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ORIGINAL ARTICLE

Floral morphology and development in *Tachigali* (Caesalpinioideae, Leguminosae), a predominantly rainforest tree genus with contrasting flower architectures

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Abstract
Comparative studies of floral development and morphology have largely contributed to the understanding of taxonomic classification, phylogenetic relationships and evolutionary trends across many angiosperm clades, particularly in the florally diverse family Leguminosae (alternatively Fabaceae). This study aimed to characterize the middle to late stages of floral development and morphological variation of the caesalpinioid genus *Tachigali*, an evolutionary radiation of predominantly neotropical rainforest trees. Floral buds and flowers of five representative species from *Tachigali* were analyzed under stereo microscopy, light microscopy and scanning electron microscopy to evaluate informative morphological and developmental characters. Although the genus displays relatively small flowers measuring up to 14 mm long, they are variable in terms of symmetry, structure and size, which have influenced the main taxonomic subdivisions among the species. Here, we show that the floral architecture of *Tachigali* involves a double whorl of stamens, anthers with dome-shaped connective extension and monosymmetrical hypanthium, owing to the unequal development of its wall at different stages of the floral ontogeny. Such developmental patterns are likely new diagnostic floral characters of *Tachigali* in the context of the early diverging caesalpinioid clades and reaffirm the circumscription of the genus in order to include the species previously classified within *Sclerolobium*.

Keywords Floral ontogeny · Hypanthium development · *Sclerolobium* · Vascularization pattern

Introduction

Comparative studies of floral development and morphology have informed taxonomic classifications, and enhanced our understanding of phylogenetic relationships and evolutionary trends across many angiosperm clades, particularly in the early diverging clades of the family Leguminosae, where the constituent genera display an extreme diversity of floral architecture (Tucker 1991, 2003; Cardoso et al. 2013a, b; Bruneau et al. 2014; Leite et al. 2014, 2015; Prenner et al. 2015; Prenner and Cardoso 2017). In the recently recircumscribed subfamily Caesalpinioideae, morphological variation in floral organs can be so high that it is difficult to recognize clear synapomorphies that best characterize the close phylogenetic affinity among florally discrepant genera (LPWG 2013, 2017; Prenner and Cardoso 2017).

The focus of this study is the caesalpinioid genus *Tachigali* Aubl., an evolutionary radiation of ant-housing trees predominantly found in neotropical rainforests (Chomicki et al. 2015). Among the 75 species described in *Tachigali*, 58 occur in Brazilian territory, and 26 are endemic to the country (Silva and Lima 2007; BFG 2018). *Tachigali* stands out for its ecological dominance, being one of the most abundant in number of species per sampling area in the Amazon region (ter Steege et al. 2013), as well as for its common mutualistic relationship with ants that inhabit the variously

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shaped leaf domatia (Fonseca 1999; Fonseca and Benson 2003; Chomicki et al. 2015).

The most recent phylogenetic classification of *Tachigali* based on molecular data placed the genus in the so-called Tachigali clade together with *Arapatiella* R.W. Cowan from the Atlantic Forest and *Jacqueshuberia* Ducke from the Amazon (Haston et al. 2005; Manzanilla and Bruneau 2012; Silva et al. 2016a, b). Traditionally, *Tachigali* was considered to be closely related to *Sclerolobium* Vogel because of their shared small flowers in large, dense panicles and cryptosamaroid legumes (Haston et al. 2005; Bruneau et al. 2008). However, these genera have been assembled in a broader circumscription of *Tachigali* based on similar wood anatomy (Barreta-Kuipers 1981; Macedo et al. 2014), pollen morphology (Graham and Barker 1981), floral and fruit morphological features (Silva and Lima 2007; van der Werff 2008), as well as results from molecular phylogenetic analyses, despite very sparsely sampled (Silva et al. 2016a, b). If *Tachigali* and *Sclerolobium* have to be recognized as distinct genera, Van der Werff (2008) pointed out that they would be separated by only one floral character: spathulate *vs*. linear petals. He also argued that the floral morphological variation of *Tachigali* was expanded to include both actinomorphic and zygomorphic flowers with spathulate and/or linear petals, as well as the ovary stipe arising in a central portion or laterally displaced in the hypanthium (van der Werff 2008).

In order to contribute to a better characterization of the floral morphological variation in *Tachigali*, we herein examine the middle to late stages of flower development to reveal the putative homologies between the actinomorphic *Sclerolobium*-like flowers and the zygomorphic *Tachigali*-like flowers. We also show how floral developmental morphology can contribute to elucidate diagnostic characters that bring more insight to the current classification of *Tachigali*.

Materials and methods

For the study of floral morphology, the following species of *Tachigali* were analyzed: *T. beaurepairei* (Harms) L.G.Silva & H.C.Lima, *T. denudata* (Vogel) Oliveira-Filho, *T. duckei* (Dwyer) Oliveira-Filho, *T. paratyensis* (Vell.) H.C.Lima & *T. spathulipetala* L.G.Silva, L.J.T.Cardoso, D.B.O.S.Cardoso & H.C.Lima. The first three species listed were previously circumscribed in *Sclerolobium*. These species were chosen as they represent the wide variation in floral morphology in *Sclerolobium*.

The floral buds and flowers of *T. paratyensis* (RB 435559) were collected at the Arboretum of the Rio de Janeiro Botanical Garden and fixed in glutaraldehyde 2.5% in a 0.1 M sodium phosphate buffer in pH 7.2 (Gabriel 1982). The samples of *T. duckei* (RB 430982; RB spirit 1617) and *T. spathulipetala* (RB 460994; RB spirit 1327; RB 459830; RB spirit 1329) were obtained from the Spirit collection of the herbarium of the Rio de Janeiro Botanical Garden and were previously fixed in ethanol 70%. The samples of *T. denudata* (RB 659134) and *T. beaurepairei* (RB 38772) were also preserved in ethanol 70% and were taken from the personal collection of Professor Haroldo Lima. The floral buds and flowers of each species were measured using the Leica MZ8 stereo microscope and analyzed and photographed with the Olympus SZ61 stereo microscope with an Olympus SC30 camera to determine the different stages of development.

The flower buds were dehydrated in ethanol series and then embedded in hydroxymethyl methacrylate (Gerrits and Smid 1983) and sectioned with the Leica RM2245 rotary microtome in order to proceed with light microscopy analysis. In this process, glass knives were used to obtain sections 1–3 µm thick, which were stained with 0.05% toluidine blue O (O'Brien et al. 1964) and observed and photographed using the BX-50 light microscope with the Olympus DP73 digital camera.

For scanning electron microscopy (SEM), the materials were dehydrated initially in ethanol series and later in acetone (Bozzola and Russel 1999, modified). The samples were submitted to Leica EM 030 critical point to finish the dehydration and fixed with a carbon tape on stubs and covered with a ca. 20 nm layer of gold (Emitech K550X Sputter Coater). The samples were observed under the Zeiss EVO 40 scanning electron microscope.

All images obtained from the different analyses were processed with Adobe Photoshop CS5 Extended software version 12.1, and the schemes were made with Adobe Illustrator CS5 software version 15.1.0.

Results

Morphological characters

In *Tachigali*, the young floral buds are protected by bracts (Fig. 1), which are deciduous and fall before anthesis. The flowers are small, with the smallest (*T. spathulipetala*) ca. 4.5 mm long and the biggest (*T. paratyensis*) ca. 14 mm long. The flowers in the other species analyzed here (*T. beaurepairei*, *T. denudata* and *T. duckei*) are ca. 5.5 mm long. The floral buds have 0.20–0.50 mm long pedicels in *T. beaurepairei* (Fig. 2d), T. *denudata* (Fig. 2a) and *T. duckei* (Fig. 2c) or 1–4 mm long in *T. paratyensis* (Fig. 2e) and *T. spathulipetala* (Fig. 2b).

The flowers and floral buds have monosymmetric hypanthium with simple and glandular trichomes on their outer surface, except for *T. paratyensis*, which only has simple trichomes. All studied species have five boat-shaped sepals (Fig. 2a–e, V) with simple trichomes on the inner and outer surface, and five petals (Fig. 2a–e, IV) varying between

Fig. 1 Upper part of inflorescence of *Tachigali paratyensis*. Floral buds (asterisks) with subtending floral bracts (arrowheads). Bar = 5 mm

spathulate (*T. paratyensis* Fig. 2e, IV), linear (*T. beaurepairei*, Fig. 2d, IV; *T. denudata*, Fig. 2a, IV; and *T. duckei*, Fig. 2c; IV) and heteromorphic in *T. spathulipetala* (Fig. 2b, IV) with spathulate and linear petals in the same flower. All petals have simple trichomes on the inner surface. In the spathulate petals, the trichomes are distributed along the main rib. *Tachigali spathulipetala* also has simple trichomes on the outer surface of its spathulate petals.

All species have ten stamens (Fig. 2a–e, III; Online Resource 1–5) arranged in two whorls (Fig. 2a–e, I; Online Resource 1–5), which are conspicuous in *T. denudata* (Fig. 2a, I; Online Resource 1) and *T. paratyensis* (Fig. 2e, I; Online Resource 2), less so in *T. beaurepairei* (Fig. 2d, I; Online Resource 3), *T. duckei* (Fig. 2c, I; Online Resource 4) and *T. spathulipetala* (Fig. 2b, I; Online Resource 5). After anthesis, the stamens are equal in size and shape in *T. beaurepairei* (Fig. 2d, III), *T. denudata* (Fig. 2a, III), *T. duckei* (Fig. 2c, III) and *T. spathulipetala* (Fig. 2b, III), but heteromorphic in *T. paratyensis* (Fig. 2e, III), with three short and thick stamens in the adaxial portion and seven thin stamens from the mid to the abaxial portion of the flower. All stamens have simple trichomes at the base of the filaments. The anthers are dorsifixed (Fig. 2a–e, III; 3a–b) with a dome-shaped connective extension apically (Fig. 3a–d), which can occasionally have simple trichomes (Fig. 3d). This connective extension was more protruded in *T. denudata*, especially in the anthers of antepetalous stamens.

In all species, the superior ovary with simple trichomes is elevated on a stipe (Figs. 2II, a–e, 4d–e). The stipe is centrally attached to the hypanthium (*T. beaurepairei*, Fig. 4d; *T. denudata*, Fig. 4a; and *T. duckei*, Fig. 4c) or laterally displaced (*T. paratyensis*, Fig. 4e; *T. spathulipetala*, Fig. 4b). The only style varies in length, being short (up to 0.65 mm long) in *T. spathulipetala* (Fig. 2b, II); medium-sized (1.00–1.50 mm long) in *T. beaurepairei* (Fig. 2d, II), *T. denudata* (Fig. 2a, II) and *T. duckei* (Fig. 2c, II); and elongated (ca. 2.0 mm long) in *T. paratyensis* (Fig. 2e, II).

Hypanthium development

In the floral buds, an unequal development of the hypanthium takes place (Fig. 4), giving an asymmetrical aspect to the floral bud from middle to late stages of floral development. This monosymmetry is evidenced by a projection in the adaxial portion of the hypanthium wall (Fig. 4a–e; Online Resource 1–5). In addition, from early stages, the ovary stipe can be found in a central position of the hypanthium in all species, while in later stages decentralization of the stipe appears in *T. paratyensis* (Fig. 4e) and *T. spathulipetala* (Fig. 4b). This positional change results from the unequal growth of the hypanthium which becomes more prominent in the adaxial portion.

Furthermore, the establishment of hypanthium monosymmetry is distinct in relation to the maturity of reproductive whorls among the analyzed species (Fig. 5). In *T. denudata,* the asymmetry begins when the ovule integuments are forming (Fig. 5a), as well as when meiosis takes place in the anthers (Fig. 5b, b'), with callose deposition. In *T. spathulipetala, T. beaurepairei* and *T. duckei*, the asymmetry arises later. In sections of *T. spathulipetala* and *T. beaurepairei*, functional megaspores are established in the ovule (Fig. 5c), and microgametogenesis with uninuclear pollen grains begins (Fig. 5d, d'). In *T. duckei*, the megaspores are at the dyad stage (Fig. 5e) and the anthers contain binuclear pollen grains (Fig. 5f, f'). In *T. paratyensis*, hypanthium asymmetry begins earlier than in the other species analyzed, and the floral buds are asymmetrical when the ovule (Fig. 5g) and the anther walls (Fig. 5h, h') develop.

Vascularization of flower buds

The hypanthium monosymmetry described above is also seen in flower bud vascularization. Among the five species analyzed, there are three distinct vascular patterns (Figs. 6, 7, 8). In all species, the intersection region between the pedicel and the basal portion of the hypanthium is similar, with a continuous cylindrical bicollateral vascular bundle (Figs. 6/1, 7/1, 8/1).

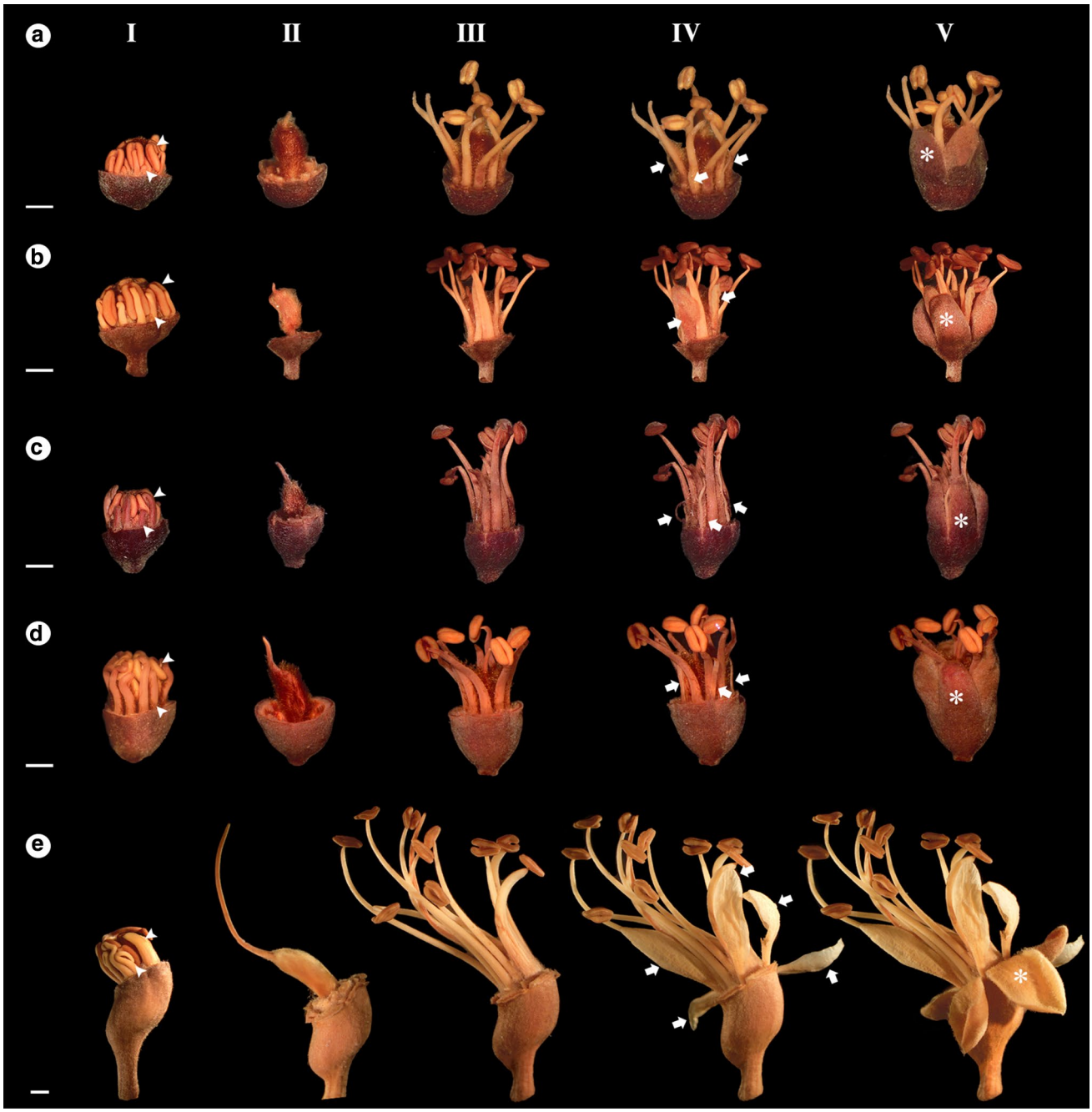

Fig. 2 **a**–**e** Flower buds, anthetic and postanthetic flowers. *Tachigali denudata* (**a**), *T. spathulipetala* (**b**), *T. duckei* (**c**), *T. beaurepairei* (**d**) and *T. paratyensis* (**e**). I) Floral buds with sepals and petal whorls removed, showing double whorl of stamens (arrowhead); II) flowers showing the gynoecium, with sepals, petals and stamens removed; III) flowers showing the androecium, with sepals and petals removed; IV) flowers showing petals (arrows), with sepals removed; V) entire flowers, showing sepals (asterisk). Bar: **a**–**e** = 1 mm

In *T. beaurepairei*, *T. denudata* and *T. duckei*, the division of five vascular bundles starts at the hypanthium base from the central cylinder in the abaxial region (Fig. 6/2–4). These vascular bundles will be part of the external circle of hypanthium bundles (Fig. 6/4). Above these bundles, the division of five more vascular bundles begins, also from the central cylinder to the abaxial region of this structure (Fig. 6/3–4). These will be part of the inner circle of hypanthium bundles (Fig. 6/4). Because of the short (cupular) hypanthium, the gap between the divisions of these vascular bundles is reduced. Immediately after the establishment of the vascular bundles in the abaxial region, the separation of bundles from the central cylinder begins (Fig. 6/4). Above the departure of the bundles, a total of twenty vascular bundles are present

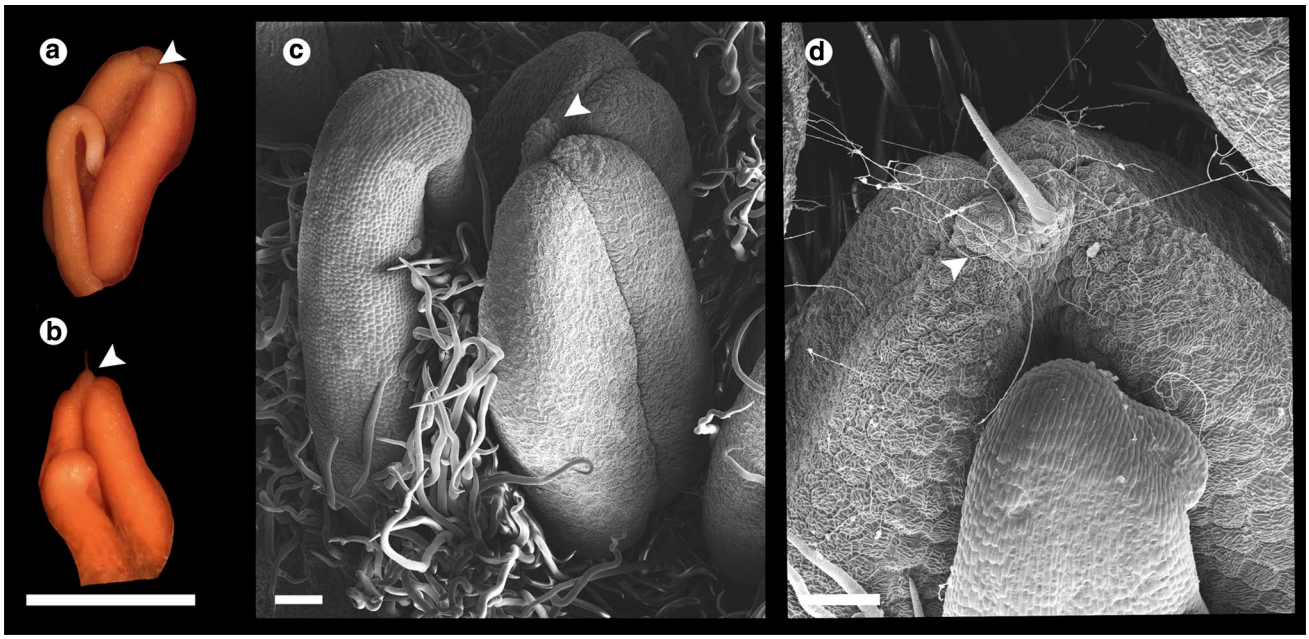

Fig. 3 **a**–**d** Anthers of *Tachigali*. **a**–**b** *Tachigali denudata* seen in stereo microscope. **c** *Tachigali duckei* seen with scanning electron microscopy. **d** *Tachigali beaurepairei* seen with scanning electron microscopy. **a** Antesepalous anther/stamen; **b** antepetalous anther/stamen; **a**–**b** arrowhead indicating dome-shaped connective extension; **c** antepetalous anther/stamen of *T. duckei*. **d** antepetalous anther/stamen of *T. beaurepairei*; **c**–**d** anther detail with dome-shaped connective extension (arrowhead). Bar: **a**–**b** = 1 mm; **c** = 100 µm; **d** = 20 µm

at the midpoint of the hypanthium composed of two circles of ten bundles (outer and inner) and a vascular cylinder in the middle, which will be part of the carpel stipe (Fig. 6/5). Above the midpoint of the hypanthium, the vascular bundles of the outer circle undergo consecutive divisions. Five of these bundles form the sepal–petal complex, giving new bundles to both sepals and petals; the other five bundles divide, forming new bundles that will only be part of the sepals (Fig. 6/5). At the hypanthium, these bundles are intercalary to the ones that divides above in new bundles in sepals and petals (Fig. 6/5). The petals of *T. beaurepairei*, *T. denudata* and *T. duckei* are linear and have only one vascular bundle from their basal portion to the apex (Fig. 6/6–7). The vascular bundles of the inner circle will be part of the stamens (Fig. 6/3–7). They divide again only when they reach the anthers toward the two thecae (Fig. 6/7). The vascular cylinder of the ovary stipe is transformed into three vascular bundles in the ovary (Fig. 6/7).

In *T. spathulipetala* (Fig. 7), significant changes were noticed from level 2 (Fig. 7/2). In Fig. 7/2–3, in the abaxial region, the internal circle of vascular bundles has ten vascular bundles arranged in five pairs, originating from the central cylinder (Fig. 7/2–7). The same was observed for the adaxial region (Fig. 7/4–5). The pairs are only separated in the anthers when each bundle becomes part of a theca (Fig. 7/7). In addition, because of petal heteromorphism in this species, all petals have one vascular bundle at the base (Fig. 7/6). However, in spathulate petals, the vascular bundles divide into two or three higher up (Fig. 7/7), increasing in number toward the apical portion.

The third pattern was observed in *T. paratyensis* (Fig. 8). As a result of the elongated tubular hypanthium, the separation of the bundles of the external and internal circle occurs at some distance from the central cylinder in the abaxial and adaxial regions (Fig. 8/2–4). The petals have one vascular bundle at their base (Fig. 8/5–6); however, they divide into three bundles (Fig. 8/6–7) and, higher up, into several bundles near the middle region.

The supplemental material (sup. material 1–5) also shows the floral development of the species analyzed.

Discussion

Taxonomically informative floral developmental characters

Although the genus *Tachigali* displays small flowers with the largest up to 14 mm long, they are variable in terms of symmetry, structure and size, resulting in well-delimited species (van der Werff 2008). Within the Tachigali clade (Haston et al. 2005), the genus *Tachigali* has the smallest flowers compared with *Arapatiella* and *Jacqueshuberia*, as one of their distinguishing characters (Silva et al. 2016a, b).

The overall flower morphology of *Tachigali* has already been described in taxonomic studies (Silva 2007; van der

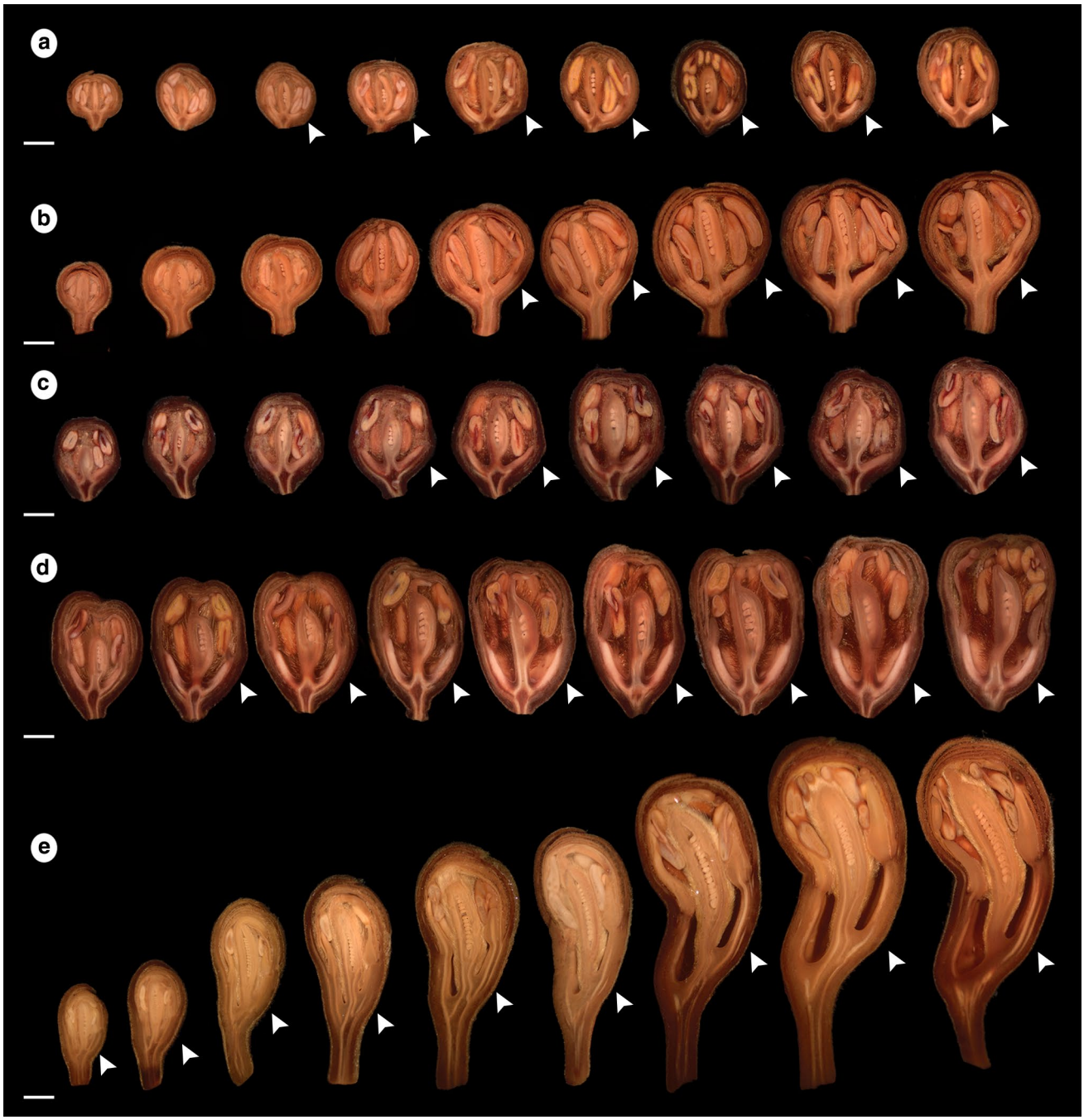

Fig. 4 **a**–**e** Floral buds in different developmental stages. *Tachigali denudata* (**a**), *T. spathulipetala* (**b**), *T. duckei* (**c**), *T. beaurepairei* (**d**) and *T. paratyensis* (**e**) in longitudinal section; arrowheads indicating the projection of the hypanthium wall. Bar = 1 mm

Werff 2008; Silva et al. 2016a, b). Within Leguminosae, two stamen whorls, five sepals, five petals and a single carpel are well known (Tucker 2003). However, we herein describe new floral features that have, so far, remained unnoticed in morphological assessments of the genus. Among the floral characters observed in the later flower development of all studied species, two stamens whorls and anthers with dome-shaped connective extension are newly reported for the genus, as well as the glandular trichomes on the outer surface of the hypanthium in *T. denudata*, *T. duckei* and *T. spathulipetala*.

Anthers with connective extensions are common among several angiosperm families, as in Crassulaceae, Proteaceae, Sapindaceae and Rutaceae for example (Endress and Stumpf, 1991). Within Leguminosae, such extensions are often present in the mimosoid clade of

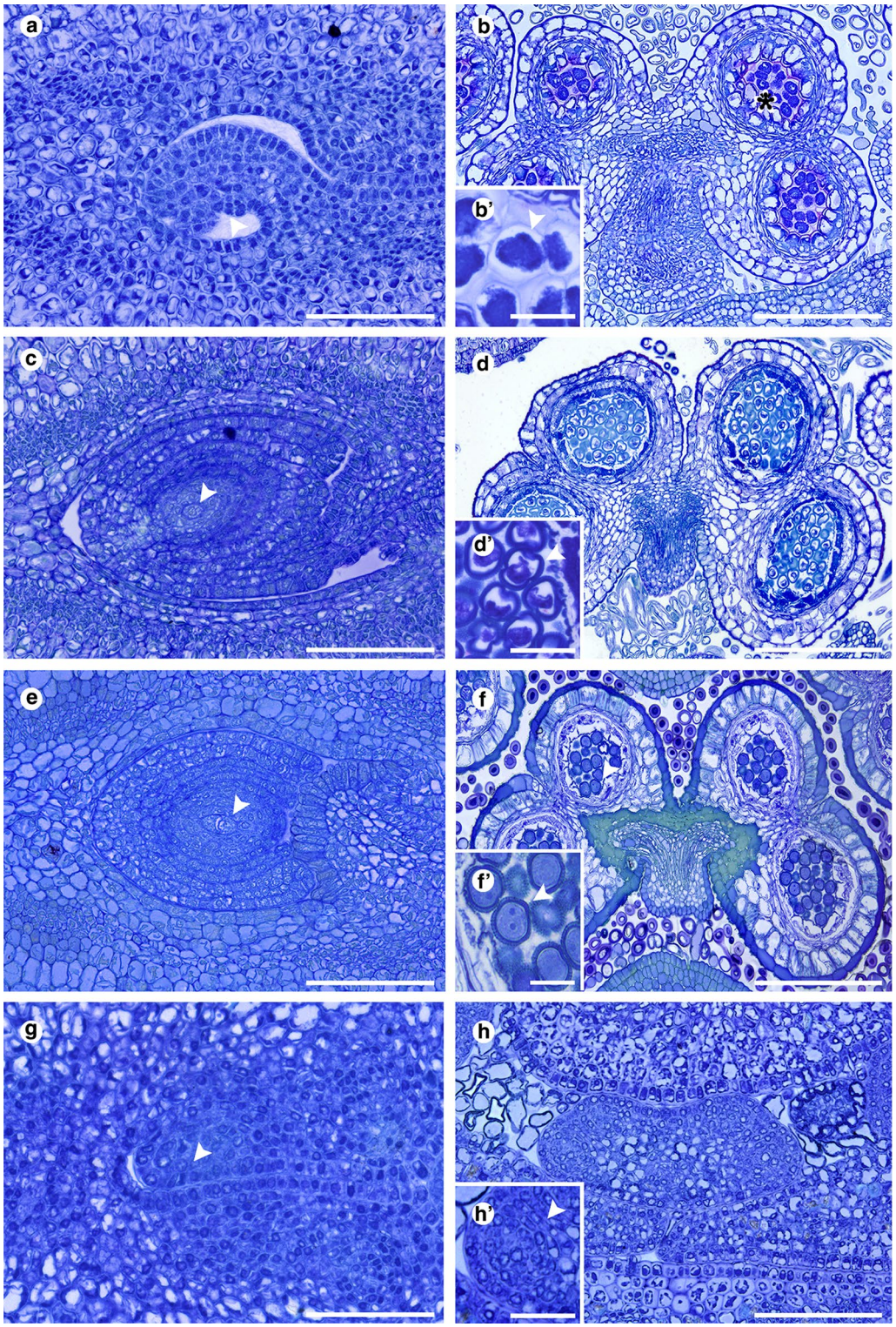

Fig. 5 **a**–**h**' Development of reproductive organs in floral buds. *Tachigali denudata* (**a**–**b**'), *T. spathulipetala* (**c**–**d**'), *T. duckei* (**e**–**f**') and *T. paratyensis* (**g**–**h**'). **a**, **c**, **e**, **g**—ovule details. **b**–**b**' **d**–**d**' **f**–**f**' **h**–**h**'—anther and androspore details. **a** Establishment of integuments (arrowhead); **b** androspore in meiosis (asterisk); **b**' detail of the callose deposition (arrowhead); **c** functional gynospore established in the ovule (arrowhead); **d** beginning of androgametogenesis; **d**' detail of unicellular pollen grains (arrowhead); **e** gynospore in meiosis (arrowhead), dyad; **f**–**f**' bicellular pollen grains (arrowhead); **g** establishment of young ovules (arrowhead); **h**–**h**' establishment of anther wall (arrowhead). Bar **a**–**h** = 100 µm; **b**'–**h**' = 25 µm

Caesalpinioideae, in which they differentiate into secretory structures (Luckow and Grimes 1997; Barros and Teixeira 2016). This feature was also observed in the Detarioideae legume *Goniorrhachis marginata* Taub. (Prenner and Cardoso 2017). Although the connective extensions observed here are not secretory, they can still be taxonomically useful as a possible diagnostic character for the genus.

Glandular trichomes are also common in Leguminosae, both in vegetative and reproductive organs (Lavin et al. 2001; Horner et al. 2003; Meira et al. 2014; Gagnon et al. 2015; Marinho et al. 2016; Silva et al. 2018; Vargas et al. 2018). Moreover, they show considerable variation in form and therefore often used as a diagnostic character at genus and species levels (Meira et al. 2014; Gagnon et al. 2015; Silva et al. 2018; Vargas et al. 2018). In *Tachigali*, glandular trichomes have already been studied in the stipules (Pipoly 1995) and hypanthium (Dwyer 1954).

The floral hypanthium is a common feature of Leguminosae (LPWG 2017). It typically appears as an elongated receptacle that elevates perianth and androecium but does not merge with the gynoecium (Weberling 1989). When present, the hypanthium in Caesalpinioideae genera varies between cupular and tubular (LPWG 2017). After its new circumscription, the genus *Tachigali* began to encompass all species with tubular (cylindrical) hypanthium, as well as the species with cupular hypanthium that were formerly classified in *Sclerolobium* (Watson and Dallwitz 1983; Silva and Lima 2007).

Van der Werff (2008) has classified the hypanthium shape in *Tachigali* by its symmetry, i.e., symmetrical when the stipe is in central position in the hypanthium and asymmetrical when the stipe is laterally displaced. This character was used to separate *Sclerolobium* from *Tachigali*. *Sclerolobium* was described as having symmetrical hypanthium and *Tachigali* as having asymmetric hypanthium (Van der Werff 2008), which was then used in infrageneric classification. However, all species analyzed here have asymmetrical hypanthium, even those with a central

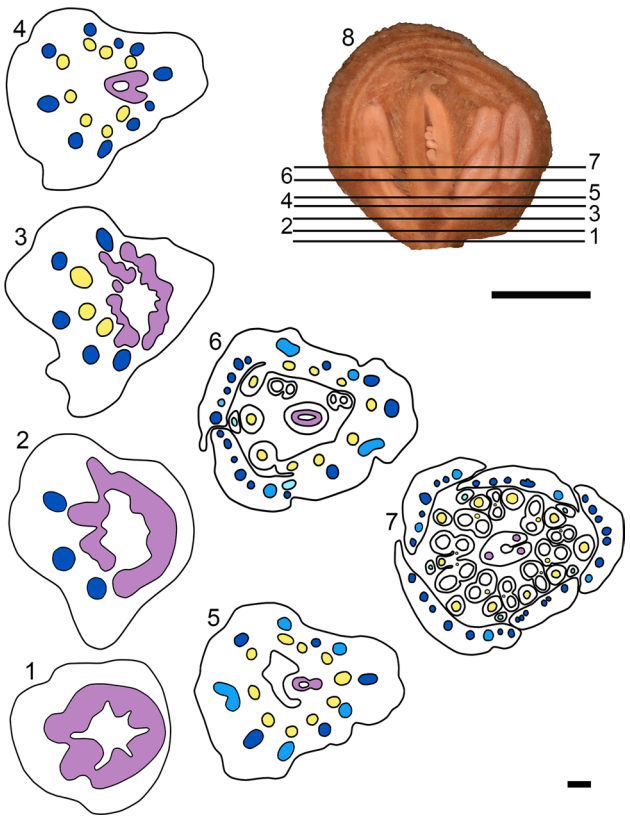

Fig. 6 Diagram of *Tachigali denudata* floral bud vascularization in seven levels (indicated in 8). The vascular bundles are indicated in different colors related to their origin and position. Central cylinder (1–3) and ovary bundles (4–7) in purple; external circle (2–5): dark blue; internal circle (3–5) and stamen bundles (6–7): yellow; light blue (5–6): sepal–petal complex bundles; cyan (6–7): petal bundles. Bar: 7 = 100 µm, 8 = 1 mm

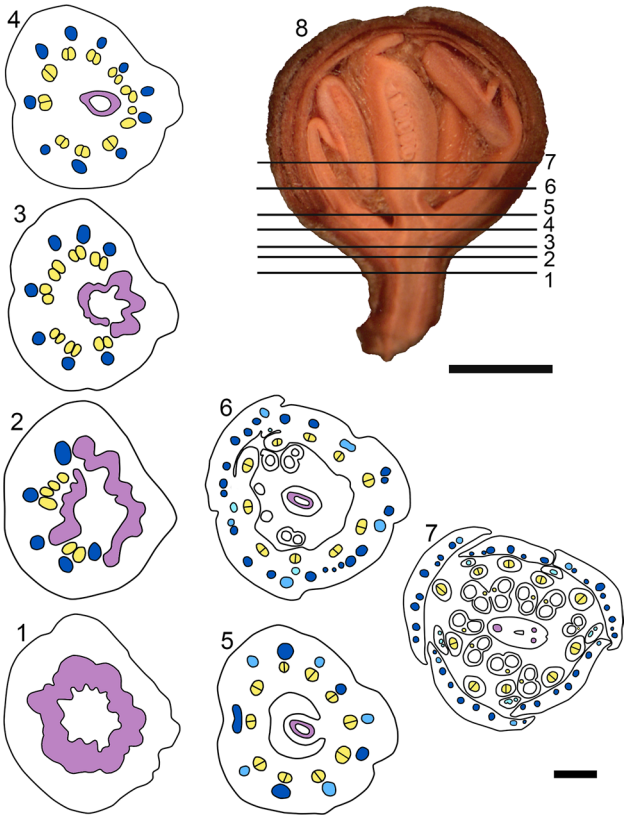

Fig. 7 Floral bud vascularization scheme of *Tachigali spathulipetala* at seven levels (indicated in 8). The vascular bundles are indicated in different colors related to their origin and position. Central cylinder (1–3) and ovary bundles (4–7) in purple; external circle (2–5): dark blue; internal circle (2–5) and stamen bundles (6–7): yellow; light blue (5–6): sepal–petal complex bundles; cyan (6–7): petal bundles. Bar: 7 = 100 µm, 8 = 1 mm

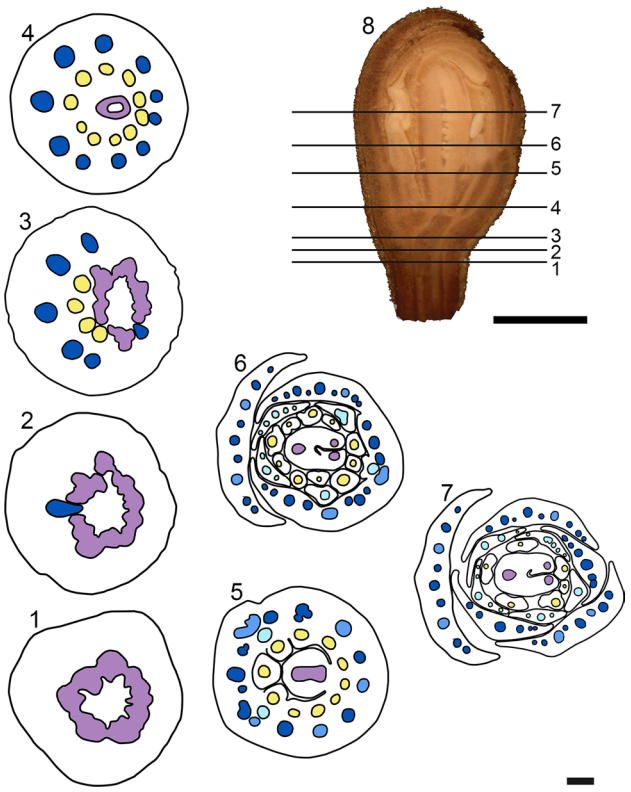

Fig. 8 Floral bud vascularization scheme of *Tachigali paratyensis* in seven levels (indicated in 8). The vascular bundles are indicated in different colors related to their origin and position. Central cylinder (1–3) and ovary bundles (4–7) in purple; external circle (2–4): dark blue; internal circle (3–4) and stamen bundles (5–7): yellow; light blue (5–6): sepal–petal complex bundles; cyan (5–7): petal bundles. Bar: 7 = 100 µm, 8 = 1 mm

stipe, meaning that stipe position is irrelevant in relation to the asymmetry of the hypanthium. Therefore, hypanthium asymmetry as described by Van der Werff (2008), was not confirmed in this study. Rather, it is suggested here that the asymmetry of the hypanthium is a consequence of unequal development of the hypanthium walls which protrude into the adaxial portion of the floral bud in middle to late stages of development. In addition, the hypanthium asymmetry in all species analyzed, including those previously classified as *Sclerolobium*, corroborates the results of the preliminary molecular phylogeny of *Tachigali* and *Sclerolobium,* which places both genera in the same monophyletic group (Silva et al. 2016a, b).

According to Tucker's (1997) hierarchical theory, floral development corresponds to a succession of cascading events in which the first changes will dictate the final changes. Even according Tucker (1997), characters that develop in middle stages, such as the relative size of the floral organs, the loss or suppression of organs, as well as the fusion of organs, enable the characterization of taxa at generic level. Characteristics that develop late in the formation of the floral bud, such as the formation of papillae and trichomes, promote few changes in flower architecture; therefore, these characteristics are better suited for differentiation of infrageneric taxa. Our results for the hypanthium developmental pattern presented here agree with Tucker's (1997) hierarchical theory since the monosymmetry in this structure becomes more evident in the middle to late stages of flower development and might supply additional support for the circumscription of *Tachigali* and *Sclerolobium*. However, some studies have shown that this hypothesis cannot be applied in all cases of legume classification (Bello et al. 2012; Cardoso et al. 2013a, b; Bruneau et al. 2014). Based on combined data of morphological floral traits and molecular analyses, Bello et al. (2012) demonstrated that the ontogenetic characters supporting the clade comprised of Leguminosae, Quillajaceae and Surianaceae in Fabales originate in middle to late stages of floral development, such as the five/six antesepalous stamen primordia and the disposition of the androecial whorl. Also, Bruneau et al. (2014) show that species differentiation within genera in Detarioidae can be caused by changes that occur at all stages of flower ontogeny.

Conspicuous changes of floral symmetry within *Tachigali*

Leguminosae are well known for the strongly zygomorphic flowers, as more emblematically exemplified by the papilionate flower of the Papilionoideae, which often involves a highly modified architecture with standard, wing and keel petals, stamens enveloping the ovary, fusion of floral organs and limited access to pollen and nectaries (Cardoso et al. 2013a, b; LPWG 2017). The Leguminosae also embraces actinomorphic, as well as monosymmetrical and zygomorphic yet non-papilionate flowers within the six subfamilies (Cardoso et al. 2013a, b; LPWG 2017).

In the Tachigali clade (Haston et al. 2005), *Jacqueshuberia* has flowers with slightly zygomorphic corolla. The *Tachigali* flowers were described as zygomorphic owing to the presence of heteromorphic stamens and an unequal tubular hypanthium (Watson and Dallwitz 1983; van der Werff 2008), as observed here in *T. paratyensis*, whereas the flowers of the species previously classified as *Sclerolobium* were described as actinomorphic (Watson and Dallwitz 1983; van der Werff 2008).

In the species analyzed in the present study (Table 1), the floral buds have a bilateral symmetry (zygomorphy) owing to hypanthium monosymmetry. However, in *T. beaurepairei*, *T. denudata* and *T. duckei* (previously *Sclerolobium*), after anthesis, flowers assume an actinomorphic aspect from the isomorphism of the sepals, petals and stamens. Finally, in addition to the monosymmetric hypanthium described above in the flower buds of *T.*

Table 1 Comparison of floral symmetry from *Tachigali beaurepairei*, *T. duckei*, *T. denudata*, *T. spathulipetala* and *T. paratyensis* from literature data (Dwyer 1954; Watson and Dallwitzz 1983; Silva 2007; van der Werff 2008; Silva et al. 2016a, b) and results obtained in this study

Species	Literature	Results
Tachigali beaurepairei	Actinomorphic flowers due to symmetrical hypanthium (ovary stipe position) and isomorphic sepals, petals and stamens	Zygomorphic floral buds due to asymmetrical hypanthium (unequal wall development); actinomorphic flowers after anthesis due to the isomorphic sepals, petals and stamens
Tachigali duckei	Ditto	Ditto
Tachigali denudata	Ditto	Ditto
Tachigali spathulipetala	Actinomorphic flowers due to symmetrical hypanthium (ovary stipe position) and isomorphic sepals and stamens; petals are and heteromorphic	Slightly zygomorphic flowers due to asymmetrical hypanthium (unequal wall development) and the heteromorphic petals; the sepals and stamens are isomorphic
Tachigali paratyensis	Zygomorphic flowers due to tubular asymmetrical hypanthium (ovary stipe position) and heteromorphic stamens; the sepals and petals are isomorphic	Zygomorphic flowers due to tubular asymmetrical hypanthium (unequal wall development) and the heteromorphic stamens; the sepals and petals are isomorphic

spathulipetala, Silva et al. (2016a, b) point out the presence of heteromorphic petals: an adaxial, standard-like petal, two lateral, linear petals and two abaxial, spathulate petals. These characteristics confer a slight zygomorphic floral architecture in that species, being considered transitional among the floral morphological variation found in the genus (Silva et al. 2016a, b).

Studies of vascularization patterns have helped in the understanding of floral morphology among angiosperms (Puri 1951; Souza et al. 2005; Novikoff and Jabbour 2014; Silva et al. 2016a, b; De Paula et al. 2018; Leme et al. 2018). Within Leguminosae, floral vascularization analyses are used to recognize floral nectaries (Honner et al. 2003; Paiva and Machado 2008; Kochanovski et al. 2018). Here, vascularization of the floral buds was also helpful to reveal the structure of the monosymmetric hypanthium. The vascular bundles that are part of the abaxial region of the hypanthium originate from the central cylinder before the vascular bundles of the adaxial region. These are only present after the establishment of bundles of the abaxial region.

Overall, three patterns were observed with respect to petal vascularization: (i) linear petals with only one vascular bundle along their entire extension (as in *T. beaurepairei*, *T. denudata* and *T. duckei*); (ii) spathulate petals, with one bundle in their basal portion, which divides into three bundles and later into several, as it approaches the apical portion (as in *T. paratyensis*); and (iii) spathulate petals in which the initial bundle divides into two bundles and later into several bundles (as in *T. spathulipetala*). This vascularization pattern agrees with the external morphology of the petals analyzed here. The vascular bundle of the stamen divides only at the thecae (as in *T. beaurepairei*, *T. denudata* and *T. duckei* and *T. paratyensis*). These petal and stamen vascularization patterns are reported here for the first time in the genus.

Here, we provide a detailed assessment of the apparently simple and small, but structurally complex flowers of *Tachigali*, a large genus of neotropical trees that has early diversified in the Caesalpinioideae phylogeny. Early-branching genera across all legume subfamilies have been largely marked by conspicuous changes in floral morphology involving symmetry, reduction or proliferation of stamens and petals, multicarpellate gynoecium and petals that can be free and equal or highly differentiated and connate (e.g., Pennington et al. 2000; Prenner and Klitgaard 2008; Cardoso et al. 2012a, b, 2013a, b; Zimmerman et al. 2013; Bruneau et al. 2014; Paulino et al. 2014; Leite et al. 2015; Prenner et al. 2015; Prenner and Cardoso 2017). In contrast to such floral evolutionary lability among closely related genera of early-branching legume clades, major changes in floral architecture at genus level seem to be rare. For example, the speciose genera *Inga* (300 spp.; Caesalpinioideae-Mimosoid), *Dalbergia* (250 spp.), *Lupinus* (230 spp.), *Indigofera* (700 spp.) and *Astragalus* (2.300 spp.) (Papilionoideae) (Lewis et al. 2005)

all have relatively conserved floral morphology. On the other hand, floral symmetry seems to mark a major subdivision within *Tachigali*, which indeed has been used to define two different genera (van der Werff 2007). Understanding why the small *Tachigali* flowers have undergone so many changes during its relatively fast diversification history (Baker et al. 2014) seems to be a promising topic to explore in the future under a robust phylogenetic framework, with new data on floral development across its entire morphological diversity, as well as insights from the developmental genetic mechanisms of MADS-box genes in regulating floral symmetry (e.g., Theissen 2001; Citerne et al. 2000, 2003, 2006; Feng et al. 2006; Wang et al. 2008; Zhang et al. 2010).

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Information on Electronic Supplementary Material

The electronic supplementary material attached to this manuscript are high-quality images of the floral development from the five *Tachigali* species analyzed in this study, whorl by whorl, which allows us to better understand their floral architecture.

Online Resource 1. Floral buds at different developmental stages of *Tachigali denudata*. **a** Floral buds showing the sepals; **b** showing the petals with the sepals removed; **c** showing the androecium with the sepals and petals removed; **d** the gynoecium with the sepals, petals and androecium removed.

Online Resource 2. Floral buds at different developmental stages of *Tachigali paratyensis*. **a** Floral buds showing the sepals; **b** showing the petals with the sepals removed; **c** showing the androecium with the sepals and petals removed; **d** showing the gynoecium with the sepals, petals and androecium removed; arrowheads indicating the projection of the hypanthium wall.

Online Resource 3. Floral buds at different developmental stages of *Tachigali beaurepairei*. **a** Floral buds showing the sepals; **b** showing the petals with sepals removed; **c** showing the androecium with sepals and petals removed; **d** showing the gynoecium with sepals, petals and androecium removed; arrowheads indicating the projection of the hypanthium wall.

Online Resource 4. Floral buds at different developmental stages of *Tachigali duckei*. **a** Floral buds showing the sepals; **b** showing the petals with the sepals removed; **c** showing the androecium with the sepals and petals removed; **d** showing the gynoecium with the sepals, petals and androecium removed; arrowheads indicating the projection of the hypanthium wall.

Online Resource 5. Floral buds at different developmental stages of *Tachigali spathulipetala*. **a** Floral buds showing the sepals; **b** showing the petals with the sepals removed; **c** showing the androecium with the sepals and petals removed; **d** showing the gynoecium with the sepals, petals and androecium removed; arrowheads indicating the projection of the hypanthium wall.

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