

Ontogeny of Inflorescences and Flowers in the Brownea Clade (Fabaceae: Detarioideae): A morphologically diverse lineage of legumes

Ana Tereza Novaes Parga Rodrigues

ana.tnovaes@gmail.com

Jardim Botânico do Rio de Janeiro: Jardim Botânico do Rio de Janeiro <https://orcid.org/0000-0002-1235-1655>

Marcus José Azevedo Falcão

Jardim Botânico do Rio de Janeiro: Jardim Botânico do Rio de Janeiro

Vidal de Freitas Mansano

Jardim Botânico do Rio de Janeiro: Jardim Botânico do Rio de Janeiro

Research Article

Keywords: Floral development, floral morphology, Heterostemon, Leguminosae, Macrolobium, Paloué

Posted Date: January 31st, 2025

DOI: <https://doi.org/10.21203/rs.3.rs-5914372/v1>

License:   This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Version of Record: A version of this preprint was published at Journal of Plant Research on July 20th, 2026. See the published version at <https://doi.org/10.1007/s10265-026-01723-2>.

Ontogeny of Inflorescences and Flowers in the Brownea Clade (Fabaceae: Detarioideae): A morphologically diverse lineage of legumes

Ana Tereza Novaes Parga Rodrigues^{1, 2*}, Marcus José de Azevedo Falcão^{1, 3}, and Vidal de Freitas Mansano^{1, 4}

¹Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, DIPEQ. Rua Pacheco Leão 915, Jardim Botânico, Rio de Janeiro, RJ, 22460–030, Brazil.

²ana.tnovaes@gmail.com; <https://orcid.org/0000-0002-1235-1655>

³jrfalcao2010@hotmail.com; <https://orcid.org/0000-0001-8337-5112>

⁴vidalmansano@gmail.com; <https://orcid.org/0000-0002-7204-0744>

*Corresponding author: ana.tnovaes@gmail.com

Abstract

The subfamily Detarioideae stands out among legumes as a clade with remarkable diversity in floral morphology. Within this subfamily, the Brownea clade, characterized by its Neotropical distribution, exhibits significant meristic variability in the perianth, androecium, and gynoecium. These structures vary in size, shape, color, and pubescence. This floral diversity is associated with different pollination syndromes, including entomophily, ornithophily, and chiropterophily. Despite the monophyly of the Brownea clade, the phylogenetic and taxonomic relationships among its seven genera remain inadequately resolved. In such groups, studies on floral ontogeny are crucial to understanding the processes driving variations in floral morphology. These studies also aim to identify potential autapomorphies, synapomorphies, plesiomorphies, and homoplasies that could aid in the systematics of the group. This study aims to expand the understanding of the morphology and development of inflorescences and flowers in six species from five morphologically diverse genera within the Brownea clade. The study provides ontogenetic descriptions of *Brownea longipedicellata*, *Browneopsis macrofoliolata*, *Heterostemon mimosoides*, *Macrolobium suaveolens*, *Paloue paraensis*, and *Paloue speciosa*, comparing these findings with existing studies on Detarioideae. In doing so, it contributes to the broader understanding of floral evolution in the Leguminosae family. In addition to supporting the systematics of the group, the study explores how floral morphological adaptations relate to their respective pollination syndromes. Given the lack of studies addressing the nectariferous nature of flowers in this clade, we also conduct anatomical analyses of the hypanthium in these species to enhance knowledge of their systematics at an anatomical level.

Keywords: Floral development; floral morphology; *Heterostemon*; Leguminosae; *Macrolobium*; *Paloue*.

Introduction

Fabaceae, or Leguminosae, is the third-largest family of angiosperms in terms of species richness. With a cosmopolitan distribution, it is renowned for its ecological and economic importance, largely due to the nitrogen-fixing capacity present in most of its species (Lewis et al. 2005). The family comprises six subfamilies (LPWG 2017): Papilionoideae, Caesalpinioideae, Detarioideae, Cercidoideae, Dialioideae, and Duparquetioideae. Among these, Detarioideae stands out. Previously classified as tribe Detarieae *sensu lato* within Caesalpinioideae, its phylogenetic relationships with other Fabaceae subfamilies remain poorly resolved (Koenen et al. 2020; LPWG 2017). Similarly, the relationships among the taxa within Detarioideae remain unclear, with recent systematic studies identifying numerous polytomies and paraphyletic groups (Estrella et al. 2018; Redden et al. 2018; Schley et al. 2018).

Members of this subfamily exhibit remarkable diversity in floral morphology (Bruneau et al. 2014; Citeli et al. in prep; Cowan & Polhill 1981a; 1981b; Kochanovski et al. 2018; Krüger et al. 1999; Ojeda et al. 2019; Pedersoli et al. 2010; Prenner & Cardoso 2017; Tucker 2000a; 2000b; 2000d; 2001a; 2001b; 2002a; 2002b; 2003a; 2003c; present work). This diversity includes variations from the typical Fabaceae floral pattern, which is commonly observed in Cercidoideae, Papilionoideae, and Caesalpinioideae. In most species of these subfamilies, flowers possess 21 organs, divided into five sepals, five petals, two whorls of five stamens, and a single carpel (LPWG 2017; Tucker 1987).

In Detarioideae, the calyx is typically pentamerous, as in most Leguminosae. However, in most genera, the two adaxial sepals are fused, giving the appearance of a tetramerous calyx at anthesis (Bruneau et al. 2014; Ferguson & Tucker 1994). Regarding the corolla and androecium, although approximately 29% of genera and 36% of species in Detarioideae retain five petals and ten stamens—consistent with other legumes—the majority of taxa (70% of genera and 64% of species) exhibit reductions in the number of petals and/or stamens.

These reductions are often variable, even among closely related taxa, with petals or stamens reduced to petaloids or staminodes. In rare cases, sepals are absent, as seen in genera such as *Aphanocalyx* Oliv., *Bikinia* Wieringa, and *Brachystegia* Benth. (Tucker 1988; 1989a; 2000a; 2000c). Tucker (1988; 1989; 2000a; 2000c) discusses various forms of meristic variation that can occur during floral development, including the fusion of organs, reduction through organ abortion, and reduction via non-initiation of organs, as observed in *Aphanocalyx* and *Crudia* Schreb. (Tucker 2000a; 2001a).

Non-initiation of organs plays a critical role in floral merism, especially as it can alter the organogenesis of subsequent floral whorls (Ronse de Craene 2016; Tucker 1988; 1989; 2000c). In the corolla and androecium, reduction commonly occurs through the abortion of initiated organs, which may remain as vestigial structures at anthesis. For example, in *Macrolobium* Schreb., the corolla is reduced to a single adaxial petal, and the androecium is almost always limited to three to five fertile stamens (Bruneau et al. 2014; Cowan 1953; Murphy et al. 2018).

These reductions often result in variations in floral symmetry. Flowers of closely related taxa in Detarioideae can range from actinomorphic to slightly zygomorphic or strongly zygomorphic, as observed within the genus *Hymenaea* L. (Kochanovski et al. 2018).

Another notable feature of Detarioideae flowers is the staminal ring, which originates from the fusion of filament bases. This fusion can, in some cases, extend along the filaments to form discontinuous monadelphous sheaths on the adaxial side or, more rarely, tubes of varying heights. Occasionally, the stamens are diadelphous (Bruneau et al. 2014; Cowan & Polhill 1981a; Tucker 2000b). While the staminal ring is not always present, it can assist in pollination either structurally or by developing into a nectary (Cowan & Polhill 1981a).

A floral characteristic of significant systematic importance in Detarioideae is the style, which curves toward the abaxial side as it elongates during floral development (present study;

Tucker 2000a; 2000b; 2000c; 2001a; 2002a; 2002b). Prenner and Cardoso (2017) proposed this characteristic as a potential synapomorphy for Detarioideae, as no records indicate its occurrence in other Fabaceae subfamilies. Another notable and common feature of the subfamily is the presence of two conspicuous and persistent bracteoles (Cowan and Polhill 1981a; 1981b; LPWG 2017; Tucker 2000a).

Historically, the morphology and function of bracteoles have played a significant role in classifying the groups now included within Detarioideae. Léonard (1957) classified African genera into the tribes Cynometreae and Amherstieae based on the imbricate or valvate aestivation of their bracteoles, respectively. Later, Cowan and Polhill (1981a) expanded this system to include Neotropical and Asian genera, reinstating Detarieae DC. as the oldest valid synonym for Cynometreae. Breteler (1995) revised Léonard's classification, suggesting that valvate bracteole imbrication is strongly linked to their protective function. He observed that, when present, bracteoles remain closed around the bud until just before anthesis and are typically large and persistent. Based on these findings, Breteler redefined the tribes as Detarieae and Macrolobieae, the latter being characterized by the presence of this type of large bracteole among its genera.

However, molecular phylogenetic studies by Bruneau et al. (2000) recovered Macrolobieae as paraphyletic within Detarieae. This necessitated the reorganization of the two tribes into a single tribe, Detarieae *sensu lato*. Despite this reorganization, the structure and function of bracteoles continued to serve as tools for systematizing groups within Detarieae *s.l.* Tucker (2000a; 2001a; 2002a; 2002b) proposed that the morphology of the floral meristem during bracteole initiation could distinguish taxonomic groupings. She described two morphological types: circular and omega. The circular type is associated with smaller bracteoles during initiation, while the omega type corresponds to cases where bracteoles are already well-developed shortly after initiation and are linked to the protective function of large, persistent bracteoles at anthesis.

However, subsequent phylogenetic studies revealed that this character is frequently homoplastic across different lineages and cannot reliably demarcate groups (Bruneau et al. 2014).

Despite its homoplastic nature, bracteoles remain of considerable systematic value within the subfamily, serving as diagnostic characters for various taxa (Breteler 2010; Cowan 1953). Additionally, bracteoles often play an ecological role, acting as attractants for pollination or providing protection to the flower bud (Breteler 1995; Cowan & Polhill 1981a; 1981b). Numerous studies on floral ontogeny also emphasize the influence of bracteole development on the final architecture of the flower (Bull-Hereñu et al. 2022; Tucker 2000a; 2000b; 2002a; 2002b).

Brownea Clade

In the phylogeny by Estrella et al. (2018), the genera of Detarioideae were grouped into six tribes: Schotieae, Barnebydendreae, Detarieae, Saraceae, Afzelieae, and Amherstieae. Among these, the tribe Amherstieae is the largest, but intra- and intergeneric relationships within it are often poorly supported. Several genera have been recovered as paraphyletic, highlighting the need for better-supported phylogenies and/or new taxonomic circumspections (Baker et al. 2022; Estrella et al. 2018; LPWG 2017).

Amherstieae exhibits great morphological variety but can be characterized by the large, persistent bracteoles. These bracteoles are typically larger than the sepals in the bud and serve a protective function (Breteler 1995). Additionally, the tribe is marked by various forms of meristic reduction and morphological modifications leading to zygomorphy (Cowan and Polhill 1981a; 1981b). The differentiation of the adaxial petal, often more prominent than the others, is a notable feature. This petal frequently remains as the sole petal in cases of monopetaly (Bruneau et al. 2014; Cowan and Polhill 1981a; 1981b).

The *Brownea* clade stands out within Amherstieae for its remarkable morphological diversity. Initially established as an informal group within Detarieae s.s. by Cowan and Polhill (1981a) based on morphological traits, the clade currently comprises seven genera: *Brownea* Jacq., *Browneopsis* Huber, *Brachycylis* (Harms) R. S. Cowan, *Ecuadendron* D.A. Neill, *Heterostemon* Desf., *Macrolobium*, and *Paloue* Aubl., all of which are Neotropical (Bruneau et al. 2000; Estrella et al. 2018; Redden et al. 2006; 2010). However, the relationships among these genera remain poorly resolved and conflict across studies.

For example, Murphy et al. (2018) recovered *Macrolobium* as monophyletic in a phylogeny focused on the genus, but some species of *Heterostemon* were grouped within *Paloue*. Meanwhile, Schley et al. (2018) showed species of *Browneopsis* interspersed with those of *Brownea*. The most comprehensive phylogenetic study of Detarioideae to date (Estrella et al. 2018) also presented poor resolution within the *Brownea* clade, recovering a polytomy that includes most genera without support for their monophyly.

The *Brownea* clade comprises approximately 130 species (POWO 2024), accounting for roughly 16% of Detarioideae's species richness. Despite its diversity, floral ontogeny studies have been conducted for only two species within the clade: *Brownea latifolia* Jacq. and *Macrolobium acaciifolium* (Benth.) Benth. (Tucker 2000b; 2002b). However, Tucker's study on *M. acaciifolium* lacks images, and much of the discussion focuses on *Macrolobium crassifolium* A. Chev., later recombined as *Anthonothea crassifolia* (Baill.) J. Léonard. (Tucker 2002b). Consequently, it is unclear whether the information presented truly pertains to *M. acaciifolium*.

A key feature of the *Brownea* clade is the significant meristic variation observed in the corolla and androecium, including reductions in the number of petals and stamens. These reductions occur through non-initiation, early-stage abortion, or transformation into petaloids or staminodes, phenomena prevalent across most species in the group (Redden and Herendeen 2006; Schley et al. 2018). Another noteworthy characteristic is the fusion of bracteoles into a tube (Bruneau et al. 2014; Cowan and Polhill 1981a; 1981b), considered a synapomorphy for the clade (Redden et al. 2010). However, in *Macrolobium*, this character is reversed, with most species displaying free bracteoles (Cowan 1953; Murphy et al. 2018).

Table 1 provides a comparative analysis of the main floral morphological characteristics across the clade's genera.

Recent phylogenetic studies focusing on the *Brownea* clade (Redden et al. 2018; Schley et al. 2018) suggest that *Brachycylis* and *Ecuadendron* are sister genera, forming a clade that is sister to the clade grouping *Brownea* and *Browneopsis*. Together, these form a sister group to a third clade comprising *Heterostemon*, *Macrolobium* and *Paloue*. In Schley et al (2018) phylogeny, several species of *Browneopsis* were nested within *Brownea*, raising questions about their monophyly. Furthermore, a later study by Schley et al. (2020) suggested high rates of intra- and intergeneric hybridization between taxa in these two genera.

Floral Diversity in the *Brownea* Clade

The approximately 20 species of *Brownea* are characterized by red, radially symmetrical flowers with a pseudotubular structure. These flowers feature fused bracteoles, 4–5 free but erect petals, and a staminal ring that forms a sheath around the carpel, interrupted in the median adaxial region. The inflorescences of *Brownea* are generally cauliflorous, forming congested, pendulous, capituliform racemes with numerous flowers (Klitgaard 1991). However, *Brownea longipedicellata* Huber stands out with its loose racemes, which bear fewer flowers with long pedicels.

Browneopsis, comprising eight species, shares several characteristics with *Brownea*, such as the staminal ring and inflorescence arrangement. However, its inflorescences are erect, and the flowers, which are sometimes pseudotubular, exhibit white to slightly greenish or yellowish hues. The androecium in *Browneopsis* is more variable, ranging from nine to more

than twenty stamens (Klitgaard 1991). Staminal proliferation, although less common than reduction, can also be observed in other genera of Detarioideae, such as *Cynometra* L. (approximately 20 species, previously included in *Maniltoa* Scheff.), and in the monospecific genera *Colophospermum* Kirk ex J. Léonard and *Polystemonanthus* Harms (Tucker 1987). However, the mechanisms underlying staminal proliferation remain poorly understood.

The clade that includes *Paloue*, *Heterostemon*, and *Macrolobium* (Redden and Herendeen 2006; Schley et al. 2018) exhibits the greatest diversity in floral morphology and represents the largest number of species within the Brownea clade (POWO 2024).

- *Paloue*: This genus, currently comprising 16 species, displays diverse floral morphotypes that vary in symmetry, corolla and androecium reduction, and inflorescence types. Flower colors range from red or pink to white, with two predominant morphologies:
 1. Flowers with 1–3 developed petals and a greater number of fertile stamens, typical of species previously circumscribed in *Paloue*.
 2. Flowers with 4–5 developed petals and an androecium commonly reduced to three fertile stamens, characteristic of species formerly included in *Elizabetha* Schomburgk ex Benth. and *Paloveopsis* R. S. Cowan (Redden et al. 2018).
- *Heterostemon*: This genus, comprising seven species, is distinguished by large, showy flowers that range in color from pink to purple. These flowers feature three petals with nectar guides, two reduced petaloids, a narrow and elongated nectariferous hypanthium, and nine stamens arranged in a monadelphous sheath. Some stamens exhibit reduced anthers (antherodes).
- *Macrolobium*: As the most diverse genus of the Brownea clade, *Macrolobium* includes 78 species (Murphy et al. 2018; POWO 2024). Its flowers exhibit relatively conserved morphology compared to other members of the clade. They are strongly zygomorphic, with the corolla reduced to a single white adaxial petal, the androecium reduced to three stamens and buds protected by a pair of large bracteoles whose morphology varies among species (Cowan 1953).

The monospecific sister genera *Brachycylix* and *Ecuadendron* display intriguing morphological affinities. The flowers of *Brachycylix* resemble those of *Heterostemon* due to shared corolla and androecium characteristics (Table 1). However, *Brachycylix* also shares similarities with *Ecuadendron*, particularly in the number of fertile stamens and the long, pendulous racemes (Neill 1998).

The Brownea clade exhibits notable morphological variation in hypanthia, which differ greatly in width, length, and depth. All species are likely nectar producers, a trait common to the subfamily (Cowan and Polhill 1981a). Investigating the nectariferous nature of their hypanthia could yield valuable insights into the pollination mechanisms of these taxa. However, no anatomical studies have yet explored the microstructural differences among the group's flowers or their relationship to pollination.

Different pollination syndromes, including ornithophily, chiropterophily, psychophily, and phallenophily, have been documented for taxa within the Brownea clade (Arroyo 1981; Banks and Klitgaard 2000; Banks and Rudall 2016; Fleming et al. 2009; Knudsen and Klitgaard 1998). According to Cowan and Polhill (1981a), the floral diversity in the subfamily Detarioideae reflects an evolutionary history of coadaptation with animals for defense and reproduction. Similarly, Arroyo (1981) suggests that the evolution of Fabaceae as a whole is closely linked to the coadaptation of plants and their pollinators, leading to a trend of increasing floral specialization, although exceptions exist across different lineages (Citeli et al. in prep).

In the Brownea clade, ornithophily—primarily involving hummingbirds—is recorded in many species of *Brownea* (Arroyo 1981; Klitgaard 1991; Snow and Snow 1972) and *Paloue* (Arroyo 1981). Chiropterophily has been documented in *Browneopsis* (Arroyo 1981; Banks

and Rudall 2016; Fleming et al. 2009; Klitgaard 1991; Knudsen and Klitgaard 1998), *Paloue* (Arroyo 1981; Banks and Rudall 2016; Carvalho 1961; Fleming et al. 2009; Rodrigues et al., personal observation), and is inferred for *Ecuadendron* (Neill 1998). Phallenophily has been recorded in *Browneopsis* (Arroyo 1981; Banks and Rudall 2016; Klitgaard 1991; Knudsen and Klitgaard 1998) and psychophily in *Macrolobium* (van Dulmen 2001). However, there is currently no data on the pollination strategies of *Brachycylis* and *Heterostemon*.

To advance our understanding of the evolutionary relationships within this group, it is crucial to expand morphological studies across these genera. These studies can help identify potential synapomorphies and autapomorphies that are useful for clade delimitation. Additionally, analyzing homoplasies through different ontogenetic pathways can clarify which character states should not be used in circumscribing certain taxa. Ontogenetic analyses of inflorescences and flowers have proven invaluable in the systematics and floral evolution of morphologically diverse Fabaceae groups, including subfamilies such as Detarioideae (Bruneau et al. 2014; Cowan and Polhill 1981a, 1981b; Tucker 2000a, 2000b, 2000c, 2002a, 2002b), Duparquetioideae (Prenner and Klitgaard 2008), Dialioideae (Tucker 1998; Zimmerman et al. 2017), and the Swartzieae clade within Papilionoideae (Paulino et al. 2013; Tucker 1990, 2003a).

Thus, this study aims to perform ontogenetic and anatomical analyses of representatives from different genera within the Brownea clade. By doing so, it seeks to address key evolutionary questions while contributing to the systematics and understanding of floral evolution in this fascinating group of Fabaceae.

Materials and methods

Six species from five genera were selected for analysis in this study (Figure 1): *Brownea longipedicellata* Huber (Fig. 1a–b) (*Novaes AT 02*), *Browneopsis macrofoliolata* Klitg. (Fig. 1c–d) (*Falcão MJ 96*), *Heterostemon mimosoides* Desf. (Fig. 1k–l) (*Novaes AT 01*), *Paloue paraensis* (Ducke) Redden (Fig. 1g–h) (*Lima HC 2156A*), *Paloue speciosa* (Ducke) Redden (Fig. 1e–f) (*Novaes AT 03*), and *Macrolobium suaveolens* Spruce ex Benth. (Fig. 1i–j) (*Pinto RB 467*). The first five species were collected at the Arboretum of the Rio de Janeiro Botanical Garden, while the latter was collected during an expedition to the state of Pará in 2014. Voucher specimens were deposited in the RB and HSTM herbariums.

For ontogenetic analysis, the collected samples were fixed in FAA 70 (formaldehyde, glacial acetic acid, and 70% alcohol; Johansen 1940) and stored in 70% alcohol. The floral materials were dissected and observed under a stereomicroscope (Leica MZ7.5). After dissection, the samples were dehydrated in an alcohol series (Tucker 1993), subjected to critical point drying (Leica EM CPD 030), and then fixed onto metal stubs with double-sided carbon tape. The samples were coated with a gold-palladium alloy using a sputter coater (Emitech K550X) and observed under a scanning electron microscope (JEOL JSM-6490LV-LABNANO-CBPF) (Tucker 2000b; 2000c).

Anatomical analyses of the flowers were conducted on floral buds fixed in 2.5% glutaraldehyde and 0.1M sodium phosphate buffer at pH 7.2. These buds were then dehydrated in an alcohol series, embedded in glycol-methacrylate resin (Gabriel 1982; Gerrits et al. 1991), sectioned transversely and longitudinally using a rotary microtome (Leica RM 2245), stained with 0.05% Toluidine Blue, and observed and photographed under a light microscope (Olympus BX50) (O'Brien et al. 1964).

Terminology for organography and organogenesis follows Tucker (1987; 2000a; 2000c; 2002; 2003b) and Harris and Harris (1994). For anatomical structure, the terminology follows Appezzatto-da-Gloria and Carmello-Guerreiro (2006) and Tolke et al. (2019).

Abbreviations used in the manuscript are as follows: F = flower; I = inflorescence; B = bract; Bl = bracteole; FM = floral meristem; S = sepal; P = petal; C = carpel; A = antesealous

stamen; a = antepetalous stamen; H = hypanthium; e = epidermis; np = nectariferous parenchyma; snp = subnectariferous parenchyma; vb = vascular bundle; Ab = abaxial side; Ad = adaxial side.

Results

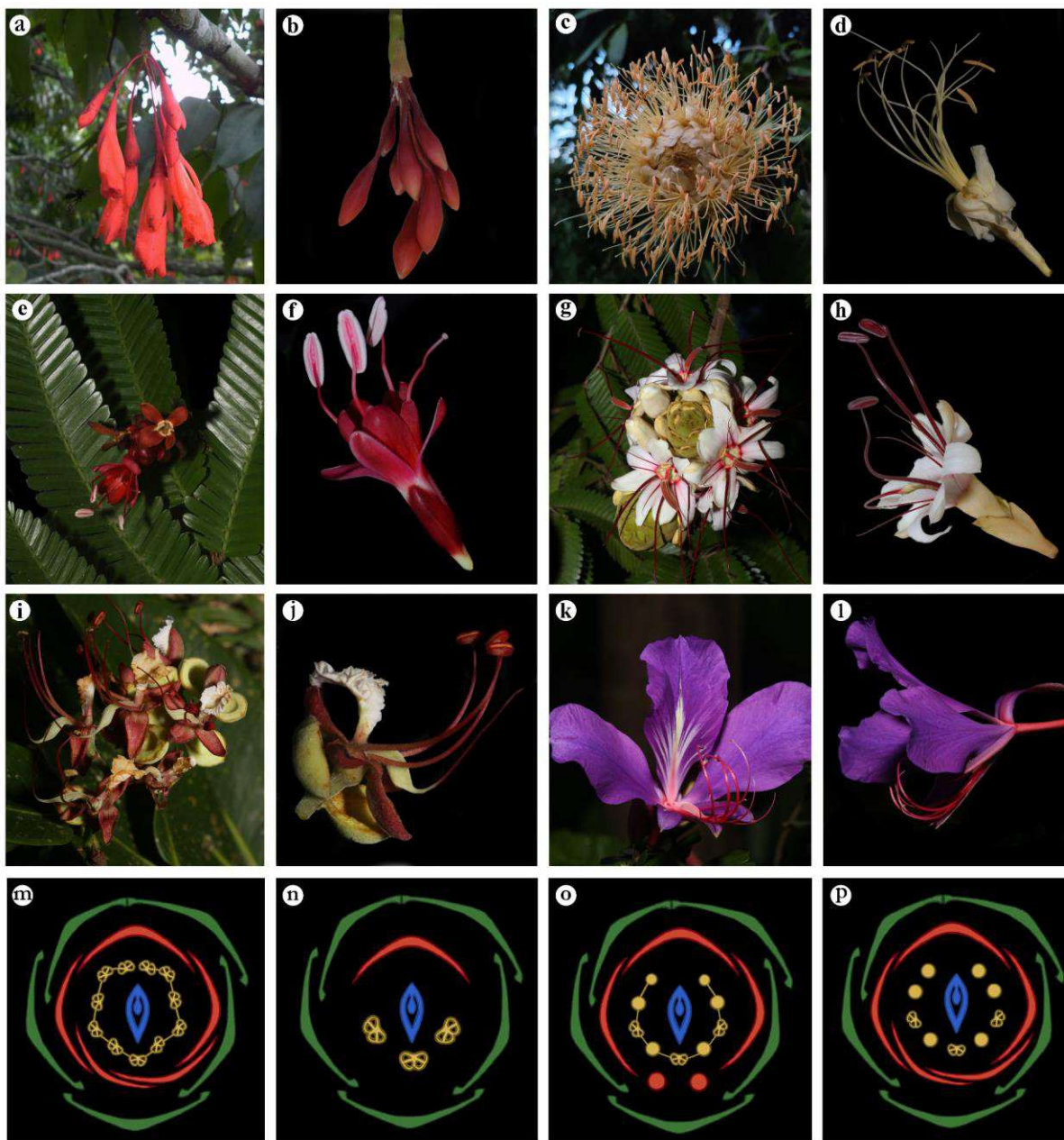
The organographies, including descriptions of the development of inflorescences and flowers, along with corresponding figures, are organized in alphabetical order of the six species: *Brownea longipedicellata*, *Browneopsis macrofoliolata*, *Heterostemon mimosoides*, *Macrolobium suaveolens*, *Paloue paraensis* and *Paloue speciosa*. Table 1 summarizes key morphological differences among the genera of the *Brownea* clade. Figure 1 contains photos and floral diagrams of the six species, and Figure 2 contains the illustrations of its inflorescences and flowers, including detailed floral structures, such as the hypanthium, anther and staminal sheath. The description of the anatomical structure of the nectaries follows as the final section.

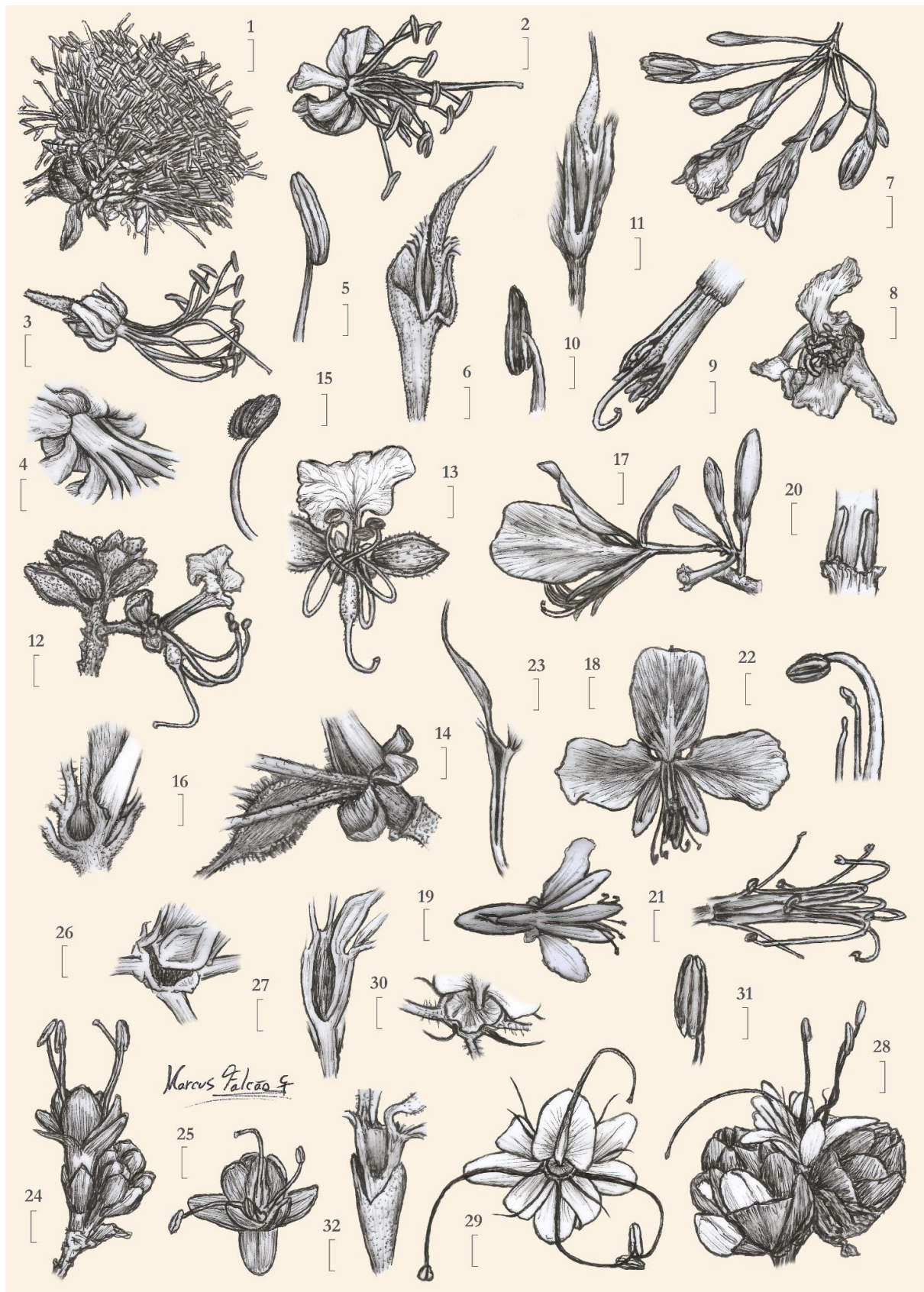
Table 1: Comparison of the main variations in floral morphology among the genera of the *Brownea* clade.

Sources: ⁽¹⁾ = Cowan 1975; ⁽²⁾ = Klitgaard 1991; ⁽³⁾ = Neill 1998; ⁽⁴⁾ = Cowan 1978; ⁽⁵⁾ = Cowan 1953; ⁽⁶⁾ = Redden et al. 2018.

Taxon	Symmetry	Bracteoles	Corolla	Androecium	Inflorescence
<i>Brachycylis</i> ¹	Strongly zygomorphic	Small, fused	3 large, 2 petaloids	9 (5 fertile); Filaments forming a sheath	Pendulous, long and lax
<i>Brownea</i> ²	Radial (usually)	Large, fused	4-5, approximately equal, erect	10-12, filaments forming a sheath	Pendulous, usually globose and congested
<i>Browneopsis</i> ²	Radial (usually)	Large, fused	3-5, approximately equal, erect or reflexed	9-26, filaments forming a sheath	Erect, globose, and congested
<i>Ecuadendron</i> ³	Slightly zygomorphic	Medium, fused	5, adaxial more expanded	9 (5 fertile); filaments fused at the base	Pendulous, long, and loose
<i>Heterostemon</i> ⁴	Strongly zygomorphic	Small, fused	3 large, 2 petaloids	9 (3 fertile); filaments forming a sheath	Erect, short, and loose
<i>Macrolobium</i> ⁵	Strongly zygomorphic	Large, free	1, rarely 2-4 petaloids	3, free	Erect, usually short and loose, rarely pendulous
<i>Paloue</i> ⁶	Slightly to strongly zygomorphic	Large, fused	1, 3, or 5 large, unequal or equal; 0, 2, or 4 petaloids	9 (3-9 fertile, 0-6 staminodes); filaments fused at the base	Erect, long to short, loose to congested; rarely globose racemes

Note: Bracteole size is quoted in comparison to flower size and not in absolute measurements.





***Brownea longipedicellata* Huber (Figures 1a–b, 1m, 2.7–11, 3a–t, 4a–h, 15a–d, 15q–r)**

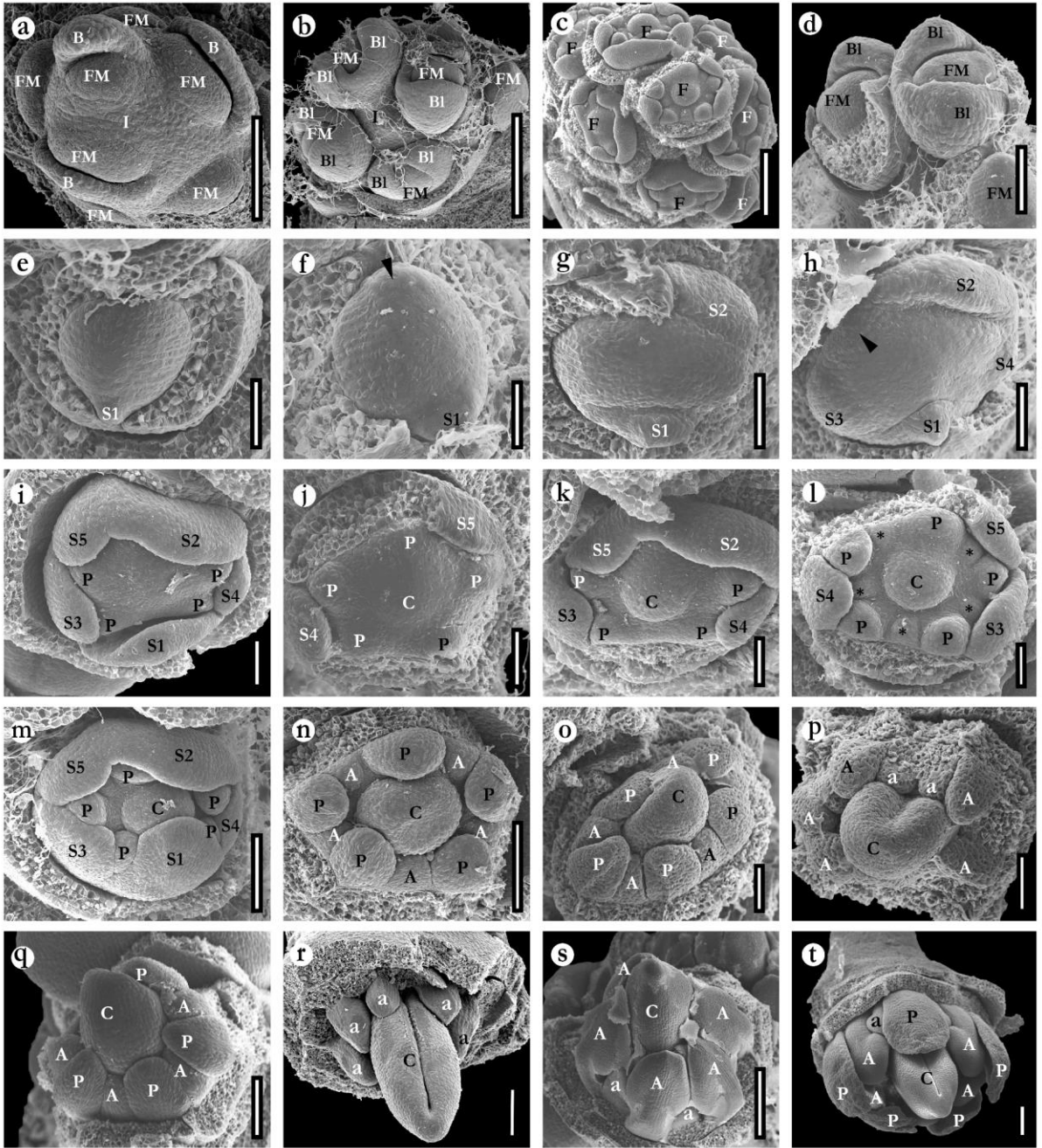
Inflorescence

Organography—Simple, pendulous, terminal, axillary, or cauliflorous raceme. The peduncle is short, approximately 1 cm long, typically bearing seven to ten flowers, though occasionally up to 15. There are two types of bracts: Type one corresponds to the proximal bracts at the base of the peduncle; these are ovate, overlapping, pubescent, alternate, and distichous, and in most cases, do not subtend any flowers except for the innermost one. Type two bracts are positioned internal to type one, oblong, acicular, long, with ciliate margins, spirally alternate, and subtend a floral bud (Fig. 1a–b, 2.7).

Organogenesis, Elongation, and Differentiation—Floral meristems and bracts initiate acropetally along the inflorescence. The first floral meristems to initiate (the most basal ones) halt their development shortly after the initiation of the bracteole pair (Fig. 3a–b). The subsequent meristems, located closer to the apex of the inflorescence, rapidly reach the same developmental stage as the basal ones (Fig. 3a–b) and may even surpass them in the organogenesis phase (Fig. 3c). Consequently, the inflorescence exhibits a partially basipetal sequential developmental character, meaning the most advanced buds, up to anthesis, are apical, despite their later initiation in the raceme. The basal buds, however, are not far behind in developmental level relative to the apical ones, with a short plastochrony between them and a limited number. Therefore, all buds in the inflorescence are at very similar developmental stages (Fig. 3b–c, 4e). The shape of the buds in intermediate and late stages is influenced by pressure from the joints between them, causing the internal/adaxial surface to become rounded or flattened (Fig. 4f).

Flower

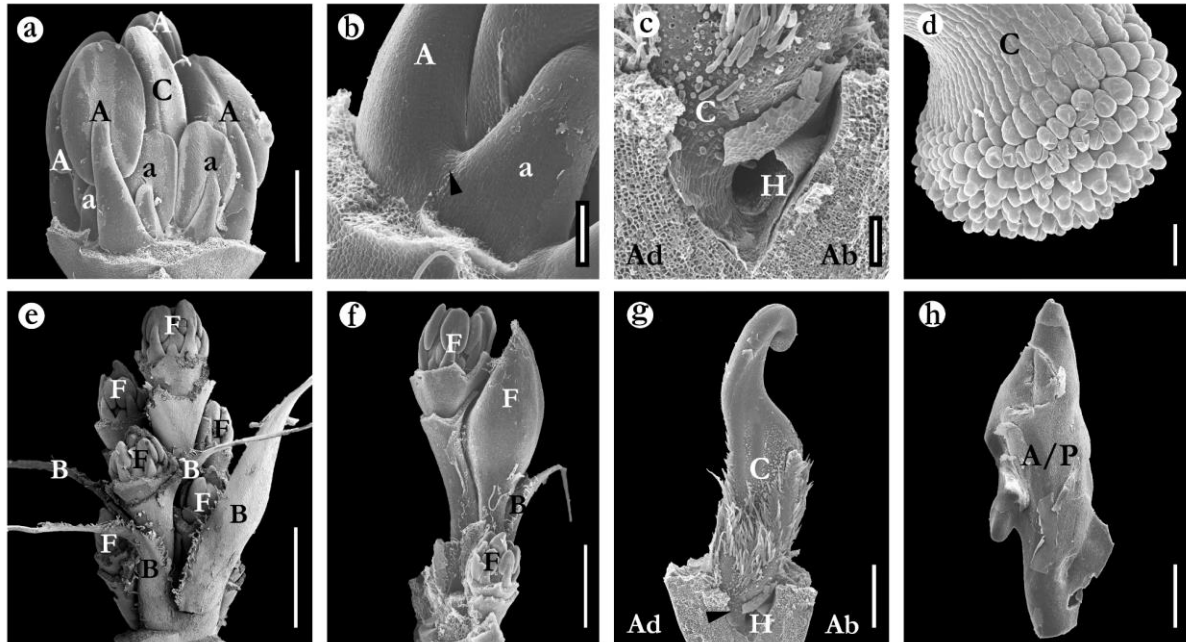
Organography—Radial flowers characterized by a long pedicel, approximately 3 cm long, pseudotubular, and orange-red. The bracteoles are fused for more than half their length and are long enough to wrap around the internal whorls, giving the flower a tubular appearance. The calyx has five sepals, appearing as four due to the fusion of two adaxial, oblong sepals with an acute apex, the adaxial one being slightly wider. The corolla consists of five equal petals, approximately 1.5 cm long, clawed, elliptical, with an acute apex and slightly wavy margins. The petals are erect, opening slightly at the anthesis, while still maintaining some level of overlap. The androecium consists of a staminal ring extending into a sheath up to 1.5 cm long, formed by the conation of the filaments of eleven stamens, with dorsifixed, introrse anthers. The free portion of the filaments reaches up to 0.8 cm in length. The six antepetalous stamens are slightly smaller than the five antesepalous stamens. The sheath, with a villous inner wall, is discontinuous at the adaxial portion of the flower, creating a gap through which the ovary and style emerge to outside the sheath. The ovary is stipitate, with a tomentose surface, and bears 3–4 ovules. The stipe is adnate to the median adaxial portion of the hypanthium. The style is about 3 cm long and slightly curved in the abaxial direction, with a globose, papillary stigma. Petaloid stamens have been observed in a small minority of pre-anthesis buds, though this is not common. In these cases, one petal is absent for each petaloid stamen; however, the total number of stamens in the androecium remains unchanged, counting the modified ones (Fig. 1a–b, 1m, 2.7–11).



Organogenesis, Elongation, and Differentiation—The first structures to form are the pair of bracteoles, with the initiation position of the first bracteole varying between the right and left sides of the meristem (Fig. 3a–b). Their margins meet, covering the floral meristem at the end of calyx initiation. Before this, the bracteoles press against the meristem, especially in the abaxial and median adaxial regions (Fig. 3d, 3f). The first sepal (S1) initiates in the median abaxial region, and the meristem acquires an obovate shape (Fig. 3e). The second sepal (S2), which forms in the adaxial region but more laterally, can sometimes be confused with the protuberance formed by the pressure of the bracteoles (Fig. 3f). The position of S2 varies between the right and left adaxial sides in different floral buds (Fig. 3h–l). The third sepal (S3) generally begins in the lateral position opposite S2, while the fourth sepal (S4) begins practically simultaneously with S3, on the opposite lateral side (Fig. 3h). The fifth and final sepal (S5) to begin is the second adaxial sepal, which starts fused with S2 congenitally (Fig. 3h–i). In the initial stages, they can be differentiated by their varying lengths and partially free

apices (Fig. 3i, 3k, 3m). Thus, the calyx initiation pattern is helical and may occur in a clockwise or counterclockwise direction.

The five organs of the corolla initiate simultaneously (Fig. 3i–j), but they may develop at different rates during organogenesis (Fig. 3j–l). Generally, the adaxial petal elongates more slowly. After the corolla, the center of the meristem rises, revealing the carpel (Fig. 3j–k). The whorl of antesepalous stamens generally initiates with the simultaneous formation of five primordia (Fig. 3l), although one or two may become evident earlier than the others without a specific position. The initiation of antepetalous stamens could not be observed, but they begin forming after the external whorls are larger and cover them (Fig. 3m–o). The whorl of antepetalous stamens typically consists of six stamens, with two opposite stamens beginning at the adaxial position, between the carpel and the adaxial petal (Fig. 3p, 4a).



After the end of organogenesis, a dorsoventral flattening of the flower bud can be observed (Fig. 3o–q). This is possibly due to the pressure exerted by the oblong bract (Fig. 4e). Later, the bud regains radial symmetry (Fig. 3s–t). The profuse elongation of the pedicel becomes more evident at later stages (Fig. 4e–f). The bracteoles elongate rapidly and close over the meristem. Their margins fuse after closing; however, the apex is not completely fused, remaining coherent by trichomes until it is ruptured at anthesis. As they elongate, the two adaxial sepals become indistinguishable from each other. The petals elongate similarly. During the differentiation process, the base of their blades tapers to form the claw (Fig. 3t). Afterwards, the antesepalous stamens differentiate into filament and anther, followed by the antepetalous stamens (Fig. 3r–t). The antepetalous stamens remain smaller than the antesepalous stamens until anthesis (Fig. 4a). In late stages of differentiation when the stamens already have differentiated microsporangia, the bases of the filaments fuse through intercalary elongation, which will later form the staminal ring (Fig. 4b). Fusion of the filaments does not occur between the pair of stamens opposite the adaxial petal, leading to the discontinuity of the staminal ring at this point. The carpel begins to form the carpel cleft before the initiation of the antepetalous stamens (Fig. 3n–p). Prior to the differentiation of the anthers and filaments, the carpel cleft is almost closed, and the carpel acquires an elongated and laterally flattened shape (Fig. 3q–r). Its acute apex gradually elongates and curves abaxially to form the style (Fig. 3s–t, 4a). Concomitantly, the stigma differentiates into a papillary surface at the apex of the carpel (Fig. 4d). At the same time, trichomes form in the ovary region, starting at the base (Fig. 4g). At more advanced stages, the style twists on itself and forms a spiral structure as it elongates (Fig.

4c, 4g). No evidence of the process leading to the formation of petaloid stamens was observed at early stages of development, nor was there any change in the standard number of initiated organs of the corolla and androecium. This is an uncommon but not rare phenomenon. Given that no evidence of this process was observed throughout the developmental study, it is likely that it is expressed only late, perhaps by the fusion of a petal and a stamen. Fig. 4h shows a petaloid stamen taken from a preanthesis bud.

***Browneopsis macrofoliolata* Klig. (Figures 1c–d, 1m, 2.1–6, 5a–p, 6a–l)**

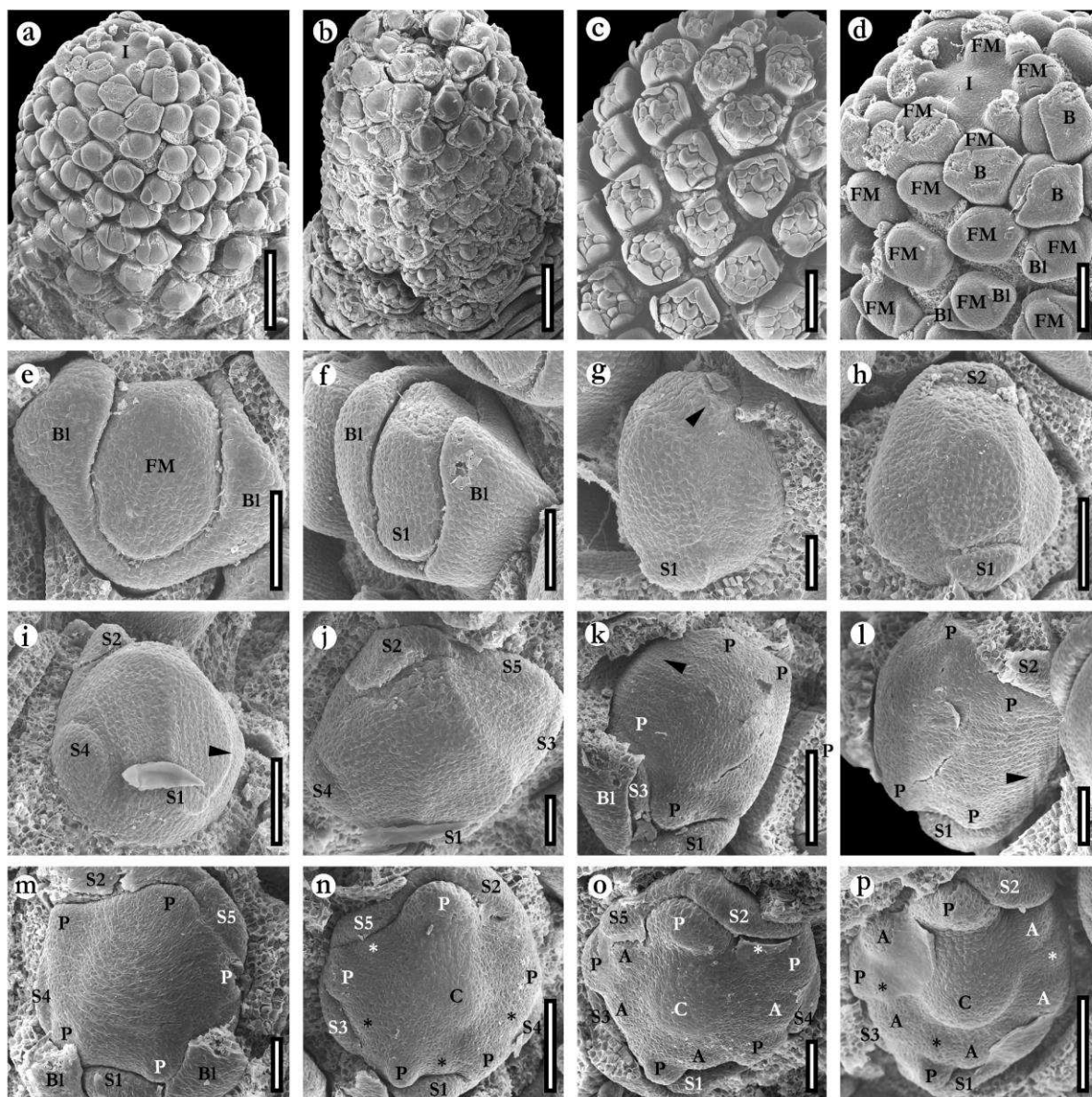
Inflorescence

Organography—Simple, terminal, erect, capituliform, globose, and compact raceme. The flowers are congested and open acropetally, the outermost first, followed by the more central ones, arranged like a pincushion and with alternate anthotaxy spiraling around the peduncle. There are two types of bracts: type one begins at the base with initially alternate anthotaxy distichous, they have an ovate to orbicular shape, a rounded apex, of rigid consistency, pubescent externally, overlapping each other and the innermost organs, with the first 20–30 being sterile, beginning to bear flowers as they become spiraling; type two bracts gradually emerge from type one, which gradually decreases in size and becomes thinner until it becomes oblong, with an acute apex, flexible consistency and a surface covered with white trichomes, so that type two occurs in the most distal positions of the raceme. There are 100–120 flower buds per inflorescence (Fig. 1c, 2.1).

Organogenesis, elongation, and differentiation—Floral meristems and bracts have acropetal initiation along the inflorescence, as well as acropetal sequential development. The meristems begin with a very short plastochrony between them, so that even with more than 100 buds on a single inflorescence, proportionally not many developmental stages can be observed (Fig. 5a–d, 6d). The peduncle is dilated (Fig. 5d) and the buds are distributed over its entire surface. In Fig. 5B, in which only bracts and bracteoles were removed, it is possible to observe the great proximity of the floral meristems to each other during organogenesis. This congested structure of the inflorescence has a profound impact on the initial stages of flower development. However, this impact is barely noticeable in later stages (Fig. 5c, 6d). Different meristems have different shapes and development rates depending on the pressure they suffer from nearby meristems. Meristems at the base of the inflorescence are wider and larger than meristems in the middle of the inflorescence, even though they are at equivalent stages (Fig. 5a–b, 5j, 6c, 6f). The flowers reach anthesis almost all simultaneously or very close to each other.

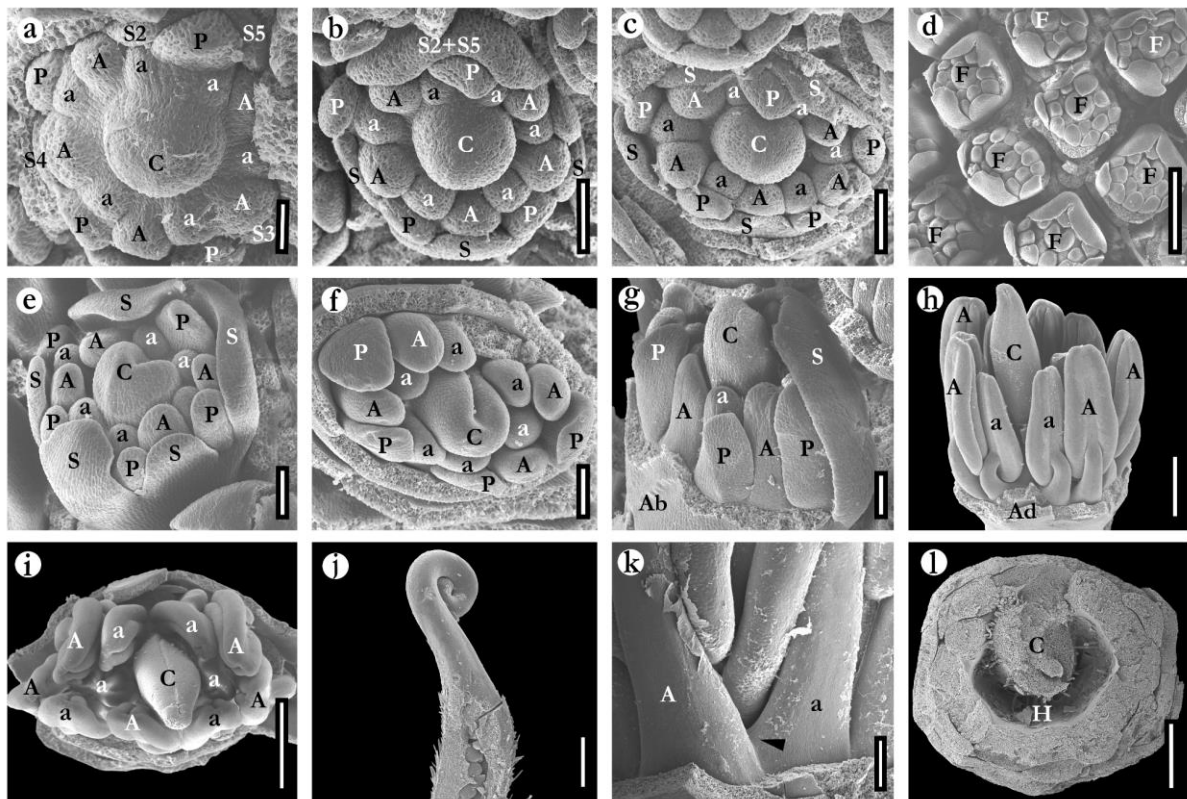
Flower

Organography—Flowers ivory to slightly yellowish with bracteoles 4–4.5 cm long, fused up to about 3.5 cm in length, oblanceolate, apex acute, flexible, outer surface woolly. Calyx composed of five sepals, the two adaxial sepals fused, up to 2.2 cm long, oblong, apex acute, reflexed at anthesis. Corolla composed of five equal petals, 3.2 cm long, clawed, claw 0.4 cm long, elliptical blades, acute apex, with rigid base and central axis, and reflexed at anthesis. Androecium composed of staminal sheath formed by the filaments of eleven stamens, connate part up to 1.7 cm long, free part 4–6 cm long, without a pattern of variation among the stamens. The sheath is woolly internally, especially at the base, and discontinuous in the adaxial portion, leaving an gap through which the carpel curves slightly out of the sheath. The anthers are dorsifixed and introrse. The carpel is stipitate and the stipe is adnate to the adaxial wall of the hypanthium. The ovary is about 1.5–1.7 cm long, has a falcate shape, is laterally compressed, has a velute surface and bears 5 ovules. The style is 6–7 cm long, curves slightly abaxially and ends in the globose stigma with a papillary surface (Fig. 1d, 1m, 2.2–6).



Organogenesis, elongation, and differentiation—The first bracteole varies between being on the left or right side of the meristem to initiate, and the second comes soon after (Fig. 5a, 5d). As they elongate, they exert pressure, especially on the medial abaxial and adaxial portions (Fig. 5e–f). Before their margins meet, the first sepal (S1) initiates in the medial abaxial position (Fig. 5f). Due to the pressure exerted on the medial adaxial position, a protuberance is formed that can be confused with the second sepal (S2) (Fig. 5g). S2 initiates in the adaxial position, relatively lateralized and converging with the protuberance in the same position (Fig. 5g–h). It varies between being on the left or right adaxial. Next come the lateral sepals (S3 and S4), whose initiation time is variable and may be simultaneous (Fig. 5h–j) or sequential (Fig. 5k–l). The fifth sepal (S5) is the second adaxial and begins fused with S2 (Fig. 5m). The initiation time of the last three sepals may occur before the initiation of the corolla (Fig. 5h–j) or after it (Fig. 5k–l). Fig. 5k and 5l represent the same meristem from two different angles to show that, although the corolla has already been initiated, S4 and S5 are not yet present. In any case, although there is an erraticism due to variable modifications in different buds due to the pressure of the bracts, bracteoles, and other floral buds, there is a general pattern of helical initiation of the calyx.

Corolla initiation appears to be simultaneous, however, with development rates varying between organs and between meristems (Fig. 5j–o). In Fig. 5k and 5l, the abaxial petals appear larger, while in Fig. 5m, they all appear the same size, although with different shapes, and in Fig. 5n and 5o, the adaxial petals appear larger. Again, this erratic development between different buds appears to result from the differential pressure of each flower in the congested inflorescence. Furthermore, the calyx and corolla organs gradually become marginalized in the meristem as the inner whorls initiate (Fig. 5n, 6a). The antesealous stamens, like the corolla, initiate almost simultaneously (Fig. 5n–o), however, initially, and at later stages as well (Fig. 6H), they present different development rates. The whorl of antepetalous stamens has unidirectional initiation (Fig. 5p, 6a), and it has six stamens since two begin opposite the adaxial petal (Fig. 6a–b). Thus, the androecium normally contains eleven stamens in total.



Sometimes, a bud with ten stamens occurs (Fig. 6f). The carpel begins posterior to the corolla and anterior to the stamens (Fig. 5m–n). The bracteoles cover the bud between the end of calyx organogenesis and during corolla organogenesis. The sepals elongate slowly, and at the beginning of organ differentiation, they have not yet covered the internal whorls (Fig. 6f–g). The sepals elongate fused at the base (Fig. 6e). The adaxial petal is the first to differentiate with tapering of the apex, followed by the others (Fig. 6b–c). In general, all stamens elongate and differentiate equally (Fig. 6g). The stamens also develop equally, although the antepetalous remain smaller than the antesealous (Fig. 6h–i).

At a much later differentiation stage, the bases of the filaments grow fused by intercalary growth (Fig. 6k). This process later forms the staminal sheath, which, however, is discontinuous between the two adaxial antepetalous stamens, whose filaments do not fuse. The carpel begins to form the carpel cleft after the end of organogenesis (Fig. 6c). After the beginning of whorl differentiation, its apex begins to elongate (Fig. 6g) and the style is slowly formed, which curves to the abaxial side (Fig. 6h–i), later forming a spiral on itself (Fig. 6j).

***Heterostemon mimosoides* Desf. (Figuras 1k–l, 1o, 2.17–23, 7a–t, 8a–h, 15e–h)**

Inflorescence

Organography—Racemes are simple, terminal, axillary, or cauliflorous. The peduncle is short, erect, 2–6 cm long, around which the flowers are attached in spirals alternating fashion with short spaces between them. The bracts are about 1 cm long, elliptical, fibrous, green, and deciduous. There are about 6–8 flowers per inflorescence (Fig. 2.17).

Organogenesis and development—Floral meristems and bracts have acropetal sequential initiation and development. Each meristem initiates at a position on the peduncle opposite to the previous one, with a very long plastochron that is more noticeable during late stages of differentiation, so that there is a large stage interval between a floral bud and its adjacent ones (Fig. 7a–b; 8g). The peduncle elongates slightly, so that even with long plastochrons between the buds, they are still very close to each other (Fig. 8g). In the same inflorescence, very few different developmental stages are observed.

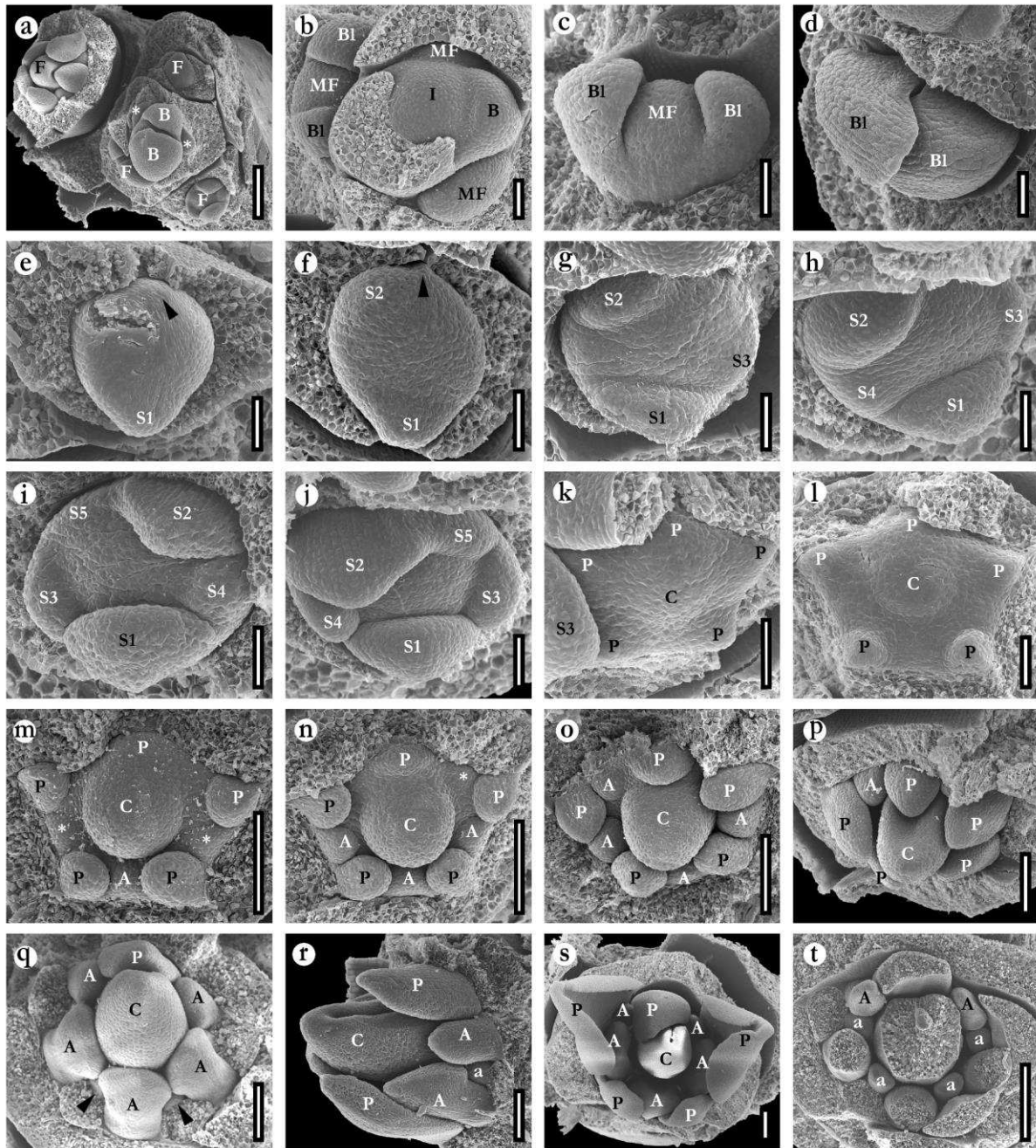
Flower

Organography—The flowers have short pedicels about 0.5 cm long. The bracteoles are short, only 0.4 cm long, and are fused up to a little more than half their length. They are fibrous and green. The calyx is formed by five sepals, the adaxial pair being fused, about 3.5 cm long, oblong in shape, with an acute apex, purple in color with a green apex. The adaxial pair is slightly wider than the others and reflexed, while the other three sepals are erect on the abaxial side of the flower. The corolla is formed by three large and showy petals, the lateral ones and the adaxial one, while the two abaxial ones are reduced to petaloids. The three petals are approximately the same size, with the adaxial petal being slightly shorter in length and wider in width. They measure approximately 6–6.3 cm × 2.8–3.1 cm, with a spatulate shape, slightly wavy margin, and a truncated and emarginate apex and attenuated base. The adaxial petal has a ciliate margin at the base. The petaloids are approximately 0.3 cm long. The petals are purple, with the adaxial petal characterized by nectar guides in the form of white linear stains that start from the base, ascending the central axis and spreading across the first half of the blade. The central stain at the base is light pink, becoming cream towards the apex of the blade. The base of the other petals is light pink (Fig. 1k–l, 1o, 2.17–20).

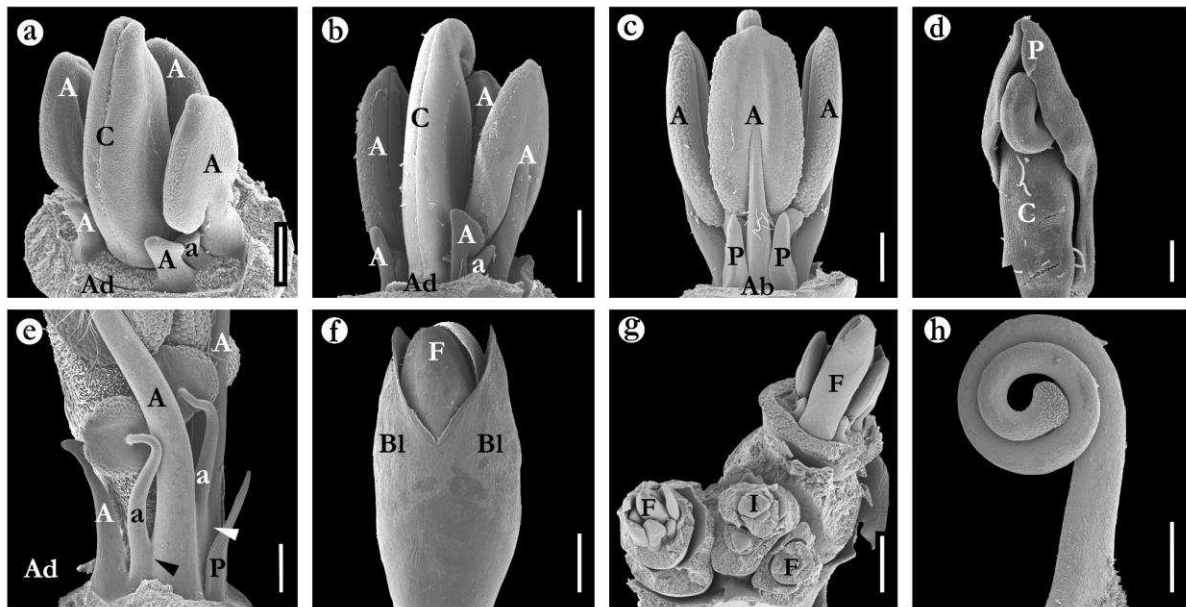
The androecium has stamens facing the abaxial side of the flower, forming a monadelphous sheath, whose filaments have different sizes and levels of conation, and is composed of three fertile stamens and six staminodes. The staminodes at the ends are the smallest, about 2 cm long, followed by two more staminodes, one on each side of the sheath, measuring 4.5–5 cm long, and two of the fertile stamens, one on each side, measuring about 6.5 cm long, and finally two more staminodes measuring about 5 cm long, and between these is the last fertile stamen, central to the sheath, measuring about 6 cm long. The staminodes have antheroid, except for those at the ends of the sheath. Thus, the distribution of the organs in the sheath shows bilateral symmetry. The sheath is curved in the abaxial direction of the flower and the height of the conation between the filaments varies, starting at 0.5 cm long at the ends and reaching 2.5 cm long. The free portion of the filaments curves in the adaxial direction of the flower, forming an arch. The sheath is pink, with its base being lighter. The androecium is glabrous, except for the free portion of the five most central filaments with a few long and sparse trichomes. The staminodes have vestigial anthers, reduced in the two smaller stamens at the ends of the sheath. The anthers of the fertile stamens are dorsifixed, introrse and light pink (Fig. 2.21–22).

The carpel is stipitate and the stipe is adnate to the adaxial wall of the hypanthium, with the free part measuring 0.9 cm in length and a pubescent surface. The ovary is 1.3 cm long, falcate in shape, slightly curved towards the abaxial side, pubescent surface with white trichomes, light pink, and bears nine ovules. The style is arched towards the abaxial side and

then turning towards the adaxial side, as are the filaments. It measures 4.5 cm in length, is pink in color, and at its apex is the globose stigma with a papillary surface (Fig 1k–l, 2.23).



Organogenesis, elongation, and differentiation—The undifferentiated floral meristem is laterally elongated (Fig. 7b). It expands and the first bracteole initiates on one side, followed by the second bracteole (Fig. 7b–d). They overlap first at the apex, leaving a small gap at the abaxial and medial adaxial positions before completely covering the meristem (Fig. 7d). They may form small projections at the adaxial medial position of the meristem where the bracteole margins meet (Fig. 7e–f). When these overlap, the first sepal (S1) initiates at the abaxial medial position (Fig. 7e). The second sepal (S2) initiates at the adaxial position, slightly displaced to the right or left of the meristem (Fig. 7f). The third sepal (S3) initiates on the side opposite to S2, quickly followed by the fourth sepal (S4) on the other side (Fig. 7g–h). The fifth sepal (S5) to initiate is the second adaxial that appears to be congenitally fused to S2 (Fig. 7i–j). Therefore, the calyx presents helical initiation.



The initiation pattern of the corolla is dubious, appearing to be a simultaneous initiation with developmental heterochrony from the beginning, but we also consider the possibility of a unidirectional initiation, starting with the abaxial pair, followed by the laterals and finally the adaxial, with an extremely short plastochrony between the abaxials and the laterals (Fig. 7k–n). The whorl of antesepalous stamens has unidirectional initiation, starting with the abaxial, followed by the laterals, and finally the adaxials (Fig. 7m–o). The carpel begins shortly after the initiation of the petals and before the stamens (Fig. 7k–l). The bracteoles elongate and cover the floral meristem during organogenesis in the calyx (Fig. 7d).

However, the calyx, in its elongation, later surpasses the bracteoles and bursts through their cover (Fig. 8f). The calyx grows faster than the other whorls and covers the internal meristem during the organogenesis of the androecium. The corolla, despite simultaneous initiation (Fig. 7k), presents an unequal rate of development of its petals (Fig. 7l–o). The abaxial petals elongate slowly and reach anthesis as petaloids (Fig. 7s, 8c), although they are the first to initiate. The lateral petals surpass the abaxial petals during the beginning of stamen differentiation (Fig. 7s). The adaxial petal is the slowest to elongate (Fig. 7l–n), but it also overtakes the abaxial ones at intermediate stages (Fig. 7s). As it elongates, it pairs with the carpel and envelops it above and laterally, elongating between the lateral stamens (Fig. 7s, 8d). The primordia of the antesepalous stamens show uneven development (Fig. 7q–r). The lateral and abaxial stamens elongate similarly (Fig. 7q, 8a–c). The two adaxial stamens elongate more and more slowly (Fig. 7t, 8a–b, 8e).

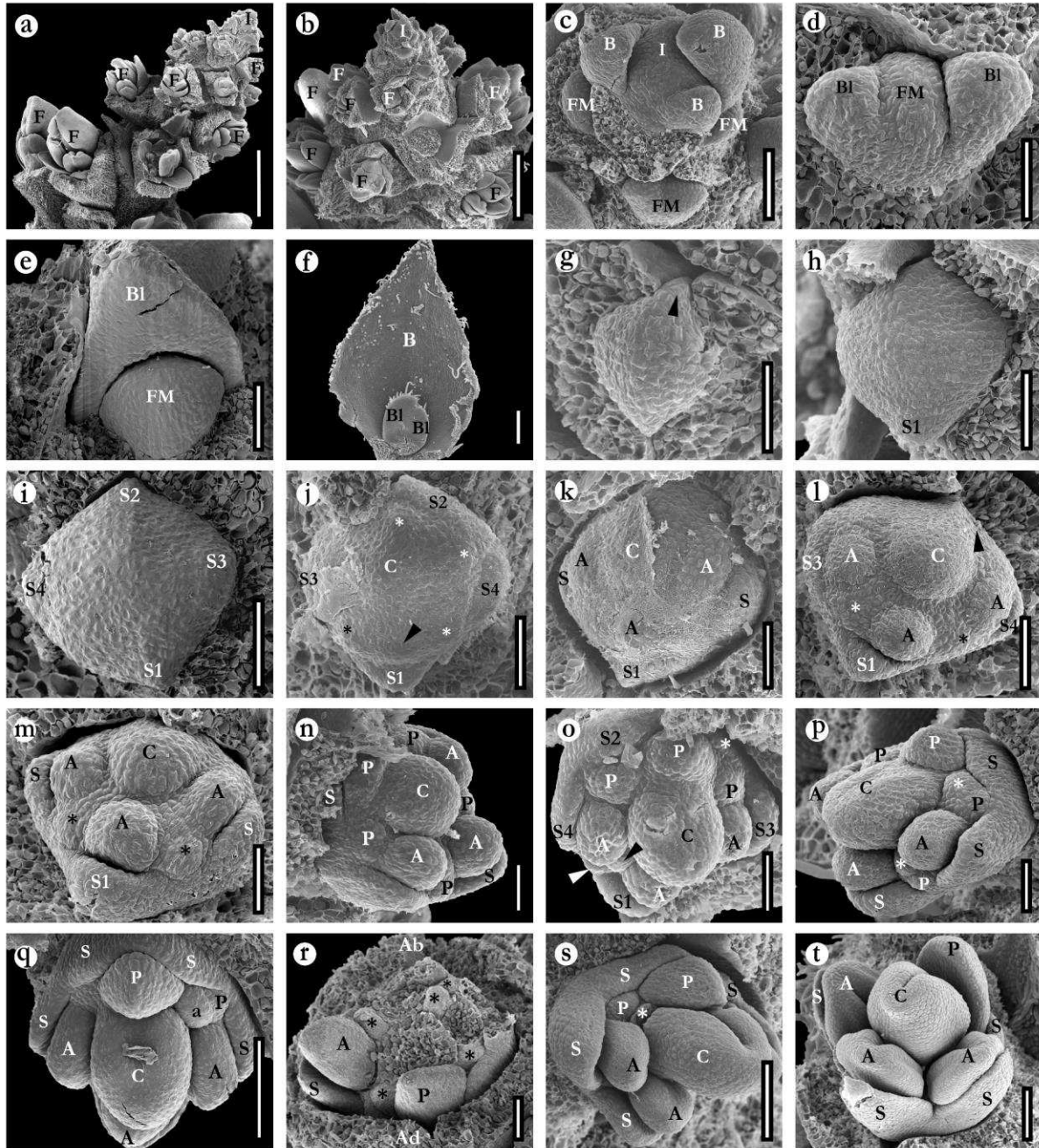
At anthesis, these form the two ends of the monadelphous sheath and are the two smallest organs of the androecium (Fig. 8e). The 4 antepetalous stamens elongate similarly and undergo differentiation but remain much smaller than the first three (Fig. 8e). Furthermore, the elevation of the sheath occurs at late stages with the fusion of the filaments by intercalary growth (Fig. 8e). The carpel begins to form the carpel cleft before the initiation of the antepetalous stamens (Fig. 7o–p). Its apex tapers and curves abaxially as it elongates to form the style, forming a spiral (Fig. 8a–b, 8d, 8h).

***Macrobium suaveolens* Spruce ex Benth. (Figures 1i–j, 1n, 2.12–16, 9a–t, 10a–h)**

Inflorescence:

Organography—Raceme simple, axillary or terminal, erect. Peduncle 6–10 cm long, with densely woolly surface and loose flowers, arranged in alternate spiral anthotaxis. Bracts about 1 cm long, ovate to elliptic, with pubescent outer surface and puberulent inner surface. About 15–25 flowers occur per inflorescence (Fig. 1i, 2.12).

Organogenesis and development—Floral meristems and bracts initiate and develop sequentially acropetal along the inflorescence. The plastochrony of meristems are short but are relatively far apart so that the development of each is not greatly impacted by its neighbors (Fig. 9a–c). As the inflorescence elongates, the buds acquire a spiral conformation around the peduncle. Bracts grow and differentiate very rapidly (Fig. 9c), where the apex of the inflorescence is still largely undifferentiated, except for the bracts.



Flower:

Organography—The pair of bracteoles plays the main protective role of the flower while it is still in bud since the calyx parts are short and do not cover the internal whorls. The bracteoles

are about 0.8 cm long, ovate in shape, with a slightly cuspidate apex, rigid in consistency, with thick, fibrous laminae, a densely pubescent outer surface, and a puberulent inner surface. The calyx has five small, slightly unequal sepals, the adaxial ones being smaller, ranging from 0.1 to 0.2 cm in length, triangular to ovate, and acute to acuminate apex. The adaxial sepals may be free or partially fused, with the level of fusion varying from flower to flower. The corolla is reduced to a clawed adaxial petal, with a 0.5 cm long claw and a blade measuring approximately 0.6 cm x 0.7 cm, with an orbicular shape and wavy margin. The lateral margins of the claw are slightly curved inward, forming a pseudotube in the petal, and its base is slightly auriculate, surrounding the stipe. The androecium is generally reduced to three stamens that correspond to the abaxial and lateral antesealous, rarely occurring a fourth stamen. Commonly, it is possible to see traces of aborted stamens. The filaments are free, measuring approximately 1.8 cm in length and pubescent at the base with a few long trichomes. The anther is dorsifixed and versatile. The stipe is adnate to the adaxial wall of the hypanthium, villous on the apical surface and it curves towards the abaxial side of the flower. The ovary is trapezoidal in shape, laterally compressed, marginally villous and bears 1–2 ovules. The style is about 1.5 cm long and at its apex is the globose and papillary stigma. The hypanthium is gibbose and short (Fig. 1j, 1n, 2.12–16).

Organogenesis, elongation, and differentiation—The undifferentiated floral meristem is laterally elongated (Fig. 9c) but acquires a rhombic shape as it expands (Fig. 9g). The first bracteole varies in position between left and right laterally of the meristem, and the second begins shortly thereafter (Fig. 9c–d). It is noticeable how quickly the bracteoles thicken, even as they begin to elongate (Fig. 9d–f). They overlap and cover the meristem (Fig. 9e–f), initially leaving a gap in the median adaxial position, which exerts physical pressure on the meristem (Fig. 9g). The shape of the still undifferentiated meristem is strongly influenced by the pressure of the bracteoles. Because of this, it is easy to confuse the abaxial and adaxial ends with already initiated organs (Fig. 9g).

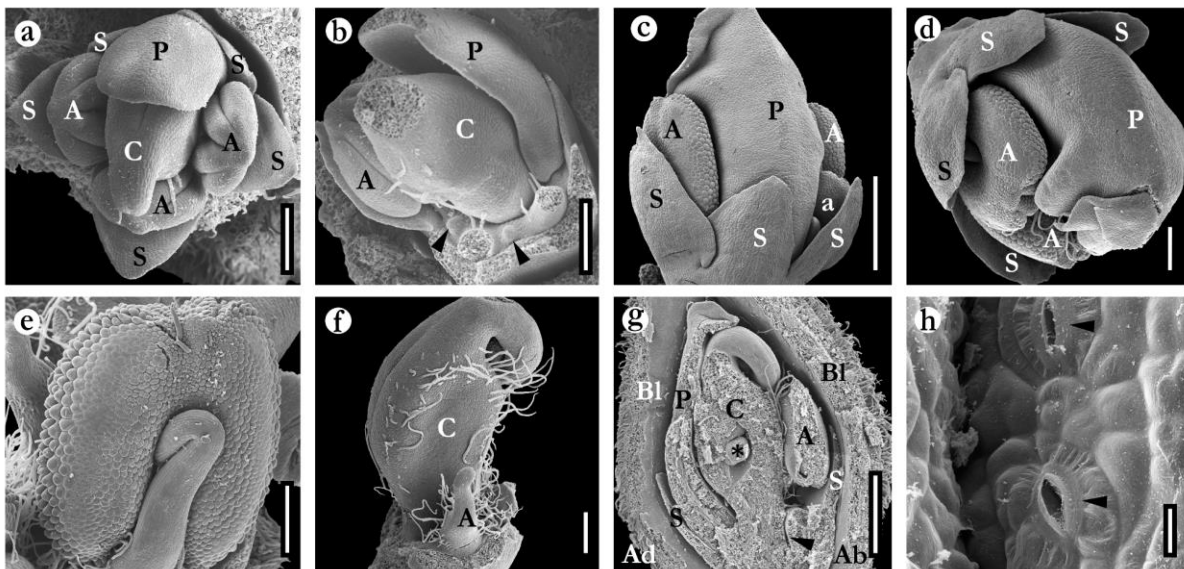
The first sepal (S1) begins in the median abaxial position (Fig. 9h). The second sepal (S2) begins in the median adaxial position, opposite to S1 (Fig. 9i), but it is difficult to distinguish the primordium from the protuberance formed previously by the pressure of the bracteoles. The second and third sepals (S3 and S4) appear simultaneously on the sides, practically simultaneously with S2 (Fig. 9i). We can see from Fig. 9i that the four sepals have a very short plastochrony between them. It was not possible to observe the moment of initiation of S5, which only becomes visible after the initiation of all the other organs (Fig. 9o). The initiation pattern of the calyx, therefore, is helical, however, with some level of erraticism.

The five petals initiate simultaneously, and the carpel initiates practically next to them (Fig. 9j). In Fig. 9j, we also see an elevation in the abaxial position of the antesealous that probably corresponds to a stamen primordium. It was not possible to distinguish the moment of initiation of these three whorls, which can be considered practically simultaneous and superimposed given the very short plastochrony between them. In subsequent stages, we can barely observe the petals, which are suppressed as the other organs elongate (Fig. 9j–m). The lateral antesealous stamens initiate shortly after the abaxial one (Fig. 9k–m). The adaxial portion of the meristem is slightly marginalized as the carpel and the first three stamens elongate, making it difficult to observe (Fig. 9k–n). The petals are visible during the intermediate stages (Fig. 9m–o).

Currently, we also see the two abaxial antepetalous stamen primordia (Fig. 9n–p). The last two stamens to initiate are opposite the lateral petal primordia, but it is uncertain whether they are of an antesealous or an antepetalous nature (Fig. 9p–s). It is possible that one or both do not initiate or, if they do initiate, they are suppressed soon after, as seen in Fig. 9q, in which one of the lateral petals is also missing. Thus, the number of initiated stamens varies from 5–7 and the initiation pattern for both stamen whorls is unidirectional. In general, floral

organogenesis presents a short plastochrony between each whorl and between the organs of the same whorl, as well as overlap in whorl initiation. On the other hand, there is a great heterochrony in organ development, observable from the early stages.

During the initial stages of floral organ elongation, it is important to note that these are arranged at different heights of the meristem, with the abaxial ones higher than the adaxial ones (Fig. 9n–s). The bracteoles elongate and stiffen rapidly, and their margins fuse, before calyx initiation (Fig. 9f–g). Fig. 10h shows stomata on the inner surface of the bracteole during advanced stages of differentiation. The sepal primordia develop slowly and do not elongate enough to cover the inner whorls. The two adaxial sepals are the ones that take the longest to elongate, remaining slightly hidden under the adaxial petal primordium (Fig. 9l–s) which, although initially slow to elongate, is the only one of the corolla to elongate, differentiate and reach anthesis (Fig. 9s–t, 10a–d). It remains practically adjacent to the carpel from the beginning of its elongation until the point at which it exceeds it in length and envelops it from above and laterally, occupying the space between it and the stamens (Fig. 10a–d).



The other petals are visible as undifferentiated primordia during intermediate stages but are subsequently suppressed and are no longer visible at anthesis (Fig. 9p–s). The first three stamens to emerge are the only ones to develop, in most cases (Fig. 9t, 10a, 10e). Rarely does a fourth stamen develop and differentiate, reaching anthesis (Fig. 10c). This fourth stamen generally corresponds to one of the lateral antepetalous. As primordia, the stamens elongate rapidly, surpassing the corolla primordia and closely following the length of the carpel (Fig. 9l–p). Their differentiation occurs at the beginning of the formation of the carpel cleft (Fig. 9q–s). The remaining stamen primordia generally do not reach anthesis but are still observable at intermediate and late stages (Fig. 9r, 10b). The uneven shape of the floral meristem surface can be confusing as to the size of the primordia, so that the organs on the abaxial side, depending on the angle, appear to be much larger (Fig. 9n–p). Soon after initiating, the carpel takes up much of the central and adaxial space of the meristem, hiding the median adaxial region (Fig. 9l–p). Differentiation of the carpel cleft begins soon after the end of the organogenetic stage (Fig. 9p–q). At later stages, the carpel tapers slightly at the base (Fig. 10b) and its apex curves almost perpendicularly to the abaxial side (Fig. 9t, 10a). The apex elongates to form the style, which gradually curves back on itself (Fig. 10f–g). Long trichomes form on the margins of the ovary (Fig. 10g).

***Paloue paraensis* (Ducke) Redden (Figures 1g–h, 1p, 2.28–32, 11a–t, 12a–t, 15i–l, 15s)**

Inflorescence

Organogenesis—Simple, terminal, erect, capituliform raceme, characterized by its globose appearance formed by very congested flowers. The relatively short peduncle is about 8 cm long and bears 40–50 flowers subtended by cuculate bracts, of slightly rigid and fibrous consistency and externally pubescent. The first bracts at the base of the peduncle have alternate distichous anthotaxy and are strongly overlapped, in addition to not subtending flowers. Later, they begin to spiral and bear flowers. The bracts of more distal buds generally overlap other more internal structures, contributing to the globose and compact appearance of the inflorescence (Fig. 1g, 2.28).

Organogenesis and development—Floral meristems and bracts have acropetal sequential initiation and development. They present a relatively short plastochrony of initiation between floral buds, and it is possible to observe many stages of development in the same inflorescence. The flower buds are very close to each other in space (Fig. 11a–c, Fig. 12h). In Fig. 11b–c, we see that the meristems tend to start in a diametrically opposite position concerning the previous one in the peduncle. During development, as the axis of the inflorescence elongates and generates new meristems, the proximity between the flower buds increases and the inflorescence acquires a spiral anthotaxy (Fig. 12h).

Flower

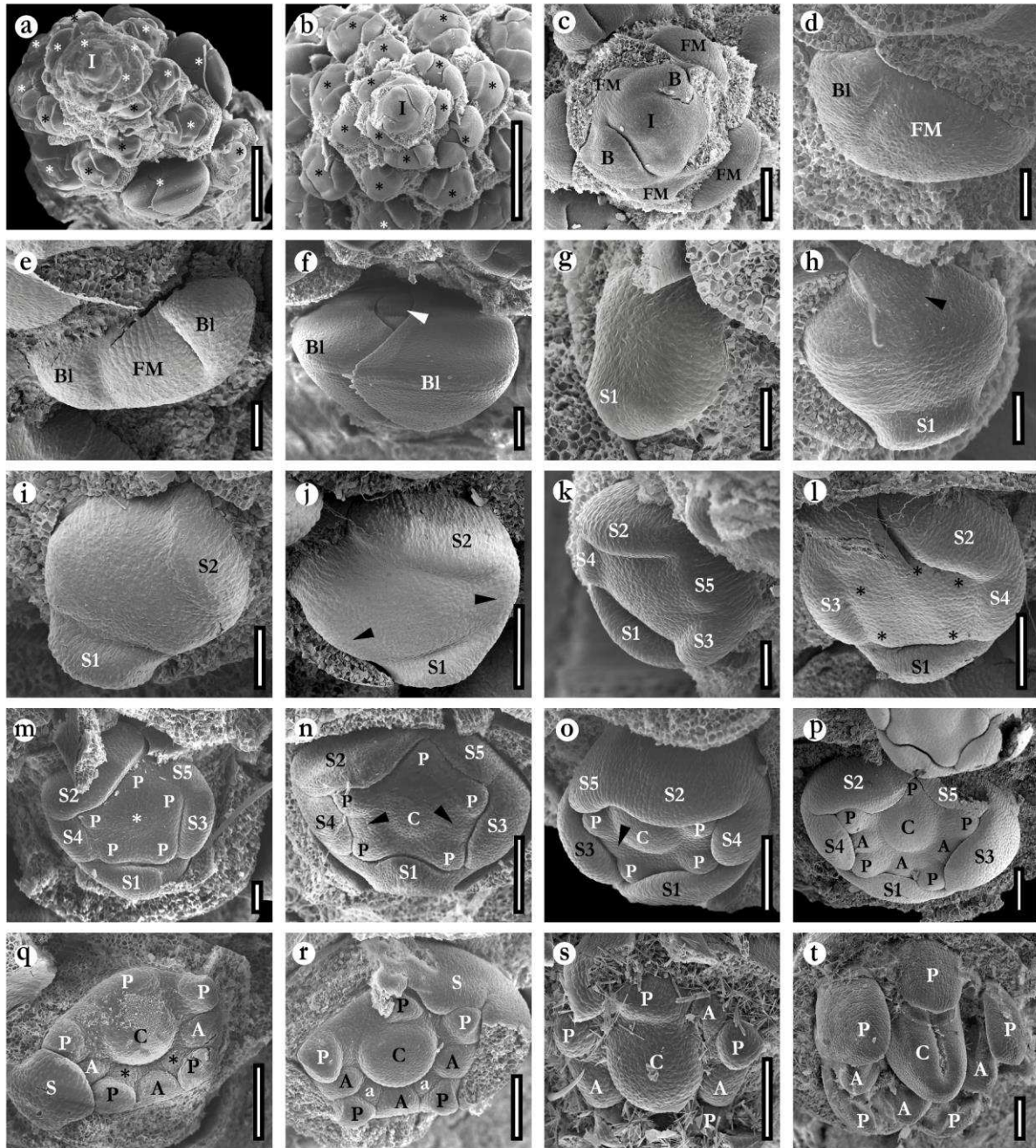
Organography—The flowers have short pedicels up to 1.5 cm long and are arranged very close to each other on the peduncle, which contributes to their compactness. The bracteoles are about 2–2.5 cm long and are fused up to almost half their length. The bracteoles are cuculate in shape, surrounding the base of the flower, have a slightly rigid and fibrous consistency, a pubescent outer surface, and are greenish brown in color. The calyx has five white sepals (two fused adaxial ones), about 2 cm long, oblong to ovate, a rounded apex, and a villous inner surface, with the adaxial one being wider than the others (Fig. 1g–h, 1p).

The corolla has five petals, the lateral and abaxial ones being smaller, up to 2.5 cm long, and the adaxial one up to 3 cm long, oblong in shape, with a rounded to slightly emarginate apex, and a white color with a vinaceous base. The adaxial may present linear pink nectar guides at the base of the central region of the blade (Fig. 2.29). The androecium is composed of a short staminal ring 1 mm long, with three fertile stamens corresponding to the abaxial and lateral antesealous, and six staminodes corresponding to the adaxial antesealous and abaxial and lateral antepetalous. The fertile stamens are up to 5 cm long, while the staminodes are up to 2.5 cm long and are wine-colored. The filaments are free above the ring, villous at the base, and the anthers are dorsifixed and introrse. The staminodes do not form anthers (Fig. 2.30–31).

The carpel is stipitate, with the stipe adnate to the adaxial wall of the hypanthium and its apex curved toward the abaxial side. The ovary is trapezoidal and laterally compressed, about 1–1.2 cm long, with a velvety surface, light pink and bearing 10–11 ovules. The vinaceous style is about 4.5 cm long, ending in a white stigma with a papillose surface (Fig. 2.32).

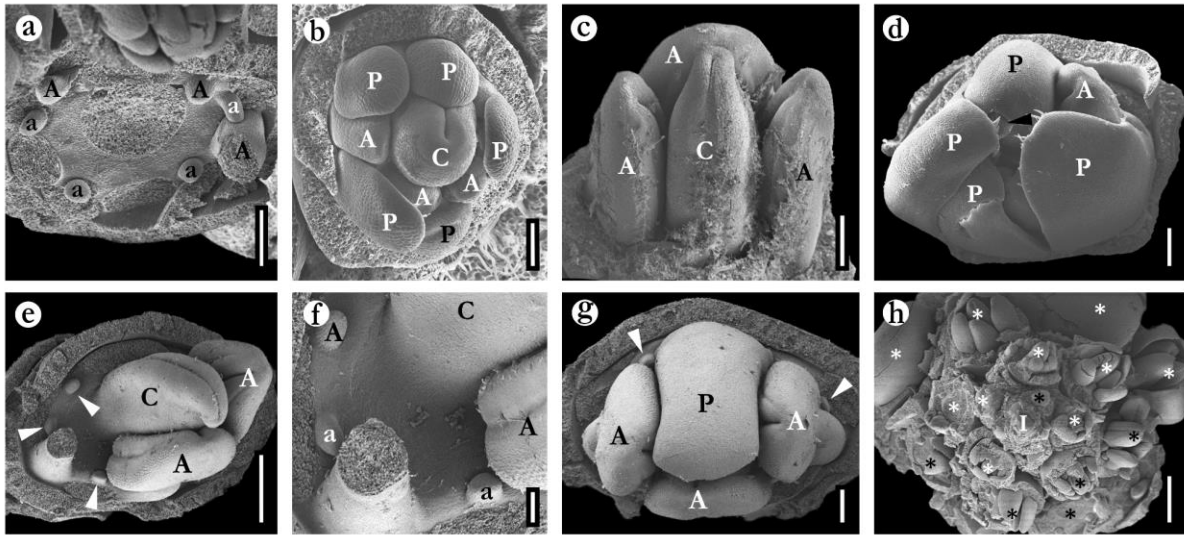
Organogenesis, elongation, and differentiation—The first products of the floral meristem are the two bracteoles, initiating one after the other, with the position of initiation of the first varying between left or right lateral (Fig. 11c–f). The bracteoles elongate more rapidly in length than in width, covering the apical surface of the meristem, while the median abaxial and adaxial regions are initially exposed (Fig. 11f). The first sepal (S1) initiates in the median abaxial position (Fig. 11g). The protuberance in the median adaxial region is formed by the mechanical pressure exerted by the margins of the bracteoles (Fig. 11f, 11h) and can be confused with the emergence of the second sepal (S2), but we observe that it initiates laterally in the adaxial region (Fig. 11i), varying, between meristems, between the right or left side (Fig. 11i–p). The second and third sepals (S3 and S4) initiate almost simultaneously in lateral positions, with a

short plastochron, with S3 generally opposite S2 (Fig. 11j). The fifth sepal (S5) is the second adaxial, and may be left or right depending on the position of S2 (Fig. 11k–p). Therefore, the initiation pattern of the calyx organs is helical.



The five corolla primordia initiate simultaneously (Fig. 11l), but have differential development. The adaxial petal takes longer than the others to elongate (Fig. 11p–t). Soon after the corolla primordia initiate, we observe a central elevation in the meristem corresponding to the initiating carpel (Fig. 11m–n). The first three primordia of antesepalous stamens arise almost simultaneously in the lateral and median abaxial positions, opposite S1, S3 and S4 (Fig. 11p). At some moments, it is possible to observe elevations of a dubious nature in lateral positions that may correspond to the primordia of stamens (Fig. 11n–o). Before the last antesepalous stamens initiate, we observe the elevation of the two abaxial antepetalous primordia, so that there is an overlap of the two whorls. The two adaxial antesepalous primordia and the lateral antepetalous primordia are observed already at the beginning of their elongation (Fig. 11s–t). No case or trace of initiation of the antepetalous adaxial stamen is observed. Thus,

both whorls present unidirectional initiation, although it is also possible that the antesepal whorl presents bidirectional initiation, but with very short plastochrons between the first three primordia.



The first bracteole overlaps the second after their margins meet. They elongate vertically and fuse, except for the apical portion that remains free. In late stages, the first bracteole becomes considerably taller, but its apical margin remains coherent with the second by trichomes. S2 and S5 begin separately, but still in the organogenesis stages they become fused by intercalary growth (Fig. 11o) and in anthesis they become indistinguishable. We can see markings on the surface of the petals made from the pressure exerted by the sepals (Fig. 11q-r). It is possible that the slower development of the adaxial petal is due to the pressure of S2 on it (Fig. 11p-r). Besides being smaller than the others during elongation (Fig. 11p-t, 12b, 12d), when the adaxial petal reaches the same length as the carpel (Fig. 11t), its lateral margins grow to envelop it from above and laterally, through the space between it and the stamens (Fig. 12d, 12g). It surpasses it in length and begins to envelop it at the beginning of style growth (Fig. 12d). The other petals develop in a similar way to each other. The first three antesepalous stamens to emerge are just slightly larger than the others in the initial stages of elongation (Fig. 11s), but they quickly distance themselves in length and are the only ones to undergo the process of differentiation into anther and filament (Fig. 11t, 12a-g). Their differentiation produces an anther that is considerably larger in proportion to the filament (Fig. 12c-g). All three reach and follow the carpel in length and width. The other six stamens elongate slowly, without differentiating into anther and filament (Fig. 12a, 12e-g). The carpel primordium grows rapidly after its initiation, taking up much of the space of the meristem (Fig. 11p-s). The carpel cleft is formed during early stages of organ elongation (Fig. 11s-t). It deepens during staminal differentiation (Fig. 11t) and begins to close during style elongation (Fig. 12c). The style bends abaxially as it elongates, gradually forming a spiral (Fig. 12e).

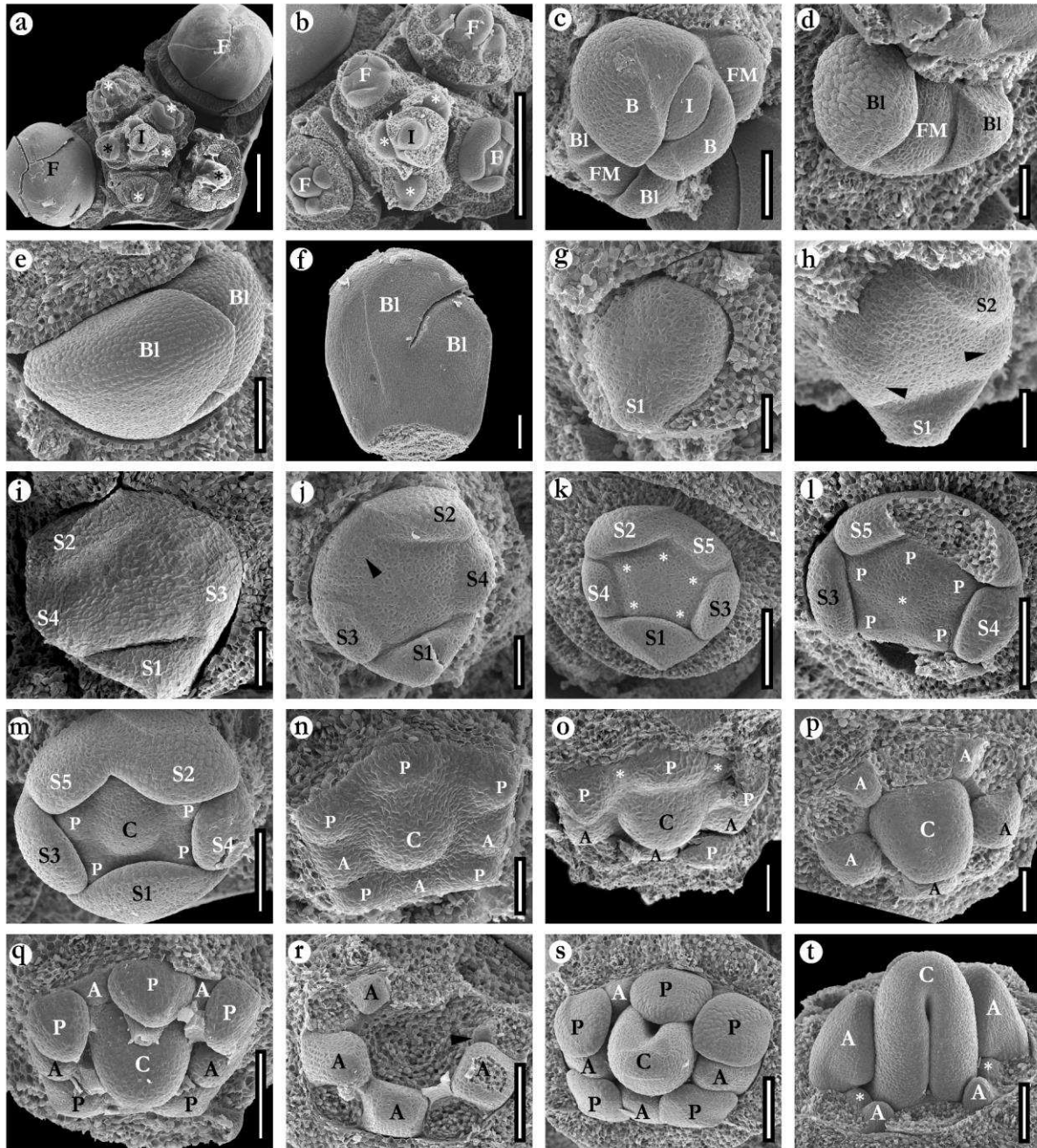
***Paloue speciosa* (Ducke) Redden (Figuras 1d-f, 1p, 2.24-27, 13a-t, 14a-h, 15m-p, 15t)**

Inflorescence

Organography—Simple, terminal, erect racemes. The peduncles are about 6–10 cm long, with slightly congested anthotaxy, spirally alternating patterns. The bracts are obovate and cuculate in shape, rigid and fibrous in consistency, wine-colored, and surround the buds in such a way

that they mold themselves to them. One to a few flowers are open at a time in the same inflorescence. There are 20–25 flower buds per inflorescence (Fig. 1e, 2.24).

Organogenesis, elongation, and differentiation—Floral meristems and bracts have acropetal sequential initiation and development (Fig. 13a–b). The meristems generally initiate in a position opposite to the previous one on the axis of the peduncle (Fig. 13c), but they have a relatively long plastochron between them. In addition, the peduncle elongates considerably. As a result, a considerable space is maintained between the flower buds.



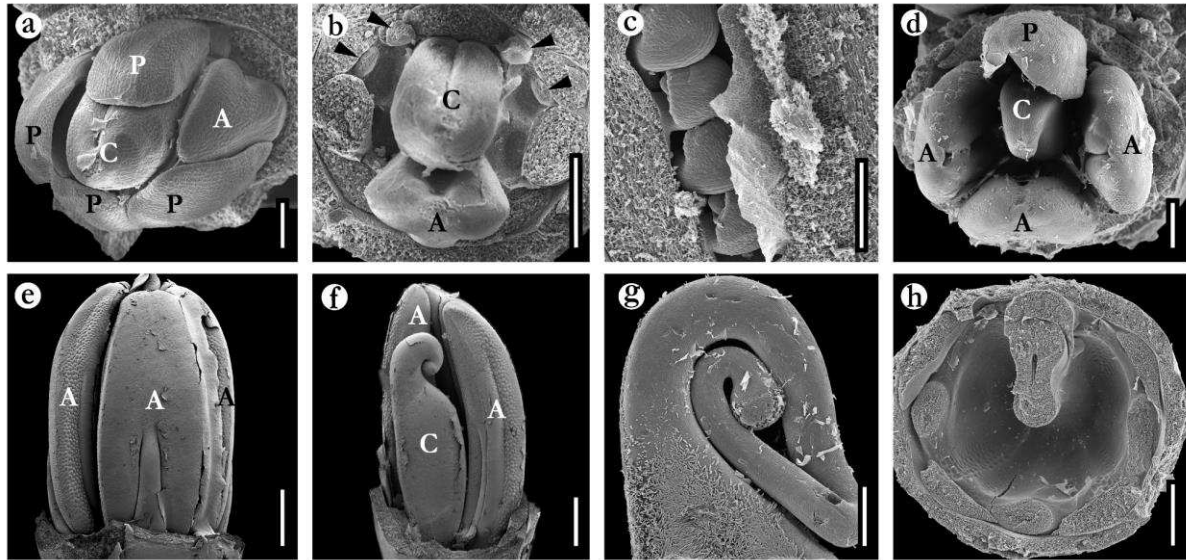
Flower

Organography—The flowers have short pedicels up to 0.5 cm long, which contributes to their compactness, although they are not very close together. The bracteoles, similar to bracts, are about 1.2 cm long, oblong and cuculated in shape, with an acute apex, rigid and fibrous consistency, wine-colored, are fused up to about half their length and tightly surround the flower up to the height of the base of the calyx. The calyx is composed of five sepals (two fused

adaxial ones) pink to red, up to 1.5 cm long, with the adaxial one being slightly wider. The corolla is composed of five equal petals, pink to red, oblong to elliptical, with an acute apex, with the adaxial one remaining surrounding the gynoecium even in anthesis, in addition to having a slightly auriculate base. The androecium consists of a staminal ring 0.1 cm high, with three fertile stamens 2.5–3 cm long and six staminodes ranging in size in the same flower from 0.8–1.2 cm long. The ring has a puberulent surface and is discontinuous in the median adaxial portion of the flower. The filaments are free above the ring, villous at the base and pink to red. The anthers are dorsifixed, introrse and light pink. The staminodes are undifferentiated. The carpel is stipitate and its stipe is adnate adaxially to the hypanthium wall (Fig. 2.27). The ovary is 6–10 cm long, oblong, and laterally compressed, with a velutinous surface and light pink, and bears eight ovules. The style is 1.6–2 cm long, pink, and at its tip is the globose stigma with a papillary surface (Fig. 1f, 1p, 2.24–26).

Organogenesis, elongation, and differentiation—The first products of the floral meristem are the pair of bracteoles (Fig. 13c–f). One of its sides develops more rapidly, giving rise to the first bracteole, whose position varies between the right and left side, and is quickly followed by the second. Both elongate more rapidly in length and overlap, covering the meristem (Fig. 13e). The first sepal (S1) initiates in the median abaxial position, while this region is still partially exposed by the bracteoles (Fig. 13g). The second sepal (S2) initiates in the adaxial position, varying between right and left lateral (Fig. 13f–m). At this time, the bracteoles have completely covered the meristem. The third and fourth sepals (S3 and S4) initiate simultaneously or nearly simultaneously in the lateral positions (Fig. 13h–i). However, despite simultaneous initiation, the sepal positioned between S1 and S2 generally develops more slowly (Fig. 13k–m). In Fig. 13i, we see that a small gap remains between the bracteoles in the median adaxial position. The margin of the bracteole presses against the surface of S2, where we can see the mark left by it. The fifth and last sepal (S5) is the second adaxial one that appears to initiate already fused with S2 by intercalary growth (Fig. 13j–m). Thus, the calyx presents a helical initiation. The meristem internal to the calyx acquires a star-shaped shape and each of the vertices represents one of the corolla primordia that will initiate simultaneously (Fig. 13k–l). Soon after, the center of the meristem rises to give rise to the carpel (Fig. 13e–m). The first three stamens initiate simultaneously in the abaxial and lateral positions, opposite to S1, S3 and S4, when the calyx is already covering the innermost whorls (Fig. 13n). Subsequently, the two adaxial antesepalous stamens initiate (Fig. 13o–p), thus following a unidirectional initiation pattern. It was not possible to observe the initiation pattern of the inner whorl of stamens, which only became visible when the other organs were already much more elongated (Fig. 13r). However, it is possible to identify that four antepetalous stamens initiate. The adaxial antepetalous stamen was not observed at any time. The proximity between the scar of the adaxial petal and the carpel in Fig. 13r indicates that there was no space in this region for the initiation of this stamen. The margins of the bracteoles fuse as they elongate, and they become fused from their base, except for the apical portion (Fig. 13f). The apical region of the larger bracteole acquires a domed shape as it covers the apical surface of the smaller one (Fig. 13f). The calyx elongates vertically with its base already fused (Fig. 13m). The corolla elongates slowly, but the petals differentiate rapidly with lateral widening of the lamina and tapering of the apex (Fig. 13q, 13s). The adaxial petal develops slightly more slowly than the others (Fig. 13s) and approaches the carpel (Fig. 14a). As it elongates, first laterally and then lengthwise, it begins to envelop it through the space between the carpel and the adjacent stamens (Fig. 14c). The base of the petal acquires a slightly auriculate shape that slightly invades the hypanthium space around the carpel (Fig. 14h). The other petals develop similarly to each other. The first three antesepalous stamens to initiate are the only ones to undergo differentiation into anther and filament (Fig. 13t), and the anthers enlarge rapidly and take up much of the space between the corolla and the carpel (Fig. 14a–c). The other stamens remain very small throughout

development, especially the antepetalous (Fig. 13t, 14b) and occur vestigially at anthesis. In Fig. 14h, it is difficult to discern whether there is any structure corresponding to the antepetalous stamens, leading to the possibility that they are suppressed. The carpel takes up most of the center of the meristem soon after its initiation (Fig. 13m–p). We observed the formation of the carpel cleft prior to the initiation of the antepetalous stamens (Fig. 13p). The cleft forms during the early differentiation process of the other organs (Fig. 13s–t). The apex of the carpel begins to taper to form the style, which elongates abaxially (Fig. 14a–c). At later stages, the style curves back on itself as it elongates (Fig. 14f–g).



General

Comments

All studied species undergo the same fundamental process of hypanthium formation, though there are variations in its depth, shape, and other specific characteristics. The hypanthium generally begins to form during the later developmental stages through a vertical invagination of the meristematic tissue in the bud receptacle. This vertical elongation occurs specifically in the region between the carpel and the androecium. However, this process does not take place between the carpel and the median adaxial region. As a result, a stipe is formed that is adnate to the adaxial wall of the hypanthium (Fig. 4c, 4g, 6l, 10g, 12e–f, 14h, 15e).

Nectariferous tissue of the hypanthium

Anatomical studies of the hypanthial region were conducted for four of the six species investigated in this work: *Brownea longipedicellata* (Fig. 15a–d, 15q–r), *Heterostemon mimosoides* (Fig. 15e–h), *Paloue paraensis* (Fig. 15i–l, 15s), and *Paloue speciosa* (Fig. 15m–p, 15t). All light microscopy images represent longitudinal anatomical sections of flower buds at late developmental stages (pre-anthesis). In the cases of *B. longipedicellata*, *P. paraensis*, and *P. speciosa*, the sections are perpendicular to the dorsoventral axis of the bud. For *H. mimosoides*, the sections are parallel to the dorsoventral axis of the bud.

All species exhibit structured nectariferous tissue divided into three distinct layers: the epidermis, nectariferous parenchyma, and subnectariferous parenchyma.

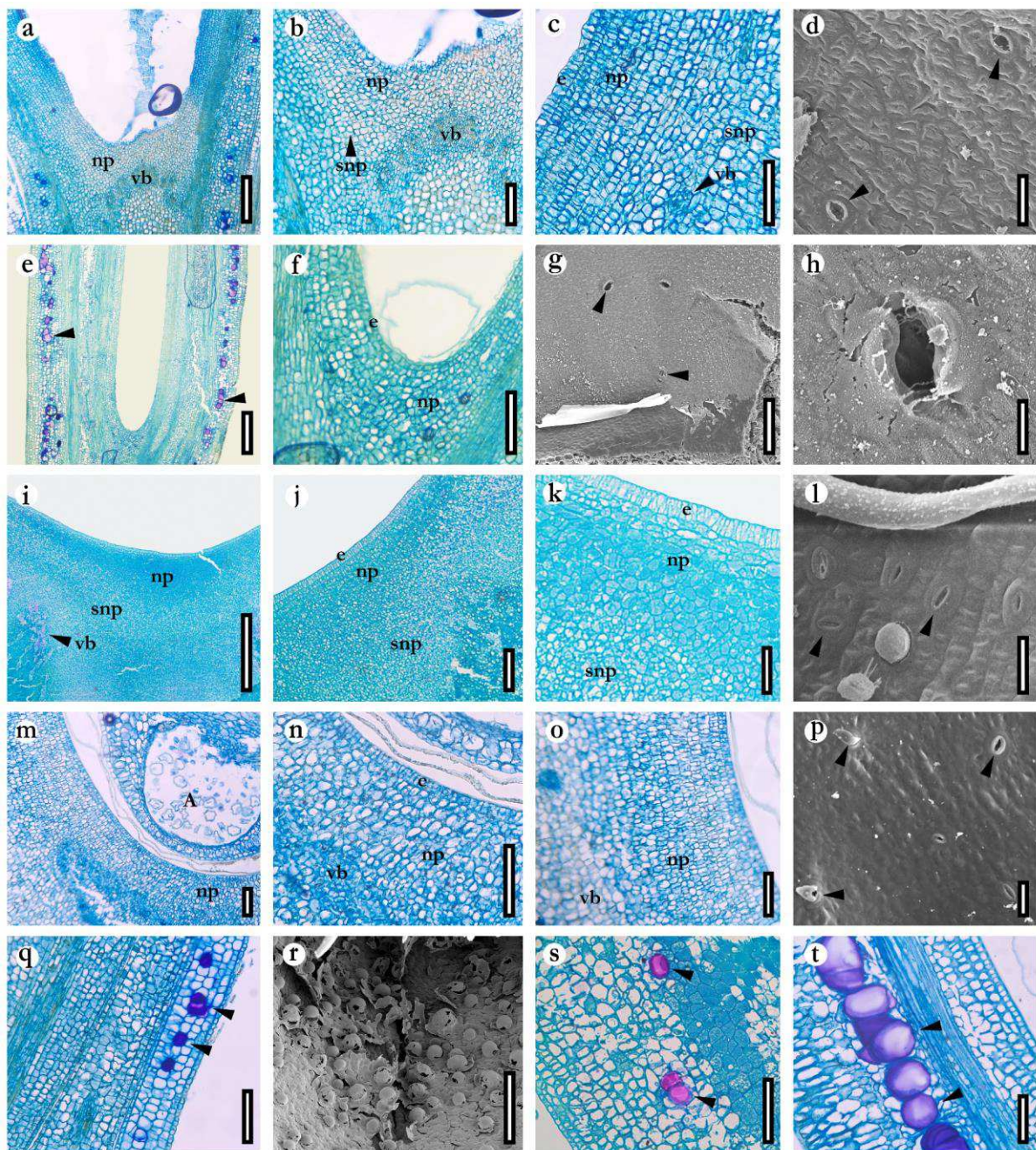
In *B. longipedicellata*, *P. paraensis*, and *P. speciosa*, the epidermis consists of elongated palisade cells (Fig. 15c, 15k, 15n). In contrast, *H. mimosoides* displays small, rectangular epidermal cells (Fig. 15f). Stomata are concentrated in the basal region of the hypanthium wall, generally more abundant on the abaxial side, opposite to stipe (Fig. 15d, 15g–h, 15l, 15p).

The nectariferous parenchyma is composed of globoid, slightly misshapen cells with dense, intensely stained cytoplasm and generally thin cell walls. These traits are most pronounced in *P. paraensis*, and *P. speciosa* (Fig. 15i–k, 15m–o). In *H. mimosoides*, the cells have slightly thicker walls (Fig. 15f), while *B. longipedicellata* exhibits more rectangular cells (Fig. 15b–c). In *P. paraensis*, 1–2 layers of smaller, misshapen, and less stained cells occur just below the epidermis, distinguishing them from the underlying nectar parenchyma (Fig. 15k).

The subnectariferous parenchyma varies greatly among species. *P. paraensis* has a prominent subnectariferous parenchyma composed of globoid, misshapen cells with thicker walls and less intense staining (Fig. 15k). Marginal vascular bundles are present but are not closely associated with the nectar parenchyma (Fig. 15i). *P. speciosa* exhibits damaged subnectariferous parenchyma in some samples, making visualization difficult. However, larger, less intensely stained, rectangular cells can still be observed, along with a vascular bundle marginal to the nectar parenchyma (Fig. 15m–o). *B. longipedicellata* displays larger subnectariferous parenchyma cells, which are slightly less stained and intersected by a vascular bundle (Fig. 15a–c). In *H. mimosoides*, the subnectariferous parenchyma was not observable.

Idioblasts were observed in all species, distributed primarily along the bracteoles and sepals (Fig. 15e, 15s, 15t). These cells are very large and intensely purple-stained, likely indicating the presence of phenolic compounds.

In *B. longipedicellata* (Fig. 15r), the abaxial wall of the hypanthium is covered with what appear to be modified trichomes. However, these structures were not observed in the anatomical sections or other buds, such as the one shown in Fig. 15d.



Discussion

Table 2 presents the order of initiation and development of flowers and inflorescences in each of the analyzed taxa. The initiation of whorls in the meristem follows a mixed acropetal pattern, beginning with the calyx, followed by the corolla, carpel, the whorl of antesealous stamens, and finally the whorl of antepetalous stamens. This pattern, where the carpel is not the last organ to form, is typical of nearly all Leguminosae (Tucker 1987).

In *Macrolobium suaveolens*, the initiation of the corolla, carpel, and antesealous stamens occurs in close succession, appearing almost simultaneous and overlapping. For *Heterostemon mimosoides*, we observed the initiation of the carpel occurring alongside the corolla. However, it was unclear whether these structures arise truly simultaneously or if there is a very short plastochrony between the emergence of the corolla and the gynoecium. *Browneopsis macrofoliolata* occasionally shows overlapping initiation of the calyx and corolla, while in *Paloue paraensis*, overlap occurs between the two stamen whorls.

Table 2: Patterns of initiation and development.

Development		Patterns of Initiation			
	Inflorescence	Calyx	Corolla	Antesepalous st.	Antepetalous st.
<i>B. longipedicellata</i>	partially basipetal	helical	simultaneous	simultaneous	-
<i>B. macrofoliolata</i>	acropetal, nearly synchronous	helical	simultaneous	simultaneous /erratic	unidirectional
<i>H. mimosoides</i>	Acropetal, sequential	helical	simultaneous	unidirectional	-
<i>M. suaveolens</i>	acropetal, sequential	unidirectional	simultaneous	unidirectional	unidirectional
<i>P. paraensis</i>	acropetal, sequential	helical	simultaneous	unidirectional	unidirectional
<i>P. speciosa</i>	acropetal, sequential	helical	simultaneous	unidirectional	-

(-) = not observed.

Development and morphology of inflorescences and bracts—The taxa analyzed in this study present a wide morphological variety in their inflorescences, however, they all consist of the same basic structure: racemes with spiral anthotaxy and, at least initially, acropetal sequential initiation. Some factors that play an important role in generating such morphological diversity are: 1) relative length of the peduncle; 2) number of flowers per inflorescence; 3) differences in plastochrony between the emergence of different floral meristems; 4) size of the pedicel and/or hypanthium; 5) relative size of the flowers. The peduncle length and the flower size are relative because they depend on the other parameters to be defined. For example, in the case of *B. macrofoliolata*, the axis of the inflorescence is short considering the large number of large flowers it bears. Table 3 shows a comparative table of the species about each of these parameters.

Most species of *Brownea* and *Browneopsis*, as well as some of *Paloue*, such as *Paloue paraensis*, have a type of raceme often called capituliform, which is characterized by many flowers grouped in a very congested way around a relatively short and thick peduncle and with reduced internodes between flowers (Arroyo 1981; Klitgaard 1991; Redden et al. 2018). Capitiform racemes, although common in the *Brownea* clade, are uncommon in Detarioideae (Bruneau et al. 2014; Cowan and Polhill 1981a; 1981b) and can be found in some species of the genus *Cynometra*, formerly included in *Maniltoa* (Lewis et al. 2005; Radosavljevic 2019). The structure of this inflorescence is achieved through the development of numerous meristems with short plastochrony between them, which develop on a central axis with reduced internodes about the number of flowers, whose pedicels are also short. *Brownea longipedicellata*, unlike the other species in the group, has non-capituliform racemes with few flowers (generally 7–10). The floral buds, although they have very short plastochrony between them, are few and have long pedicels that give the inflorescence a looser appearance. Besides, *B. longipedicellata* presents basipetal sequential development, that is, the most apical meristems, during organogenesis, surpass the most basal ones by developing faster and reaching anthesis earlier. Bull–Hereñu et al. (2022) comment on some records of this type of development in species of Araceae, Asteraceae, among others, in which the most basal meristems present a delayed development due to the pressure of specialized protective organs such as involucre and spathes. The case of *Brownea latifolia* (Tucker 2000b), whose meristems still in early stages synchronize their development, is also rare in Detarioideae and uncommon in Fabaceae in general, although it is common in the tribe Mimoseae (Caesalpinioideae) (Tucker 1987). In Detarioideae, Tucker (2002b) also recorded initially synchronous development of flower buds

for *Berlinia grandiflora* (Vahl) Hutch. & Dalziel, in addition to indicating that *Paramacrolobium coeruleum* (Taub.) J.Léonard presents apical buds that enlarge earlier than the basal ones, that is, with basipetal development. However, there are no images of these records nor information about later stadiums.

Table 3: Morphological diversity variables of the inflorescence

Species	Inflorescence Axis	Flowers per inflorescence	Plastochron between flowers	Pedicel/Hypanthium	Flower Size
<i>B. longipedicellata</i>	Short	8–10	Short	Long pedicel/medium hypanthium	Large
<i>B. macrofoliolata</i>	Short and robust	100–120	Short	Short pedicel/medium hypanthium	Large
<i>H. mimosoides</i>	Short	6–8	Long	Short pedicel/long hypanthium	Large
<i>M. suaveolens</i>	Medium	15–20	Medium	Both short	Small
<i>P. paraensis</i>	Short and robust	35–40	Short	Both short	Large
<i>P. speciosa</i>	Long	20–25	Long	Short pedicel/medium hypanthium	Medium

The inflorescence of *Browneopsis macrofoliolata* produces floral meristems with very short plastochrony between them, and its flowers almost all reach anthesis at the same time. The numerous meristems are very close together, generating mechanical pressure and competition for space between each meristem and its adjacent ones. The meristems of the base of the inflorescence (Figs. 5j, 6c, 6f) are generally much wider than meristems that are at the same developmental stage, but located in the middle of the inflorescence (Figs. 5i, 6b, 6e). In addition, the erraticity, especially of the elongation of the whorls, as well as the variable shape of adjacent meristems at very similar stages, are some examples of the impact generated by the mechanical pressures of such proximity (Bull–Hereñu et al. 2022; Endress 2006). Comparing young inflorescences (Fig. 5a–b) to others more advanced in development (Fig. 5c, 6d), we see that the competition for space generates a visibly greater impact during stages of organogenesis. It is possible to trace several similarities between the development of the inflorescence of *Browneopsis macrofoliolata* and development patterns observed in genera of the Mimoseae tribe in the subfamily Caesalpinioideae, such as in the genera *Inga*, *Parkia*, among several others, whose inflorescences are commonly capitula, glomeruli or capituliform racemes, congested, with numerous flowers, simultaneous or almost simultaneous development of one or more whorls (generally the corolla and androecium), radial symmetry and, sometimes, with staminal proliferation that can exceed a hundred (Paulino et al. 2016; Pedersoli and Teixeira 2016; Prenner 2004; Ramirez-Domenech and Tucker 1990; Tucker 1987). Furthermore, Arroyo (1981) highlights species of *Parkia* and *Inga* with chiropterophilous flowers, a pollination syndrome also cited for *Browneopsis* (Knudsen and Klugaard 1998). Arroyo (1981) describes the inflorescence of *Parkia clappertoniana* Keay (synonym of *Parkia biglobosa* (Jacq.) R.Br. ex G.Don) as bearing “up to 200 flowers supported by robust peduncles projecting away from the foliage”, a structure that resembles the inflorescences of *B. macrofoliolata*. Many of these floral architectural patterns are also seen in the flowers of some *Brownea* species, such as the more or less simultaneous initiation patterns of meristems and whorls, congested capituliform inflorescences, and numerous radial flowers, but structured in the form of a pseudotube (Arroyo 1981; Bruneau et al. 2014; Klitgaard 1991), highlighting that the species studied here, *Brownea longipedicellata*, is an exception to most of these character states found in most of its genus. Among these characteristics, only the formation of a pseudotube

does not occur in *B. macrofoliolata*, which has a reflexed corolla and a shallow staminal ring, without sheath formation. On the other hand, it is interesting to note that in both cases, the inflorescence acts as an attractive unit structure for the pollinator (Arroyo 1981). It is also worth highlighting that the erraticity observed in the organogenetic patterns of *Browneopsis* is also present in some of the Mimoseae genera with similar inflorescences, such as, for example, in the genera *Senegalia* and *Vachellia* (Alvarado-Reyes et al. 2024; Gomez-Acevedo et al. 2007; Gomez-Acevedo 2021), highlighting the possibility that the impact of this type of inflorescence is one of the factors acting on floral ontogeny.

The major ontogenetic differences between *Paloue paraensis* and *Paloue speciosa* lie in the divergence of their inflorescence development. While *P. speciosa* has a loose raceme with few flowers, *P. paraensis* has a capituliform and congested raceme with many more flowers. The divergence between the pathways that lead to these two structures is evident from the beginning of development, due to the different plastochrony between the emergence of the floral meristems of each species, longer in *P. speciosa* and shorter in *P. paraensis*. This may be one of the main factors enabling the formation of so many flowers in the inflorescences of *P. paraensis* (Figs. 11a–b, 12h), while in *P. speciosa*, the long plastochrony causes more basal flowers to already be very developed (Fig. 13a–b) when the flowers just above them appear, which raises questions not only about mechanical forces, but also about the distribution of resources along the inflorescence. The formation of inflorescences with many more flowers and, consequently, much larger, heavier and with a greater need for resource input, also explains the thin and soft peduncles of *P. speciosa* and the thick and rigid ones of *P. paraensis*. Interestingly, despite the great difference in the number of flowers, these two species, as well as in another similar species in the genus (*P. princeps*), have few flowers open per inflorescence at the same time, contrasting with, for example, *Browneopsis*, where almost all of the numerous flowers of an inflorescence are in anthesis simultaneously. This characteristic is not, however, universal in *Paloue*, since at least one species (*Paloue durissima* (Ducke) Redden) has short inflorescences with few flowers, similar to those of *P. speciosa*, but almost all of which are in anthesis simultaneously (present study). It is interesting to note that the main differences in floral morphology between the two species occur at late stages, while the processes of organogenesis and elongation are very similar, which is usually observed among closely related taxa, notably within the same genus (Tucker 1984; 1997), although several cases contradict this pattern (Bruneau et al. 2014). On the other hand, we can see that differences in the development of the inflorescence as a whole, which are prior to organogenesis, also play an important role in the differentiation of closely related taxa. This phenomenon can also be observed between *B. longipedicellata* and *B. latifolia* (Tucker 2000b). *Heterostemon mimosoides*, like *B. longipedicellata*, has racemes with short internodes and few flowers with large plastochrons between the emergence of their meristems, in addition to long hypanthia. *Macrolobium suaveolens* presents a typical raceme with intermediate characteristics concerning the five factors of morphological variability in Table 3. It is possible to see how recombinations of these factors generate morphologically variable inflorescences without necessarily changing the basic structure of the raceme. Another interesting feature found in the development of the inflorescences of almost all species of the clade studied here (except *Macrolobium suaveolens*) is the presence of sterile bracts with a distichous arrangement at the base of the inflorescence that, from a certain height on the main axis of the inflorescence, gradually begin to bear floral buds and become spiral, a pattern common to the extreme majority of species of Detarioideae and Leguminosae as a whole, with rare distichous exceptions in Detarioideae in the genera *Sindora*, *Goniorrhachis*, *Copaifera*, *Plagiosiphon* and *Cynometra* (Dwyer 1951; Maior et al. in prep.; Radosavljevic 2019; Tucker 1987; 2003c). In Leguminosae, fully distichous inflorescences are a synapomorphy of the subfamily Dialioideae (Falcão et al. 2020; 2023) and are present in a few genera of Papilionoideae (Monteiro et al. in

prep; Prenner 2013; Tucker 1987). The distichy present in the basal portions of the inflorescences of taxa of the *Brownea* clade may also be related to a continuity of the pattern observed for their leaves, since these species have strongly distichous phyllotaxis (Klitgaard 1991; Redden et al. 2018; present work). Despite the possibility that these partially distichous bracts, found in almost all studied taxa of the *Brownea* clade, are a synapomorphy for this group, studies focused on the origin of the inflorescence are necessary for other lineages of Detarioideae since such stages are commonly not treated in ontogenetic studies.

It is worth noting that in the *Brownea* clade, this character was found in the present study in much greater expression in the two species with congested capituliform inflorescences (*Browneopsis macrofoliolata* and *Paloue paraensis*) and in a species with lax racemes (*Brownea longipedicellata*), where the basal, sterile and distichous bracts are larger in relation to the inflorescence and, apparently, more numerous. However, this species of *Brownea* is inserted in a genus where practically all the other species have congested capituliform inflorescences and, despite the need for studies to reconstruct ancestral character states, it can be conjectured that the lax inflorescences with few flowers of *B. longipedicellata* represent a reduction of the ancestral congested and capituliform character. However, during ontogeny, some of the ancestral characters, such as the different types of bracts, some distichous and many of them without flowers, could still be observed. Furthermore, more than one bract morphology may occur in the same raceme, as is the case of *B. longipedicellata* and *B. macrofoliolata*, whose basal bracts, which are mostly sterile, are ovate and rigid, while the innermost bracts are oblong and flexible. It is worth considering the possibility that this is a synapomorphy for the group, since phylogenetic studies indicate *Brownea* and *Browneopsis* as sister genera or even as a single genus (Schley et al. 2018; 2020).

In all taxa studied, the initiation of the first bracteole varies in position in relation to the right or left side of the meristem. This generates a cascade effect that leads to the development of flowers where the organogenesis of the calyx also occurs in a mirrored manner, with flowers where the helicoid pattern occurs in a clockwise direction, with the second sepal to form being the left adaxial one, and other flowers where the direction is counterclockwise and the second sepal to form is the right adaxial one. Consequently, sepals three, four and five will follow these clockwise and counterclockwise patterns. Such variations may also extend to the corolla, allowing different imbrication patterns at anthesis. In this study, this phenomenon was not observed only in *M. suaveolens*. In general, the variation in position occurs between meristems of the same inflorescence, except in *P. speciosa*, in which, through the analysis of several inflorescences, it was observed that the variation occurs only between meristems of different inflorescences. The variation that occurs with the first bracteole is possibly caused by pressure on one side of the meristem by a bract further up the inflorescence axis (Figs. 11b–c, 13c), but this can only be seen more clearly in the case of *P. paraensis* and *P. speciosa*, while in the others the cause is not so clear.

In the case of sepals, we observed that in most species S2 begins opposite the largest/first-to-emerge bracteole; however, in *P. speciosa*, where all meristems of a given inflorescence present S2 in the same position, this pattern is broken. One possible explanation is that, at the time of S2 initiation, the largest bracteole is further away from the surface of the meristem because it is already overlapping the smaller bracteole. The latter, in turn, is closer to the meristem and, therefore, causes greater pressure on the side on which it is located (Figs. 13e–f). *Heterostemon mimosoides* has few stages in the same inflorescence, making this type of analysis difficult, since it requires comparing several meristems in organogenesis. The inflorescences of *P. paraensis* and *B. macrofoliolata*, on the other hand, have numerous buds in different stages, which generates many variables of pressure and positioning of one meristem in relation to the other, which is why it was not possible to find a pattern in the variation of the position of the bracteoles and sepals of the meristems along the axis of the inflorescence. The

inflorescences of *B. longipedicellata* have few buds and all are in very close stages, which generates another difficulty, which is to understand divergences in longer intervals of time along the same inflorescence. In the case of *M. suaveolens*, S2 begins in the median adaxial position, in addition to the initiation of S5 not having been observed until much later stages, and both take a long time to elongate compared to the other sepals of the bud, which makes their observation difficult. Other studies mention this variation between the right and left sides in cases of helical calyx initiation pattern (Prenner 2004; Prenner and Cardoso 2017; Tucker 1984; 2000a; 2000b; 2000c; 2001a), however, without delving into the cause of such variations. Particularly in the subfamily Dialioideae, this effect mirrored in the development of bracteoles and perianth is present in several taxa, extending, in the genus *Dicorynia*, to the androecium and gynoecium and culminating in enantiostyly during anthesis (Falcão et al. 2023). Enantiostyly was also observed in the subfamily Cesalpinioideae and plays an important role in floral biology (Marazzi and Endress 2008). In the Brownea clade, although there is no striking evidence of enantiostyly, several flowers commonly have the style turned to one side. Further studies are needed to verify whether this phenomenon may be a subtle type of enantiostyly and whether it may be a consequence of the “mirror effect” observed during several stages of the group's ontogeny.

Bracteoles, reduction events, and evolutionary parallelism in Detarioideae—Partially fused bracteoles are considered a synapomorphy for the Brownea clade. This character is present in most taxa of the clade, with reversal only in *Heterostemon ingifolius* Sandwith and most *Macrolobium* species, whose bracteoles open fully at anthesis (Bruneau et al. 2014; Cowan 1978; Redden et al. 2010; Tucker 2000b). In the *Stenosolen* section of *Macrolobium*, there is partial fusion of the bracteoles on the adaxial side of the flower (Cowan 1953). Both cases of reversal may have occurred through different pathways of floral development. In the case of *H. ingifolius*, it is possible that the loss of this characteristic occurred due to the reduction of the bracteoles, which are free and deciduous (Cowan 1978). On the other hand, in the case of *Macrolobium*, it is possible that this loss occurred through the enlargement and thickening of the bracteoles. In the floral development of *M. suaveolens*, this thickening process precedes the fusion process observed in the other taxa studied.

Tucker (2000a; 2000b; 2000d; 2001a; 2001b; 2002a; 2002b; 2003b; 2003c), in her studies of floral development for the current Detarioideae, divided the taxa of the subfamily into two groups based on the shape of the floral meristem at a stage prior to corolla initiation and after the beginning of bracteolar elongation: the circular and the omega. In general, the circular group corresponds to species whose meristem, during this stage, has a circular shape and is paired with relatively small bracteoles, while the omega group presents species whose meristem has a dorsoventrally elongated shape and the bracteoles are large and voluminous already during the organogenesis of the calyx. In the analysis by Bruneau et al. (2014), it was established that not all taxa with large bracteoles at the beginning of floral development are of the omega type, but that all of the omega type have large and thick bracteoles already at the beginning of organogenesis. Tables 4 and 5 show the list of Detarioideae species ontogenetically addressed to date. Table 4 contains the representatives of the omega group and Table 5 contains the representatives of the circular group.

Tucker studied at least one species from each genus that makes up the current Babijt + *Microberlinia* clade (Estrella et al. 2018), with the exception of *Icuria*, and all were considered to be in the omega group (*Microberlinia*, *Brachystegia*, *Bikinia*, *Julbernardia* and *Tetraberlinia*), in addition to other closely related taxa, such as *Gilbertiodendron*, *Berlinia*, *Isoberlinia*, among others from the tribe Amherstieae (Tucker 2000a; 2002a; 2002b; 2003c). Species from other current tribes of Detarioideae were also included in the omega group, such as *Afzelia quanzensis* Welw, *Sindora klaineana* Pierre ex Pellegr. and *Barnebydendron ridelii*

(Tul.) J.H.Kirkbr, belonging to the tribes Afzelieae, Detarieae and Barnebydendreae, respectively. However, there are no images of the floral development of *B. riedelii*, as the author indicates that it closely resembles that of *Neochevalierodendron stephanii* (A.Chev.) J.Léonard (Tucker 2002b). Other species without images of their development, but described ontogenetically by the author, were included in Table 4. Furthermore, the images of the floral development of *S. klaineana* make it unclear whether the author would place it in the omega group (Tucker 2003c), as the few images available of this stage suggest that the taxon would be better positioned in the circular group (present study).

Most of the genera represented in Table 4 (11 of the 18) belonged to the ancient tribe Macrolobieae (Breteler 1995), which is characterized by the presence of large bracteoles that generally play a protective role in the floral bud. Both the Macrolobieae tribe and the omega group are artificial circumscriptions (Bruneau et al. 2000; 2001; 2008; 2014; Estrella et al. 2018), however, they draw attention to the occurrence of several lineages in Detarioideae, especially in the Amherstieae tribe, in which there was a profuse elongation and thickening of the bracteoles that generated different consequences for floral development, which is why they are being addressed here.

Table 5 contains 18 species from five tribes. *Saraca*, from the Saraceae tribe, is not included in the table because, although it is considered part of the circular group, its species ontogenetically addressed present particularities of floral development that do not apply to the variables in the table (Tucker 2000d). In addition, *Goniorrhachis marginata* Taub., *Colophospermum mopane* (J. Kirk ex Benth.) J. Léonard, *Copaifera langsdorfii* Desf., *Hymenaea verrucosa* Gaertn. and *Brodriguesia santosii* R.S. Cowan were classified as belonging to the circular group based on our observations of data made available by other studies (Citeli et al. in prep; Kochanovski et al. 2018; Krüger et al. 1999; Pedersoli et al. 2010; Prenner and Cardoso 2017). All other taxa in both tables, except those analyzed in this study, follow the classifications made by the author in the ontogenetic studies that address them (Tucker 2000a; 2000b; 2000d; 2001a; 2001b; 2002a; 2002b; 2003b; 2003c).

Comparing the two tables, we see that, proportionally, the omega group presents more cases of corolla reduction (16 of 20) than the circular group (seven of 18). On the other hand, androecium reduction is practically as frequent in the circular group (four of 18) as in the omega group (six of 20). The calyx, although showing few cases of reduction in numbers, notably in the genera *Colophospermum*, *Aphanocalyx* and *Bikinia*, presents several cases of reduction in size and shape during late stages of development until anthesis, especially in the omega group, as in *Gilbertiodendron klainei* (Pierre ex Pellegr.) J. Léonard, *Tetraberlinia tubmaniana* J. Léonard, *Microberlinia brazzavillensis* A. Chev., *Brachystegia tamarindoides* Welw. ex Benth., among others (Tucker 2000a; 2002a; 2002b).

The same applies to petals, which, although present, are often reduced in size and shape, reinforcing the idea that, in Detarioideae, the reduction is, in its vast majority, due to suppression or interruption of growth events in intermediate to late stages and, rarely, due to absence since initiation or suppression in early stages of development, which contrasts, for example, with the frequent reduction events observed in the subfamily Dialioideae, which are, in the majority, due to suppression immediately after emergence, in early stages of development or, more rarely, absence since initiation (Zimmerman et al. 2013; Falcão et al. 2020; 2023). It is important to emphasize that these data of Tables 4 and 5 correspond only to the scope of ontogenetic studies of Detarioideae, therefore, they do not contemplate the complete morphological diversity of flowers in the subfamily, in addition to being subject to a bias in the choice of taxa by the authors.

Table 4: Omega-type taxa and floral reduction events. Sources: ⁽¹⁾ = Tucker 2000a; ⁽²⁾ = Tucker 2002a; ⁽³⁾ = Tucker 2002b; ⁽⁴⁾ = Tucker 2003c.

Taxa	S	P	Initiated P.	Stamens	Initiated st.	Staminods	Tribe
------	---	---	--------------	---------	---------------	-----------	-------

<i>Barnebydendron</i> ³ <i>riedelii</i> (no images)	5	3	5	10	10	0	Barnebydendreae
<i>Sindora klaineana</i> ⁴	5	1(4)	5	2	10	8	Detarieae
<i>Tessmannia africana</i> Harms ² (no images)	5	5	5	10	10	0	Detarieae
<i>Afzelia quanzensis</i> ³	5	1(4)	5	7	9	0	Afzelieae
<i>Macrolobium suaveolens</i>	5	1	3-5	3	5-7	0	Amherstieae
<i>Paramacrolobium</i> <i>coeruleum</i> ³ (no images)	5	1(4)	5	3	9	6	Amherstieae
<i>Neochevalierodendron</i> <i>stephanii</i> ³	5	3	5	10	10	0	Amherstieae
<i>Hymenostegia klainei</i> Pierre ex Pellegr ² (no images)	5	3(2)	5	10	10	0	Amherstieae
<i>Isoberlinia angolensis</i> (Welw ex Benth.) Hoyle & Brenan ²	5	5	5	10	10	0	Amherstieae
<i>Berlinia grandiflora</i> ³ (no images)	5	1(4)	5	10	10	0	Amherstieae
<i>Anthonothea crassifolia</i> ³ (no images)	5	1(4)	5	3	10	0	Amherstieae
<i>Microberlinia bisulcata</i> ² <i>Microberlinia brazzavilensis</i> ²	4-5	5	5	10	10	0	Amherstieae
<i>Brachystegia boehmii</i> Taub ¹ <i>Brachystegia tamarindoides</i> ¹	5	0	4	10	10	0	Amherstieae
<i>Julbernardia pellegriniana</i> Troupin ⁴	5	3(2)	5	10	10	0	Amherstieae
<i>Aphanocalyx djumaensis</i> ¹	1-3	1(0-2)	3	10	10	0	Amherstieae
<i>Bikinia durandii</i> ¹	1-5	1	3	10	10	0	Amherstieae
<i>Tetraberlinia tubmaniana</i> ³	5	3(2)	5	10	10	0	Amherstieae
<i>Gilbertiodendron klainei</i> ³	5	1(4)	5	3	10	0	Amherstieae

Note: in column P, the numbers of petalodides are indicated in parentheses.

Comparing the floral development of *M. suaveolens* with that of other omega-type taxa, it is possible to trace significant similarities, especially at the beginning of organogenesis, such as the shape of the meristem and bracteoles, the overlapping initiation of whorls, reduction events that involve the non-initiation of organs or organs that initiate but are later suppressed and/or reduced at anthesis (Tucker 2000a; 2002a; 2002b; 2003c). *M. suaveolens*, during organogenesis, especially resembles *Aphanocalyx djumaensis* (D.Wild) J.Léonard (Tucker 2000a). However, *Macrolobium* is not a genus closely related phylogenetically to any of the omega-group taxa (Bruneau et al. 2000; 2001; Estrella et al. 2017). The pronounced development of bracteoles soon after their emergence and its relationship with reduction events in Detarioideae has been previously discussed (Bull–Hereñu et al. 2022; Tucker 2000a), as well as other variations in organogenesis caused by changes in the shape or presence/absence of

bracteoles have already been identified for other groups of Leguminosae (Prenner 2004b). However, it is worth noting that these reduction events occur more frequently in the perianth and that androecium reduction events are possibly more frequently motivated by other causes, not related to the bracteole. In addition, some cases of extreme corolla reduction such as *Crudia*, *Copaifera* and *Colophospermum* also involve different ontogenetic processes. Finally, it is worth noting that despite the ontogenetic similarities between the different lineages of the omega group, they still retain numerous differences, evidencing the analogy of these processes. The main point in common is the pair of highly developed bracteoles, so that the reduction events, each in their own way, are possibly a consequence of this. Thus, the evolutionary parallelism of these taxa is also detectable at the level of floral development.

Table 5: Circular taxa and floral reduction (or rarely proliferation) events. Sources: ⁽¹⁾: Tucker 2000b; ⁽²⁾ = Tucker 2001a; ⁽³⁾ = Tucker 2001b; ⁽⁴⁾ = Pedersoli et al. 2010; ⁽⁵⁾ = Prenner and Cardoso 2017; ⁽⁶⁾ = Kochanovski et al. 2018; ⁽⁷⁾ = Citeli et al. in prep; ⁽⁸⁾ = Krüger et al. 1999.

Taxa	S	P	Initiated P	Stamens	Initiated st.	Staminods	Tribe
<i>Schotia afra</i> ³							
<i>Schotia brachypetala</i> ³	5	5	5	10	10	0	Schotieae
<i>Schotia latifolia</i> ³							
<i>Goniorrhachis marginata</i> ⁵	4	5	5	10	10	0	Barnebydendreae
<i>Colophospermum mopane</i> ⁸	2	0	0	20	20	0	Detarieae
<i>Copaifera langsdorffii</i> ⁴	5	0	5	10	10	0	Detarieae
<i>Hymenaea verrucosa</i> ⁶	5	3(2)	5	10	10	0	Detarieae
<i>Brodriguesia santosii</i> ⁷	5	5	5	10	10	0	Afzelieae
<i>Amherstia nobilis</i> ¹	5	3(2)	5	9	9	0	Amherstieae
<i>Tamarindus indica</i> ¹	5	3(2)	5	3	9	0	Amherstieae
<i>Brownea latifolia</i> ¹	5	5	5	10-11	10-11	0	Amherstieae
<i>Brownea longipedicellata</i>							
<i>Browneopsis macrofoliolata</i>	5	5	5	10-11	10-11	0	Amherstieae
<i>Heterostemon mimosoides</i>	5	3(2)	5	3	9	6	Amherstieae
<i>Paloue paraensis</i>	5	5	5	3	9	6	Amherstieae
<i>Paloue speciosa</i>							
<i>Crudia acuminata</i> Benth. ²	5	0	5	10	10	0	Amherstieae
<i>Cynometra webberi</i> Baker f. ³	5	5	5	10	10	0	Amherstieae

Note: In column P, the numbers of petaloids are indicated in parentheses. The taxa studied in this work are marked in gray.

Symmetry and floral architecture—There is a great variety in meristic and floral symmetry within the *Brownea* clade. Among the seven genera, actinomorphy predominates in two (*Brownea* and *Browneopsis*) and five genera are zygomorphic (*Brachycylis*, *Ecuadendron*, *Heterostemon*, *Macrolobium*, *Paloue*). Zygomorphy can be more or less intense and results only from the reduction and/or heteromorphy of the corolla parts and/or their positions at

anthesis, as well as from the reduction and/or heteromorphy of the stamens and staminodes. Therefore, two main questions arise: 1) what are the different floral developmental pathways that lead to these divergences; 2) which types of merism and symmetry are plesiomorphic for the clade and which are apomorphic.

In *Brownea longipedicellata* and *Browneopsis macrofoliolata*, simultaneous or nearly simultaneous initiation patterns predominate for almost all whorls, except the calyx (Table 2). Even when some organ initiates earlier than others in a whorl, all of them are later equalized. The flowers of *B. longipedicellata* present synorganization without fusion of the calyx and corolla, but rather through partial fusion of their bracteoles, which, as they are also exceptionally large in comparison to the size of the flower, surround the internal whorls and structure the pseudo-tubular architecture of the flower at anthesis, preventing the petals from opening completely. In certain species of *Brownea*, such as *B. macrophylla*, this structuring is less evident and the flowers are more open. In *Paloue speciosa*, the petals also remain nearly erect at anthesis, not opening to a patent or even reflexed shape present in *P. paraensis* and other species of the *Brownea* clade, although a pseudotube like that observed in *B. longipedicellata* is not present in *P. speciosa*, this last species, with also red flowers, presents an intermediate appearance in this direction. The formation of at least partially pseudotubule flowers has sometimes occurred independently in different subfamilies of Leguminosae, such as in Cercidoideae (*Lysiphyllum cunninghamii* (Benth.) de Wit), Detarioideae (genera *Barnebydendron*, *Schotia* and some species of *Eperua* and *Humboldtia*), Dialioideae (*Zenia*), Caesalpinioideae (*Colvillea*, some species of *Delonyx*, among others) and Papilionoideae (*Erythrina*, *Camptosema*, *Butea*, *Swainsona* Salisb., *Dahlstedtia*, among others), and is commonly associated with ornithophily, which can also be evidenced by another parallelism in most of these lineages, the red coloration of the flowers, which is otherwise uncommon in Leguminosae (Banks 1997; Falcão et al. 2023; Ferreira 2010; Franklin 1999; Jusaitis 1994; Kiepiel et al. 2022; Lewis et al. 2005; Missagia et al. 2014; Souza et al. 2024; Tandon et al. 2003; ter Steege et al. 2023; Warwick et al. 2008). It is important to emphasize that considerable erraticity was observed in the present work for organogenesis in *Browneopsis*. The correlation between actinomorphy and erraticity in organogenesis has already been considered by Tucker (1999).

Paloue paraensis and *Paloue speciosa* have zygomorphic symmetry, which is more subtle in *P. speciosa*. In both cases, the adaxial petal, narrower (*P. speciosa*) or wider (*P. paraensis*) than the others, the dorsoventral flattening of the flower (*P. paraensis*) and the heteromorphic androecium with three fertile stamens in the abaxial region, unidirectional initiation and intense heterochrony, contribute to this symmetry (Endress 2006; Tucker 1999). In *P. speciosa*, this zygomorphy is more subtle because the perianth remains slightly closed, with the calyx and corolla organs more erect, compared to *P. paraensis*. The genus *Paloue*, with a diverse floral morphology, presents cases of corolla reduction, possibly by similar pathways to that of *H. mimosoides*, in addition to different cases of androecium reduction, of flowers with three or nine fertile stamens (Redden et al. 2018). Future ontogenetic studies addressing the flowers of other taxa of the genus are necessary in order to compare the processes that generate these differences.

M. suaveolens presents corolla and androecium reduction pathways that are, in some ways, similar to those of *P. paraensis*, *P. speciosa* and *H. mimosoides*, all of which are marked by strong organ heterochrony. However, as mentioned in the previous section, the bracteoles of *M. suaveolens* have a disruptive influence on the subsequent development of the meristem, especially in relation to the perianth, which profoundly differentiates its floral development from all other species studied. The vast majority of taxa identified as being of the omega type have strongly zygomorphic flowers, with the exception of *Isobertinia* and *Tessmannia*, which have practically actinomorphic flowers (Table 4).

In the *Brownea* clade, zygomorphy predominates in the *Macrolobium*, *Heterostemon* and *Paloue* clade. In the *Brachycylix*, *Ecuadendron*, *Brownea* and *Browneopsis* clade, *Brachycylix* and *Ecuadendron* constitute the clade with zygomorphy, being more intense in *Brachycylix*. In relation to the studied taxa, we see that the cases of corolla zygomorphy involve, in some cases, heterochrony processes during intermediate and late stages of floral development, which suggests that this is possibly a derived characteristic in the evolution of these lineages (Tucker 2000c), specially in relation to the variation in size of the adaxial petal in *Paloue* and to the reduction to petaloids of the two abaxial petals of *Heterostemon*. The heteromorphic development of the adaxial petal of *Heterostemon* occurs from early stages of development, with this organ developing much later than the others and only surpassing them in size at intermediate stages of development. The suppression of the lateral and abaxial petals in *M. suaveolens* also occurs at early stages of development, leading to a strongly bilateral flower at anthesis. The zygomorphy of the androecium, on the other hand, is present from organogenesis, with unidirectional initiation, later accompanied by heterochrony. It is possible that the actinomorphic corolla is a more derived character of the clade, a possible synapomorphy of *Brownea* + *Browneopsis*, but the same cannot be said for the androecium. In order to better understand these issues, it is necessary to expand the ontogenetic studies of the clade, especially of the genera *Brachycylix* and *Ecuadendron*, not yet addressed, as well as of other floral morphotypes of *Paloue*, besides the necessity to carry out studies to reconstruct ancestral characters for the group.

Corolla and androecium—In Table 2, we see that all species analyzed present simultaneous initiation of the corolla, however, with different development rates soon after organogenesis. In general, the adaxial petal initially presents a slower elongation, but with subsequent equalization, and sometimes surpassing the others in length. *H. mimosoides* is an interesting example, because, initially, the abaxial petals are the largest, while the adaxial is the smallest (Fig. 7l–o) and, later, this situation is reversed, with the abaxial pair becoming petaloids. In *M. suaveolens*, similarly, although all five petals initiate simultaneously (Fig. 9j), the adaxial takes longer to elongate (Fig. 9l–n), although it is the only one to reach anthesis. This is a process common to several taxa of Detarioideae such as *Hymenaea* (Kochanovski et al. 2018), *Amherstia*, *Crudia*, *Schotia*, *Neochevalierodendron* (Tucker 2000b; 2001a; 2001b; 2002b) and *Brodriguesia* (Citeli et al. in prep), and is possibly due to the pressure exerted by S2+S5. After sepal elongation, the pressure reduces, which then creates space for the petal to develop. Some of the taxa in which this process occurs, such as *Schotia brachypetala* Sond., *Schotia afra* Thunb., *Schotia latifolia* Jacq. (Tucker 2001b) and *Neochevalierodendron stephanii* (Tucker 2002b), the author indicates that these taxa present corolla with unidirectional initiation, however, from the images of the works, it seems to be cases of simultaneous initiation, but with different development rates soon after the appearance of the organs.

The differential elongation of the corolla that is in fact reflected in the flower in anthesis occurs at later stages, through processes of heterochrony of the primordia, such as we see in *H. mimosoides*. The development of *M. suaveolens* involves processes of heterochrony not only between organs of the same whorl, but between whorls, and it is possible to observe the impact that the more accelerated elongation of the abaxial and lateral antesealous stamens has on the elongation of the petals (Fig. 9l–n).

In general, in legumes, initiation of a whorl begins after initiation of the previous one has finished, however, overlapping initiation of two or more whorls is not uncommon (Bruneau et al. 2014; Tucker 2003a). In *Paloue paraensis*, the two stamen whorls overlap (Fig. 11q–r), possibly due to the long plastochrony between the primordia of the antesealous whorl. This type of overlap is common in Papilionoideae, where unidirectional whorl initiation predominates (Tucker 1989). On the other hand, in *M. suaveolens*, as well as in *Brachystegia*,

Julbernardia, *Bikinia*, *Aphanocalyx*, among others of the omega group (Tucker 2000a; 2003c), the overlapping of the corolla with the androecium is probably caused by the impact of the pressure of the bracteoles on organogenesis, which shortens the available space in the floral meristem and delays the initiation of the outermost whorls (calyx and corolla), so that they overlap the following whorls (androecium and carpel) (Tucker 2000d; 2002a). Tucker (2000a; 2002a) related this overlapping phenomenon to the emergence of a meristematic ring in *Aphanocalyx djumaensis*, *Bikinia durandii* (F. Hallé & Normand) Wieringa, *Microberlinia bisulcata* A. Chev. and *Brachystegia boehmii* Taub. However, the structure that the author identifies as a meristematic ring is quite different from those that occur in *Colophospermum mopane* (Krüger et al. 1999) or in the tribe Swartzieae of Papilionoideae (Paulino et al. 2013; Tucker 1990; 2003a) and Mimoseae of Caesalpinioideae (Alvarado-Reyes et al. 2024; Paulino et al. 2016; Prenner 2011), in which the meristematic ring is related to the expansion of a region of the meristem in a ring shape, which often results in staminal proliferation, in addition to, more rarely, reductions in the corolla. Such an exception is the case of *Ateleia*, of the tribe Swartzieae, which presents a meristematic ring, but, in general, without staminal proliferation neither cases of reduction (Tucker 1990). In the case of *Aphanocalyx*, *Bikinia*, *Microberlinia* and *Brachystegia*, in which Tucker (2000a; 2002a) suggested the occurrence of a meristematic ring, there was, on the contrary, a restriction of space in the meristem with consequent overlapping of whorls and without alteration in the standard number of ten stamens. It is possible that, in these cases, the overlapping whorls, combined with the shortened plastochrony between the organs, as well as the delayed elongation of the outer whorls, generated a ring-shaped conformation around the carpel like a meristematic ring, however, with different causes and implications for floral development, compared to those we see in the tribes Swartzieae and Mimoseae. Thus, we do not consider the idea of these meristematic conformations in *Aphanocalyx*, *Brachystegia*, *Bikinia* and *Microberlinia* as a meristematic ring to be parsimonious.

A striking difference between *M. suaveolens* and several other omega-type taxa is the intense reduction of the androecium from the standard number of ten to three fertile stamens at anthesis, through a process like that which occurs in *Heterostemon mimosoides*, *Paloue paraensis* and *Paloue speciosa*, being marked by unidirectional initiation and strong heterochrony of stamen primordia. In all four cases, only three of the nine initiated stamens become fertile, however, *M. suaveolens* does not present any remaining staminodes in the flower at anthesis, unlike *P. paraensis*, *P. speciosa* and *H. mimosoides*, in which the other six primordia become visible staminodes at anthesis. In *H. mimosoides*, unlike *Paloue*, whose staminodes are only filiform and without any differentiated structures at their apices, the six staminodes of *Heterostemon* differentiate into antheroids and filament. It is worth noting that, among the nine stamens of *Heterostemon*, three of them (two outermost in the sheath and one of the innermost) have poorly developed anthers that are most likely infertile staminodes, and three of the central stamens that present the largest and most developed anthers are commonly understood as fertile stamens. The remaining three stamens have developed anthers, only of reduced size regarding the other three anthers. These three stamens are considered staminodes in the literature (Cowan 1978), but in-depth studies regarding their real fertility have not yet been carried out, so the real nature of these three intermediate organs is not entirely certain. *Paloue* presents two groups of species, one that includes those with a reduction of the androecium to three fertile stamens and six staminodes, and the other that includes, for the most part, those with nine fertile stamens (Redden et al. 2018). *Macrolobium* consistently presents only three fertile stamens among its species (Cowan 1953; 1978). It is possible that the reduction from ten to nine initiated stamens is a plesiomorphic characteristic, not only for the group that encompasses these three genera, but also for the Brownea clade, given the occurrence of this character state for *Brachycylix* and *Ecuadendron*, as well as in other genera

outside the clade, but closely related phylogenetically, such as *Amherstia* and *Tamarindus* (Tucker 2000b; 2002b). However, it is difficult to say whether the reduced state with three fertile stamens is a plesiomorphic character for the group of *Macrolobium*, *Paloue* and *Heterostemon*, synapomorphic for it, or whether it would consist of independent apomorphies for different lineages within this group, thus consisting of homoplasies. Considering this character as homoplastic, it would have arisen at least three times in the group: in the *Macrolobium* lineage, in *Heterostemon*, and in a lineage within *Paloue* with staminal reduction. On the other hand, considering it as synapomorphic for the trio of genera, or even plesiomorphic, there would be reversion in most of the *Paloue* group with nine fertile stamens, except in *Paloue emarginata* (R.S.Cowan) Redden, which is positioned in this group, but has only three fertile stamens (Redden et al. 2010; 2018). Thus, evolutionary reconstruction studies are necessary.

Given the above, considering the reduction from ten to nine stamens initiated in the meristem as a synapomorphic or even plesiomorphic character for the *Brownea* clade, this implies that there was a reversal of this character state in the clade that includes *Brownea* and *Browneopsis*, whose species generally have ten or more stamens. In the case of *B. longipedicellata* and *B. macrofoliolata*, the extra stamen always occurs in the adaxial region adjacent to the adaxial petal, so that a pair of stamens is always formed in this position, although they are slightly separated from each other (Fig. 3p, 6a–b). In *Brownea latifolia*, the position of the extra stamen varies (Tucker 2000b). In the case of taxa with a reduction from ten to nine stamens, the missing stamen always corresponds to this same position between the carpel and the adaxial petal, according to current ontogenetic data. More cases need to be evaluated, especially concerning *Brachycylis* and *Ecuadendron*, which have not been addressed ontogenetically, and other species of *Brownea* and *Browneopsis*, such as *Browneopsis disepala* (Little) Klitgaard, which presents staminal proliferation of up to 26 stamens (Klitgaard 1991), to better understand this process and why this specific region of the meristem appears to present greater lability, being more subject to changes in space availability. One possibility is the dorsoventrally flattened shape of the floral meristem, which, in this adaxial region (Fig. 3n–p, 6a–c), provides more space than that present in other species. Such space availability may facilitate the emergence of extra organs (Claßen-Bockhoff and Meyer 2016).

In taxa in which only nine stamens are initiated, the adaxial antepetalous region that would normally be occupied by a stamen becomes a region occupied by the expanding carpel, so that it is very close to the adaxial petal during elongation. We see this in *H. mimosoides*, *M. suaveolens*, *P. paraensis* and *P. speciosa* (Figs. 7s, 9s, 12b, 13s), as well as in *Amherstia nobilis* Wall., *Tamarindus indica* L. and *Azelia quanzensis* (Tucker 2000b; 2002b). Tucker (2002b) states that the *Gilbertiodendron* species analyzed ontogenetically had ten initiated stamens, but from the images it was only possible to observe nine, the missing one corresponding to the adaxial antepetalous region. In *Gilbertiodendron* species, there is also an approximation between the carpel and the adaxial petal. *Paramacrolobium coeruleum* has nine initiated stamens; however, it was not possible to verify this characteristic, since no images were available. In taxa not belonging to the *Brownea* clade in which this occurs, the adaxial petal involves, to a greater or lesser extent, the innermost whorls (stamens and carpel) as a whole (Tucker 2000b; 2002b). However, in *H. mimosoides*, *M. suaveolens*, *P. paraensis* and *P. speciosa*, we see that the adaxial petal only involves the carpel between the stamens during the late stages of development (Fig. 8d, 10c–d, 12g, 14d), remaining so until pre-anthesis. This is a characteristic not previously observed in other ontogenetic studies for Detarioideae, and is possibly a synapomorphy of the clade that includes *Heterostemon*, *Macrolobium* and *Paloue*, and does not occur in *Brownea* and *Browneopsis*, where there are 1–2 stamens between the carpel and the adaxial petal. In *Ecuadendron*, with five fertile stamens and four staminodes, it was observed that the adaxial petal surrounds the carpel and the stamens equally in the bud

(present study). This is a striking morphological characteristic, but it may go unnoticed because it is not visible at anthesis. However, observations regarding this character are still necessary in the genus *Brachycylis* and it is also necessary to carry out a more comprehensive survey to verify whether this characteristic does not actually occur in other closely related taxa of Detarioideae.

Hypanthium and nectariferous tissue—Most Detarioideae have hypanthiums, which are often internally lined with nectariferous parenchyma tissue (Bruneau et al. 2014; Cowan and Polhill 1981a). In general, the hypanthium is tubular in shape, but a wide morphological variety of this structure can be observed among the taxa studied (Fig. 2.6, 2.11, 2.16, 2.23, 2.30, 2.32).

Brownea longipedicellata and *Paloue speciosa* have a more typical tubular hypanthial structure, with nectariferous tissue concentrated in the basal region of the hypanthium, although that of *B. longipedicellata* is longer and more tapered (Fig. 15a–d, 15m–p). Both have flowers with a pseudotubular architecture and reddish colors, to a greater or lesser extent, which characterizes them as flowers adapted to ornithophily, a syndrome recorded for closely related taxa (Arroyo 1981). Furthermore, both species have an ovary inclined toward the adaxial side of the flower, which emerges through the opening of the staminal ring in *B. longipedicellata*, a strategy that possibly aims to facilitate pollinator access to the hypanthium.

The hypanthium of *Browneopsis macrofoliolata* is deep, but relatively narrow and laterally long, forming a crescent shape around the stipe. *Paloue paraensis* has the shallowest hypanthium among the six species, making it quite exposed to floral visitors, and its nectariferous tissue is relatively extensive compared to the others (Fig. 15i–l), producing abundant amounts of nectar, which is consistent with large pollinators with high energy needs such as bats (Arroyo 1981; Carvalho 1961; Rodrigues et al. personal observation). In *P. paraensis*, the ovary leans slightly to the adaxial side, as in *P. speciosa*, but the flower of *B. macrofoliolata* greatly restricts access to the hypanthium, narrowing the opening of the staminal ring around the ovary, so that only visitors such as bats and moths would be able to access it without damaging the flower, its likely pollinators (Knudsen and Klitgaard 1998).

Heterostemon mimosoides has nectar guides on the adaxial petal and receptacle, as well as a long and narrow hypanthium, while that of *Macrolobium suaveolens* is short and gibbose. However, both have the same strategy of restricting access to the hypanthium, in which the ovary lean to the abaxial side, next to the stamens, a common characteristic in Detarioideae (Cowan and Polhill 1981a). Both have different morphological characteristics of adaptation for pollination by Lepidoptera. The nectariferous tissue of *H. mimosoides* is concentrated at the base of its hypanthium, making access to the nectar very difficult for other types of visitors (Fig. 15e–h) and favoring Lepidoptera with their long proboscises. The claw of the adaxial petal of *M. suaveolens* is strongly auriculate, forming a kind of extremely narrow duct that leads to the hypanthium. There is a record of butterfly pollination for only one species of *Macrolobium* (van Dulmen 2001), but it is important to emphasize that the white petals of the genus may indicate a greater association with nocturnal pollinators such as moths.

It is important to emphasize that the anatomical studies carried out on the hypanthial structure of *B. longipedicellata*, *H. mimosoides*, *P. paraensis* and *P. speciosa* were carried out with flower buds close to anthesis, and there may be modifications in the nectariferous tissue of the flower in anthesis regarding to what is illustrated in Figure 15.

Final considerations—This study provides new data on floral development within the *Brownea* clade, a morphologically diverse group within Detarioideae that has previously received limited attention in terms of ontogenetic research. The findings contribute to discussions on the factors influencing inflorescence morphology and meristic and symmetry variation, from an evolutionary standpoint—not only for the clade itself but for the subfamily as a whole.

A key factor in the morphological differentiation of inflorescences is variation in plastochrony between meristems. This is evident when comparing *Paloue paraensis* and *Paloue speciosa*, or even *Brownea longipedicellata* and *Browneopsis macrofoliolata*. Notably, *B. longipedicellata* displays basipetal sequential development, which means apical meristems surpass basal ones in their rate of development during organogenesis, marking it as a distinctive morphological trait.

Bracteoles play a critical role in the evolutionary history of Detarioideae, particularly within the tribe Amherstieae. They not only contribute to the floral architecture at anthesis but also significantly influence floral development in several lineages. The pressure exerted by the bracteoles, combined with the unidirectional initiation of the androecium and heterochrony of floral organs, are primary factors behind meristic reduction. However, the exact cause of the non-initiation of the stamen opposite the adaxial petal in various lineages remains unclear. This reduction has led to a process of convergence between the adaxial petal and the carpel. In the *Heterostemon* + *Paloue* + *Macrolobium* clade, the adaxial petal laterally envelops the carpel through the space between the stamens and the carpel—a unique characteristic within Detarioideae, which may represent a synapomorphy for the clade.

Finally, the remarkable diversity of pollination strategies among the studied taxa is noteworthy. Even species adapted to the same type of pollinator, such as *Paloue paraensis* and *Browneopsis macrofoliolata*, exhibit distinct differences in their pollination mechanisms. The anatomical structure of the nectariferous tissue is similar across species, but the variation in the shape, depth, and width of the hypanthium, as well as the methods by which the pollinator accesses it, highlight the extensive array of adaptations present within the clade.

Acknowledgments

The authors are grateful to the Jardim Botânico do Rio de Janeiro (JBRJ), where most of the work was conducted; to the staff of the Laboratório de Botânica Estrutural (LBE), specially to Rogério Figueiredo; we would also like to thank the staff of the CBPF (Centro Brasileiro de Pesquisas Físicas), who provided the SEM and sputter coater, especially to Prof. Dr. André Rossi and to Ayla Poltronieri; the staff of CENANO (Centro de Caracterização em Nanotecnologia para Materiais e Catálise) of the INT (Instituto Nacional de Tecnologia), who provided the critical point apparatus and the sputter coater, especially to MSc. Alan Menezes; to the team at the laboratory of Prof. Dr. Simone de Pádua Teixeira, at FCFRP (Faculdade de Ciências Farmacêuticas de Ribeirão Preto) from USP (Universidade de São Paulo), where a large part of the anatomical study was conducted, with the provision of space, microtome and light microscope, with a special thanks to Dr. Viviane Leite and to Edimárcio da Silva Campos, for all their help and teachings; to Dr. Marcus Nadruz for allowing us to collect some of the specimens approached in this work in the arboretum of the JBRJ; to Dr. João Paulo Basso-Alves, Dr. Juliana Paulino and Dr. Juliana Santos Silva, for all the advices, teachings and theoretical support; to the PPGA of ENBT (Escola Nacional de Botânica Tropical), especially to Prof. Dr. Cássia Sakuragui, for the financial assistance that paid for the trip to FCFRP; to Dr. Rafael Barbosa Pinto, for the collection of *Macrolobium suaveolens*; to MSc. Anderson Alvarado who sent us photographs of several important manuscripts from the library of the New York Botanical Garden, as well as photographs of *Ecuadendron*. Funding: Ana Tereza Novaes is grateful to CAPES (Fundação Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) for the master's scholarship [process number 88887.823272/2023.00]; Marcus Falcão is grateful to FAPERJ (Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro) for the postdoc scholarship [E-26/200.124/2024]. Vidal Mansano is grateful to CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico) [303053/2018-6] and to FAPERJ [E-26-/203.007/2017].

Competing interests

On behalf of all authors, the corresponding author states that there is no conflict of interest.

References

- Alvarado-Reyes AJ, Paulino JV, Terra V, Mansano VF (2024) Floral ontogeny reveals potential synapomorphies for *Senegalia* sect. *Monacantha* pp (Leguminosae). *Journal of Plant Research* 137(5): 907-925.
- Arroyo MTK (1981) Breeding systems and pollination biology in Leguminosae. In: Polhill, R. M.; Raven, P. H. *Advances in Legume Systematics, Part 2*. Royal Botanical Gardens, Appezzato-da-Glória B, Carmello-Guerreiro SM (2006) *Anatomia Vegetal*. 2ed. UFV, Universidade Federal de Viçosa.
- Baker WJ et al. (2022) A comprehensive phylogenomic platform for exploring the angiosperm tree of life. *Systematic biology* 71(2): 301-319.
- Banks H (1997) The pollen of *Delonix* (Leguminosae: Caesalpinioideae: Caesalpinieae). *Kew Bulletin*, 417-434.
- Banks H, Klitgaard BB (2000) Palynological contribution to the systematics of detarioid legumes (Leguminosae: Caesalpinioideae). In: Herendeen, P. S. & Bruneau, A. *Advances in Legume Systematics, Part 9*. Royal Botanical Gardens, Kew, 79-106.
- Banks H, Rudall PJ (2016) Pollen structure and function in caesalpinoid legumes. *American Journal of Botany* 103(3): 423-436.
- Breteler FJ (1995) The boundary between Amherstieae and Detarieae (Caesalpinioideae). In: *Advances in Legume Systematics, Part 7*. Royal Botanical Garden, Kew, 53-62.
- Breteler FJ (2010) Revision of the African genus *Anthonotha* (Leguminosae, Caesalpinioideae). *Plant Ecology and Evolution* 143(1): 70-99.
- Bruneau A, Breteler FJ, Wieringa JJ, Gervais GF, Forest F (2000) Phylogenetic relationships in tribes Macroblobiae and Detariae as inferred from chloroplast trnL intron sequences. In: Herendeen, P. S., & Bruneau, A. *Advances in Legume Systematics, Part 9*. Royal Botanical Garden, Kew, 121-149.
- Bruneau A, Forest F, Herendeen PS, Klitgaard BB, Lewis GP (2001) Phylogenetic relationships in the Caesalpinioideae (Leguminosae) as inferred from chloroplast trnL intron sequences. *Systematic Botany* 26(3): 487-514.
- Bruneau A, Mercure M, Lewis GP, Herendeen PS (2008) Phylogenetic patterns and diversification in the caesalpinoid legumes. *Botany* 86: 697-718.
- Bruneau A, Klitgaard BB, Prenner G, Fougere-Danezan M, Tucker SC (2014) Floral evolution in the Detarieae (Leguminosae): phylogenetic evidence for labile floral development in an early-diverging legume lineage. *International Journal of Plant Sciences* 175(4): 392-417.
- Bull-Hereñu K et al. (2022) Mechanical forces in flower development. *Plants* 11: 661.
- Carvalho CT (1961) Sobre os hábitos alimentares de *Phillostomídeos* (Mammalia: Chiroptera). *Revista de Biologia Tropical* 9(1): 53-60.
- Claßen-Bockhoff R, Meyer C (2016) Space matters: meristem expansion triggers corona formation in *Passiflora*. *Annals of Botany* 117(2): 277-290.
- Cowan RS (1953) A taxonomic revision of the genus *Macrobium* (Leguminosae-Caesalpinioideae). *Memoirs of The New York Botanical Garden* 8(4): 257-342.
- Cowan RS (1975) *Brachycylix*, a new genus of tropical leguminosae (Caesalpinioideae). *Proceedings of the Koninklijke nederlandse akademie van wetenschappen* 78(1): 464-467.
- Cowan RS (1976) A taxonomic revision of the genus *Heterostemon* (Leguminosae-Caesalpinioideae). *Proceedings of the Koninklijke nederlandse akademie van wetenschappen* 79: 42-60.
- Cowan RS, Polhill RM (1981a) Detarieae DC. In: Polhill RM and Raven PH. *Advances in Legume Systematics, Part 1*. Royal Botanical Gardens, Kew, 117-134.

Cowan RS, Polhill RM (1981b) *Amherstieae* Benth. emend. J. Léon (1957). In: Polhill RM and Raven PH. *Advances in Legume Systematics, Part 1*. Royal Botanical Gardens, Kew, 135-142.

Dwyer JD (1951) The central American, west Indian, and South American species of *Copaifera* (Caesalpinioideae). *Brittonia* 7(3): 143-172.

Estrella M et al. (2018) A new phylogeny-based tribal classification of subfamily Detarioideae, an early branching clade of florally diverse tropical arborescent legumes. *Scientific Reports* 8(1): 1-14.

Endress PK (1990) Patterns of floral construction in ontogeny and phylogeny. *Biological Journal of Linnean Society* 39: 153-175.

Endress PK (2006) Angiosperm floral evolution: morphological development framework. *Advances in Botanical Research* 44: 1-61.

Falcão MJA, Paulino JV, Kochanowski FJ, Figueiredo RC, Basso-Alves JP, Mansano VF (2020) Development of inflorescences and flowers in Fabaceae subfamily Dialioideae: An evolutionary overview and complete ontogenetic series for *Apuleia* and *Martiodendron*. *Botanical Journal of the Linnean Society* 193: 19–46.

Falcão MJA (2023) *Sistemática, Biogeografia Histórica e Evolução em Dialioideae (Fabaceae)*. Tese de Doutorado. ENBT-JBRJ. Rio de Janeiro. 241pp.

Ferguson IK, Tucker SC (1994) *Advances in Legume Systematics, Part 6*. Royal Botanical Gardens, Kew.

Ferreira MH, Fagundes IB, da Paz Silva TF (2010) Floral nectar dynamics and spectrum of visitors in *Camptosema coriaceum* (Nees & Mart.) Benth. (Leguminosae, Papilionoideae): an ornithophilous plant robbed by bees in a rupestrian field from Chapada Diamantina, Brazil. *Biologia e Ecologia da Polinização*, 91.

Fleming TH, Geiselman C, Kress WJ (2009) The evolution of bat pollination: a phylogenetic perspective. *Annals of botany* 104(6): 1017-1043.

Franklin DC (1999) Opportunistic nectarivory: an annual dry season phenomenon among birds in monsoonal northern Australia. *Emu* 99(2): 135-141.

Gabriel BL (1982) *Biological Electron Microscopy*. Van Nostrand Reinhold Company, New York, 264p.

Gerrits PO, Eppinger B, Goor HV, Horobin RW (1991) A versatile, low toxicity glycol methacrylate embedding medium for use in biological research, and for recovered biomaterials prostheses. *Cells and Materials* 1: 189-198.

Gomez-Acevedo SL, Magallon S, Rico-Arce L (2007) Floral development in three species of *Acacia* (Leguminosae, Mimosoideae). *Australian Journal of Botany* 55: 30–41

Gomez-Acevedo SL (2021) Floral development of the myrmecophytic *Acacia cornigera* (Leguminosae). *Botanical Sciences* 99: 588–598.

Harris JG, Harris MW (1994) *Plant identification terminology: an illustrated glossary*. Spring Lake, Utah: Spring Lake Publishing. p. 198.

Johansen DA (1940) *Plant microtechnique*. Mc Graw Hill, New York.

Jusaitis M (1994) Floral development and breeding system of *Swainsona formosa* (Leguminosae). *HortScience* 29(2): 117-119.

Kiepiel I, Brown M, Johnson SD (2022) A generalized bird pollination system in *Schotia brachypetala* (Fabaceae). *Plant Biology* 24(5): 806-814.

Klitgaard BB (1991) Ecuadorian *Brownea* and *Browneopsis* (Leguminosae-Caesalpinioideae): taxonomy, palynology, and morphology. *Nordic Journal of Botany* 11(4): 433-449.

Knudsen JT, Klitgaard BB (1998) Floral scent and pollination in *Browneopsis disepala* (Leguminosae: Caesalpinioideae) in western Ecuador. *Brittonia* 50(2) 174-182.

Kochanowski FJ, Paulino JV, Teixeira SP, Tozzi AMGA, Mansano VF (2018) Floral development of *Hymenaea verrucosa*: an ontogenetic approach to the unusual flower of Fabaceae subfamily Detarioideae. *Botanical Journal of Linnean Society* 187(1): 46-58.

- Koenen EJ et al. (2020) Large-scale genomic sequence data resolve the deepest divergences in the legume phylogeny and support a near-simultaneous evolutionary origin of all six subfamilies. *New Phytologist*, 225(3), 1355-1369.
- Krüger H, Tiedt LR, Wessels DCJ (1999) Floral development in the legume tree *Colophospermum mopane*, Caesalpinioideae: Detarieae. *Botanical Journal of Linnean society* 131: 223-233.
- Legume Phylogeny Working Group (2017) A new subfamily classification of the Leguminosae based on a taxonomically comprehensive phylogeny. *Taxon* 66: 44-77.
- Léonard J (1957) Genera des Cynometreae et des Amherstieae africaines (Leguminosae–Caesalpinioideae). *Memoires Academie Royale de Belgique, Classe Sciences*, 30: 1–314.
- Lewis GP, Schrire B, Mackinder B, Lock M (2005) *Legumes of the World*. Royal Botanic Gardens. Kew, UK.
- Marazzi B, Endress PK (2008) Patterns and development of floral asymmetry in *Senna* (Leguminosae, Cassiinae). *American Journal of Botany* 95(1): 22-40.
- Missagia CC, Vercoza FC, Alves MAS (2014) Reproductive phenology and sharing of floral resource among hummingbirds (Trochilidae) in inflorescences of *Dahlstedtia pinnata* (Benth.) Malme. (Fabaceae) in the Atlantic forest. *Anais da Academia Brasileira de Ciências* 86: 1693-1702.
- Murphy B, Estrella M, Schley R, Forest F, Klitgaard B (2018) On the monophyly of *Macrolobium* Schreb., an ecologically diverse neotropical tree genus (Fabaceae-Detarioideae). *International Journal of Plant Sciences* 179(1): 75-86.
- Neill DA (1998) *Ecuadendron* (Fabaceae: Caesalpinioideae: Detarieae): a new arborescent genus from western Ecuador. *Novon* 45-49.
- O'brien TP, Feder N, McCully ME (1964) Polychromatic staining of plant cell walls by toluidine blue O. *Protoplasma* 59: 368-373.
- Ojeda DI et al. (2019) Phylogenomic analyses reveal an exceptionally high number of evolutionary shifts in a florally diverse clade of African legumes. *Molecular Phylogenetics and Evolution* 137: 156-167.
- Paulino JV, Mansano VF, Teixeira SP (2013) Elucidating the unusual floral features of *Swartzia dipetala* (Fabaceae). *Botanical Journal of the Linnean Society* 173(2): 303-320.
- Paulino JV, Mansano VF, Prenner G, Teixeira SP (2016) High developmental lability in the perianth of *Inga* (Fabales, Fabaceae): a Neotropical woody rosoid with gamopetalous corolla. *Botanical Journal of the Linnean Society* 183(1): 146-161.
- Pedersoli GD, Paulino JV, Leite VG, Teixeira SP (2010) Elucidating enigmatic floral issues in *Copaifera langsdorffii* Desf. (Leguminosae: Caesalpinioideae). *International Journal of Plant Sciences* 171(8): 834-846.
- Pedersoli GD, Teixeira SP (2016) Floral development of *Parkia multijuga* and *Stryphnodendron adstringens*, two andromonoecious mimosoid trees (Leguminosae). *International Journal of Plant Sciences* 177(1): 000.
- Plants of the World Online (2024) Facilitated by the Royal Botanical Gardens, Kew. <https://powo.science.kew.org>. Accessed 10 October 2024.
- Prenner G (2004a) Floral ontogeny in *Calliandra angustifolia* (Leguminosae: Mimosoideae: Ingeae) and its systematics implications. *International Journal of Plant sciences* 165(3): 417-426.
- Prenner G (2004b) New aspects in floral development in Papilionoideae: initiated but suppressed bracteoles and variable initiation of sepals. *Annals of Botany* 93: 537-545.
- Prenner G, Klitgaard BB (2008) Towards unlocking the deep nodes of Leguminosae: floral development and morphology of the enigmatic *Duparquetia orchidacea* (Leguminosae, Caesalpinioideae). *American Journal of Botany* 95(11): 1349-1365.

- Prenner G (2011) Floral ontogeny of *Acacia celastrifolia*: an enigmatic mimosoid legume with pronounced polyandry and multiple carpels. *Flowers on the Tree of Life* 1: 256-278.
- Prenner G (2013) Papilionoid inflorescences revisited (Leguminosae-Papilionoideae). *Annals of Botany* 112(8): 1567-1576.
- Prenner G, Cardoso C (2017) Flower development of *Goniorrhachis marginata* reveals new insights into the evolution of florally diverse detarioid legumes. *Annals of Botany* 119(3): 417-432.
- Ramirez-Domenech JI & Tucker SC (1990) Comparative ontogeny of the perianth in Mimosoideae Legumes. *American Journal of Botany* 77: 624-635.
- Redden KM, Herendeen PS (2006) Morphology and phylogenetic analysis of *Paloue* and related genera in the *Brownea* clade (Detarieae, Caesalpinioideae). *International Journal of Plant Sciences* 167(6): 1229-1246.
- Redden KM, Herendeen PS, Wurdack KJ, Bruneau A (2010) Phylogenetic relationships of the northeastern South American *Brownea* clade of tribe Detarieae (Leguminosae: Caesalpinioideae) based on morphology and molecular data. *Systematic botany* 35(3): 524-533.
- Redden KM, Herendeen PS, Lewis GP (2018) Understanding *Paloue* (Leguminosae: Detarioideae): revision of a predominantly Guiana Shield endemic. *Smithsonian Contributions to Botany* 109: 1-44.
- Radosavljevic A (2019) The rise of *Cynometra* (Leguminosae) and the fall of *Maniltoa*: a generic re-circumscription and the addition of 4 new species. *PhytoKeys* 127: 1.
- Ronse de Craene LP (2010) *Floral diagrams: an aid to understanding flower morphology and evolution*. Cambridge, Royal Botanical Garden Edinburgh.
- Ronse de Craene LP (2016) Meristic changes in flowering plants: how flowers play with numbers. *Flora-Morphology, Distribution, Functional Ecology of Plants* 221: 22-37.
- Ronse de Craene LP (2010) *Floral diagrams*. Cambridge: UK: Cambridge University Press.
- Schley RJ, de la Estrella M, Pérez-Escobar OA, Bruneau A, Barraclough T, Forest F, Klitgaard B (2018) Is Amazonia a ‘museum’ for Neotropical trees? The evolution of the *Brownea* clade. *Molecular Phylogenetics and Evolution* 126: 279-292.
- Schley RJ, Pennington RT, Pérez-Escobar OA, Helmstetter AJ, de la Estrella M, Larridon I, Alberto I, Kikuchi BS, Barraclough T, Forest F & Klitgaard B (2020) Introgression across evolutionary scales suggests reticulation contributes to Amazonian tree diversity. *Molecular Ecology* 29: 4170-4185.
- Souza LGMP, Falcão MJA, Basso-Alves JP, Mansano VF (2024) Floral developmental insights into two species of *Erythrina* (Fabaceae: Papilionoideae: Phaseoleae) pollinated by humming birds and passerines. *Journal of Plant Research*.
- Tandon R, Shivanna KR, Mohan Ram HY (2003) Reproductive biology of *Butea monosperma* (Fabaceae). *Annals of Botany* 92(5): 715-723.
- ter Steege H et al. (2013) Hyperdominance in the Amazonian tree flora. *Science* 342: 1243092.
- ter Steege H et al. (2023) Molecular phylogeny and evolution of inflorescence types in *Eperua*. *American journal of botany* 110(10): e16229.
- Tolke ED, Capelli NV, Pastori T, Alencar AC, Cole TCH, Demarco D (2019) Diversity in floral glands and their secretions in pollinator attraction. In: Merillon JM & Ramawat K (eds) *Co-evolution of secondary metabolites Reference Series in Phytochemistry*. Springer, Cham. https://doi.org/10.1007/978-3-319-76887-8_48-1.
- Tucker SC (1984). Unidirectional organ initiation in leguminous flowers. *American Journal of Botany* 71(8): 1139-1148.
- Tucker SC (1987) Floral initiation and development in legumes. In: Stirton CH, ed. *Advances in Legume Systematics, Part 3*. Royal Botanical Gardens, Kew, 183-239.

- Tucker SC (1988) Loss versus suppression of floral organs. In: Leins P, Tucker SC & Endress PK. Aspects of floral development, 69–82.
- Tucker SC (1989a) Evolutionary implications of floral ontogeny in legumes. In: Stirton CH & Zarucchi JL, ed. Advances in legume biology, Missouri Botanical Garden Monographs in Systematic Botany 59–76.
- Tucker SC (1989b) Overlapping organ initiation and common primordia in flowers of *Pisum sativum* (Leguminosae: Papilionoideae). *American Journal of Botany* 76(5): 714–729.
- Tucker SC (1990) Loss of floral organs in *Ateleia* (Leguminosae: Papilionoideae: Sophoreae). *American Journal of Botany* 77(6): 750–761.
- Tucker SC (1993) Floral ontogeny in Sophoreae (Leguminosae: Papilionoideae). 1. *Myroxylon* (*Myroxylon* group) and *Castanospermum* (*Angylocalyx* group). *American Journal of Botany* 80: 65–75.
- Tucker SC (1997) Comparative floral development and evolution in tribe Caesalpinieae (Leguminosae: Caesalpinioideae). *Haematoxylum*. *American Journal of Botany* 84(8): 1047–1063.
- Tucker SC (1998) Floral ontogeny in legume genera *Petalostylis*, *Labichea*, and *Dialium* (Caesalpinioideae: Cassieae), a series in floral reduction. *American Journal of Botany* 85: 184–208.
- Tucker SC (1999) Evolutionary lability of symmetry in early floral development. *International Journal of Plant Sciences* 160(S6): S25–S39.
- Tucker SC (2000a) Evolutionary loss of sepals and/or petals in detarioid legume taxa *Aphanocalyx*, *Brachystegia*, and *Monopetalanthus* (Leguminosae: Caesalpinioideae). *American Journal of Botany* 87(5): 608–624.
- Tucker SC (2000b) Floral development in tribe Detarieae (Leguminosae: Caesalpinioideae): *Amherstia*, *Brownea*, and *Tamarindus*. *American Journal of Botany* 87(10): 1385–1407.
- Tucker SC (2000c) Organ loss in Detarioid and other leguminous flowers, and the possibility of saltatory evolution. In: Herendeen PS & Bruneau A. Advances in Legume Systematics, Part 9. Royal Botanical Gardens, Kew, 107–120.
- Tucker SC (2001a) The ontogenetic basis for missing petals in *Crudia* (Leguminosae: Caesalpinioideae: Detarieae). *International Journal of Plant Sciences* 162(1): 83–89.
- Tucker SC (2002a) Comparative floral ontogeny in Detarieae (Leguminosae: Caesalpinioideae). 1. Radially symmetrical taxa lacking organ suppression. *American Journal of Botany*. 89(6): 875–887.
- Tucker SC (2002b) Comparative floral ontogeny in Detarieae (Leguminosae: Caesalpinioideae). 2. Zygomorphic taxa with petal and stamen suppression. *American Journal of Botany*. 89(6): 888–907.
- Tucker SC (2003a) Floral ontogeny in *Swartzia* (Leguminosae: Papilionoideae: Swartzieae): distribution and role of the ring meristem. *American Journal of Botany* 90(9): 1271–1292.
- Tucker SC (2003b) Floral development in legumes. *Plant Physiology* 131: 911–926.
- Tucker SC (2003c) Comparative floral ontogeny in Detarieae (Leguminosae: Caesalpinioideae). III. Adaxially initiated whorls in *Julbernardia* and *Sindora*. *International Journal of Plant Sciences* 164(2): 275–286.
- van Dulmen A (2001) Pollination and phenology of flowers in the canopy of two contrasting rain forest types in Amazonia, Colombia. *Plant Ecology* 153: 73–85.
- Warwick MC, Lewis GP, Lima HD (2008) A reappraisal of *Barnebydendron* (Leguminosae: Caesalpinioideae: Detarieae). *Kew Bulletin* 63: 143–149.
- Zimmerman E, Prenner G, Bruneau A (2013) Floral ontogeny in *Dialiinae* (Caesalpinioideae: Cassieae), a study in organ loss and instability. *South African Journal of Botany* 89: 188–209.

Zimmerman E, Herendeen PS, Lewis GP, Bruneau A (2017) Floral evolution and phylogeny of the Dialioideae, a diverse subfamily of tropical legumes. *American Journal of Botany* 104: 1019-1041.

Figure legends

Fig. 1 Flowers and inflorescences of the studied genera: **a–b** Inflorescences of *Brownea longipedicellata*. **c–d** Inflorescence and flower of *Browneopsis macrofoliolata*. **e–f** Inflorescence and flower of *Paloue speciosa*. **g–h** Inflorescence and flower of *Paloue paraensis*. **i–j** Inflorescence and flower of *Macrolobium latifolium* (a morphologically similar species, included here for illustrative purposes). **k–l** Flowers of *Heterostemon mimosoides*. **m** Floral diagram of *B. longipedicellata* e *B. macrofoliolata*. **n** Floral diagram of *M. suaveolens*. **o** Floral diagram of *H. mimosoides*. **p** Floral diagram of *P. paraensis* e *P. speciosa*

Fig. 2 Illustration of inflorescences and flowers of the studied species. **1–6** *Browneopsis macrofoliolata*. **7–11** *Brownea longipedicellata*. **12–16** *Macrolobium suaveolens*. **17–23** *Heterostemon mimosoides*. **24–27** *Paloue speciosa*. **28–32** *Paloue paraensis*. **1, 7, 12, 17, 24, 28** Inflorescence. **2, 8, 13, 18, 25, 29** Polar view of the flower. **4, 9, 21** Detail of staminal sheath. **5, 10, 15, 31** Detail of the anther. **6, 11, 16, 23, 27, 32** Detail of the longitudinally sectioned hypanthium with stipe adnate to its adaxial wall. **3** Lateral view of the flower. **14** Lateral detailed view of the flower with reduced sepals. **19** Abaxial view of the flower **20** Detail of the two petaloids. **22** Detail of anther, medium antheroid (middle one) and small antheroid (left one). **26, 30** Detailed polar view of the hypanthium aperture and staminal sheath showing staminodes. Scale bars: **1** = 2 cm; **2** = 1.2 cm; **3, 18, 29** = 1.5 cm; **4, 5, 11** = 3.5 mm; **6, 30** = 8 mm; **7, 17, 32** = 1 cm; **8, 24** = 5 mm; **9, 27, 31** = 4 mm; **10, 15** = 0.6 mm; **12** = 2.5 mm; **13, 22** = 2 mm; **14, 16** = 1 mm; **19** = 9 mm; **20, 26** = 3 mm; **21, 23** = 7 mm; **22** = 2 mm; **25** = 6 mm; **28** = 1.8 cm

Fig. 3 Development of flowers and inflorescences of *Brownea longipedicellata* (SEM). All type 1 bracts and some type 2 bracts were removed in **a**. All bracts were removed in **b** and **d**. All bracts and bracteoles were removed in **c** and **e–t**. **a** Bracts subtending undifferentiated meristems and bracteole organogenesis. **b** Floral meristems at very similar stages and surrounded by bracteoles. **c** End of organogenesis, with apical buds more advanced in floral development than basal ones. **d** Lateral view of two meristems surrounded by bracteoles. **e** Initiation of the first median abaxial sepal. **f** Protuberance formed by the pressure of the bracteoles on the adaxial region (arrow). **g** S1 and S2. **h** The first four sepals and the possible initiation of S5 (arrow). **i** S2 and S5 fused and petals evident (except adaxial). **j** Carpel initiation (S1, S2 and S3 removed). **k** Petals and carpel more elongated (S1 removed). **l** Petals with different development rates and primordia of antesealous (asterisk) stamens (S1 and S2 removed). **m** Sepals covering the bud. **n** Carpel begins to show in its adaxial portion the beginning of the formation of the carpel cleft. **o** Dorsoventrally flattened flower with petals and stamens covering the innermost part. **p** Showing only carpel, antesealous stamens and antepetalous, drawing attention to the pair of antepetalous opposite the adaxial petal that was removed and to the carpel cleft in formation. **q** Petals differentiating and carpel apex tapering. **r** Carpel cleft almost closed and stamens beginning to differentiate. **s–t** Stamens differentiated into anther and filament. **t** Petal base narrowing. Scale bars: **a, e–l, o–p** = 50 µm; **b–d, m–n, q–r, t** = 100 µm; **c, s** = 200 µm

Fig. 4 Differentiation and details of floral structures and inflorescences of *Brownea longipedicellata* (SEM). **a** Adaxial side of the bud with sepals and petals removed to show differentiated stamens and carpels and “extra” stamen. **b** Detail of the base of two fused

filaments (arrow). **c** Detail of the developing hypanthium and stipe of the ovary adnate to the adaxial wall. **d** Detail of the stigma differentiating. **e** Inflorescence with oblong bracts and flower buds in late stages. **f** Inflorescence showing the elongated pedicel of the buds and an entire flower bud to show the fit that forms between them. **g** All organs of the bud were removed, except the carpel, showing its differentiation into the ovary, stipe adnate to the hypanthium (arrow), style curved to the abaxial side, and stigma. **h** Petaloid stamen removed from a flower in preanthesis. Scale bars: **d** = 50 μ m; **b–c** = 100 μ m; **a, g–h** = 500 μ m; **e–f** = 1 mm.

Fig. 5 Development of flowers and inflorescences of *Browneopsis macrofoliolata* (SEM). Bracts were completely removed in **b–c** and **e–p** and partially removed in **a** and **d**. Bracteoles were completely removed in **b–c** and **g–p**, and partially removed in **a** and **d**. **a–c** Lateral view of inflorescences, from youngest to oldest. **d** Detail of the apex of the same inflorescence as in **a**. **e** Floral meristem with elongating bracteoles. **f** Initiation of S1. **g** Protuberance in the adaxial position formed by the pressure of bracts and bracteoles (arrow). **h** Initiation of S2. **i** Polar view slightly displaced to the abaxial side, showing S1, S2, S4 and possibly S3 (arrow). **j** Dorsoventrally flattened meristem, S5 initiating. **k** Slightly lateralized polar view showing the 5 initiated petals, but with different developments, and S5 not being visible (arrow). **l** Same bud as in **k**, but from another angle, showing that S4 is not visible (arrow) (S2 partially cut). **m** Bud with all sepals and petals present. **n** Initiated carpel and signs of antesepalous stamens (asterisk). **o** Antesepalous stamens emerging (asterisk). **p** Antepetalous abaxial stamens emerging (asterisk). Scale bars: **g, j, l–m, o** = 50 μ m; **e–f, h–i, k, n, p** = 100 μ m; **d** = 200 μ m; **a–c** = 500 μ m

Fig. 6 Development and details of floral structures of *Browneopsis macrofoliolata* (SEM). Bracteae and bracteoles removed in **a–l**. Polar view of floral buds in **a–f, i** and **l**, with the abaxial side down. Lateral view of buds and floral structures in **g–h, j–k**. **a** All antepetalous stamens initiated, highlighting the two opposite the adaxial petal (asterisk). **b** Bud with all floral organs initiated and adaxial petal differentiating. **c** Dorsoventrally flattened bud and beginning of carpelar cleft formation. **d** Floral buds at very similar stages of elongation. **e** Fusion of the calyx base and elongating organs. **f** Dorsoventrally flattened bud with 10 stamens instead of 11. **g** Organs differentiating. **h** Sepals and petals removed, stamens well differentiated and carpel with tapered and slightly curved apex. **i** Bud flattened dorsoventrally, petals and sepals removed, stamens differentiated and of different sizes. **j** Carpel differentiated with an open ovary showing ovules, style elongated and curving towards the abaxial side and differentiated stigma. **k** Detail of the base of the filaments merging (arrow). **l** All organs removed to show the hypanthium forming and the stipe adnate to the adaxial wall. Scale bars: **a** = 50 μ m; **b–c, e–g** = 100 μ m; **k** = 200 μ m; **d, i–j, l** = 500 μ m

Fig. 7 Development of inflorescence and flowers of *Heterostemon mimosoides* (SEM). Bracts were removed totally or partially in **a–t**. Bracteoles were removed in **e–t**. Sepals were removed in **k–t**. Petals were removed totally or partially in **q–r** and **t**. Polar view of flower buds in **d–t**. **a** Inflorescence showing different stages of meristem development (asterisk) and flower buds. **b** Meristematic apex of the inflorescence. **c** Lateral view of a meristem with two elongating bracteoles. **d** Bracteoles covering the meristem. **e** S1 emerging and highlighting the bulge in the median adaxial position (arrow). **f** S2 emerging and highlighting the bulge in the median adaxial position (arrow). **g** S3 emerging. **h** S4 emerging. **i** S5 emerging. **j** Complete calyx and highlighting S2 and S5 fused. **k** Petals in evidence and the carpel emerging in the center. **l** Petals with different development rates. **m** Abaxial and lateral antesepalous stamens emerging (asterisk) and adaxial petal barely visible. **n** Abaxial and lateral antesepalous stamens visible

and adaxial ones emerging (asterisk). **o** Adaxial antesepalous stamen visible. **p** Petals differentiating and beginning of carpel cleft formation. **q** Antesepalous stamens differentiating and antepetalous already emerged (arrow). **r** Lateral antepetalous stamen appearing (asterisk), adaxial antesepalous stamen smaller. **s** Lateral petals larger, adaxial petal surrounding the carpel. **t** Lateral and abaxial antesepalous stamens and petals removed to show antepetalous stamens and adaxial antesepalous stamens. Scale bars: **b–l** = 50 μ m; **m–s** = 100 μ m; **a, t** = 200 μ m

Fig. 8 Development of inflorescence and flowers and details of floral structures of *Heterostemon mimosoides* (SEM). Bracts removed in **a–h**. Bracteoles and sepals removed in **a–e** and **g–h**; Petals completely or partially removed in **a–e** and **g–h**. Lateral view of buds or floral structures in **a–f** and **h**. **a–b** Adaxial side of two different stages, highlighting the lateral and abaxial antesepalous stamens that are much more developed than the others, in addition to the apex of the carpel curved toward the abaxial side. **c** Abaxial side showing the abaxial petaloids. **d** Abaxial side of the detail of the carpel being enveloped by the adaxial petal. **e** Formation of the monadelphous sheath (arrow) with heteromorphic stamens and a petaloid. **f** Entire bud with partially fused bracteoles. **g** Polar view of the inflorescence showing different stages of floral development. **h** Detail of the style forming a spiral and differentiated stigma. Scale bars: **a, d** = 200 μ m; **b–c, e–h** = 500 μ m

Fig. 9 Development of inflorescences and flowers of *Macrolobium suaveolens* (SEM). Bracts were removed in whole or in part in **a–e** and **g–t**. Bracteoles were removed in whole or in part in **a–b** and **g–t**. Lateral view of inflorescence and flower bud in **a, e–f** and **n–q**. Polar view of inflorescence and flower buds in **b–c, h–m** and **r–t**. Abaxial side facing downward in **d** and **g–t**. **a–b** Inflorescences at different angles with several buds at different stages of development. **c** Meristematic apex of inflorescence. **d** Meristem with two developing bracteoles. **e** One bracteole was removed to show the size ratio of the bracteole to the meristem. **f** Bract with bud with closed bracteoles. **g** Protuberance formed by the pressure of the bracteoles (arrow). **h** S1 emerging. **i** S2, S3 and S4 emerging. **j** Petals (asterisks), carpel and abaxial antesepalous stamen (arrow) emerging. **k** Abaxial and lateral antesepalous stamens. **l–m** Abaxial and lateral antesepalous stamens more developed than petals (asterisks) and S2 is barely visible (arrow). **n** Petals visible and highlight on the unevenness of the bud. **o** Highlight on S5 (asterisk), adaxial, lateral and one abaxial petals (white arrow) and one abaxial antepetalous stamen (black arrow). **p** Adaxial petal developing and antepetalous stamen primordia (asterisk). **q** Adaxial side, only one side with petal and stamen primordia, in addition to carpel forming carpel cleft. **r** Adaxial petal, carpel and one lateral stamen removed to show undeveloped primordia of dubious nature (asterisk). **s** Formation of carpel cleft and primordia of one lateral petal and antepetalous stamen (asterisk). **t** Stamens, sepals and adaxial petal differentiated, and carpel apex slightly curved. Scale bars: **d–f, h–p, r** = 50 μ m; **c, q, s–t** = 100 μ m; **g** = 200 μ m; **b** = 500 μ m; **a** = 1 mm

Fig. 10 Floral development and details of structures of *Macrolobium suaveolens* (SEM). Bracts completely removed and bracteoles completely or partially removed in **a–g**, Sepals completely or partially removed in **b** and **e–g**. Polar view of flower buds in **a–b** and **d**, with abaxial side facing downwards. Lateral view of flower buds in **c** and **e–h**. **a** Inner whorls larger than sepals and formation of the style. **b** Two stamens and two sepals removed to show the remains of undeveloped primordia (arrow). **c** Adaxial petal covering the carpel and a fourth stamen that developed on the right side. **d** Adaxial petal embracing the carpel from above. **e** Detail of the surface of a differentiated anther. **f** Detail of the carpel with marginal trichomes, style curved toward the abaxial side, other flower structures removed (except one filament). **g** Longitudinal

section of a bud showing the formation of the hypanthium (arrow) and an ovule in the ovary (asterisk). **h** Detail of stomata (arrow) on the inner surface of the bracteole. Scale bars: **h** = 10 μm ; **a–b, d–f** = 200 μm ; **c, g** = 500 μm

Fig. 11 Development of inflorescences and flowers of *Paloue paraensis* (SEM). Bracts were removed totally or partially in **a–t**. Bracteoles were removed totally or partially in **a–b** and **g–t**. Sepals were removed totally or partially in **q–t**. Polar view of inflorescences in Fig. **a–c** and of meristems/flower buds in **d–t**. **a–b** Different inflorescences showing the proximity of numerous flower buds (asterisk) to each other. **c** Detail of the inflorescence apex with bracts and floral meristems differentiating. **d** Meristem with one bracteole formed and another forming (arrow). **e** Meristem with two bracteoles formed. **f** Bracteoles covering the meristem, except for the gap in the median adaxial region (arrow). **g** S1 emerging. **h** Protuberance formed by the pressure of the bracteoles (arrow). **i** S2 initiated. **j** Initiation of S3 and S4 simultaneously (arrow). **k** Initiation of S5 fused to S2. **l** Petals initiating (asterisk). **m** Carpel initiating (asterisk). **n** Initiation of lateral antesealous stamens (arrow). **o** Calyx, corolla, and carpel elongating and initiation of lateral antesealous stamen. **p** Bud with initiated abaxial and lateral antesealous stamens. **q** Initiation of antepetalous abaxial stamens (asterisk), poorly developed adaxial petal. **r** Organs elongating. **s** Bud with artifacts that hinder visualization, but an antesealous adaxial stamen can be seen. **t** Organ differentiation and carpel cleft forming. Scale bars: **d–e, g–i, k** = 50 μm ; **c, f, j, l–t** = 100 μm ; **a–b** = 500 μm

Fig. 12 Development of flowers and inflorescences and details of floral structures of *Paloue paraensis* (SEM). Bracts, bracteoles, and sepals completely or partially removed in **a–h**. Petals completely or partially removed in **a, c, e–g**. Polar view of flower buds in **a–b, d–g**, with the abaxial side facing downwards, and of the inflorescence in **h**. **a** Carpel and two antesealous stamens removed to show traces of poorly developed stamens and the already enlarged hypanthium. **b** Differentiated petals and adaxial petal “touching” the carpel. **c** Adaxial lateral view of a bud with differentiated stamens and style curving towards the abaxial side. **d** Four imbricated petals, one of the lateral ones has been removed and the innermost petal is the adaxial one, enveloping the carpel. **e** Lateral stamen removed to show traces of poorly developed stamens (arrow) and the hypanthium forming. **f** Detail of staminodes. **g** Vestigial stamens (arrow) and adaxial petal surrounding the carpel. **h** Inflorescence with numerous stages of floral development and spiral arrangement of buds (asterisk). Scale bars: **b, f** = 100 μm ; **a, c–d, g** = 200 μm ; **e, h** = 500 μm

Fig. 13 Development of inflorescences and flowers of *Paloue speciosa* (SEM). Bracts were removed in whole or in part. Bracteoles were removed in whole or in part in **a–b** and **g–t**. Sepals were removed in whole or in part in **l** and **n–t**. Polar view of inflorescences in **a–c** and of meristems/flower buds in **d–e** and **g–s**, with abaxial side facing downwards. **a** Inflorescence with different stages of floral development (asterisk). **b** Detail of inflorescence of **a**. **c** Inflorescence apex with elongating bracts. **d** Undifferentiated meristem with a pair of bracteoles. **e** Bracteoles covering the meristem and leaving a gap in the abaxial position (arrow). **f** Closed flower bud with overlapping bracteoles. **g** Initiation of S1. **h** S2 initiated, and S3 and S4 initiating (arrows). **i** Initiation of S3 and S4. **j** S5 initiating (arrow). **k** Petals initiating (asterisk) and S5 fused to S2. **l** Carpel initiating (asterisk). **m** Calyx, corolla, and carpel elongating. **n** initiation of abaxial and lateral antesealous stamens. **o** Initiation of adaxial antesealous stamens (asterisk). **p** Petals removed to show stamens, and carpel forming carpel cleft. **q** Petals differentiating. **r** one lateral antepetalous stamen visible (arrow). **s** Organs differentiating. **t** Adaxial lateral view of bud without petals showing differentiating stamens

and four poorly developed staminodes, including two antepetalous (asterisk). Scale bars: **d, g–j, n–p** = 50 μm ; **c, e–f, k–m, q–t** = 100 μm ; **a–b** = 500 μm

Fig. 14 Final stages of floral development and detail of structures of *Paloue speciosa* (SEM). Bracts, bracteoles, and sepals removed. Petals completely or partially removed in **b–h**. Polar view of flower buds in **a–b, d** and **h**, with the abaxial side facing downwards. Lateral view of flower buds and structures in **c, e–g**. **a** Stamens differentiating into anther and filament. **b** Lateral stamens removed to show staminodes (arrow). **c** Detail of ovules. **d** Adaxial petal surrounding the carpel and style curving towards the abaxial side. **e** Abaxial side of bud showing developed stamens. **f** Lateral stamen removed to show style curving. **g** Detail of style forming spiral and differentiated stigma. **h** Whorls removed to show hypanthium and stipe adnate to the adaxial wall. Scale bars: **a** = 100 μm ; **b–d** = 200 μm ; **e–h** = 500 μm

Fig. 15 Anatomical structure of the nectariferous tissue of the hypanthium of *B. longipedicellata*, *H. mimosoides*, *P. paraensis* and *P. speciosa*. **a–c, e–f, i–k, m–o, q, s–t** are taken from light microscopy. Fig. **d, g–h, l, p** and **r** are scanning electron micrographs. *B. longipedicellata* in **a–d**. **a** General view of the hypanthial region. **b** Nectariferous tissue with vascular bundles. **c** Detail of the nectariferous parenchyma. **d** Stomata on the surface of the hypanthium (arrow). *H. mimosoides* in **e–h**. **e** General view of the hypanthial region with a highlight to the presence of idioblasts (arrow). **f** Detail of the nectariferous parenchyma and epidermis. **g** Stomata on the surface of the hypanthium. **h** Detail of the stoma. *P. paraensis* in **i–l**. **i** General view of the hypanthium region with a highlight to the vascular bundles (arrow). **j** Color difference between the nectariferous parenchyma and the subnectariferous parenchyma. **k** Detail of the nectariferous parenchyma and epidermis. **l** Stomata on the surface of the hypanthium (arrow). *P. speciosa* in **m–p**. **m** General view of the hypanthium region (note that the base of the anther invades the lumen of the hypanthium). **n** Detail of the nectariferous tissue. **o** Color difference between the nectariferous parenchyma and the subnectariferous parenchyma. **p** Stomata on the surface of the hypanthium, some of them with unidentified substances at the operculum (arrow). **q** Detail of the idioblasts of *B. longipedicellata*. **r** Detail of the modified trichomes of *B. longipedicellata*. **s** Detail of the idioblasts of *P. paraensis*. **t** Detail of the idioblasts of *P. speciosa*. Scale bars: **h** = 10 μm ; **d, l, p** = 20 μm ; **b–c, f, k, m–o, q, t** = 50 μm ; **a, e, j, r, s** = 100 μm ; **i** = 500 μm