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SHORT COMMUNICATION

New records of pollen tube shower in species of *Bertolonia* (Melastomataceae) suggest that autogamy may be the rule in the genus

Luan Salles Passos[1] · **Renato Goldenberg**[2] · **Lucas F. Bacci**[3] · **Francismeire Jane Telles**[4] · **Fabiano Rodrigo Maia**[1,5]

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Abstract

Previous molecular phylogenetic analyses showed that *Bertolonia* (Melastomataceae), an endemic genus to the Brazilian Atlantic Forest (AF) with 35 species, presents a strong correlation regarding species distribution and some floral traits. The same analyses showed that all species belong to three clades: marmorata (species mostly distributed in northern AF), formosa (species only occurring in central AF), and nymphaeifolia (species mostly distributed in southern AF). A rare delayed selfing mechanism, the pollen tube shower (PTS), was recently described for two species in the nymphaeifolia clade; however, this mechanism may also be prevalent in species of the other clades. Here, we investigated the potential occurrence of PTS in two other species of the genus: *B. violacea* (marmorata clade) and *B. acuminata* (nymphaeifolia clade). We also investigated species, as well as herbarium specimens, searching for potential evidence of floral traits that could suggest the presence of an autonomous selfing mechanism in other *Bertolonia* species. Both *B. violacea* and *B. acuminata* produced seeds through PTS. We also observed the occurrence of PTS in two exsiccates from two different species: *B. maculata* (marmorata clade) and *Bertolonia* sp. Taxonomic data across all clades of the genus indicate the absence of herkogamy, presence of post-anthesis petal closure and corolla persistence on the floral receptacle, all traits associated with the occurrence of PTS. We present here empirical evidence and descriptions of floral traits that indicate that the genus *Bertolonia* is predominantly autogamous, an uncommon characteristic in Melastomataceae.

Keywords Autonomous self-pollination · Bertolonieae · Delayed selfing · Poricidal anthers · Reproductive assurance

Introduction

Bertolonia Raddi is a genus of Melastomataceae with 35 herbaceous species (Baumgratz 1990; Bacci et al. 2020a; Bisewski et al. 2020). Its distribution is restricted to eastern Brazil, with all species endemic to the Atlantic Forest (AF) domain (Bacci et al. 2019). The genus was informally divided into three clades: "marmorata," "formosa," and "nymphaeifolia" (Bacci et al. 2020b). These clades present a strong correlation with the geographical distribution of their species, with the members of the marmorata clade occurring more often in the northern AF, the members of the formosa clade in central AF and species of the nymphaeifolia clade (together with the type of the genus: *B. nymphaeifolia* Raddi) distributed in the southern AF (Bacci et al. 2020b). In addition to geographic congruence, some floral traits such as the orientation of the anther pore dehiscence, petals and

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Luan Salles Passos
luan.spassos@gmail.com

[1] Programa de Pós-Graduação em Botânica, Departamento de Botânica, Universidade Federal do Paraná, Curitiba, Paraná, Brazil

[2] Departamento de Botânica, Universidade Federal do Paraná, Curitiba, Paraná, Brazil

[3] Florida Museum of Natural History, University of Florida, Gainesville, FL, USA

[4] Programa de Pós-Graduação em Ecologia e Conservação de Recursos Naturais, Universidade Federal de Uberlândia, Uberlândia, Minas Gerais, Brazil

[5] Departamento de Biologia Geral, Universidade Estadual de Ponta Grossa, Ponta Grossa, Paraná, Brazil

anthers color were also somewhat conserved in each one of these clades (Bacci et al. 2020b).

Bertolonia species share a set of attributes with some other Melastomataceae genera, such as *Monolena* Triana ex. Benth & Hook.f., *Triolena* Naudin, and *Macrocentrum* Hook f., among others. The main traits are herbaceous habit, scorpioid inflorescences, angular fruits, seed dispersal by raindrops, and even vivipary (Bacci et al. 2019, 2021). The delimitation of the tribe Bertolonieae s.l. based on these shared traits has always been discussed in melastome classifications (see Bacci et al. 2019). However, based on molecular evidence, Bacci et al. (2019) recircumscribed Bertolonieae only with *Bertolonia*, excluding the aforementioned genera in addition to others. Thus, these shared traits can be understood as morphological convergence in response to selective pressures from environmentally similar habitats (Bacci et al. 2019).

In a recent survey, a new delayed selfing mechanism was described for two species belonging to the nymphaeifolia clade: *Bertolonia paranaensis* (Wurdack) Baumgratz and *B. mosenii* Cogniaux (Passos et al. 2021). In this mechanism called *pollen tube shower* (PTS), pollen grains from post-anthetic flowers (the anthesis in both species is shorter than one day) germinate inside the poricidal anthers and the pollen tubes reach the stigmas, penetrate the transmission tissue, and then fertilize the ovules; resulting in perfect seeds (Passos et al. 2021). For these species, PTS ensures reproductive success in unsuccessful pollination or even in the absence of pollinators, providing reproductive assurance, since it occurs after cross-pollination events or in their absence (Passos et al. 2021).

Autonomous self-pollination events (hereafter autonomous selfing) are rarely documented in Melastomataceae. This peculiarity is probably a consequence of the presence of poricidal anthers, a trait conserved in the family, whose pollination usually depends on an active vector for pollen removal from these structures (e.g., buzzing bees; Buchmann 1983). It is also a consequence of the pronounced herkogamy evident in most species (Renner 1989). However, despite the presence of poricidal anthers in *Bertolonia paranaensis* and *B. mosenii*, (1) the absence of herkogamy resulting from the movement of the stamens throughout the flower life cycle, associated with (2) the return of the corolla to the same position as in the bud stage and its retention in the floral receptacle allows pollen tubes exiting the anther pore to reach the ovules in post-anthetic flowers (Passos et al. 2021). Therefore, based on the absence of significant variation in the floral attributes of *Bertolonia* species (e.g., pronounced herkogamy), we hypothesize that this autonomous selfing mechanism is widespread in the genus.

In this study, we aimed to investigate whether this autonomous selfing mechanism also occurs in species of other clades within the genus *Bertolonia*. For this purpose, we investigated living and herbarium specimens from all three *Bertolonia* clades, in order to assess putative PTS events. In addition, we searched morphological descriptions in taxonomic papers for features that could indicate the potential occurrence of selfing in other species with similar floral traits.

Materials and methods

To investigate fruit set resulting from the PTS mechanism we selected two species: *Bertolonia violacea* Bisewski, Bacci & R.Goldenb. (marmorata clade; Fig. 1a), in which we conducted pollination experiments in greenhouse ($n = 27$ flowers; plants from the Instituto Nacional da Mata Atlântica, Santa Teresa, Espírito Santo, Brazil), and in a natural population of *B. acuminata* Gardner (nymphaeifolia clade; Fig. 1b, c; $n = 12$ flowers; plants in Serra da Graciosa, Morretes, Paraná, Brazil; 25° 21′ 49″ S, 48° 52′ 37″ W). Thus, we performed autonomous self-pollination experiments by isolating the flowers of both species with *voile* bags to avoid visits from potential pollinators. We also performed floral biology observations for *B. violacea*, recording the time of anthesis and post-anthesis, and the arrangement and dynamics of the floral whorls during these events.

When PTS occurs, the anthers and stigma are joined by a weft of pollen tubes (Passos et al. 2021). This can be seen in herbarium specimens, and consequently could provide us with evidence of this phenomenon in different species. We gathered all *Bertolonia* (except *B. paranaensis*, *B. mosenii*, and *B. acuminata*) specimens deposited in the herbarium UPCB (Thiers 2020), totaling 26 exsiccates. We removed flowers from the exsiccates, rehydrated them in heated water, and observed them under a stereoscopic microscope (ZEISS Stemi 305, Germany).

We gathered published taxonomic descriptions and monographs of *Bertolonia* (references in Table 1) to collect data on style and stamen length for each species. We also surveyed field information (e.g., floral features, time of anthesis), searching for evidence of floral traits related to autonomous selfing events (i.e., brief floral lifespan and retention of floral pieces in post-anthesis; Passos et al. 2021). We used the style and stamen length data to calculate Pearson's correlation coefficient, in order to assess whether there is a linear association between the size of both reproductive structures and the herkogamy index (HI; Robertson & Lloyd 1991). The HI may range from negative (with the stigma below the anthers; reverse herkogamy) to positive values (when the stigma is above the anthers; approach herkogamy). We assume that species presenting HI values between −4 and 4 mm are prone to perform autonomous selfing (see Lázaro et al. 2020). For both calculations, we used the absolute

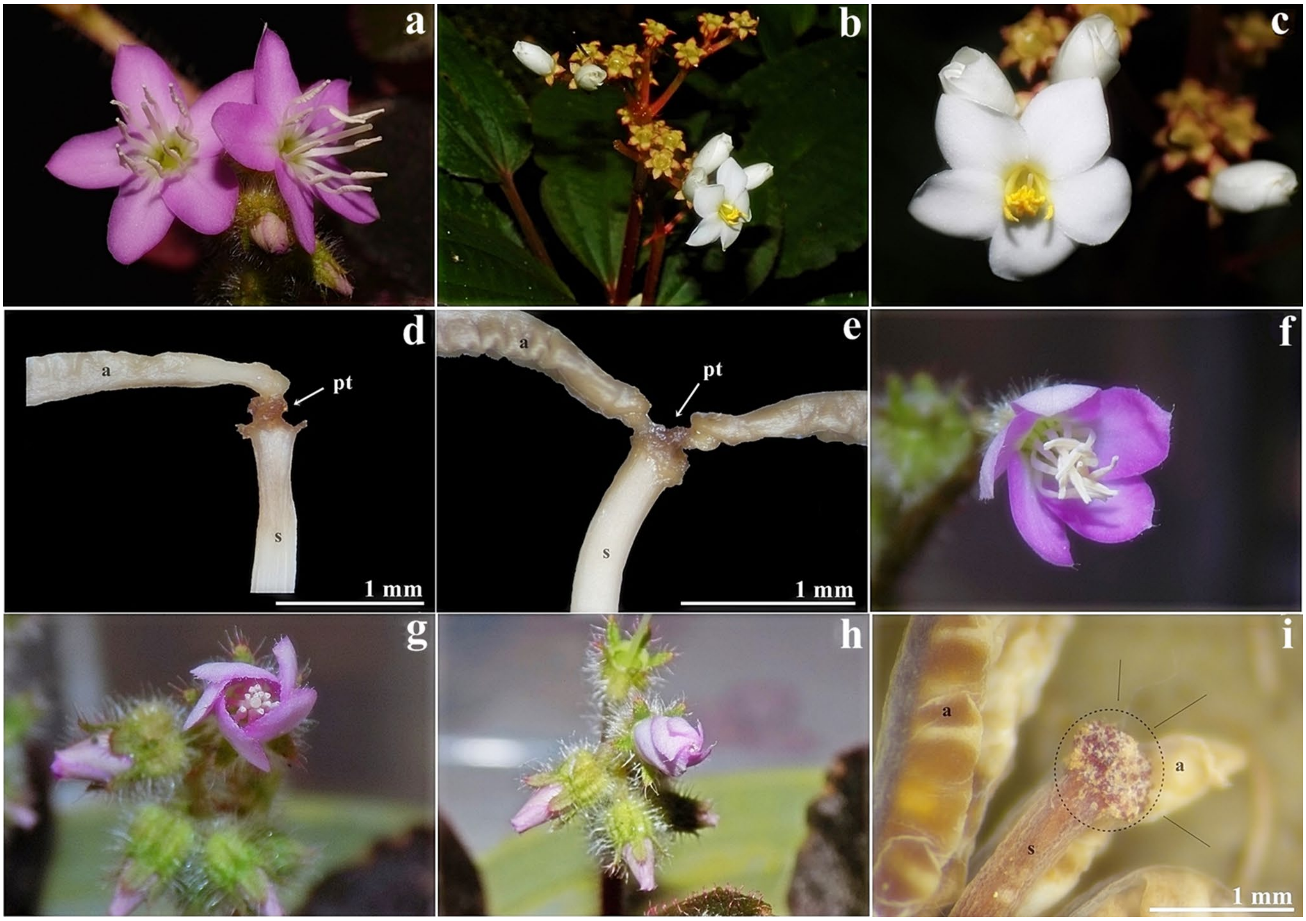

Fig. 1 **a** Flowers of *Bertolonia violacea*, **b** *B. acuminata*. **c** Flower detail of *B. acuminata*. **d** Mass of pollen tubes leaving the anther and penetrating the stigma in *B. violacea* and **e** in *B. acuminata*. **f** Flower of *B. violacea* at the end of the anthesis: stamens gathering in the center of the flower, around the style; **g** petals closing with stamens and style included, and **h** flower in post–anthesis with reproductive structures included. **i** Pollen on stigma of *B. maculata*, anther and stigma were connected through pollen tubes but were separate during handling. Subtitle: *a* anthers, *s* style and *pt* pollen tubes

values of the length of either structure, or the mean values when the measures were distributed in a range (Table 1).

Results and discussion

Both *Bertolonia violacea* (14/27—51.9%) and *B. acuminata* (6/12—50%) produced fruits and perfect seeds through autonomous selfing. We observed that the reproductive structures in post-anthetic flowers of *B. violacea* (Fig. 1d) and *B. acuminata* (Fig. 1e) were joined by pollen tubes exiting the anther pore and penetrating the stigmatic surface of the respective flowers, as reported in *B. paranaensis* and *B. mosenii* (Passos et al. 2021). *Bertolonia violacea* exhibited a short flower lifespan, with anthesis starting at 5 a.m., corolla fully opening between 6–6:30 a.m., and the beginning of the corolla closure around 11:30 a.m., fully closing at 2 p.m. During anthesis, the stamens were radially arranged and away from the stigma. Once the petals started to close, the stamens were pushed to the center of the flower (Fig. 1f, g), with the anther pores approaching the stigma. The post-anthetic petals (Fig. 1h) remained on the floral receptacle until 48 h after anthesis. We also observed the production of exudate on the stigmatic surface in post-anthetic flowers. These same floral traits (i.e., a brief period of anthesis, transitory herkogamy, petal closure and retention on the receptacle, and exudate formation in post-anthesis) were described in *B. paranaensis* and *B. mosenii* and may be associated with PTS events (Passos et al. 2021).

Most exsiccates of *Bertolonia* that were analysed (81%) had only old fruits or flower buds. Therefore, it was not possible to investigate the occurrence of PTS in these specimens. Exsiccates with post-anthetic flowers were rare, which seems to be a pattern in several *Bertolonia* collections (Bacci et al. 2020b). However, we observed that some anthers were "connected" to the stigma by pollen

Table 1 Orientation of pore dehiscence in anthers, length (in mm) of stamens and style, and herkogamy index (HI) of *Bertolonia* Raddi species

Species	Pore orientation	Lenght (mm)			References
		Stamens	Style	HI	
Bertolonia acuminata Gardner	Introrse	3.6–5.5	4–6.5	0.70	Goldenberg et al. (2016)
Bertolonia alternifolia Baumgratz et al.	Extrorse	6.6–9.9	7.5–11.4	1.20	Bisewski et al. (2020)
Bertolonia angustifolia Cogniaux	Introrse	No data	No data	No data	Baumgratz (1990)
Bertolonia angustipetala Bacci & R.Goldenb.*	Introrse	6–7.5	5–6	−1.25	Bacci et al. (2018)
Bertolonia bullata Baumgratz et al.	Introrse	3.7–4.5	3.8–4.5	0.05	Bisewski et al. (2020)
Bertolonia carmoi Baumgratz	Introrse	8.2–9.5	6–11	0.15	Baumgratz (1990)
Bertolonia cuspidata Bacci & Amorim	Introrse	4.4–5.9	3.6–5.9	−0.40	Bisewski et al. (2020)
Bertolonia duasbocaensis Bacci & R.Goldenb.	Introrse	6–7	5	−1.50	Bacci et al. (2016b)
Bertolonia formosa Brade	Introrse	8.0–9.7	7.5–8.0	−1.10	Baumgratz (1990)
Bertolonia foveolata Brade	Introrse	5.5–6	5–5.5	−0.50	Baumgratz (1990)
Bertolonia grazielae Baumgratz	Introrse	6.2–7.2	6	−0.70	Baumgratz (1990)
Bertolonia hirsutissima Bacci et al.	Extrorse	6–7	5	−1.50	Bacci et al. (2016a)
Bertolonia hoehneana Brade	Introrse	5.5–6	6–6.5	0.50	Baumgratz (1990)
Bertolonia igrapiuna Bisewki et al.	Extrorse	4.5–6.5	4.3–6.4	−0.15	Bisewski et al. (2020)
Bertolonia kollmannii Bacci & R.Goldenb.*	Extrorse	4.5–5.5	6	1.00	Bacci et al. (2018)
Bertolonia leuzeana (Bonpl.) DC.	Introrse	5–5.6	5	−0.30	Baumgratz (1990)
Bertolonia linearifolia Bacci & Michelang.*	Extrorse	5–7	7	1.00	Bacci et al. (2018)
Bertolonia lucernula Bacci et al.	Introrse	5.5–8	4.5–5.5	−1.75	Bacci et al. (2020a)
Bertolonia macrocalyx Bacci & R.Goldenb.	Introrse	6.3	5	−1.30	Bacci et al. (2016b)
Bertolonia maculata DC.	Apical	5.8–8.7	7–7.6	0.05	Baumgratz (1990)
Bertolonia margaritacea Naudin	Extrorse	6.5–7**	3–6	−2.25	Goldenberg et al. (2016)
Bertolonia marmorata (Naud.) Naudin	Introrse	4–6	4.8–6	1.00	Baumgratz (1990)
Bertolonia michelangeliana Bacci & R.Goldenb.	Extrorse	10.9–11.5	12	0.80	Bacci et al. (2016b)
Bertolonia mosenii Cogniaux	Extrorse (two pores)	3.6–8.8	6.5–8.2	1.15	Baumgratz (1990)
Bertolonia nymphaeifolia Raddi	Introrse	7–10.5	8–8.5	−0.50	Baumgratz (1990)
Bertolonia organensis Baumgratz et al.	Introrse	5.5–7.5	6	−0.50	Silva-Gonçalves et al. (2016)
Bertolonia paranaensis (Wurd.) Baumgratz**	Introrse	5.8–7	5.6–5.8	−0.70	Baumgratz (1990)
Bertolonia riocontensis Bisewski et al.	Extrorse	7–8	8	0.50	Bisewski et al. (2020)
Bertolonia reginatoi Bacci & Michelang.*	Introrse	5–7.5	8–10	2.75	Bacci et al. (2018)
Bertolonia ruschiana Bacci & R.Goldenb.	Introrse	6–7.5	6	−0.75	Bacci et al. (2016b)
Bertolonia sanguinea Safd. ex Cogniaux var. *sanguinea*	Introrse	18–19	12.5–13	−5.75	Baumgratz (1990)
Bertolonia sanguinea var. *santos-limae* (Brade) Baumgratz	Introrse	18–19	12.5–13	−5.75	Baumgratz (1990)
Bertolonia valenteana Baumgratz	Introrse	12.1	9.7	−2.40	Baumgratz (1990)
Bertolonia violacea Bisewki et al.	Extrorse	5.7–5.9	5.7–7.3	0.70	Bisewski et al. (2020)
Bertolonia vitoriana Bacci & Amorim*	Introrse	6.3	5.1	−1.20	Bacci et al. (2018)
Bertolonia wurdackiana Baumgratz	Introrse	5.6–6.6	5.3–5.5	−0.70	Baumgratz (1990)

*Stamen length: filaments plus anther lengths (Goldenberg et al. 2016; Bacci et al. 2018)

***Bertolonia paranaensis* was described in Goldenberg et al. (2016) with anthers dehiscing through an extrorse pore, but, we observed introrse pores. Confirmed in Baumgratz (1990) and Passos et al. (2021)

tubes that came out of anthers, providing evidence of PTS in two exsiccates, each one from a distinct species. One of these species was *B. maculata* DC. (marmorata clade; voucher UPCB79510). We also noticed that the stigmas of other flowers in the same specimen were impregnated with pollen between their stigmatic papillae (Fig. 1i). The other species was recently collected in Bahia state (UPCB 98210), northern AF (therefore probably also part of the marmorata clade), but it is probably an undescribed species (G. Bisewski pers. comm).

The length of the reproductive structures of *Bertolonia* species (i.e., style and stamens) showed a positively strong correlation (Pearson's correlation coefficient = 0.86; $p < 0.001$), suggesting that herkogamy (or its absence) is continuous across the species of the genus. Moreover, except for *Bertolonia sanguinea* Sald. ex Cogniaux var. *sanguinea*

(HI = −5.75; Table 1), *Bertolonia sanguinea var. santos-limae* (Brade) Baumgratz (HI = −5.75; Table 1), and for *Bertolonia angustifolia* Cogniaux, for which we found no data (Baumgratz 1990), most species of *Bertolonia* do not present herkogamy (Table 1). When there is a difference in size between the style and stamens (−4 > HI > 4), the latter are longer (reverse herkogamy). Thus, for most of these species, the stamens may bend toward the stigma at the end of anthesis, as observed in *B. paranaensis* and *B. mosenii* (Passos et al. 2021), as well as evidenced in *B. violacea* (this paper), which may facilitate the deposition of pollen tubes on the stigmatic surface.

Besides the absence of herkogamy, we highlight other morphological features from taxonomic descriptions for the flowers of some species. First, in *Bertolonia bullata* Baumgratz, Amorim & A.B.Jardim (formosa clade), *B. sanguinea* var. *sanguinea* and *B. nymphaeifolia* Raddi (both from nymphaeifolia clade), the corollas were described as cupuliform (Baumgratz 1990; Baumgratz et al. 2011). This feature suggests a tendency toward autonomous selfing in these species, considering that either species exhibit some degree of cleistogamy or investment in autogamous seed production as opposed to attracting pollinators (see discussion in Passos et al. 2021). Moreover, in the recent description of *B. lucernula* Bacci, D.T.Iglesias & R.Goldenb., Bacci et al. (2020a; formosa clade) points out that in post-anthetic flowers the petals return to the floral bud position and remain on the receptacle, a factor associated with autonomous selfing events in *Bertolonia* (Passos et al. 2021).

Up to now, there are at least six taxa with conclusive evidence of autonomous selfing; these belong to two different clades of *Bertolonia*: *B. maculata* and *B. violacea* (marmorata clade); *B. paranaensis*, *B. mosenii* and *B. acuminata* (nymphaeifolia clade), and *Bertolonia* sp. (without phylogenetic position at the present moment). Although we have not found concrete evidence of autonomous selfing in species of the formosa clade, due to the lack of herbarium vouchers or in vivo plants for floral biology studies, taxonomic records such as the absence of herkogamy have been found in almost all species in this clade (Table 1). Moreover, the cupuliform corolla in *B. bullata* (Baumgratz et al. 2011) and the closing of the persistent petals in post-anthetic flowers of *B. lucernula* (Bacci et al. 2020a) indicate that autonomous selfing is also occurring in this clade and, therefore, in all lineages across the genus.

The genera *Monolena*, *Triolena*, *Macrocentrum* and *Boyania* Wurdack, that once belonged to Bertolonieae s.l., share similar floral traits (Cogniaux 1891; Renner 1993; Clausing & Renner 2001; Goldenberg et al. 2012; Bacci et al. 2019) and inhabit similar environments as *Bertolonia* (herbaceous humid and shaded forest strata; Bacci et al. 2019), a factor that may be associated with lower visitation rates by pollinating bees (Passos et al. 2021). Therefore, if PTS also occurs in these genera as in *Bertolonia* species, we hypothesize that autonomous selfing mechanisms may have evolved independently in the two groups; a PTS-like mechanism has already been suggested for *Monolena trichopoda* R.H.Warner (Warner 2002).

Finally, our work points out an important finding, considering that at least five species of *Bertolonia* (14.2% of all species) can produce fruits and perfect seeds by autonomous selfing. The morphological and functional traits found in the flowers of the genus are an excellent indication of the existence of a Melastomataceae group capable of reproducing by autonomous selfing, a rare phenomenon in the family. The autonomous selfing events in *Bertolonia* may ensure the reproductive success of these species in cases of insufficient pollen deposition to fertilize the ovules or even in the absence of pollinators. Furthermore, it favors cross-pollination, since it occurs only after anthesis (i.e., delayed selfing), avoiding ovule discounting. Therefore, PTS is an important adaptive trait for these species, since this mechanism reduces the effects of pollen limitation and provides reproductive assurance. Thus, future surveys will be essential to confirm our findings, as well as investigate the occurrence of potential autonomous selfing events in species that share similar floral traits, such as in *Monolena*, *Triolena*, and *Macrocentrum*.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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