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Research article

Palynological characterization and taxonomical delimitation of the subgenera within *Passiflora* L. (Passifloraceae: Malpighiales), the largest genus of lianas in the Neotropics

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Abstract. *Passiflora* L., the largest genus of Neotropical lianas, belongs to the family Passifloraceae and encompasses 615 accepted species as concluded in the present research. Historically, various taxonomic classifications have been proposed for the genus. One such proposal divided the genus into 23 subgenera. Subsequent revisions reduced this number to four and later expanded it to the six currently recognized subgenera. Recent phylogenetic analyses using molecular markers have confirmed the monophyly of these subgenera. However, no study has used pollen characteristics for the taxonomic delimitation of subgenera of *Passiflora*. Given the importance of pollen morphology in taxonomy, this study aims to present taxonomic and palynological descriptions, illustrations, an identification key, and a list of species of the subgenera *Astrophea*, *Deidamioides*, *Decaloba*, *Passiflora*, *Tetrapathea*, and *Tryphostemmatoides*.

Keywords. *Astrophea*, *Decaloba*, *Deidamioides*, *Tetrapathea*, *Tryphostemmatoides*.

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Introduction

Passiflora L., a genus encompassing 600 to 700 species mostly native to the Americas, belongs to the family Passifloraceae Juss. ex Roussel and is the largest genus of lianas in the Neotropics (Acevedo-Rodríguez *et al.* 2015; Feuillet & Acevedo-Rodríguez 2020; Kuethe 2024). About 20 species are found in India, China, Southeast Asia, Australia, and Oceania (Bernacci 2003; Ulmer & MacDougal 2004; Krosnick *et al.* 2009). The first classification within *Passiflora* (Supp. file 1) was proposed by de Candolle (1822). Based on vegetative and reproductive morphology, especially floral morphology, this classification was further refined (Harms 1925; Killip 1938; Escobar 1988, 1989), resulting in a total of 23 subgenera, which remained unchanged until the end of the twentieth century (Cervi 1997).

A morphological phylogenetic analysis was then conducted, resulting in the division of the genus *Passiflora* into only four subgenera. Although significant changes were made to the delimitation of subgenera (except for *Astrophea* (DC.) Mast.), Feuillet & MacDougal (2003) did not present circumscriptions or identification keys, as their publication focused on validating new taxa and combinations.

Molecular phylogenetic analyses have confirmed the monophyly of the genus *Passiflora*, but there is no consensus on infrageneric classifications (Yockteng & Nadot 2004; Hansen *et al.* 2006). Some studies supported the monophyly of only three subgenera: *Passiflora*, *Decaloba* (DC.) Rchb., and *Astrophea* (Muschner *et al.* 2003, 2012). Others suggested incorporating *Hollrungia* K.Schum. into *Passiflora* and creating a fifth subgenus, *Tetrapathea* (DC.) P.S.Green (Krosnick *et al.* 2009, 2013). Additionally, discussions on the restoration of the subgenus *Tryphostemmatoides* (Harms) Killip eventually led to its acceptance as a sixth subgenus (Supp. file 1) in recent taxonomic publications (Yockteng & Nadot 2004; Muschner *et al.* 2012; Krosnick *et al.* 2013; Buitrago *et al.* 2018; Chávez-Corcuera & Fernandez-Hilario 2019; Restrepo *et al.* 2019). Of the six currently recognized subgenera, *Astrophea* and *Tryphostemmatoides* are the most basal lineages in the genus *Passiflora*, whereas *Deidamioides* (Harms) Killip is closely related to *Passiflora* and *Tetrapathea* to *Decaloba* (see Krosnick *et al.* 2013).

Karyotype analyses revealed independent polyploidization events in *P. tetrandra* Banks ex DC. and *P. deidamioides* Harms (Sader *et al.* 2019), supporting the distinctiveness of *P.* subgen. *Tetrapathea* from *P.* subgen. *Deidamioides*. Chloroplast DNA analysis confirmed the polyphyletic nature of *P.* subgen. *Deidamioides* (sensu Feuillet & MacDougal 2003) and indicated *P.* subgen. *Tryphostemmatoides* as a distinct sister group of *P.* subgen. *Astrophea*, which had already been suggested by Krosnick *et al.* (2013) (Pacheco *et al.* 2020). However, since Feuillet & MacDougal's (2003) recognition of four subgenera of *Passiflora*, no morphological circumscriptions have been presented for these or subsequent subgeneric classifications.

Several studies have used pollen morphology for species recognition and taxonomic treatment within the Passifloraceae (Presting 1965; Spirlet 1965; Araújo & Santos 2004; Milward-de-Azevedo *et al.* 2004, 2010, 2014; Dettke & Santos 2009; Mezzonato-Pires *et al.* 2015a, 2015b, 2017, 2019, 2020; Richardo & Silvério 2019; Araújo *et al.* 2020; Cruz *et al.* 2020). Pollen morphology has proven diagnostic for distinguishing species of the subgenera *Passiflora* and *Decaloba*, particularly features such as aperture type and exine ornamentation pattern (Soares *et al.* 2018). The subgenus *Passiflora* was described as having 6-syncolpate pollen, with large-lumen exines. *Passiflora* subgen. *Decaloba* was characterized by 6- or 12-colporate or 12-colpate pollen with exines having smaller lumina. Additionally, pollen morphology was shown to have diagnostic value for species of these subgenera (Soares *et al.* 2018). A comprehensive study including these subgenera and representatives of the subgenus *Astrophea* reported that pollen grains from *P.* subgen. *Passiflora* could be recognized by their large size and absence of endoaperture (Richardo & Silvério 2019). Analysis of pollen grains from representatives of the subgenus *Deidamioides* (sensu Feuillet & MacDougal 2003) showed a lack of uniformity in pollen characters and suggested that the subgenus was polyphyletic, sharing characteristics with members of the *P.* subgen. *Astrophea*,

P. subgen. *Decaloba*, and *P.* subgen. *Passiflora* (Araujo *et al.* 2021). Other studies on pollen morphology have primarily focused on species within *P.* subgen. *Decaloba* (Milward-de-Azevedo *et al.* 2010, 2014) and *P.* subgen. *Astrophea* (Mezzonato-Pires *et al.* 2015b, 2017), failing to conduct thorough comparisons. No palynological study has characterized the six currently recognized subgenera of *Passiflora*.

This study aims to identify pollen characteristics to assist in delimiting the six currently recognized subgenera of *Passiflora*: *Astrophea*, *Deidamioides*, *Decaloba*, *Passiflora*, *Tetrapathea*, and *Tryphostemmatoides*. Addressing the lack of comprehensive circumscriptions, this article provides detailed morphological and palynological descriptions, illustrations, an identification key, and an updated list of species.

Material and methods

Morphological analysis was based on the experience acquired by our research group over numerous scientific investigations and supported by bibliographical sources on *Passiflora*, including historical literature (Biodiversity Heritage Library, <https://www.biodiversitylibrary.org/>), and recent complementary examinations of specimens (Supp. file 2).

In the delimitation system adopted herein, *P.* subgen. *Deidamioides* includes both the species forming a sister group to *P.* subgen. *Passiflora* (Krosnick *et al.* 2013) and species taxonomically related to *P. ovalis* Vell., i.e., *P.* sect. *Tetrastylis* (Barb.Rodr.) Harms (listed in Bernacci *et al.* 2025). *Passiflora* subgen. *Tryphostemmatoides* includes the species indicated by Restrepo *et al.* (2019) based on a monophyletic group (Krosnick *et al.* 2013). Each entry of the list of species used as a reference (Kuethe 2024) was checked for correspondence to the accepted name and had the authorship formatted according to current standards (IPNI 2024; <https://www.ipni.org/about#about-authors>).

Pollen material (flower buds) was obtained from national and international herbaria (CESJ, HAMAB, IAC, INPA, MBM, MEXU, MO, NY, R, RB, RBR, UB, and UPCB, acronyms according to Thiers 2021). Pollen grains were collected from representative species of the six subgenera and analyzed by light microscopy and scanning electron microscopy (SEM). In total, 33 species were examined (see vouchers in Supp. file 2), including 7 from *P.* subgen. *Astrophea*, 11 from *P.* subgen. *Decaloba*, 2 from *P.* subgen. *Deidamioides*, 10 from *P.* subgen. *Passiflora*, 2 from *P.* subgen. *Tetrapathea*, and 1 from *P.* subgen. *Tryphostemmatoides*. For light microscopy, samples were prepared by the acetolysis method of Erdtman (1952) with the modifications proposed by Melhem *et al.* (2003). Measurements and photomicrographs of pollen grains were taken using a Zeiss Axiostar Plus microscope at the Álvaro Xavier Moreira Laboratory of Palynology, Department of Botany, National Museum, Federal University of Rio de Janeiro, Brazil. For SEM analysis, anthers were excised from flowers of voucher specimens and opened with flame-sterilized tweezers and a cutting knife. Thus, it was possible to release the pollen grains directly onto a metal stub covered with double-sided carbon tape. The non-acetolyzed material was sputtered with pure gold for 3 min. Electron micrographs were taken using a JEOL JSM-6510 microscope at the Laboratory of Optical and Scanning Electron Microscopy Imaging of the Institute of Biology, Federal University of Rio de Janeiro, and a Zeiss DS M960 at the Laboratory of Cell Ultrastructure of the Institute of Biophysics, Federal University of Rio de Janeiro.

The following studies were considered reference sources of information on the genus and used to support and complement palynological descriptions of subgenera: Spirlet (1965), Araújo & Santos (2004), Milward-de-Azevedo *et al.* (2010, 2014), Evaldt *et al.* (2011), Mezzonato-Pires *et al.* (2015a, 2015b, 2017), Richardo & Silvério (2019), Araújo *et al.* (2020), Cruz *et al.* (2020), and Araújo *et al.* (2021). The number and species studied in the current and reference articles are listed in Supp. file 3. The terminology adopted for the operculum type of Passifloraceae pollen grains (Fig. 1) follows those of Wodehouse (1935), Erdtman (1952), Spirlet (1965), Presting (1965), and Punt *et al.* (2007). The operculum is defined according to the concepts of Wodehouse (1935) and Punt *et al.* (2007): a distinct region of sexine/ektexine

that covers part of the aperture and is completely isolated from the rest of the sexine. For Presting (1965), what is commonly referred to as the operculum corresponds to the secondary operculum. The definition for the pontoperculum follows those of Erdtman (1952), Spirlet (1965), and Punt *et al.* (2007), namely a type of operculum that is not completely isolated from the rest of the sexine but connected to it by the ends of the apertures. For Presting (1965), the so-called pontoperculum corresponded to the primary operculum. The pseudoperculum is defined according to Presting (1965), who described it as a region delimited by the fusion, in pairs, of the ends of the apertures and that functions as an operculum during the growth of the pollen tube and is easily detached from the rest of the exine during palynological preparations. Lumina are classified according to their width into small (1.0–10.9 μm) and large (11.0–25.0 μm).

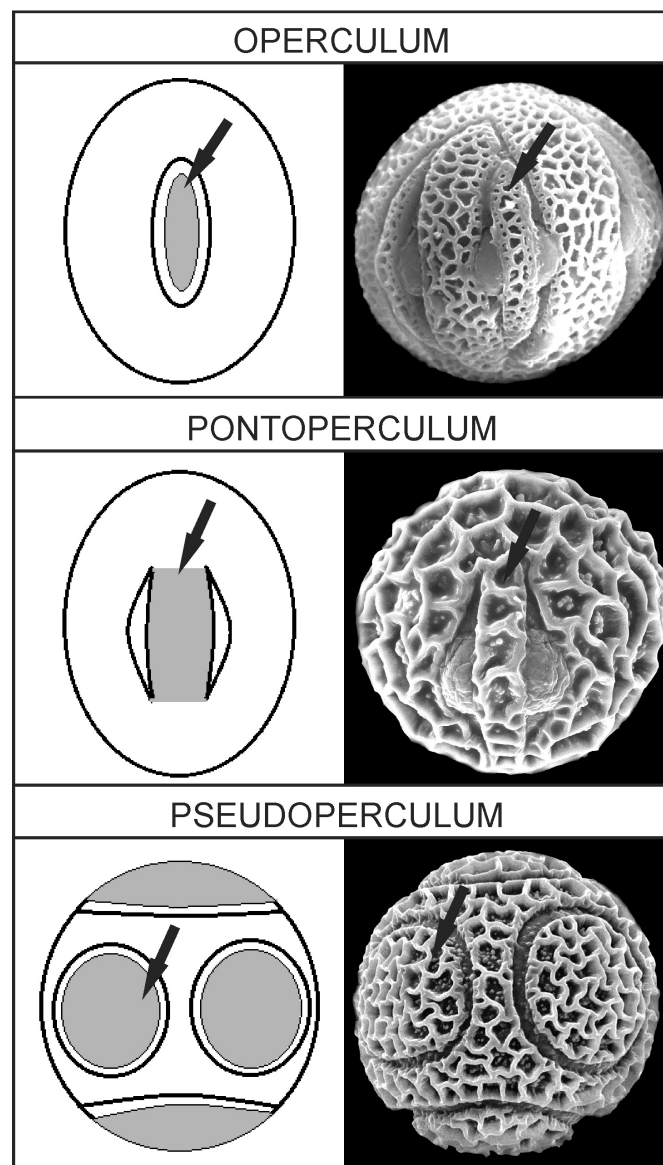


Fig. 1. Types of opercula (black arrows) found in pollen grains of *Passiflora* L. Operculum in *Passiflora konzattiana* Killip (*E. Carranza* 688, MO). Pontoperculum in *Passiflora maguirei* Killip (*B. Maguire & D.B. Fanshawe* 23285, NY). Pseudoperculum in *Passiflora actinia* Hook (*A.C. Cervi et al. s.n.*, MBM 385343).

Macromorphological plates are arranged, whenever possible, by habit, petiolar gland, leaf blade, stipule, bract, and flower characters. Palynological plates are organized according to the pollen characters that exhibits the highest variability within each subgenus (Figs 2–11). The image created by Krosnick *et al.* (2013) to depict the framework of their phylogenetic hypothesis based on combined nuclear markers (nrITS, ncpGS, *trnL-F*, and *ndhF*) was adapted and is presented here (Fig. 12) to discuss the analyzed characters.

Results

The most conspicuous vegetative characteristics of species of the subgenus *Astrophea* include two glands near the apex of the petiole, simple and entire leaves, and small stipules. As for floral characteristics, species belonging to *P.* subgen. *Astrophea* have small bracts and absent limen. Pollen grains exhibit four types of sexine (intectate, partially tectate, semitectate with continuous muri, and semitectate with discontinuous muri), two of which (intectate and partially tectate) are unique, differing from those of other subgenera. Furthermore, *P.* subgen. *Astrophea* has the greatest variability in exine structure and ornamentation.

Vegetatively, *P.* subgen. *Decaloba* is characterized by slender stems and lobed leaves with ocelli in most species. Flowers are small. The subgenus finds ample palynological support, as it bears all types of opercula (operculum, pseudoperculum, and pontoperculum) and an increased number of apertures and endoapertures. The subgenus *Passiflora* has no endoapertures but may contain a large number of apertures (14). The only types of opercula are the pseudoperculum and, in a few species, the pontoperculum.

Species of the subgenus *Deidamioides* may possess or not adhesive disks, and most species have entire, simple leaves. It is the only group that can have composite leaves, such as those found in *Passiflora cirrhiflora* Juss. and *Passiflora deidamioides*. Bracteoles and limina are always present. Some species have three styles and stigmas whereas others have four. Species with four styles were originally described in the genus *Tetrastylis* Barb.Rodr., now synonymized under *Passiflora* subgen. *Deidamioides*. The subgenus has pollen grains with only one type of aperture (6-colporate), sexine semitectate with continuous or discontinuous muri, and simpliculumellate, forming small lumina (1.0–10.4 µm). These characteristics are not exclusive to *P.* subgen. *Deidamioides*; they also occur in species of other subgenera. Large lumina are only observed in the subgenera *Astrophea* and *Passiflora*, and, in *Astrophea*, lumina may measure up to 24.5 µm in width, because of the discontinuous muri.

In summary, ornamentation of the sexine proved to be the most differentiating aspect for recognizing species of *P.* subgen. *Astrophea*, *P.* subgen. *Deidamioides*, and *P.* subgen. *Tetrapathea*. Aperture number and type were the most distinctive characters for *P.* subgen. *Decaloba*; polarity, aperture number and type, and ornamentation for *P.* subgen. *Passiflora*; and aperture type for *P.* subgen. *Tryphostemmatoides*.

A dichotomous key was constructed based on morphological characters conventionally used in taxonomic studies, as well as on pollen characters, which allowed the six currently recognized subgenera of *Passiflora* to be distinguished, as follows.

Key to six currently recognized subgenera of *Passiflora*

- 1 Plants dioecious, with differences in the size of the gynoecium and/or androecium and/or in the number of parts of the gynoecium and presence/absence of nectariferous disk between plants of different sexes; hypanthium flat, petals and sepals (3)4 or (4)5, stamens 4 (*P. tetrandra*) or variable number, (3)4–5 in *P. aurantioides* (K.Schum.) Krosnick or 6–8 in *P. kuranda* Krosnick & A.J.Ford, bracts 2, minute; leaves simple, entire, ocelli present; pollen 6-colporate, polar area very small, amb subcircular. Species exclusively native to Oceania *Tetrapathea* (DC.) P.S.Green

- Plants monoecious; nectariferous disk absent and/or present, hypanthium flat to tubular, petals and sepals 5 (petals rarely absent), stamens 5, bracts (2)3, minute to foliaceous; leaves simple or compound, lobed or entire, ocelli present or not; pollen 6- or 12-colpate or 6- or 12-colporate or 6-syncolporate or 5–10-, 12-, or 14-syncolpate, polar area very small, small or large, amb circular, subcircular to subtriangular. Species native to the Americas, Asia, or Oceania 2
- 2 Tendrils branched; leaves simple, entire, ocelli absent; hypanthium shortly campanulate to campanulate; pollen 6-syncolporate or 6-colporate, amb subcircular or subtriangular. Species exclusively native to the Americas *Tryphostemmatoides* (Harms) Killip
- Tendrils simple (rarely absent); leaves simple or compound, entire or lobed, ocelli present or absent; hypanthium shortly campanulate to campanulate, cylindrical to cylindrical-campanulate or funnellform; pollen 6- or 12-colpate or 6- or 12-colporate or 5–10-, 12-, or 14-syncolpate, amb circular to subtriangular. Species native to the Americas, Asia, or Oceania 3
- 3 Leaves simple, entire, ocelli absent; petiolar glands 2, sessile, concave, near or at the apex or at the junction with the leaf blade on the abaxial surface; styles 3; pollen 6-colporate, colpi short or long, endoapertures lalongate. Species exclusively native to the Americas *Astrophea* (DC.) Mast.
- Leaves simple or compound, lobed or entire, ocelli present or absent; petiolar glands (0)2–many, sessile or stipulate, never on the abaxial surface; styles 3(4); pollen 6- or 12-colpate or 6- or 12-colporate or 5–10-, 12-, or 14-syncolpate, colpi long, endoapertures often lolongate or absent or lalongate or circular. Species native to the Americas, Asia, or Oceania 4
- 4 Leaves simple and entire with tendrils bearing an adhesive disk or leaves 3- or 5–7(9)-compound; ocelli absent; styles/stigmas 4; pollen 6-colporate, colpi narrow, amb subcircular or subtriangular. Species exclusively native to the Americas *Deidamioides* (Harms) Killip
- Leaves simple, lobed or entire, tendrils without adhesive disk (present only in *P. obovata* Killip ex Standl.); ocelli present or absent; styles/stigmas 3; pollen grains 6- or 12-colpate or 6- or 12-colporate or 5–10-, 12-, or 14-syncolpate, colpi narrow or wide, amb circular or subcircular. Species native to the Americas, Asia, or Oceania 5
- 5 Stipules foliaceous (rarely minute); petiolar glands (0)2–many; bracts well developed, often verticillate (rarely minute or alternate); hypanthium campanulate, cylindrical, cylindrical-campanulate, funnellform, or flat; corona 1–many-seriate, whitish, purple, violet, pink, red, or a combination of these colors; operculum smooth (plicate in the series *Kermesinae*), entire or filamentous at the apex; pollen 6-colpate or 5–10-, 12-, or 14-syncolpate, endoapertures absent. Species exclusively native to the Americas *Passiflora* L.
- Stipules minute (rarely foliaceous); petiolar glands 2 or absent; bracts minute, alternate; hypanthium flat, very rarely campanulate or tapered; corona 1–2-seriate, whitish or banded red or purple, operculum plicate; pollen 12-colpate or 6- or 12-colporate, endoapertures often lolongate or lalongate or circular. Species native to the Americas, Asia, or Oceania *Decaloba* (DC.) Rchb.

Using morphological and palynological characters (Figs 2–12) and published data, it was possible to construct descriptions (detailed below) and determine the distribution of species within subgenera (Supp. file 2). A total of 615 currently accepted species were listed, including 3 additions to the reference list, 48 synonyms, 30 unpublished names, 1 dubious name, 6 new combinations (taxa not currently at species status), and 3 hybrids excluded (Supp. file 2).

Class Magnoliopsida Brongn.
Order Malpighiales Juss. ex Bercht. & J.Presl
Family Passifloraceae Juss. ex. Roussel
Tribe Passifloreae DC.
Genus *Passiflora* L.

Passiflora subgenus *Astrophea* (DC.) Mast.
Figs 2–3

Passiflora subgenus *Astrophea* (DC.) Mast. (Masters 1871: 629). — *Passiflora* section *Astrophea* DC. (de Candolle 1822: 435).

(69 spp.)

Taxonomic description

Vines slender to woody, shrubs, or trees; monoecious; *tendrils* absent or present (in most species), entire, without adhesive disks; *stipules* minute, most often deciduous; *glands* 2, at or near the apex or on the abaxial surface at the leaf–petiole junction; *leaves* simple, entire, *ocelli* absent; *main rib* 1; *inflorescences* 1-flowered, 2-flowered, or racemose; *bracts* 3, minute, most often deciduous; *hypanthium* cylindrical, cylindrical-campanulate, funnellform, or campanulate; *flowers* whitish, yellowish-orange, pink, or orange to reddish-orange, corona of the same color; *sepals* 5; *petals* 5; *corona* with (1)2–many series of filaments; *operculum* erect or flexed, tubular or not, papillate or not, fimbriate, lacerate, lacinate, flabellate; *nectariferous disk* absent; *limen* absent; *trochlea* present or absent, *stamens* 5; *styles* 3, *stigmas* 3; *fruit* a berry (Fig. 2).

Pollen description

Pollen grains medium or large; isopolar; subprolate, oblate-spheroidal, or prolate-spheroidal; polar area small or large; amb subcircular, circular, or subtriangular; 6-colporate; colpi short or long, narrow or wide; endoapertures 3, lalongate, one for each pair of colpi; pontopercula 3; mesocolpia 3; sexine diversely ornamented, intectate (granulate-baculate-spinulose), partially tectate, muri around apertures in higher or lower amounts; sexine duplicolumellate, with lumina lacking; pila and bacula present and very conspicuous or pila densely distributed and conspicuous and bacula sparsely distributed, or semitectate (muri continuous or discontinuous, simplicolumellate or duplicolumellate; lumina large (11.3–24.5 µm) or small (1.2–8.6 µm); bacula and/or pila present or absent). Sexine thicker than nexine, total exine 1.9–7.6 µm (Fig. 3).

Passiflora subgenus *Tryphostemmatoides* (Harms) Killip
Fig. 4A–F

Passiflora subgenus *Tryphostemmatoides* (Harms) Killip (Killip 1938: 24). — *Passiflora* section *Tryphostemmatoides* Harms (Harms 1925: 500).

(6 spp.)

Taxonomic description

Vines slender to woody; monoecious; *tendrils* branched (2–4), adhesive disks present or absent; *stipules* minute (0.2–3 × 0.1–1 mm), sometimes deciduous; *glands* 0–2–4–6, at the petiole apex at the leaf–petiole junction; *leaves* simple, entire; *main rib* 1; *ocelli* absent; *inflorescences* 1- or 2-flowered, ending or not in a tendril, *bracts* 2–3, usually minute (0.5–2 × <0.1 mm), long in *P. tryphostemmatoides* (8–12 mm) and *P. arbelaezii* L.Uribe (5–13 mm), in which it can be wide (<5 mm), bracteoles present or absent; *hypanthium* shortly campanulate to campanulate; *flowers* greenish, yellowish-green, with corona banded white and yellow or yellow-orange, apex white; *sepals* 5; *petals* 5; *corona* with 1–3 series of filaments;

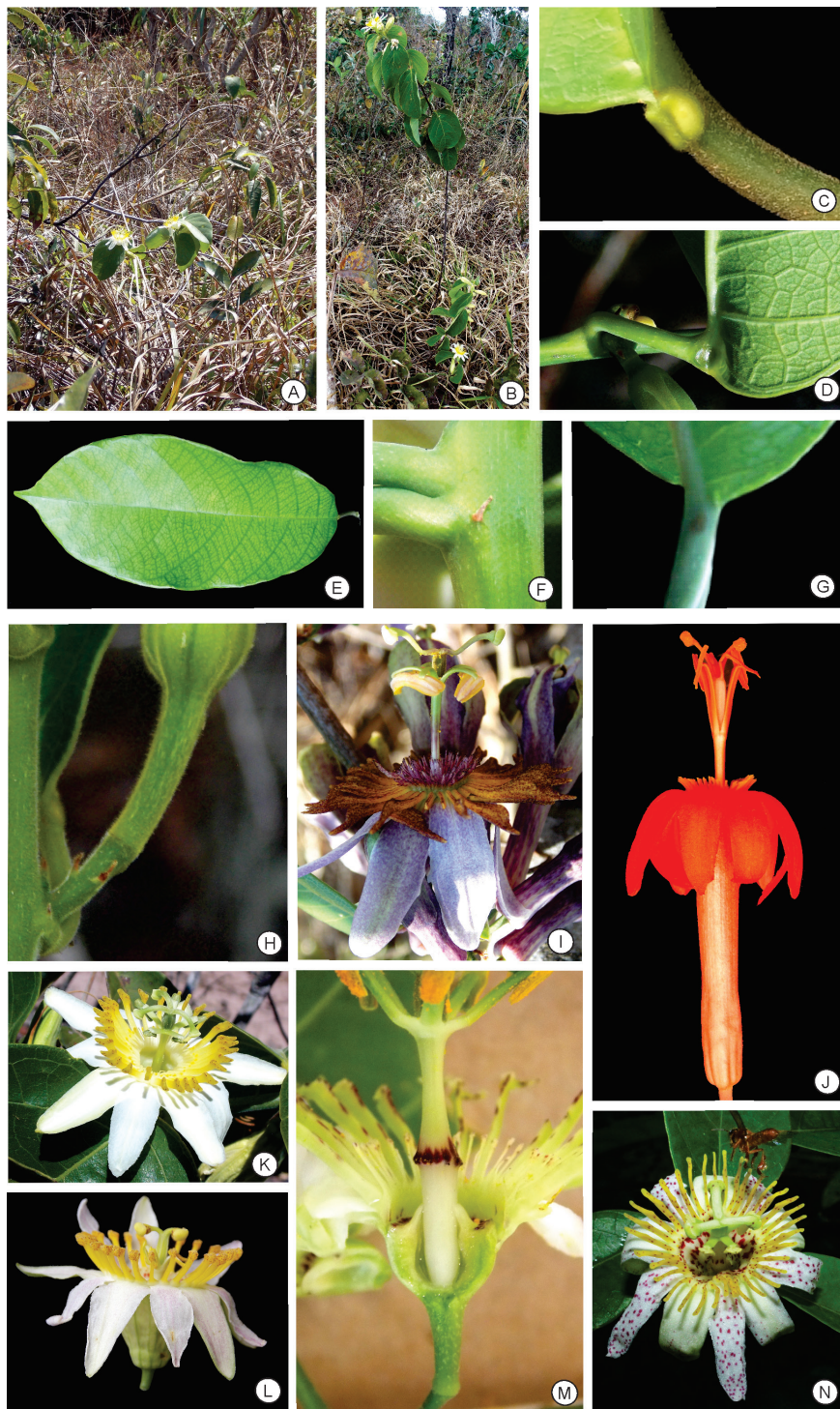


Fig. 2. External morphology of *Passiflora* subgen. *Astrophea* (DC.) Mast. **A.** Lianescent habit of *P. mansoi* (Mart.) Mast. **B.** Undershrub habit of *P. mansoi* (Mart.) Mast. **C.** Detail of the glands of *P. candida* (Poepp. & Endl.) Mast. **D.** Detail of the glands of *P. faroana* Harms. **E.** Leaf blade of *P. candida* (Poepp. & Endl.) Mast. **F.** Stipule of *P. costata* Mast. **G.** Detail of the glands of *P. pittieri* Mast. **H.** Bracts of *P. haematostigma* Mart. ex Mast. **I.** Flower of *P. cerradensis* Sacco. **J.** Flower of *P. securiclata* Mast. **K.** Flower of *P. mansoi* (Mart.) Mast. **L.** Flower of *P. hexagonocarpa* Barb.Rodr. **M.** Longitudinal section of the flower of *P. rhamnifolia* Mast. **N.** Flower of *P. phaeocaula* Killip. Photographs were taken by A.C. Mezzonato (A–M) and L.O. Demarchi (N).

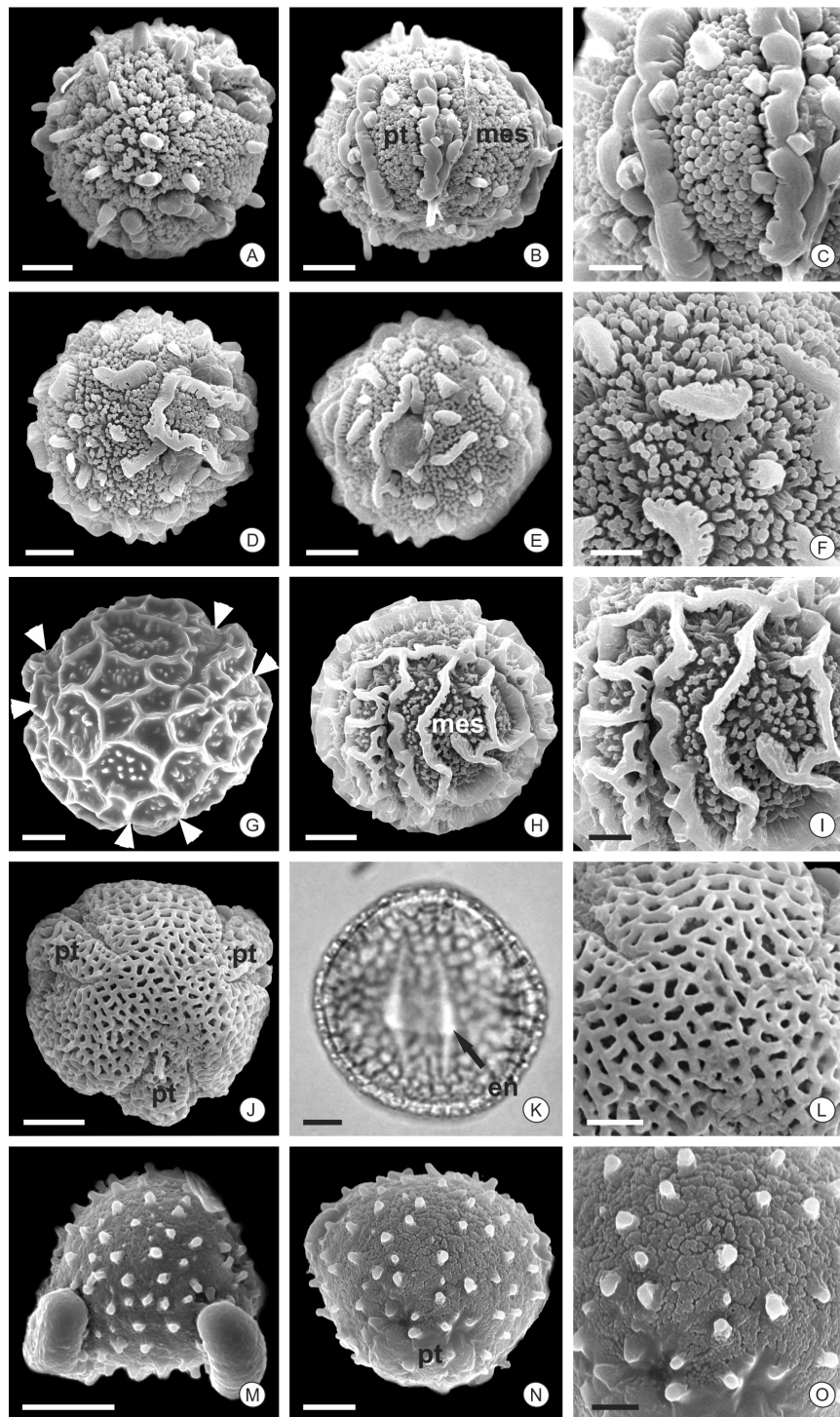


Fig. 3. Pollen grains of *Passiflora* subgen. *Astrophea* (DC.) Mast. **A–C.** *P. cauliflora* Harms (*A. Ducke s.n.*, RB 34968). **D–F.** *P. jussieui* Feuillet (*C.A.C. Ferreira 8915*, INPA). **G.** *P. maguirei* Killip (*B. Maguire & D.B. Fanshawe 23285*, NY). **H–I.** *P. cardonae* Killip (*R. Ziesner et al. 21139*, NY). **J, L.** *P. mansoi* (Mart.) Mast. (*A.C. Mezzonato & R.M. Souza-Souza 101*, R). **K.** *P. amoena* L.K.Escobar (*S.V. Costa Neto et al. 2818*, HAMAB). **M–O.** *P. macrophylla* Spruce ex Mast. (*A.J. Gilmartin 513*, NY). Polar view (A, D, G, J, M–N), equatorial view (B, E, H, K), detail of ornamentation (C, F, I, L, O). Abbreviations: en = endoaperture; mes = mesocolpium; pt = pontoperculum; arrowheads = apertures. Scale bars: A–B, D–E, G–H, J–K, N = 10 µm; C, F, I, L, O = 5 µm; M = 20 µm.

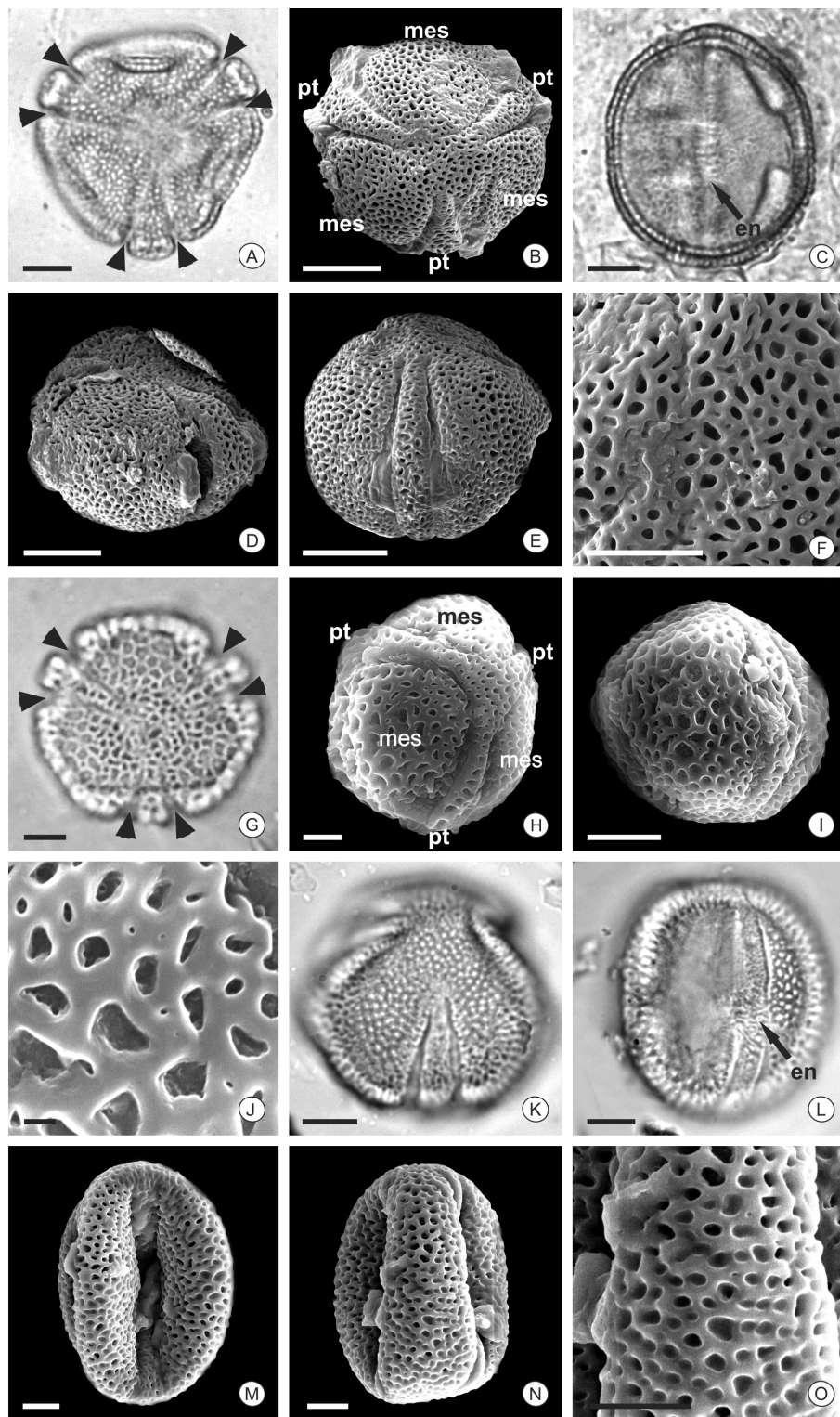


Fig. 4. Pollen grains of *Passiflora* subgen. *Tryphostemmatoides* (Harms) Killip (A–F) and *P.* subgen. *Tetrapathea* (DC.) P.S.Green (G–O). A–F. *P. tryphostemmatoides* Harms (*Idrobo, Pinto & Bischler* 2874, MBM). G–J. *P. aurantioides* (K.Schum.) Krosnick (*W. Takeuchi & D. Ama* 16355, MO). K–O. *P. tetrandra* Banks ex DC. (*K. Wood* 28426, MO). Polar view (A–B, G–H, K), equatorial view (C–E, I, L–N), detail of ornamentation (F, J, O). Abbreviations: en = endoaperture; mes = mesocolpium; pt = pontoperculum; arrowheads = apertures. Scale bars: A–E, G, I, K–L = 10 μ m; F, H, M–O = 5 μ m; J = 1 μ m.

operculum plicate, smooth, or laciniate, erect, membranaceous; *nectariferous disk* present (not described for *P. nebulosae* J. Restrepo & Ocampo); *limen* cupuliform to anneliform, membranaceous; *trochlea* present or absent in most species, *stamens* 5; *styles* 3, *stigmas* 3; *fruit* a berry.

Pollen description

Pollen grains medium or large; isopolar; oblate, subprolate, or prolate-spheroidal; polar area very small; amb subcircular or subtriangular; 6-syncolporate or 6-colporate, colpi long and wide; endoapertures 3, lalongate, one for each pair of colpi, or endoapertures 6, circular, one for each colpus; pontopercula 3 and mesocolpia 3 or pontopercula 3 and pseudopercula 3; sexine semitectate (muri continuous, simplicolumellate, lumina small (0.5–2.3 µm); bacula absent). Sexine as thick as or less thick than nexine, total exine 2.1–3.0 µm (Fig. 4A–F).

Passiflora subgenus *Deidamioides* (Harms) Killip Figs 5–6

Passiflora subgenus *Deidamioides* (Harms) Killip (Killip 1938: 25). — *Passiflora* section *Deidamioides* Harms (Harms 1923: 58).

(6 spp.)

Taxonomic description

Vines slender to woody; monoecious; *tendrils* missing or present (in most species), entire, adhesive disks present or absent; *stipules* minute (0.1–4 × 0.1–2 mm); *glands* 2–4–6, at the base of the lamina, below the lamina, near the base or middle of the petiole, or distributed in pairs near the petiole; *leaves* single, entire, or 5–9-composite; *ocelli* absent; *main rib* 1; *inflorescences* 1-flowered, 2-flowered, or racemose; *bracts* 3, very narrow (up to 2 mm), generally short (up to 5(7) mm) but longer in *P. contracta* Vitta (up to 20 mm), bracteoles present; *hypanthium* shortly campanulate, campanulate to infundibuliform; *flowers* whitish, white-green, yellow, with corona whitish to yellowish, reddish, lilac, and orange; *sepals* 5; *petals* 5; *corona* with 2–5 series of filaments; *operculum* plicate or not, apex laciniate, fimbriate; *nectariferous disk* present or absent; *limen* tubular, cupuliform, membranaceous; *trochlea* present or absent, *stamens* 5; *styles* 3–4, *stigmas* 3–4; *fruit* a berry (Fig. 5).

Pollen description

Pollen grains medium or large; isopolar; subprolate, oblate-spheroidal, or prolate-spheroidal; polar area small; amb subcircular or subtriangular; 6-colporate; colpi long and narrow; endoapertures 3, lalongate, one for each pair of colpi or endoapertures 6, circular, one for each colpus; pontopercula 3, mesocolpia 3; sexine semitectate (muri continuous or discontinuous, simplicolumellate; lumina small (1.0–10.4 µm); bacula present). Sexine as thick as or thicker than nexine, total exine 2.4–5.6 µm (Fig. 6).

Passiflora subgenus *Passiflora* Figs 7–9

(287 spp.)

Taxonomic description

Vines slender to woody; monoecious; *tendrils* entire, adhesive disks absent; *stipules* minute to foliaceous in most species; *glands* (0)2–many, distributed across the petiole; *leaves* simple, entire to lobed in most species; *ocelli* absent; *main ribs* 3; *inflorescences* 1-flowered (in most species), 2-flowered, racemose, or cymose; *bracts* 3, minute to well-developed in most species, bracteoles absent; *hypanthium* campanulate,



Fig. 5. External morphology of *Passiflora* subgen. *Deidamioides* (Harms) Killip. **A.** Climbing habit of *P. deidamioides* Harms. **B.** Leaf blade of *P. deidamioides* Harms. **C.** Flower of *P. contracta* Vitta. **D.** Blades and petiole glands of *P. contracta* Vitta. **E.** Detail of the inflorescence of *P. contracta* Vitta. **F.** Fruit of *P. contracta* Vitta. **G.** Flower of *P. deidamioides* Harms. Photographs were taken by A.C. Mezzonato.

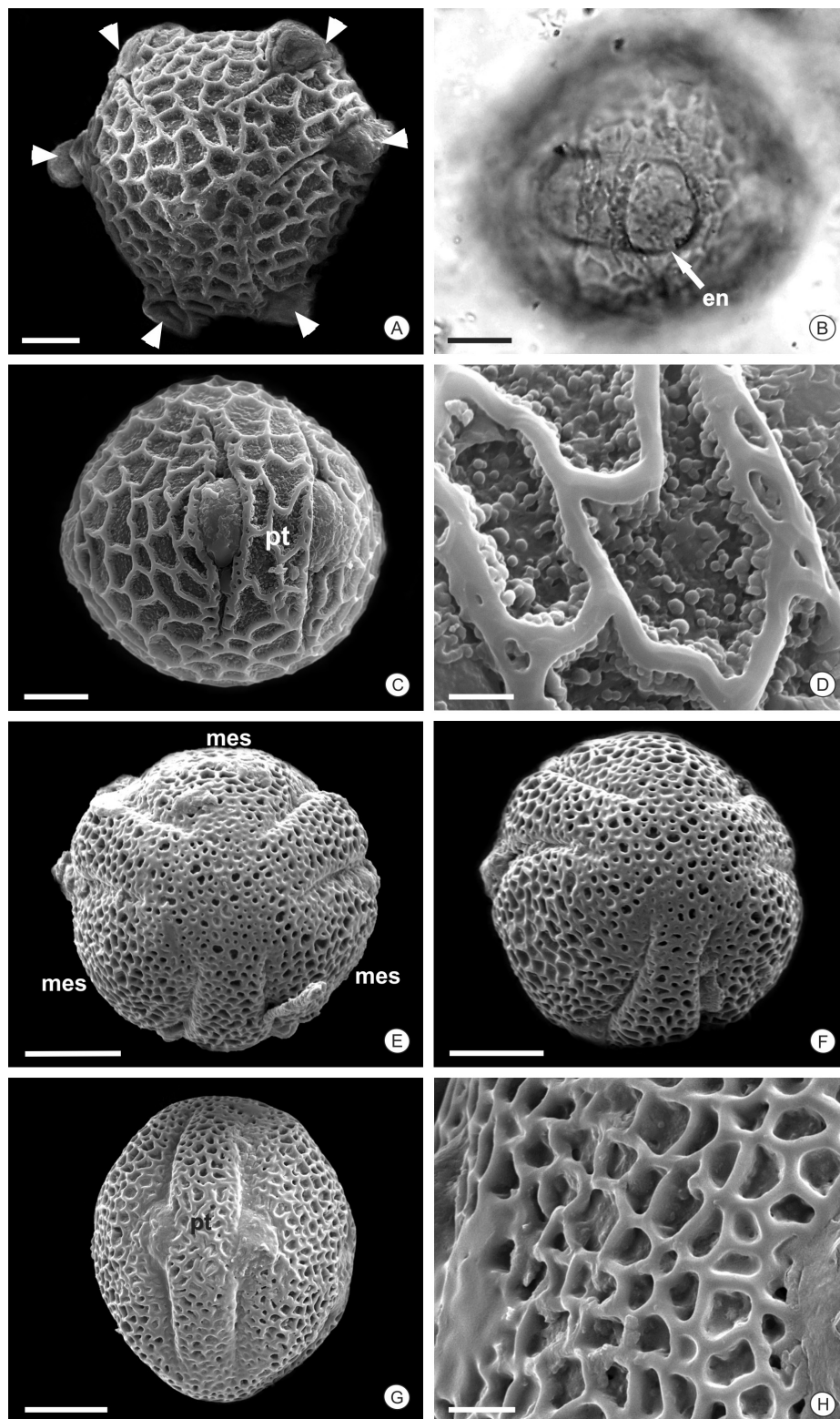


Fig. 6. Pollen grains of *Passiflora* subgen. *Deidamioides* (Harms) Killip. **A–D.** *P. contracta* Vitta (S.C.San’Ana *et al.* 265, MBM). **E–H.** *P. deidamioides* Harms (F.R.G. Salimena *et al. s.n.*, CESJ 27554). Polar view (A, E–F), equatorial view (B–C, G), detail of ornamentation (D, H). Abbreviations: en = endoaperture; mes = mesocolpium; pt = pontopericulum; arrowheads = apertures. Scale bars: A–C, E–G = 10 μ m; D, H = 2 μ m.

cylindrical, cylindrical-campanulate, funnellform, or patelliform; *flowers* whitish, purple, violet, pink, red, or their combination, with corona presenting these colors and colored bands; *sepals* 5; *petals* 5; *corona* with 1–20 series of filaments; *operculum* present, curved or erect, filamentous at the apex; *nectariferous disk* present, rarely inconspicuous or absent; *limen* absent, annular, membranaceous, or cupuliform; *trochlea* absent in most species, *stamens* 5; *styles* 3, *stigmas* 3; *fruit* a berry (Figs 7–8).

Pollen description

Pollen grains medium, large, or very large; isopolar or non-polar; when isopolar, oblate-spheroidal, prolate-spheroidal, suboblate, or prolate; polar area small or large; amb circular; 6-colpate, 5-, 6-, 7-, 8-, 9-, 10-, 12-, and/or 14-syncolpate, colpi long and narrow or wide; endoaperture absent; pseudopercula 3, 5–10, 12, 14, pontopercula 0 or 3; sexine semitectate (muri continuous, simplicolumellate, or duplicolumellate; lumina large (11.1–16.1 μm) or small (4.4–10.6 μm); bacula numerous). Sexine thicker or less thick than nexine, total exine 6.0–16.2 μm (Fig. 9).

Passiflora subgenus *Decaloba* (DC.) Rchb.

Figs 10–11

Passiflora subgenus *Decaloba* (DC.) Rchb. (Reichenbach 1828: 132). — *Passiflora* section *Decaloba* DC. (de Candolle 1822: 435).

(244 spp.)

Taxonomic description

Vines slender; monoecious; *tendrils* present, entire, adhesive disks absent; *stipules* minute; *glands* 2, present or absent on the petiole; *leaves* simple, entire, or 2–3-lobed in most species; *ocelli* present or absent; *main ribs* 3; *inflorescences* 1-flowered, 2-flowered, or cymose; *bracts* 3, minute, bracteoles absent; *hypanthium* flat; *flowers* yellow-green to white or reddish, corona with red or purplish bands; *sepals* 5; *petals* 0 or 5; *corona* with 1 or 2 series of filaments; *operculum* plicate; *nectariferous disk* present or absent; *limen* annular, lobulate, recurved, or cuculiform; *trochlea* absent, *stamens* 5; *styles* 3, *stigmas* 3; *fruit* a berry or a fleshy capsule (Fig. 10).

Pollen description

Pollen grains medium to large; isopolar; subprolate, oblate-spheroidal, prolate, or prolate-spheroidal; polar area very small or small; amb circular; 6-colporate, 12-colporate, or 12-colpate; colpi long and narrow or wide; endoapertures 0, 6, or 12, lolongate (in most species), lalongate or circular; opercula 0, 3, 6, or 12, pseudopercula 0, 3, or 6, pontopercula 0 or 3, and/or mesocolpia 3 or 6; sexine semitectate (muri continuous, simplicolumellate; lumina small (0.7–8.7 μm); bacula present or absent). Sexine thicker than nexine, total exine 1.0–5.6 μm (Fig. 11).

Passiflora subgenus *Tetrapathea* (DC.) P.S.Green

Fig. 4G–O

Passiflora subgenus *Tetrapathea* (DC.) P.S.Green (Green 1972: 552). — *Passiflora* section *Tetrapathea* DC. (de Candolle 1822: 435).

(3 spp.)

Taxonomic description

Vines slender to woody; dioecious plants, with differences in the size of the gynoecium and/or androecium and/or in the number of parts of the gynoecium and presence/absence of nectariferous disk between plants of different sex; *tendrils* entire, adhesive disks absent; *stipules* minute (0.25–3 \times 0.25–1 mm);

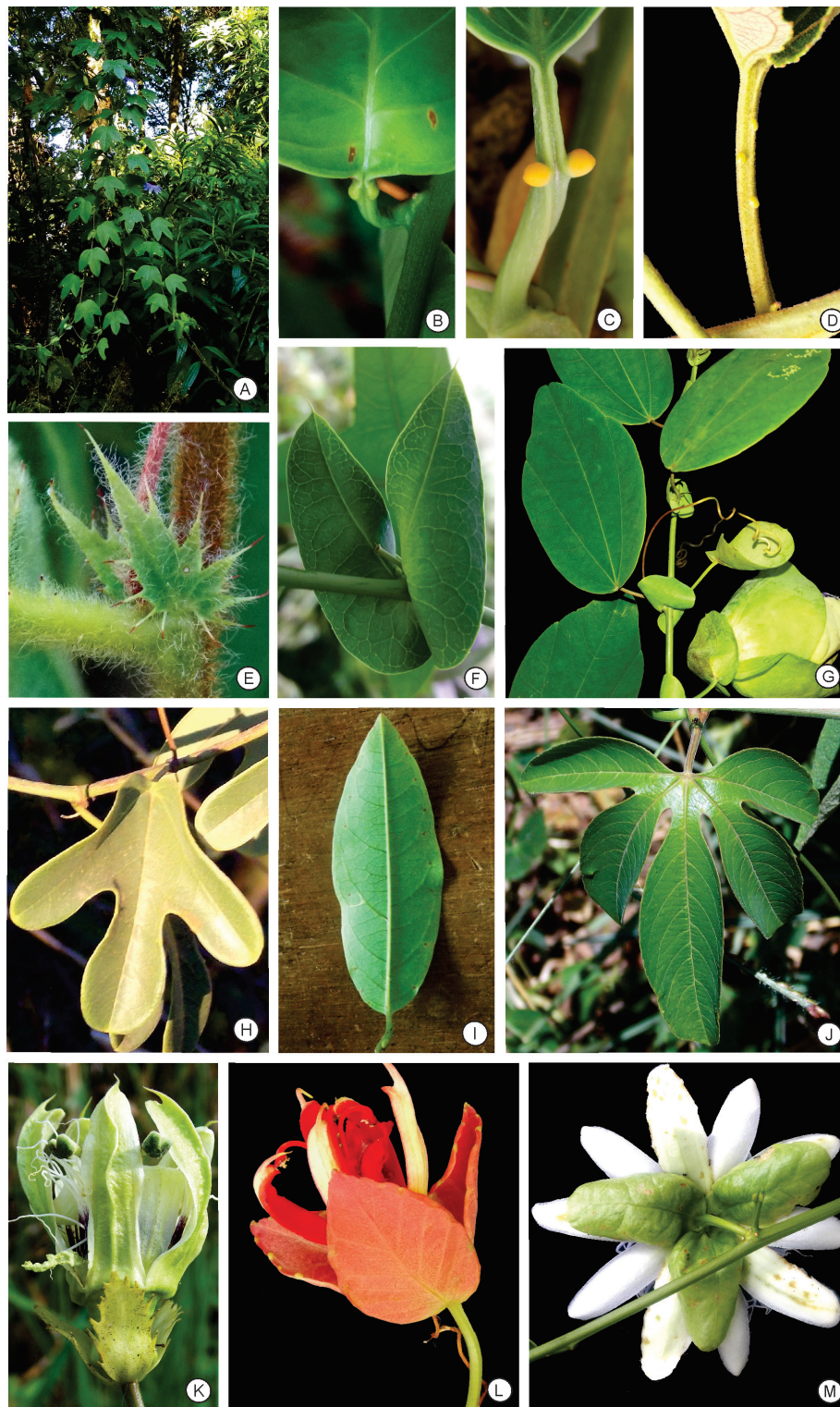


Fig. 7. External morphology of *Passiflora* subgen. *Passiflora*. **A.** Climbing habit of *P. amethystina* J.C.Mikan. **B.** Detail of the glands of *P. nitida* Kunth. **C.** Detail of the glands of *P. alata* Curtis. **D.** Detail of the glands of *P. araujoii* Sacco. **E.** Detail of the stipules of *P. villosa* Vell. **F.** Detail of the stipules of *P. amethystina* J.C.Mikan. **G.** Arrangement of stipules in *P. sidifolia* M.Roem. **H.** Leaf blade of *P. recurva* Mast. **I.** Leaf blade of *P. glandulosa* Cav. **J.** Leaf blade of *P. cincinnata* Mast. **K.** Bracts of *P. edulis* Sims. **L.** Bracts of *Passiflora* sp. **M.** Bracts of *P. nitida* Kunth. Photographs were taken by A.C. Mezzonato.



Fig. 8. Floral morphology of *Passiflora* subgen. *Passiflora*. **A.** *P. edmundoi* Sacco. **B.** *P. alata* Curtis. **C.** *P. cincinnata* Mast. **D.** *P. amethystina* J.C.Mikan. **E–G.** *P. acuminata* DC. Photographs were taken by A.C. Mezzonato.

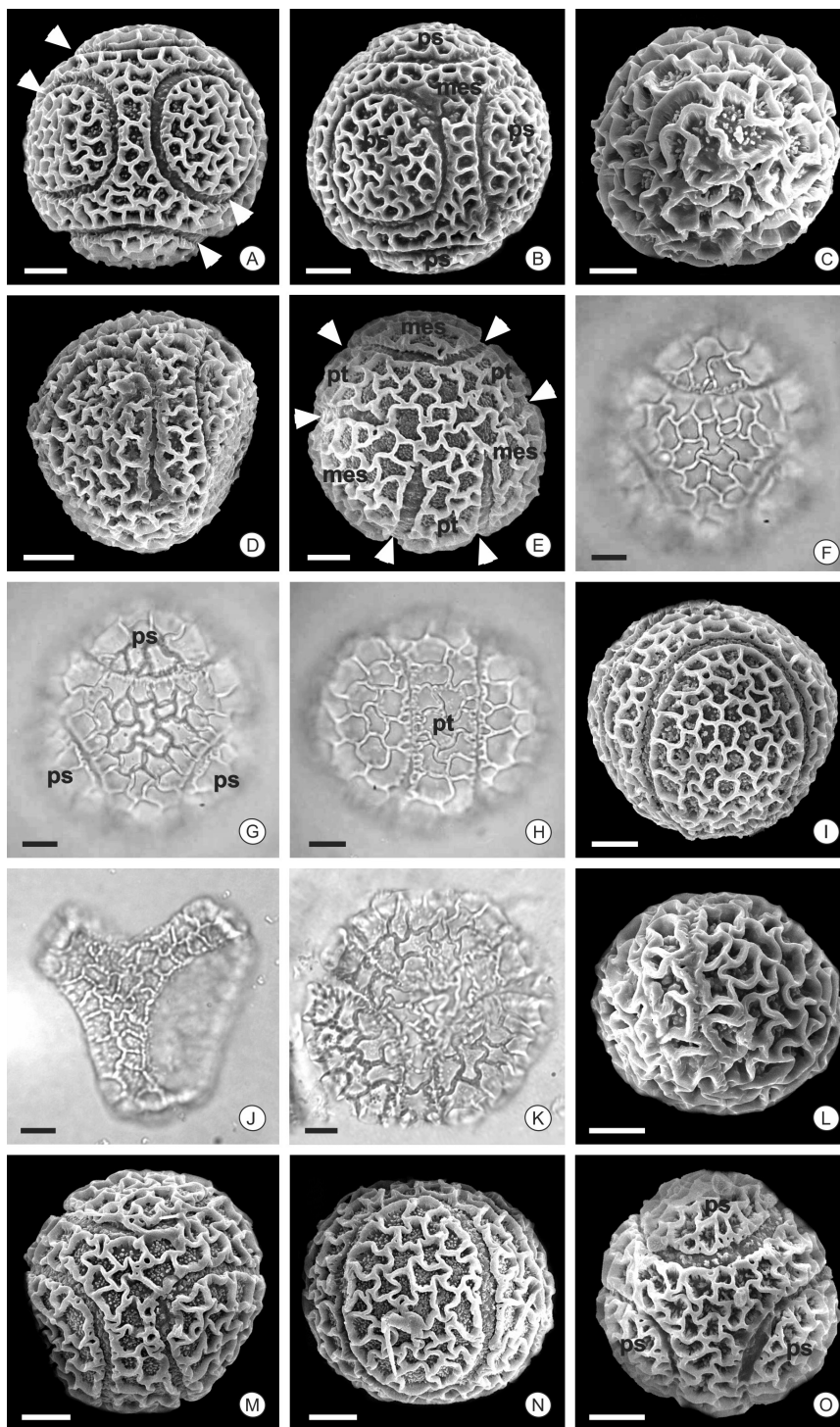


Fig. 9. Pollen grains of *Passiflora* subgen. *Passiflora*. **A–B.** *P. actinia* Hook (A.C. Cervi *et al. s.n.*, MBM 385343). **C.** *P. mediterranea* Vell. (A.S. Grotta *et al. s.n.*, RBR 23995) **D.** *P. tenuiflora* Killip (G.M. Hastschbach *et al.* 23133, MBM). **E.** *P. mucronata* Lam. (A. Costa *et al. s.n.*, R 208564). **F–H.** *P. alata* Curtis (A.C. Mezzonato *et al.* 55, R) **I.** *P. caerulea* L. (G.M. Hastschbach *et al.* 78178, MBM). **J.** *P. edulis* Sims (A.C. Mezzonato & M. Milward 77, R). **K–L.** *P. racemosa* Brot. (J.G. Silva *et al.* 615, R). **M–N.** *P. silvestris* Vell. (M.M. Souza *s.n.*, UPCB 60269) **O.** *P. subrotunda* Mast. (J. Sacco 2391, R). General aspect (A–D), polar view (E–G, J–K, M, O), equatorial view (H, I, L, N). Abbreviations: mes = mesocolpium; ps = pseudopericulum; pt = pontopericulum; arrowheads = apertures. Scale bars = 10 μ m.

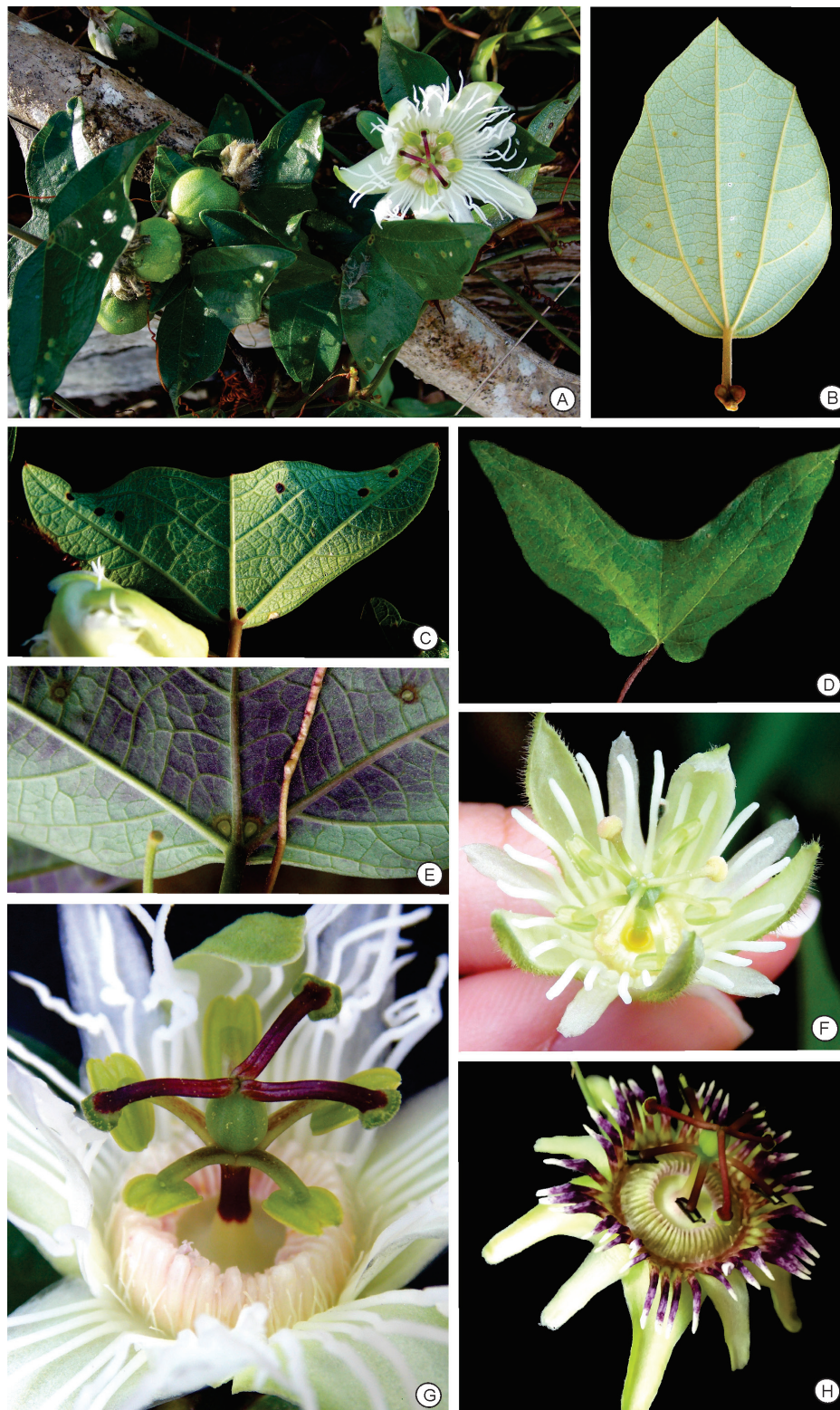


Fig. 10. External morphology of *Passiflora* subgen. *Decaloba* (DC.) Rehb. **A.** Climbing habit of *P. vespertilio* L. **B.** Leaf blade of *P. auriculata* Kunth. **C.** Abaxial face of the leaf blade with detail of the ocelli of *P. vespertilio* L. **D.** Variegated leaf blade of *P. capsularis* L. **E.** Detail of the ocelli of *P. misera* Kunth. **F.** Flower of *P. capsularis* L. **G.** Flower detail of *P. vespertilio* L. **H.** Flower of *P. porophylla* Vell. Photographs were taken by A.C. Mezzonato.

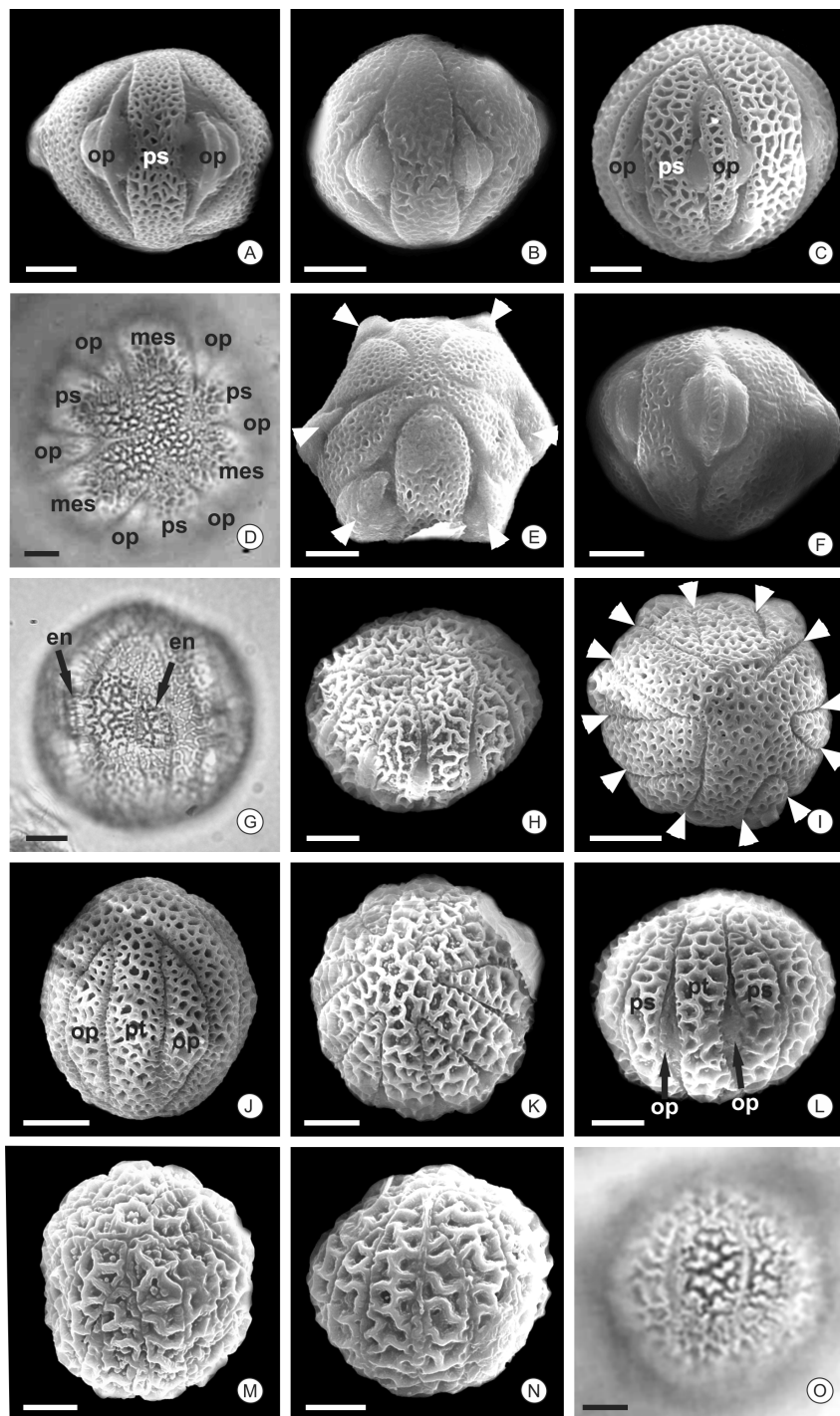


Fig. 11. Pollen grains of *Passiflora* subgen. *Decaloba* (DC.) Rchb. **A.** *P. brevipes* Killip (J.C. Soto *et al.* 21520, MEXU). **B.** *P. citrina* J.M.MacDougal (R. Evans 1421, MO). **C.** *P. conzattiana* Killip (E. Carranza 688, MO). **D.** *P. porophylla* Vell. (A.C. Mezzonato *et al.* 211, R). **E–F.** *P. tenella* Killip (E. Aspland 5189, MBM). **G.** *P. candollei* Triana & Planch. (I.S. Ribeiro *et al.* s.n., UPCB 5234). **H.** *P. cervii* M.A.M.Azevedo (E.P. Heringer 6578, UB). **I–J.** *P. misera* Kunth (A.C. Mezzonato & M. Milward 78, R). **K–L.** *P. quinquangularis* S.Calderón ex J.M.MacDougal (A. Sermeño 141, MO). **M.** *P. rubra* L. (R. Carter 5174, MO). **N–O.** *P. capsularis* L. (A.C. Mezzonato & Y. Tavares 62, R). Polar view (D–E, I, K), equatorial view (A–C, F–H, J, L–O). Abbreviations: en = endoaperture; mes = mesocolpium; op = operculum; ps = pseudoperculum; pt = pontoperculum; arrowheads = apertures. Scale bars = 10 μ m.

glands 0–2(–4) on the lower half or third of the petiole; *leaves* simple, entire; *ocelli* present; *main rib* 1; *inflorescences* with (1)2–4(5) axes, 2–6(8–16)-flowered (rarely 1-flowered); *bracts* 2, small (1–2(4) × 0.25–1 mm), bracteoles absent; *hypanthium* flat; *flowers* whitish to whitish-greenish, with corona whitish to yellow or whitish-greenish; *sepals* (3)4 or (4)5, petals (3)4 or (4)5; *corona* with 2 series of filaments; *operculum* absent or present, when present, erect, membranaceous, apex fimbriate; *nectariferous disk* present, absent only in male flowers of *P. tetrandra*; *limen* present or absent; *trochlea* absent, *stamens* 4 or variable number, (3)4–5 or 6–8, between species; *styles* 2–7, *stigmas* 2–7, variable within and between species; *fruit* a berry.

Pollen description

Pollen grains medium or large; isopolar; subprolate; polar area very small; amb subcircular; 6-colporate; colpi long to very long and wide; endoapertures 3, lalongate, one for each pair of colpi; pontopercula

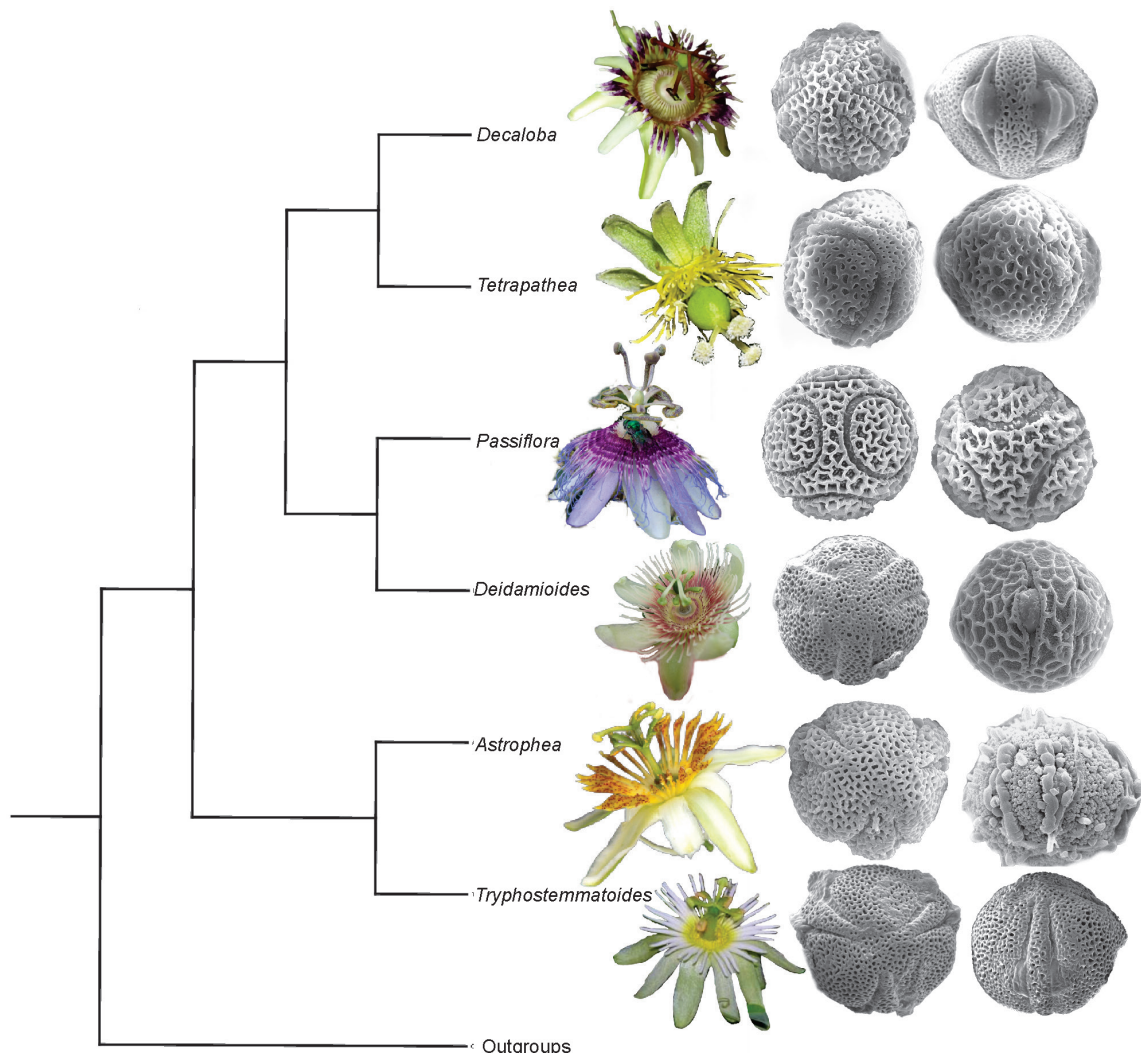


Fig. 12. Phylogenetic tree (adapted from Krosnick *et al.* 2009) based on combined nrITS, ncpGS, *trnL-F*, and *ndhF* data. Photographs showing the morphological characters that represent the six subgenera of *Passiflora* L. Photographs were taken by the authors, except the flowers of *P.* subgen. *Tetrapathea* P.S.Green (Lawrence Jensen) and *P.* subgen. *Tryphostemmatoides* (Harms) Killip (Miguel Molinari).

3, mesocolpia 3; sexine semitectate (muri continuous, simplicolumellate, or duplicolumellate; lumina small (4.2–8.0 μm); bacula present). Sexine as thick as or thicker than nexine, total exine 2.1–4.2 μm (Fig. 4G–O).

Discussion

Passifloraceae exhibits an exceptional morphological diversity and is considered the family with the largest variability in both floral (including bracts) and vegetative (mainly leaves and stipules) characters (MacDougal 1994). Pollen characters are also noteworthy for their variability, as evidenced by the results of this study. Therefore, the diversity of floral characters becomes more visible when pollen grains are included in the analysis. Pollen type, aperture number, presence/absence of endoapertures, sexine ornamentation, and operculum type are the most informative characters for differentiating *Passiflora* infrageneric categories.

Passiflora subgen. *Astrophea* is the only one that has an arboreal or shrubby habit and no tendrils, morphological characteristics that are considered ancestral. Its sister group *P.* subgen. *Tryphostemmatoides* (Krosnick *et al.* 2013) has branched tendrils as an ancestral character. The pollen affinity of these subgenera is evidenced by the presence of 6-colporate pollen, with 3 unique lalongate endoapertures for each pair of colpi. The pollen grains of *P.* subgen. *Tryphostemmatoides* have a very small polar area and sexine as thick as or narrower than the nexine. In *P.* subgen. *Astrophea* pollen, the polar area varies between small and large and the sexine is always thicker than the nexine. The characteristics of the polar area (very small) and sexine thickness (as thick as or narrower than the nexine) serve to distinguish the subgenus *Tryphostemmatoides* (apart from the wide colpi and absence of bracts) from *P.* subgen. *Deidamioides* (small polar area, sexine as thick as or thicker than the nexine, narrow colpi, and presence of bracts).

In all subgenera, with the exception of *P.* subgen. *Passiflora*, there are species with 6-colporate pollen, which is the only type occurring in *P.* subgen. *Astrophea*, *P.* subgen. *Deidamioides*, and *P.* subgen. *Tetrapathea*. The absence of 6-colporate pollen in *P.* subgen. *Passiflora* and its occurrence in *P.* subgen. *Deidamioides*, considered its sister group (Krosnick *et al.* 2013), is not difficult to explain. The 6-colporate type is considered the most primitive (Presting 1965; Dettke & Santos 2009), from which the other types were derived. In other words, the common ancestor of *P.* subgen. *Passiflora* and *P.* subgen. *Deidamioides* likely had 6-colporate pollen, with the loss of the 6-colporate type having occurred at some point in the lineage of the subgenus *Passiflora*.

Pollen grains with six colpi can be found in the subgenus *Passiflora*; however, endoapertures have been lost in all species of this subgenus and in some of *P.* subgen. *Decaloba*. The occurrence of pollen with fused colpi and the subsequent formation of different types of opercula (opercula, pontopercula, and pseudopercula) are prominent features in the subgenus *Decaloba*. Some species of *P.* subgen. *Decaloba* exhibit pollen with 12 apertures and simultaneously all types of opercula, demonstrating that the group has the most morphologically complex pollen grains. In the subgenus *Passiflora*, an even greater number of apertures can occur, and pseudopercula, resulting from the fusion of colpi, are widespread, with some occurrence of pontopercula.

The subgenera *Decaloba* and *Passiflora* are the most diverse with regard to both morphology and palynology. As hypothesized by Presting (1965), there has been an increase in the number of pollen apertures throughout evolution in both subgenera. A greater number of apertures may represent a selective advantage, as it increases the number of possible pollen germination sites, thereby facilitating contact between at least one aperture and the stigmatic surface (Furness & Rudall 2004). The increase in aperture number enables the diversification of operculum types and may result in an increase in fertilization rate, promoting evolutionary success, as observed in the subgenera *Decaloba* and *Passiflora*.

It was found that the subgenus *Passiflora* is the largest and most morphologically diverse group in the Passifloraceae. Leaf shape, as well as the number, shape, and position of petiolar glands, can vary greatly. Individuals can have large bracts and very colorful flowers with several coronal series (1–20). However, the circumscription of the subgenus is supported by its pollen characters. It is the only group in which all species have very thick exine (up to 16.2 μm) and no endoapertures.

Passiflora subgen. *Tetrapathea* and *P.* subgen. *Tryphostemmatoides* exhibit the smallest range of exine thickness, reaching a maximum of 4.2 μm . Both subgenera have pollen with very small polar areas and 6-colporate apertures (6-syncolporate only in *P.* subgen. *Tryphostemmatoides*). Bacula are present in *P.* subgen. *Tetrapathea* (even if in small quantities) but absent in *P.* subgen. *Tryphostemmatoides*. Phylogenetic analyses indicated the placement of *P. tetrandra* in *P.* subgen. *Decaloba* (Yockteng & Nadot 2004) or as a sister group of *P.* subgen. *Decaloba* (Hearn 2006; Krosnick *et al.* 2009, 2013). Palynologically, there is no support for placing this species in *P.* subgen. *Decaloba*, as the pollen grains of *P. tetrandra* have a fixed number of endoapertures (3). The number of endoapertures varies among species of *P.* subgen. *Decaloba* (0, 6, or 12) but is never 3.

It can be concluded that, despite the great morphological diversity among the Passifloraceae, there is an overlap of characters, both floral and vegetative. Furthermore, it is very difficult to recognize diagnostic characters for subgenera of *Passiflora*. The dichotomous key presented here is an attempt to facilitate the identification of subgenera. The highlighted characters, when used together, make it possible to distinguish subgenera. This unprecedented combination of characters has proved to be unique among different subgenera. Similarly, the inclusion of pollen characteristics has significantly contributed to the distinction of subgenera by providing additional reliable traits for observation, while also resolving uncertainties regarding the classification and recognition of subgenera (and how many and which subgenera need to be recognized). In addition to the morphological, macromolecular (e.g., Krosnick *et al.* 2013; Pacheco *et al.* 2020), and chromosomal (Sader *et al.* 2019) characteristics of subgenera of *Passiflora*, distinct pollen features have been identified. For example, *P.* subgen. *Decaloba* exhibits a wide variety of operculum types, some representatives of *P.* subgen. *Astropheia* have non-reticulate sexine, and all species of *P.* subgen. *Passiflora* have lost endoapertures.

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Supplementary files

Supp. file 1. First and current infrageneric categories within *Passiflora* L. and the main taxonomic changes related to the genus, followed by the numbering system or sequence in which taxa were presented (delimited by the polygon). Authorship information is presented only after the first mention of each taxon. ¹ = *Granadilla* DC.; ² = Established by Reichenbach (1828); ³ = Established by Schumann (1888); ⁴ = Established by Barbosa Rodrigues (1892); ⁵ = *Granadilla* (Medic.) Mast.; ⁶ = *Plectostemma* Mast. <https://doi.org/10.5852/ejt.2025.981.2829.12899>

Supp. file 2. List of accepted names of species of *Passiflora* L. (not hybrids), in their respective subgenera. <https://doi.org/10.5852/ejt.2025.981.2829.12901>

Supp. file 3. Table of species studied in the main palynological works and in the present study. <https://doi.org/10.5852/ejt.2025.981.2829.12903>