
TAXONOMIC HISTORY,
MORPHOLOGY, AND
REPRODUCTIVE BIOLOGY OF
THE TRIBE POSOQUERIEAE
(RUBIACEAE, IXOROIDEAE)¹

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ABSTRACT

The tribe Posoquerieae was recently described to include the genera *Posoqueria* Aubl. and *Molopanthera* Turcz. based on floral morphology, palynology, the presence of the pollen catapult mechanism, and molecular phylogenetic evidence. The floral morphology of these two genera was first recognized as unique in the Rubiaceae by Schumann. Both genera have stamens initially united into an ellipsoidal structure held at an oblique position, with the ventral stamen that springs forward when touched, while the two lateral stamens fold outward. Since their descriptions were published, *Posoqueria* and *Molopanthera* have been positioned in several distantly related tribes within the Rubiaceae. The close relationship between the two genera was only recently revealed by molecular phylogenetic studies. The taxonomic history of *Posoqueria* and *Molopanthera* is reviewed, and a general morphological comparison (particularly of stamen morphology and pollen catapult mechanism, and observations about pollination biology) of both genera is presented here. The pollen catapult mechanism of *Molopanthera* is described here in detail for the first time and concluded to be practically identical to that of *Posoqueria*.

Key words: Gardenieae, *Molopanthera*, Neotropics, pollen catapult mechanism, *Posoqueria*, Posoquerieae, Rubiaceae.

The genus *Posoqueria* Aubl. was established by Aublet (1775) based on his material from French Guiana and on *P. longiflora* Aubl. He explained that the generic name was derived from the name used by the Galibi tribe, “Aymara-Posoqueri,” because the fish Aymara eats the fruits of this plant. However, the typical laterally bent floral buds of this genus were not depicted in the drawing.

De Candolle (1830) included *Posoqueria* in the tribe Gardenieae (as “Gardeniaceae”) and, more specifically, in the subtribe Gardeniinae (as “Gardenieae”; de Candolle, 1830: 368), among genera now positioned in several other tribes. In *Posoqueria*, de Candolle recognized seven species, namely *P. longiflora*, *P. latifolia* Roem. & Schult., *P. decora* DC., *P. trinitatis* DC., *P. havanensis* DC., *P. gracilis* Roem. & Schult., and *P. revoluta* Nees [*P. revoluta* Schrad.].

Turczaninow (1848) published *Molopanthera* Turcz., describing *M. paniculata* Turcz., and treated

it as a genus with uncertain tribal position, differing from all the Rubiaceae genera with a multi-ovulate ovary. He derived the generic name from the Greek μόλωψ- (molops- = bruise or weal) and -ανθηρα (anthera = anther) meaning bruised anthers, probably in allusion to the dark ends of the anthers, which are the points of fusion of the anthers in two pairs (the other anther remaining solitary).

Karsten (1849) described the genus *Stannia* H. Karst., based on *S. formosa* H. Karst., which he distinguished from *Posoqueria* based mostly on stamen length (all equal in *Posoqueria*; three out of five longer and curved in *Stannia*). Müller (1866), probably unaware of Karsten’s *Stannia*, also described the genus as *Martha* F. J. Müll., which he distinguished from *Posoqueria* because of the unequal stamens. In this work, he was the first to describe, in great detail, the catapult mechanism for throwing the pollen onto the flower visitors, observed on plants

¹This research was realized during a Visiting Scientist fellowship from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) at the Institute of Biological Sciences of the Universidade Federal de Goiás (UFG), Goiânia, Goiás, Brazil. Observations of flowering individuals of *Molopanthera* were made at the Feliciano Miguel Abdala Natural Heritage Private Reserve (commonly known as the “Caratinga Biological Station”), Minas Gerais, Brazil. Special thanks are due to the administration and guides of the reserve for help in locating a healthy population of this rare species. Additional observations were made at the herbarium of the Universidade Federal de Minas Gerais, Belo Horizonte, and the curator Alexandre Salino, and Marcos Sobral, are kindly acknowledged. A travel grant for the presentation of this work at the Third International Rubiaceae Congress was provided by the Fund for Scientific Research–Flanders (FWO N. WO.005.05) and the Laboratory of Plant Systematics of the Katholieke Universiteit, Leuven, Belgium.

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doi: 10.3417/2006192

growing in his private garden at Desterro, Santa Catarina, southern Brazil. The peculiar mechanism was later commented on by Charles Darwin (1876, 1877), based on the notes and material sent to him by Müller.

Hooker (1873: 8–9) positioned *Posoqueria* in the Gardenieae, which he distinguished from the Catesbaeeae by having (translated from Latin) “corolla narrowly contorted, seeds few to many, large, compressed, or small, angled” (vs. “corolla valvate, seeds many, large to very large, compressed” in the Catesbaeeae). He divided the Gardenieae into several informal groups based on flower sexuality, inflorescence position, style morphology, number of locules, and ovules biseriate or multiseriate. Hooker positioned *Posoqueria* in the group with terminal inflorescence and hermaphroditic flowers, rarely polygamo-dioecious. He further distinguished *Posoqueria* from the other genera of this group with its corymbose inflorescence, flowers with elongated corolla tube, corolla lobes gibbous in bud, five exerted anthers, and a bifid stigma. Under this genus, he synonymized *Solena* Willd., *Cyrtanthus* Schreb., *Kyrtanthus* J. F. Gmel., and *Stannia*. However, Hooker did not include *Martha* in the list of synonyms, probably unaware of its publication. In *Posoqueria*, he recognized 12 species distributed in tropical America. Although he described the flower buds as laterally gibbous and the filaments as erect or curved, he did not mention the peculiar pollen catapult mechanism. At the same time, Hooker placed *Molopanthera* in the Cinchoneae in the group with imbricate corolla lobes (one or two exterior) and stamens inserted at the base of the corolla. In addition, he described a second species, *M. burchellii* Hook. f., which he distinguished from the typical species by having pubescent vegetative parts.

Baillon (1880) included the Gardenieae into his broadly circumscribed Genipa Series or Genipeae, where he positioned *Posoqueria* (Baillon: 435; including *Solena*, *Cyrtanthus*, *Kyrtanthus*, *Posoria* Raf., and *Stannia*). He stated that *Posoqueria* “closely approaches the Genipas with elongated corolla” and treated it as closely related to *Oxyanthus* DC. and *Kutchubaea* Fisch. ex DC. In the same work, he maintained *Molopanthera* in the Cinchoneae, following the position and definition suggested by Hooker (1873), and positioned it near *Calycophyllum* DC. because of the 4- to 5-merous flowers, 2-locular capsules, and seeds with unequally dentate wing.

The generic delimitations of *Posoqueria* and *Stannia* were repeatedly debated among Karsten (1849, 1856, 1860, 1887) and Planchon (1850), and Hooker (1873) and Baillon (1880), resulting in a complex diatribe of heated arguments published in a series of publications. Karsten put forward that *Stannia* has unequal stamens (with three stamens

curved and longer) and leathery or lignified berries, while *Posoqueria* has equal stamens and juicy or fleshy berries. The other authors considered these characters trivial and preferred to synonymize the two genera. Because the flower buds have the portion with the corolla lobes curved on one side, the stamens located on the inner portion of the curvature are shorter. This debate was summarized by Schumann (1888: 351–360; see annotated translation by Delprete et al., 2005a: 50–58). Schumann agreed with most authors in synonymizing the two genera and stressed that in both taxa the stamens are unequal. In addition, he used the morphology of the anthers as the unifying character and stated that (translated from German; Delprete et al., 2005a: 55): “The anthers have a wide, dorsal area that is slightly curved from top to bottom and also from right to left. They are of rather firm consistency, and are truly introrse, whereby the two parallel, closely touching thecae are flattened with inclined, slightly angled sides like normal ones. These are not tapered at the top nor at the base, but the anthers are rather bounded by firm, solid ends on both sides. There are stiff, short bristles located at the sides of the anthers, in addition to very shallow papillae, which are only visible with a lens, and which give the surface an iridescent appearance” (Schumann, 1888: 356).

Most importantly, Schumann (1888, 1891) was the first to notice the overall similarity of the pollen catapult mechanism of *Posoqueria* and *Molopanthera* and its uniqueness within the family. He observed the flower buds of *Molopanthera* in herbarium specimens, noticed that the anthers are initially united in an ellipsoidal structure while in flower bud, and suspected the stamen catapult mechanism. He wrote, “I think it is not impossible that this movement is executed with certain vehemence. But this question can only be investigated with living material, which is something I should like to point out to those botanists, who are lucky enough to be in a position to do this” (Schumann, 1888: 357, translated from German; Delprete et al., 2005a: 56). Schumann also compared the floral morphology and pollen catapult mechanism with that of *Posoqueria* and declared that they correspond entirely. Furthermore, he compared the corolla aestivation of the two genera and described them with lobes variably overlapping, stating that in *Molopanthera* “the two lowermost lobes overlap the two middle ones, and these two [in turn] cover the one on top. This aestivation is constant, and without a doubt the result of corolla genesis. Inconsistent is only the overlapping of the two front corolla lobes, and this I have also always found in ascending aestivation. Here the right lobe sometimes overlaps the one to the left and vice versa. Bearing these observations in

mind, I examined, with some difficulty, the aestivation of *Posoqueria*, and I was finally able to definitely ascertain that it was exactly the same as in *Molopanthera*" (Schumann, 1888: 359, translated from German; Delprete et al., 2005a: 58).

Schumann (1891: 9–10) positioned both genera in the subfamily Cinchonoideae. However, probably because of the capsular fruits, he included *Molopanthera* in the tribe Cinchoneae, subtribe Cinchoniinae (as "Cinchoninae–Cinchoneae"), near *Coutarea* Aubl., the only other genus of this group with zygomorphic flowers. On the other hand, he positioned *Posoqueria* in the tribe Gardenieae, subtribe Gardeniinae (as Eugardenieae), probably because of its leathery berries, and distinguished it from the other genera by having flower buds laterally bent at the lobes portion.

Bremekamp (1934a) criticized the classification proposed by Schumann (1888, 1891) and contributed several important improvements. In addition, he proposed the ixoroid pollination syndrome (pollen presentation at the style apex) as a strong taxonomic character for the subfamily Ixoroideae. However, his classification was focused on genera occurring in Suriname, thus he did not discuss the systematic position of *Molopanthera*. He placed the Gardenieae within the Ixoroideae and, in the three works dedicated to the *Flora of Surinam* (Bremekamp, 1934a, b, 1937), maintained *Posoqueria* in the Gardenieae. However, following Schumann's observations (1888, 1889, 1891), he stated that *Posoqueria* does not belong to this tribe, but did not suggest any other position in the family. In fact, the pollen catapult mechanism of *Posoqueria* (and *Molopanthera*) is not a form of secondary presentation, as the pollen is thrown directly from the anther onto the pollinator.

Verdcourt's (1958) family classification was profoundly influenced by the taxonomic observations of Bremekamp, and he agreed with that author that *Posoqueria* "will have to be excluded [from the Gardenieae], but do not know where it should be put. It has a higher chromosome number than has been reported for any other Rubiaceae, peculiar horny anthers like some Apocynaceae and it does not show the ixoroid pollen mechanism that other members of the tribe possess" (Verdcourt, 1958: 246).

Bremekamp (1966: 25–26), in his last notes on Rubiaceae classification, declared that "[t]he true Gardenieae are recognizable by their many seeded, comparatively large fruits, which are provided with a thick, leathery or more or less woody pericarp and gelatinous endocarp in which the numerous seeds are embedded. They are not rarely dioecious, in which case the male flowers are provided with a style of which the upper part serves as 'receptaculum pollinis.'

Fruits of the kind described above are found in the genera *Gardenia* Ellis, *Randia* Houst. [*Randia* L.], *Rosenbergiodendron* Fagerl., *Tocoyena* Aubl., *Genipa* L., *Alibertia* A. Rich., *Ibetrulia* Bremek. [= *Kutchubaea*], *Duroia* L. f. and perhaps some other ones." In addition, he maintained that *Posoqueria* is excluded from the Gardenieae as a genus probably related to *Cladoceras* Bremek. because of the unique pollination mechanism.

Robbrecht and Puff (1986) presented a comprehensive survey of the Gardenieae–Ixoreae complex using data from morphology, anatomy, cytology, and reproductive biology. However, several Neotropical genera traditionally positioned in the Gardenieae were not mentioned in the study, among them *Melanopsidium* Colla, *Posoqueria*, and *Botryarrhena* Ducke.

Robbrecht (1988) proposed a system of classification highly influenced by that of Bremekamp (1966), complemented by a synthesis of all the data available to him at that time. He divided the family into four subfamilies and 44 tribes and positioned the Gardenieae in the subfamily Ixoroideae. He delimited the Gardenieae according to the conclusions presented by Robbrecht and Puff (1986) and divided it into the Diplosporinae and Gardeniinae, positioning *Posoqueria* in the second subtribe without any additional comments.

Andersson and Persson (1991) presented a phylogenetic study with an attempt to define the tribe Cinchoneae. In this work, *Molopanthera* was found in a basal position near *Condaminea* DC. in the two analyses using a hypothetical taxon (combining the characters of the Loganiaceae genera *Antonia* Pohl and *Gelsemium* Juss.) as outgroup, and as sister genus with *Condaminea* in the analyses using *Gelsemium* as outgroup. These results prompted the authors to include *Molopanthera* among the genera that they provisionally transferred to the Condamineae.

Delprete (1993) presented a preliminary phylogeny using morphological characters focused on representative genera of the Chiococceae, Catesbaeeae, Condamineae, and Rondeletieae. Based on the results of this study, he indicated that the subtribe Portlandiinae of the Condamineae should be separated as the informal *Portlandia* group in which the genera *Catesbaea* L. and *Phyllacanthus* Hook. f. (Catesbaeeae) should be included. In addition, he indicated that *Molopanthera* might be tentatively included within the Rondeletieae.

Robbrecht (1993), in a supplement to his 1988 classification and following Delprete's preliminary results, separated the "genera associated with *Portlandia*." He positioned this informal group near the Condamineae, with the note "If the Catesbaeeae are

included (see tribus incertae), they will provide a tribal name for this group" (Robbrecht, 1993: 176). Within this informal group, he included *Molopanthera* without any further comments.

Delprete (1996) published an expanded phylogenetic study based on morphological characters presented in 1993. In the analysis using *Cinchona* L. and *Joosia* H. Karst. as outgroup, *Molopanthera* appeared at a basal unresolved position. In the analyses using solely *Coffea* L. as outgroup and in that with *Coffea*, *Cinchona*, and *Joosia* as outgroup, *Molopanthera* was positioned in a clade with *Parachimarrhis* Ducke and *Simira* Aubl. These results prompted Delprete to propose *Molopanthera* as a member of the Condamineae–Rondeletiae complex (Rondeletiae s.l.).

Persson (1996) published a phylogenetic study of the tribe Gardenieae using morphological characters. In the cladograms obtained, *Posoqueria* was positioned within the outgroup, with the following parallelisms: apical extension of connective absent, placental pulp present, and exotesta without radial and tangential wall thickenings. Based on these results, Persson excluded *Posoqueria* from the Gardenieae, but did not further indicate its position in the family.

Delprete (1999) included *Molopanthera* in his widely delimited Rondeletiae (including Sipaneeae and Condamineae p.p.) as related to *Chimarrhis* Jacq. because of its narrowly imbricate corollas and placentation. In his taxonomic revision, he maintained it as a monospecific genus, with the same two varieties recognized by Schumann (1889).

Rova et al. (2002), with a molecular phylogeny using *trnL-F* sequences, were the first to demonstrate the close phylogenetic relationship between the *Posoqueria* and *Molopanthera*. In turn, they were found to be closely associated with the tribes Henriquezieae and Sipaneeae, as further supported by the molecular phylogenies of Delprete and Cortés-B. (2004) and Cortés-B. et al. (2005), using *trnL-F* and *rps16* sequences.

Delprete (2004), based on morphological, palynological, and phylogenetic evidence, described the new tribe Posoquerieae, with these genera as shrubs or small to tall trees, with stipules triangular or oblong-lanceolate; terminal inflorescences; flower buds gibbous (*Posoqueria*) or curved (*Molopanthera*); corolla zygomorphic, long-tubular (*Posoqueria*) or rotate, small (*Molopanthera*); anthers apiculate, base agitate or caudate, organized in bud in two pairs with a single one bearing a pollen mass released by all the anthers; pollen grains 3-colporate; ovary bilocular; fruits baccate (*Posoqueria*) or capsular (*Molopanthera*); and seeds many, large, and wingless with testa coriaceous,

perlaceous (*Posoqueria*) or seeds minute with wing lacerate-dentate and testa membranaceous (*Molopanthera*).

Robbrecht and Manen (2006) proposed a new family classification based on a phylogeny obtained from nuclear and chloroplast DNA sequences (supertree technique). In this new system, they divided the Rubiaceae into two subfamilies and several supertribes. They reduced the tribes Henriquezieae and Posoquerieae to subtribes of the expanded Henriquezieae (sister to the tribe Sipaneeae). However, despite these recent results, I prefer to maintain the Henriquezieae and Posoquerieae as sister tribes. The remarkable floral morphological characters and the pollen catapult system unique to the Posoquerieae warrant recognition at the tribal level. Furthermore, the Henriquezieae show some very different characters, e.g., the half-superior to superior ovaries.

CHARACTERIZATION OF THE TRIBE POSOQUERIEAE

Genera with zygomorphic flowers are uncommon in the Rubiaceae; however, the trademark of the tribe Posoquerieae is the peculiar pollen catapult mechanism that requires a composition of morphological and functional characters in order to undergo the various stages of anthesis (see below). With the goal of having a general view of the morphological variation in the tribe and a comparison between the two genera included, an itemized characterization is presented below.

GEOGRAPHIC DISTRIBUTION

Posoqueria is a genus of about 17 species distributed throughout the Neotropics, from Central America to southern Brazil (Macias, 1988; Taylor & Cortés-B., 1999; Boom & Delprete, 2002; Macias & Kinoshita, 2003; Delprete et al., 2005b). *Molopanthera* is a monospecific genus (Delprete, 1999) endemic to the Atlantic forests of Brazil, with two varieties distinguished by the type of vestiture of the vegetative parts.

HABIT

Posoqueria species are large shrubs (1.5–)2–7 m tall or, exceptionally, trees to 15(–20) m tall (especially the Amazonian species), with bark usually smooth, or rarely shallowly fissured in old trees. *Molopanthera* is represented by trees 5–10(–30) m tall, with the main trunk 15–30(–80) cm DBH, and the bark longitudinally fissured (Fig. 1B) and pale brown.

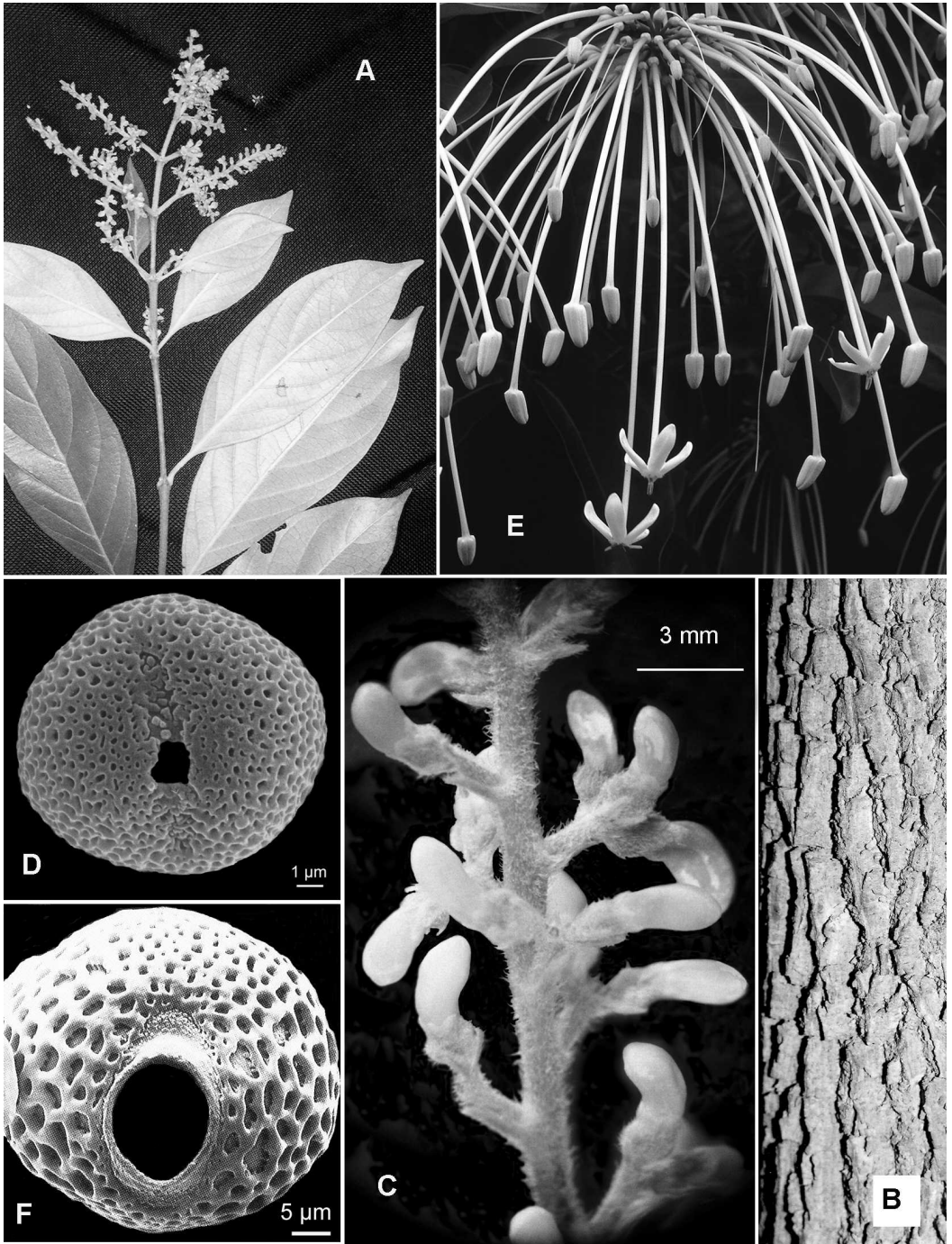


Figure 1. *Molopanthera* and *Posoqueria*. A–D. *Molopanthera paniculata*. —A. Inflorescence. —B. Bark. —C. Detail of inflorescence with flower buds. —D. Pollen. E, F. *Posoqueria longiflora*. —E. Inflorescence with flower buds and open flowers. —F. Pollen. (A–C photos by P. Delprete; D reproduced with permission from Huysmans et al., 1999; E photo by L. Westra; F reproduced with permission from Persson, 1993.)

LEAVES

The leaves of both genera are ovate, elliptic, or oblong-elliptic and have brochidodromous venation (Fig. 1A), which is the common condition in the family.

STIPULES

As in most members of the family, the stipules of both genera are interpetiolar and free at the base, although they differ in several characters. In *Posoqueria*, they are ovate, narrowly triangular, oblong, ligulate, or lanceolate and are readily caducous, while those of *Molopanthera* are broadly triangular at the base, acuminate at the apex, and persistent.

INFLORESCENCE

In both genera, the inflorescences are terminal. In *Posoqueria*, they are cymose or corymbose, and few- to many-flowered. On the other hand, those of *Molopanthera* are laxly paniculate, many-flowered, with secondary branches subtended by leaf-like bracts (perophylls), tertiary branches thyrsoid, and with 1- to 3-flowered terminal units (Fig. 1A, C).

FLOWERS

In both genera, the flowers are zygomorphic, 5-merous, bisexual, and protandrous, with a glabrous corolla that is white to cream-white during anthesis, commonly turning pale yellow to yellow after anthesis. However, the main contrast between the two taxa is the difference in corolla size and shape. In *Posoqueria*, the flower buds are narrowly cylindrical and laterally bent at the apex (corolla lobes); the corollas are hypocrateriform, 7–35(–38) cm long (28–35[–38] cm long in *P. longiflora*; Fig. 1E), with a long, narrowly cylindrical tube, 5–32(–34) cm long; and the corolla lobes are equal or unequal, imbricate or left-contorted, ovate, oblong-ovate, or oblong to lanceolate, and obtuse or round at apex. In *Posoqueria*, the flowers are odorless or slightly fragrant during the daytime, becoming strongly fragrant from dusk to the middle of the night. They are visited and probably pollinated by long-tongued sphingid moths (Bawa & Beach, 1983; and pers. obs.).

In *Molopanthera*, the flower buds are curved, slightly wider medio-distally (at the anther position); the corollas are rotate, deeply lobed, 3–4 mm long, with a short, cylindrical tube, 0.3–0.5 mm long (Fig. 1C); and the corolla lobes are unequal in length (shorter on the ventral side of the bud), imbricate, oblong-linear, and round at apex. In *Molopanthera*, the flowers are sweet-scented and open during the

daytime. They are visited and probably pollinated by small bees (pers. obs.).

STAMENS

In most species of *Posoqueria*, the two dorsal filaments are the longest, the two lateral ones are of intermediate length, and the ventral one is the shortest. However, in a few species (e.g., *P. taraiensis* C. M. Taylor & Cortés-Ballén), the filaments are of equal length and during anthesis they separate independently. This species does not show the typical pollen catapult mechanism. Only a few species of *Posoqueria* have been closely examined for the unequal length of the filaments, and even fewer were directly observed during anthesis.

In *Molopanthera*, stamen morphology and pollen release are very similar to those of *Posoqueria*. As in *Posoqueria*, the anthers are initially united in an ellipsoidal structure held slightly oblique (Fig. 2A) according to the flower bud curvature; the two dorsal stamens are the longest, the two lateral ones are of intermediate length, and the solitary one (inserted at the ventral portion) is the shortest. The anthers are all of equal length, although those connected in pairs are slightly narrower than the solitary one (responsible for throwing the pollen onto the pollinator).

POLLEN PRESENTATION

Most species of *Posoqueria* display the characteristic pollen catapult mechanism, which is the trademark feature of the Posoquerieae. However, the presence of this peculiar mechanism has not been observed in all the species of the genus, as some species apparently have equal or subequal stamens that separate freely, without performing the pollen catapult (as reported by Burk [1884] in "*Posoqueria hirsuta*," a name of doubtful application). In other species, the separation of the stamens occurs only after the pollen dispersal. Therefore, even though most species have been reported to display the typical pollen catapult mechanism, this remains to be confirmed in a number of species.

The pollen catapult mechanism of *Posoqueria latifolia* was first described, in much detail, by Müller (1866) and later by Hallé (1967), Beach (1983), and Puff et al. (1995). In addition, I have personally observed *P. latifolia* in several natural populations in Costa Rica and central and southern Brazil (states of Goiás, Minas Gerais, and Santa Catarina), and this species is used here as an example for the several stages in the anthesis. In *P. latifolia*, the five anthers are initially united into an ellipsoidal structure, which is held in an oblique position in relation to the corolla

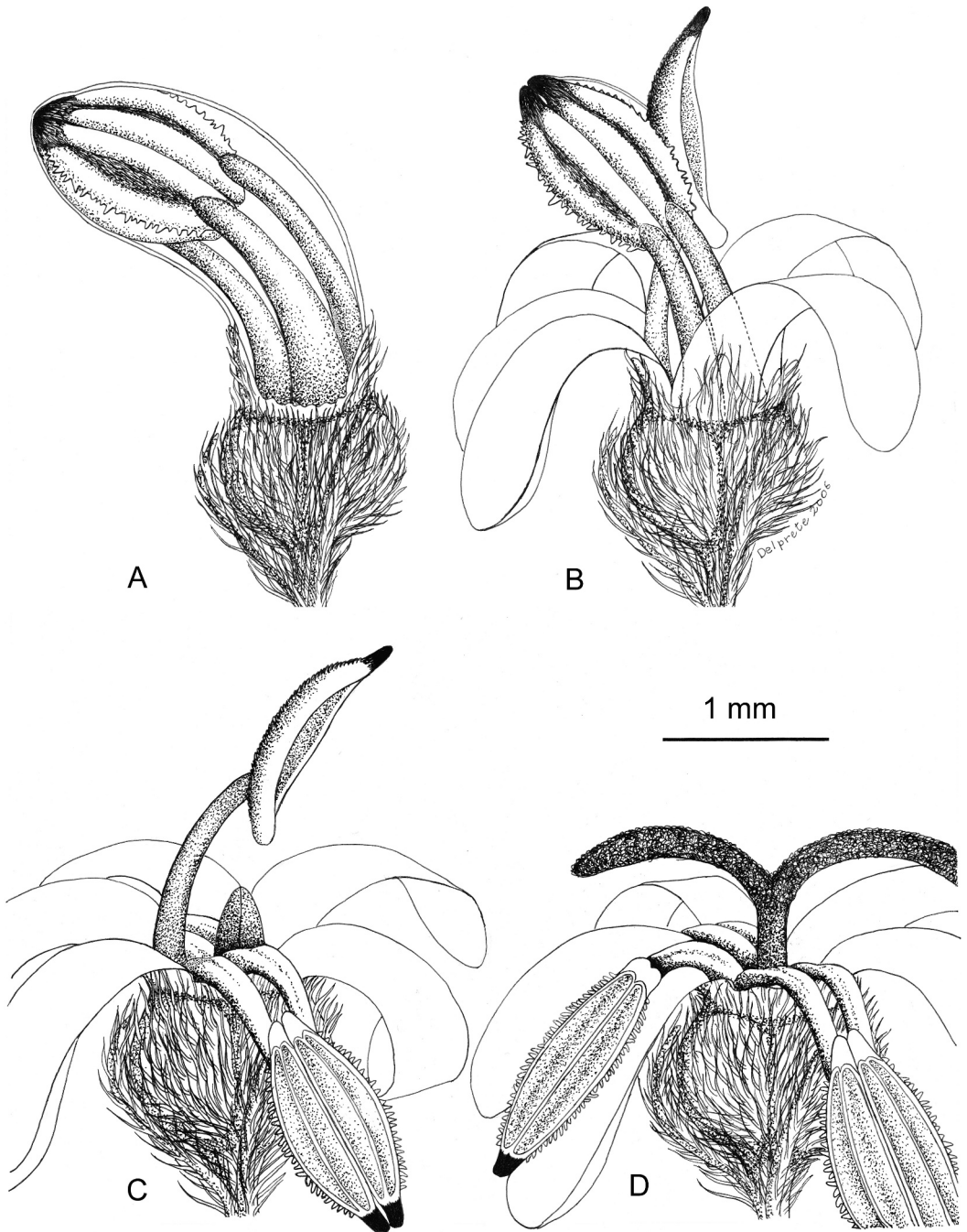


Figure 2. Stages of anthesis of *Molopanthera*. —A. Flower bud, with anthers held in ellipsoidal structure. —B. Pollen catapult mechanism. —C. Stage following the pollen catapult, with the two stamen pairs folded backward and the solitary stamen remaining erect above the corolla mouth. —D. Final stage with solitary anther folded backward and the style branches expanded and receptive.

tube, as it can be seen in the flower bud (Fig. 3A). Each anther has two basal and two apical appendages, which are sterile extensions of the thecae, usually much darker. These function as a contact zone for the

two anther couples. The anthers dehisce longitudinally and, while they are still united, they release a loose pollen mass at the center of the structure (Puff et al., 1995: fig. 14E). Müller (1866) and Puff et al.

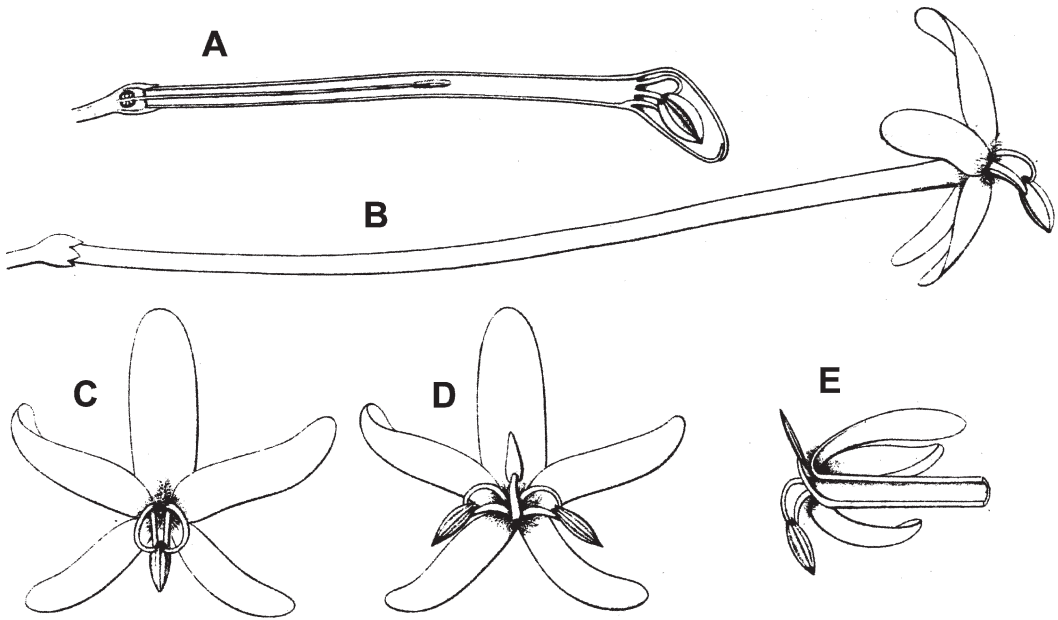


Figure 3. *Posoqueria latifolia*, diagrammatic representation of the pollen catapult mechanism. —A. Flower bud, with anthers in ellipsoidal structure. —B, C. Anthers held in ellipsoidal structure above the corolla. —D, E. Stage following the pollen catapult, with the two lateral stamen pairs folded backward, and the solitary stamen remaining erect above the corolla mouth. (Modified from F. Müller, 1866.)

(1995) reported that the anther structure points downward, as the flowers are pendulous; however, according to personal observation, they might also point upward or sideways, especially in some other species that may also have erect flowers (e.g., *P. gracilis* (Rudge) Roem. & Schult.; pers. obs. in Suriname). The corolla may open prior to pollination, exposing the anther ellipsoid structure (Fig. 3B, C), or may remain closed, with the anther structure enclosed inside the corolla lobes; this variation is possible even within the same individual (e.g., *P. latifolia*; pers. obs. in Santa Catarina). In flowers with the ellipsoid structure exposed, as soon as the hawkmoth touches the anther structure, the ventral stamen makes a violent forward movement (Fig. 3D, E), throwing a dust (or minute clumps of grains) of pollen onto the visitor (pers. obs.; not a globose mass, as reported by Hallé [1967]). In flowers with the anther structure included, it was observed that some hawkmoths forced the entrance of their proboscis at the top of the flower bud (pers. obs.), causing the corolla lobes to open and resulting in the sudden movement of the catapulting anther, releasing a dust of pollen onto the hawkmoth. At the moment of throwing the pollen, the two lateral pairs of anthers remain momentarily erect, folding backward shortly after, with the solitary stamen remaining erect above the corolla mouth. This stage has the obvious function of preventing the visitation of potential pollinators, as the flower at this point is devoid of pollen and the

stigma is not yet receptive. The third stage of anthesis is represented by the solitary anther folding backward (in ventral position), probably due to cell shrinkage, which liberates the mouth of the corolla. This is followed by the expansion of the style and a final receptive stage, with the style either remaining included (e.g., *P. latifolia*, pers. obs.) or further elongating and becoming exerted (e.g., *P. longiflora*, pers. obs. in Ecuador, Suriname, and the Brazilian state of Tocantins), depending on the species. The same catapult mechanism described in *P. latifolia* was also observed and photographed in *P. longiflora* (Fig. 4A, B).

Molopanthera paniculata is a species becoming quite rare in nature, as the Brazilian Atlantic forest is now almost completely destroyed. I was able to find a healthy population at the Feliciano Miguel Abdala Natural Heritage Private Reserve (also known as the "Caratinga Biological Station"), in Minas Gerais, Brazil. Studies on the pollination biology of this genus are planned for the near future. The pollen catapult mechanism of *Molopanthera* was personally observed for the first time at this locality, and although the flowers are much smaller, the process is practically identical to that in *Posoqueria*. The five anthers are initially united into an ellipsoidal structure held at an oblique position, as the flower bud is curved (Fig. 2A). As in *Posoqueria*, each anther has basal and apical appendages, which are sterile extensions of the thecae, much darker, and which function as a

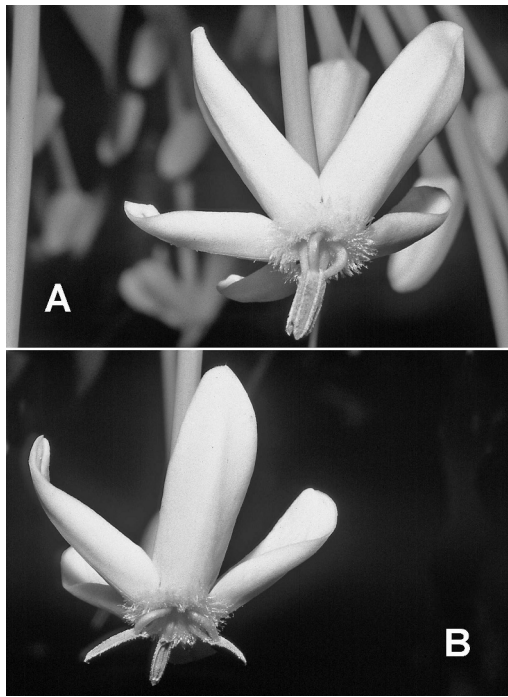


Figure 4. *Posoqueria longiflora*, flowers in two stages of anthesis. —A. Flower with anthers held in ellipsoidal structure above the corolla, before the pollen catapult. —B. Later stage of anthesis following the pollen catapult, with the two lateral stamen pairs folded backward and the solitary stamen folded backward liberating the corolla mouth; the style is in the process of expansion and is still included within the corolla tube. (Photos by L. Westra.)

contact zone for the two anther pairs. While still united, the anthers dehisce longitudinally and release a loose pollen mass at the center of the anther structure. When the visitor (most probably a small bee) touches the anther structure, the ventral stamen springs forward (Fig. 2B), throwing a dust of pollen, while the two lateral pairs of anthers remain momentarily erect. However, the flowers were not directly observed while visited by the pollinators, but the catapult movement was stimulated by lightly touching the tip of the flower buds with a small pin. Shortly after the catapult movement, the two lateral stamen pairs fold outward, and the solitary stamen remains erect above the corolla mouth (Fig. 2C). As in *Posoqueria*, the erect stamen has the function of obstructing the visitation of possible pollinators, as the flower at this point is devoid of pollen and the stigma is not yet receptive. At the final stage of anthesis, the solitary stamen shortens and folds backward, liberating the mouth of the corolla, and the style and style branches expand, exposing the receptive stigmas (Fig. 2D).

POLLEN

According to the information provided by Persson (1993) and Huysmans et al. (1999), the pollen grains of *Molopanthera* (Fig. 1D) and *Posoqueria* (Fig. 1F) are very similar. They are spheroidal (or oblate), tricolporate, and with ectocolpi acute at both ends. The exine is reticulate with lumina gradually decreasing in size toward the poles, and supracteal processes are absent. However, this combination of characters is one of the most common in the family. The main difference between the pollen of the two genera is found in the size, $34\text{--}57 \times 40\text{--}59 \mu\text{m}$ in *Posoqueria* (Persson, 1993) and $14\text{--}16 \times 14\text{--}17 \mu\text{m}$ in *Molopanthera* (Huysmans et al., 1999), which is positively correlated with the flower size in each genus.

OVARY

In both genera, the ovary is 2-locular (sometimes with incomplete placenta and 1-locular in *Posoqueria*), the placenta has a basal stalk, elevating the portion where the ovules are attached to the central septum, and the ovules are numerous. The placental extensions are quite different, terminating with two lateral lamellas in *Posoqueria*, and with a globose structure in *Molopanthera*.

STYLE

The style of *Posoqueria* is bilobed with oblong-ovate stigmatic branches. In most species, it elongates in the female stage of the flower, becoming exerted and receptive after the anthers have folded backward. However, in some species (e.g., *P. taraiensis*), the style apparently remains included even during the receptive stage.

Similarly, the style of *Molopanthera* is bilobed, with the stigmatic branches narrowly oblong and slightly reflexed at maturity (Fig. 2D). It functions much in the same way as that of *Posoqueria*. However, with the first stage of anthesis, the style is about the same length as the corolla tube and not receptive. After the anthers have folded backward, the style expands and the style branches eventually elongate and become receptive.

FRUITS

Aside from the flower size, the most impressive difference between *Posoqueria* and *Molopanthera* lies in fruit size, seed type, and dimensions. Obviously, this set of characters influenced most rubiologists in keeping the two genera far apart in all historical classifications.

The fruits of *Posoqueria* are leathery or woody berries, globose, ovoid to ellipsoid, and 2.5–5 cm in diameter. The large seeds are found in the central portion, immersed in a white, gelatinous pulp.

The fruits of *Molopanthera* are capsular, 2–3.5 × 3.5–5 mm, thin, woody, strongly bilobed, with the two sides subglobose, and with loculicidal dehiscence.

SEEDS

The seeds of *Posoqueria* are attached to the two lamellar extensions of the placenta, which is somewhat difficult to detect in mature fruits. They are 6–15 mm in diameter, round or ovate in outline, obtusely angled or flattened. According to Persson (1995), the exotesta cells are isodiametrical to elongate and parenchymatic. Following personal observations, the seeds are perlaceous, with the outer portion of gelatinous consistency, sweetish and edible, and dispersed by birds (e.g., parrots, pers. obs.) and mammals (e.g., monkeys, capivaras, pers. obs.).

The seeds of *Molopanthera* are peltately attached to the globose placental extensions. They are 0.8–3 × 1–2.2 mm, very irregular, deeply fringed in outline, with a central hylum, and wind dispersed. The testa is shallowly reticulate. Exotesta cells are elongated, with radial orientation, and interspaces have foveolate-reticulate thickenings (Delprete, 1999: 38, fig. 11B). Because of these features, they are very similar to those of *Chimarrhis*, which explains Delprete's (1999) positioning within the Rondeletieae.

CONCLUSION

As discussed here, apparently not all the species of *Posoqueria* display the catapult mechanism typical of this tribe. In the species reported to have stamens with equal length, the flower buds are supposedly straight, as can be seen in the illustration of *P. taraiensis* (Taylor & Cortés-B., 1999: fig. 1), and not laterally bent, as in species with the pollen catapult mechanism. This feature definitely needs further morphological, anatomical, and phylogenetic studies in order to detect patterns of evolution within the genus. Additional field observations of both *Posoqueria* and *Molopanthera* are necessary for a complete understanding of the pollination biology and the identification of the pollinators of this peculiar tribe.

This work corroborates that the pollen catapult mechanism of *Molopanthera* and *Posoqueria* is generally identical, as originally pointed out by Schumann (1888, 1889, 1891). This confirms the close relationship between the two genera.

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