Acta Botanica Brasilica - 33(4): 672-682. October-December 2019.
doi: 10.1590/0102-33062019abb0140

Synflorescence morphology of species of *Typha* L. (Typhaceae): anatomical and ontogenetic bases for taxonomic applications

Jordano Dorval Tavares de Carvalho[1] and Jorge Ernesto de Araujo Mariath[1*]

Received: April 15, 2019
Accepted: June 11, 2019

ABSTRACT

The inflorescence of plants of the genus *Typha* L. consists of a polytelic system with the fertile region containing staminate flowers in the terminal portion and pistillate flowers in the basal portion. Although some useful morphological information has been provided to characterize species of the genus, various divergent typologies have arisen due to mistaken interpretations that ignore the different degrees of branching in this indeterminate system. The present study aimed to identify structural homologies by comparing the morphology and ontogeny of the synflorescences of *Typha domingensis*, *T. latifolia* and their putative hybrid, *T. x provincialis*, using standard micro-techniques for light and electron microscopy. Analysis revealed that the synflorescence of species of *Typha* should be considered a homothetic triple raceme. New diagnostic characters are proposed for both the pistillate and staminate portions. Differences among the apices of the pistillate portions are compared for the first time, and mainly involve the rate of lengthening of the second order branch, which is species specific. The data and interpretations proposed in this study should serve as a basis for proposing homologies for different structures of the synflorescences of species of *Typha*.

Keywords: compound spike, inflorescence, panicle, prophyll, raceme, synflorescence, *Typha*

Introduction

The genus *Typha* contains 10 to 15 species of aquatic plants that are characterized mainly by their cylindrical synflorescences with thousands of diclinous flowers packed in a terminal fertile zone subtended by a long peduncle. The fertile zone comprises two sectors: a terminal sector with staminate flowers formed by a few nodes, and a subterminal sector with many indeterminate branches and where the pistillate flowers are also densely packed but in a single node (Smith 1967; Krattinger 1975; Finlayson *et al.* 1985; Grace & Harrison 1986; Smith 1986). *Typha* and the genus *Sparganium* compose Typhaceae (APG IV 2016). These genera are similar not only because of the extreme reduction of floral components, but also because they produce densely packed diclinous flowers. The pistillate flowers of species of *Sparganium*, however, are not located in a single cylindrical structure at one node, but in series of small fascicles at different nodes. Some species of *Typha* possess an apparent gap without flowers or branches between the staminate portion and the pistillate portion of the synflorescences, such as with *Typha domingensis*, *T. angustifolia* and *T. minima*. This gap is a common diagnostic characteristic for species, although it is recurrently variable in populations, mainly due to the presence of hybrids or intraspecific variation (Kim & Choi 2011). Besides this morphology, other characteristics of synflorescences are used for taxonomic purposes, such as the color of the surface of the pistillate portion, the

---

[1] Laboratório de Anatomia Vegetal, Departamento de Botânica, Instituto de Biociências, Universidade Federal do Rio Grande do Sul, 91509-900, Porto Alegre, RS, Brazil

[*] Corresponding author: jorge.mariath@ufrgs.br

presence of bracteoles and the proportion of the pistillate portion in relation to the staminate portion in the fertile region. These characteristics are considered stable in some infrageneric clades, but extremely variable if hybrids and phenotypic variation among populations is considered, which makes it difficult to identify most of the species and established hybrids (notospecies) (Kim & Choi 2011).

The comparative typological approach for inflorescences *sensu* Troll (1964; 1969), adopted by Weberling (1989), has resulted in hypotheses to discuss homologies for compact and complex inflorescences (Nogueira *et al*. 2017). However, as discussed by Stützel & Trovó (2013), a purely typological approach may not be ideal for inflorescences with more complex branching systems, as may be the case for *Typha*. Considering the location of pherophylls and the quantity of nodes and branches, the synflorescence of species of this genus are a polytelic, and thus ramified, system, in which an axis with an indeterminate apex generates lateral branches, which are also indeterminate, in the axil of each pherophyll. However, each pherophyll involves a node with flowers or many densely packed branches, which makes correct typological interpretation much more difficult when analyzing only the mature synflorescence, besides the fact that the pherophylls are deciduous. From a purely typological standpoint, it would be sufficient to consider the inflorescence of species of *Typha* as a compound spike with sessile flowers, or a panicle as proposed by several authors (Krattinger 1975; Wilder 1990), which is an inappropriate nomenclature for the densely ramified polytelic system. This morphological complexity has already reported by Müller-Doblies (1970) for *Typha* and *Sparganium*, who only classified this synflorescence generally as a truncated polytelic inflorescence. In a more recent approach for inflorescence typology and morphology, Endress (2010) prioritized the relative length of the primary and secondary branches and proposed broader concepts for the spike and raceme: the first type having an indeterminate inflorescence with a elongated primary axis and short secondary axes, and the second type having an indeterminate inflorescence with both primary and secondary axes elongated. However, the different orders of branching that represent the complex synflorescence of *Typha* and the relative length of this polytelic system are not properly specified to apply this new perspective.

The present study intended to discuss the different typologies adopted to classify the synflorescence of *Typha* and to propose a typology that considers the different orders of branching and relative lengths of the branches of this structure. Furthermore, this study aimed to provide new diagnostic morphological characteristics for synflorescences of *Typha domingensis*, *Typha latifolia* and *Typha x provincialis* and to evaluate aspects of the anatomy and ontogeny of the synflorescences of *T. domingensis* and *T. latifolia*.

Materials and methods

Botanical material

Inflorescences of five to 10 specimens of *Typha latifolia* L., *Typha domingensis* Pers. and *Typha x provincialis* A. Camus (*T. domingensis* x *latifolia*) were collected from natural populations in wetlands of the state of Rio Grande do Sul, Brazil. Vouchers, with collection information of inflorescences at different phases of development, are deposited in the ICN herbarium at Universidade Federal do Rio Grande do Sul (UFRGS), under registration numbers ICN 196908, ICN 196909, ICN 196910 and ICN 196911 for *T. domingensis*; ICN 196912, ICN 196913 and ICN 196914 for *T. latifolia*; and ICN 196915, ICN 196916, ICN 196917 and ICN 196918 for *T. x provincialis*. Specimens were identified using keys for species and hybrids (Reitz 1984), and consulting specific literature for identifying hybrids (Smith 1967) and specimens preserved in herbaria.

Micro-technique and microscopy

All analyses under light microscopy and micro-technique were performed in the Laboratório de Anatomia Vegetal (LAVeg) at the Universidade Federal do Rio Grande do Sul (UFRGS). Fresh mature synflorescences of *Typha latifolia*, *Typha domingensis* and *Typha x provincialis* were used for morphological analysis under a stereomicroscope. For ontogenetic and anatomical analyses, inflorescences of *T. domingensis* and *T. latifolia* were collected at specific phases of development obtained from synflorescences longer than 4 mm. Immature (still covered by pherophylls) and mature synflorescences were desiccated, fixed in 1 % glutaraldehyde and 4 % formaldehyde (McDowell & Trump 1976) in 0.1 M sodium phosphate buffer, pH 7.2 (Gabriel 1982), washed in the same buffer, washed in distilled water and finally dehydrated in an ethyl alcohol series (O'Brien & McCully 1981). The material was pre-infiltrated in a solution of 2-hydroxyethyl methacrylate (HEMA) and pure ethanol (1:1) for 12h, followed by inclusion in HEMA for approximately 8h and embedding in a Teflon holder until polymerization was completed (Gerrits & Smid 1983). Sections (4-µm thick) made using a Zeiss Mikron HM 340E rotary microtome were deposited on histological slides and dried on a hot plate at 50 °C. The material was then stained with 0.05 % Toluidine Blue O in sodium benzoate buffer, pH 4.4 (Sidman *et al*. 1961), for observation under light microscopy (O'Brien & McCully 1981). Images were analyzed and recorded either under a Leica DMR HC microscope with a Zeiss Axiocam HRc digital camera using the image capture program Axiovision SE 64 v. 4.9.1, or under a Leica M165 FC stereomicroscope with a Leica DFC 500 digital camera using the program LAS version 4.1.

For analysis by scanning electron microscopy the samples were dehydrated in an ascending acetone series and dried using the critical point method (Gerstberger & Leins 1978), with a BAL-TEC CPD 030 apparatus. The samples were adhered to aluminum stubs and covered with gold using BAL-TEC SCD 050 equipment. Observations and digital electromicrographs were made using a JEOL 6060 SEM with 10kV.

Terminology

The terminology used for inflorescence morphology followed Troll (1964; 1969) and Weberling (1989), with the new interpretations proposed by Endress (2010). Given the highly compact and complex nature of the synflorescences, the concepts of these authors were merged to more accurately classify the type of inflorescence of *Typha*.

Results

Mature synflorescence

The analyzed species of *Typha* have polytelic synflorescences with a cylindrical, narrow peduncle, which subtends the fertile region of the synflorescence up to 2m, with its height sometimes reaching over the nomophiles (Fig. 1A-D). The mature fertile region is long and narrowly cylindrical with two different portions (Fig. 1A-D): a terminal portion with staminate flowers (Fig. 1E-J) formed by some nodes, which culminates in an indeterminate apex, and a subterminal portion with pistillate flowers (Fig. 1K-R) compacted in many indeterminate branches (Fig. 1M, P-R) at a single node.

There is a conspicuous 1 to 3-cm gap with a smooth axis (without flowers or branches) at the apex of the pistillate portion (pp) in *T. domingensis* (Fig. 1A). This gap is generally not perceptible in *T. latifolia* (Fig. 1B), but when it is apparent it measures a few millimeters, as is also the case for *T. x provincialis* (Fig. 1C, D).

The staminate portion (sp) is formed by a few nodes below the indeterminate apex (Fig. S1 in supplementary material). It has achlamydeous staminate flowers that, as with its bracteoles (prophylls), appear to be inserted directly in the axis of synflorescence (Fig. 1E-H). This portion generally comprises 50-60 % of the fertile region in *T. domingensis* (Fig. 1A) and 30-40 % in *T. latifolia* (Fig. 1B). This character is highly variable (30-60 %) in *T. x provincialis*, even in a same population (Fig. 1C, D). Anthesis of staminate flowers is not perceived externally in *T. domingensis* (Fig. 1A) and is noticed only by anther dehiscence. The prophylls in this species are brown in color in their distal portions, are conspicuous and cover the apices of the staminate flowers during all phases of synflorescence development (Fig. 1E, I, asterisks). Anthesis of staminate flowers is perceptible in *T. latifolia* (Fig. 1B) due to the sudden lengthening of the filaments (about 3x in a few hours) (Fig. 1H). The prophylls in this species resemble trichomes (Fig. 1F, J, asterisks). Populations of *T. x provincialis* have individuals with one or the other behavior of the staminate flowers in the anthesis (Fig. 1C, D, S1 in supplementary material), although the prophylls are never conspicuous (Fig. 1G, asterisk), such as those of *T. domingensis*.

The pistillate portion contains fertile and sterile flowers that are densely arranged in many branches of a single node (Fig. 1M, P-R). The mature pp of *T. domingensis* has a brown surface formed by the apices of the prophylls and stigmas; they are often deciduous, thus exposing the sterile flowers (Fig. 1K). In contrast, the surface of the pp of *T. latifolia* is formed exclusively by apices of the stigmas (Fig. 1L, M), which overlap densely and cover the sterile flowers. Only the bases of the branches remain in this region after fruit is dispersed in *T. domingensis* (Fig. 1P). The axes of branches remain entire after fruit is dispersed in *T. latifolia* (Fig. 1Q, R), which is also the case for *T. x provincialis*. Prophylls at the apex of the pp (Fig. 1 N, O) are distinguished by size and density in *T. domingensis* (Fig. 1N), whereas *T. latifolia* does not have prophylls (Fig. 1O); prophylls of *T. x provincialis* may occur only in this region or be absent throughout the pp.

Pherophylls were not observed in the mature synflorescences, although long bracts are clearly seen in the basal node of the pistillate portion and in the nodes of the staminate portion before maturing of the synflorescence in *T. latifolia* and *T. x provincialis* (Fig. S1 in supplementary material).

Synflorescence anatomy and development

The synflorescences of the analyzed species develop at the apex of a reproductive branch with few phytomers (Fig. 2A). Pherophylls emerge from each node and wrap their sheaths completely around the internode, giving the primary branch the aspect of a rosette. The peduncle is formed by some phytomers with pherophylls without axillary buds (Fig. 2A). Some nodes below the apical meristem, occur undifferentiated buds (lateral branches or second order branches) in the axil of each pherophyll of the fertile zone (Fig. 2B). The bud surrounds the axis of the synflorescence and consists of a meristem whose surface expands with synflorescence elongation (concaulescent bud), through predominantly anticlinal proliferation, initially not producing branches, be they flowers or third order branches (Fig. 2C, D).

In the first phases of synflorescence development it is impossible to distinguish the buds that give rise directly to staminate flowers from those that will produce indeterminate third order branches, except for their position (Fig. 2B-D). The surface of the undifferentiated buds grows until the synflorescence becomes several centimeters long, at which point the differentiation of the staminate portion (sp) begins (Fig. 2C, D). Only after this phase do the indeterminate branches rise in the pistillate portion (pp)

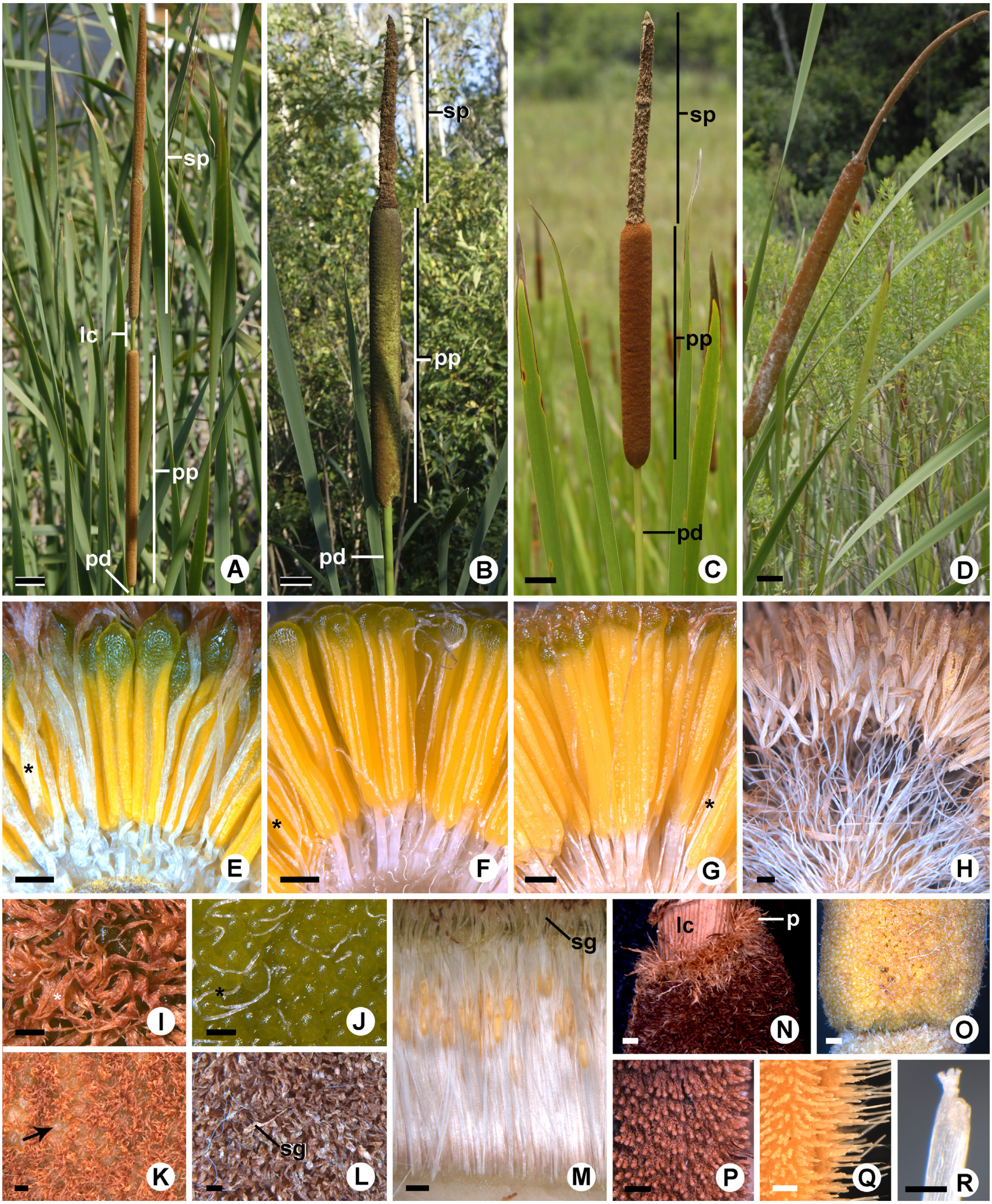

Figure 1. Morphology of the mature synflorescence. **A, E, I, K, N, P, R.** *T. domingensis*. **B, F, L, M, Q.** *T. latifolia*. **C, D, G, H, K, O.** *T. x provincialis*. **A-D.** synflorescence morphology after dispersion of the pollen grains. **E-H.** transverse sections of the axes of the staminate portions of the synflorescences (staminate flowers seen longitudinally). **H.** elongated filaments and twisted anthers in anthesis. **I-L.** surface of the two portions of the synflorescences. **M.** cross section of the axis of the pistillate portion of the synflorescence (pistillate flowers seen longitudinally). **N-O.** apices of pistillate portion. **P-R.** branches of the pistillate portion. lc: gap between the staminate and pistillate portions. p: bracteoles (prophylls), at the apex of the pistillate portion in *T. domingensis*. pd: peduncle. pp: pistillate portion. sg: stigma. sp: staminate portion. Arrow: exposed apices of sterile pistillate flowers. Bars: A-D = 2 cm; E-L = 500 μm; M-Q = 1 mm; R = 100 μm.

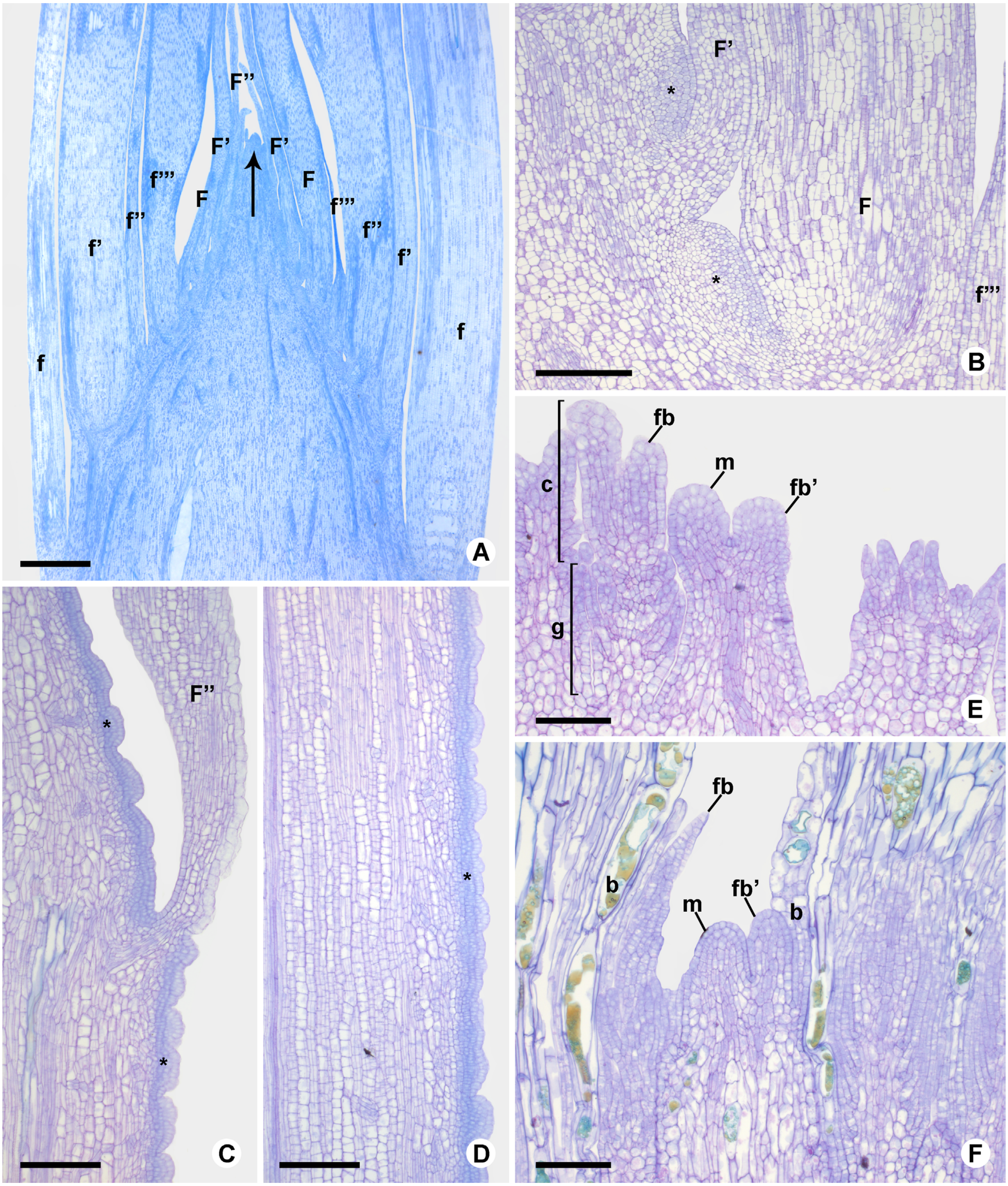

Figure 2. Initial development of the synflorescence. **A-E.** *T. latifolia*. **F.** *T. domingensis*. **A.** primary branch at the initial development of the synflorescence. **B.** detail of the axillary buds (second order branches). **C, D.** expansion of the surface of the axillary buds. **E, F.** third order branches in the pistillate portion. f; f'; f'', f''': sequence of pherophylls from the inhibition zone (no axillary buds) corresponding to the peduncle nodes. F, F', F'': sequence of pherophylls of the fertile zone. b: bracteole (prophyll) c: carpellary leaf. g: gynophore. fb and fb': floral buds in the development sequence. m: apical meristem. Asterisks: axillary buds (second order branches). Arrow: indeterminate apex of the primary branch. Bars: A-D = 500 µm; E-F = 200 µm.

(Fig. 2E, F), although its surface continues to grow until the inflorescence measures several centimeters. The staminate flowers arise directly from the bud (secondary branch), which does not produce third order branches (Fig. 3A). The third order branches arise similarly in both *T. domingensis* and *T. latifolia* as protuberances on the surface of the bud that produce, initially, flowers that appear to rise directly from the surface of the bud (Fig. 3B). The first flowers to appear are fertile and initially develop by elongation of the gynophore (Fig. 2E), which gradually produces many verticillate trichomes at different heights (Fig. 3C, D). While the gynophore becomes longer, the locule develops by apical

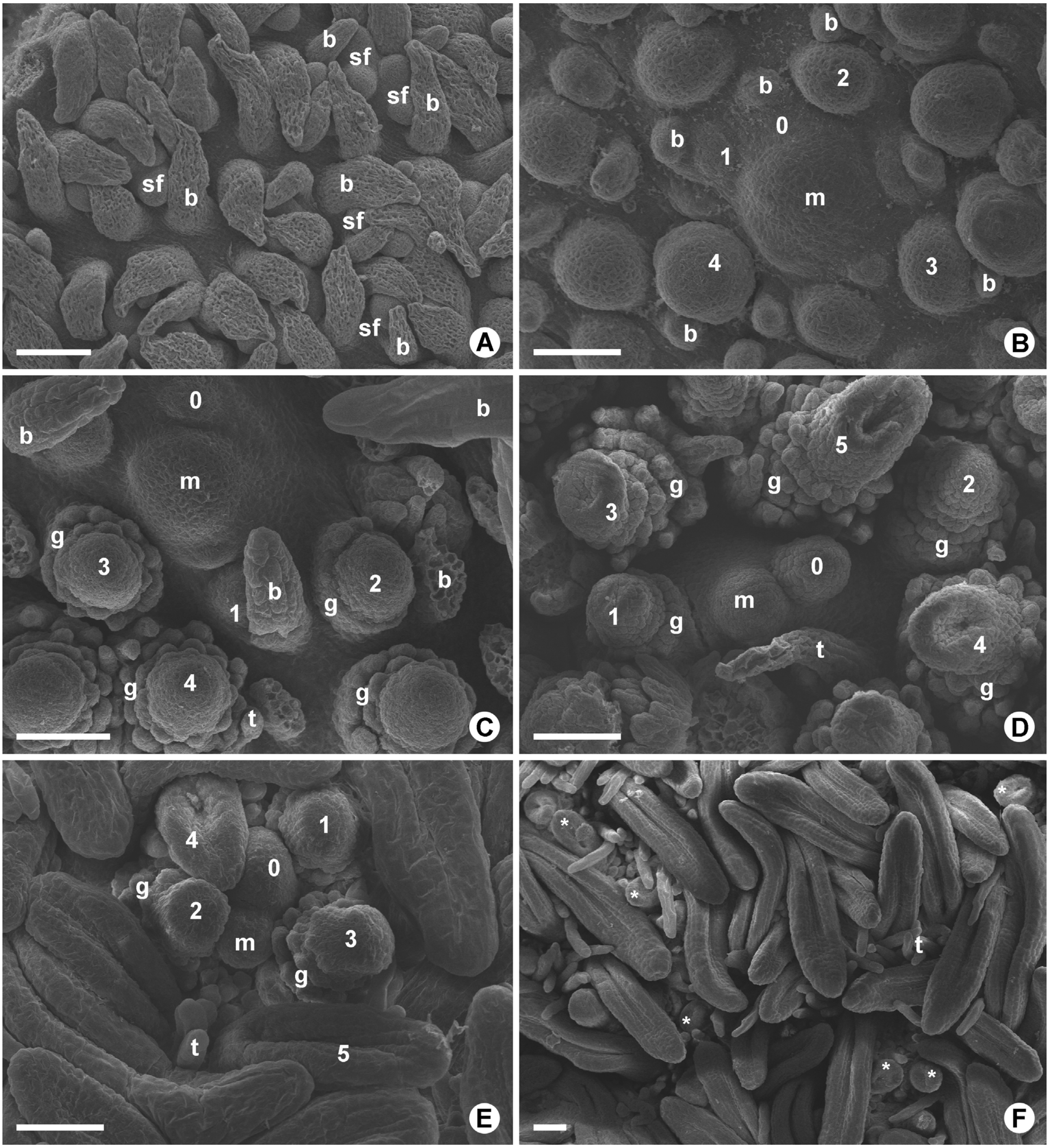

Figure 3. Morphology and development of immature synflorescences under scanning electron microscopy. A-C**.** *T. domingensis*. D-F**.** *T. latifolia*. A: staminate portion at the initiation of flower development. Some prophylls (bracteoles) and flowers are indicated. A-E**.** development of the third order branches in pistillate portion. b: bracteole (prophyll). m: apical meristem of the third order branches. g: gynophore. The numbers from 0 to 5 represent development sequences of the flowers in the context of each image. Asterisks: sterile flowers. Bars: A- D = 50 µm; E = 100 µm; F-G = 500 µm.

invagination of the carpellary primordium, and is initially cupulate, becoming concave (Fig. 3D), until the still sessile stigma differentiates to the ovarian region (Fig. 3E). With the elongation of the third order axes of the pp, new fertile flowers develop until a given height, at which point sterile flowers that do not develop stigmas are produced, although they are also invaginated to form the locule (Fig. 3F). In *T. domingensis*, each flower is subtended by a prophyll that early-on lengthens and covers the undifferentiated flowers (Fig. 3C).

In the mature inflorescence (Fig. 4A-E), the third order branches are organized similarly in both species, with fertile flowers at the base and a sterile flower at the apex (Fig. 4A), both with many trichomes in the gynophore. At the apex of the pp of *T. latifolia*, the differentiating bud produces a prolongation that wraps around the apical portion of the internode (non-concaulescent portion) (Fig. 4B, C), which appears to be covered by branches and flowers. In *T. domingensis* the apex of the pp is covered by large, vascularized prophylls and by its respective flowers, which are contiguous with the apical portion of the internode, which is smooth (Figs. 1N, 4D, E).

Discussion

Structural characteristics of the inflorescences of species of *Typha* have been used for taxonomic purposes by several authors, especially to characterize species and hybrids (Smith 1967; Krattinger 1975; Finlayson *et al.* 1985; Grace & Harrison 1986; Smith 1986). The presence of bracteoles (prophylls) in the pistillate flowers, the gap separating the two portions of the synflorescence, the coloring and surface of the pistillate portion and the relative proportion of these two portions in the fertile region of the synflorescence were the main diagnostic characteristics of synflorescences used by these studies. We confirmed the efficacy of these characters to delimit species and hybrids, including those that are difficult to observe, such as the color of the mature inflorescence. However, these characters must be meticulously evaluated for the correct identification of species; the failure to do so has led to many mistakes, not only because there is overlap in the characters, but also because there has been no consensus about morphological nomenclature, as proposed in the present study. Furthermore, several of these characteristics are exclusive to the pistillate portion of the synflorescence, while there has been no specific study of the different forms of anthesis of staminate flowers, probably because the latter are absent at the time fruit are dispersed (Wilder 1990). The two behaviors of staminate flowers observed in the present study — elongation of the filaments in *T. latifolia*; anthesis not perceptible in *T. domingensis* — are combined with other characters that are related to two distinct pollination strategies, which tend to facilitate or prevent self-pollination in the two species. Some of these characteristics have been reported in the literature (Krattinger 1975) for several species. For example, *T. domingensis* and *T. angustifolia* have pollen grains in monads, which are lighter, and a greater distance between pistillate and staminate flowers (a tendency to avoid self-pollination). In contrast, *T. latifolia* and *T. shutterworthii,* for instance, have pollen grains in tetrads, which are thus heavier, and contiguous portions of the synflorescence (characteristics that facilitate self-pollination). These characters have been related to greater reproductive success in *T. angustifolia* compared to *T. latifolia* in natural populations (Krattinger 1975). The dimorphism of prophylls in the pistillate portion of *T. domingensis* and the elongation of the stamens in *T. latifolia* are first reported here for the genus. These characteristics may also have implications in the reproductive success, and so they need to be investigated from a functional standpoint.

Hybrids among species of *Typha* may have even greater reproductive success than their respective parental species, and may even overtake *T. latifolia* in natural populations (Smith 1967; Krattinger 1975). These authors relate this success to the presence of viable pollen grains and seed in naturalized hybrids and to variation in these characters in hybrid populations, as often occurs with the different phenotypes of *T. x provincialis*, although this morphological variation has not been investigated by combining data of pollination biology and genetics.

The structure of the inflorescence of *Typha* was interpreted by Müller-Doblies (1970) as an indeterminate branched system, with the node of the pistillate portion being homologous with each of the nodes of the staminate portion, but with many third order branches that are also indeterminate. Thus, from the structural standpoint, the inflorescence of both *Sparganium* and of *Typha* consists of a polytelic system with many nodes, and therefore represents a synflorescence that is interpreted here as a homothetic compound raceme (therefore without flowers directly inserted in the main florescence) with sessile flowers. Specifically, since one of the secondary axes of the raceme generates third order branches, this synflorescence is a triple homothetic raceme, which is very distinct from the different non-homologous interpretations presented for the typology of this synflorescence, exemplified in Figure 5 (I, II and III).

The compact synflorescence of *Typha*, with indeterminate second order branches and third order branches on only one distal node, was recurrently treated as a compound spike to avoid new nomenclature (Krattinger 1975; Wilder 1990). The difficulty in interpreting this system arises because it contradicts two concepts for spikes and racemes: *sensu* Troll (1964; 1969) adopted by Weberling (1989) and a more current revision proposed by Endress (2010). The first authors prioritize the presence of sessile flowers in an indeterminate system to distinguish spikes from racemes.

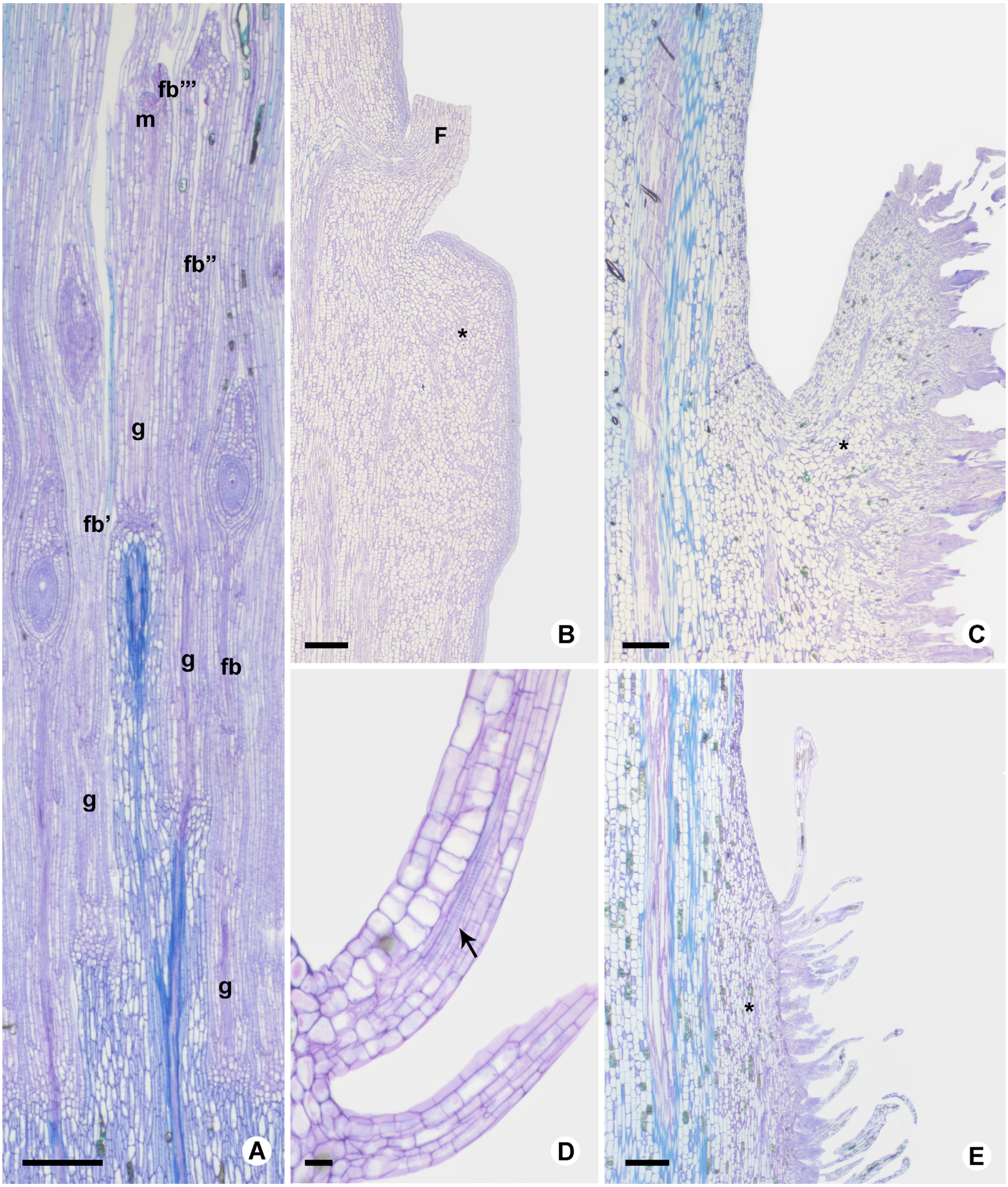

Figure 4. Anatomy of the pistillate portion. A-C**.** *T. latifolia*. D-E**.** *T. domingensis*. A**.** third order branch with fertile flowers at the base and sterile at the apex. B-E**.** apices of the pistillate portion. B**.** at immature synflorescence. C**.** at mature synflorescence. D**.** detail of vascularized prophyll. E**.** apex of the mature pistillate portion in *T. domingensis*. fb, fb', fb'' and fb''': floral buds in the development sequence. fb and fb': fertile flowers. fb'' and fb''': sterile flowers. g: gynophore. m: apical meristem of the third order branches. F. pherophyll of the first node of the staminate portion. Asterisk: apex of the pistillate bud (second order branch). Arrow: vascular bundle. Bars: A-B = 500 µm; C, E = 1000 µm; D = 50 µm.

Endress (2010) considers a raceme to be any indeterminate inflorescence with primary and secondary long branches, independently of the presence of pedicels, and spikes as inflorescences with long primary, but short secondary branches. According to this definition, however, how would a double heterothetic raceme be classified since it has short (flowers) and long (indeterminate) second-order branches? There is thus a need to extend the concepts of both authors to classify more complex synflorescences. The type proposed here, therefore, is not in accordance with both definitions for spikes, since the primary axis of the synflorescence of *Typha* do not contain directly-inserted (second order

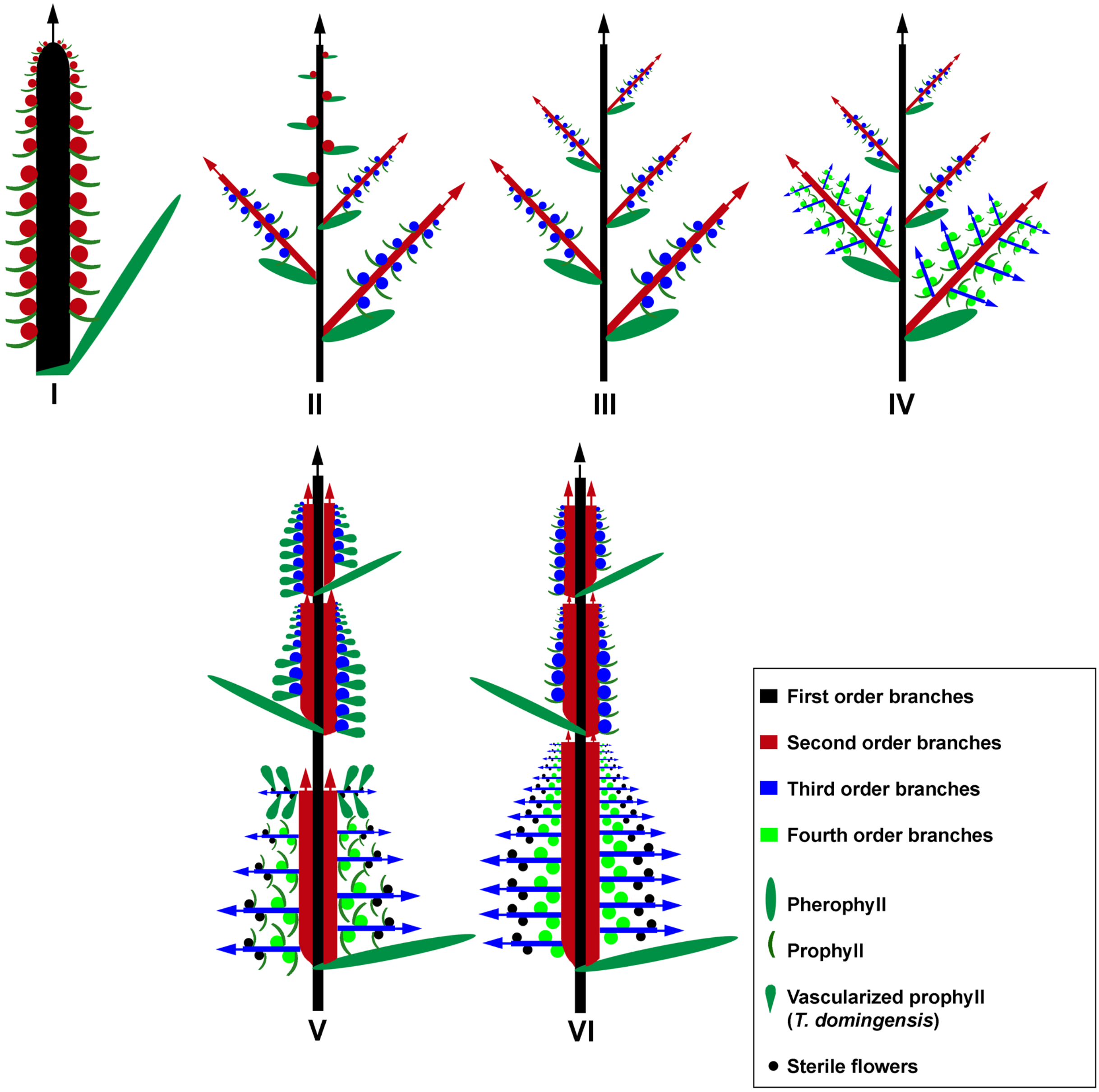

Figure 5. Diagram of the synflorescences of *T. domingensis* and *T. latifolia* and different indeterminate inflorescences. I, II and III: non-homologous models for the synflorescence of *Typha*. I: spadix, a type of simple spike. In this case the pherophyll of the apical bud is called the spathe. Flowers are second order branches. II: compound spike or heterothetic double raceme with sessile flowers. The main florescence (apical) produces flowers directly as second order branches, while below it, in the enrichment zone, indeterminate second order branches produce flowers as third order branches. III: homothetic double raceme with sessile flowers. All of the indeterminate branches produce flowers directly (third order branches). In this case, there is no apical florescence with directly inserted flowers. IV: homothetic triple raceme with sessile flowers, a type homologous to the synflorescence of *Typha*. In this case the distal second order branches again generate indeterminate branches (third order branches), and the flowers are fourth order branches in this portion. V and VI: synflorescences of *T. domingensis* (V) and *T. latifolia* (VI). The inflorescence of *Typha* is homologous to a homothetic triple raceme (IV), but with only a single distal second order branch (pistillate portion) with third order indeterminate branches. Details of the structure of these synflorescences are discussed in the text.

branches) flowers. A compound spike (*sensu* Weberling 1989) or heterothetic double raceme with sessile flowers (Endress 2010) has flowers directly inserted in the axis of the synflorescence apex (subtended by pherophylls), below which indeterminate branches appear in the axils of the pherophylls (Fig. 5-II). In *Typha*, on the other hand, the first apical phytomer is minimal and does not directly produce flowers. The staminate flowers are formed from second-order branches many nodes below the apical meristem, which characterizes a homothetic compound raceme (without flowers inserted in the primary axis). However, given the third order branches in the pistillate portion, it is not possible to classify this synflorescence as a double raceme (Fig. 5-III), but instead as a triple raceme (Fig. 5-IV), although with a single second order branch (the pistillate portion) generating third order branches. The impression that the flowers appear directly from the primary axis comes from the form of growth of the second order branches of the raceme, which are contiguous to the superior internode and expand on its surface (Fig. 5-V and VI), a phenomenon also observed by Müller-Doblies (1970).

The similarities in the development of the pistillate portion of the synflorescence of *T. domingensis* and *T. latifolia* allow generalizing the stages of development of the flower and the third order branches for the two species, with the exception being the presence of prophylls in the pistillate flowers, which is exclusive to *T. domingensis* (Fig. 5-V and VI). The presence of a smooth region at the apex of the axis of the pistillate portion in different species of *Typha* is considered one of the main diagnostic characteristics for species, although there is variation in the length of this region even in individuals of the same population, and especially in hybrid populations (Smith 1967). *Typha latifolia* is characterized by the absence of this gap in the mature inflorescence (Krattinger 1975; Kim & Choi 2011), although there may be a small gap in young inflorescences. The additional data presented here allow the absence of this gap to be interpreted as the concaulescence of the bud (second order branch) hiding the upper portion of the internode because of its surface expansion. This does not occur in *T. domingensis*, in which concrescence of the second order branch of the pistillate portion does not occur, which also accounts for the smaller proportion of the pistillate portion in relation to the staminate portion in this species.

Conclusions

This study proposes new morphological characteristics for the synflorescences of *Typha domingensis*, *T. latifolia* and *T.* x *provincialis*, that are effective in delimiting these species and the putative hybrid. These characteristics include different morphologies of the prophylls in each of the portions of synflorescence and two different forms of anthesis of the staminate flower. The synflorescence is classified as a homothetic triple raceme based on anatomical and ontogenetic evidence. Anatomical and developmental analyses of the pistillate portion were also important for understanding the formation of the gap or the proximity between the two portions of synflorescence in *T. domingensis* and *T. latifolia*. This gap is related to the concrescence of the secondary branch (bud) to the superior internode. The application of these data and the interpretations proposed in this study to other species would help to better understand the evolution of these characteristics in *Typha* and should serve as a basis for the interpretation of homologies between the different structures of the synflorescences of species of the genus.

Acknowledgements

We thank the Laboratório de Anatomia Vegetal (LAVeg: Plant Anatomy Laboratory) at the Universidade Federal do Rio Grande do Sul (Federal University of Rio Grande do Sul -UFRGS) for technical support. This work was supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq: National Council for Scientific and Technological Development) and the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES: Coordination of Improvement of Higher Education Personnel).

References

APG – Angiosperm Phylogeny Group IV. 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Botanical Journal of the Linnean Society 181: 1-20.

Endress PK. 2010. Disentangling confusions in inflorescence morphology: patterns and diversity of reproductive shoot ramification in angiosperms. Journal of Systematics and Evolution 48: 225-239.

Finlayson M, Forrester RI, Mitchell DS, Chick AJ. 1985. Identification of native *Typha* species in Australia. Australian Journal of Botany 33: 101-107.

Gabriel BL. 1982. Biological electron microscopy. New York, Van Nostrand Reinhold Company.

Gerrits PO, Smid L. 1983. A new less toxic polymerization system for the embedding of soft tissue in glycol methacrylate and subsequent preparing of serial sections. Journal of Microscopy 132: 81-85.

Gerstberger P, Leins P. 1978. Rasterelektronmikroskopische Untersuchungen an Blutenknospen von *Physalis philadelphica* (Solanaceae). Anwendung einer neuen Praparationsmethode. Berichte der Deutschen Botanischen Gesellschaft 91: 381-387

Grace JB, Harrison S. 1986. The biology of Canadian weeds. 73. *Typha latifolia* L., *Typha angustifolia* L. and *Typha x glauca* Godr. Canadian Journal of Plant Science 66: 361-379.

Kim C, Choi H-K. 2011. Molecular systematics and character evolutivon of *Typha* (Typhaceae) inferred from nuclear and plastid DNA sequence data. Taxon 60: 1417-1428.

Krattinger K. 1975. Genetic mobility in *Typha*. Aquatic Botany 1: 57-70.

McDowell EM, Trump BR. 1976. Histological fixatives for diagnostic light and electron microscopy. Archives of Pathology & Laboratory Medicine 100: 405-414.

Müller-Doblies U. 1970. Über die Verwandtschaft von *Typha* und *Sparganium* im Infloreszenz-und Blütenbau. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 89: 451-562.

Nogueira FM, Kuhn SA, Palombini FL, *et al*. 2017. Tank-inflorescence in *Nidularium innocentii* (Bromeliaceae): three-dimensional model and development. Botanical Journal of the Linnean Society 185: 413-424.

O'Brien TP, McCully ME. 1981. The study of plant structure – principles and selected methods. Melbourne, Termarcarphi Pty.

Reitz R. 1984. Tifáceas. In: Reitz R. (ed.) Flora Ilustrada Catarinense. Itajaí, Herbário Barbosa Rodrigues.

Sidman RL, Mottla PA, Feder N. 1961. Improved polyester wax embedding for histology. Stain Technology 36: 279-284.

Smith SG. 1967. Experimental and natural hybrids in North America *Typha* (Typhaceae). The American Midland Naturalist 78: 257-287.

Smith SG. 1986. The cattails (*Typha*): interspecific ecological differences and problems of identification, Lake and Reservoir Management 2: 357-362.

Stützel T, Trovó M. 2013. Inflorescences in Eriocaulaceae: taxonomic relevance and practical implications. Annals of Botany 112: 1505-1522.

Troll W. 1964. Die Infloreszenzen. Typologie und Stellung im Aufbau des Vegetionskörpers, Bd. 1. Jena, Fisher.

Troll W. 1969. *Die* Infloreszenzen. Typologie und Stellung im Aufbau des Vegetionskörpers, Bd. 2, 1. Stuttgart, Fisher

Weberling F. 1989. Morphology of flowers and inflorescences. Cambridge, Cambridge University Press.

Wilder GJ. 1990. Normal and teratological pistillate spikes of *Typha angustifolia* (Typhaceae): gross aspects of morphology, anatomy, symmetry, and inflorescence dehiscence. Canadian Journal of Botany 69: 321-335.