MORPHOLOGY AND ANATOMY OF *GUACAMAYA SUPERBA* (RAPATEACEAE) AND SCHOENOCEPHALIEAE WITH NOTES ON THE NATURAL HISTORY OF THE *FLOR DE INÍRIDA*

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Abstract. Rapateaceae are a monophyletic family of 17 genera with greatest species diversity on the mountains and savannas of the Guiana Shield. The family has intrigued botanists because of their interesting and unusual inflorescence and leaf morphologies. The small tribe Schoenocephalieae (three genera and seven species) are regionally prized for their showy inflorescences that are harvested as everlasting flowers. Here, we report on local cultivation efforts to minimize harvesting from wild populations and examine vegetative morphology and anatomy, reporting for the first time the presence of a lateral thickening meristem in Rapateaceae. Schoenocephalieae exhibit possible adaptations to their oligotrophic, open, and fire-prone habitats such as abundant mucilage, idioblasts containing a tannin-like substance, leaf fibers, presence of epidermal silica, the formation of telmata in *Guacamaya*, and vesicular-arbuscular mycorrhizal fungi.

Keywords: Guiana Shield, *Kunhardtia*, oligotrophic, phytotelmata, Rapateaceae, secondary thickening meristem, white-sand savanna

Rapateaceae (Poales) are a remarkable family due to their unusual leaf morphology, inflorescence structure, anatomy, and phylogenetic and biogeographic histories (Arber, 1925; Maguire, 1958; Carlquist, 1961, 1966, 1969; Venturelli and Bouman, 1988; Stevenson et al., 1998; Givnish et al., 2000; Crayn et al., 2001). The family is considered monophyletic (Givnish et al., 2000; Davis et al., 2004; Givnish et al., 2006; Bouchenak-Khelladi et al., 2014) comprising 16 or 17 genera and about 100 species (Stevenson et al., 1998; Berry, 2004), the placement of which within early-diverging Poales is not yet clear (Givnish et al., 2000; Bremer, 2002; Michelangeli et al., 2003; Bremer and Janssen, 2004; Davis et al., 2004; Chase et al., 2006; Givnish et al., 2006; 2010; Bouchenak-Khelladi et al., 2014). The family is thought to have evolved in the late Cretaceous, with estimates of about 36–80 million years before present (Givnish et al., 2000; Bremer, 2002; Janssen and Bremer, 2004; Bouchenak-Khelladi et al., 2014).

Rapateaceae are hypothesized to have evolved in wet, open habitats (Bouchenak-Khelladi et al., 2014) in the flooded lowlands on the Guiana Shield (Givnish et al., 2000; 2004), where they are presently most diverse (Stevenson et al., 1998; Berry, 2004; Stevenson, 2004). Most species occur in savannas, on *tepui* slopes and summits, inselbergs, or in low elevation forests on the Guiana and Brazilian Shields of northern South America (Stevenson et al. 1998; Berry, 2004, 2012) as lithophytic or understory plants, but most distinctively as dominants in herbaceous communities (Huber, 1995a, 2006; Fig. 1A). Rapateaceae exhibit elevation (on the Guiana Shield; Huber, 1987) as well as geographical disjunctions. The epiphytic genus *Epidryos* is distributed in Panama (Davidse, 1994), the Andes (Berry, 2004), as well as on the Guiana Shield (Givnish et al., 2004; Rodrigues and Flores, 2010), and the single amphiatlantic species, *Maschalocephalus dinklagei* Gilg and K. Schum., is known from tropical Africa (Liberia and Sierra Leone) presumably through a recent long-distance dispersal (Givnish et al., 2000, 2004).

Two subfamilies of Rapateaceae were recognized in the past, supported by pollen morphology and vegetative anatomical studies (Carlquist, 1961; Shoichi Kawano in Maguire, 1965; Carlquist, 1966, 1969): Rapateoideae and Saxofridericioideae, each with two tribes (Maguire, 1958; Stevenson et al., 1998). In the current infrafamilial classification Givnish and Berry (in Givnish et al., 2000) segregated Monotremeae from Rapateoideae, recognizing it as a third subfamily and erected a new tribe: Stegolepideae for all of Saxofridericieae except the type genus. In both the traditional and current classifications, Saxofridericioideae include the tribe Schoenocephalieae, which consists of three genera: *Guacamaya* (1 sp.), *Kunhardtia* (2 spp.), and *Schoenocephalium* (4 spp.; Fig. 1B–D).

Rapateaceae are perennial herbs; many are rhizomatous and have long-pedunculate inflorescences with colorful bracts. Among the principal morphological and anatomical characteristics known in the family are: highly thickened endodermal cell walls in the root (Carlquist, 1966); presence of aerenchyma in the roots and peduncles; and broad stems, usually with inconspicuous internodes, and ground tissue with sclerenchyma, slime canals (Schoenocephalieae), and starch (Carlquist, 1966, 1969; Stevenson et al., 1998; Ferrari et al., 2014). The leaves have conspicuous, conduplicate

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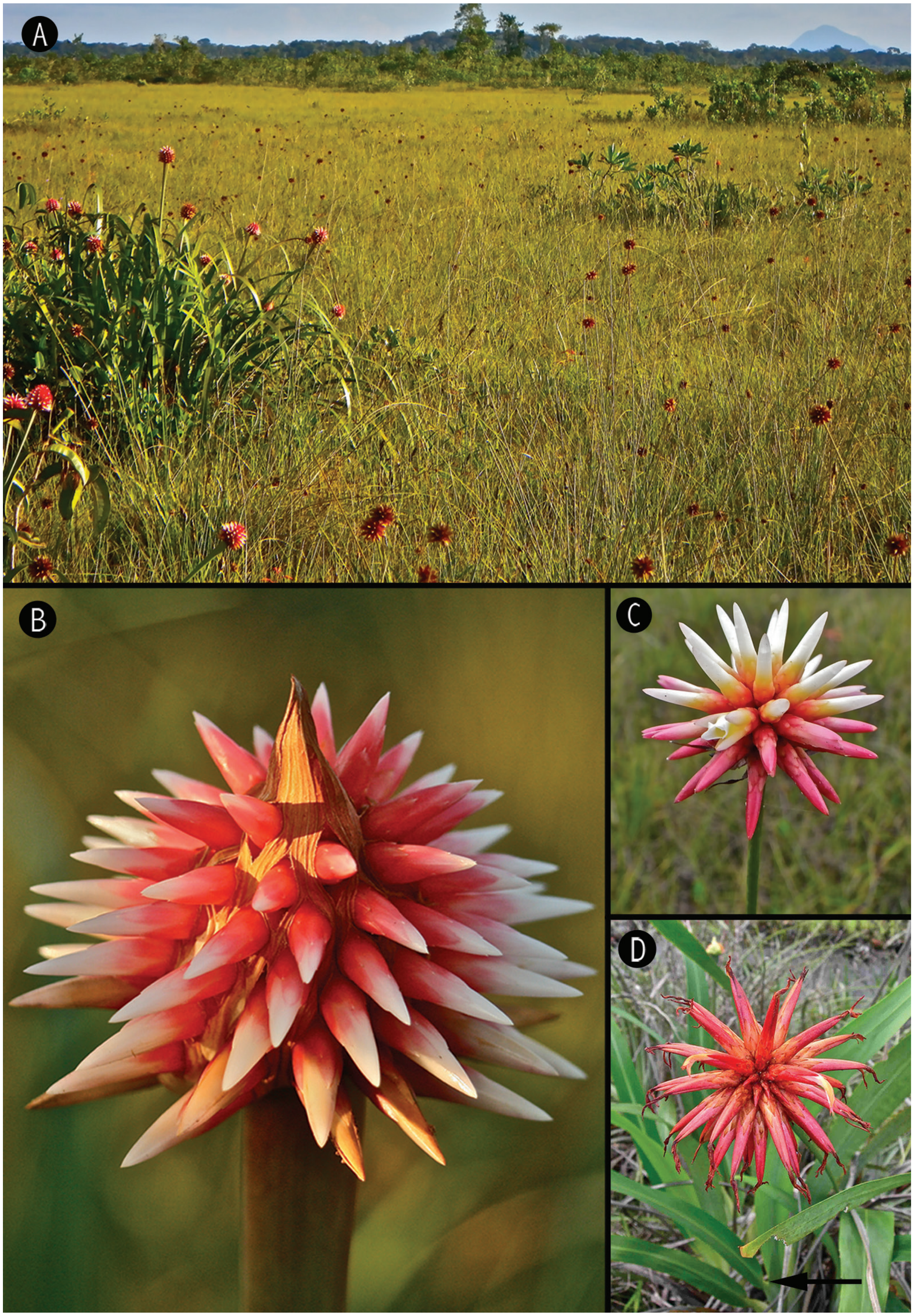

FIGURE 1. Species of Schoenocephalieae (Rapateaceae) and their habitat. **A**. White-sand savanna in Inírida, Colombia (Guainía state). A broad savanna landscape with isolated inselbergs (one seen at the right in the background). *Guacamaya superba* is blooming at the left, and dried infructescences of *Schoenocephalium teretifolium* are at the right. **B**. Detail of the conical inflorescence of *G. superba*, with a pair of involucral bracts (brown) that are pierced at maturity by the individual flowers. **C**. Globose inflorescence of *S. teretifolium*, note the open flower. **D**. Globose inflorescence of *Kunhardtia radiata*, the petals withered. The constriction between the conduplicate sheath and lamina can be seen below. (See arrow; photograph by G. A. Romero-González).

leaf sheaths (Boubier, 1895; Arber, 1922, 1925; Solereder and Meyer, 1929; Pilger, 1930; Carlquist, 1969), paracytic stomata, silica bodies in the adaxial epidermis, a hypodermis is sometimes present (Solereder and Meyer, 1929; Carlquist, 1969; Ferrari et al., 2014), subdermal fiber strands (Carlquist, 1969), buttressed vascular bundles surrounded by a fibrous sheath (Carlquist, 1969; Ferrari et al., 2014), large colorless cells in the mesophyll, and, in some genera, uniseriate, slime-secreting trichomes associated with vegetative and floral structures (Carlquist, 1969; Oriani and Scatena, 2013). Peduncle anatomy appears to have taxonomic utility in Rapateaceae (Carlquist, 1969; Oriani and Scatena, 2013), although it has not been exhaustively studied. In addition to silica bodies, idioblastic tannin cells are found in various organs (Carlquist, 1969; Ferrari et al., 2014). Both the inflorescences and flowers are bracteate, the anthers dehiscence by apical or subapical pores, and the seeds have silica bodies (Tiemann, 1985; Venturelli and Bouman, 1988; Oriani and Scatena, 2013).

The white-sand savanna habitats of many Rapateaceae are complex ecosystems that occur in tectonically stable regions although the massive sandstones are constantly eroding (Goodland, 1966; Kroonenberg, 1985; Gibbs and Barron, 1993). This ecosystem experiences a bimodal seasonality. Heavy precipitation causes flooding during the rainy season (Domínguez, 1985; Huber 1995b), although many savannas drain quickly limiting water availability (Campbell and Stevenson, 2005). High temperatures and insolation make the vegetation vulnerable to scorching when a shallow layer of water remains on the savanna (pers. obs.), and accentuate the effects of natural and anthropogenic fires in the dry season (Hernández, 1987; Huber, 1995a; Biddulph and Kellman, 1998; Rodríguez, 2004. The hydrologic regime; high insolation; and the soil acidity (Medina et al. 1990; Cárdenas, 2007), with low concentration of essential nutrients, and often high levels of aluminum (Huber, 1995b) are profound physio-ecological challenges for plants occurring in white-sand savannas (Klinge and Medina, 1979; Medina et al., 1990).

Symbiotic mycorrhizae improve plants' ability to endure environmental stress, influencing nutrition (Fitter et al., 1987; Sylvia, 1990) and seed germination (Dickison, 2000). Although a symbiotic relationship has not been demonstrated, the mycorrhizal fungus *Scutellospora* sp. has been reported from soil samples taken from areas occupied by populations of Rapateaceae (Walker et al., 1998) and the endophytic fungus *Stegolerium kukenani* Strobel, Hess & Ford was isolated from *Stegolepis* leaves (Rapateaceae; Strobel et al., 2001).

Among the most locally common Schoenocephalieae, *Guacamaya superba* Maguire (Fig. 1B), *Schoenocephalium cucullatum* Maguire, and *S. teretifolium* Maguire (Fig. 1C; 9B, C) often occur in sympatric populations, and are known locally as *Flor de Inírida* in Colombia (Avellaneda and Herrera, 1998) or *Flor de Maroa* in Venezuela (Stevenson, 2004; *M. Colella et al. 1275*, NY). These species are restricted to white-sand savannas of the western Guiana Shield, in southeastern Colombia (Amazonas and Guainía states; ICN, 2014) and southwestern Venezuela (Guainía and Amazonas states; GBIF, 2012). Generally, *Schoenocephalium* grows in more exposed sites where *G. superba* is not successful, but sometimes inhabits marshy places with *G. superba*. Due to their differing phenology, *G. superba* and *Schoenocephalium* are further distinguished in Colombia as *Flor de Inírida de invierno* and *Flor de Inírida de verano*, respectively (Avellaneda and Herrera, 1998; Rojas et al., 2001). Less easily differentiated are the two species of *Schoenocephalium*, which are thought to hybridize in zones of contact (Berry, 2004). The red floral bracts, whitish perianth, and long peduncles give *Guacamaya* inflorescences their appealing beauty that inspired Maguire (1958, 1982) to use the local name for the beautiful and revered scarlet macaw (*Ara macao*) in naming the genus. Often occurring in dense populations, with the inflorescences held above other savanna vegetation (Fig. 1A), many Rapateaceae are iconic of Guiana Shield savannas, and it is not surprising that the inflorescences of *Guacamaya* are an important emblem for local people (see Maguire, 1958; Fig. 9D, E), who harvest Schoenocephalieae for decorative bouquets (Schultes, 1954; Berry, 2004; Fig. 9A, D, F). The larger dried infructescences of *Kunhardtia* are likewise collected, but are relatively unknown because the remoteness of where they occur.

In spite of the regional and scientific interest, information on many biological aspects (Avellaneda and Herrera, 1998) of some Rapateaceae is scanty due to the difficult access for researchers to regions where many species are endemic (see Funk and Hollowell, 2007), making long term field studies difficult. Schoenocephalieae have been examined anatomically; however, material was limited (Carlquist, 1966).

The objective of this paper was to examine the morphology and anatomy of *Guacamaya* in comparison with other Schoenocephalieae and to characterize their habitats and possible adaptations to them, as well as natural history information.

MATERIALS AND METHODS

Study Sites

Intensive descriptive fieldwork was conducted documenting morphological and ecological features of *Guacamaya superba* in white-sand savannas of Inírida (Guainía state, Colombia, in the Orinoco river basin), supplemented by years of observations there and in the vicinity of Maroa (Municipio Autónomo Maroa, Amazonas state, Venezuela, in the Río Negro and therefore the Amazon river basin). Both sites (3°49.129'N, 67°53.894'W and 37°25.8'N, 122°05.36'W) are below 120 m, and are characterized by isolated savannas within *bana* or Amazonian *caatinga* (see Prance, 1996; Huber, 1995a; Fig. 1A). The geomorphology of the upper Río Negro also includes numerous inselbergs, or *lajas* (Fig. 1A). Annual averages for Inírida are 83–85% relative humidity, over 3000 mm rain, and 26°C (for 1972–2010, IDEAM—Instituto de

Hidrología, Meteorología y Estudios Ambientales, pers. com.; Mejía and Mejía, 1980; Cárdenas, 2007). Both study sites experience greater evapotranspiration in December–March (Huber, 1995b; Cárdenas, 2007); however, Maroa, located approximately 100 km to the southeast of Inírida, is in a region with greater precipitation (Mejía and Mejía, 1980; and "…a barely pronounced" (Huber, 1995b: 13) and much shorter dry season. Details of the specimens collected are presented in Table 1.

Plant Samples and Preparations

Individual plants of *Guacamaya superba* were excavated, dissected, measured, and photographed *in situ*. Data were obtained to characterize growth patterns, morphology, and general ecological features. Samples (Table 1) were fixed in formalin-propionic acid-alcohol (FPA; 1:1:18 v/v, 50% EtoH; Johansen, 1940) and then transferred to 70% EtoH. Some samples of *G. superba* were directly collected into ethanol. Observations were also made on herbarium specimens at NY, and some material was rehydrated with Aerosol®OT solution (10%; Fisher Scientific Inc.; Ayensu, 1967). A free-hand peel of leaf epidermis was stained with Johansen´s safranin (Johansen, 1940). For sectioning, samples were paraffin embedded (Paraplast®X-Tra, M^{c}Cormic™) using standard procedures, except for some hard tissues that were resin embedded (Technovit H7100). Sections were cut 4–11μm thick using a rotary microtome (AO Spencer 820). Paraffin samples were stained with Johansen´s safranin and counterstained with astrablue (Roeser, 1962), whereas Toluidine Blue O (O'Brien et al. 1964) was used for resin embedded sections. The presence of lignin was detected with saturated phloroglucinol, acidified with HCL (Jensen, 1962). To evaluate the presence of mycorrhizae in roots and root nodules, roots were cleared with 10% KOH and stained with Trypan blue (Phillips and Hayman, 1970) and cotton blue (Aniline blue W.S.; Rawlins, 1993). Leaves of *G. superba* were cleared modifying the protocol of Vasco et al. (2014); stained with Safranin in 95% EtOH and mounted in Caroplastick® (Carolina®, Burlington, North Carolina). Slides were observed on a Zeiss Axioplan light microscope and photographed with a Nikon digital camera (DXM1200c) using the ACT-1 software (Nikon Instruements, Inc.®). For scanning electron microscopy, samples were dehydrated in a series to 100% acetone and then critical point dried in a DCP-1 apparatus (Denton Vacuum, LLC). Samples were coated with gold palladium in a sputter coating system (Hummer 6.2, Anatech USA, Union City, CA) and observed at 10 kV in a JEOL JSM-5410LV microscope (JEOL USA, Inc., Peabody, MA). Images were obtained using ORION software (ver. GA02870/1, ©2000–2004 JEOL USA, Inc.) and edited using Adobe Photoshop. Terminology follows Barthlott et al. (1998) for wax. Abbreviations are used for longitudinal and transverse sections (l.s.; t.s.) and vascular bundle(s) (v.b.; v.bs.).

TABLE 1. Samples, their vouchers, and the structures used for this anatomical research.

SAMPLE	ROOT	STEM	LEAF	PEDUNCLE
Guacamaya superba Maguire *Campbell et al. 505* (NY)				X
G. superba Maguire *Fernández-L. 104* (ANDES)	X	X	X	X
Kunhardtia radiata Maguire & Steyerm. *Campbell et al. 684* (NY)				X
K. radiata Maguire & Steyerm. *Maguire et al. 31834* (NY)*			X	
K. rhodantha Maguire *Campbell et al. 767B* (VEN)	X	X	X	
Schoenocephalium teretifolium Maguire *Campbell s.n.* (NY)				X
S. teretifolium Maguire *Huber 5957* (NY)*	X	X	X	

* Denotes herbarium samples rehydrated with a 10% Aerosol®OT solution (Fisher Scientific Inc.; Ayensu, 1967), otherwise samples were originally collected in fluid.

Morphological and Anatomical Observations

Schoenocephalieae

The three genera studied are perennial herbs of oligotrophic savannas or rock surfaces (*Kunhardtia*) with erect stems; open, conduplicate leaf sheaths; no evidence of Kranz anatomy; and long, distally compressed peduncles.

Guacamaya

Guacamaya superba has a terminal inflorescence and sympodial renewal shoots (Fig. 2A). Mature individuals (leaves and peduncles) ranged from 50 cm to 180 cm high. Impounding phytotelma, composed of marcescent leaf sheaths that persist for years, were observed. Up to 25% of juvenile shoots were found dead in the leaf axils before the bud elongated (n = 16 individuals; Fig. 3E). A community of other plant species (Fig. 3F), invertebrates, and small vertebrates were observed in the phytotelma.

Root. 9–11 mm diam., endogenous, grows laterally through the cortex (Fig. 4A), before piercing the leaf sheaths, growing closely along the stem providing mechanical support (Fig. 3H, 4A). Plagiotropic growth and root branching (Fig. 4B) begins in less than 20 cm of substrate, some negatively or more-or-less horizontal roots, to 15 mm diam., occur inside the phytotelma, branching and producing root nodules (Fig. 3D, 4B, C). Roots with nodules were also found piercing through the marcescent leaf sheaths.

A velamen is present during development, and is later sloughed off (Fig. 4G). Exodermis of 3 or 4 cell layers (Fig. 4G), cell walls lignified. Cortex broad, a narrow band of irregular, densely compact cells below the exodermis, middle cortex composed of large arm parenchyma, many cells collapsed, parenchyma towards the central cylinder more regular in shape and progressively smaller near the endodermis. Tannin cells scattered throughout the ground tissue, denser near the central cylinder, which they nearly completely surround in 3 or 4 layers. Endodermis uniseriate, cells narrow and anticlinally elongate. Pericycle bilayered, cells periclinally broad, squarish to irregular in shape, stele polyarch with over 30 poles, cells of the pith highly lignified, except those immediately surrounding the metaxylem vessels (Fig. 4D, E).

Fungal hyphae present as vesicular-arbuscular endomycorrhizae were in parenchyma near the periphery of the root cortex and mycelia also in parenchyma cells of roots and root nodules (Fig. 4E).

Stem. Covered by indurate leaf sheaths, tightly surrounded by shoot-borne roots (Fig. 3H, 4A), ca. 3–5 cm diam. when mature. Cortical cells small and densely arranged, elliptical to spherical, with abundant starch (Fig. 2G), and scattered tannin idioblasts (Fig. 5), slightly less abundant in the stele of younger stems. Large slime cavities with uniseriate, multicellular trichomes in the outer cortex. Endodermis apparently biseriate. Radial files of cells produced from meristematic activity near the pericycle (Fig. 5). Vascular bundles are amphivasal and coalesced (Fig. 5).

Leaf. 35–185 cm long, sheath ca. ¼ the length of the leaf, phyllotaxis spirodistichous, sheath open, asymmetrically conduplicate (Fig. 6D, F), the fold conspicuous, edge hard, tapered to a constriction below the lamina (Fig. 6A, B).

Leaf sheath with mucilage-secreting hairs on the adaxial surface, wax covered spherical glands (Fig. 7G), and coiled tubules (Fig. 7F) more abundant on the sheath, lamina also with wax plates and granules (Fig. 7E) in the medial region of the lower surface, and arachnoid crystaloids over some guard cells (Fig. 7A). In surface view epidermal cells squarish, intercostal and costal cells of similar size, the anticlinal walls sinuous (Fig. 2C). In t.s. the cells short, of similar size on both surfaces of the lamina (Fig. 2D); silica bodies present. Predominantly hypostomatic, occasionally distally amphistomatic, stomata paracytic, in randomly arranged rows (Fig. 2C). Cuticle thick on the adaxial surface (Fig. 2D). Hypodermis of small, densely compact cells and large tannin filled cells on the adaxial surface of the sheath, tannin filled cells continuous on the abaxial surface except where interrupted by v.b. buttresses, in the lamina subepidermal tannin cells continuous in one or more layers in the underside, interrupted by v.b. buttresses on the upper side. Remaining mesophyll of the sheath composed of mostly isodiametric cells with abundant starch, those of the adaxial surface small and compact, centrally some small lysigenous cavities and arm parenchyma, and scattered tannin filled cells. Cavities becoming regularly spaced air canals in the lamina (Fig. 6H). Phloem with a cap of fibers, buttress sclerenchyma cells with a very small lumen. Conduplication narrower than the rest of the sheath, with a small v.b., the midvein off center. Other v.bs. more or less at two levels, those toward the abaxial surface large and small, toward the adaxial large. Vascular bundles collateral, surrounded by a sheath of parenchyma and tannin filled cells. Vessel elements with sclariform plates.

Peduncle. 40 to 180 cm long. Easily detached from the rhizome, base slimy (Fig. 2A). Ovate medially in t.s., 0.5–1 cm diam., distally flattened, more than twice the median width, twice as wide as thick (Fig. 8A). Epidermis narrow, uniseriate, cells radially elongate, silica bodies present, stomata paracytic, in longitudinal grooves. Hypodermis a single layer of colorless or tannin filled cells (Fig. 8A, D–F), subdermal layer interrupted by sclerenchyma of v.b. buttresses and substomatal chambers. Subdermal chlorenchyma larger than the epidermal cells, isodiametric, lobed and larger toward the center at the base, lobed and becoming stellate and aerenchymatous towards the center in the medial portion of the axis, distally nearly all subepidermal cells lobed (Fig. 8F). Starch grains present in the base, idioblastic tannin more abundant proximally (Fig.8F). Vascular bundles numerous, collateral, phloem with a cap of fibers, peripherally the v.bs. solitary, smaller, in a single subdermal ring, buttressed with sclerenchyma, towards the center the bundles coalesced or solitary, without a common sheath, but surrounded by a few lignified cells (Fig. 8 A, 8D–F).

Kunhardtia

Root. Endogenous, piercing the leaf sheaths, growing closely along the stem providing mechanical support. Exodermis 3 or 4 cell layers. Cortex broad, below the

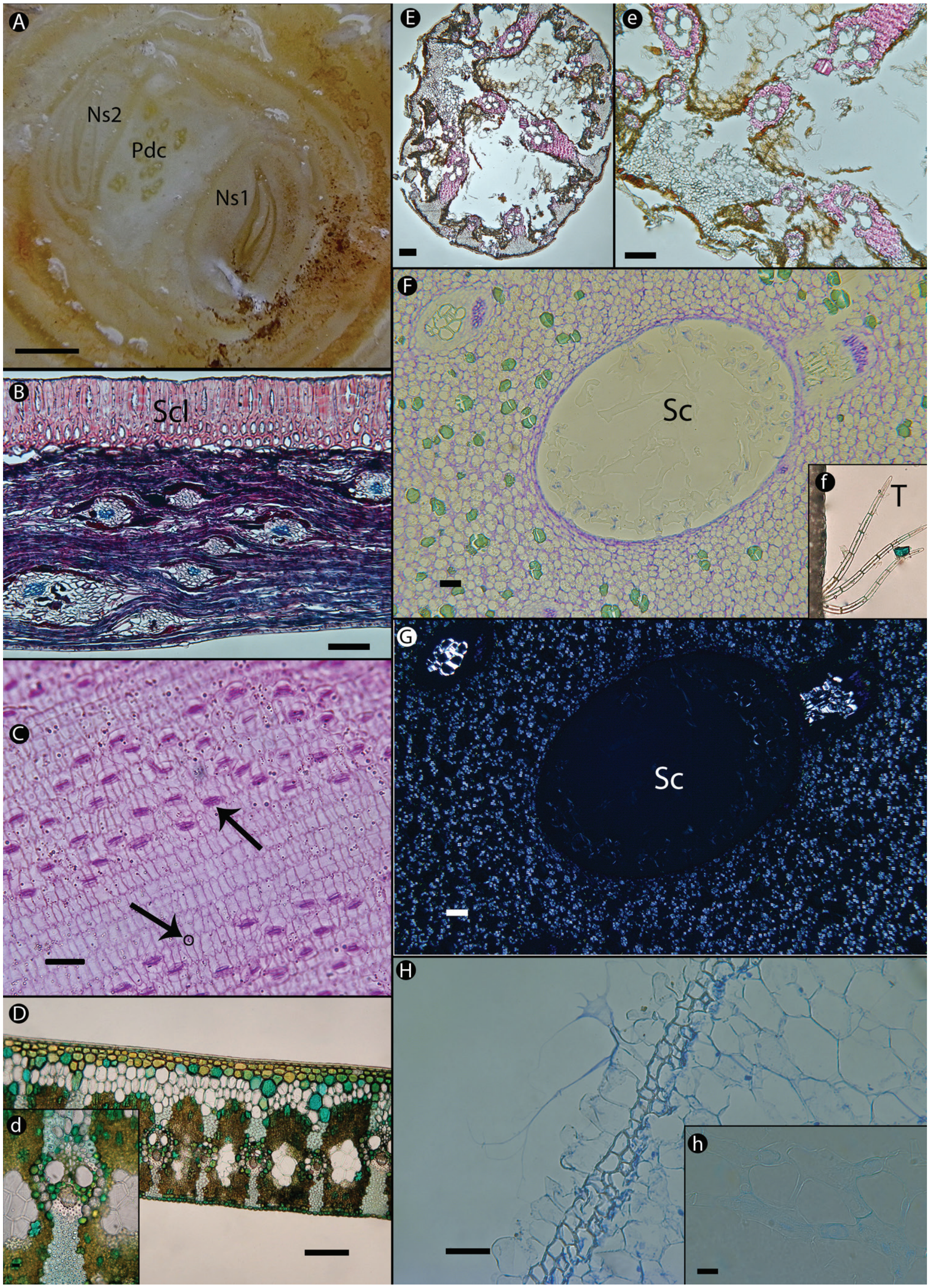

FIGURE 2. Sections of stems and leaves of *Guacamaya superba* (A, C, D, F–H), *Kunhardtia radiata* (B), and *Schoenocephalium teretifolium* (E). **A**. A transverse (t.s.) section of the slimy stem apex. Note the terminal position of the peduncle (Pdc), with visible vascular bundles, and two shoots (Ns1, Ns2). **B**. Transverse section of a base of a marcescent leaf sheath from a tank, with elongate, highly lignified sclerenchyma (Scl). **C**. Leaf epidermis. Note the nearly linear arrangement of the intercostal stomata, and the presence of silica bodies (downward arrow). **D**. Transverse section of the leaf blade showing arrangement of the buttressed vascular bundles, large colorless parenchyma, and tannin cells. Detail of a vascular bundle (d). **E**. Transverse section through the proximal portion of an elliptic, terete *Schoenocephalium* lamina. **F**. Stem (t.s.) with a wide slime canal lined with uniseriate trichomes (f). **G**. The same section as F as viewed under polarized light revealing abundant cortical starch. **H**. Fungal infection of a root; a hypha is evident, penetrating the epidermis and terminating as an external arbuscule. A branched hypha inside an arm-parenchyma cell (h). Abbreviation: t.s., transverse section. Ns, renewal shoot; Pdc, peduncle; Sc, slime canal; Scl, sclerenchyma. Scale bars: A: 5 mm; B, D, E: 0.1 mm; C, F–H: 50 μm; d, h: 10 μm.

FIGURE 3. Aspects of the morphology and habitat of *Guacamaya superba*. **A**. A termite mound in a white-sand savanna that burned during the previous year. In the rainy season this individual of *G. superba* and other species resprouted. **B**. A partially disected plant showing the spirodistichous phyllotaxis and water impounding leaf sheaths. Mature individuals can have up to 50 shoots, and dead leaves remain attached to the stem for several years forming a massive tank system. **C**. A fallen inflorescence decomposing in the phytotelma. **D**. Branched root system in an impounding tank (removed). Note the mucilage from the stem cortex. **E**. Buds of many shoots were found decomposing inside the phytotelmata. **F**. Plants of various species utilize the habitat inside the phytotelmata, in this case an orchid in the favorable, moist conditions. **G**. A termite mound associated with *G. superba*, an association that is common among plants in oligotrophic, white-sand savannas. **H**. A stem with old leaves removed. Roots emerge from the cortex, piercing the leaf sheaths, and course vertically, firmly adhering to the stem, providing mechanical support, even when dead (dark roots).

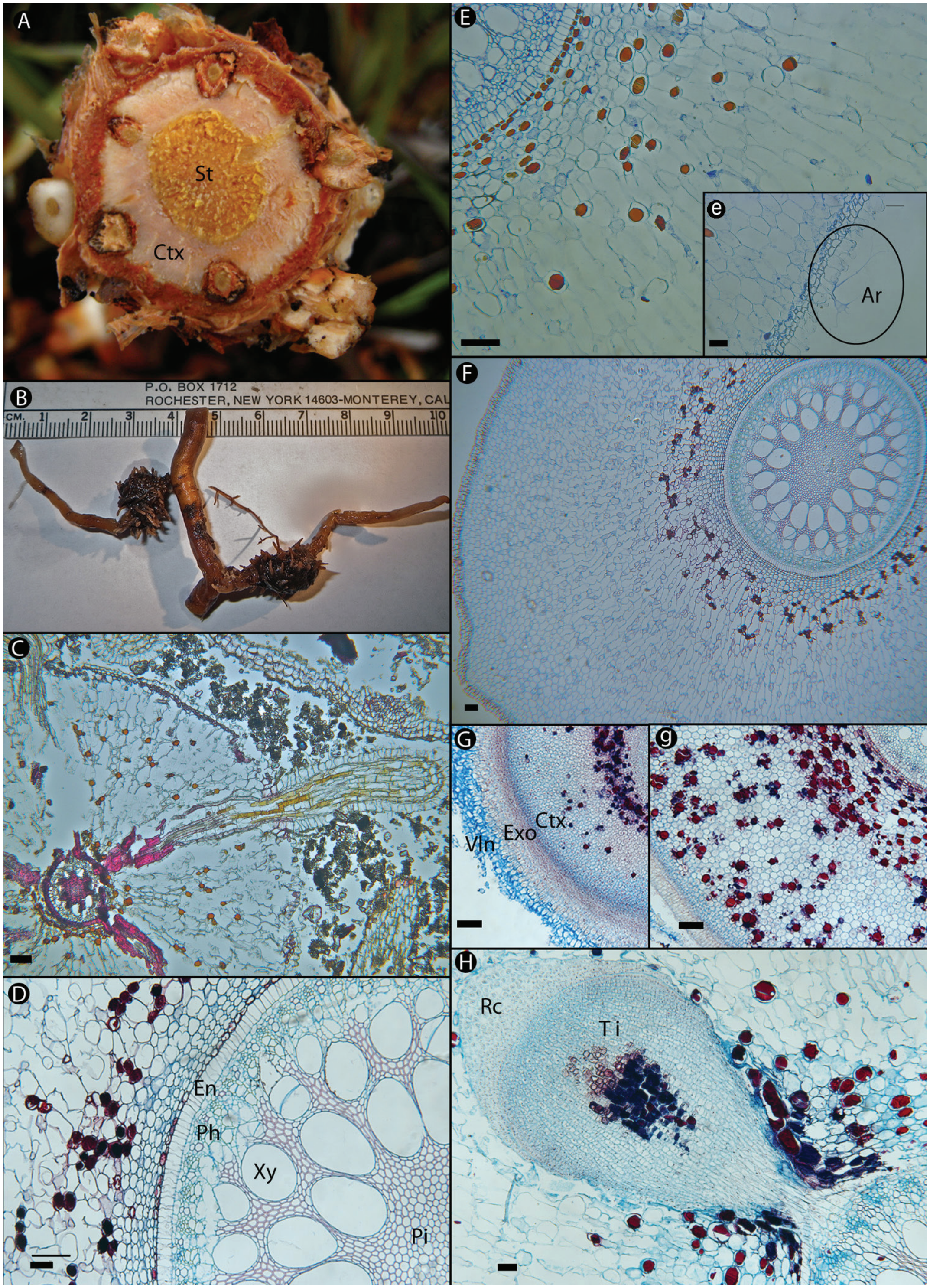

FIGURE 4. Roots of *Guacamaya superba* (A–E, G, H) and *Kunhardtia rhodantha* (F). **A**. Medial portion of a rhizome (t.s.), with roots emerging from the cortex (Ctx). Note the yellow stele (St). **B**. A branched root with nodules excavated from a phytotelma. **C**. Root nodule (t.s.) showing rootlets and the lignified endodermis (darkly stained). **D**. Detail of a vascular cylinder, pericycle, and endodermis. **E**. Root (t.s.) with mychorrhizal arbuscules (e). **F**. Mature root (t.s.) of *Kunhardtia* with tannin containing cells concentrated near the vascular cylinder. **G**. Transverse section of a young root, note the tannin cells becoming more dispersed with age (g) and presences of a velamen (Vln) present during early stages of development. **H**. Early stage of root branching (l.s.). Abbreviations: l.s., longitudinal section; t.s., transverse section. Ar, arbuscular mychorrhiza; Ctx, cortex; En, endodermis; Exo, exodermis; Ph, phloem; Pi, pith; Rm, root cap overlying the meristem; Ti, tannin idioblasts; Vln, Velamen; Xy, xylem. Scale bars: C, E, F, G: 0.1 mm; D, H: 50 μm.

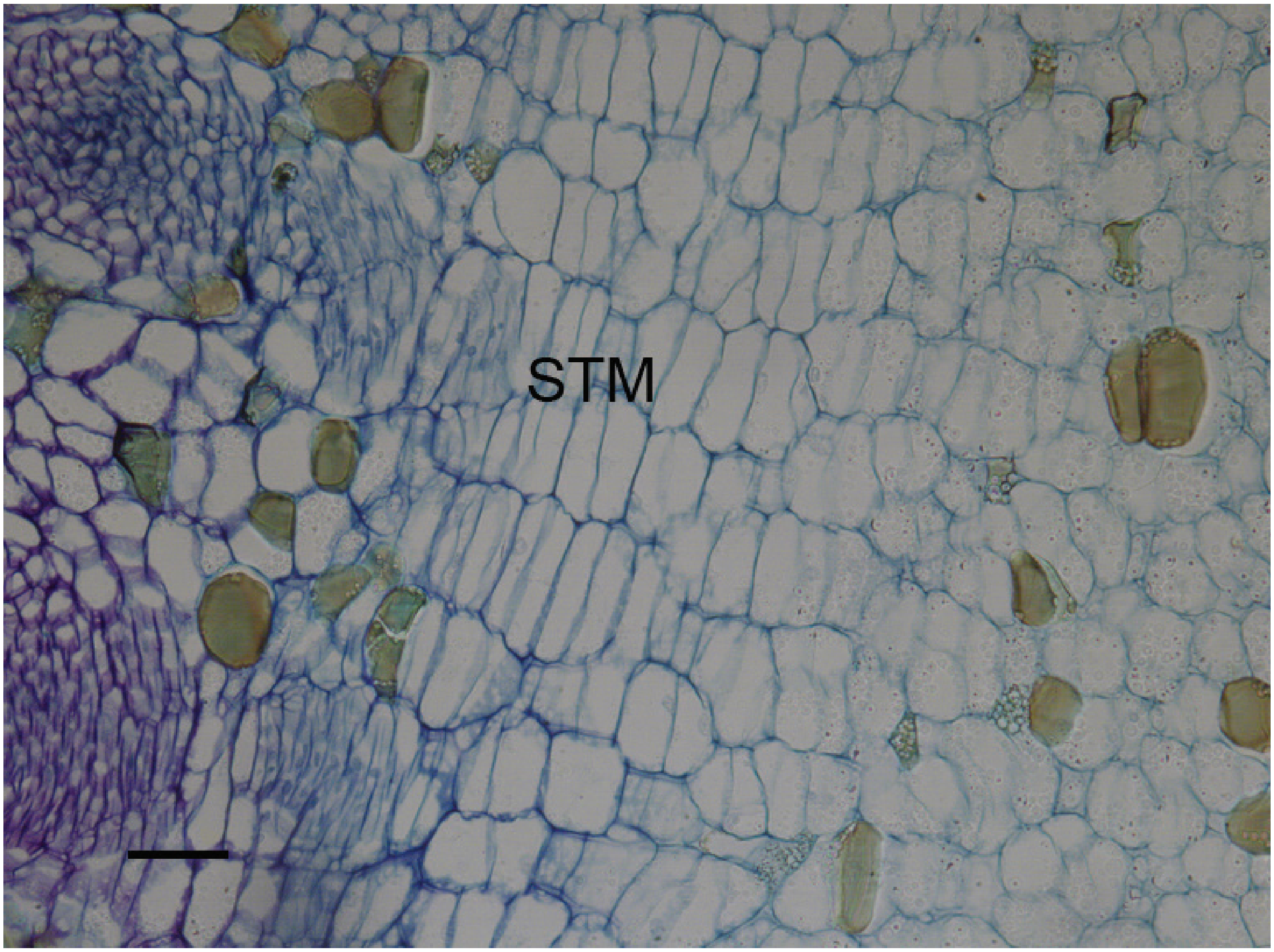

FIGURE 5. Stem of *Guaycamaya superba*, showing radial files of cells of the secondary thickening meristem (STM; scale bar: 0.1 mm).

exodermis cells isodiametric, densely compact, cells grading into arm parenchyma, many collapsed. Tannin idioblasts present in a ring near the periphery of the cortex, 4–7 layers of elliptic, densely compact cells surround the endodermis. Endodermis uniseriate, cells anticlinally elongate. Cells of the pericycle large, periclinally broad, stele polyarch, phloem scanty, cells of the pith highly lignified, except those immediately surrounding the metaxylem vessels (Fig. 4F).

Stem. Epidermis with silica bodies. Cortex with slime cavities lined with uniseriate trichomes, abundant starch in young tissue.

Leaf. Distichous, equitant. Sheath evenly conduplicate, with uniseriate, multicellular mucilage-secreting hairs on the adaxial surface, epidermis multilayered, sclerotic, silica bodies present, hypodermal cells lignified, vascular bundles large and small, with a cap of phloem fibers, often a partial tannin sheath, fiber buttresses to one or both surfaces. Vascular bundles of the lamina amphivasal, buttressed to one or both surfaces.

Peduncle. Distally broad, flattened and elliptic in t.s. Epidermis narrow, uniseriate, cells radially elongate, with silica bodies, hypodermis a single layer of tannin filled cells, cortex fibrous at the periphery, sometimes a greater number of fiber layers present above v.bs. Distally, most chlorenchyma lobed, becoming stellate toward the center. Vascular bundles numerous, collateral, phloem with a cap of fibers, v.bs. surrounded by lignified cells, a single ring peripherally of smaller v.bs. with fibrous buttresses, bundles toward the center coalesced.

SCHOENOCEPHALIUM

Root. Exodermis bilayered, cells sclerified. Cortex wide, aerenchyma radially arranged throughout, innermost parenchyma radially elongate, thick-walled, deeply stained, endodermal cells highly lignified, the walls evenly thickened, lumen extremely narrow. Pith lignified.

Stems. Narrower than the other species examined, cortex with slime canals and abundant starch.

Leaf. Spirodistichously inserted. Sheath conduplicate, broad, tapered to a terete lamina, less than 1 cm diam. (Fig. 2E). Cuticle thick, epidermis of the lamina compact, cells darkly stained. Mesophyll cells isodiametric near the periphery, arm-cells toward the center forming aerenchyma with large air spaces. Vascular bundles collateral, surrounded by a fibrous sheath, larger ones buttressed to the epidermis by an obdeltoid patch of sclereids.

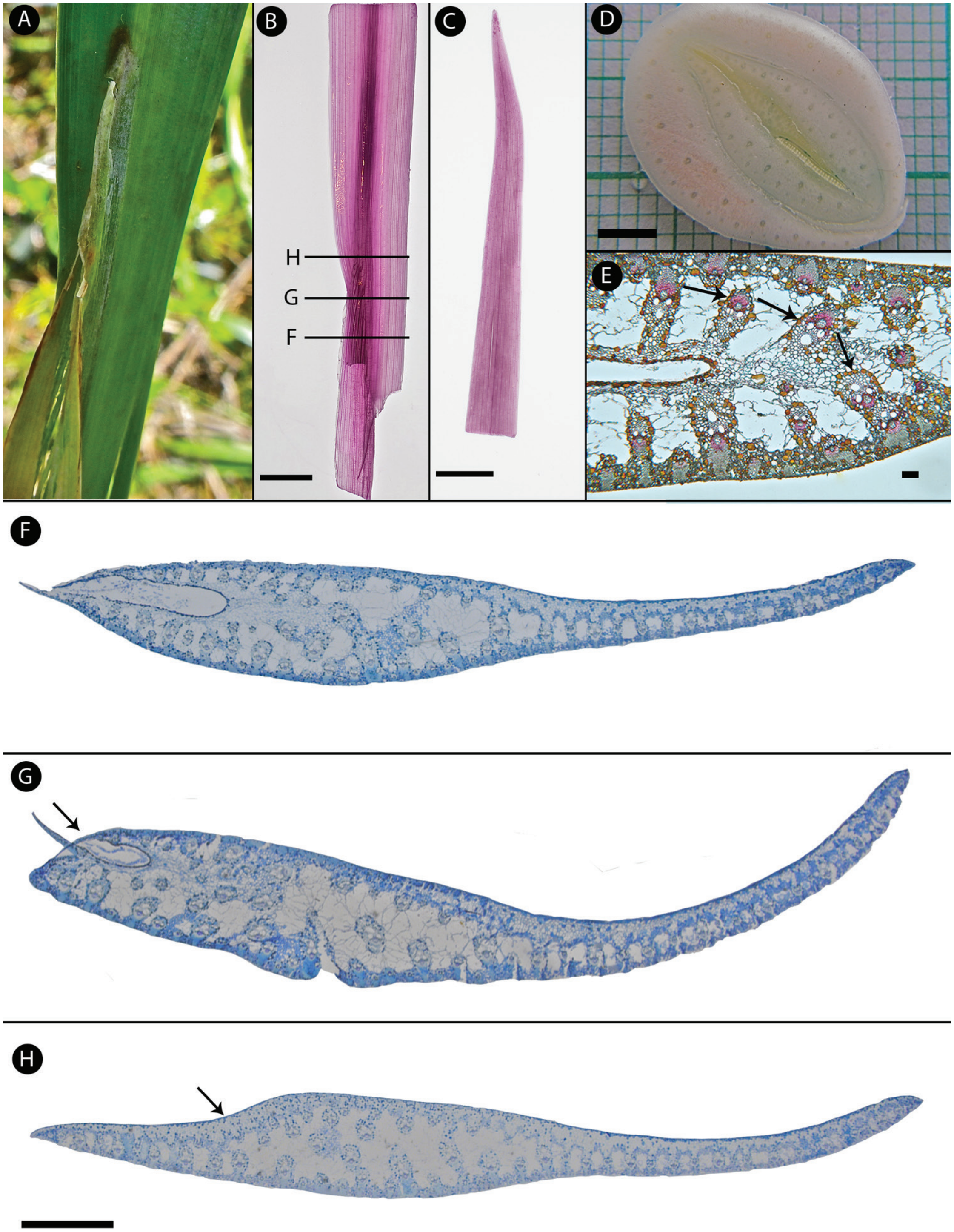

FIGURE 6. Leaves of *Guacamaya superba*. The asymmetric conduplicate sheath tapers to a constriction beneath the transition to an isolateral lamina. **A**. Leaf in situ. B, C. A cleared leaf. **B**. In the region shown in A. Lettered bars refer to sections in F–H. **C**. The dorsiventral lamina with the midvein central in the apex, and a characteristic distal curve. **D**. Juvenile leaves showing equitant insertion of the conduplicate sheath, and vascular bundles in more than one series. **E**. Orientation of the vascular bundles near the fold in the region near F. Note the aerenchyma. F–H. Transverse sections through the constricted region and broadened lamina (see B). **F**. The asymmetrical conduplicate sheath. **G**. The asymmetry continues in development. **H**. Base of the lamina where both surfaces are of abaxial origin. Scale bars: B: 2 cm; C: 1 cm; D: 0.3 cm; E: 0.1 mm ; F–H: 1 mm.

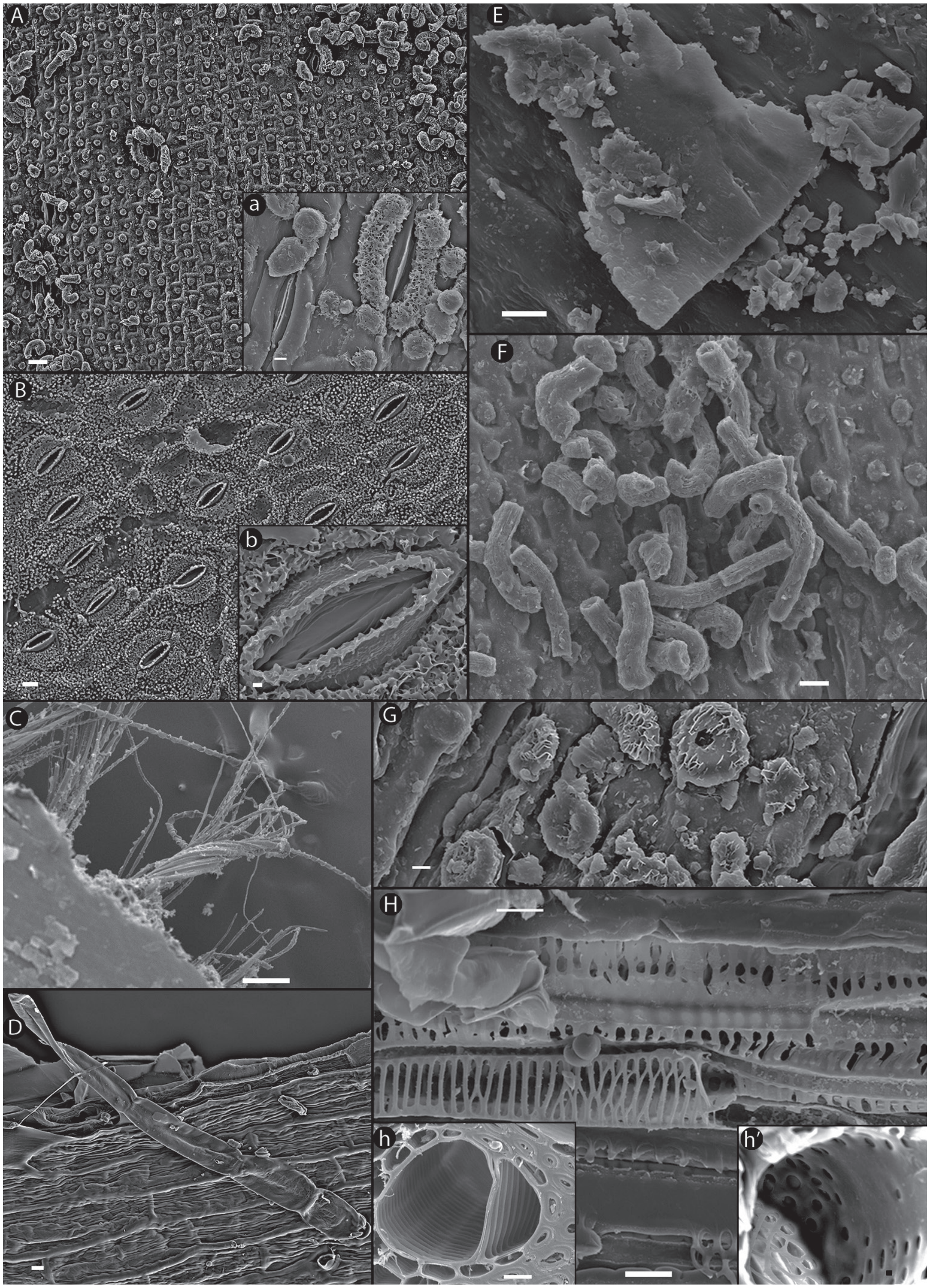

FIGURE 7. Scanning electron micrographs of leaves of Schoenocepahlieae (*Guacamaya superba*, A, C–G; *Kunhardtia radiata*, B; *Schoenocephalium teretifolium*, H) **A**. Lamina with glands and epicuticular waxes, as coiled tubules and crystaloids, (a) forming a dense, arachnoid covering on the guard cells of the paracytic stomata. **B**. Linear arrangement of stomata on a lamina with abundant epicuticular waxes, including crystaloids on the guard cells (b). **C**. Abundant fibers that surround the vasculature (t.s.). **D**. Uniseriate, multicellular, slime-secreting trichome on a leaf sheath. **E**. Wax plates and granules on the lower surface of a median region. **F**, **G**. The adaxail surface of a leaf sheath. F. Wax in the form of coiled tubules on. G. Detail of *g*landular trichomes covered with wax. **H**, h. Sclariform vessel elements and (h') pitted walls. Abbreviation: t.s., transverse section. Scale bars: A: 20 μm; a, G: 3 μm; B, C: 0.1 mm; b, h, h': 1 μm; D–F, H: 10 μm.

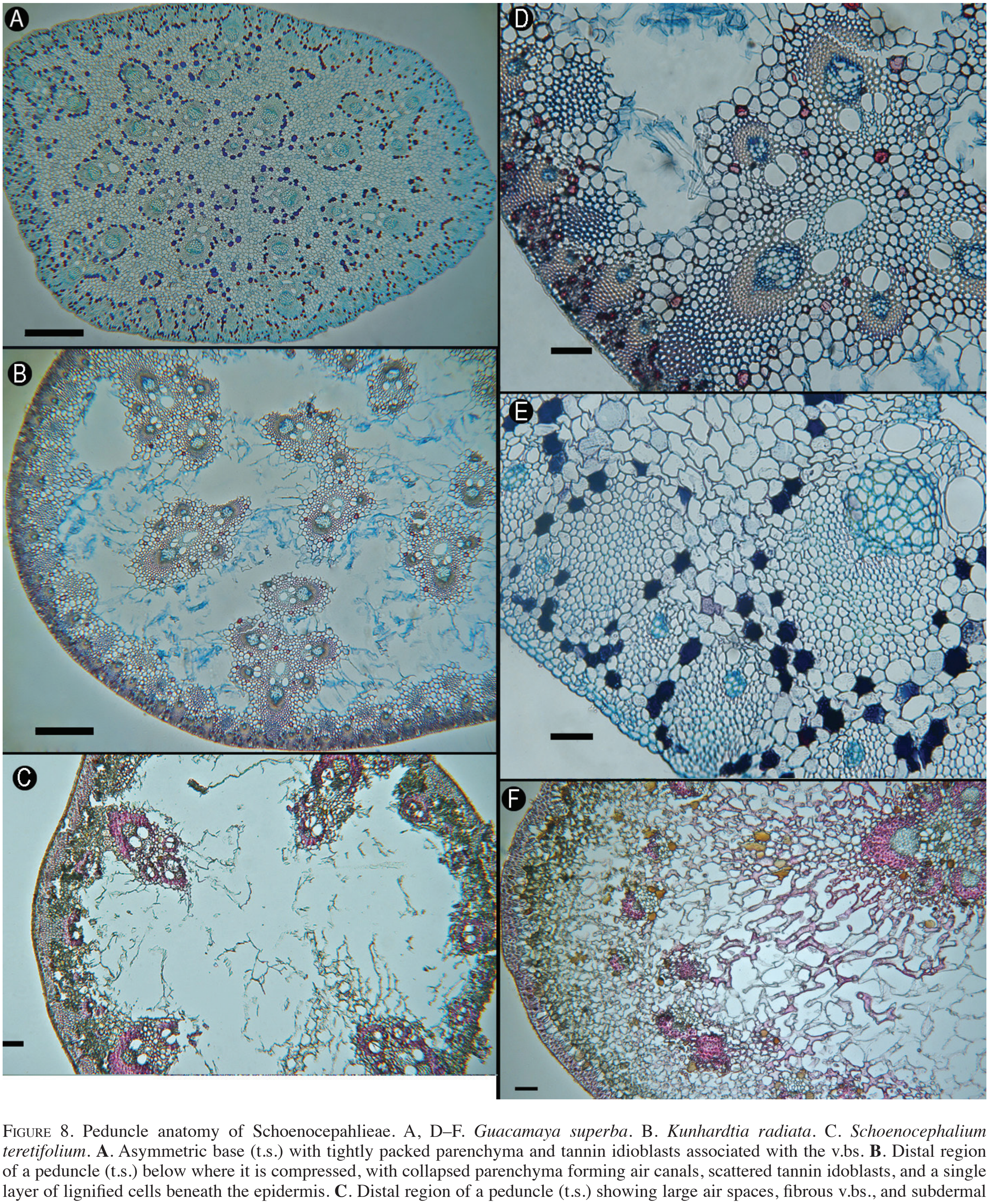

FIGURE 8. Peduncle anatomy of Schoenocepahlieae. A, D–F. *Guacamaya superba*. B. *Kunhardtia radiata*. C. *Schoenocephalium teretifolium*. **A**. Asymmetric base (t.s.) with tightly packed parenchyma and tannin idioblasts associated with the v.bs. **B**. Distal region of a peduncle (t.s.) below where it is compressed, with collapsed parenchyma forming air canals, scattered tannin idoblasts, and a single layer of lignified cells beneath the epidermis. **C**. Distal region of a peduncle (t.s.) showing large air spaces, fibrous v.bs., and subdermal sclerenchyma. **D**. Medial region (t.s.) showing 1 (2) layers of in compact, isodiametric subdermal parenchyma cells, interrupted by v.b. buttresses. **E**. Tannin idioblasts are more abundant in the proximal regions. **F**. Distal portion (t.s.) where the peduncle is elliptic and the periphery of the cortex is lignified. Abbreviations: t.s., transverse section; v.bs., vascular bundles. Scale bars: A, B, C: 0.5 mm ; D, E, H: 0.1 mm; F, G: 50 μm.

Peduncle. In t.s. round nearly throughout, distally slightly wider and elliptic. Cuticle thick, epidermis narrow, cells radially elongate, and tannin filled, underlain by several layers of fibers. Distally, chlorenchyma isodiametric, densely arranged with tannin idioblasts scattered near the periphery, parenchyma becoming arm-cells towards the center, stellate with large air spaces in the pith. Vascular bundles collateral, large and small bundles form a ring near the periphery, some buttressed to the epidermis.

Natural History

The beautiful infructescences of the *Flor de Inirída* and *Flor de Maroa* are prized by residents of the upper Río Negro, where the species are endemic. They have a history of cultural importance (see Schultes, 1954; pers. obs.) and appear as icons in Inírida's anthem, legends, souvenir carvings, and a symbolic statue of the *Schoenocephalium* was erected along the river in Inírida (Fig. 9B, C, E). As mentioned above, the fresh inflorescences with colorful bracts of *Guacamaya superba*, and dried infructescences of Schoenocephalieae (Schultes, 1954; Berry, 2004; pers. obs.) are harvested for everlasting bouquets (Fig. 9A, D, F). Schultes (1954: 191) reported that inflorescences of *S. martianum* Seub. (*Estrellitas del sur*) were used to decorate a rural Christmas altar, and abundant bouquets from Caquetá state, Colombia were sold in Bogotá. In recognition of the cultural and floristic importance of the *Flor de Inirída*, the Instituo Amazónica de Investigaciones Cientificas uses *Guacamaya* in its insignia (Instituto SINCHI, 2011).

Conservation, management, and cultivation

Although not included in the IUCN Red List of Threatened Species (IUCN, 2014; see SIB, 2012), the extractive practices and natural and anthropogenic fires, coupled with the restricted distribution and edaphic specificity of *Guacamaya superba*, have caused extirpation of some populations (pers. obs.). Conservation concerns lead to the Colombian environmental authority (Corporación Para el Desarrollo Sostenible del Norte y el Oriente Amazónico—CDA) to prohibit the harvest, transport, and commercialization of species of *Flor de Inírida* (resolution 526 of November 29 of 1998).

Environmental and social concerns prompted the creation of a grassroots organization in Inírida (Asociación Para el Desarrollo Integral, Humano y Sostenible—AKAYÚ; CDA, undated). A management plan for wild harvesting and propagation of *Guacamaya* and *Schoenocephalium* was developed with technical assistance from the Instituto Amazónico de Investigaciones Científicas—SINCHI, and permits for controlled, local harvesting of the *Flor de Inírida* was granted to AKAYÚ. Species from these habitats with particular edaphic conditions are known to be difficult to cultivate (G. Romero-G., pers. comm.) and attempts to grow *S. martianum* (Schultes, 1954) and *S. teretifolium* (Avellaneda and Herrera, 1998) from seed ex situ were unsuccessful. However, the project in Inírida developed species-specific protocols to propagate *G. superba* and *Schoenocephalium teretifolium* from lateral shoots, including the required size of the shoot, spacing in raised beds, and water regimes (PRONATTA, undated). Cutting with secuters rather than pulling inflorescences was used to harvest, minimizing damage to the plants (PRONATTA, undated). A mortality rate of less than 1% in the local nursery was achieved, and some threatened populations were successfully re-established.

Discussion

Schoenocephalieae (Saxofridericioideae) have erect stems and branch sympodially following production of a terminal inflorescence, as in some other Rapateaceae (e.g., *Duckea,* Rapateoideae; Colella, 1999). Roots grow along the stem protected by the leaf sheaths, providing mechanical support, a pattern frequent in monocots (e.g., Juncaceae, Velloziaceae; Weber, 1953), rather than through the cortex, as in many Bromeliaceae (Weber, 1954). We suggest this is likely the common architecture in Rapateaceae as it has been observed in other genera (e.g., *Stegolepis*; pers. obs.).

Roots of Rapateaceae have a sclerotic velamen (Solereder and Meyer, 1929), generally a well developed exodermis, and a conspicuous endodermis of thick walled sclerotic cells (Solereder and Meyer, 1929; Carlquist, 1969). A persistent root epidermis and starch sheath (Carlquist, 1969) were not observed here, perhaps due to the maturity of the material. The number of pericycle layers varies within the family (Carlquist, 1969); Schoenocephaleae are characterized by a bilayered pericycle. Carlquist (1969) found the pericycle in *Guacamaya* to be slightly lignified, which was not observed in our material. The ground tissue in the stele is sclerotic in Saxofridericoideae (Carlquist, 1969). In Schoenocephaleae the outer cortex contains irregular arm parenchyma with air spaces (Solereder and Meyer, 1929; Carlquist, 1969; Stevenson et al., 1998).

Stem thickening through lateral meristematic activity is known from several families of Poales (see Rudall, 1991), and is reported here for the first time in Rapateaceae as a secondary meristem (i.e., distal from the apex). A lateral meristem is likely also present in *Kunhardtia* (see Fig. 1D)—as well as other large-stemmed Rapateaceae—although it may not be present in the narrower stems of *Schoenocephalium*.

A variety of plant structures such as tree cavities (Kitching, 1983, 2000); inflorescence bracts (e.g., *Heliconia caribaea* Lam.; Machado Allison et al., 1993); closely inserted, laterally broadened or inflated leaf bases (e.g., *Cochliostema*; Troll, 1961; Hardy, 2001); or leaves individually fused creating a container (e.g., *Nepenthes*; Bell, 2008); impound water, forming an aquatic habitat (Kitching, 2000). In addition to water, these structures may passively accumulate insects and other small animals, soil particles, as well as plant (Fig. 3C) and animal debris (Fish, 1983; Kitching, 2000), and may provide a habitat for other plants as was observed in *Guacamaya* (Fig. 3F). The phytotelm environment and the organisms occurring there may be

FIGURE 9. Regional cultural importance of Schoenocepahlieae (*Flora de Inírida* and *Flora de Maroa*). **A**. A fresh bouquet of *Guacamaya superba*. B, C. *Schoenocephalium teretifolium*. **B**. Statue in Inírida, Colombia. **C**. The state flag of Guainía, Colombia. D–F. *Guacamaya superba*. **D**. A bouquet including *Lycopodiella* sp. on the door to the air terminal welcomes travelers in Maroa, Venezuela. *Guacamaya* occurs in the savanna (the type locality) that is used as the airstrip. **E**. Iconography inside the air terminal. **F**. Harvesting inflorescences from wild populations of *Guacamaya*.

part of complex food webs (Beaver, 1983; Kitching, 2000), and some tank-producing plant species secrete digestive enzymes, deriving nutritional benefit from their contents (Fish, 1983; Benzing, 2000). Impounding phytotelma in *Guacamaya*, composed of enlarged, marcescent leaf sheaths that may persist for years, contain mycorrhizal roots, other organisms (Fig. 3B), water, and debris. The impounding leaf bases in the rosulate genus *Cochliostema* similarly protect masses of entangled roots consisting of primary shoot-borne roots that are shorter than the secondary ones (Troll, 1961).

Unequally conduplicate leaf sheaths has been associated with leaf phyllotaxis in Rapateaceae (Stevenson et al., 1998); our interpretation of an equal conduplication and spriodistichous arrangement in Schoenocephalium warrants further examination. Leaves of Rapateaceae are generally described as hypostomatic (Boubier, 1895; Solereder and Meyer, 1929; Carlquist, 1969; Stevenson et al., 1998); however, *Monotrema* leaves are amphistomatic (Ferrari et al., 2014), and distally the leaves of *Guacamaya* are weakly so. Rapateaceae are characterized by randomly arranged, paracytic stomates (Solereder and Meyer, 1929; Carlquist, 1969), or tetracytic stomates (*Monotrema*; Ferrari et al., 2014). Previous examination of the family for epicuticular wax relied on herbarium material and found unordered crystaloids (Barthlott and Frölich, 1983), eroded wax (*Guacamaya*), or apparently none (Frölich and Barthlott, 1988). Epicuticular waxes may form an impervious boundary layer and are often interpreted as an adaptation to reduce water loss (Barthlott et al., 1998). The hydrophobic waxes on the surface of the leaf sheath in *G. superba* may have a protective function against microbial activity and the continuous contact with water (Cutter, 1978). Isolated surface wax was thought to facilitate trapping insects in a digestive container system (Martin and Juniper, 1970). Schoenocephaleae and *Monotrema* leaves have air canals (Carlquist, 1966; Ferrari et al., 2014), and layers of clear subdermal cells are common in Rapateaceae leaves; this tissue is often interrupted by fiber strands (Carlquist, 1969; Ferrari et al., 2014) or tannin filled cells.

Schoenocephalieae, and nearly all other Rapateaceae, have an elongate and photosynthetic peduncle that elevates the inflorescence above the leaves, *Maschalocepahalus* Gilg & K. Schum. and most species of *Rapatea* Aubl. being notable exceptions (Pilger, 1930; Maguire, 1958; Stevenson et al., 1998). In Schoenocephalieae the inflorescence is usually red (yellowish in other Rapateaceae) and the peduncle is distally flattened, where stellate cells forming aerenchyma, are more pronounced. A hypodermis of sclerenchyma or parenchyma is present in the peduncle (Solereder and Meyer, 1929; Carlquist, 1969) and may be present on both or only the abaxial leaf surface (Carlquist, 1966; Ferrari et al., 2014).

Rapateaceae are characterized by having amphivasal and smaller, collateral vascular bundles (Carlquist, 1966, 1969; Stevenson et al. 1998), or all bundles collateral (Ferrari et al., 2014). Vascular bundles are sheathed by fibers or thin-walled cells, and may be buttressed to the lower or both leaf surfaces. Cheadle and Kosakai (1982) found all levels of tracheary element specialization in a large sampling of Rapateaceae, with vessels with sclariform perforation plates, the form observed here in leaves, to be the most common; imperforate tracheary element also occur in Schoenocephalieae leaves (Carlquist, 1969).

Our observations on cellular inclusions are consistent with those previously reported (Solereder and Meyer, 1929; Carlquist, 1966, 1969; Stevenson et al., 1998; Ferrari et al., 2014). Epidermal silica bodies are characteristic of Rapateaceae (Carlquist, 1966, 1969; Stevenson et al., 1998) and occur in some other families of Poales including Bromeliaceae, but not Typhaceae (Prychid et al., 2004), two families suggested to be related to Rapateaceae (Givnish et al., 2000; Givnish et al., 2006; Bouchenak-Khelladi et al., 2014). Furthermore, silica bodies are associated with drought resistance and tolerance to metal accumulation (Hodson et al., 2005). The contents of Rapateaceae idioblasts have been referred to as tannins since Solereder and Meyer (1929; Carlquist, 1966, 1969; Stevenson et al., 1998; Ferrari et al., 2014); however, further characterization of these constituents is needed because their staining properties are not always consistent (Carlquist, 1966). Both tannins and mucilage may prevent desiccation.

Many Rapateaceae produce copious mucilage from roots, stems, and leaves (Carlquist, 1966; Stevenson et al., 1998; pers. obs.), which was observed in this study secreted from external, uniseriate, trichomes and in vertically-oriented cortical cavities that also occur horizontally in *Guacamaya* (Carlquist, 1966).

Fire has an important role in the ecology of savannas (Gillon, 1983; Hernández, 1987). Plant species that inhabit savannas exhibit structural and life history strategies enabling tolerance or resistance to periodic fires (e.g., Soderstrom, 1981; Appessato da Gloria and Cury, 2011; Marais et al., 2014). Mucilage contains a high water content (Roth and Lindorf, 1991) and has been suggested as an adaptation in Rapateaceae for withstanding fires (Givnish et al., 2000). The humidity and thermal isolation provided by the telmata should also protect meristems against fires, as do the persistent leaf bases in *Bulbostylis paradoxa* (Spreng.) Lindm. (pers. obs.), and tightly arranged leaves of *Vellozia* (Kubitzki, 1998).

Plants occurring in the oligotrophic white sand may experience flooding, although ample available water may be temporarily limited, even during the rainy season due to the high drainage capacity of the sandy substrate. Thus, they may exhibit a combination of characters associated with both flooded and drought prone habitats (see Campbell, 2004). Aerenchyma is common in wetland plants (Jung et al., 2008), and is well-documented in Poales. Although Carlquist (1969) considered this tissue common only in stems and peduncles of Rapateaceae, lysigensous air spaces, as we found particularly in the sheath, are known in leaves of the tribe (Solereder and Meyer, 1929), as well as in some *Monotrema* species (Ferrari et al., 2014).

Documentation of modern uses of tropical plants has focused on agricultural crops; timber; and extraction of non-timber forest products, such as fibers, building materials, medicinal plants, gums, and latex (ACTI, 1975; Mejía and Mejía, 1980; Nepstad and Schwartzman, 1992; Cárdenas López and López Camacho, 2000; van Andel et al., 2003), whereas there is little in the literature about extraction or cultivation of tropical plants for ornamental purposes (Burman, 1991; Giulietti et al., 1996; Cárdenas López and López Camacho, 2000; Huber and Foster, 2003; van Andel et al., 2003; Schmidt et al., 2006; Oliveira et al., 2014). Forest species have been emphasized and little has been described for savanna plant species (Burman, 1991; Giulietti et al., 1996; Schmidt et al., 2006; Oliveira et al., 2014), although use of *Mauritia flexuosa* L.f., a forest species that also occurs as isolated stands (*morichales* or *buritizais*) or as gallery forests in savannas is well known (Pittier, 1926; ACTI, 1975; Padoch, 1988; Ponce et al., 2000). In the upper Río Negro region, local cultivation programs are usually aimed at promoting agroforestry practices (e.g., Vélez and Vélez, 1999). The experiments observed in this study to cultivate and sustainably extract *Guacamaya* show promise not only for Schoenocephalieae, which has a long history of regional use (Schultes, 1954; Fig. 9), but also for other native species. The edaphic specificity of species endemic to white-sand savannas have generally rendered them unsuitable for ex situ cultivation, but the success in using local soil, likely combined with the presence of vesicular-arbuscular mycorrhizae (see St. John, 1988) may serve as an example for other re-introduction programs in an ecologically important habitat that has little or no other agricultural use but that is often degraded for other purposes (Hernández, 1987; Fölster and Dezzeo, 1994; Huber, 1995c; Huber and Foster, 2003; Rodríguez 2004; see Miranda et al., 2002; Cook and Corbett, 2003; Ferreira et al., 2013). Cultivation and/or the management of harvesting inflorescences of Schoenocephalieae is critical because the removal of wild plants for handicrafts and other decorative uses raises conservation concerns, in part due to depletion of the seed bank (e.g., Burman, 1991; Giulietti et al., 1996; Schmidt et al., 2006; Oliveira et al., 2014).

Aspects about the biology of Schoenocephalieae that remain to be addressed include characterization of the telmata habitat, their use, and dynamics; a possible nutritive association with termites (Fig. 3A, G; Avellaneda, M. and C. A. Herrera, 1998); characterization of endophytic fungi, and their possible economic value (see Strobel et al., 2001), and the role, if any, of mycorrhizae in aluminum accumulation in Rapateaceae (see Chenery, 1949); whether aluminum or phenolics deter herbivory of the starchy roots and stems; and the species' potential in bioremediation of aluminum contaminated soils. Further examination of liquid-preserved material may reveal a greater distribution of surface wax, which may have taxonomic value (see Frölich and Barthlott, 1988). As noted by Carlquist (1966), the chemistry of tannin-like substances remains unknown in Rapateaceae.

Although hummingbird visitation is known in *Guacamaya* (Berry, 2004; pers. obs.), the number of phoric mites we observed was low (unpubl. data) and pollination, dispersal, germination, and phenology have never been documented for species in the tribe.

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