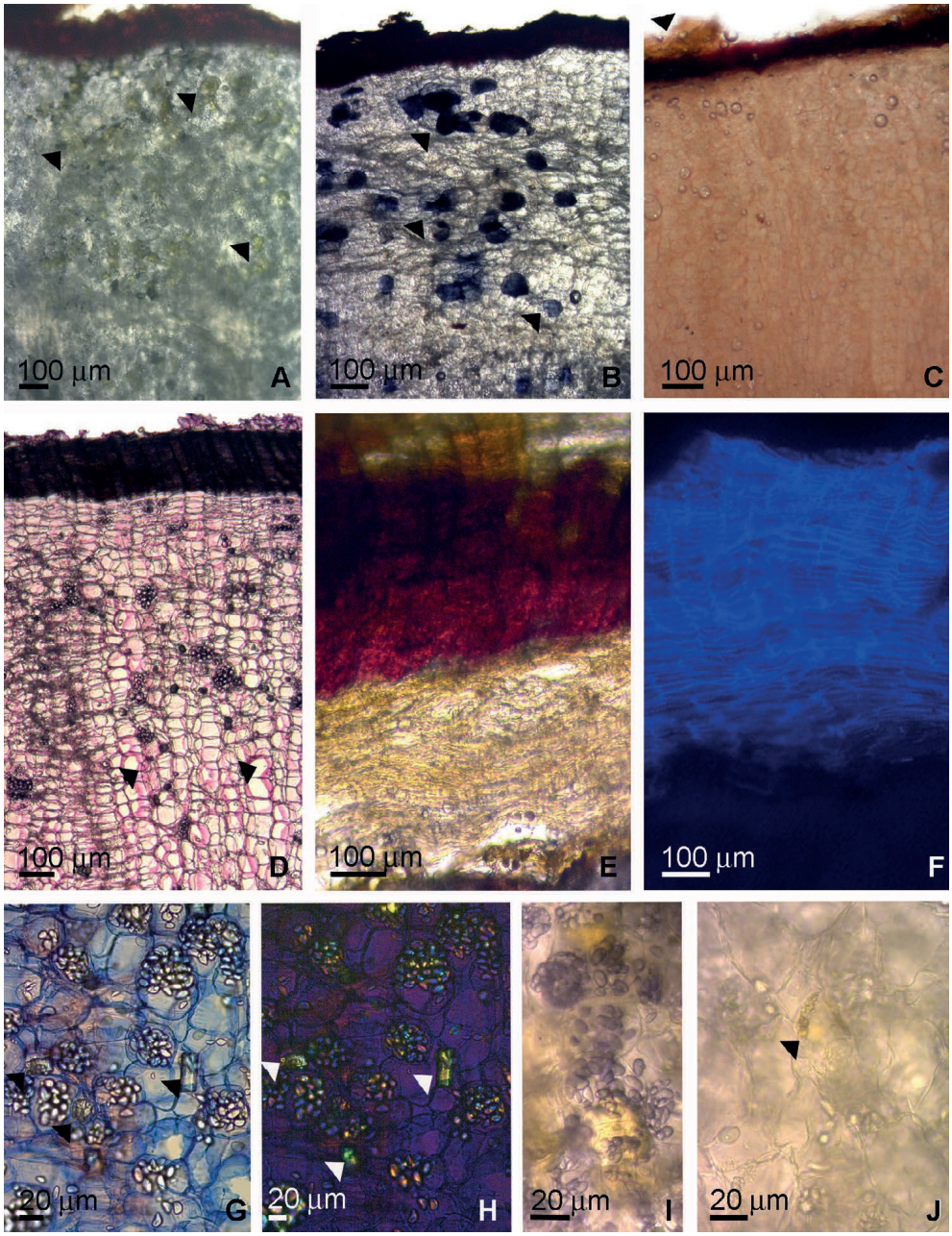

Fig. 10. *Hypseocharis pimpinellifolia*. Tuberous roots, histochemistry of the periderm and reserve parenchyma at the distal region in relation to the rhizome. A) Unstained fresh section of periderm and cortex with amber-colored idioblast (arrowhead). B) Ferric chloride positive staining for phenolic compounds (arrowhead). C) Sudan IV positive staining for lipids, cutin, and suberin (arrowhead). D) Pectins in primary cell walls of the cortical reserve parenchyma stained with ruthenium red (arrowhead). E) Vanillin-sulfuric acid positive reaction for tannins at the periderm (red color). F) Neu's reagent positive for staining for phenols indicated by bright blue fluorescence at periderm. G) Starch and calcium oxalate crystals (arrowhead) in reserve parenchyma, under bright light. H) Starch and calcium oxalate crystals (arrowhead) in the reserve parenchyma under polarized light. I) Starch visualized by Lugol's reagent. J) Proteins (arrowhead) revealed with picric acid in the reserve parenchyma.

Fig. 10. *Hypseocharis pimpinellifolia*. Raíces tuberosas, histoquímica de la peridermis y el parénquima de reserva en la región distal en relación con el rizoma. A) Peridermis y corteza en sección fresca sin teñir con idioblasto de color ámbar (punta de flecha). ➤

B) Tinción positiva con cloruro férrico para compuestos fenólicos (punta de flecha). C) Tinción positiva con Sudán IV para lípidos, cutina y suberina (punta de flecha). D) Pectinas en las paredes celulares primarias del parénquima cortical de reserva, teñidas con rojo de rutenio (punta de flecha). E) Reacción positiva de vanillin-ácido sulfúrico para taninos en la peridermis (color rojo). F) Reactivo de Neu positivo para fenoles revelando fluorescencia azul brillante en la peridermis. G) Almidón y cristales de oxalato de calcio (punta de flecha) en el parénquima de reserva, bajo luz brillante. H) Almidón y cristales de oxalato de calcio (punta de flecha) en el parénquima de reserva bajo luz polarizada. I) Almidón visualizado mediante el reactivo de tinción de Lugol. J) Proteínas (punta de flecha) reveladas con ácido pícrico en el parénquima de reserva.

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AUTHORS CONTRIBUTIONS

MIM, MII, and ICZ contributed equally to this work.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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