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Reproductive morphoanatomy of *Tripodanthus belmirensis* (Loranthaceae), a key nectar and fruit source for native birds in Colombia's Central Cordillera

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ABSTRACT

Floral diversification in the widespread Loranthaceae reaches its greatest expression in the Andes, spanning entomophilous species to ornithophilous taxa. *Tripodanthus*, a genus restricted to South America, comprises three species with medium-sized flowers. Among them, the threatened *T. belmirensis*, endemic to Colombia's Central Cordillera, displays ornithophilous red to orange corollas that contrast sharply with the entomophilous, whitish flowers of its congeners *T. acutifolius* and *T. flagellaris*. We examined the reproductive traits of the little-known *T. belmirensis*. Its flowers possess six free petals that form an actinomorphic, tubular, fenestrate corolla, and three long stamens alternating with three short ones, all epipetalous. The ovary is three-locular, each locule containing a highly reduced ovule. Only a single dicotyledonous embryo develops per flower, surrounded by a massive compound endosperm, whereas the remaining embryo sacs arrest early in development. The viable embryo is pendulous. The fruits consist of a dry, indehiscent pericarp enclosed by a viscin-rich epicarp. In the absence of a seed coat, the embryo and endosperm lie directly against the pericarp. Together, the substantial viscin layer and endosperm provide abundant nutritive resources for frugivorous birds, particularly the Indigo-winged parrot (*Hapalopsittaca fuertesi*, Psittacidae: Arinae), an endemic and critically endangered species of Colombia's Central Cordillera.

Resumen: La diversificación floral de la familia Loranthaceae, ampliamente distribuida, alcanza su máxima expresión en los Andes, abarcando desde especies entomófilas hasta ornitófilas. *Tripodanthus*, género restringido a Sudamérica, comprende tres especies con flores de tamaño mediano. Entre ellas, *T. belmirensis*, especie amenazada y endémica de la Cordillera Central de Colombia, presenta corolas ornitófilas de color rojo a naranja que contrastan marcadamente con las flores blanquecinas y entomófilas de sus congéneres *T. acutifolius* y *T. flagellaris*. Estudiamos los caracteres reproductivos de *T. belmirensis*, especie poco conocida. Sus flores poseen seis pétalos libres que forman una corola actinomorfa, tubular, fenestrada, y tres estambres largos que alternan con tres cortos, todos epipétalos. El ovario es trilocular; cada lóculo contiene un óvulo muy reducido. Solo se desarrolla un embrión dicotiledóneo por flor, rodeado por abundante endosperma compuesto, mientras que los sacos embrionarios restantes detienen su desarrollo en etapas tempranas. Los frutos constan de un pericarpo seco e indehiscente, envuelto por un epicarpo rico en viscina. Debido a la ausencia de cubierta seminal, el embrión y el endosperma se encuentran en contacto directo con el pericarpo. En conjunto, la masiva capa de viscina y el endosperma proporcionan abundantes recursos nutritivos para las aves frugívoras, en particular para la cotorra aliazul (*Hapalopsittaca fuertesi*, Psittacidae: Arinae), una especie endémica y críticamente amenazada de la Cordillera Central de Colombia.

Palabras clave: Antesis fenestrada, frugivoría por aves, ornitofilia, plantas parasíticas, muérdagos de subpáramo, Santalales.

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1. Introduction

Flowers in the mistletoe family Loranthaceae Juss. (Santalales) reach their highest degree of morphological diversification in the Andes. However, most of the studies on floral morphoanatomy and reproductive biology have been carried out in Old World members of the family (e.g. Blakely, 1922; Maheshwari et al., 1957; Johri, 1963; Bhatnagar and Johri, 1983; Feehan, 1985; Ladley & al.,1997). The New World genus *Tripodanthus* Tiegh. (Loranthaceae) comprises three species restricted to South America: *T. acutifolius* (Ruiz & Pav.) Tiegh., which is widespread across tropical and subtropical regions of the continent, except Chile; *T. belmirensis* F.J. Roldán & Kuijt, confined to the Central Andes of Colombia; and *T. flagellaris* (Cham. & Schltdl.) Tiegh., occurring in northern Argentina and western Uruguay (Eichler, 1868; Rizzini, 1952; Kuijt, 1986; Roldán and Kuijt, 2005; Amico et al., 2012; Dettke and Waechter, 2014; Kuijt and Hansen, 2015). *Tripodanthus* belongs to the subtribe Psittacanthinae, together with the genera *Aetanthus* (Eichler) Engler, *Cladocolea* Tiegh., *Dendropemon* (Blume) Rchb., *Maracanthus* Kuijt, *Oryctanthus* Eichler, *Oryctina* Tiegh., *Panamanthus* Kuijt, *Passovia* H.Karst., *Phthirusa* Mart., *Psittacanthus* Mart., and *Struthanthus* Mart. (Wilson and Calvin, 2006b; Vidal-Russell and Nickrent, 2008; Nickrent et al., 2010; Su et al., 2015; Galván-González et al., 2024). However, the precise phylogenetic relationships within the subtribe remain poorly resolved. Preliminary analyses suggest that *Tripodanthus* is sister to all other members of the subtribe, with this divergence estimated to date back to the Oligocene (Liu et al., 2018) or possibly even earlier, in the Eocene (Grímsson et al., 2017). Given the pivotal phylogenetic position of *Tripodanthus* as a likely early-diverging lineage, and the remarkable variation in floral and fruit anatomy and morphology across the subtribe Psittacanthinae (Amico et al., 2012; Grímsson et al., 2017; Liu et al., 2018), the features present in *T. belmirensis* are of particular importance for understanding patterns of character evolution within the group. The genus *Tripodanthus* is characterized by epicortical adventitious roots that penetrate stems and, occasionally, roots of their hosts; indeterminate inflorescences that are mostly terminal on foliose branches and composed of groups of two, or more commonly three flowers; and by medium-sized (1–4 cm long) tubular flowers with dimorphic stamens and a three-locular ovary. The epicortical roots arise from shoots that function either as secondary haustoria or as tendrils facilitating climbing, and have been reported to develop in response to wounds (Kuijt, 1982; J. 1989; Calvin and Wilson, 2006; Wilson and Calvin, 2006a, 2006b; Heide-Jørgensen, 2008). Despite the current understanding of its vegetative and parasitic structures, including the haustorial system, information on the morphoanatomy and development of the flowers and fruits of *Tripodanthus* remains limited, as its species are rare in the wild.

To address the need for documenting floral and fruit traits in this poorly known genus, we studied a population of *Tripodanthus belmirensis*, endemic to the Central Cordillera of Colombia. This species inhabits a limited number of high-Andean cloud forests, subpáramos, and páramos in the departments of Antioquia, Caldas, Risaralda, and Valle del Cauca, at elevations ranging from 3000 to 3693 m. (Fig. 1). The species represents the northern limit of the genus distribution, and its range is disjunct with respect to its congeners. Along with *Aetanthus, Gaiadendron* G. Don, and *Tristerix* Mart., it is among the few members of the Loranthaceae that reach páramo vegetation in Colombia. The habitats occupied by these species are increasingly threatened by agricultural expansion and severe disturbance. Except for the widespread *G. punctatum* G. Don., the remaining species of these genera qualify as Critically Endangered under IUCN (2022) criteria B1 (Extent of Occurrence < 100 km^2) and B2 (Area of Occupancy severely fragmented or limited number of locations), owing to the very low numbers of known individuals (González and Pabón-Mora, 2023). Beyond its restricted

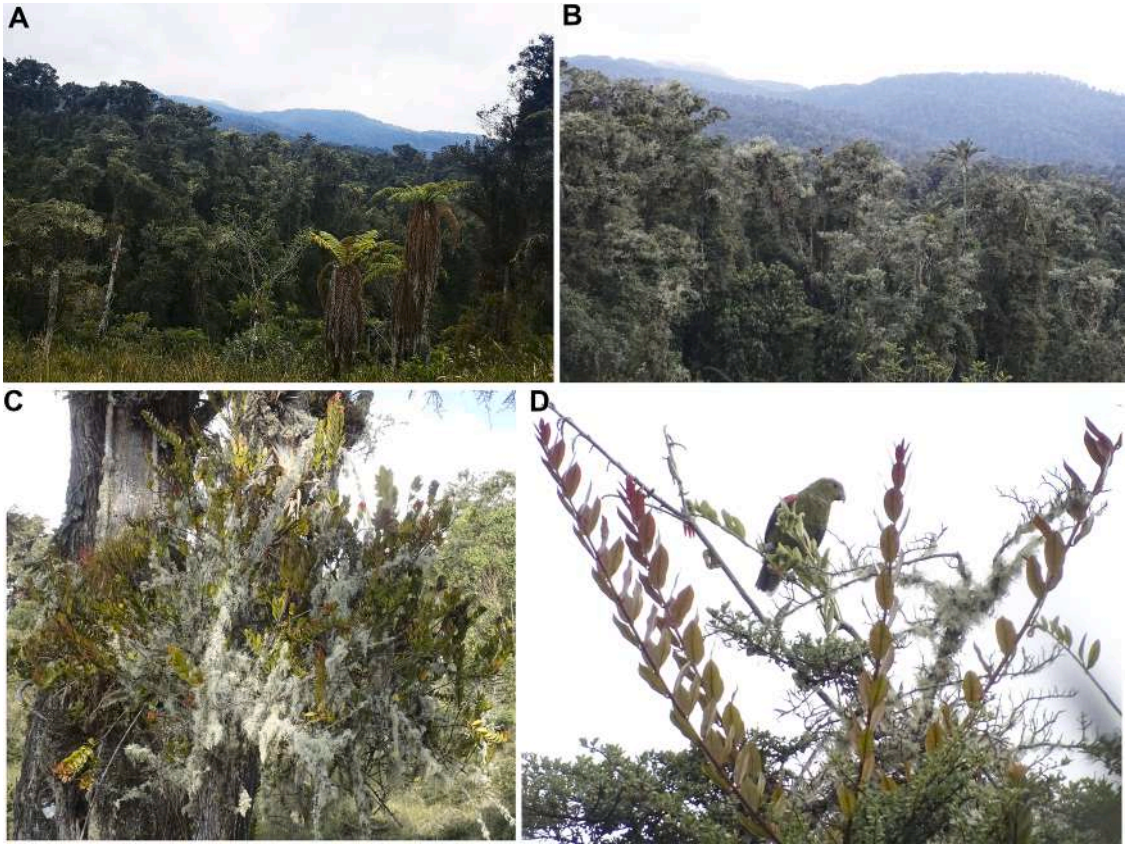

Fig. 1. Site study and life form of *Tripodanthus belmirensis,* and its associated parrot. A-B. High-Andean cloud forests. C. Stem hemiparasitic habit. D. Indigo-winged parrot, *Hapalopsittaca fuertesi* (Psittacidae: Arinae), pearching near *T. belmirensis*.

distribution and conservation status, understanding the ecological role of *Tripodanthus belmirensis* is crucial, as mistletoes are widely recognized as keystone resources, particularly for vertebrates (Watson, 2001). Birds play a critical role in mistletoe dispersal, germination, and establishment (Docters van Leeuwen, 1954; Ladley and Kelly, 1996; Ladley et al., 1997; Robertson et al., 1999) and may also act as important drivers of mistletoe diversification (Restrepo et al., 2002; Amico et al., 2007). In this context, *T. belmirensis* likely contributes to sustaining local biotic interactions as its fruits constitute an important food source for the Indigo-winged parrot, *Hapalopsittaca fuertesi* (Chapman, 1912) (Psittacidae: Arinae; Fig. 1D), an endemic species of Colombia's Central Cordillera that is considered critically endangered (Díaz-González et al., 2024). Additionally, foliage of related mistletoe species, such as *Tripodanthus acutifolius* (Loranthaceae) and *Antidaphne viscoidea* Poepp. & Endl. (Santalaceae), serves as primary food for the larvae of Pieridae butterflies (Pierini: Aporiina) (Biezanko, 1958; Remillet, 1988; Braby and Nishida, 2010; González et al., 2021), suggesting that *T. belmirensis* may play a comparable role within high-Andean ecosystems.

In light of the limited knowledge of *Tripodanthus belmirensis*, its restricted distribution, and its potential ecological significance, this study examines the morphoanatomy of its reproductive structures to enhance our understanding of the species and to document traits that may influence its survival and long-term persistence as a critically endangered Andean endemic mistletoe. Specifically, we aim to: (1) provide a detailed account of floral and fruit morphology, anatomy, and development in *T. belmirensis*; (2) identify structural features that inform interpretations of its reproductive biology and functional ecology; (3) clarify characters relevant to understanding evolutionary patterns within Psittacanthinae and Loranthaceae; and (4) establish a morphological and anatomical framework to support future ecological, evolutionary, and conservation studies of the species.

2. Material and methods

2.1. Plant material

Three individuals of *Tripodanthus belmirensis* were collected in the locality of Cortaderal, municipality of Santa Rosa de Cabal, department of Risaralda, on November 30th, 2023, at an elevation of 3177 m (coordinates: 4.855645, –75.481913) (Fig. 1). Voucher specimens were deposited in the herbarium Unisarc (CUS-P), Santa Rosa de Cabal (Risaralda), and in the National Herbarium of Colombia (COL), Universidad Nacional de Colombia, Bogotá, under the number *S. Quintero García 970*. We examined three to four flowers per individual at two developmental stages—preanthesis and anthesis. Because fruits were actively consumed by birds, fewer developmental stages could be analyzed, and samples were obtained from only two individuals. The fruits examined measured 0.5, 1, and 2 cm in length.

2.2. Tissue processing

Reproductive organs at different developmental stages (from preanthesis flowers to mature fruits) of *Tripodanthus belmirensis* were initially preserved in 70 % ethanol. Flowers in pre-anthesis and anthesis, as well as fruits of various sizes, were dissected in 90 % ethanol under a Leica MZ7.5 stereomicroscope (Leica Microsystems, Heerbrugg, Switzerland). Samples were dehydrated through a standard ethanol–Histochoice series (90 %, 95 %, and 100 % × 2; 30 min each) and embedded in Paraplast X-tra (Fisher Healthcare, Houston, Texas, USA). Both, transverse and longitudinal serial sections (10–14 μm thick) were obtained using a Leica RM2125 rotary microtome. Sections were stained with Johansen's Safranin and 0.5 % Astra Blue, and permanently mounted in Permount (Fisher Scientific, Pittsburgh, Pennsylvania, USA). Additional free-hand sections were stained with Potasium Iodide (KI, Lugol; ThermoFisher Scientific), in order to test for the presence of starch. All protocols followed Johansen (1940). Observations and digital images were made using a Leica DM500 optical microscope equipped with a Leica ICC50W camera, operated with LAS EZ software. ImageJ (imageJ.net/ij/) was used to measure and estimate the percentages of viscin and endosperm in both a transverse and a longitudinal section of fully mature fruits.

2.3. Landmarks and terminology

Terminology follows Weberling (1981), Suaza-Gaviria et al. (2016, 2017), González & Pabón-Mora (2017a, 2017b, 2018, 2019), and Botero-Castaño et al. (2026). The histological zones of the flowers and fruits were defined using the vascular system as a positional landmark, as follows: the vascular bundles shared by petals and stamens delimit the extracarpellary-derived epicarp externally and the carpellary-derived pericarp internally.

3. Results

Tripodanthus belmirensis is a robust, shrubby, obligate stem hemiparasite characterized by upright branches, predominantly decussate leaves, although some may be alternate on the proximal portions of the shoots (Figs. 1C, D, 2A, B, D, E). The specimen examined for the anatomical studies presented here was collected growing on a species of *Escallonia* Mutis ex L.f.(Escalloniaceae). Individuals branch profusely from early elongation stages, shortly after seedling establishment. Young stems are somewhat fleshy and tetragonal in transverse section, becoming woody, terete and lenticellate at maturity. The leaves are shortly petiolate, with elliptic blades bearing a cuneate base, an acuminate apex, a pronounced midvein, inconspicuous higher-order veins, and a slightly succulent texture. They are light green in color, with distinctly red margin (Fig. 2E, F).

Flowering shoots are upright, reaching up to 1 m in length (Fig. 2A, B, D, E). The inflorescences are indeterminate thyrses borne on the terminal portion of the first and second order branches (Fig. 2B, D, E). Each thyrse comprises 5 to 8 partial inflorescences, each consisting of simple dichasia (i.e. one central and two lateral flowers) that develop in the axils of inconspicuous bracts (Fig. 2C, E). The central flower of each dichasium develops first, although it often aborts or fails to develop, resulting in two-flowered partial inflorescences. The proximal flowers of the thyrse open and transition to fruits earlier than the distal flowers.

Flowers are borne on pedicels 4–6 mm long (Fig. 2C). The calyx is glabrous and green, with a rounded red apex that is scarcely six-lobed (Fig. 2C). The corolla is actinomorphic, measuring 3.5–4 cm in length and 3–8 mm in diameter (Fig. 2B–E), and exhibits valvate aestivation. The six petals are entirely free, although their marginal epidermal cells remain interlocked until anthesis, forming a narrow, straight tube. The petals are orange to red externally and light yellow internally. Anthesis is fenestrate *ab initio* as the petals begin to separate at mid-lenght (Fig. 2C); subsequently, the distal third of the petals expands and becomes symmetrically reflexed, fully exposing the epipetalous stamens (Fig. 2C–E).

The androecium is dimorphic, consisting of three long stamens alternating with three short ones. The stamens are upright and adnate to the petals along their proximal half, with the zone of coherence between petals and filaments extending up to 1.7 cm in length. The long stamens are nearly as long as the petals. The free portions of the filaments are light yellow with red apices, and measure 10–12 mm in length. The anthers are dorsifixed, versatile, dithecal and tetrasporangiate; they are isomorphic, ovoid, and short (2–3 mm long), and with a small terminal apiculum and a dull creamy-yellow color (Figs. 2C–E, 3E, F, I).

The gynoecium is composed of six congenitally fused carpels, as indicated by the six vascular bundles (see below) and the alternating edges between petals and stamens, although only three poorly defined locules are discernible in the ovary (Fig. 3B). The ovary is inferior, 5–7 mm long and is crowned by a prominent six-lobed nectary, whose lobes alternate with the petals and stamens. The style is upright, slender, and

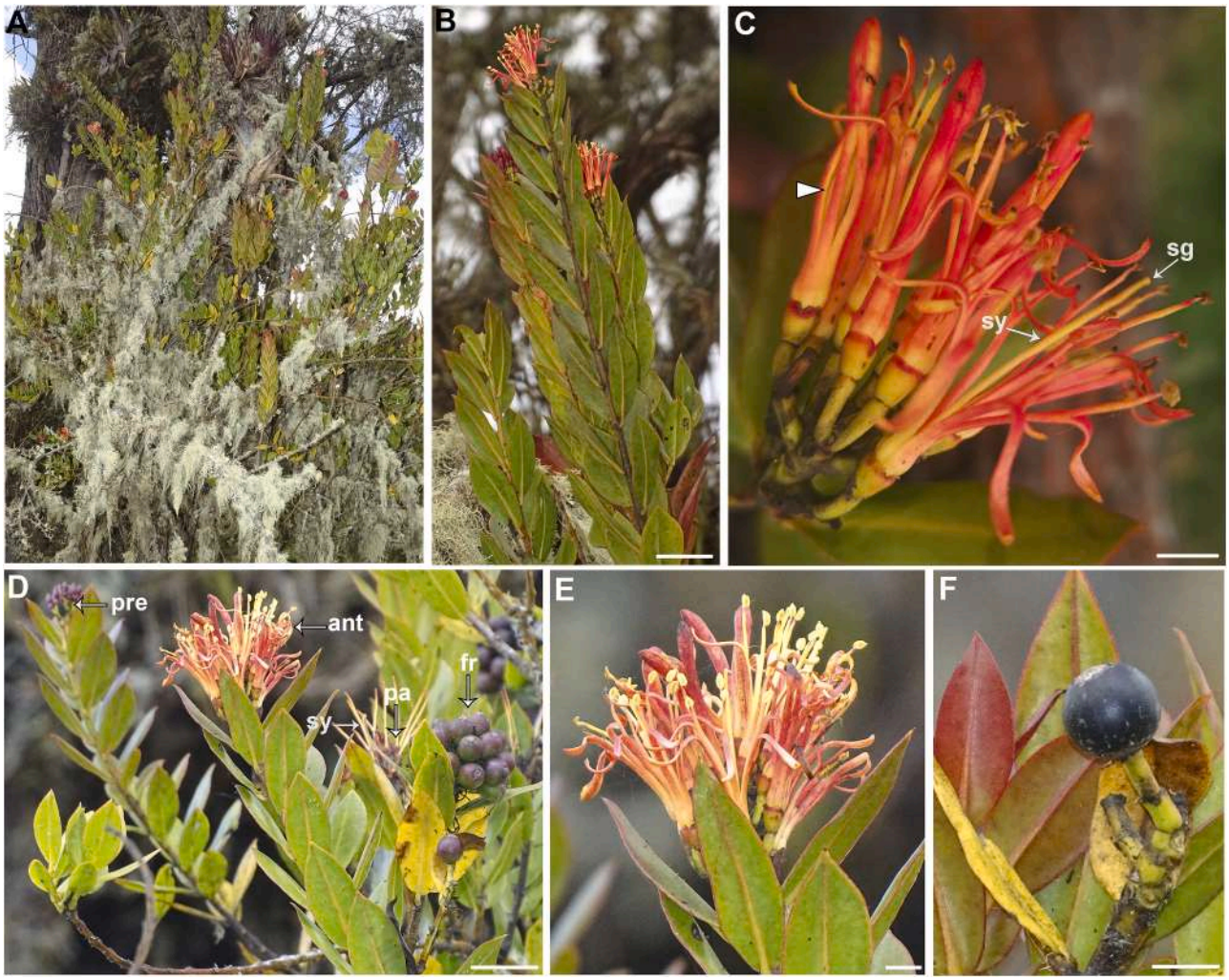

Fig. 2. *Tripodanthus belmirensis* flowers and fruits. A. Individual from which samples were collected for the present study (voucher *S. Quintero García 970*). B. Flowering shoots with terminal inflorescences. C. Detail of inflorescence; note *ab initio* fenestrate corolla anthesis (arrowhead), style (sy) and stigma (sg). D. Reproductive shoots showing (from left to right) flowers at preanthesis (pre), anthesis (ant), post-anthesis (pa) and fruits (fr); note persistent styles (sy) in post-anthetic flowers. E. Flowers at full anthesis showing truncate calyx, reflexed petals, and versatile dorsifixed stamens. F. Fully formed fruit. Scale bars: 3 cm in B, D; 5 mm in C, E; 1 cm in F.

light yellow, except for a narrow zone immediately below the capitate stigma, and it nearly equals the stamens in length (Fig. 2B–E). The style persists through the early stages of fruit development.

The fruits of *Tripodanthus belmirensis* are globose to subglobose, 1–1.5 cm in diameter, and enclosed by the calyx, to which they are fused except at the apical portion. The outer surface of the calyx in mature fruits gradually shifts in color from dull green and vinaceous when young to dark purple at full maturity (Fig. 2D, F), and exudes a copious green secretion.

Floral anatomy: Six vascular bundles enter the pedicel and split radially at the mid-level of the ovary into outer and inner bundles (Fig. 3A, B). The outer bundles supply the common petal-stamen bases, whereas the inner traces serve the gynoecium. The vascular trace entering the common petal-stamen base further divides radially into separate petal and stamen traces (Fig. 3C, D).

The hypanthium is massive and covered by a unistratified epidermis (Fig. 3A, B). The 6–8 outermost layers of the mesophyll consist of large tannin-like filled cells. In the upper hypanthium, the calyx exhibits a mesophyll composed of 3–4 layers, bounded by an outer epidermis and a narrower inner epidermis (Fig. 3C, D). No stomata or vascular traces irrigating the hypanthium were detected.

Each petal is supplied by a central vascular trace and two submarginal traces (Fig. 3E-H). In transverse section, the petals display a rectangular and slightly curved outline. Both the inner and outer epidermis consist of a single layer of small, slightly tangentially elongate cells. Along the inner half of the petal margins, papilliform epidermal cells form a tightly interlocked surface during pre-anthesis and early anthesis (Fig. 3D–H). The petal mesophyll comprises 10–15 cell layers, with the outer half composed of large tannin-like filled cells and the inner half formed by smaller, isodiametric to ovoid cells. Patches of nectariferous mesophyll, interspersed with intercellular spaces (lacunae), occur within this inner region (Fig. 3H).

Each stamen receives a single vascular trace (Fig. 3E–I). The abaxial and lateral mesophyll of the filament consists of 4–6 layers of large, isodiametric, tannin-like filled cells (Fig. 3G). The two pollen sacs of each theca dehisce through a common latrorse stomium (Fig. 3E, F, I). The anther wall comprises a thin unistratified epidermal layer of tangentially elongated cells, a thick, fibrous endothecium of radially elongate to cuboidal cells with ring-like to spiral wall tickenings, and one or two ephemeral middle layers of thin, tangentially elongated cells (Fig. 3I–L). The tapetum is secretory, uni- to bistratified, and degenerates by late preanthesis (Fig. 3I–L). Pollen grains are radially symmetrical, isopolar, oblate, deeply trilobed, and fossaperturate (Fig. 3L).

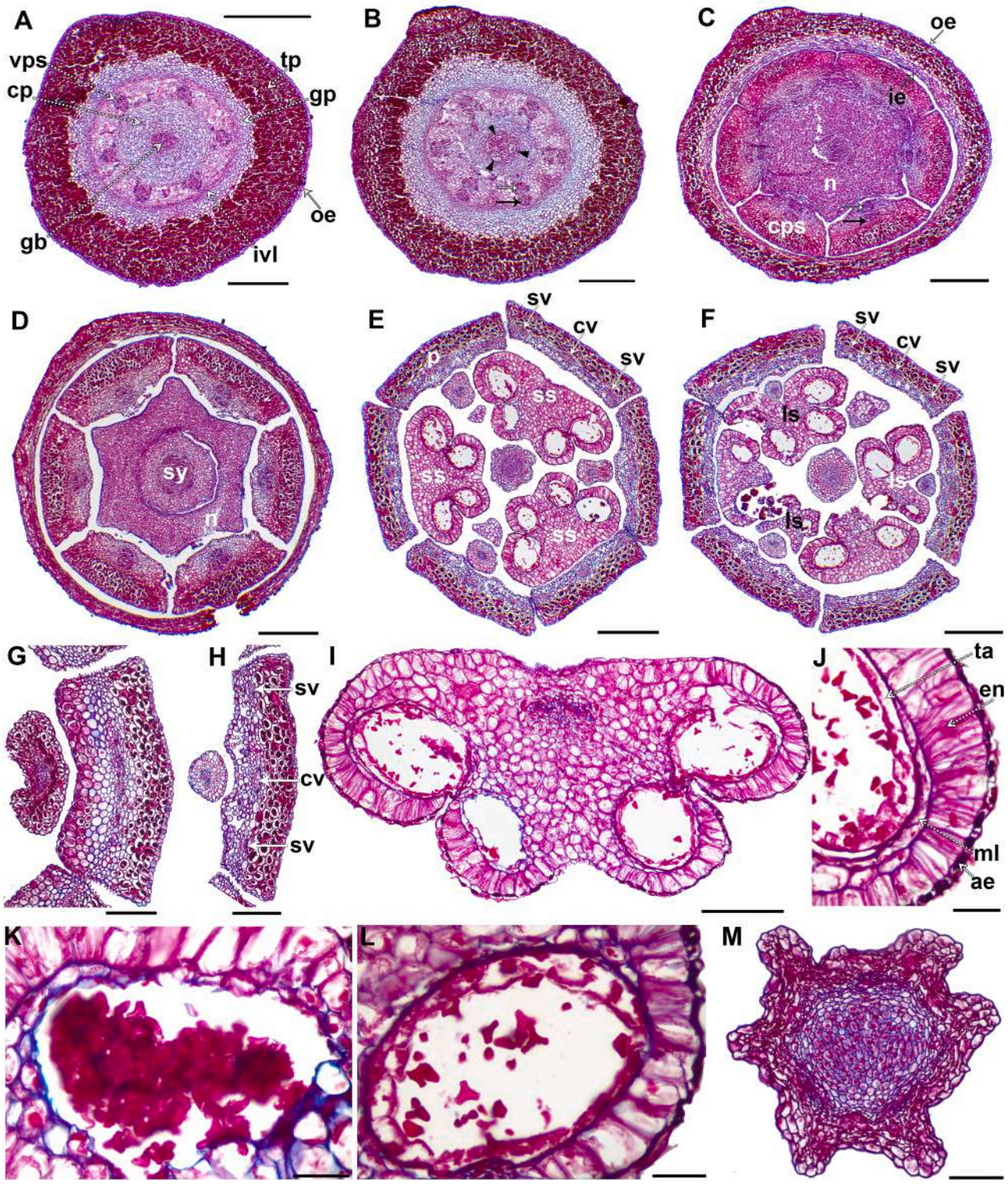

Fig. 3. *Tripodanthus belmirensis*, floral anatomy. A-F. Successive transections from the base (A) to mid-level (F) of the flower. A. Histology (from the outside in): outer epidermis; tanniferous parenchyma; ground parenchyma; initials of the viscine layer; six common petal/stamen vascular bundles; carpellary parenchyma; and base of the gynoecium. B. Transection at the level of the three gynoecial locules (arrowheads); note the radial split of petal (black arrow) and stamen (white arrow) vascular traces. C, D. Sections at the level of the 6-lobed nectary (C) and the base of the style (D); note the epidermal interlocking of petal margins and the outer tanniferous parenchyma of the petals; black and white arrows point to petal and stamen vascular traces, respectively. E, F. Sections showing the three short stamens (in E) alternating with the three long stamens (in F). G, H. Transection of young (G) and fully formed (H) petal; note the epidermal interlocking of petal margins and the outer tanniferous parenchyma. I. Anther. J. Anther wall. K. L. Anther locule with pollen clumps (K) and loose pollen grains (L). M. Transection of style. Abbreviations: ae, anther epidermis; cp, carpellary parenchyma; cps, common petal-stamen base; cv, central vein of petal; en, endothecium; gb, gynoecium base; gp, ground parenchyma; ie, inner epidermis of calyx; ivl: initials of viscine layer; ls, long stamen; ml, middle layer; n, nectary; oe, outer epidermis of calyx; p, petal; ss, short stamen; sv, submarginal vein of petal; sy, style; ta, tapetum; tp, tanniferous parenchyma; vps, common petal/stamen vascular bundles. Scale bars: 500 μm in A-F. 200 μm in G-I; 50 μm in J-L; 100 μm in M.

The ovary is trilocular and served by six small vascular traces (Fig. 3B). The locules are evident at the base and mid-level of the ovary, each containing a highly reduced, ategmic ovule (Figs. 3B, 4B, C). Immediately above the ovary, a massive nectarial disk is formed exhibiting a strong Lugol-positive signal indicative of high starch accumulation (Figs. 3C, D, 4A, D-G). The style is solid, slightly six-lobed and supplied by an equal number of poorly developed vascular traces (Fig. 3D-F, M). The style epidermis is unistratified and formed by small, slightly papilliform cells surrounding a mesophyll composed predominantly of isodiametric cells. The central transmitting tissue is heavily amyliferous, exhibiting intense Lugol-positive staining (Figs. 3M, 4A, D-G). The stigma is terminal, solid and undifferentiated except for the short papilliform epidermal cells.

Fruit anatomy: Two stages of fruit development were sampled

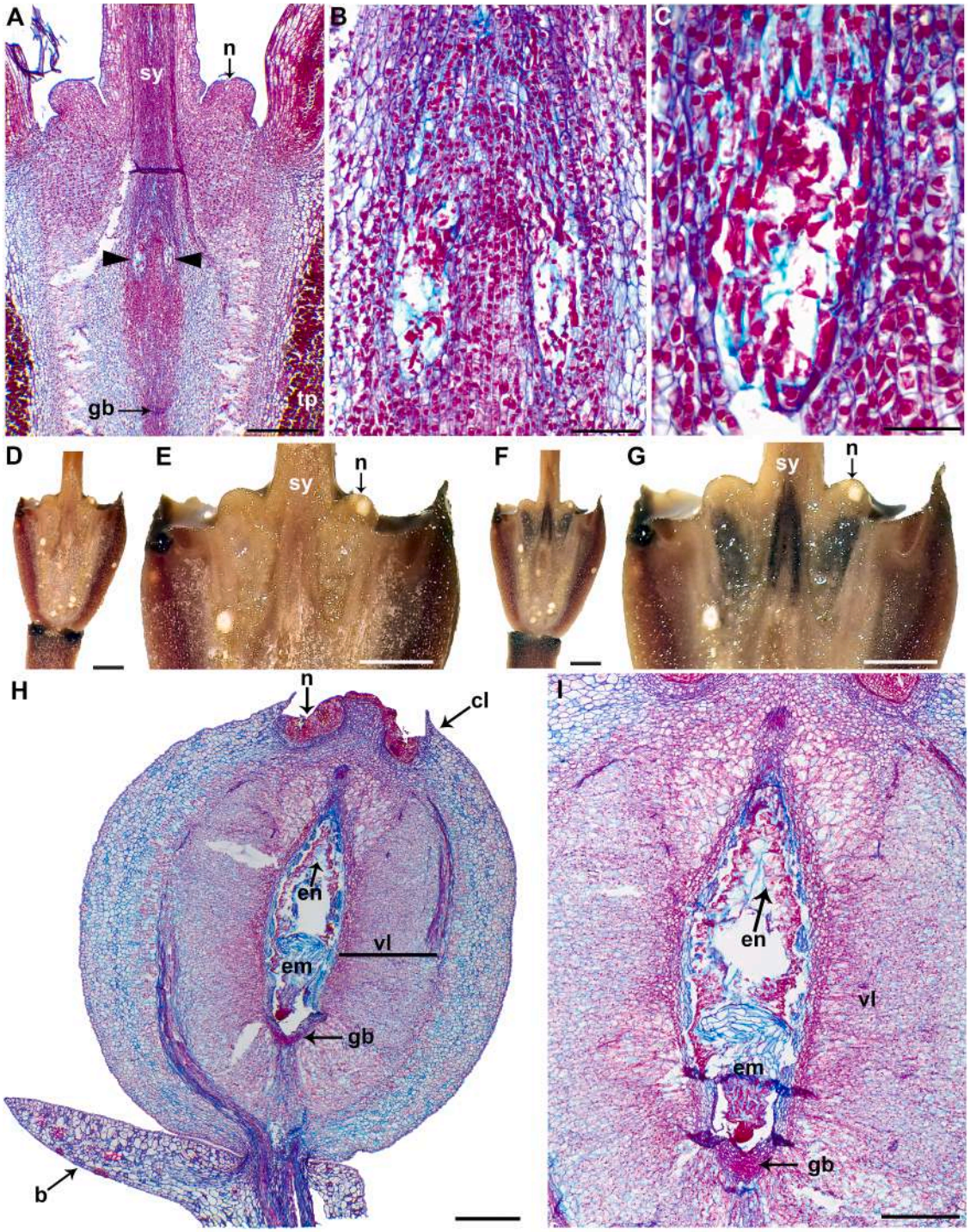

Fig. 4. *Tripodanthus belmirensis,* flower-to-fruit transition. A. Long section of ovary through two of the three locules (arrowheads). B, C. Details of ategmic, reduced ovules. D. Longitudinal section of a flower in anthesis at the level of the ovary prior to lugol-staining. E. Detail of D showing the nectary and the style. F. Long section of a flower in anthesis at the level of the ovary after lugol-staining. G. Detail of F showing intense stain indicating strong carbohydrate accumulation in the nectary and the style. H, Section of a fruit (ca. 0.5 mm long), showing the young pendulous embryo and endosperm surrounded by viscin layer. I. Detail of embryo and endosperm. Abbreviations: b, bract; cl, calyx lobe; em, embryo; en, endosperm; gb, gynoecium base; n, nectary; sy, style; tp, tanniferous parenchyma; vl, viscin layer. Scale bars: 500 μm in A, H; 100 μm in B; 50 μm in C; 200 μm in D-G, I.

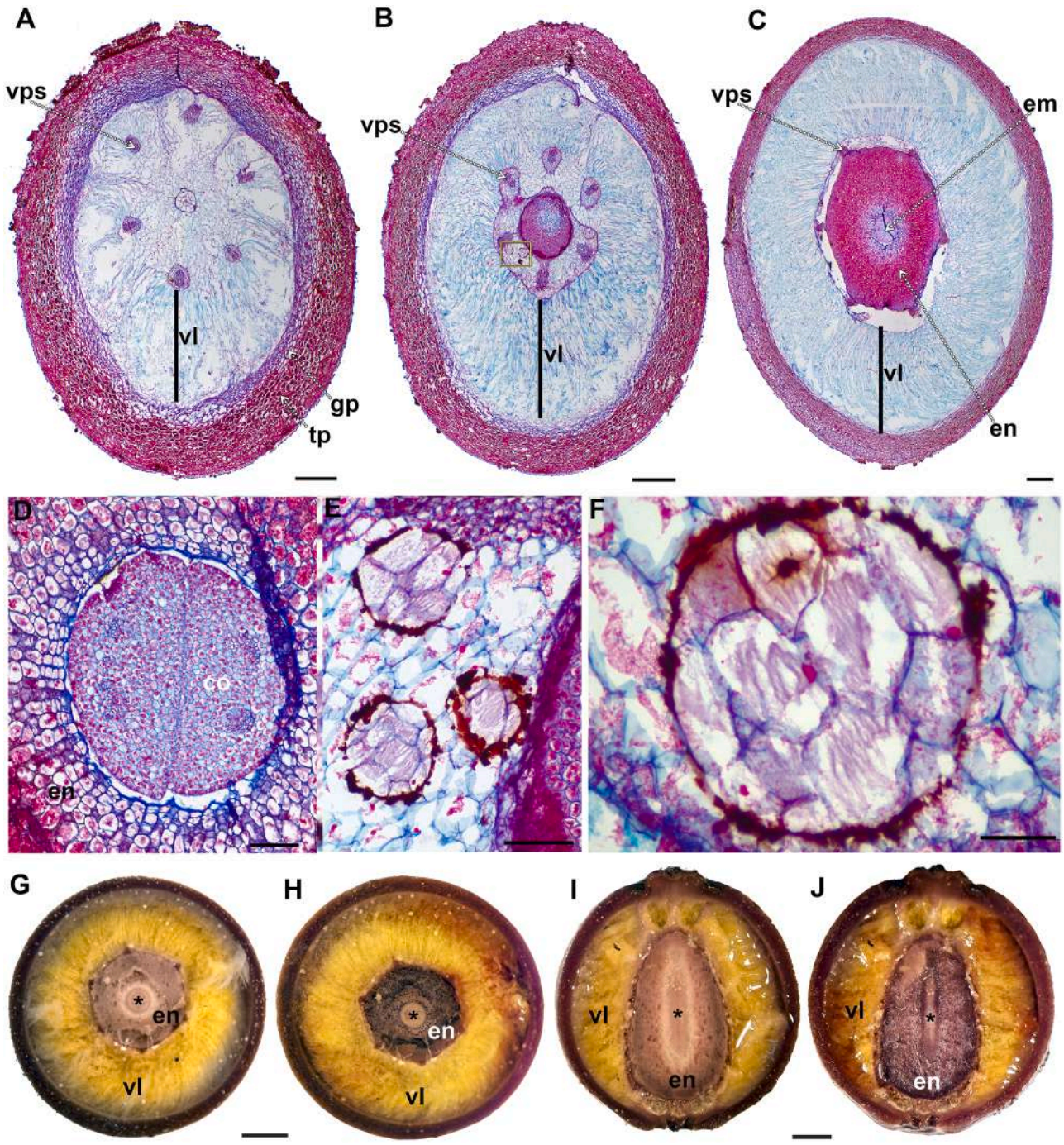

Fig. 5. *Tripodanthus belmirensis,* fruit. A-C. Transverse sections of a fruit (ca. 1 cm in diameter) at proximal (A), middle (B), and distal (C) levels. D. Cotyledons surrounded by endosperm. E-F. Ectopic arrested embryos (E, detail of inset in B). G. Transverse section of a 1 cm fruit prior to Lugol staining. H. Same section after staining, showing intense starch signal in the endosperm. I. Longitudinal section of a 1 cm fruit prior to staining. J. Same section after staining, revealing strong starch signal in the endosperm. Abbreviations: co, cotyledon; em, embryo; en, endosperm; gp, ground parenchyma; tp, tanniferous parenchyma; vl, viscin layer; vps, common petal/stamen vascular bundle. Asterisks in G-J mark the embryo. Scale bars: 500 μm in A-C; 200 μm in D; 250 μm in G-J; 100 μm in E; 50 μm in F.

(Figs. 4,5). The first stage sampled corresponds to a fruit 0.5 cm in diameter. At this stage the viscin layer is clearly differentiated and surrounds the pendulous embryo and the forming endosperm (Fig. 4H, I). The growing embryo tip is in close contact with the sclerenchymatic gynoecium base. At this stage the hypanthial tissue outside of the viscin layer is formed by ca. 15 layers of ground parenchyma (Fig. 4H).

When fruits have reached 1 cm in diameter, the hypanthium is enclosed by a unistratified epidermis, followed by 10–12 layers of large isodiametric, tannin-like filled cells. The inner mesophyll comprises 6–8 layers of tangentially elongate cells with thinner walls and no tannins, followed by a massive viscin layer composed of radially elongate cells (Fig. 5A–C). All tissues up to here correspond to the extra-carpellary epicarp. The six main vascular bundles that supply the petal/stamens remain evident in the fruit as they are persistent outside the carpellary tissue (Fig. 5A–C). The pericarp is reduced to 1–3-layers that crush at maturity. The lack of a seed coat causes the embryo and endosperm to lie directly against a vestigial, dry pericarp, a condition characteristic of Loranthaceae (Fig. 5G–J). The embryo is large, with two massive

cotyledons, and is surrounded by a six-angled, starch-rich abundant endosperm (Fig. 5C, D, G-J). Several arrested, non-viable embryos are also evident (Fig. 5E, F).

4. Discussion

Floral traits of *Tripodanthus belmirensis*. *Tripodanthus belmirensis* conforms to Hofmeister's rule between sepals and petals on one side, and stamens and carpels on the other, but this rule is disrupted between petals and stamens, as is typical in Loranthaceae (Suaza-Gaviria et al., 2016; González and Pabón-Mora, 2019). Furthermore, the most relevant floral traits that are plesiomorphic in Loranthaceae, namely, the irregular development of the calyx, the uniseriate corolla and androecium, the epipetalous stamens, and the actinomorphic corolla, consistently appear in all species of *Tripodanthus*.

We report here, for the first time, the fenestrate anthesis of corollas in *Tripodanthus belmirensis,* a mechanism in Loranthaceae first described in Old World mistletoes by Evans (1895). This mode of anthesis consists of the opening of lateral narrow, window-like slits between the petals prior the opening of the corolla tip (Fig. 2C), evoking the appearance of "lighted candles" (Evans, 1895: 235) or "Chinese lanterns" (Bernhard & al., 1980: 441). This mode of anthesis, rare among New World Loranthaceae (e.g. *Tristerix*; Amico et al., 2007; González and Pabón-Mora, 2017 a), is far more common in Old World members of the family. Reports exist for species of the Australian *Amyema* Tiegh. (Blakely, 1922; Dixit, 1958 a; Bernhard et al., 1980), the African *Erianthemum dregei* (Eckl. & Zeyh.) Tiegh. and *Englerina woodfordioides* (Schweinfurth) Balle ex M.G. Gilbert (Werth 1915; Kirkup, 1998), the New Zealand *Alepis flavida* Tiegh., *Peraxilla colensoi* (Hook. f.) Tiegh., *P. tetrapetala* (L. f.) Tiegh. and *Trilepidea adamsii* Tiegh. (Evans, 1895; Feehan, 1985; Aluri and Subba Redi, 1995), as well as the Bornean *Amylotheca duthieana* (King) Danser (Yumoto et al., 1997). Fenestrate corollas have also been illustrated in *Agelanthus platyphyllus* Hotchst. ex A. Rich. (Fig. 72 in Engler and Krause, 1935) and *Helicanthes elastica* (Desr.) Danser (Figs. 4 and 5 in Johri et al., 1957). Because these taxa are phylogenetically scattered, it is likely that fenestrate anthesis represents a convergent trait that evolves through different developmental mechanisms, which reinforces Vidal-Russell & Nickrent's (2008) statement that tubular, bird-pollinated flowers have evolved independently from insect-pollinated ancestors.

Fenestrate corollas have been associated with ornithophily, the primary pollination mechanism in both Old and New World Loranthaceae, including *Tripodanthus* and *Tristerix* (Reiche, 1904; Werth, 1915; Blakely, 1922; Feehan, 1985; Galetto et al., 1990; Kirkup, 1998; Aizen, 2003, 2005; Amico et al., 2007; González and Pabón-Mora 2017a). However, this mode of anthesis is not restricted to cross-pollinated mistletoes, as it also occurs in self-compatible and even cleistogamous species, such as *Peraxilla colensoi* and *P. tetrapetala* (Ladley et al., 1997).

Four large, orange- to red-flowered lineages of Psittacantheae (sensu Nickrent et al., 2010), *Tristerix* (Ligarinae) and *Aetanthus, Psittacanthus*, and *Tripodanthus* (Psittacanthinae), converge in Colombia, all of which commonly exhibit hummingbird pollination (González and Pabón-Mora 2017a, 2019). *Tripodanthus belmirensis* fits this pattern: its fragrance-free, bright orange to red tubular corollas (up to 3 cm long) appear adapted for ornithophily, and our field observations confirm the tourmaline sunangel (*Heliangelus exortis*, Trochilidae: Lesbiini) as a frequent floral visitor, consistent with previous reports in related genera such as *Aetanthus, Psittacanthus*, and *Tristerix* (Rivera et al., 1996; Aizen, 2003; Azpeitia and Lara, 2006; González and Pabón-Mora, 2017a). The floral morphology of *T. belmirensis* contrasts sharply with that of its congeners *T. acutifolius* and *T. flagellaris*, which bear fragrant, white to pale yellow, shorter, insect-pollinated flowers (Jacobi and Do Carmo 2011). Following the phylogeny of *Tripodanthus* (Amico et al., 2012), the ornithophilous, orange-red corollas of *T. belmirensis* are therefore interpreted as autapomorphic, derived from the entomophilous condition present in its sister species.

Embryological traits of *Tripodanthus belmirensis*. In general, our observations on *Tripodanthus belmirensis* align with those reported for its congeners by Cocucci and Venturelli (1982), Venturelli (1983), and Forstreuter and Weber (1991), particularly with respect to the trilocular ovary surrounded by a massive viscin layer, the formation of a single ovule per locule, the morphology of the single viable embryo, and the compound hexagonal endosperm (Figs. 3- 5).

Full development of a single embryo and a massive compound endosperm, and the occurrence of vestigial, non-viable and arrested proembryos (Fig. 5E, F), is here detected for the first time in *Tripodanthus*. Similar observations are limited to two New World genera of Loranthaceae, namely, *Ligaria* (as *Psittacanthus*; Bhatnagar and Chandra, 1968) and *Tristerix* (as *Phrygilanthus*, Reiche, 1904; González and Pabón-Mora, 2017b, 2018). Conversely, these embryological traits are widely known in numerous Old World representatives of four families of Santalales. Within Loranthaceae, these have been documented in species of *Amyema* (Schaeppi and Steindl, 1942; Dixit, 1958a), *Atkinsonia* (Garg, 1958; Prakash, 1961), *Barathranthus* (Schaeppi and Steindl, 1942; Prakash, 1963), *Dendrophthoe* (Singh, 1952; Narayana, 1954, 1956), *Helicanthes* (Johri and Agrawal, 1954; Johri et al. 1957), *Helixanthera* (Maheshwari and Johri, 1950), *Lepeostegeres* (Dixit 1955, 1958b), *Lysiana* (Narayana, 1958a), *Macrosolen* (as *Loranthus*, Treub, 1885; Maheshwari and Singh, 1952), *Nuytsia* (Van Tieghem, 1898; Narayana, 1958b), *Peraxilla* (Prakash, 1960), *Tapinanthus* (as *Loranthus*; Pienaar, 1951), *Taxillus* (Schaeppi and Steindl, 1942; Subrahmanyam et al., 2015), *Tolypanthus* (Dixit, 1961), and *Tupeia* (Van Tieghem 1895b; Smart, 1952). Comparable patterns also occur in Olacaceae (species of *Olax* and *Strombosia*; Agarwal, 1961, 1963a, 1963b), in Santalaceae (species of *Arceuthobium, Exocarpos, Ginalloa, Leptomeria, Mida, Osyris, Santalum, Scleropyrum* and *Thesium*; Johnson, 1888; Van Tieghem, 1895a, 1895b; Rao, 1942; Bhatnagar, 1959, 1960; Ram, 1959a, 1959b; Bhatnagar and Agarwal, 1961; Jones and Gordon, 1965; Sedgley, 1982; Ma et al., 2006), and in Viscaceae (species of *Dendrophthora, Kortharsella, Phoradendron* and *Viscum*; Jost, 1888; Van Tieghem, 1895b; Billings, 1933; Stevenson, 1935).

Kuijt and Hansen (2015) described the presence of endosperm in *Tripodanthus* as a distinguishing trait separating it from the closely related genera *Aetanthus* and *Psittacanthus*, which were though to lack endosperm. However, this diagnostic trait should be reconsidered, as the presence of endosperm in species of both of these latter genera has now been documented (Engler and Krause, 1935; González and Pabón-Mora 2017b, 2018; Botero-Castaño et al., 2026).

Ecological role of *Tripodanthus belmirensis*. This report increases to 19 the number of species known to contribute fruits or seeds to the diet of the Indigo-winged parrot, *Hapalopsittaca fuertesi* (Psittacidae: Arinae), a species endemic to the Central Cordillera of Colombia and considered as critically endangered. Five of these species (the Loranthaceae *Gaiadendron punctatum* and *Tripodanthus belmirensis*; the Santalaceae *Antidaphne andina* and *A. viscoidea*, Santalaceae; and the Viscaceae *Dendrophthora* sp.) are mistletoes native to the Colombian flora (González and Pabón-Mora, 2023). Collectively, these mistletoes represent the primary lineage of flowering plants in the diet of *H. fuertesi* (Díaz-González et al., 2024). Among them, *Tripodanthus belmirensis* produces the largest fruits in the region. It is also likely that *Tristerix longibracteatus* (Loranthaceae), another mistletoe species inhabiting the study area (González and Pabón-Mora 2017a, 2019) also contributes to the parrot diet, as its fruits are even larger than those of *T. belmirensis*. Notably, mistletoe viscin is rich in proteins, polysaccharides (especially glucose, xylose and arabinose), and uronic acids (Geladovich-Shedletsky et al., 1988; E. 1989), and can constitute up to 42 % of the epicarp (Geladovich-Shedletsky et al., 1988). Our observations suggest that *Tripodanthus belmirensis* fruits contain remarkably high levels of viscin, accounting for 70–80 % of the fruit, and approaching 90 % when the starch-rich endosperm is considered (Fig. 5A–C).

Given the dual ecological role of birds as primary pollinators or dispersers of mistletoes, it is worth investigating whether dispersal is less

constrained than pollination in *Tripodanthus* and other large-flowered New World mistletoes, as has been reported for New Zealand Loranthaceae (Kelly et al., 2004).

Finally, we incidentally observed significant floral damage on the corolla tube of *Tripodanthus belmirensis* prior to anthesis, consisting of randomly distributed punctures caused by the larvae of an unidentified coleopteran species (not shown) that feed on the floral tissues. Because this type of damage can destroy the anthers, it warrants detailed study to assess its impact on floral viability.

5. Conclusion

In summary, our study provides the first comprehensive account of flower and fruit morphology, anatomy, and development in *Tripodanthus belmirensis*, placing this species in a comparative framework with its congeners. *T. belmirensis* retains the plesiomorphic floral architecture typical of *Tripodanthus* and other members of Loranthaceae, such as a uniseriate corolla and androecium, epipetalous stamens, and an inferior ovary surrounded by a massive viscin layer. Conversely, it also exhibits distinctive features, including fenestrate anthesis and an ornithophilous floral syndrome, that set it apart from its primarily entomophilous sister species. Embryologically, the confirmation of a single functional embryo accompanied by a massive compound endosperm and vestigial proembryos strengthens developmental parallels with other New World genera while aligning *Tripodanthus* with broader patterns documented across Santalales. These structural and developmental traits clarify key aspects of reproductive biology, such as pollination mode, breeding system, seed development, and dispersal potential, and refine character interpretations within Psittacanthinae and Loranthaceae. By integrating floral, embryological, and ecological data, this work establishes a robust framework for future studies addressing the evolution of pollination syndromes, developmental convergence, host–parasite interactions, and the conservation significance of *T. belmirensis*, particularly in light of its role in sustaining threatened Andean frugivores.

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Declaration of generative AI use

Authors declare no use of generative AI in the manuscript preparation process upon submission of the paper.

CRediT authorship contribution statement

Favio González: Formal analysis, Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Estefanía Elejalde-Baena:** Data curation, Formal analysis, Methodology. **Sthepany Quintero-García:** Methodology, Investigation, Formal analysis, Data curation. **María Clara Díaz-González:** Methodology, Investigation, Formal analysis, Data curation. **Natalia Pabón-Mora:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation.

Declaration of competing interest

The authors declare no conflict of interest.

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Data availability

No data was used for the research described in the article.

References

Agarwal, S.J., 1961. The embryology of *Strombosia* Blume. Phytomorphology 11, 269–272.
Agarwal, S.J., 1963a. Morphological and embryological studies in the family olacaceae. I. *Olax* L. Phytomorphology 13, 185–196.
Agarwal, S.J., 1963b. Morphological and embryological studies in the family Olacaceae. II. *Strombosia* Blume. Phytomorphology 13, 348–356.
Aizen, M.A., 2003. Down-facing flowers, hummingbirds and rain. Taxon. 52, 675–680.
Aizen, M.A., 2005. Breeding system of *Tristerix corymbosus* (Loranthaceae), a winter-flowering mistletoe from the southern Andes. Aust. J. Bot. 53, 357–361. https://doi.org/10.1071/BT04088.
Aluri, R.J.S., Subba Redi, S., 1995. Explosive pollen release and pollination in flowering plants. Proc. Indian Natl. Sci. Acad. B61, 323–332.
Amico, G.C., Vidal-Russell, R., García, M.A., Nickrent, D.L., 2012. Evolutionary history of the South American mistletoe *Tripodanthus* (Loranthaceae) using nuclear and plastid markers. Syst. Bot. 37, 218–225. https://doi.org/10.1600/036364412x616783.
Amico, G.C., Vidal-Russell, R., Nickrent, D.L., 2007. Phylogenetic relationships and ecological speciation in the mistletoe *Tristerix* (Loranthaceae): the influence of pollinators, dispersers, and hosts. Amer. J. Bot. 94, 558–567. https://doi.org/10.3732/ajb.94.4.558.
Azpeitia, F., Lara, C., 2006. Reproductive biology and pollination of the parasitic plant *Psittacanthus calyculatus* (Loranthaceae) in central México. J. Torrey Bot. Soc. 133, 429–438.
Bernhard, P., Knox, R.B., Calder, D.M., 1980. Floral biology and self-incompatibility in some Australian mistletoes of the genus *Amyema* (Loranthaceae). Aust. J. Bot. 28, 437–451. https://doi.org/10.1071/BT9800437.
Bhatnagar, S.P., 1959. Some observations on the post-fertilization development of the embryo sac of *Santalum*. Phytomorphology 9, 87–91.
Bhatnagar, S.P., 1960. Morphological and embryological studies in the family Santalaceae – IV *Mida salicifolia*. Phytomorphology 10, 198–207.
Bhatnagar, S.P., Agarwal, S., 1961. Morphological and embryological studies in the family Santalaceae – VI *Thesium* L. Phytomorphology 11, 273–282.
Bhatnagar, S.P., Chandra, S., 1968. Endosperm in *Psittacanthus*. Curr. Sci. 24, 704–706.
Bhatnagar, S.P., Johri, B.M., 1983. Embryology of the Loranthaceae. In: Calder, M., Bernhardt, P. (Eds.), The Biology of Mistletoes. Academic Press, Sydney, pp. 47–67.
Biezanko, C.M., 1958. Pieridae da Zona Sueste do Rio Grande do Sul (Contribuição ao conhecimento da fisiografia do Rio Grande do Sul). Arq. Entomol. Esc. Agron. "Eliseu Maciel" Pelotas, Ser. A. Ib 1–15.
Billings, F.H., 1933. Development of the embryo-sac in *Phoradendron*. Ann. Bot. 47, 261–278.
Blakely, W.F., 1922. The Loranthaceae of Australia. Proc. Linn. Soc. New South Wales 47 (1–25), 199–222, 391-414.
Botero-Castaño, V., González, F., Pabón-Mora, N., 2026. Morphological and anatomical changes during the flower-to-fruit transition in Andean species of the parasitic family Loranthaceae. Intl. J. Plant Sci. 187 (3), 1–10.
Braby, M.F., Nishida, K., 2010. The immature stages, larval food plants and biology of neotropical mistletoe butterflies (Lepidoptera: pieridae). II. The *Catasticta* group (Pierini: aporiina). J. Nat. Hist. 44 (29–30), 1831–1928.
Calvin, C.L., Wilson, C.A., 2006. Comparative morphology of epicortical roots in Old and New World Loranthaceae with reference to root types, origin, patterns of longitudinal extension and potential for clonal growth. Flora 201, 51–64.
Cocucci, A.E., Venturelli, M., 1982. El óvulo y el gineceo en Loranthaceae. Bol. Soc. Argent. Bot. 21, 131–141.
Dettke, G.A., Waechter, J.L., 2014. Estudo taxonômico das ervas-de-passarinho da Região sul do Brasil: I. Loranthaceae e santalaceae (taxonomic study of mistletoes from South Brazil: I. Loranthaceae and Santalaceae). Rodriguésia 65, 939–953. https://doi.org/10.1590/2175-7860201465408.
Díaz-González, M.C., Soler-García de Oteyza, E., Noreña-Tobón, J.C., Espitia-Pachón, D. F., Quintero-García, S., Sánchez-Salazar, A., Zamora-Padrón, R., 2024. Seis especies de plantas nuevas para la dieta de la cotorra aliazul (*Hapalopsittaca fuertesi*), especie endémica de Colombia en riesgo de extinción. Ornitología Colombiana 25, 25–32. https://doi.org/10.59517/oc.e578.
Dixit, S.N., 1955. The embryology of *Lepeostegeres gemminiflorus* Bl. Curr. Sci. 8, 278–279.
Dixit, S.N., 1958a. Morphological and embryological studies in the family Loranthaceae - IV. *Amyema* van Tiegh. Phytomorphology 8, 346–364.
Dixit, S.N., 1958b. Morphological and embryological studies in the family Loranthaceae - V. *Lepteostegeres gemminiflorus* (Bl.) bl. Phytomorphology 8, 365–376.
Dixit, S.N., 1961. Morphological and embryological studies in the family Loranthaceae - VIII. *Tolypanthus* Bl. Phytomorphology 11, 335–345.
Docters van Leeuwen, V.M., 1954. On the biology of some Javanese Loranthaceae and the role birds play in their life-story. Beaufortia 4, 105–208.
Eichler, A.W., 1868. Loranthaceae. In: von Martius, C.F.P. (Ed.), Flora Brasiliensis 3(1). Wilhelm Engelmann, Leipzig, pp. 156–198.
Engler, A., Krause, K., 1935. Loranthaceae. In: Engler, A., Prantl, K. (Eds.), Die Natürlichen Pflanzenfamilien, 2 Aufl. 16b. Wilhelm Engelmann, Leipzig, pp. 98–203.

Evans, M.S., 1895. The fertilisation of "*Loranthus krausianus* and "*L. dregei*.". Nature 51, 235.
Feehan, J., 1985. Explosive flower opening in ornithophily: a study of pollination mechanisms in some Central African Loranthaceae. Bot. J. Linn. Soc. 90, 129–144. https://doi.org/10.1111/j.1095-8339.1985.tb02205.x.
Forstreuter, W., Weber, H.C., 1991. Untersuchungen zur morphologie und anatomy des Embryos und des Keimlings von *Tripodanthus acutifolius* (Ruiz & Pav.) Tiegh. (Loranthaceae). Flora 185, 153–164.
Galetto, L., Bernardello, L., Juliani, H.R., 1990. Acerca del nectario, néctar y visitantes florales en *Ligaria cuneifolia* (Loranthaceae). Darwiniana 30, 155–161. http://www.jstor.org/stable/23222525.
Galván-González, L.G., Cerros-Tlatilpa, R., Espejo-Serna, A., Steinmann, V.W., 2024. Phylogenetic relationships of the genera *Cladocolea* and *Struthanthus* (Loranthaceae) with emphasis on the Mexican species. Syst. Bot. 49, 396–411. https://doi.org/10.1600/036364424x17194277229601.
Garg, S., 1958. Embryology of *Atkinsonia ligustrina* (A. Cunn. Ex F. Muell.) F. Muell. Nature 182, 1615–1616.
Geladovich-Shedletsky, E., Kuijt, J., Carpita, N.C., 1988. Chemical composition of viscin, an adhesive involved in dispersal of the parasite *Phoradendron californicum* (Viscaceae). Phys. Mol. Plant Path. 32, 61–76.
Geladovich-Shedletsky, E., Delmer, D.P., Kuijt, J., 1989. Chemical composition of viscin mucilage from three mistletoe species—a comparison. Ann. Bot. 64, 249–252.
González, F., Pabón-Mora, N., 2017a. Inflorescence and floral traits of the Colombian species of *Tristerix* (Loranthaceae) related to hummingbird pollination. Anal. Jard. Bot. Madrid. 74, e061.
González, F., Pabón-Mora, N., 2017b. On the supposed polycotyledony and lack of endosperm in *Psittacanthus* (Loranthaceae). Brittonia 69, 176–185. https://doi.org/10.1007/s12228-017-9461-9.
González, F., Pabón-Mora, N., 2018. On embryo polarity, polycotyly, and the homology test of conjunction: a reply to Kuijt's (2017) critique. Brittonia 70, 150–154. https://doi.org/10.1007/s12228-017-9503-3.
González, F., Pabón-Mora, N., 2019. Flower development of *Tristerix* confirms irregular calyx formation and obhaplostemony as plesiomorphies in New World Loranthaceae (Santalales). Intl. J. Plant Sci. 180, 403–410. https://doi.org/10.1086/703263.
González, F., Pabón-Mora, N., 2023. The remarkable diversity of parasitic flowering plants in Colombia. Bot. Rev. 89, 331–385. https://doi.org/10.1007/s12229-023-09294-w.
González, F., Suaza-Gaviria, V., Pabón-Mora, N., 2021. Floral development and morphology of the mistletoe *Antidaphne viscoidea*: a case of extreme flower reduction in the sandalwood family (Santalaceae). Aust. J. Bot. 69, 152–161. https://doi.org/10.1071/BT21010.
Grímsson, F., Kapli, P., Hofmann, C.-C., Zetter, R., Grimm, G.W., 2017. Eocene Loranthaceae pollen pushes back divergence ages for major splits in the family. PeerJ. 5, e3373. https://doi.org/10.7717/peerj.3373.
Heide-Jørgensen, H.S., 2008. Parasitic Flowering Plants. Brill, Leiden, Netherlands. https://doi.org/10.1163/ej.9789004167506.i-438.
IUCN Standards and Petitions Committee, 2022. Guidelines for using the IUCN red list categories and criteria. Version 15.1. Prep. Stand. Petitions Comm. [Last accessed 19 March 2025] https://www.iucnredlist.org/documents/RedListGuidelines.pdf.
Jacobi, C.M., Fonseca do Carmo, F., 2011. Life-forms, pollination and seed dispersal syndromes in plant communities on ironstone outcrops, SE Brazil. Acta Bot. Bras. 25, 395–412.
Johansen, D.A., 1940. Plant Microtechnique. McGraw-Hill, New York.
Johnson, T., 1888. *Arceuthobium oxycedri*. Ann. Bot. 2, 137–160.
Johri, B.M., 1963. Embryology and taxonomy. In: Maheshwari, P. (Ed.), Recent Advances in the Embryology of angiosperms. International Society of Plant Morphologists. University of Delhi, India, pp. 395–444.
Johri, B.M., Agrawal, J.S., 1954. Morphology and embryology of *Helicanthes elastica* (Desr.) Dans. Curr. Sci. 3, 96–98.
Johri, B.M., Agrawal, J.S., Garg, S., 1957. Morphological and embryological studies in the family Loranthaceae. – I. *Helicanthes elastica* (Desr.) Dans. Phytomorphology 7, 336–354.
Jones, B.L., Gordon, C.C., 1965. Embryology and development of the endosperm haustorium of *Arceuthobium douglasii*. Amer. J. Bot. 52, 127–132.
Jost, L., 1888. Zur kenntnis der Blüthenentwickelung der Mistel. Bot. Zeit. 46, 357–372.
Kelly, D., Ladley, J.J., Robertson, A.W., 2004. Is dispersal easier than pollination? Two tests in New Zealand Loranthaceae. N. Z. J. Bot. 42, 89–103.
Kirkup, D., 1998. Pollination mechanisms in African loranthaceae. In: Polhill, R., Wiens, D. (Eds.), Mistletoes of Africa. Royal Botanic Gardens, Kew, pp. 37–60.
Kuijt, J., 1982. Epicortical roots and vegetative reproduction in Loranthaceae (s.s.) of the New World. Beitr. Biol. Pfl. 56, 307–316.
Kuijt, J., 1986. Eremolepidaceae, Loranthaceae and Viscaceae. In: Harling, G., Sparre, B. (Eds.), Flora of Ecuador, Flora of Ecuador, 24. Swedish Research Councils, Stockholm, pp. 1–197.
Kuijt, J., 1989. Additional notes on the parasitism of New World Loranthaceae. Beitr. Biol. Pfl. 64, 115–125.
Kuijt, J., Hansen, B., 2015. Loranthaceae. In: Kubitzki, K. (Ed.), The Families and Genera of Vascular Plants. Vol 12. Flowering Plants. Eudicots: Santalales, Balanophorales. Springer International Publishing, Cham, pp. 73–119. https://doi.org/10.1007/978-3-319-09296-6.
Ladley, J.J., Kelly, D., 1996. Dispersal, germination and survival of New Zealand mistletoes (Loranthaceae): dependence of birds. N. Z. J. Ecol. 20, 69–79.
Ladley, J.J., Kelly, D., Robertson, A.W., 1997. Explosive flowering, nectar production, breeding systems, and pollinators of New Zealand mistletoes (Loranthaceae). N. Z. J. Bot. 35, 345–360. https://doi.org/10.1080/0028825X.1997.10410160.
Liu, B., Le, C.T., Barrett, R.L., Nickrent, D.L., Chen, Z., Lu, L., Vidal-Russell, R., 2018. Historical biogeography of Loranthaceae (Santalales): diversification agrees with emergence of tropical forests and radiation of songbirds. Mol. Phylog. Evol. 124, 199–212. https://doi.org/10.1016/j.ympev.2018.03.010.
Ma, G.-H., Bunn, E., Zhang, J.-F., Wu, G.-J., 2006. Evidence of dichogamy in *Santalum album*. L. J. Integr. Pl. Biol. 48, 300–306.
Maheshwari, P., Johri, B.M., 1950. Development of the embryo sac, embryo and endosperm in *Helixanthera ligustrina* (Wall.) Dans. Nature 165, 978–979.
Maheshwari, P., Johri, B.M., Dixit, S.N., 1957. The floral morphology and embryology of the Loranthoideae (Loranthaceae). J. Madras. Univ. 27, 121–136.
Maheshwari, P., Singh, B., 1952. Embryology of *Macrosolen cochinchinensis*. Bot. Gaz. 114, 20–32.
Narayana, R., 1954. Contribution to the embryology of *Dendrophthoe* Mart. Phytomorphology 4, 173–179.
Narayana, R., 1956. Morphological and embryological studies in the Loranthaceae-Loranthoideae. III. *Dendrophthoe neelgherrensis* (W. & A.) van Tiegh. J. Mysore Univ. 16, 185–205.
Narayana, R., 1958a. Morphological and embryological studies in the family Loranthaceae. II. *Lysiana exocarpi* (Behr.) Van Tieghem. Phytomorphology 8, 146–168.
Narayana, R., 1958b. Morphological and embryological studies in the Loranthaceae – III. *Nuytsia floribunda* (Labill.) R. Br. Phytomorphology 8, 306–323.
Nickrent, D.L., Malécot, V., Vidal-Russell, R., Der, J.P., 2010. A revised classification of Santalales. Taxon 59, 538–558.
Pienaar, R., de, V., 1951. The origin and development of the embryo sac and young embryo of *Loranthus rubromarginatus* Engler. Trans. R. Soc. S. Afr. 33, 223–237. https://doi.org/10.1080/00359195109519885.
Prakash, S., 1960. Morphological and embryological studies in the family Loranthaceae - VI. *Peraxilla tetrapetala* (Linn. f.) van Tiegh. Phytomorphology 10, 224–234.
Prakash, S., 1961. Morphological and embryological studies in the family Loranthaceae - VII. *Atkinsonia ligustrina* (Cunningh.) F v. Muell. Phytomorphology 11, 325–335.
Prakash, S., 1963. Morphological and embryological studies in the family Loranthaceae - X. *Barathranthus axanthus* (Korth.) Miq. Phytomorphology 13, 97–103.
Ram, M., 1959a. Morphological and embryological studies in the family Santalaceae – II. *Exocarpus*, with a discussion on its systematic position. Phytomorphology 9, 4–19.
Ram, M., 1959b. Morphological and embryological studies in the family Santalaceae – III. *Leptomeria* R. Br. Phytomorphology 9, 20–33.
Rao, L.N., 1942. Studies in the Santalaceae. Ann. Bot. 6, 150–175.
Reiche, K., 1904. Bau und Leben der chilenischen Loranthacee *Phrygilanthus aphyllus*. Flora 93, 271–297.
Remillet, M., 1988. Catalogue Des Insectes Ravageurs Des Cultures En Guyane Française. ORSTOM, Paris (France).
Restrepo, C., Sargent, C., Levey, D.J., Watson, D.M., 2002. The role of vertebrates in the diversification of New World mistletoes. In: Levey, D.J., Silva, W.R., Galetti, M. (Eds.), Seed Dispersal and Frugivory: Ecology, Evolution and Conservation. CABI Publishing, Wallingford, UK, pp. 83–98.
Rivera, G.L., Galetto, L., Bernardello, L., 1996. Nectar secretion pattern, removal effects, and breeding system of *Ligaria cuneifolia* (Loranthaceae). Can. J. Bot. 74, 1996-2001.
Rizzini, C.T., 1952. Pars generalis prodromi monographiae Loranthacearum brasiliae terrarumque finitinarum. Arq. Jard. Bot. Rio de Janeiro 12, 39–126.
Robertson, A.W., Kelly, D., Ladley, J.J., Sparrow, A.D., 1999. Effects of pollinator loss on endemic New Zealand mistletoes (Loranthaceae). Conserv. Biol. 13, 499–508. http://www.jstor.org/stable/2641864.
Roldán, F.J., Kuijt, J., 2005. A new red-flowered species of *Tripodanthus* (Loranthaceae) from Colombia. Novon 15, 207–209.
Schaeppi, H., Steindl, F., 1942. Blütenmorphologische und embryologische Untersuchungen an Loranthoideen. Viert. Naturf. Gesel. Zürich 87, 301–372.
Sedgley, M., 1982. Floral anatomy and pollen tube growth in the Quandong *(Santalum acuminatum* (R. Br.) A. DC.). Aust. J. Bot. 30, 601–609.
Singh, B., 1952. A contribution to the floral morphology and embryology of *Dendrophthoe falcata* (L. f.) Ettingsh. Bot. J. Linn. Soc. 53, 449–473. https://doi.org/10.1111/j.1095-8339.1952.tb01557.x.
Smart, C., 1952. The life history of *Tupeia* Cham. Et schl. (Loranthaceae). Trans. R. Soc. N. Z. 79, 459–466.
Stevenson, G.B., 1935. The life history of the New Zealand species of the parasitic genus *Kortharsella*. Trans. Proceed. Royal Soc. N. Z. 64, 175–190.
Su, H.-J., Hu, J.-M., Anderson, F.E., Der, J.P., Nickrent, D.L., 2015. Phylogenetic relationships of Santalales with insights into the origins of holoparasitic balanophoraceae. Taxon 64, 491–506. https://doi.org/10.12705/643.2.
Suaza-Gaviria, V., González, F., Pabón-Mora, N.L., 2017. Comparative inflorescence development in selected Andean Loranthaceae and Viscaceae. Amer. J. Bot. 104, 1–15. https://doi.org/10.3732/ajb.1600253.
Suaza-Gaviria, V., Pabón-Mora, N., González, F., 2016. Development and morphology of flowers in Loranthaceae. Intl. J. Plant Sci. 177, 559–578. https://doi.org/10.1086/687280.
Subrahmanyam, P., Rama Gopal, G., Pullaiah, T., 2015. Embryology of *Taxillus heyneanus* (Schult.f.) Danser (Loranthaceae). Intl. J. Plant Reprod. Biol. 7, 147–152.
Treub, M., 1885. Observations sur les Loranthaceés. Annal. Jard. Bot. Buitenzorg 2, 54–76.
Van Tieghem, P., 1895a. Sur le genre *arceuthobium* considéré comme type dune tribu distincte dans la famille des Loranthacées. Bull. Soc. Bot. France 42, 625–642.
Van Tieghem, P., 1895b. Sur la structure et les affinités des *tupeia, Ginalloa, Phoradendron* et *Dendrophthora*, de la famille des loranthacées. Bull. Soc. Bot. France 42, 643–652.
Van Tieghem, P., 1898. Structure du fruit, germination, et structure de la plantula de la nuytsie. Bull. Soc. Bot. France 45, 213–220.

Venturelli, M., 1983. Estudos embriologicos em Loranthaceae: gênero *Tripodanthus*. Kurtziana 16, 71–90.
Vidal-Russell, R., Nickrent, D.L., 2008. Evolutionary relationships in the showy mistletoe family (Loranthaceae). Amer. J. Bot. 95, 1015–1029. https://doi.org/10.3732/ajb.0800085.
Watson, D.M., 2001. Mistletoe—a keystone resource in forests and woodlands worldwide. Annu Rev. Ecol. Syst. 32, 219–249.
Weberling, F., 1981. Morphology of Flowers and Inflorescences. Cambridge University Press, Cambridge, UK.
Werth, E., 1915. Kurzer Überblick über die gesamtfrage der Ornithophilie. Bot. Jahrb. 53, 314–378.
Wilson, C.A., Calvin, C.L., 2006a. An origin of aerial branch parasitism in the mistletoe family. Loranthaceae. Amer. J. Bot. 95, 787–796. https://doi.org/10.1111/j.1095-8339.2006.00488.x.
Wilson, C.A., Calvin, C.L., 2006b. Character divergences and convergences in canopy-dwelling Loranthaceae. Bot. J. Linn. Soc. 150, 101–113.
Yumoto, T., Itino, T., Nagamasu, H., 1997. Pollination of hemiparasites (Loranthaceae) by the spider hunters (Nectariniidae) in the canopy of a Bornean tropical rain forest. Selbyana 18, 51–60. http://www.jstor.org/stable/41759942.