DEVELOPMENT AND MORPHOLOGY OF FLOWERS IN LORANTHACEAE

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Premise of research.   Loranthaceae flowers exhibit exceedingly variable ground plan, size, and pollination syndromes. The homology of floral organs (especially the calyculus and the perianth), the evolutionary shifts from bisexual to unisexual flowers, and the trends in ovary and ovule reduction, primarily studied in Old World taxa, have been controversial. We investigate the development and morphoanatomy of early- and late-diverging Neotropical lineages with broad floral diversity to test organ homology and postulate floral plesiomorphies and apomorphies throughout the family.

Methodology.   We examined eight species from six genera, all native to the Colombian Andes. Standard LM and SEM methods were used.

Pivotal results.   All species studied exhibit bisexual flowers, but partial or total stamen sterilization was observed in the small-flowered *Passovia pyrifolia* and *Peristethium archeri*. All flowers examined possess an irregular calyx developed from a ring primordium, distinct from the four to seven petals initially free but postgenitally fused, and four to seven epipetalous stamens. Additionally, a cupular pedicel is present, either free from the calyx in *Aetanthus* and *Psittacanthus* or fused to the calyx in *Passovia*. Polysporangiate anthers were detected in *Aetanthus mutisii*; they dehisce prior to anthesis, which suggests cleistogamy. The ovary is six- or seven-chambered in *Gaiadendron punctatum*, but it is variously reduced or even solid in the remaining taxa.

Conclusions.   Plesiomorphies in the family include sessile, bisexual flowers lacking a cupular pedicel; an irregularly developed, distinct calyx; free, simultaneous petal primordia; versatile and tetrasporangiate anthers; and an ovary with six or seven locules and mamelons. The cupular pedicel is apomorphic in some Psittacanthinae genera. Other apomorphies include the basifixed, polysporangiate anthers with preanthetic dehiscence in *A. mutisii*. Unisexual flowers are homoplasious and linked to small-flowered taxa; anther sterilization occurs by either reduction in the number of sporangia or a proliferating endothecium. The modification of the ovary across Loranthaceae likely reflects pseudomonomery.

Keywords: *Aetanthus*, flower development, flower anatomy, *Gaiadendron*, *Oryctanthus*, *Psittacanthus*, hemiparasitic plants, Loranthaceae, *Passovia*, *Peristethium*, Santalales.

Introduction

Of the 12 families currently recognized in the order Santalales, the Loranthaceae Juss. (77 genera and ca. 950 hemiparasitic spp.) is the most diversified and successful family worldwide (Heide-Jørgensen 2008; Kuijt 2015). Flowers in the family, primarily bisexual and with inferior ovary, exhibit several traits that are highly variable, such as the presence or absence of a calyculus; the shape of the calyx; the shape, size, color, and number of petals; the number and relative size of stamens; and the variously reduced ovary-ovule complex. Flower length in the family ranges from 2 mm in *Passovia* spp. to 22 cm or more in *Aetanthus* spp. Perianth color, size, and shape have also been

linked to shifts from entomophily in small-flowered taxa to ornithophily in large-flowered taxa.

Some of these traits, including the atypical embryological modifications in most members of the Loranthaceae and allied families of the order Santalales, have been pivotal to the taxonomy of the order (Johri 1963; Johri et al. 1992). However, flower morphology has been examined in more detail in African, Asian, and Australian taxa, compared to Neotropical taxa (Schaeppi and Steindl 1942; Maheshwari and Johri 1950; Singh 1952; Smart 1952; Narayana 1956; Maheshwari et al. 1957; Johri 1963; Johri et al. 1992, among others). The goal of our research is to investigate the flower development, morphology, and anatomy in Neotropical species with small, medium-sized, and large flowers that exhibit variation on all floral traits mentioned above. Particular attention will be given to the overlooked or ambiguously interpreted features, such as the calyculus and the sporangiate condition of the anthers. Both have been used as tax-

onomic characters since the early classification of the family by Eichler (1868, 1878) and Van Tieghem (1893, 1894, 1895), among others, as well as in the modern systems based on Barlow (1964).

Material and Methods

We selected eight Neotropical species from six genera exhibiting different floral traits with respect to the floral size; the presence or absence of a calyculus; the gross morphology and organ number of calyx, corolla, and androecium; and the presence or absence of locules at the level of the ovary. All vouchers were collected in Colombia and deposited at the herbaria COL and HUA: *Aetanthus mutisii* Engl.: Boyacá, Sogamoso, 3360 m, 1 Feb 2013, *González 4480*; *Gaiadendron punctatum* G. Don: Boyacá, Villa de Leyva, Iguaque, 3300 msnm, 10 May 2008, *González 4314*; *Oryctanthus callicarpus* Kuijt: Antioquia, Urrao, 1098 m, 30 Jul 2013, *Idárraga 5396*; *Passovia pedunculata* (Jacq.) Kuijt: Santander, Piedecuesta, Pescadero, 760 m, 25 May 2008, *González 4324*; *Passovia pyrifolia* (Kunth) Tiegh.: Antioquia, Medellín, 1800 m, 13 Dec 2013, *Suaza-Gaviria 03*; *Peristethium archeri* (A. C. Sm.) Kuijt: Antioquia, Parque Arví, 2000 m, 4 Apr 2015, *Pabón-Mora 353*; *Psittacanthus acinarius* (Martius) Martius: Casanare, Tauramena, 260 m, 23 Dec 2007, *González 4282*; *Psittacanthus krameri* Kuijt: Antioquia, San Carlos, 1000 m, 7 Oct 2014, *Suaza-Gaviria 11*, 7 Jan 2016, *Suaza-Gaviria 12*.

SEM. Flowers in several developmental stages were fixed in 70% ethanol. For SEM studies, buds were dissected in 90% ethanol under a Zeiss Stemi DV4 stereoscope and then dehydrated in an absolute ethanol series (90%, 95%, and 100% × 2 ethanol, 30 min each). Dehydrated material was then critical-point dried using a Balzers 790 CPD (Balzers, Liechtenstein), coated with gold and palladium in a Hummer 6.2 sputter-coater, and examined using a JEOL (Tokyo) JSM-5410 LV SEM at 10 kV.

LM. Fixed material was dehydrated through an alcohol-toluene series in a Leica TP-1020 automatic tissue processor and embedded in Paraplast X-tra (Fisher Healthcare, Houston) using an AP 280 Microm (Thermo Fisher Scientific, Waldorf, Germany) tissue-embedding center. The samples were sectioned at 12 μm with an AO Spencer 820 (GMI, Ramsey, MN) rotary microtome. Sections were stained with two alternative protocols. One used Johansen's safranin and 0.5% astra blue in 2% tartaric acid w/v in distilled water. The second was based on a mix of Johansen's safranin and alcian blue (Tolivia and Tolivia 1987). Last, slides were permanently mounted in Permount (Fisher Scientific, Pittsburgh). Sections were viewed and digitally photographed with a Nikon Eclipse 80i compound microscope equipped with a Nikon DXM1200C digital camera with ACT (1) software.

Results

Large Loranthaceae Flowers: Aetanthus mutisii, Psittacanthus acinarius, *and* Psittacanthus krameri

Aetanthus mutisii. The genus *Aetanthus* comprises 15 species from the northern Andes in South America (Kuijt 2015). Individuals of *A. mutisii* are formed by woody, horizontal, or patent branches up to 1 m long, with pendant, bright red flowers reaching up to 22 cm in length and 4.5 mm in diameter (fig. 1A–1E). Flowers are arranged in numerous ramiflorous dyads (fig. 1A, 1B). A vestigial terminal flower is found in early developmental stages of the inflorescence, which renders the two flowers of the dyad as the lateral flowers of a dichasium (V. Suaza-Gaviria, F. González, and N. Pabón-Mora, unpublished manuscript).

Flower development begins from a more or less radial primordium. The distal portion of the pedicel becomes dilated and cup shaped, hereafter called the cupular pedicel (fig. 2A–2C). This structure is not integrated into the flower at any developmental stage. The calyx initiates as a ring meristem, from which five or six irregular lobes become evident (fig. 2A–2C). Soon after the expansion of the calyx lobes, six petal primordia arise almost simultaneously (fig. 2A, 2B). Six stamen primordia opposing the petals then become apparent (fig. 2D); by this stage, the young petals are massive and thickened at their distal portion. The elongation of each petal is accompanied by the fusion of the corresponding filament (fig. 2D–2F). The gynoecium then initiates as a dome-shaped structure with an asymmetric apex (fig. 2E–2H).

At maturity, the cupular pedicel turns purple and reaches 5 mm in length (fig. 1A, 1E). The calyx is greenish, has irregular lobes, and is slightly longer than the cupular pedicel, reaching 6 mm in length (fig. 1A). Petal aestivation is valvate (figs. 1A, 1B, 3C, 3D). During elongation, petal margins superficially interlock through the epidermal cells; thus, sympetaly is late and occurs through postgenital fusion (fig. 3C, 3D). Petals reach 22 cm in length (fig. 1B); during anthesis, petals split only by their short (ca. 3 cm) distal portions, which slightly recurve, exposing the anthers, the tip of the style, and the stigma (fig. 1B, 1D). The six stamens reach almost the same level of the petals; the basifixed anthers are connivent and form a bright yellow anther tube that surrounds the style (figs. 1B–1D, 3E). Individual anthers reach 1.5 cm in length at maturity, including the arrow-shaped base and the tapered apex (figs. 1B–1D, 3E). The filiform style reaches approximately the same length as the petals, and the stigma is capitate and overtops the anther tips (figs. 1B–1D, 3E). Nectar is secreted from a nectarial disk at the base of the corolla but accumulates mostly around the base of the anthers, as flowers are pendant (fig. 1D). By postanthesis, the corolla and the anthers wither, leaving the persistent filiform style completely exposed (fig. 1B).

Floral anatomy. The cupular pedicel possesses a single epidermal layer and a parenchymatous mesophyll (fig. 3A, 3B). Six vascular bundles enter the base of the flower (fig. 3A). The abaxial epidermis of the calyx has some stomata slightly sunken and papillary cells scattered (fig. 3C). The calyx mesophyll is formed by 10–12 layers of parenchymatous cells at its base, of which the four or five adaxial layers are considerably smaller than the remaining cells (fig. 3B, 3C); the mesophyll is reduced to four or five layers of isodiametric cells in the calyx lobes (fig. 3D). The calyx is poorly vascularized, and only a few tracheids were observed (fig. 3A–3C). The petals are massive, with a single-layer epidermis formed by small cuboidal cells; their mesophyll is formed by five or six abaxial layers of large isodiametric parenchymatic cells and five to seven adaxial layers of smaller tangentially elongated cells. Six median vascular bundles enter the common corolla-androecium base, and they radially split into an outer trace running to the tip of each
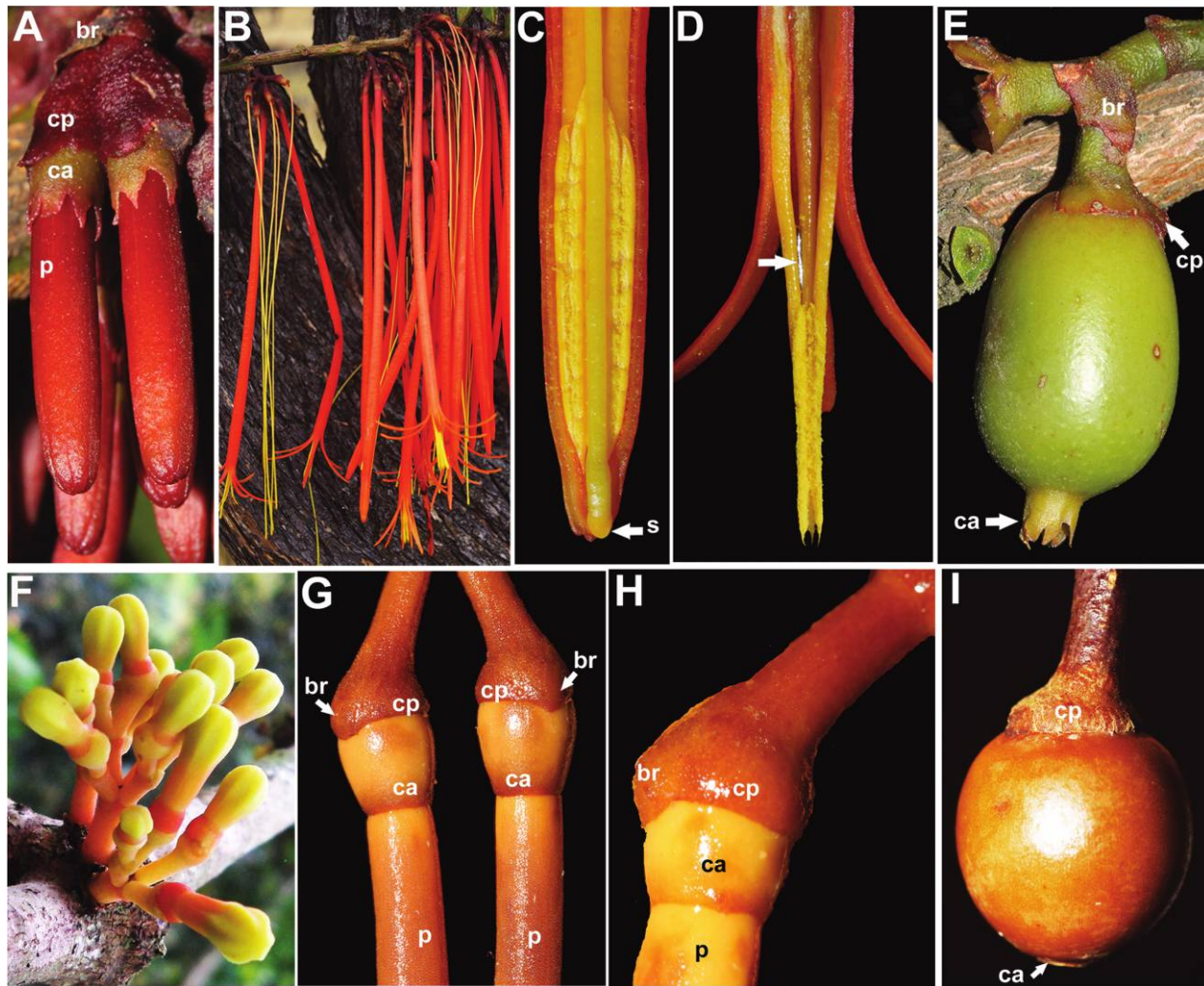
Fig. 1 Large-flowered Loranthaceae studied in this article. *A–E, Aetanthus mutisii. A,* Floral buds. *B,* Flowers at anthesis. *C,* Preanthetic flower showing the polysporangiate anthers surrounding the style. *D,* Anthetic flower with dehiscent anthers; the arrow points to nectar accumulation at the base of the anthers. *E,* Fruit. *F–I, Psittacanthus krameri. F,* Preanthetic flowers. *G, H,* Detail of the bracteole, the cupular pedicel, the calyx, and the corolla base. *I,* Fruit showing the cupular pedicel and the persistent calyx. br = bracteole, ca = calyx, cp = cupular pedicel, p = petal, s = stigma.

petal and an inner trace serving the filament (fig. 3*B*–3*D*). The connective is massive; the anthers are dithecal and tetrasporangiate, but each locule secondarily divides by transverse parenchymatic septa, resulting in polysporangiate anthers at maturity (figs. 1*C*, 3*F*, 3*G*). The apical portion of each anther is tapered and sterile (fig. 3*F*). The anther wall is reduced at maturity to one layer of undifferentiated exothecium, an adjacent single layer of endothecium formed by cuboidal cells with ring-like thickenings, and a single ephemeral middle layer (fig. 3*G*, 3*H*). Anther dehiscence is latrorse and occurs during preanthesis; the stomia of adjacent anthers face each other, and most of the pollen load is released toward the style (figs. 1*C*, 1*D*, 3*E*); pollen grains are already formed by preanthesis (figs. 1*C*, 3*E*, 3*H*, 3*I*). The tapetum is unistratified and secretory, and it is prematurely degraded by preanthesis (fig. 3*G*–3*I*); orbicules are present (fig. 3*I*). A narrow locule was observed in the ovarial region (fig. 3*J*). The epidermis of the style is formed by isodia-

metrical cells similar to those of the stylar mesophyll; three or four vascular bundles are apparent at the midlevel of the style (fig. 3*D*, 3*K*). The capitate stigma is densely covered by small unicellular papillae.

Psittacanthus. The genus *Psittacanthus* consists of approximately 120 species distributed from the southern United States, Mesoamerica, Central America, the Antilles, and most of South America (Kuijt 2009, 2015), being the most diversified genus among the taxa with large flowers. The two species here examined are shrubby, with pendant twigs up to 1 m long. The inflorescences are formed at the distal portions of the twigs in *Psittacanthus acinarius*, whereas in *Psittacanthus krameri* they are also ramiflorous (fig. 1*F*). The bisexual flowers are ultimately organized in dyads (fig. 1*G*). By anthesis, they are patent to pendant. Unlike *Aetanthus*, where anthers remain connivent for most of the anthesis, corolla expansion in *Psittacanthus* during
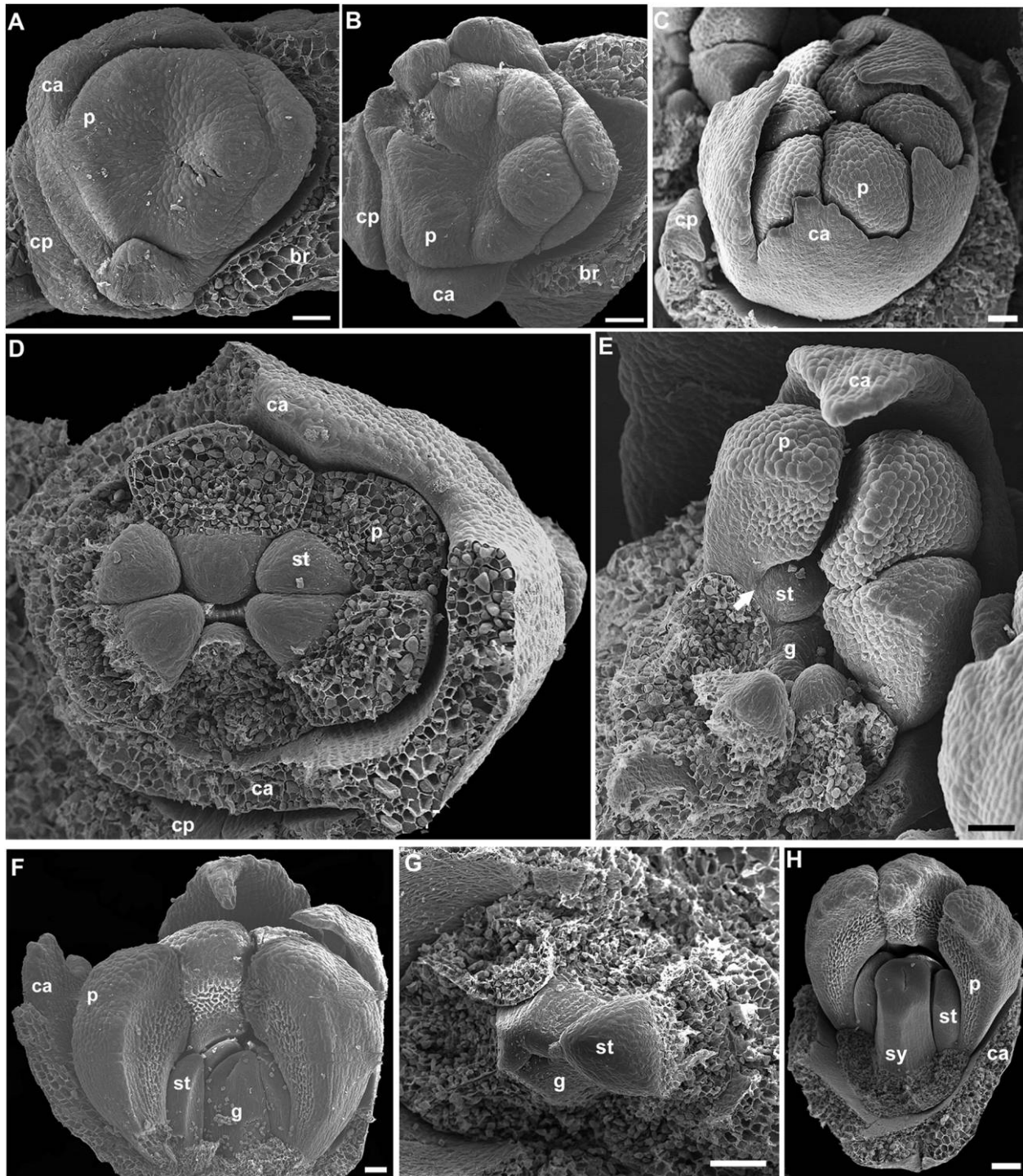
Fig. 2 SEM micrographs of *Aetanthus mutisii*. *A–C*, Successive stages of the developing flower during initiation and elongation of the calyx and the corolla; note the cupular pedicel below the irregularly initiating calyx. *D*, Initiation of stamens. *E*, Floral bud during initiation of gynoecium. *F*, Early elongation of the stamens and the gynoecium; the cupular pedicel is removed. *G, H*, Successive stages of style elongation. Note the asymmetric stigma; the cupular pedicel is removed. Scale bars = 100 μm. br = bracteole, ca = calyx, cp = cupular pedicel, g =gynoecium, p = petal, st = stamen, sy = style.
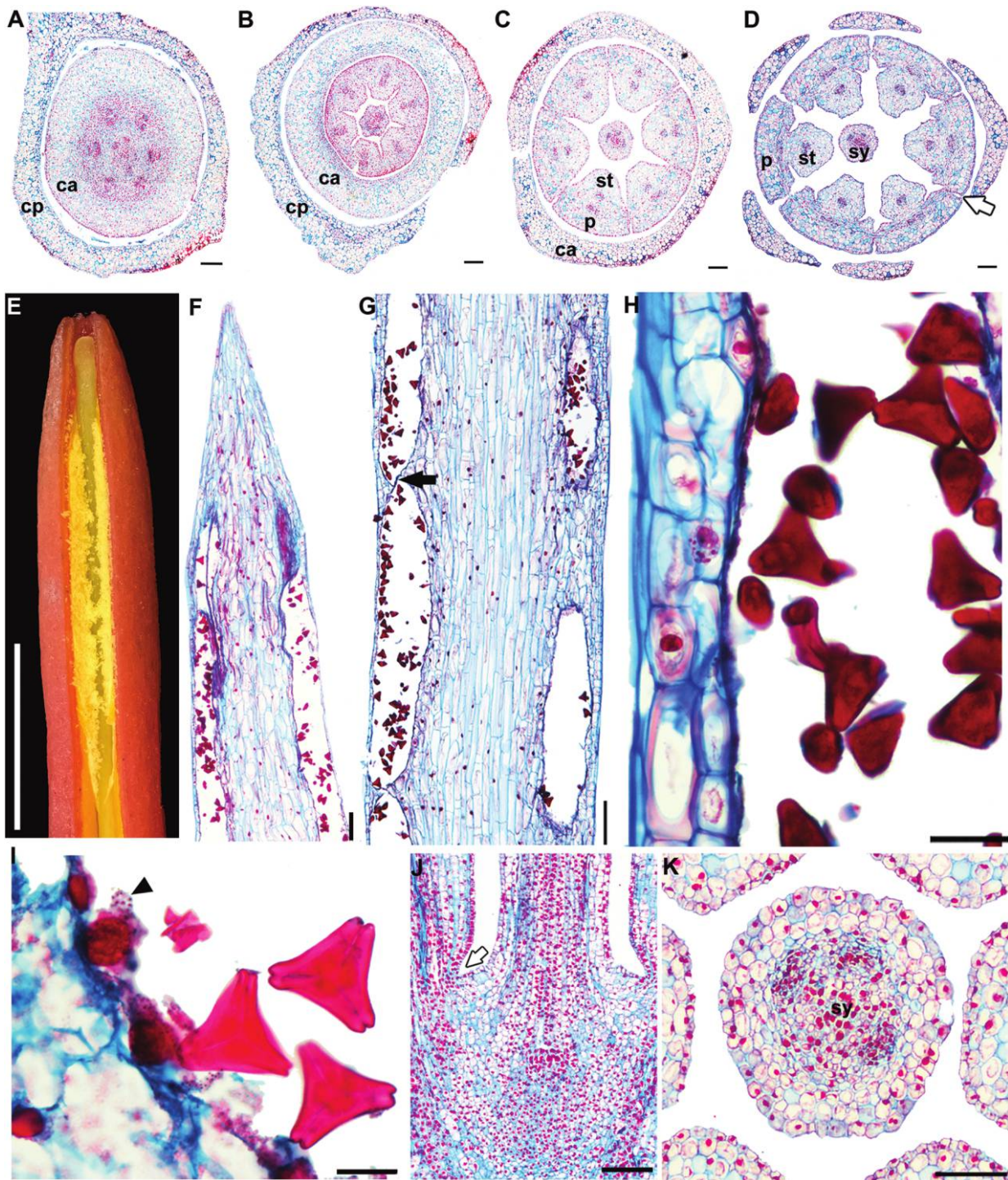
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Fig. 3 Floral anatomy of *Aetanthus mutisii*. *A–D*, Transverse sections at levels of the cupular pedicel and the floral base (*A*), the base of the calyx and the corolla (*B*), the base of the flower above the cupular pedicel (*C*), and the calyx lobes (*D*); note the interlocking of petals (arrow). *E*, Tip of the preanthetic flower used for sections *F–I*; note the premature anther dehiscence. *F, G*, Longitudinal sections of the tip (*F*) and the midlevel (*G*) of a polysporangiate anther in a preanthetic flower; note the transverse septum (arrow) and the mature pollen. *H*, Detail of the anther wall showing the endothecium, the tapetal cells, and the mature pollen grains. *I*, Pollen grains and the degraded tapetum with an orbicule (arrowhead). *J*, Longitudinal section of the unilocular ovary; note the common base of petals and stamens (arrow). *K*, Transverse section of the style. Scale bars: *A–D, F, G* = 250 μm; *E* = 5 mm; *H, I* = 25 μm; *J, K* = 100 μm. ca = calyx, cp = cupular pedicel, p = petal, st = stamen, sy = style.

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anthesis reaches the midlevel of petals, which separates the versatile, dorsifixed anthers.

Flowers in the two species here examined are attached to a cupular pedicel that is more evident in *P. acinarius* than in *P. krameri*. In the latter species, it is reduced to a flange of yellowish to pale orange tissue below the reddish calyx (fig. 1F–1H). The calyx in both species is truncate (figs. 1F–1H, 4A–4D). The corolla aestivation is valvate (fig. 4A–4E). The six petals are bright orange except in the yellow apical portion and have papillate epidermal cells (fig. 4B, 4E–4G). Petals remain adnate in a tube that reaches 8 cm in length in *P. acinarius* and 6.5 cm in *P. krameri* (figs. 1F, 1G, 4F, 4G). An inner ligule formed near the apex of the petal, and a series of long, villous trichomes formed at the petal-stamen junction are restricted to flowers of *P. krameri* (fig. 4D–4G). Anthers are dorsifixed and undergo latrorse dehiscence. In *P. acinarius*, three stamens are shorter and alternate to the other three stamens during preanthesis; however, by anthesis the anthers reach about the same level. The stamens in *P. krameri* are of the same size (fig. 1C, 1D, 1F). The stigma is slightly capitate and minutely papillate in both species (fig. 4D, 4F).

Floral anatomy (not shown) is similar to that found in *A. mutisii*. The main differences are found in the anthers. The anthers of *Psittacanthus* are dorsifixed and lack lateral sagittate sterile extensions, the apex is obtuse (not tapered), and the thecae remain tetrasporangiate throughout development, as no parenchymatic septae are secondarily formed.

Medium-Sized Loranthaceae Flowers: Gaiadendron punctatum

The genus *Gaiadendron* consists of two species distributed from Nicaragua to Bolivia (Kuijt 2015). Individuals of *G. punctatum* are root hemiparasitic, profusely branched trees ≥5 m tall, with white tubular flowers up to 2 cm long (fig. 5A). Flowers are ultimately organized in dichasia (fig. 6A–6C, 6E).

The floral primordia are radial. The terminal flower initiates first, followed by the simultaneous initiation of the two lateral, bracteolate flowers (fig. 7A). Flowers lack a cupular pedicel because they are sessile (fig. 5A). The sepals initiate irregularly from a ring primordium (fig. 6A–6D). Seven petal primordia then initiate almost simultaneously from a common ring primordium (fig. 6A). Soon after petal initiation, the calyx overtops the growing petals; at this stage, stamens have not initiated yet (fig. 6E, 6F). Numerous stomata and some sunken mucilage dots are scattered in the abaxial epidermis of the growing calyx (fig. 6D, 6G). Next, seven free stamen primordia arise almost simultaneously, opposite to the growing petals (fig. 6H). From early stages, stamens
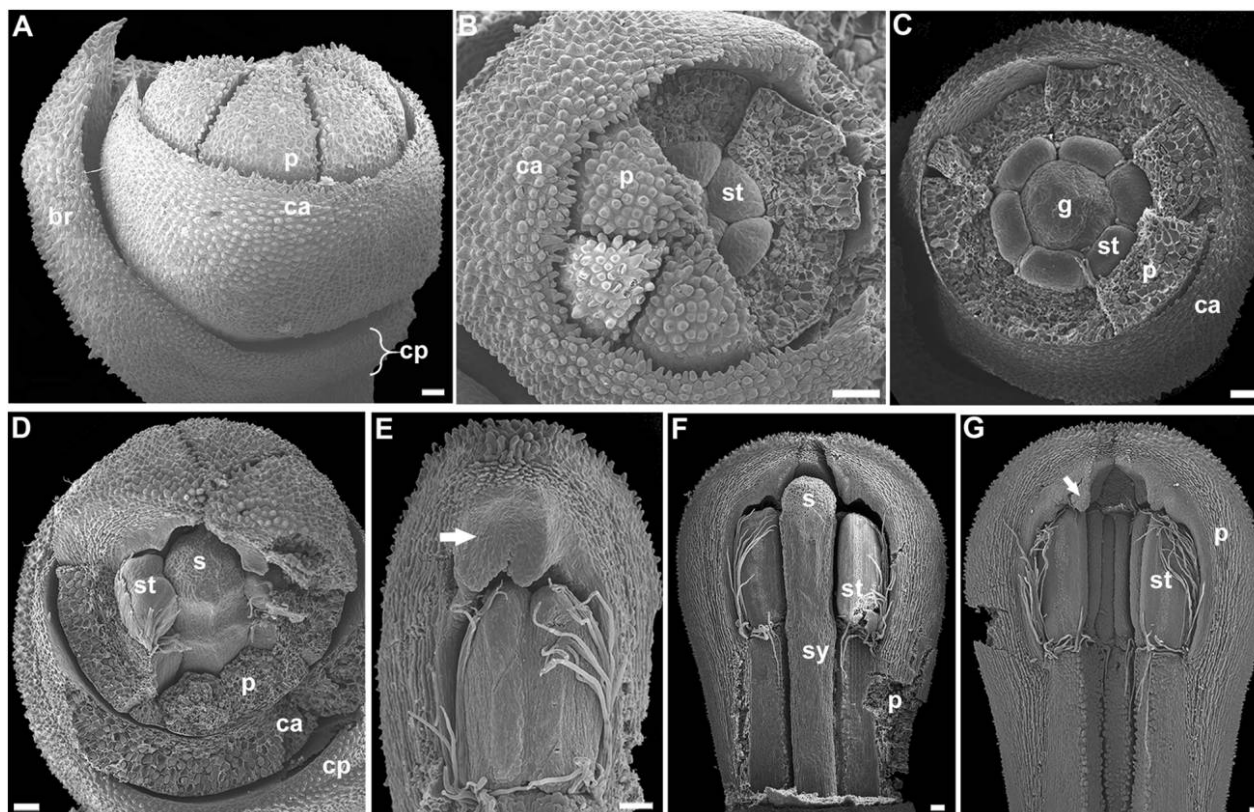

Fig. 4 SEM micrographs of *Psittacanthus krameri*. *A*, Young lateral flower of a dichasium with its subtending bracteole fused with the short cupular pedicel; note the truncate calyx and the petals. *B*, Stamen initiation; some petals are removed. *C*, *D*, Successive stages of gynoecium initiation. *E*, Petal with a rooflike ligule (arrow) above the stamen; note the long, stiff trichomes formed at the petal-filament joint. *F*, *G*, Young flowers showing the relative position of the style and the interlocked epidermis of petal margins. Scale bars = 100 μm. br = bracteole, ca = calyx, cp = cupular pedicel, g = gynoecium, p = petal, s = stigma, st = stamen, sy = style.
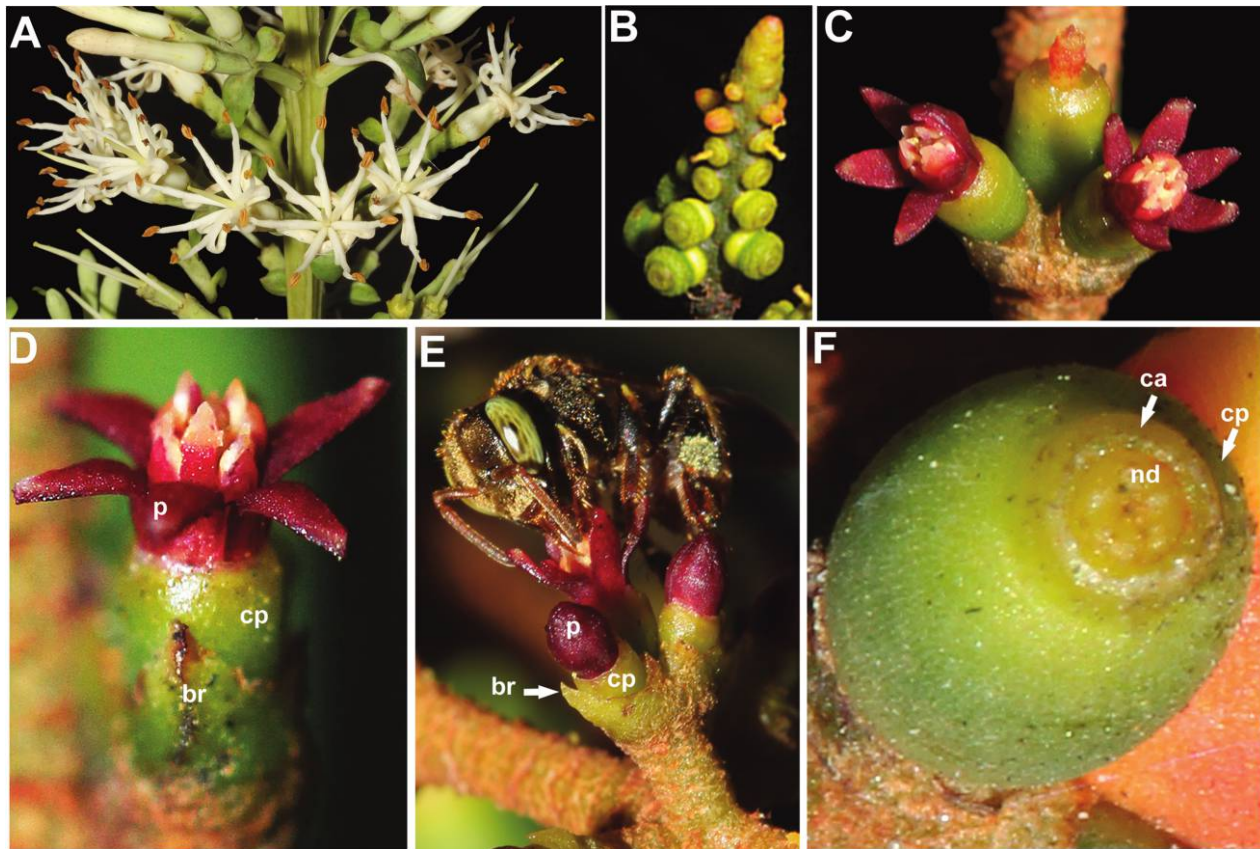
Fig. 5   Small- and medium-size-flowered Loranthaceae studied in this article. *A*, *Gaiadendron punctatum*, anthetic flowers. *B*, *Oryctanthus callicarpus*, inflorescence. *C–F*, *Passovia pyrifolia*. *C*, Dichasium with the central flower becoming fruit and the lateral flowers at anthesis. *D*, Anthetic, lateral flower showing the subtending bracteole, the accrescent cupular pedicel, and the corolla; the calyx (not apparent) is tightly enclosed by the accrescent cupular pedicel. *E*, Floral visitor. *F*, Forming fruit surrounded by the accrescent cupular pedicel; note the calyx and the nectarial disk apparent at the fruit apex. br = bracteole, ca = calyx, cp = cupular pedicel, nd = nectarial disk, p = petal.

show slightly different sizes from larger to smaller in an abaxial-adaxial gradient (fig. 6*H*, 6*I*). Prior to anthesis, two long, three medium-sized, and two short stamens are evident, but this size difference is not obvious at anthesis (fig. 5*A*). Finally, the gynoecium and the nectarial disk around the base of the style are formed (fig. 6*I*).

The mature calyx is light and dull green and has six to nine irregular teeth, which overtop the ovary (fig. 5*A*). Anthesis is acropetal along the indeterminate axis of the inflorescence, but flowers of the same node open simultaneously (fig. 5*A*). Petal aestivation is valvate (fig. 6*H*, 6*I*). The proximal half of the postgenitally fused petals remains tubular, but their distal halves split, and each petal becomes strongly reflexed (fig. 5*A*). The stamens have a white, slightly laminar filament, which remains adnate to the corresponding petal for most of their length; the dorsifixed and versatile anthers become brown during anthesis, and their dehiscence is longitudinal and latrorse.

Floral anatomy. The adaxial layers of the subtending bract and the two bracteoles of the dichasium develop abundant sclerenchyma at maturity (fig. 7*H*). Seven (or, less often, six) vascular bundles enter the base of the flower. Each vascular bundle soon splits radially; the inner traces irrigate the ovarial cavity and are smaller than the outer traces that con-

tinue upward to serve the corolla and the androecium (fig. 7*B*, 7*C*). Seven locules and seven discrete ategmic ovules are apparent at the midlevel of the ovary (fig. 7*B*, 7*H*–7*J*). The ovules are oriented downward (fig. 7*I*, 7*J*). The abaxial epidermis of the calyx is formed by small cuboidal cells. The calyx mesophyll contains six outer layers of isodiametric cells plus six inner layers of radially elongated cells (fig. 7*B*, 7*H*). The fused portion of petals and stamens has an epidermis formed by small cuboidal cells and a parenchyma formed by isodiametric cells (fig. 7*E*). Petals are nearly rectangular in transverse section, and their margins postgenitally fuse by interlocking of their epidermis (fig. 7*C*). Each petal has one central and two lateral vascular bundles surrounded by a mesophyll formed by about seven layers of isodiametric cells (fig. 7*C*); some mucilage cavities are scattered in the abaxial epidermis. Each stamen is served by one vascular bundle that reaches the abaxial junction of the filament and the anther (fig. 7*B*, 7*E*, 7*F*). The anthers are tetrasporangiate, and each locule has its own stomium (fig. 7*F*). The anther wall is formed by a single layer of exothecium with cuboidal cells, a single layer of endothecium formed by radially elongated cells, and one or two middle layers of tangentially elongated cells. The tapetum is secretory and formed by uninucleate cells. The style is hollow and irrigated by at least five vascular
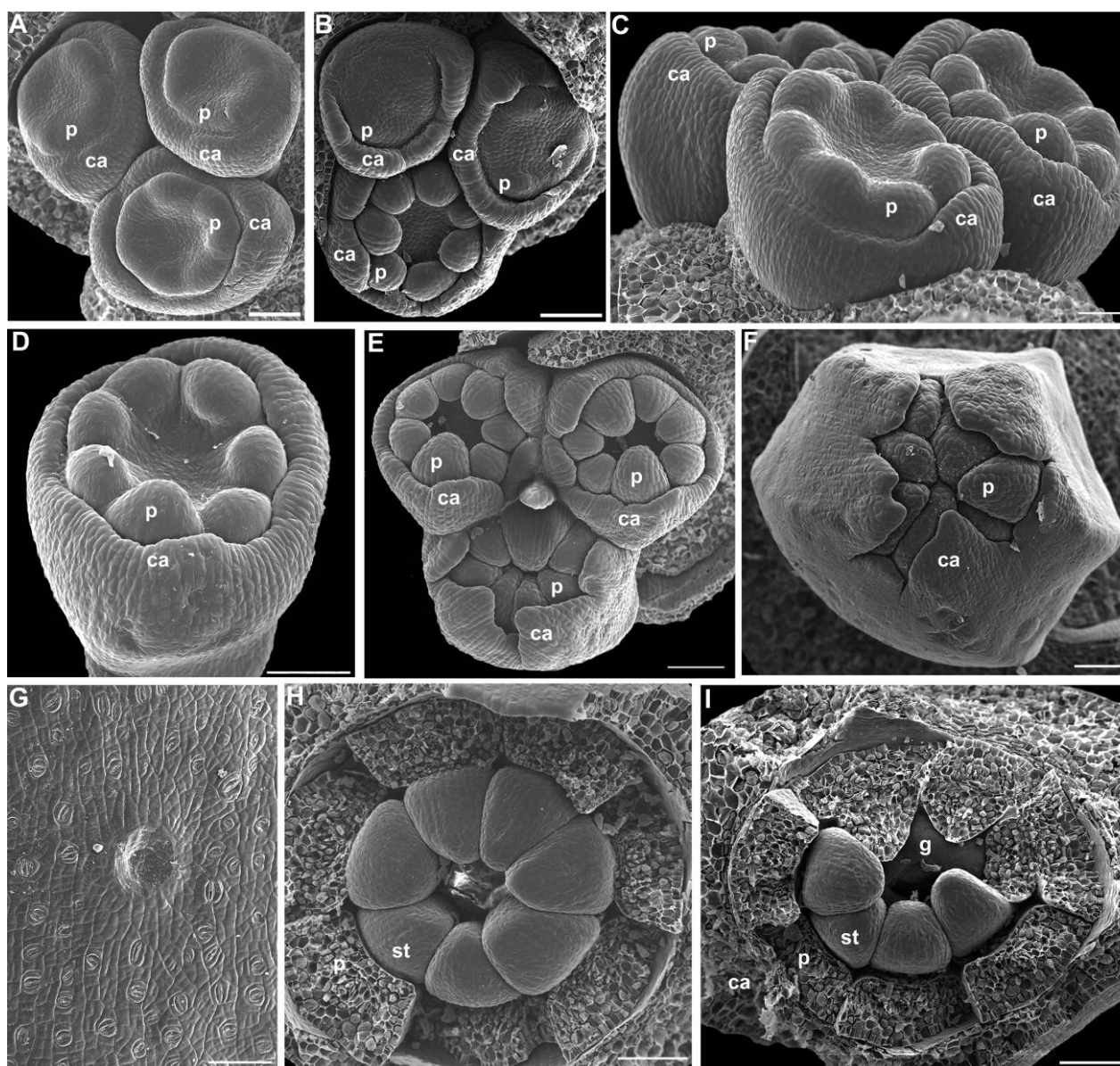
Fig. 6 SEM micrographs of *Gaiadendron punctatum* (*González 4314*). *A*, *B*, Successive stages of flower initiation; note the early organ initiation in the middle flower. *C*, *D*, Initiation of the calyx and the corolla. *E*, *F*, Late floral organogenesis; note the irregular lobes of the forming calyx, which gradually cover the forming petals and stamens. *G*, Detail of the abaxial surface of the calyx, with stomata and sunken epidermal mucilage cavities. *H*, *I*, Late stamen initiation; some primordia are removed in *I* to show the initiation of gynoecium. Scale bars = 100 μm. ca = calyx, g = gynoecium, p = petal, st = stamen.

bundles that reach the stigma (fig. 7*C*, 7*D*, 7*G*). The stigma is oblique and covered with unicellular papillae (fig. 7*G*).

Small Loranthaceae Flowers: Oryctanthus callicarpus, Passovia pedunculata, Passovia pyrifolia, *and* Peristethium archeri

Oryctanthus callicarpus. The genus *Oryctanthus* comprises 13 species distributed in Mesoamerica, Central America, and the tropical belt of South America (Kuijt 2015). Individuals of *O. callicarpus* are formed by shrubby, pendant branches

up to 1 m long. The individual flowers are located along short spikes (fig. 5*B*). All examined flowers were bisexual. The mature flower reaches 2.5 mm in length and is formed by a short calyx, an actinomorphic corolla formed by six valvate orange-yellow petals almost totally free, six stamens of unequal size, subglobose anthers, and an ovary crowned by a massive nectarial disk (fig. 5*B*).

Each flower is flanked by two sterile bracteoles, one of which develops first (fig. 8*A*, 8*B*, 8*D*). Young floral buds develop sunken into a fossula, and they gradually emerge during preanthesis (figs. 5*B*, 8*F*, 8*G*). The calyx initiates as a ring pri-
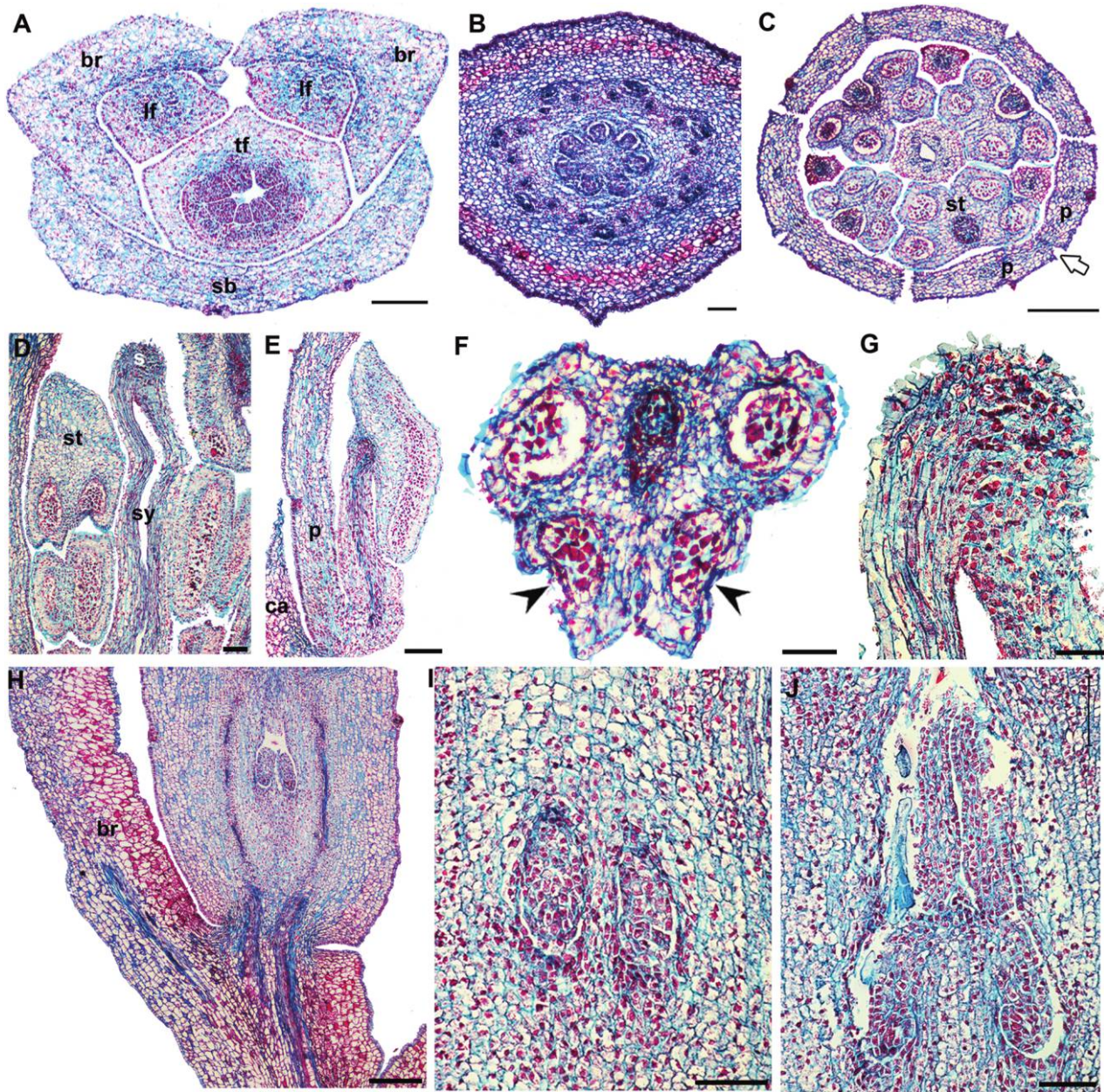
Fig. 7 Floral anatomy of *Gaiadendron punctatum*. *A*, Transverse section at the base of lateral flowers. *B*, Transverse section of the ovary showing seven main vascular bundles and seven locules. *C*, Transverse section at the level of petals and anthers; note the interlocking of the petals (arrow). *D*, Longitudinal section of four anthers of different lengths surrounding the apex of the style and the stigma. *E*, Longitudinal section of a petal and its corresponding stamen. *F*, Transverse section of an anther; arrowheads point to stomia. *G*, Detail of stigma. *H*, Longitudinal section of the ovary with two ovules. *I*, *J*, Details of ovules. Scale bars: *A–D*, *H* = 250 μm; *E*, *F* = 100 μm; *G* = 50 μm; *I*, *J* = 25 μm. br = bracteole, ca = calyx, lf = lateral flower, p = petal, s = stigma, sb = subtending bract of the dichasium, st = stamen, sy = style, tf = terminal flower.

mordium that remains entire or with irregular but shallow lobes at its apex (fig. 8*B*, 8*C*, 8*E*, 8*F*); the calyx is very short and remains partially sunken in the fossula (figs. 5*B*, 8*B*, 8*E*, 8*F*). The corolla initiates in two successive whorls of three alternate petals each (fig. 8*B*–8*D*); the petals remain free except for a slight epidermal interlocking of the margins at their base (fig. 8*E*, 8*F*, 8*H*). Next, the six stamens initiate almost simultaneously (fig. 8*E*), but soon they follow the petal growth sequence, with three long

stamens alternate to three short stamens (fig. 8*F*–8*H*). An adaxial thickening in the base of the filament is formed at early stages (fig. 8*H*). The anthers are basifixed and tetrasporangiate (fig. 8*F*–8*H*). The ovary is solid. By preanthesis, a thick nectarial disk is formed around the base of the elongating style; the relatively short and straight style (fig. 8*H*) is covered by isodiametric epidermal cells arranged in transverse rows and ends up as a capitate stigma densely covered by unicellular papillae.

Passovia pedunculata **and** ***Passovia pyrifolia***. The genus *Passovia* includes 30 or more species distributed in Mesoamerica, Central America, the West Indies, and the tropical belt of South America (Kuijt 2015). Individuals of *P. pedunculata* possess climbing twigs up to 1 m long. Those of *P. pyrifolia* are shrubs profusely ramified from the main haustoria, with epicortical roots up to 60 cm long; hanging twigs reach up to 1 m in length. In both species, the small, purple, bell-shaped flowers are arranged in small opposite dichasia along indeterminate inflorescences (figs. 5*C*–5*E*, 9*A*–9*C*, 10*B*–10*D*). Each dichasium is formed by three sessile flowers, from which the terminal flower develops first, followed by the asynchronous initiation of the two bracteolate, lateral flowers (figs. 9*A*–9*C*, 10*B*–10*D*). Individual flowers reach 3 mm in length (fig. 5*C*–5*E*).

Floral development is similar in the two species of *Passovia* examined. The floral primordia are radial (fig. 10*B*). The initiation of an irregular cupular pedicel precedes that of the calyx and the corolla (figs. 9*A*–9*D*, 10*A*–10*D*). The calyx also initiates irregularly as a short flange, and it is soon overtopped and covered by the rapid expansion of the cupular pedicel (figs. 9*A*–9*D*, 10*B*–10*E*). From this stage on, the calyx remains tightly enclosed by the cupular pedicel and becomes apparent again as a fringe of tissue between the cupular pedicel and the nectarial disk during fruit formation (fig. 5*F*). As in *O. callicarpus*, the corolla initiates in two successive whorls of three alternate petals each; the petals that develop last remain slightly smaller during floral growth (figs. 9*C*, 9*D*, 10*A*–10*D*). All six petals reach approximately the same size by preanthesis (figs. 5*C*–5*E*, 10*E*). Petal aestivation is valvate and free, but the epidermal cells of their margins remain interlocked until anthesis (figs. 9*G*, 10*D*, 10*E*, 11*B*, 11*C*). The initiation and growth of the six unequal stamens keeps pace with that of the petals (fig. 10*D*, 10*F*). The filaments are laminar (figs. 9*F*, 10*F*), and in *P. pyrifolia* they are wider in the proximal and distal portions (fig. 10*F*). The anthers are ovoidal, basifixed, and tetrasporangiate in *P. pedunculata* (fig. 9*F*, 9*G*) and bi- or tetrasporangiate in *P. pyrifolia* (fig. 11*G*). The sporogenous tissue is restricted to the lower flanks at the wider portion of each anther; dehiscence is latrorse through a very short slit (fig. 10*G*–10*I*). Anthers in *P. pyrifolia* can fail to produce sporogenous tissue due to endothecial proliferation into the anther locule (fig. 11*F*, 11*G*). The apex of the connective is tapered (figs. 9*F*, 10*F*, 10*G*, 11*F*). The short style is straight and massive and has shallow impressions left by the anthers that tightly surround it during preanthesis; the stigma is capitate, asymmetric, and covered by unicellular papillae (figs. 9*G*, 10*G*, 11*I*).

Floral anatomy. Six vascular bundles enter the floral base (fig. 11*A*). The massive cupular pedicel is clearly differentiated from the calyx and lacks vascularization (fig. 11*A*, 11*D*, 11*H*). Its abaxial epidermis is formed by unicellular papillae and a few sunken, scattered mucilage glands; the mesophyll is formed by eight to 10 layers of parenchymatic cells (fig. 11*A*, 11*D*, 11*H*). An endothelium is apparent between the mesophylls of the cupular pedicel and the calyx (fig. 11*A*, 11*D*, 11*H*). The solid ovary is surrounded by a sheath of collenchymatous cells. The calyx is squeezed between the cupular pedicel and the petals (fig. 11*D*, 11*H*). A single vascular bundle enters the common petal-stamen base and radially splits farther up into an outer trace for the petal and an inner trace for the stamen (fig. 11*A*–11*D*, 11*H*). The petals are thick, with an epidermis formed by a single layer of cuboidal cells; petal mesophyll is formed by five or six layers of

parenchymatous cells (fig. 11*B*). The mesophyll of the petals and the filaments becomes heavily tanniferous by anthesis (fig. 11*E*, 11*F*). The anther wall is rich in a thickened endothecium, which proliferates and invades most of the anther mesophyll (fig. 11*F*, 11*G*). A nectarial disk is formed around the base of the style (figs. 5*F*, 11*D*, 11*H*, 11*I*). The style is formed by a slightly papillose epidermis, a mesophyll of five layers of isodiametric cells, and a core of radially elongated cells that are tightly appressed (fig. 11*I*–11*K*); three vascular bundles serve the style and reach the stigma (fig. 11*K*). The stigma is covered by unicellular papillae.

Peristethium archeri. The genus *Peristethium* comprises 15 species distributed in Central America and tropical South America (Kuijt 2015). Individuals of *P. archeri* are formed by slightly woody pendant branches up to 80 cm long with upright to horizontal indeterminate inflorescences up to 4 cm long. The flowers are bisexual and sessile or occasionally pedicellate (fig. 12*A*–12*C*). The calyx is truncate to minutely dentate and shifts from green when juvenile to light brown at maturity (fig. 12*A*–12*C*). Flowers with four or five petals and stamens were found in the same inflorescence, but tetramerous flowers are more frequent (fig. 12*B*–12*F*). Petal aestivation is valvate (fig. 12*B*–12*F*). By anthesis, the petals become light yellow and reach 5 mm in length and the anthers look sessile, as the filament is almost completely adnate to the petal (fig. 12*B*); the style is straight, and the stigma is clavate.

The flower primordia are radial (not shown). The calyx initiates as a ring primordium with a slightly irregular border (fig. 12*A*). The petal primordia then arise almost simultaneously, rapidly followed by the initiation of the stamens. Last, the gynoecium primordium with an oblique apex becomes apparent.

Floral anatomy. There is no morphoanatomical evidence of a cupular pedicel in this species at any developmental stage, although sporadic formation of pedicellate flowers occurs at the base of the inflorescence (fig. 12*C*). The epidermis of the calyx is formed by a single layer of cuboidal cells that surround a mesophyll of about 12 layers of isodiametric cells (fig. 12*D*); no vascular traces were found irrigating the calyx. Each petal is served by a middle vascular bundle, the petal mesophyll is formed by seven layers of isodiametrical cells, the petal epidermis consists of a single layer, the adaxial epidermis is formed by papillose unicellular cells, and the marginal epidermis is postgenitally fused by interlocking (fig. 12*E*, 12*F*). The anthers are served by a single vascular trace (fig. 12*E*, 12*F*); they are bisporangiate, and each locule dehisces latrorsely throughout its own stomium (fig. 12*F*, 12*G*). The anther wall is formed by a single layer of exothecium of small tangentially elongated cells and an endothecium of larger, radially elongated cells; the tapetum is secretory and unistratified (fig. 12*G*). The style is irrigated by four or five vascular traces that do not enter the stigma (fig. 12*D*–12*F*); the epidermis of the latter is formed by unicellular papillae (fig. 12*H*). A single locule almost completely surrounded by a collenchymatous pad is formed in the ovary (fig. 12*I*, 12*J*).

Discussion

Variation of floral structure in Loranthaceae is extreme. Our study included sampling of *Gaiadendron*, one of the earliest
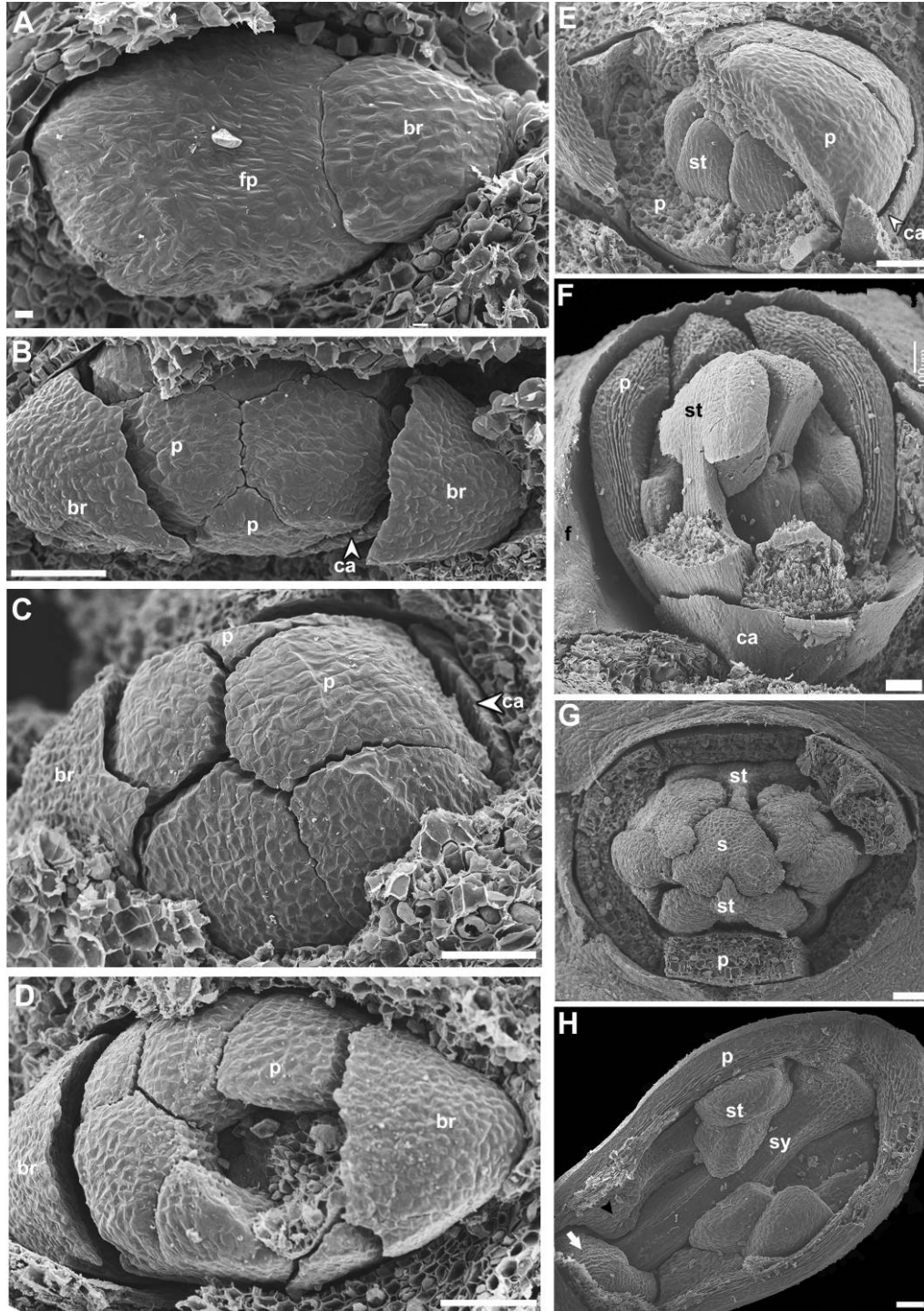
Fig. 8 SEM micrographs of *Oryctanthus callicarpus*. *A*, Floral meristem of the terminal flower; note the early initiation of one of the two flanking sterile bracteoles. *B*, Initiation of the calyx and the corolla. *C, D*, Successive stages of petal elongation. *E*, Initiation of the stamens. *F, G*, Lateral (*F*) and frontal (*G*) views of a young flower during stamen and gynoecium elongation. *H*, Longitudinal section of a preanthetic flower; note the unequal-sized stamens, the thickened stamen bases (arrowhead), and the nectarial ring at the base of the style (arrow). Scale bars = 100 μm. br = bracteole, ca = calyx, f = fossula, fp = floral primordium, p = petal, s = stigma, st = stamen, sy = style.
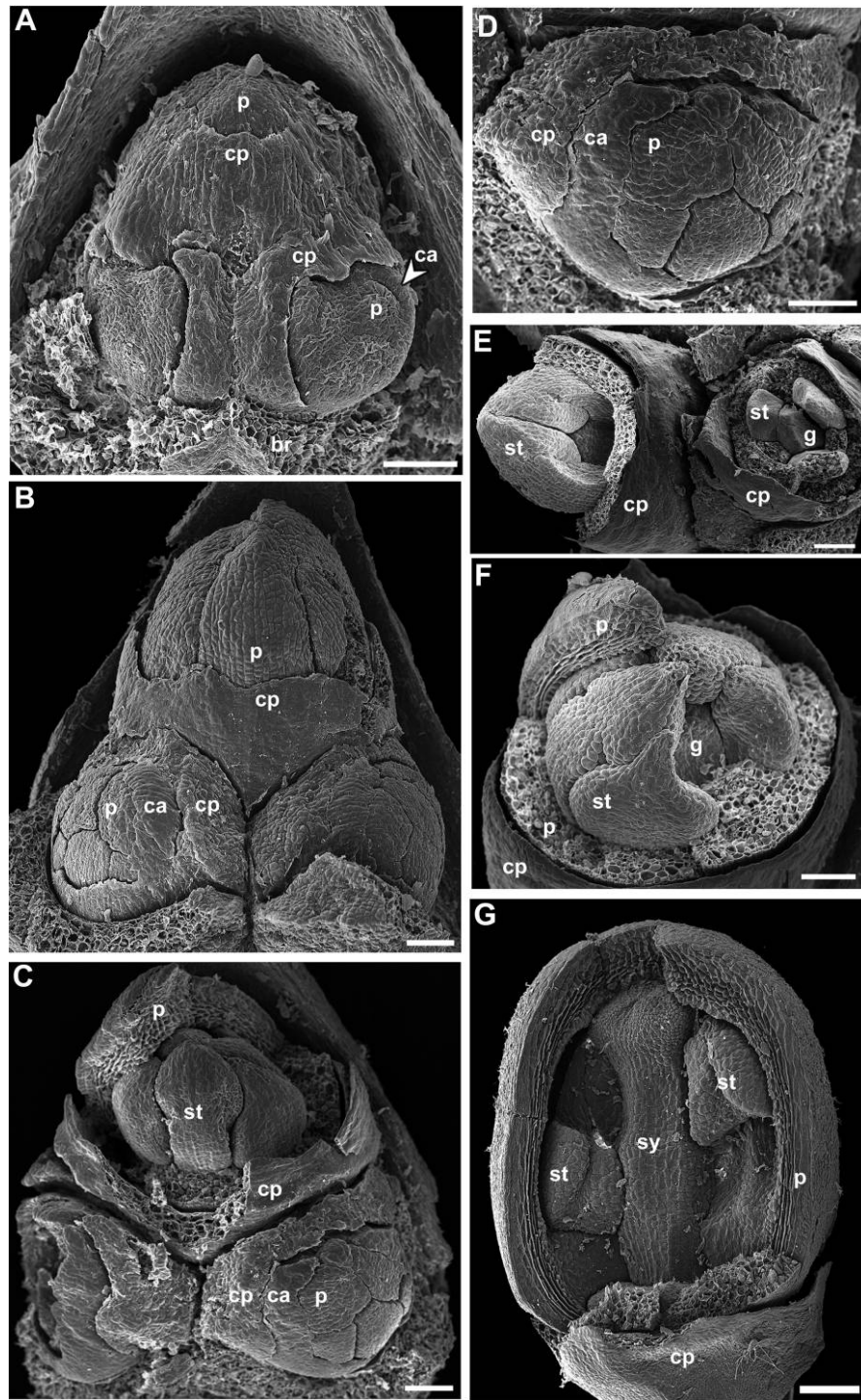
Fig. 9 SEM micrographs of *Passovia pedunculata*. *A–C*, Successive developmental stages of a dichasium during initiation of the cupular pedicel, the calyx, and the corolla. *D*, Detail of a lateral flower with the cupular pedicel, the calyx, and the corolla. *E*, Initiation of the stamens and the gynoecium in the lateral flower (*right*) and later stamen growth in the terminal flower (*left*). *F*, *G*, Successive stages of the short and the long stamen development. Scale bars = 100 µm. br = bracteole, ca = calyx, cp = cupular pedicel, g = gynoecium, p = petal, st = stamen, sy = style.
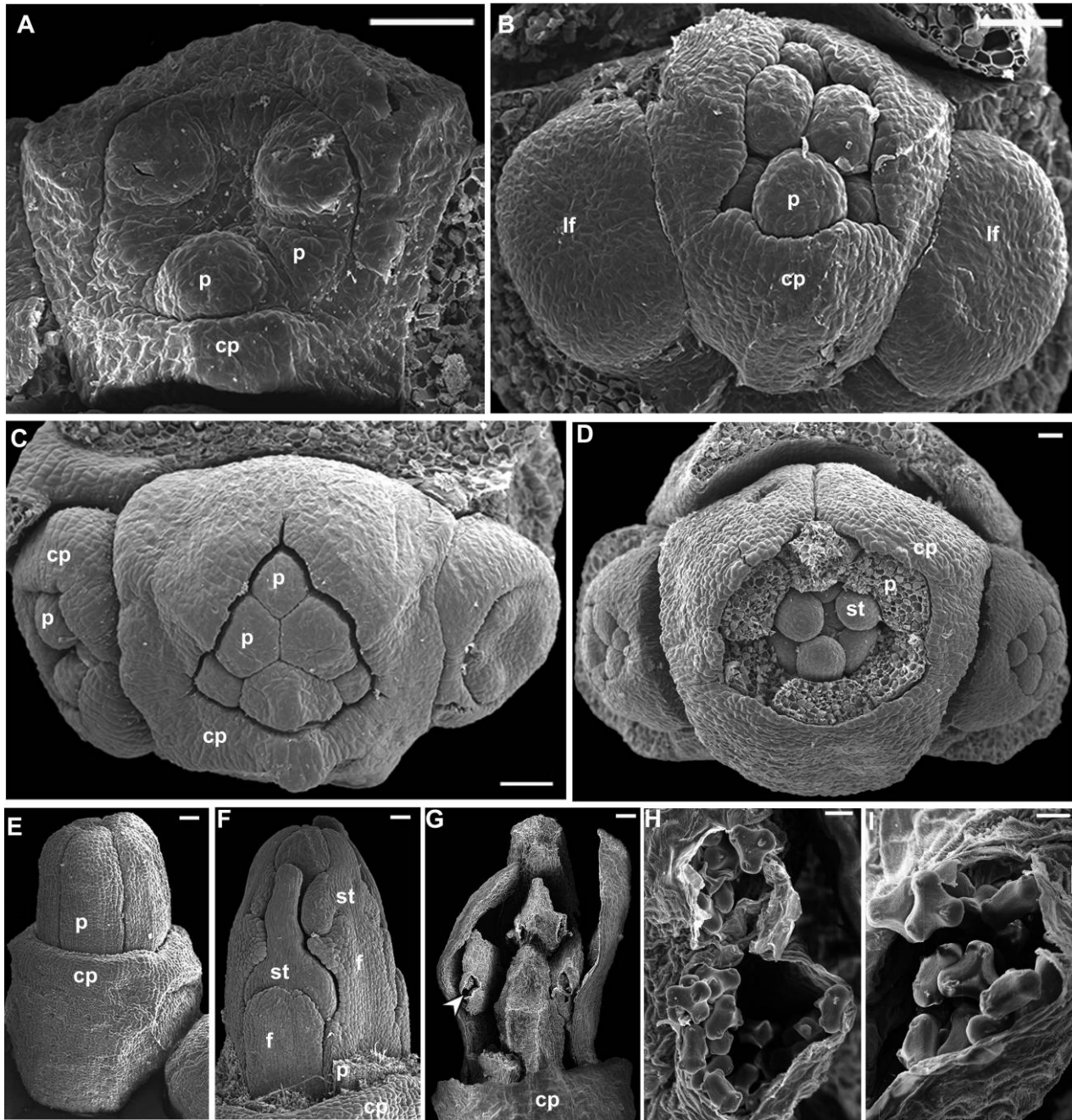
Fig. 10   SEM micrographs of *Passovia pyrifolia*. *A–C*, Flower buds during petal initiation; note the delayed organogenesis in the lateral floral buds. *D*, Stamen initiation; petals are removed. *E*, Preanthetic flower. *F*, Short and long stamens at late preanthesis; petals are removed. *G*, Anthetic flower with latrorsely dehisced anthers (arrowhead); note the impressions in the style left by the anthers. *H, I*, Detail of the stomia and the pollen grains. Scale bars = 100 μm. cp = cupular pedicel, f = laminar filament, lf = lateral flower bud, p = petal, st = stamen.

diverging lineages in the Loranthaceae, as well as species of four genera that belong to a more recent diverging clade, the subtribe Psittacanthinae (cf. phylogenetic analyses by Wilson and Calvin 2006; Vidal-Russell and Nickrent 2008; Nickrent et al. 2010). A number of evolutionary hypotheses will be discussed hereafter in the context of current phylogenetic frameworks.

Bisexual versus Unisexual Flowers

Bisexual flowers are plesiomorphic in Loranthaceae. The shift to unisexual flowers has occurred at least five times, once in *Barathranthus* Miquel (subtribe Amyeminae Nickrent and Vidal-Russell), once in *Ileostylus* (subtribe Ileostylinae Nickrent and Vidal-Russell), once in *Loranthus* Jacq. (subtribe Loranthinae
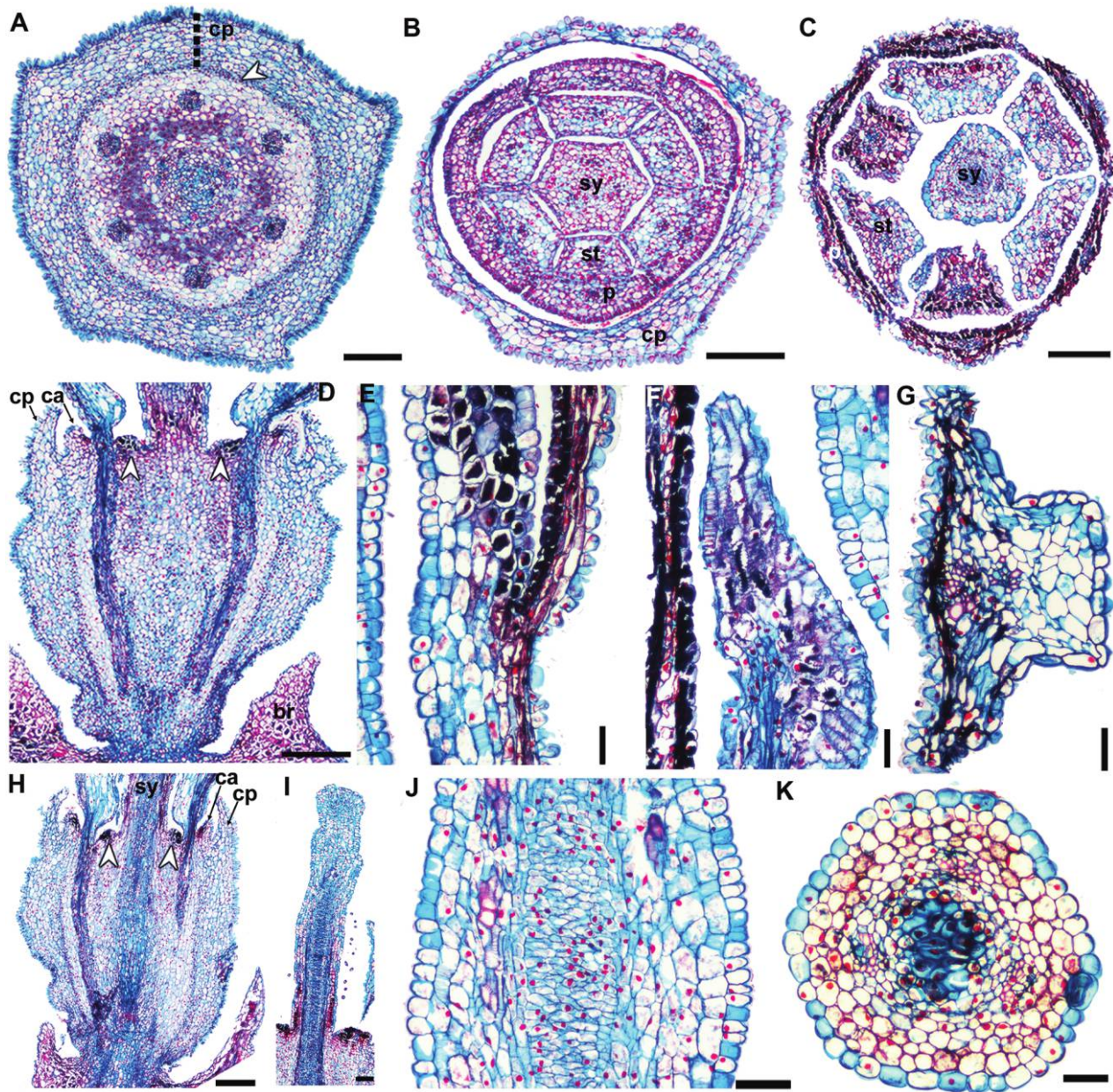
Fig. 11 Floral anatomy of *Passovia pyrifolia*. *A*, Transverse section through the floral base; note the inner epidermis of the cupular pedicel (arrowhead). *B*, *C*, Transverse sections through the proximal (*B*) and the distal (*C*) levels of a preanthetic flower. *D*, Longitudinal section of the solid ovary showing the accrescent cupular pedicel, the calyx, the common petal-stamen vascular bundles, and the nectarial ring (arrowheads). *E*, Longitudinal section of the petal-anther common base; note the tanniferous cells in the petal parenchyma and the stamen abaxial epidermis. *F*, *G*, Longitudinal (*F*) and transverse (*G*) sections of an anther; note the proliferative endothecium filling most of the entire anther locule. *H*, Sagittal section of the ovary surrounded by the cupular pedicel and the calyx; note the nectarial ring (arrowheads) around the stylar base. *I*, Detail of the nectarial ring, the style, and the stigma. *J*, *K*, Longitudinal (*J*) and transverse (*K*) sections of the style. Scale bars: *A–D*, *H* = 250 μm; *E–G*, *J*, *K* = 100 μm; *I* = 10 μm. br = bracteole, ca = calyx, cp = cupular pedicel, p = petal, st = stamen, sy = style.

Engler), once in *Tupeia* (subtribe Tupeinae Nickrent and Vidal-Russell), and several times across the subtribe Psittacanthinae Engl. in species of *Cladocolea*, *Maracanthus*, *Passovia*, *Peristethium*, *Phthirusa*, and *Struthanthus*. In the latter subtribe, unisexual flowers are restricted to small-flowered taxa (Kuijt 2015), and this trait is still labile in some species that also have bisexual

flowers, such as *Passovia pyrifolia* (see below). Both unisexual and bisexual flowers in *P. pyrifolia* were reported by Eichler (1868). The formation of both bisexual and unisexual flowers in the same inflorescences of the early-diverging *Nuytsia* R. Brown (Kuijt 2015) suggests that such lability evolved early in the family. Despite the fact that unisexual flowers and even dioe-
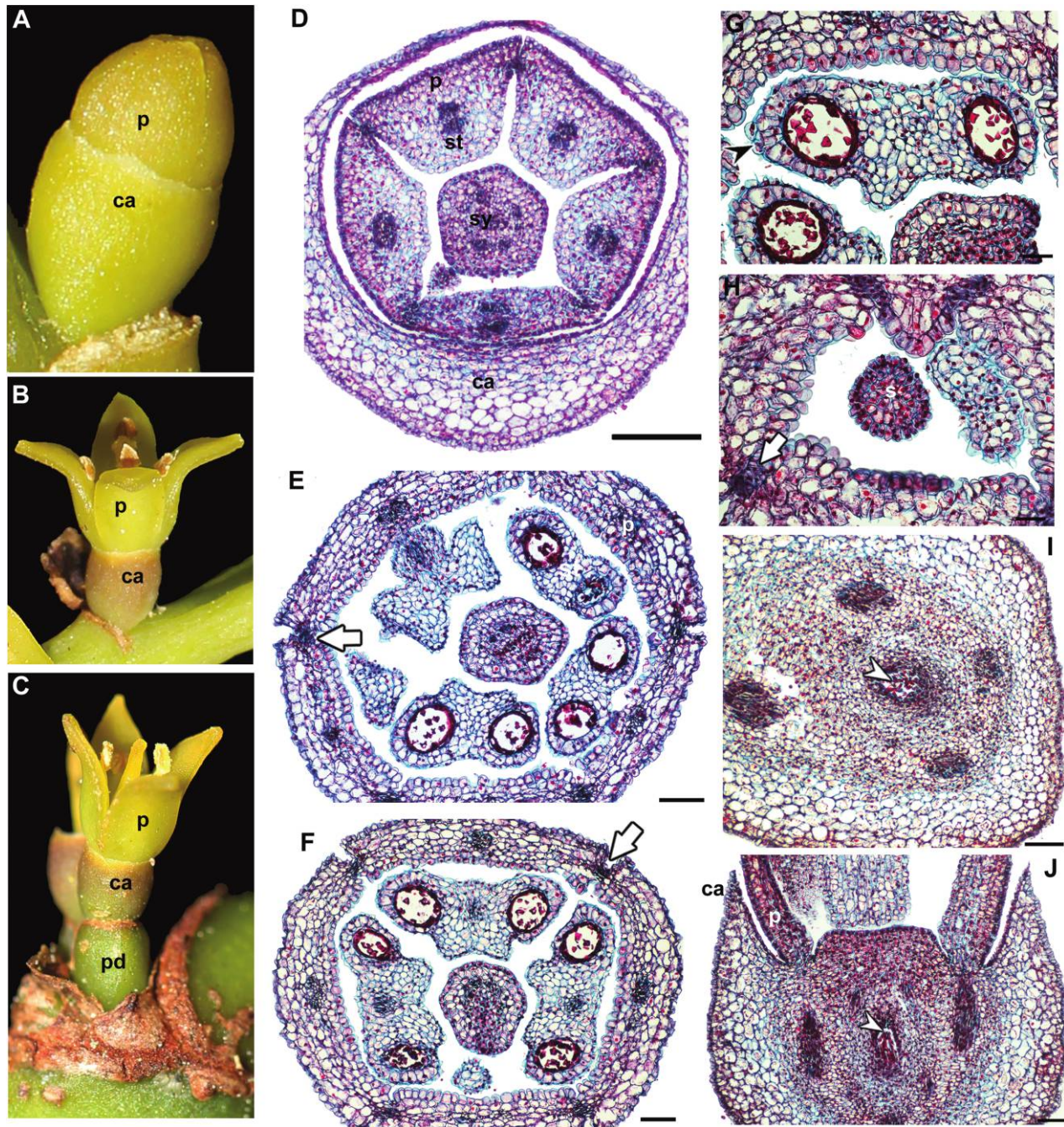
Fig. 12 Floral morphoanatomy of *Peristethium archeri*. *A*, *B*, Young (*A*) and anthetic (*B*) flowers. *C*, Pedicellate flower formed at the base of the inflorescence. *D*, *E*, Transverse sections through the proximal (*D*) and the distal (*E*) levels of a pentamerous flower; note the valvate, interlocking petals (arrow). *F*, Transverse section of a tetramerous flower. *G*, Transverse section of an anther. *H*, Transverse section of the style. *I*, *J*, Transverse (*I*) and longitudinal (*J*) sections of the unilocular ovary (arrowheads). Scale bars: *D*, *F* = 250 μm; *E*, *J* = 100 μm; *G*, *H* = 50 μm. ca = calyx, p = petal, pd = pedicel, s = stigma, st = stamen, sy = style.

cious plants have been described in Loranthaceae, it is not a straightforward feature to assess in "female" flowers, because the structure and the function of the ovary is more or less reduced throughout the family, without affecting the embryo sacs and embryo formation.

Calyculus and Cupule

The calyculus (calycode or calycodium) was first described in Loranthaceae by Brown (1810) as the outer perianth whorl outside the corolla, which encloses the pericarp. Since then, the meaning of the term has been equivocal, as it was used to refer to either an expansion of the peduncle (Planchon and Decaisne

1855) or the variously modified calyx-like structures that re-place the missing calyx in Loranthaceae (Baillon 1862*a*, 1862*b*). Eichler (1868, 1878) unambiguously equated calyx and calyculus and abandoned the use of the latter, as it was un-necessary and misleading; in addition, Eichler (1868) intro-duced the term "cupule" to describe the cuplike expansion of the pedicel (i.e., axial in origin) formed outside of the calyx in some Loranthaceaous flowers. Eichler's interpretations were followed by Engler (1889), Engler and Krause (1935), and Schaeppi and Steindl (1942). A reinterpretation of the calyculus as bracteolar in origin by Venkata Rao (1963) and Wanntorp and Ronse De Craene (2009) revived the controversy over the morphological homology of the calyculus (cf. Kuijt 2013). Wanntorp and Ronse De Craene (2009) described the calyculus as an organ positioned outside the perianth and suggested that it should be considered an epicalyx that replaces the calyx after the latter is lost in members of Santalales, including some Lo-ranthaceae.

Our developmental, morphological, and anatomical studies support Eichler's (1868, 1878) interpretations, as we have shown that the cupule is an additional structure outside of the calyx formed by a cuplike expansion of the pedicel. Accordingly, we have used the term "cupular pedicel," as it reflects both shape and origin. We have avoided the term "cupule" alone because it is also used to refer to the involucre formed by branched systems at the base of an acorn (Endress 2010), among other meanings.

We have clearly shown that flowers of five out of the eight examined species develop cupular pedicels, either below the calyx and free from it (in *Aetanthus mutisii*, *Psittacanthus acinarius*, and *Psittacanthus krameri*; figs. 1*A*, 1*E*, 1*G*–1*I*, 2*A*–2*D*, 3*A*, 3*B*, 4*A*, 4*D*) or completely fused with the calyx and tightly surrounding it (in *Passovia pedunculata* and *P. pyrifolia*; figs. 5*F*, 9*A*–9*D*, 11*A*, 11*D*, 11*H*). Our results also indicate that the cupular pedicel is not foliar (i.e., bracteolar, bracteal, or prophyllar) in origin, contrary to Wanntorp and Ronse De Craene's (2009) interpretation; in that respect, we agree with Kuijt (2013, p. 251), in that the "prophyllar hy-pothesis for the calyculus must be rejected in Loranthaceae." Altogether, these positional and structural criteria of homology clarify the controversial interpretation of the calyculus, as we provide evidence of its structural separation (such as in the large flowers of *Aetanthus*, *Psittacanthus*, or *Tapinanthus*) and histo-logical differentiation (such as in the small flowers of *Passovia*).

Flowers in *Psittacanthus* deserve further discussion. They are ultimately organized either in dichasia formed by a central flower and two lateral flowers or in dyads; the lateral flowers are subtended by a bracteole each (fig. 1*G*, 1*H*). Our results corroborate Eichler's (1868) observations that the cupule (=cupular pedicel) is formed in both the central (if present) and the lateral flowers in *Psittacanthus* and that the subtending bracteole in the lateral flowers is often fused with the cupular pedicel (figs. 1*G*, 1*H*, 4*A*). The fusion of the bracteole in the lat-eral flowers causes a slight asymmetry on the cupular pedicel (fig. 1*G*, 1*H*), contrasting with that in the central flower, which remains symmetric. This is apparent in, e.g., *Psittacanthus biternatus* Hoffmannsegg G. Don and *Psittacanthus cordatus* (Hoffmannsegg) G. Don (Eichler 1868, pls. 9-V-29 and 8-16, respectively). The free cupular pedicel is likely widespread across the large-flowered Psittacanthinae genera, such as *Aetanthus*, *Li-garia*, *Psittacanthus*, and *Tapinanthus*. This structure has been

clearly illustrated in, e.g., *P. acinarius* (Eichler 1868, pl. 4 as *Psittacanthus warmingii*), *Psittacanthus calyculatus* (DC) G. Don (as *Loranthus calyculatus* in de Candolle 1830, pl. X), *Psittacanthus cinctus* (Martius) Martius, *Psittacanthus clusii-folius* Willdenow ex Eichler, and *Psittacanthus robustus* (Martius) Martius (see Eichler 1868, pls. 6, 2-II, and 3, respec-tively), as well as in *Psittacanthus cuneifolius* (Ruiz and Pavon) G. Don (now *Ligaria cuneifolia* (Ruiz and Pavon) Tiegh.; see fig. 19 in Abbiatti 1946), *P. cordatus* (Hoffmannsegg) G. Don (see fig. 20 in Abbiatti 1946), and *Tapinanthus pentagonia* (DC.) Tiegh. (de Candolle 1830, pl. VIII as *Loranthus pentagonia*).

The presence of a cupular pedicel completely fused with the calyx and tightly surrounding it in *P. pedunculata* and *P. pyrifolia* (figs. 5*F*, 9*A*–9*D*, 11*A*, 11*D*, 11*H*) has previously been overlooked. Kuijt and Weberling (1972, p. 475) detected the double envelope around the ovary in *P. (Phthirusa) pyrifolia*, but they interpreted the calyx as a "ring-like prolif-eration of parenchyma tissue developed between the petals and the calyculus" and called it a "calycular ring." In addi-tion, Wanntorp and Ronse De Craene (2009) did not notice the presence of an outer cupular pedicel and an inner ringlike calyx in *P. pyrifolia*, although these two structures were clearly apparent in their figure 5*L*.

In the case of *Oryctanthus callicarpus*, it is likely that the fossula that surrounds the base of the flower corresponds to a cupular ped-icel that has undergone syndesmy with the inflorescence axis (V. Suaza-Gaviria, F. González, and N. Pabón-Mora, unpublished manuscript). Last, we found no evidence for the formation of cu-pular pedicels in the flowers of *Gaiadendron punctatum* (figs. 5*A*, 6*A*–6*D*) and *Peristethium archeri* (fig. 12*A*–12*C*, 12*J*), although in the latter species sporadic formation of pedicellate flowers occurs at the base of the inflorescence (fig. 12*C*). Pedicellate flowers in *Peristethium* are rare and occur in, e.g., *Peristethium aequatoris* (Kuijt) Kuijt and *Peristethium peruviense* (Kuijt) Kuijt (Kuijt 2012); however, in none of these cases does the pedicel be-come expanded or accrescent, and it remains clearly below the ovary (fig. 12*C*). Given that the cupular pedicel is lacking in flowers of the early-diverging *Nuytsia* (Blakely 1922), *Atkinsonia* (Blakely 1922), and *Gaiadendron* (figs. 5*A*, 6*A*–6*E*), this condi-tion could be plesiomorphic in the family.

Despite its ambiguous meaning, the term "calyculus" has continuously been used in the recent literature, mostly to refer to a modified or reduced calyx in Loranthaceae (e.g., Abbiatti 1946; Maheshwari and Johri 1950; Pienaar 1951; Narayana 1956; Maheshwari et al. 1957; Stauffer 1961; Kuijt 2009, 2013, 2014, 2015, among others). We advocate here that the use of ca-lyculus to refer to the variously modified calyces in Larantha-ceae should be abandoned, as Eichler (1868, 1878) did, as it is unnecessary and misleads the structural interpretation of the floral and extrafloral organs in the family.

Perianth

The interpretation of the perianth members as sepals or petals in Loranthaceae has been controversial, mostly because they are opposite to the stamens. Authors such as Van Tieghem (1893, p. 352; 1895) considered that the inner whorl of the perianth in his "Loranthacées parasites" (that is, in-cluding *Aetanthus* and *Psittacanthus* but excluding *Nuytsia*) corresponds to petaloid sepals and that true petals are lack-

ing. Conversely, de Candolle (1830), Eichler (1868, 1878), and Van Tieghem (1893, only for *Nuytsia*), among others, explained the perianth of Loranthaceae as formed by sepals and petals.

Our research indicates that the perianth in Loranthaceae is biseriate, dichlamydeous, and formed by an unusually irregular calyx that initiates as a ring primordium and a corolla formed by four to seven petals that initiate either simultaneously (*Aetanthus*, *Gaiadendron*, and *Psittacanthus*) or successively (*Oryctanthus* and *Passovia*). In *Oryctanthus* and *Passovia*, petal and stamen initiation occurs in two alternating groups of three parts. In all cases investigated here, there are clear developmental, positional, morphological, and anatomical differences between the calyx and the corolla that do not support Van Tieghem's interpretation. Furthermore, given that the calyx encloses and participates in the formation of the ovary (figs. 1*A*, 1*E*, 1*G*–1*I*, 3*B*, 4*A*, 7*B*, 7*H*, 11*A*, 11*D*, 11*H*, 12*A*–12*C*, 12*J*), the interpretation of the ovary as inferior should be based on its position with respect to the nectarial disk, the petals, and the stamens.

As a rule in the family, petals often have valvate aestivation. Petals are free, but their margins become interlocked postgenitally, which appears to be the plesiomorphic condition in the family. Kuijt (2015) mentioned some gamopetalous taxa, including one Mexican species of *Cladocolea* (*Cladocolea biflora*) and species of the Old World *Alepis* Tiegh., *Amylotheca* Tiegh., *Distrianthes* Danser, *Elythranthe* Blume, *Helicanthes* Danser, *Lampas* Danser, *Lepeostegeres* Blume, *Lepidaria* Tiegh., *Lysiana* Tiegh., *Macrosolen* (Blume) Reichenb., *Papuanthes* Danser, *Scurrula* L., *Sogerianthe* Danser, *Taxillus* Tiegh., *Thaumasianthus* Danser, *Trilepidea* Tiegh., and *Trithecanthera* Tiegh. Thus, gamopetaly appears to have evolved multiple times from dialypetalous corollas.

With respect to the perianth symmetry and merosity of the perianth in Loranthaceae, it is difficult to state these traits in the calyx, as it develops irregularly from a ring primordium. However, the early irregular development of the calyx in the family appears to be a plesiomorphic condition. This trait is found in early-diverging taxa, such as, e.g., *Nuytsia* (cf. Van Tieghem 1893) and *Gaiadendron* (fig. 6*A*–6*F*), as well as in more recently diverging lineages, such as *Aetanthus* (figs. 1*A*, 2*A*–2*C*). The opposite trend occurs in corolla evolution. A radially symmetrical corolla formed by five or more petals appears to be plesiomorphic, whereas few late-diverging taxa have monosymmetric corollas (restricted to Old World taxa, such as some species of *Dendrophthoe* Mart. and *Taxillus* Tiegh.; Wilson and Calvin 2006; Kuijt 2015). Tetramerous corollas in taxa such as *Peristethium* (fig. 12*C*, 12*F*) appear to be derived and intraspecifically labile. According to Wilson and Calvin (2006), a reduction of floral parts leading to tetramerous flowers has independently appeared several times from the hexamerous to the pentamerous condition.

Variation in the number of petals concurs with that in the number of stamens. Although the number of petals and stamens is labile even in the same species, overall evolution of this trait appears to proceed from flowers with six to eight petals and stamens (as in *Aetanthus*, *Gaiadendron*, *Nuytsia*, *Oryctanthus*, *Passovia*, and *Psittacanthus*; figs. 1*C*, 1*D*, 5*A*, 5*D*) to flowers with four or five petals and stamens (as in *P. archeri*; fig. 12*B*, 12*C*, 12*E*, 12*F*). Wilson and Calvin (2006) have mapped this reduction at least seven times inde-

pendently across the family. Flower size appears not to affect the number of petals or stamens; however, stamen sterilization was observed only in *P. pyrifolia*, the species with the smallest flowers in Loranthaceae.

The presence of an inner ligule in the petals of *Psittacanthus* appears to be species specific and of high taxonomic value in the genus (Eichler 1868; Kuijt 2009). Our finding of a subapical ligule in *P. krameri* (fig. 4*E*–4*G*) demonstrates that this structure is not limited to the base of the petals, as described by Kuijt (2009, 2015). The inner ligule appears independently in the South American *Ligaria* (subtribe Ligarinae) and in some Old World taxa (Kuijt 2009, 2015).

Androecium

Several accounts related to modifications of the anther wall structure and dehiscence and the sporangia organization in Old World Loranthaceae exist (Van Tieghem 1895; Staedtler 1923; Singh 1952; Davis 1966; Johri et al. 1992). According to Kuijt (2010), the gross morphology and size of stamens in New World taxa, particularly in *Gaiadendron* and *Psittacanthus*, are more variable than that found in the Old World taxa.

Given that the early-diverging members *Nuytsia*, *Atkinsonia*, and *Gaiadendron* (fig. 7*C*, 7*E*) and the members of the ((*Alepis*, *Peraxilla*) Elytranthinae) clade in the Loranthaceae (cf. Vidal-Russell and Nickrent 2008) have tetrasporangiate anthers, this condition appears to be plesiomorphic in the family. In this study, the polysporangiate anthers resulting from the formation of sterile parenchymatic transverse septa were observed only in *A. mutisii* (figs. 1*C*, 3*E*, 3*G*) and also appear in a number of *Psittacanthus* species (Kuijt 2009). These anthers maintain, however, a primarily thecal, tetrasporangiate organization. Polysporangiate anthers in Loranthaceae were already noticed by Eichler (1868) and Staedtler (1923). The formation of transverse parenchymatous septa could facilitate nutrition to developing microspores and pollen in long, massive anthers (González and Rudall 2010), although this hypothesis was questioned by Lersten (1971), who proposed that these septa could be indicative of an evolutionary shift toward size reduction of the anthers. The occurrence of polysporangiate anthers might also play a role in the maintenance of synchrony between sporogenous tissue and the tapetal cells (Endress and Stumpf 1990).

It is likely that the anthers with poricidal dehiscence reported by Kuijt (2009, 2015) in a few species of *Psittacanthus* in the New World (e.g., *Psittacanthus baguensis* Kuijt, *Psittacanthus crassifolius* (Martius) Martius, and *Psittacanthus ophiocephalus* Kuijt) correspond to an extreme form of polysporangiate anthers. In the Old World Loranthaceae, the polysporangiate anthers have evolved independently at least six times in species of *Amyema* Tiegh. (subtribe Amyeminae), *Dendrophthoe* and *Helixanthera* (subtribe Dendrophthoinae), *Elytranthe* (tribe Elytrantheae), *Phragmanthera* Tiegh. (subtribe Emelianthinae), *Septulina* Tiegh. (subtribe Tapinanthinae), and *Taxillus* Tiegh. (subtribe Scurrulinae; Engler and Krause 1935; Schaeppi and Steindl 1942; Maheshwari and Johri 1950; Endress and Stumpf 1990; Johri et al. 1992; Kuijt 2013, 2015).

The stamens in the two early-diverging lineages of Loranthaceae *Nuytsia* and *Atkinsonia* are uniform in size (Kuijt 2010), which indicates that this condition is plesiomorphic. According to Kuijt (2015), unequal (short and long) stamens occur almost

exclusively in New World taxa. We detected two forms of development of unequal stamens, one in *Gaiadendron*, where the stamens initiate almost simultaneously (fig. 6*H*) but exhibit two sizes in preanthesis and shift back to equal sizes by anthesis (fig. 5*A*), and a second one in which the three slightly longer stamens initiate first and alternate with the remaining three long stamens, as in, e.g., *P. pyrifolia* (fig. 10*D*) and *P. acinarius*. The rare trimorphic stamens described for species of *Gaiadendron* and *Psittacanthus* by Kuijt (2010, 2015) were not observed in our research.

The formation of the anther wall was described by Davis (1966) as of monocotyledonous type, as the primary parietal layer gives rise to two secondary parietal layers, one of which gives rise to the endothecium and the other to the middle layer and the tapetum. However, the anther wall in at least *Taxillus heyneanus* (Schult. f.) Danser has been described as being of the dicotyledonous type (Subrahmanyam et al. 2015). Thus, more detailed studies are needed to corroborate this trait across Loranthaceae, given that the anther wall undergoes significant modifications in several members of the family, including the ephemeral epidermis and the middle layers (Staedtler 1923; Johri et al. 1992).

Sterilization via reduction of the sporogenous tissue (as in *Passovia*) or reduction in the number of sporangia (as in *Peristethium*) appears to be the ongoing mechanism that has led to floral unisexuality and evolution of dioecy in these taxa. In *P. pyrifolia* the sporogenous tissue is strongly reduced to small flanking areas of the anthers (figs. 10*G*–10*I*, 11*F*, 11*G*; see also Kuijt and Weberling 1972). This particular type of anther was called the "Passovian anther" by Kuijt (2015, p. 76) and appears to occur in some other species of this genus, as well as in the closely related *Dendropemon* (Blume) Schult. and Schult. f., another member of the subtribe Psittacanthinae. On the other hand, anthers in *Peristethium*, reported by Kuijt (2012, 2015) as tetrasporangiate, have only two sporangia in all the flowers examined here (fig. 12*E*–12*G*).

Gynoecium and Mamelon

The extreme reduction of the ovary and the ovule as well as the ectopic growth and elongation of the embryo sacs upward into the style and the stigma in Loranthaceae was already reported in the seminal work by Griffith (1838, 1842). Thus, carpel number is particularly difficult to assess, except in the early-diverging genera *Nuytsia*, *Atkinsonia*, and *Gaiadendron*. The presence of six or seven locules and vascular traces and at least four mamelons in *Nuytsia* and *Gaiadendron* (fig. 7*B*; see also Van Tieghem 1893, 1894; Barlow 1964) suggests that this could be the plesiomorphic condition in the family.

Based on a number of embryological accounts in Loranthaceae (cf. Maheshwari and Singh 1952; Singh 1952; Narayana 1956; Maheshwari et al. 1957; Kapil and Vasil 1963, among others), Johri and Ambegaokar (1984) and Johri et al. (1992) summarized the reduction of the ovary in one series of six gradual steps: (1) ovary tetralocular with a fourlobed placenta (in, e.g., *Lysiana* Tiegh. and *Peraxilla* Tiegh.), (2) ovary trilocular with a threelobed placenta (*Amylotheca* Tiegh., *Lepeostegeres* Blume, and *Nuytsia*), (3) ovary unilocular with a threelobed placenta (e.g., *Elytranthe* Blume and *Macrosolen* (Blume) Reichenb.), (4) ovary unilocular and entire placenta (e.g., *Amyema gravis*, *Helicanthes*, and *Ta-*

pinostemma Tiegh.), (5) placenta transitory (e.g., *Amyema miquelii*, *Dendrophthoe pentandra*, *Dendrophthoe neelgherrensis*, *Scurrula montana*, *Struthanthus vulgaris*, and *Tolypanthus involucratus*), and (6) placenta absent (in, e.g., *Barathanthus* Miquel, *Dendrophthoe falcata*, and *Helixanthera* Lour.; see also lack of placenta in *Taxillus* reported by Subrahmanyam et al. 2015). Interestingly, the phylogenetic analyses by Wilson and Calvin (2006) and Vidal-Russell and Nickrent (2008) coincided in questioning the monophyly of *Amyema*, a genus with at least two species-specific reduction steps, i.e., ovary unilocular and placenta entire in *A. gravis* and placenta transitory in *A. miquelii* (Johri and Ambegaokar 1984; Johri et al. 1992).

In contrast to the one-way series of the reduction of ovary-ovule complex proposed by Johri and Ambegaokar (1984), Cocucci (1983) suggested a two-way series of gynoecium reduction and embryo specialization starting from tribe Nuytsieae, one way leading to tribes Tapinostemeae and Lorantheae and the second leading to tribes Elytrantheae and Lysianeae. In addition, Cocucci (1983) employed these characters to revise the tribal classification of the family (including the proposal of the new tribes Lysianeae and Tapinostemeae), which remains to be tested and compared with the recent phylogenetic analyses of the family by Wilson and Calvin (2006), Vidal-Russell and Nickrent (2008), and Nickrent et al. (2010).

Griffith (1838, p. 74) coined the term "nipple-shaped process" (called "mamelon" or "ovarian papilla" by later authors such as Treub [1881, 1883] and Johnson [1888], respectively) and considered this structure as "rather analogous to a placenta." More recent authors (e.g., Maheshwari and Johri 1950; Maheshwari et al. 1957; Dixit 1958; Johri 1963; Barlow 1964; Johri and Ambegaokar 1984; Johri et al. 1992) have also been in favor of considering the mamelon as a modification of the placenta, mainly because it possesses tracheids and is sometimes lobed (as in, e.g., *Elythranthe* and *Macrosolen*; Maheshwari et al. 1957). However, such a simplistic explanation was challenged by Cocucci (1983, p. 67), who stated that "not all 'mamelons' should be regarded as homologous structures," as in some taxa these reduced structures contain archesporial tissue. The latter observation suggests that the mamelon may correspond to a modified ovule, an interpretation that received support by a recent evolutionary developmental study using gene expression to assess organ homology (Brown et al. 2010). These authors found canonical integument identity genes such as *AINTEGUMENTA* and *BELL1* in unitegmic ovules as well as in ategmic ovules or mamelons (Brown et al. 2010). Thus, gene expression suggests that the mamelon (at least in the species tested) may correspond to an ovule that has undergone extreme reduction, likely due to the fusion between nucellar and integument tissues and reduced cell division. Given that typical ovules are not formed in the early-diverging *Nuytsia*, *Atkinsonia*, and *Gaiadendron*, reduced ovules appear to be the plesiomorphic condition in the family.

The potential use of ovary and ovule characters in the phylogenetic analysis of the family is challenging due to (1) the lack of extensive embryological studies; (2) the difficulty in studying reduced structures, some of them intraindividually variable; and (3) the presence of several reduction steps in genera such as *Dendrophthoe*, whose monophyly has not been tested (Wilson and Calvin 2006; Vidal-Russell and Nickrent 2008). Also, some taxa show intermediate states in the series proposed by Johri

and Ambegaokar (1984) and Johri et al. (1992). For example, *P. pyrifolia* lacks a cavity, but an entire mamelon is present (Johri and Ambegaokar 1984), whereas members of *Tripodanthus* were described by Cocucci (1983) as having a trilocular ovary with a single placenta.

Whether the reduction of the ovary and the ovules occurs independently and whether it occurs in one way or two ways are questions beyond the scope of this article. The two scenarios explained above coincide, in that a multilocular ovary and a lobed placenta are plesiomorphic in the Loranthaceae and that the solid ovary is likely acquired via pseudomonomery (see González and Rudall 2010 for a review on this trait). Interestingly, this reduction of the ovary does not compromise the formation of the nectarial disk, the style, or the stigma, which are functionally and structurally specialized (figs. 1*D*, 2*H*, 3*E*, 3*H*, 4*D*, 4*F*, 7*D*, 7*G*, 8*G*, 8*H*, 9*G*, 11*J*, 11*K*, 12*D*–12*F*, 12*H*), or the production of viable embryo sacs, proembryos, and embryos, which develop ectopically in the style and the stigma.

A Comment on Pollination

According to Kuijt (2015), the extreme floral diversity found in Loranthaceae is related to the pollination mechanisms in the family. Entomophyly and ornitophyly appear to occur in both early- and late-diverging lineages and in taxa from both the Old World and the New World, and shifts between these two types of pollination have likely occurred in parallel in Old World and New World taxa (Vidal-Russell and Nickrent 2008). However, entomophyly appears to be more common in small-flowered taxa. Ladley et al. (1997) have also documented the occurrence of explosive flowers in species of at least eight genera, mainly from the Old World. Ladley et al. (1997) detected that taxa with hermaphroditic flowers are bird pollinated, whereas the dioecious or subdioecious taxa are insect pollinated.

Birds are considered to be the primary pollen vectors in most Loranthaceae of the Old World (e.g., Bernhard and Knox 1983; Feehan 1985; Yumoto et al. 1997) and the New World (Amico et al. 2007). In members of the New Zealand *Peraxilla*, ornitophyly appears to be critical in the conservation and reproductive success (Robertson et al. 1999).

Hummingbirds have been considered the primary pollinators of *Aetanthus* and *Psittacanthus* (Azpeitia and Lara 2006; Kuijt 2009, 2014). However, our findings that anthers open during preanthesis, releasing mature pollen grains in *Aetanthus* (figs. 1*C*, 3*E*–3*I*), and that some older flowers transition to fruit without entering anthesis in *Psittacanthus* (V. Suaza-Gaviria, personal observations) indicate that cleistogamy might occur, considering that the anthers form a tube that tightly encloses the style and that it is in close contact to the stigma. Thus, ornitophyly in *Aetanthus* and *Psittacanthus* could be an additional mechanism that may increase cross-pollination. Far from being uncommon, self-compatibility is known to occur in *Alepis* (Ladley et al. 1997), and anther dehiscence and formation of fertilized embryo sacs and embryos in preanthetic flowers have been reported in *Amyemia* (Blakely 1922) and *Helixanthera* (Maheswari and Johri 1950; Bernhard et al. 1980), both Old World Loranthaceae.

Conclusion

The flower development and anatomy of species from both early-diverging (*Gaiadendron*) and late-diverging (*Aetanthus*, *Oryctanthus*, *Passovia*, *Psittacanthus*) New World genera indicate that plesiomorphic conditions in Loranthaceae include bisexual, dichlamydeous flowers with six or seven petals and stamens; an ovary with discrete locules and mamelons (up to seven in *Gaiadendron*); and tetrasporangiate stamens, with versatile, latrorsely dehiscent anthers. The formation of a cupular pedicel with structural and developmental differences was found in both small-flowered (*Passovia*) and large-flowered (*Aetanthus* and *Psittacanthus*) taxa, which suggests independent acquisition events within the subtribe Psittacanthineae. The reduction that leads to staminate flowers in *Passovia* and *Peristethium* might be caused by endothecial invasion of the anther locules in the former and by loss of the anther locules in the latter. The autapomorphic polysporangiate anthers were found in *Aetanthus mutisii*. In this species, cleistogamy may occur, followed by additional facultative hummingbird pollination. Finally, pseudomonomery drives the reduction of the ovary without compromising the formation of embryo sacs, fertilization, nectar disks, styles, or stigmas.

Acknowledgments

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