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UNDERSTANDING SPIKELET ORIENTATION IN PANICEAE (POACEAE)[1]

CHRISTIAN A. ZANOTTI[2], RAÚL POZNER, AND OSVALDO MORRONE

Instituto de Botánica Darwinion, Labardén 200. C.C. 22, B1642HYD San Isidro, Buenos Aires, Argentina

Spikelet structure and grouping are key characters to identify grasses. Here we tested the possibility that spikelet pairs, a distinctive morphological structure of many Andropogoneae and Paniceae, are the starting point for a secondary single spikelet condition that can also explain the change of spikelet orientation among Paniceae genera. As a first approach, we studied the inflorescence development of *Paspalum simplex*, *P. stellatum*, and *Axonopus sufultus* to clarify the origin of the spikelet orientation and other basic homologies. The results support that solitary spikelets of *A. suffultus* are homologous to the subsessile spikelets of *P. simplex* and that solitary spikelets of *P. stellatum* are homologous to the pedicellate spikelet of *P. simplex*. This last homology supports that spikelet orientation results from a differential reduction/abortion of either the pedicellate or the subsessile spikelet primordia. We also discuss the possibility that the RAMOSA and polar auxin pathways could play a role in the abortion of the lateral subsessile spikelets in *P. stellatum*. However, the apical meristem inhibition observed in *A. suffultus* and *P. stellatum* seems to depend on a very different genetic control, suggesting that the single spikelet condition is homoplasic within Paniceae and derived from at least two different genetic mechanisms.

Key words: *Axonopus*; development; homology; inflorescence; Paniceae; *Paspalum*; Poaceae; spikelet.

Grasses form one of the largest angiosperm families, and their classification is very difficult to assess. Many efforts have been recently made to improve the classification of the grass family using several molecular markers as well as morphological characters (GPWG, 2001). Among the latter, the structure and organization of spikelets in the inflorescence are two of the most relevant morphological characters. Within an inflorescence, spikelets may be borne as single units or in pairs. Spikelet pairs are very significant for grass systematics and evolution, and their production is an important synapomorphy, particularly for the tribes Andropogoneae (Le Roux and Kellogg, 1999; Kellogg, 2000) and Paniceae (*Paspalum* [Kellogg, 2000], *Urochloa* [R. Reinheimer, Universidad Nacional del Litoral, Santa Fe, Argentina, unpublished data], *Ixophorus* [Kellogg et al., 2004], and the bristle clade [Doust and Kellogg, 2002b]). The spikelet pair is also an important evolutionary unit as a starting point for the origin of solitary spikelets, particularly when the spikelets of the pair are not identical, because that could also explain the change of single spikelet orientation among genera of Paniceae. A recent study of maize (Wu et al., 2009) has shown that mutants of the *suppressor of sessile spikelets1* (*sos1*) produce solitary spikelets instead of paired ones, supporting the origin of solitary spikelets from spikelet pairs, at least in Andropogoneae. These data become even more interesting when applied to Paniceae because the same phenomenon could explain why some Paniceae members produce solitary spikelets with the fertile lemma toward the rachis (adaxial position or adaxial spikelet), while others produce spikelets with inverted orientation (abaxial position or abaxial spikelet). The genera *Paspalum* L. and *Axonopus* P. Beauv constitute a representative case study of this problem. *Paspalum* is one of the most important genera of Paniceae, gathering about 330 species mainly from tropical, subtropical, and temperate areas of America (Zuloaga and Morrone, 2005). *Paspalum* forms a highly supported monophyletic clade together with the species of *Thrasya* (Duvall et al., 2001; Giussani et al., 2001; Aliscioni, 2002; Denham, 2005; Denham and Zuloaga, 2007; Souza-Chies et al., 2006), being *Anthenantiopsis* its closest genus. Although opinions still differ about the phylogenetic relationship between *Axonopus* and *Paspalum* (Gómez-Martínez and Culham, 2000; Giussani et al., 2001; Aliscioni et al., 2003), both genera are morphologically so close (Black, 1963; Hsu, 1965; Webster, 1992; Aliscioni, 2002) that the only difference between them is the spikelet orientation: solitary, subsessile, adaxial spikelets in *Axonopus* and paired (one pedicellate abaxial and one subssesile adaxial) or solitary, pedicellate, abaxial spikelets in *Paspalum* (Webster, 1988; Giraldo-Cañas, 2000, 2007; Zuloaga and Morrone, 2005). That change of spikelet orientation has been explained by means of two hypotheses: (1) the rotation hypothesis, which states that there is a 180° rotation of the pedicel (Clifford, 1987; Crins, 1991), and (2) the differential abortion hypothesis, which states that there is a differential abortion of the pedicellate abaxial spikelet in *Axonopus* (Cámara-Hernández and Rua, 1991; Rua, 1993). The rotation hypothesis lacks morphological support (Clifford, 1987; and O. Morrone, personal anatomical observations), whereas the differential abortion hypothesis is based on typological analysis (Cámara-Hernández and Rua, 1991; Rua, 1993) without developmental support. In a wider context of understanding inflorescence evolution in Paniceae, we tested the possible origin of change in spikelet orientation with a comparative developmental study of the inflorescences of *Paspalum simplex* Morong ex Britton (subgen. *Anachyris*; paired spikelets), *P. stellatum* Humb. & Bonpl. ex Flüggé (subgen. *Ceresia*; solitary, abaxial spikelets)

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[2] Author for correspondence (e-mail: czanotti@darwin.edu.ar)

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and *Axonopus suffultus* (J. C. Mikan ex Trin.) Parodi (solitary, adaxial spikelets).

The developmental sequences of *P. simplex*, *P. stellatum*, and *A. suffultus* inflorescences differ in (1) initiation and differentiation of the primary branches, (2) branching level and timing of truncation process, and (3) spikelet initiation. We suggest homologies between the main parts of adult inflorescences. The results support that the change in spikelet orientation is not produced by a 180° rotation in the pedicel, but by a differential reduction/abortion of the pedicellate or the subsessile spikelet primordium. Considering the close phylogenetic relationship between Andropogoneae and Paniceae, we discuss the possibility that the RAMOSA and polar auxin control pathways are involved in the reduction of spikelet pairs in *P. stellatum*. The case of *Axonopus suffultus*, where the single spikelet state has developed by suppression of the pedicellate, terminal spikelet suggests a very different genetic control affecting only apical meristems of a particular branching level, thus suggesting that apical meristem inhibition is sensitive to the branching order.

MATERIALS AND METHODS

Buds from *Paspalum simplex*, *P. stellatum*, and *Axonopus suffultus* at different stages of their reproductive development, taken from plants collected in the field and cultivated at the Darwinion Institute, Buenos Aires, Argentina (IBODA-CONICET-ANCEFN), were fixed in formalin-acetic acid-alcohol (FAA, Ruzin, 1999) from September 2007 until January 2009 (vouchers listed in Appendix 1). Buds were dissected with a Nikon SMZ-2T stereoscope. All the dissected, fixed material was dehydrated with a graded ethanol series up to absolute ethanol, transferred to pure acetone, and dried in a critical point drier (Baltec CPD 030) with CO_2 as the intermediate fluid. Mounted, metallized samples were photographed with a Philips XL30 scanning electron microscope at the scanning micrococopy service from the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Buenos Aires, Argentina). Mature, fresh inflorescences were photographed at the Darwinion Institute from plants in cultivation. Appendix 1 lists the vouchers consulted for the structural analysis of mature inflorescences. Descriptions of development and structure were based on the model used by R. Reinheimer (National University of Litoral, unpublished data) and Reinheimer et al. (2009).

RESULTS

Structure of the mature inflorescence—*Paspalum simplex* has radiate inflorescences with 4–21 primary branches that are spiral, alternate, and distant from each other. The main axis may either be truncated, ending in a sterile appendage (Figs. 1, 14) or end in a raceme morphologically identical to the primary branches (terminal raceme) (Figs. 2, 13). The distal primary branches are usually shorter than the basal, proximal primary branches (Fig. 2). The primary branches and the terminal raceme usually end with a terminal spikelet, although some samples showed the most distal primary branches also differentiated as sterile appendages like the main axis in truncate inflorescences. Spikelets are arranged in two rows of spikelet pairs (each pair containing a pedicellate spikelet and a subsessile spikelet). In some cases, the subsessile spikelet is reduced, and only the pedicellate one remains on the abaxial side of the primary branches and in the terminal raceme.

Paspalum stellatum produces either one (Fig. 4) or two unequal paired racemes (Fig. 6), truncated, with the rachis ending in a sterile appendage (Fig. 4). The main axis is reduced. Usually, the most distal spikelets of each raceme are not fully developed. There is an abcission zone at the base of the racemes, and two membranous scales usually grow between that joint and the racemes (Figs. 5, 26).

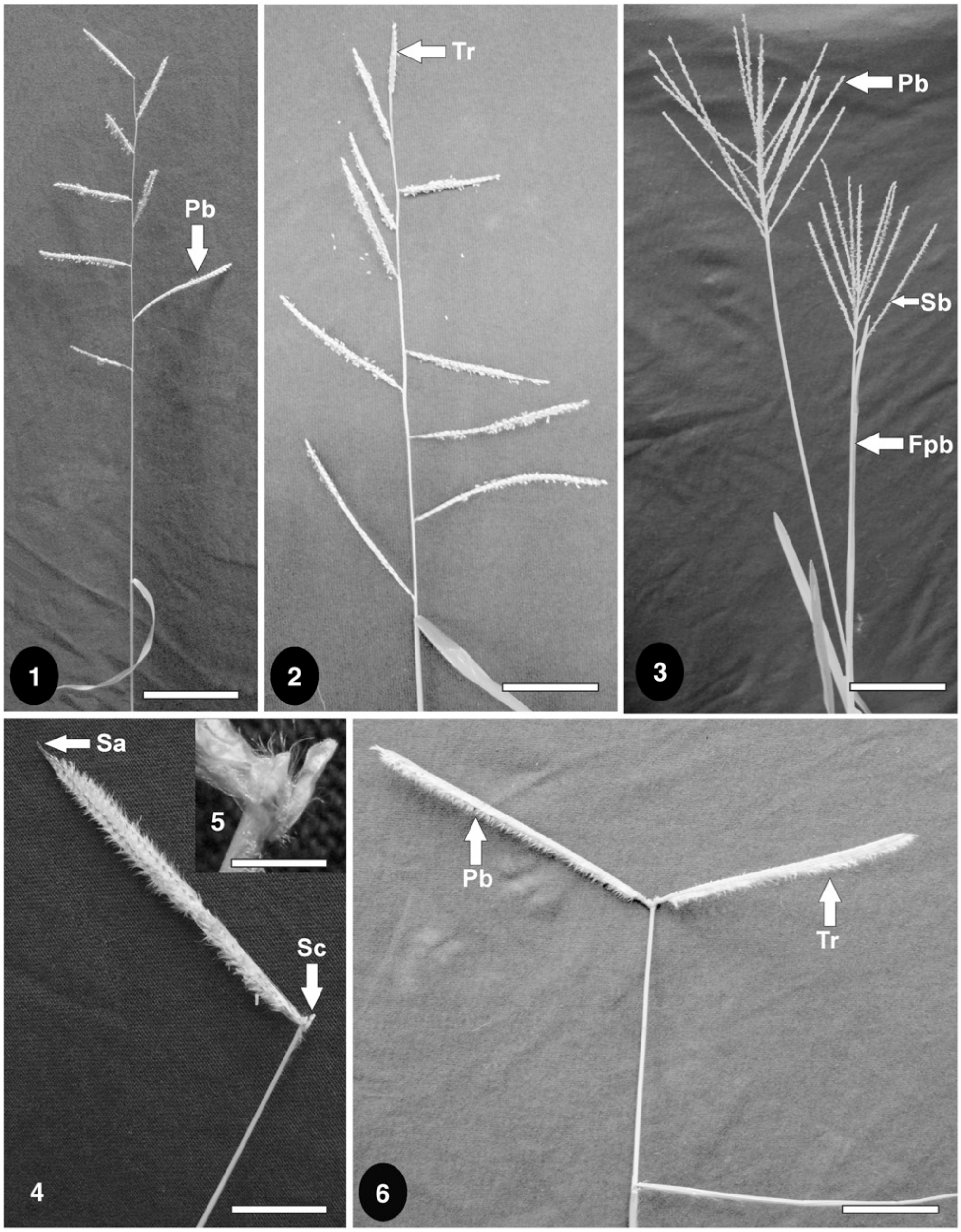
Axonopus suffultus develops a main axis with 12 to 23 primary branches, each of which always ends in a fertile spikelet. The main axis ends in a terminal raceme that ends in a fertile spikelet. The first basalmost primary branch develops 10 to 20 secondary branches, also ended in a terminal fertile spikelet. Primary and secondary branches are alternate, subopposite or verticillate, ascending, and divergent (Fig. 3). Spikelets are solitary, and the lateral ones are arranged with the upper lemma opposite to the bearing rachis (Fig. 43).

Development of the main axis and initiation of primary branches—In *P. simplex*, during vegetative growth, the apical meristem produces leaf primordia in a distichous array (Fig. 7). The first step indicating the switch to the reproductive phase in *P. simplex* is the elongation of the apical meristem above the last leaf primordium (Fig. 8). At the same time, the apical meristem initiates the primary branch primordia in a spiral pattern, giving a radiate symmetry to this first stage of the inflorescence development (Fig. 9). As the apical meristem progresses with the initiation of primary branch primordia, basal internodia begin their elongation, and basal primary branch primordia differentiates as primary branches (Fig. 10). The apical meristem of *P. simplex* may finally produce (1) a raceme morphologically identical to the primary branches (terminal raceme) (Figs. 11–13) or (2) a sterile appendage just after the last, most distal primary branch (Fig. 14), resulting in a truncated inflorescence. Primary branch primordia initiate acropetally in both truncate and nontruncate patterns.

Usually, the apical meristem of *P. stellatum* differentiates directly into a terminal raceme, an extreme case of inflorescence reduction (Fig. 24). Sometimes the apical meristem splits, before its elongation, into two meristems: one against the last leaf primordium and the other one opposite (see Figs. 18 and 19, last leaf primordium removed). Each apical meristem may develop into a raceme. The axillar one (primary branch, the one closer to the bract) is always delayed and shorter than the distal one (Figs. 20–22), resulting into bilateral inflorescences (or zygomorphic, if we also consider the bract) (Figs. 19, 23). Sometimes, only the distal meristem develops into a raceme, while the proximal lateral meristem (the one closer to the bract) remains arrested with only two lateral, flat appendages, that later become basal scales (Figs. 25, 26). Other cases of 1-raceme inflorescence do not show any remnant of a second meristem nor lateral appendages (Fig. 24).

The apical meristem elongation in *A. suffultus* does not clearly delimit the vegetative phase from the reproductive phase, and primary branches initiate before and after meristem elongation with different phyllotaxy. The first basalmost primary branch arises before the elongation of the apical meristem (during the vegetative phase, Fig. 32). The following two primary branches arise acropetally in a distichous arrangement after the apical meristem elongation (Fig. 33), substended by a bract (Fig. 34). The following primary branches continue the acropetal origin with a spiral arrangement; therefore, the inflorescence has a bilateral symmetry. The apical meristem finally differentiates a terminal raceme (Figs. 36–38).

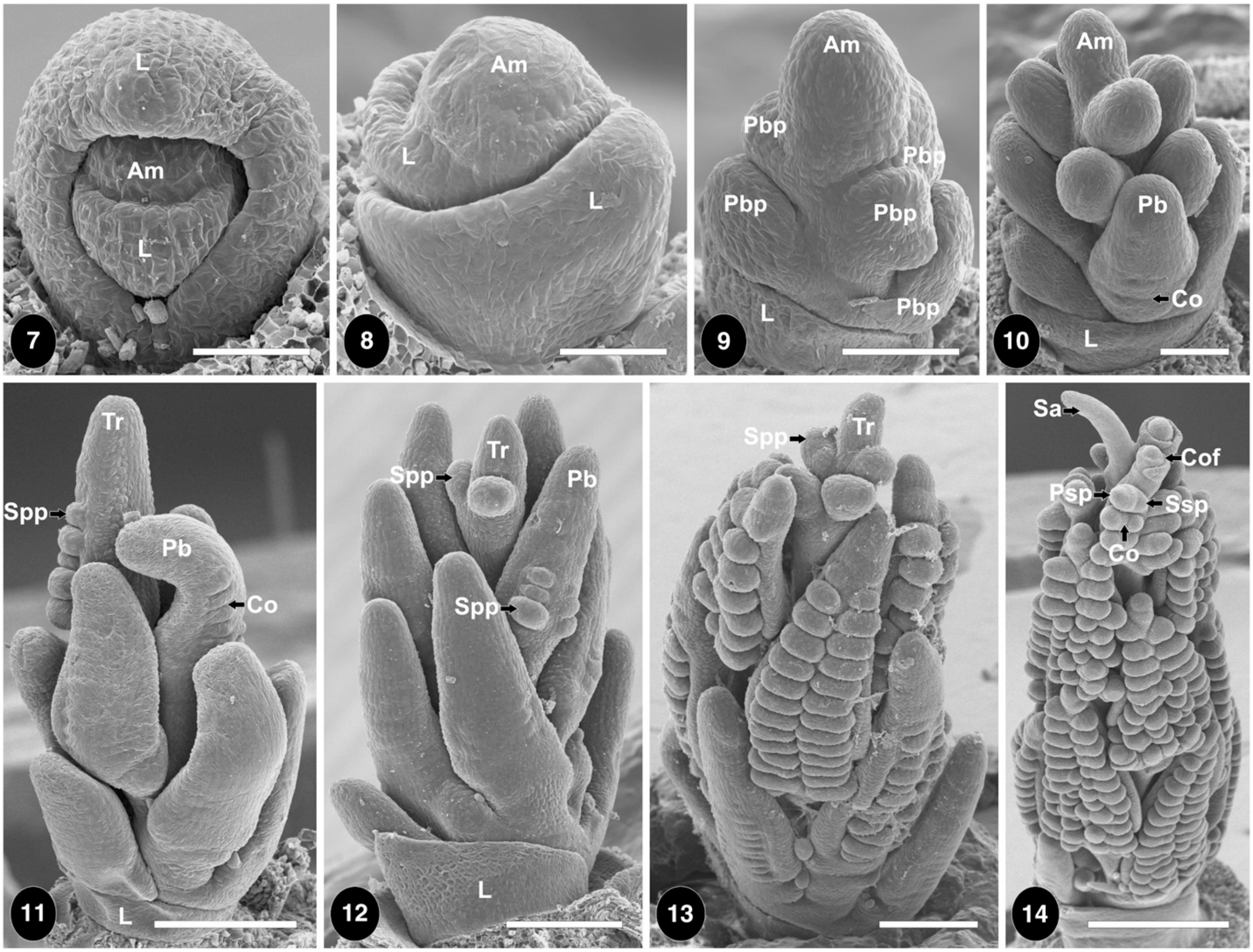
Differentiation of primary branches—The three species studied begin to differentiate the primary branches with two morphological changes before the initiation of spikelet primordia



Figs. 1–6. General morphology and structure of mature inflorescences of *Paspalum simplex*, *Axonopus suffultus*, and *P. stellatum*. **1.** *P. simplex*, truncated inflorescence. Bar = 5 cm. **2.** *P. simplex,* nontruncated inflorescence. Bar = 5 cm. **3.** *A. suffultus*, primary and secondary branches. Bar = 5 cm. **4.** *P. stellatum,* solitary inflorescence. Bar = 2 cm. **5.** Detail of the scales at the inflorescence base. Bar = 0.2 cm. **6.** *P. stellatum*, inflorescence with two racemes. Bar = 2 cm. *Figure abbreviations*: Am, apical meristem; Br, bract; Co, constriction; Cof, coflorescence; Fl, flower; Fm**,** floral meristem; Fpb, first basalmost primary branch; Gp, gynoecium primordium; L, leaf primordium (flag leaf); Lg, lower glume; Ll, lower lemma; Mf, main florescence; Mh, macrohair primordium; Pb, primary branch; Pbp, pimary branch primordium; Pr, prophyll of the first basalmost primary branch; Ps, pedicellate spikelet; Psb; secondary branches primordia; Psp, pedicellate spikelet primordium; Sa, sterile appendage; Sb, secondary branches of the first basalmost primary branch; Sb2, secondary branch of the basal primary branches; Sc, scales; Sp, stamen primordium; Spp, spikelet pair primordium; Ss, sessile spikelet; Ssp, sessile spikelet primordium; Tr, terminal raceme; Ug, upper glume; Ul, upper lemma; Up, upper palea; Wr, winged rachis.

or spikelet pair primordia: elongation and dorsiventral compression (*P. simplex*, Fig. 11; *P. stellatum*, Fig. 22; *A. suffultus*, Fig. 35). The terminal raceme of *P. simplex* shows an inverted order of developmental steps: first, the initiation of spikelet pair primordia (Figs. 12, 13), and then the elongation and dorsiventral flattening. In *P. stellatum*, the elongation of the apical meristems (1 or 2) is simultaneous with the elongation of the flag leaf (Figs. 20, 21), and the compression is deeper on the adaxial side of the primary branches and the terminal raceme (Fig. 22).

The differentiation of primary branches continues with the initiation of spikelet pair primordia (*P. simplex*) or spikelet primordia (*P. stellatum* and *A. suffultus*) in acropetal direction and subalternately arranged along each primary branch and terminal raceme



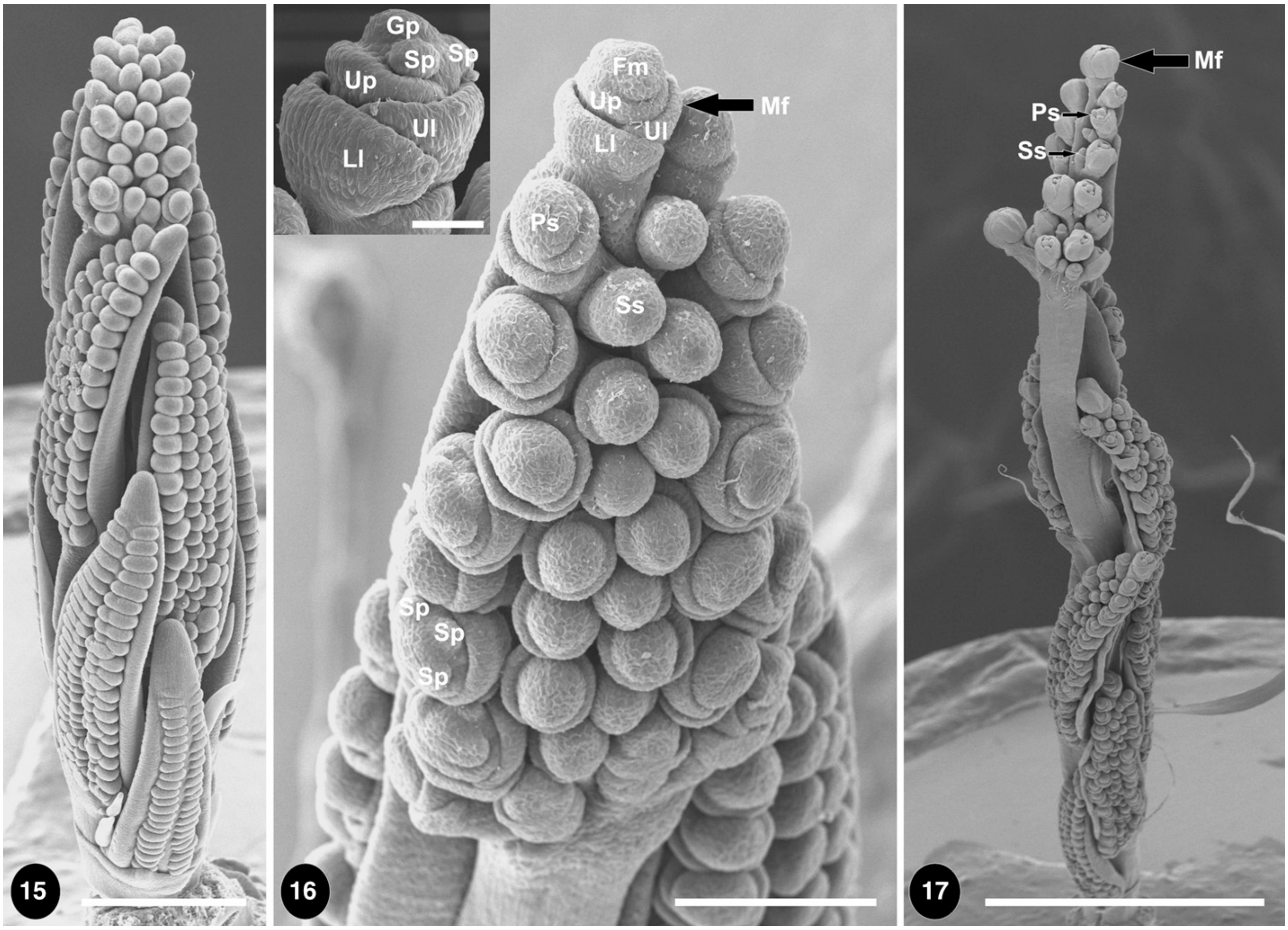
Figs. 7–14. Development of the main axis and primary branches in *Paspalum simplex* inflorescences. **7.** Apical meristem and two leaf primordia (vegetative phase). Bar = 50 µm. **8.** Transition to flowering. Bar = 50 µm. **9.** Acropetal initiation of primary branch primordia. Bar = 100 µm. **10.** Acropetal differentiation of primary branches and elongation of internodes. Bar = 100 µm. **11–13.** Basipetal differentiation of the terminal raceme and primary branches, and initiation of the pair-spikelet primordia. Bar = 200 µm. **14.** Sterile appendage in a truncate inflorescence, initiation of the pedicellate and subsessile spikelet primordia, and beginning of the differentiation of the distal primary branches. Bar = 500 µm.

(*P. simplex*, Fig. 10; *P. stellatum*, Fig. 22; and *A. suffultus*, Fig. 36). A few samples of *P. simplex* showed an acropetal pattern (Fig. 10), while most inflorescences followed a basipetal differentiation (Figs. 11–14). The acropetal pattern was observed only in the earliest stages of primary branch differentiation (Fig. 10).

Each spikelet pair primordium of *P. simplex* begins as a transverse constriction (Figs. 10, 11) and a further elongation followed by a dorsiventral compression on the abaxial side of each primary branch and in the terminal raceme (Fig. 13). Initiation of both the pedicellate and subsessile spikelet primordia in *P. simplex* occurs on the abaxial side of each primary branch and in the terminal raceme, and it is evident by an axial constriction (Fig. 14). This constriction originates two unequal primordia: the larger, outer one differentiates into a pedicellate spikelet, and the smaller, inner one forms the subsessile spikelet (Fig. 14). Spikelet primordia initiate acropetally along each primary branch and the terminal raceme, but follow a basipetal direction of initiation along the entire inflorescence (Fig. 15).

Spikelet primordia in *P. stellatum* arise dorsiventrally compressed from their very beginning (see Fig. 23). Initiation of spikelet primordia occurs together with the lateral expansion of the winged rachis, a typical feature of species of the subgenus *Ceresia*. The rachis expands laterally and progressively after the initiation of spikelet primordia, also in an acropetal direction (Fig. 23), sometimes entirely covering the spikelets (Fig. 31).

Spikelet primordia of *P. stellatum* and *A. suffultus* initiate as tranversal constrictions in the racemes (Figs. 22, 36), followed by a further elongation. Although spikelet initiation in *A. suffultus* occurs acropetally among primary branches, the first basalmost primary branch (the one initiated just before the switch to the reproductive phase) remains delayed in relation to the second and following distal primary branches (Figs. 35–37) that differentiate acropetally (Figs. 38, 39). By the time the distalmost primary branches begin to differentiate spikelets, the first basalmost primary branch initiates acropetally and differentiates secondary branch primordia (Fig. 39). In some cases,



Figs. 15–17. Spikelet differentiation in *Paspalum simplex*. **15.** Acropetal differentiation of spikelets within each primary branch and the terminal raceme. Bar = 500 μm. **16.** Acropetal initiation of bracts and fertile floral whorls. Bar = 200 μm. Bar of the upper left figure = 50 μm. **17**. Basipetal differentiation of spikelets considering the entire inflorescence. Bar = 2000 μm.

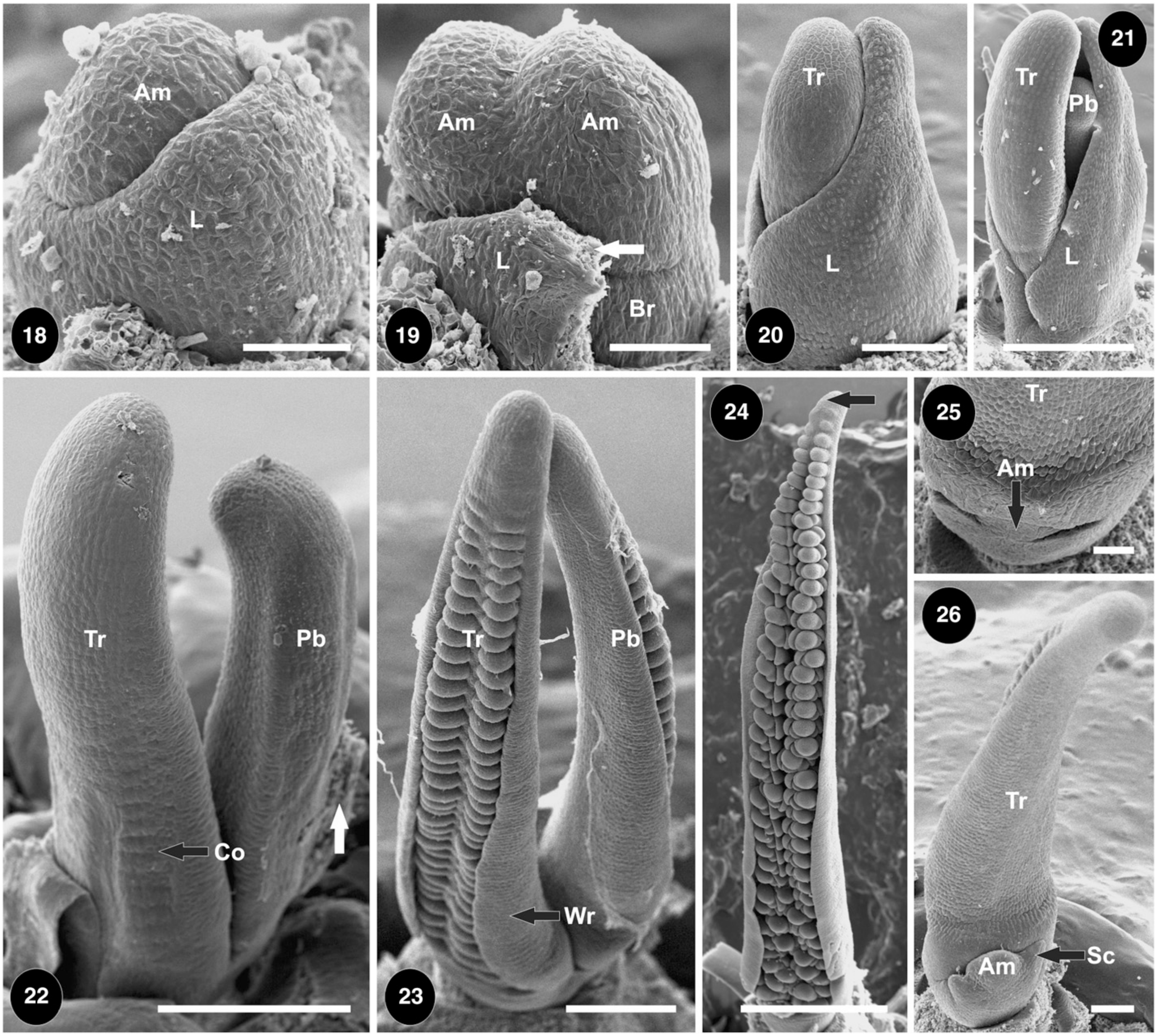
primordia of secondary branches differentiate on the basal primary branches (Figs. 39, 40), but do not progress and are not seen in the adult structure.

The differentation of secondary branches over the first basal-most primary branch is acropetal (Fig. 41).

Spikelet differentiation and initiation of floral whorls—Spikelet differentiation in *P. simplex* begins with a change in shape in both the pedicellate and subsessile spikelet primordia (Fig. 16), as well as in the coflorescence primordium of each primary branch (Fig. 14) and in the main florescence in nontruncate cases (Fig. 16). This change is evident by the initiation of the floral bracts (Figs. 14–16), which arise distichally surrounding the floral meristem in the following order: lower lemma, upper lemma, and upper palea. There is no evidence of glume initiation. The three stamen primordia arise simultaneously, followed by the initiation of the gynoecium. Both floral whorls arise soon after the initiation of the upper palea (Fig. 16). All spikelet structures arise acropetally. Both spikelet types initiate and differentiate acropetally along each primary branch and in the terminal raceme. However, in some cases, the coflorescence of the most distal primary branches (Fig. 14), as well as the main florescence in nontruncate cases (Fig. 16), are more differentiated than the proximal spikelets. Considering the entire inflorescence, spikelet initiation and differentiation is basipetal (Fig. 17). Pedicellate spikelets differentiate before subsessile spikelets, following an acropetal pattern (Fig. 16).

During spikelet differentiation in *P. stellatum* and *A. suffultus*, the shape of spikelet primordial also changes and follows an acropetal pattern along each raceme. Spikelet differentiation in *A. suffultus* starts with the inception of the upper glume, opposite to the subtending branch (Fig. 42). The lower lemma of the lower neuter floret initiates in second term toward the subtending branch, followed by the lemma (opposite to the subtending branch) and palea of the upper floret (Fig. 43). Both lateral stamens arise almost simultaneously, followed by the dorsal stamen (Fig. 44) and later by the gyneocium (Fig. 45). There was no evidence of lower gluma, lower palea, or lower floret. In a few cases, a meristem arises in adaxial position, but it does not differentiate bracts or fertile parts (Fig. 42).

Spikelet differentiation in *P. stellatum* follows the same pattern as that described for the other species studied (Figs. 27–29), but the upper glume is in abaxial position. The floral meristem of the lower flower is not formed. Stamen primordia arise simultaneously and begin when the upper glume covers the upper lemma completely (Fig. 30). At the same time, the upper glumes



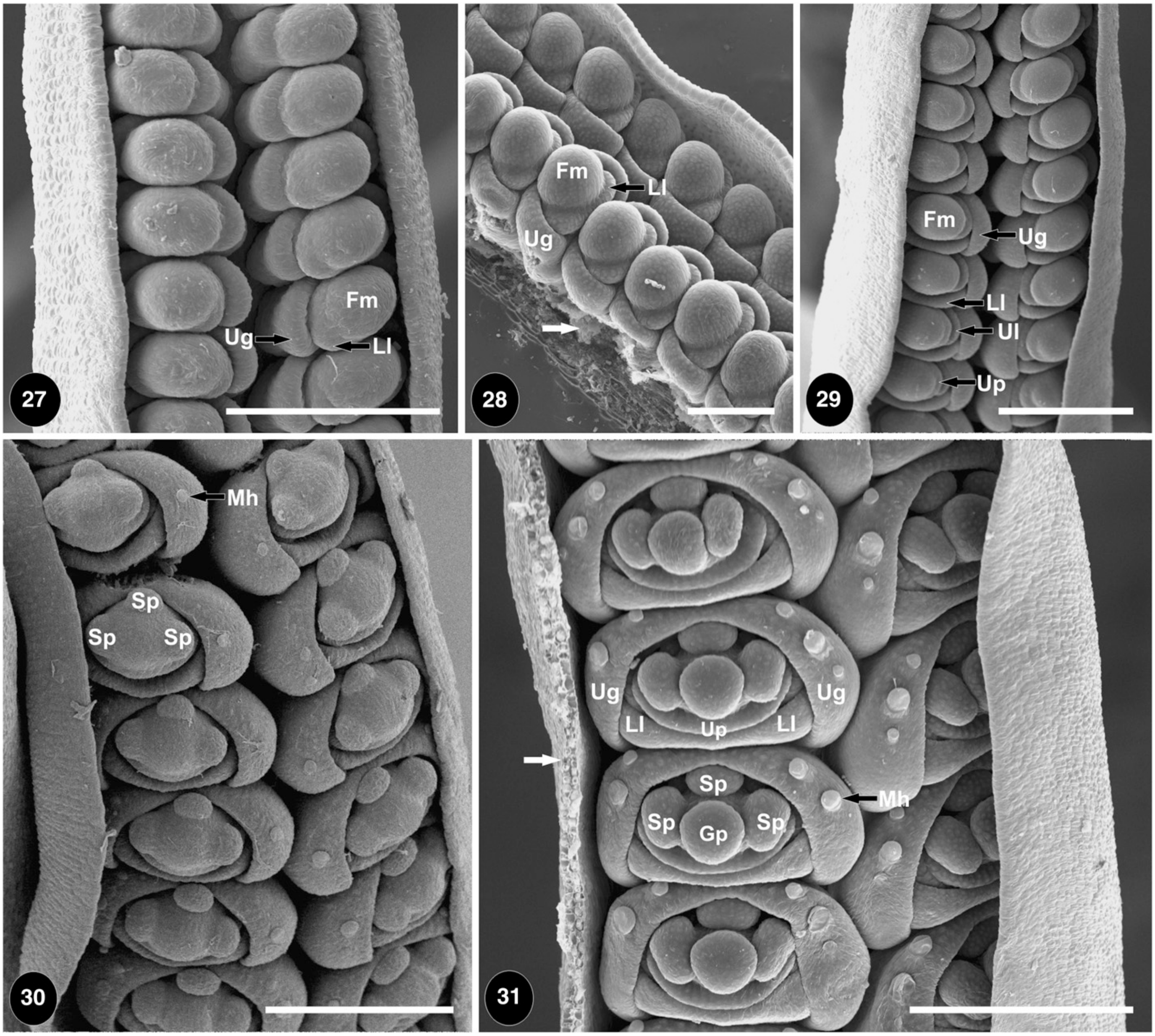
Figs. 18–26. Development of the primary branch and terminal raceme in *P. stellatum*. **18.** Transition to flowering. Bar = 50 µm. **19.** Initiation of the primary branch and the terminal raceme. Before its elongation, the apical meristem splits into two meristems. The leaf primordia covering the two meristems were removed to allow observation (arrow). Bar = 50 µm. **20.** Differentiation of the terminal raceme and elongation of the last formed leaf. Bar = 100 µm. **21.** Beginning of the differentiation of the terminal raceme and the primary branch (elongation). Bar = 200 µm. **22.** Differentiation of both the terminal raceme and primary branch, acropetal initiation of spikelet primordia. The bract covering both racemes was removed to allow observation (arrow). Bar = 200 µm. **23.** Initiation of spikelets (dorsiventrally compressed) and differentiation of the winged rachis. Bar = 200 µm. **24**. Spikelet differentiation along the terminal raceme, and beginning of truncation (black arrow). Bar = 500 µm. **25.** Detail of the undifferentiated, reduced apical meristem, at the base of the terminal raceme. Bar = 50 µm. **26.** Reduced apical meristem with two scales at the base of the terminal raceme. Bar = 200 µm.

initiate macrohairs (Fig. 30). Finally, the gynoecium primordium is formed (Fig. 31).

DISCUSSION

The comparative analysis of inflorescence development in *Paspalum simplex, P. stellatum*, and *Axonopus sufultus* showed differences in (1) apical meristem trasnsition to the reproductive phase; (2) initial branching of the apical meristem; (3) initiation and differentiation of primary branches; (4) initiation of secondary branches; (5) inflorescence symmetry; (6) extension, intensity, branching level, and timing of truncation; (7) spikelet initiation; and (8) stamen initiation.

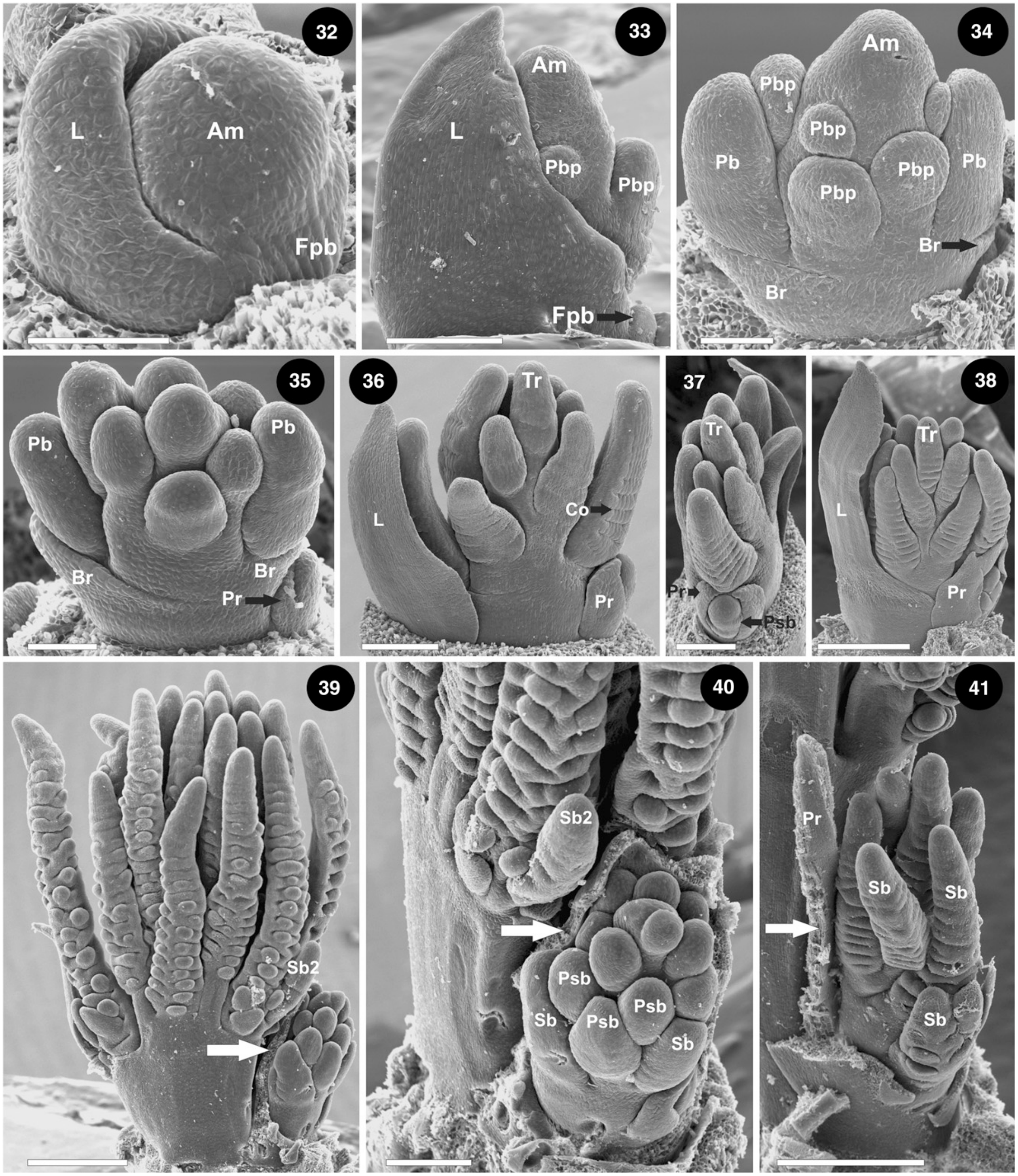
Transition to the reproductive phase—The apical meristems of *Axonopus suffultus* and *Paspalum stellatum* do not follow the regular transition to the reproductive phase. Apical meristems



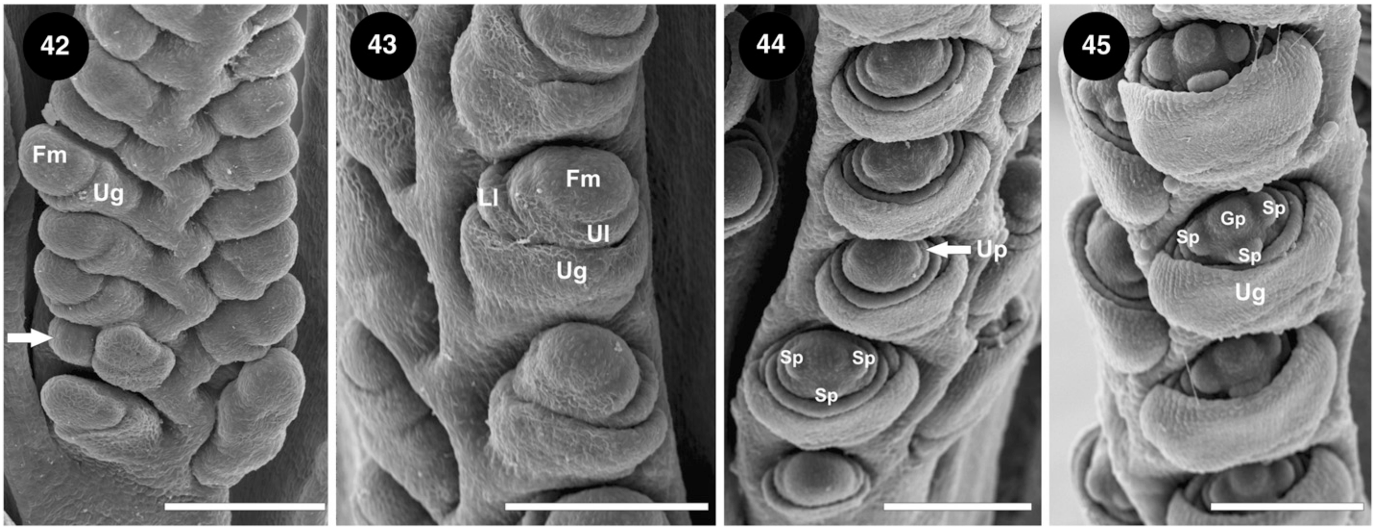
Figs. 27–31. Spikelet differentiation in *Paspalum stellatum.* **27.** Acropetal initiation of the upper glume and lower lemma, surrounding the floral meristem. Bar = 200 µm. **28.** Later upper glume and lower lemma development, surrounding the floral meristem. The winged rachis of the inflorescence was removed to allow observation (arrow). Bar = 100 µm. **29.** Initiation of upper lemma and palea of the upper floret. Bar = 200 µm. **30.** Stamen and macrohair initiation when the upper glume completely covers the upper lemma. Bar = 200 µm. **31.** Gynoecium initiation. The winged rachis of the inflorescence was removed to allow observation (arrow). Bar = 200 µm.

of Poaceae, and particularly those of Paniceae species, are usually hidden by the last formed leaf primordium and elongate beyond the last leaf primordium (flag leaf) just before the differentiation of the inflorescence main axis and initiation of primary branches (see Stür, 1986; Doust and Kellogg, 2002a; Orr et al., 2002; Orr and Sundberg, 2004; Bess et al., 2005; Reinheimer et al., 2005, 2009; Liu et al., 2007). *Paspalum simplex* follows this pattern (Fig. 8), but the apical meristem of *P. stellatum* splits before elongation (Fig. 19), and *A. suffultus* produces the first basalmost primary branch before meristem elongation (Fig. 32) and the remaining primary branches after meristem elongation (Fig. 33). Therefore, the transition to the reproductive phase may occur before apical meristem elongation.

Initial branching of the apical meristem—*Paspalum stellatum* has a very particular initial branching during the change to the reproductive phase: its apical meristem splits into two domes of similar size, resembling a dichotomous branching. Although typical dichotomous branching has been defined by meristems based on one initial cell, this equivalent meristem splitting also has been observed in meristems with tunica-corpus structure, specifically, other monocotyledons like Flagellariaceae (Tomlinson and Posluszny, 1977) and Arecaceae



Figs. 32–41. Development of the primary branch and terminal raceme in *A. suffultus*. **32.** Initiation of the first basalmost primary branch (during the vegetative phase). Bar = 100 µm. **33.** Acropetal initiation of primary branches after the apical meristem elongation. Bar = 200 µm. **34.** Later stage of development. The leaf primordia that was covering the primary branch meristem was removed to allow observation. Bar = 100 µm. **35.** Beginning of the differentiation of the primary branches (elongation and compression). The leaf primordia were removed. Bar = 100 µm. **36.** Acropetal differentiation of basal primary branches. Bar = 200 µm. **37.** Initiaton of secondary branches on the first basalmost primary branch. Bar = 200 µm. **38.** Acropetal differentiation of the first basalmost primary branch. Bar = 500 µm. **39.** Initiation of primordia of secondary branches of the basal primary branches (see also Fig. 40). Bar = 500 µm. **40.** Beginning of the differentiation of the secondary branches of the first basalmost primary branch. The prophyll was removed to allow observation (see arrow). Bar = 200 µm. **41.** Acropetal differentation of the secondary primary branches on the first basalmost primary branch. The prophyll was removed to allow observation (see arrow). Bar = 500 µm.



Figs. 42–45. Spikelet differentiation in *Axonopus suffultus.* **42.** Acropetal initiation of the upper glume, surrounding the floral meristem. The arrow indicates a meristem that arises in adaxial position. Bar = 200 µm. **43.** Later lower lemma and upper lemma development, surrounding the floral meristem. Bar = 200 µm. **44.** Stamen initiation Bar = 200 µm. **45.** Gynoecium initiation. Bar = 200 µm.

(Tomlinson, 1971). However, differences in growth between paired racemes in *P. stellatum,* as well as the eventual presence of basal scales in one raceme (homologous to the prophylls, see below), suggest that the initial ramification of the apical meristem in *P. stellatum* is not a true case of dichotomy but a very reduced form of normal branch production.

Primary branch initiation and differentiation—Inflorescences of *P. stellatum* may have two scales at the base of one raceme, both in inflorescences with single or paired racemes. Different authors have interpreted those basal scales as reduced racemes (i.e., primary branches; Chase, 1929; Sendulsky and Burman, 1978; Rua and Weberling, 1995), and because of that idea, some have suggested that the production of primary branches in the subgenus *Ceresia* follows a basipetal direction (Rua and Weberling, 1995). Others have understood those scales as bracts (Denham et al., 2002; Zuloaga and Morrone, 2005). The early elongation of paired racemes in *P. stellatum* is similar to the elongation of the first primary branch in some *Urochloa* species with basipetal, de novo origin of primary branches (except for the first primary branch, see Reinheimer et al., 2009); however, as suggested by Rua and Weberling (1995), *P. stellatum* does not produce any basipetal primary branch. Early stages of *P. stellatum* inflorescences show that basal scales derive from two flat expansions on each side of one of the meristems, which may either develop or not into a raceme (Figs. 25, 26), and that they are very much like the initial shape of the prophyll on the first basalmost primary branch of *Axonopus suffultus* (Fig. 37). The fact that the splitting of the apical meristem in *P. stellatum* occurs before meristem elongation may also relate one of the twin meristems to the first basalmost primary branch primordium of *A. suffultus*. Based on timing and position of primary branch initiation and morphology, we understand basal scales of *P. stellatum* as a modified prophyll primordium of a lateral raceme that may either develop or not (both the raceme and the scales).

The elongation and compression of branch primordia as the first changes toward the differentiation on the primary branches and the terminal raceme are steps common to other species of Paniceae (Reinheimer et al., 2009). That dorsiventral compression of branch primordia in *P. stellatum* may be related to the winged rachis state, typical of species of the subgenus *Ceresia* (Denham et al., 2002; Zuloaga and Morrone, 2005), because the dorsiventral symmetry could be a requirement for the differentiation of the marginal meristems responsible for the lateral expansion. However, elongation and dorsiventral compression do not seem to be related to spikelet initiation: both changes may occur before and after spikelet initiation in *P. simplex* (see Figs. 11–13). In spite of the morphological resemblance between the terminal raceme and primary branches, the inverted order of elongation/compression and spikelet primordia initiation may be denoting the nonhomologous condition. Concerning the direction of differentiation of primary branches, *P. simplex* follows a general basipetal pattern, although some very early stages suggest an initial acropetal differentiation of primary branches followed by an arrest and a basipetal resumption of the process (Figs. 10–13).

Although racemes of *P. stellatum* are not deciduous, they can be easily removed by handling during dissection. "Deciduous racemes" is a synapomorphy of the informal Racemosa group of the subgenus *Paspalum*, morphologically related to the subgenus *Ceresia* (Morrone et al., 1995). This characteristc of the inflorescence of *P. stellatum* could be understood as a nonfunctional abscision zone and possible link to other species with deciduous racemes.

Initiation of secondary branches—Adult inflorescences of *Axonopus suffultus* show secondary branches only on the first basalmost primary branch (Fig. 3). That basalmost primary branch reproduces the developmental pattern of the main axis, and considering its earlier origin before the elongation of the apical meristem of the main axis, it may be understood both as a primary branch or a new inflorescence. The secondary branching level on the following primary branches is evident only in early stages of development along the basal primary branches (Figs. 39, 40). That secondary branch development in *A. suffultus* inflorescence relates *Axonopus* to the richly branched panicle

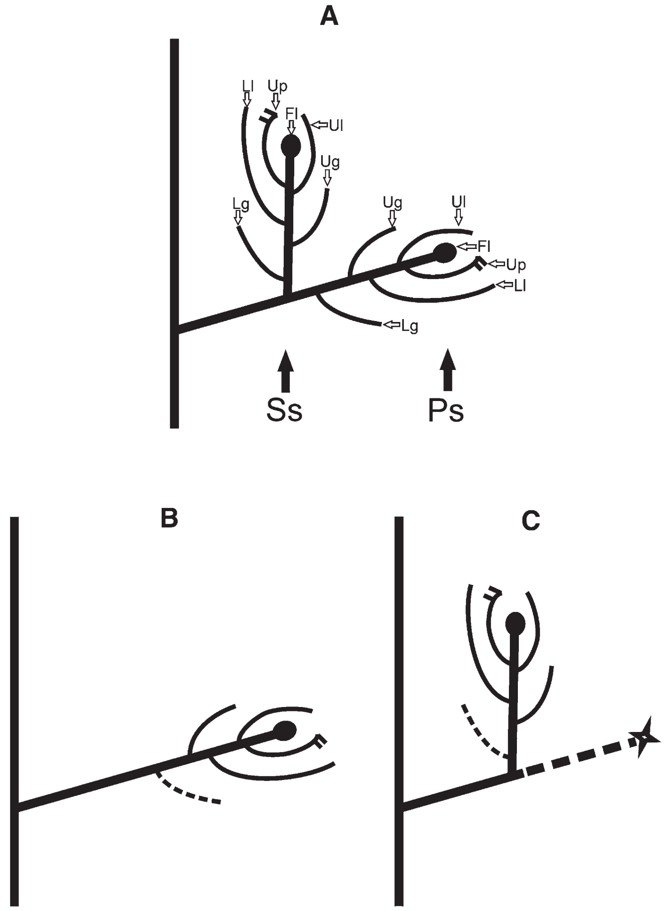


Fig. 46. Spikelet orientation in Paniceae. (A) Paniceae typical spike pair (one pedicellate, abaxial spikelet and one subsessile, adaxial spikelet; only one floret per spikelet to simplify the diagram). (B) Single pedicellate, abaxial spikelet of *P. stellatum* (the subsessile spikelet does not develop). (C) Single subsessile, adaxial spikelet of *P. suffultus* (the pedicellate spikelet is truncate).

of *Panicum* (plesiomorphic, nonhomogenized inflorescence). Homogenized inflorescences of other *Axonopus* species (such as *A. compressus*) confirm that inflorescence homogenization has occurred more than once (*Paspalum* and *Axonopus*) within the *Panicum+Axonopus+Anthenantiopsis+Paspalum* clade.

Inflorescence symmetry—Previous research on inflorescence development in Paniceae members has shown that phyllotaxis switches from distichous to spiral during the meristematic change from the vegetative to the reproductive phase, so that primary branches of the inflorescence use to be spirally arranged (Doust and Kellogg, 2002a, b; Kellogg, et al., 2004; Bess et al., 2005; Kellogg, 2006; Reinheimer et al., 2009). However, some Paniceae retain the distichous vegetative phyllotaxis in their inflorescence (like some *Urochloa* species, see Reinheimer et al., 2005, 2009). *Paspalum simplex* follows the spiral phyllotaxis model, and *P. stellatum* does not produce enough primary branches to establish an arrangement pattern. *Axonopus suffultus* forms a mixed structure with the two basal primary branches in distichous arrangement (see Fig. 35) and the following ones with spiral phyllotaxis. There is no evident relation between phyllotaxis, the presence of bracts in basal primary branches, acropetal or basipetal initiation of primary branches, and initiation of primary branches before of after apical meristem elongation.

Extension, intensity, branching level, and timing of truncation—Truncation operates with different degrees of intensity and extension, at different branching levels and stages of inflorescence development. In terms of intensity and extension, truncation can reduce the development of the most distal spikelets (*P. stellatum*, see Fig. 24), or suppress all spikelets, reducing the terminal raceme to a sterile appendage (Fig. 14), partially affecting the development of the most distal primary branches (in *P. simplex*).

When truncation reduces or aborts spikelets, it works either at second level of branching (*P. stellatum*) or at primary level of branching, completely reducing the most distal primary branches or truncating directly the main axis (*P. simplex*). Truncation may also occur at third level if we consider the eventually aborted meristems of pedicellate spikelets in *Axonopus* (Fig. 42). Concerning timing, truncation occurs before primary branch differentiation in *P. simplex* and after primary branch differentiation in *P. stellatum* and in *A. suffultus*.

According to Vegetti (1987) and Rua and Weberling (1995), *P. simplex* and *P. stellatum* produce truncate inflorescences (referred only to the main axis), but our results for *P. simplex* showed that truncation may occur as a variable process giving truncate and nontruncate inflorescences in the same individual.

Spikelet initiation—Primordia of secondary branches produce solitary spikelets in *P. stellatum* and *A. suffultus* and spikelet pairs in *P. simplex*. In spite of the different fate, both branch primordia compress dorsiventrally, although the timing of compression is different: after elongation (*P. simplex*) or before elongation (*P. stellatum*, *A. suffultus*). However, dorsiventral compression precedes spikelet differentiation in the three species.

Stamen initiation—The basal condition of the androecium of Poaceae is represented by two whorls of three stamens each (Clifford, 1987; Cocucci and Anton, 1988). On the basis of developmental and anatomical data, the three-stamen condition of most Poaceae is understood to consist of two lateral stamens from the inner whorl that arises first, plus one frontal stamen from the outer whorl that arises later (Cocucci and Anton, 1988). This is the case observed in *A. suffultus* (Figs. 44, 45). Usually, the lateral stamens are slightly smaller than the frontal one, although the opposite condition may also occur (Clifford, 1987; R. Reinheimer, Universidad Nacional del Litoral, Argentina, unpublished data). In addition, Reinheimer (R. Reinheimer, unpublished data) found that the lateral stamens in *Urochloa* and related taxa may appear either before or after the frontal one. Stamens of *P. simplex* (Fig. 16) and *P. stellatum* (Fig. 30) show a similar size and arise simultaneously, suggesting two interpretations: (1) that the three stamens belong to the same whorl or (2) that the initiation of the frontal stamen is less inhibited than in other Poaceae.

Homologies—The comparative analysis of inflorescence development of *P. simplex*, *P. stellatum*, and *A. suffultus* suggests the following homologies: (1) the terminal raceme of *P. simplex* (in nontruncate inflorescences) and the terminal appendage (in truncate inflorescences) are homologous to the terminal raceme of *A. suffultus* and to the largest raceme of paired inflorescences (or to the solitary raceme) in *P. stellatum*; (2) the reduced bud at the base of the main raceme in *P. stellatum* is homologous

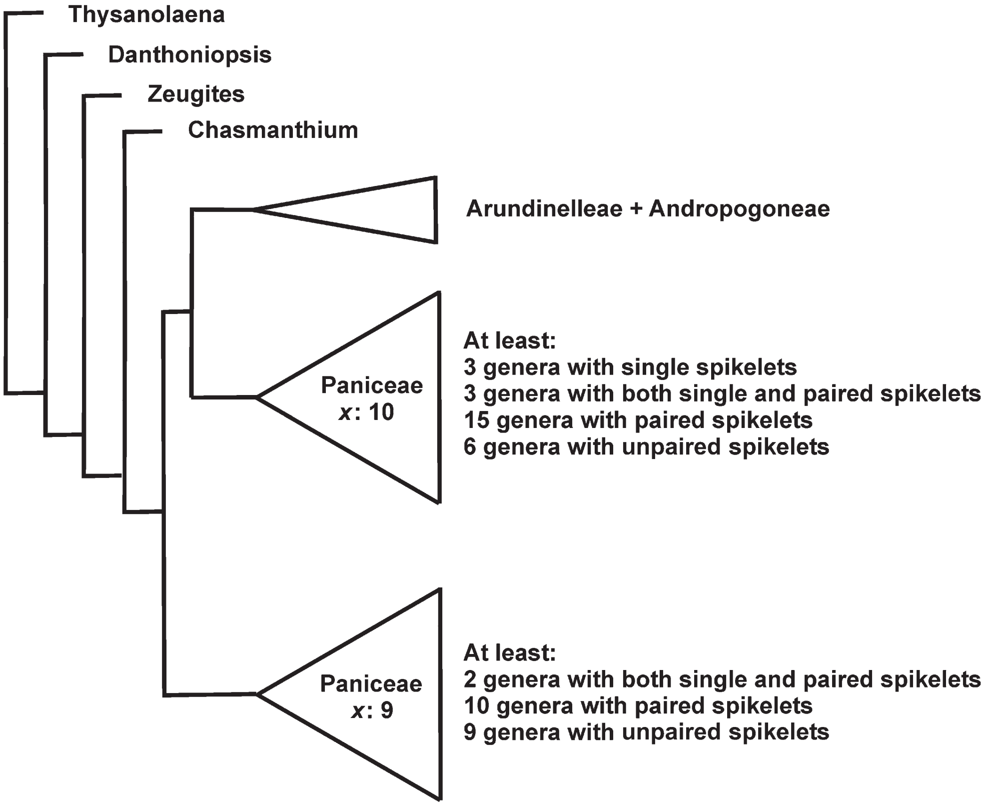


Fig. 47. Phylogenetic relationship between Arundinelleae+Andropogoneae and the two main clades of Paniceae, with a general distribution of the single spikelet and paired spikelet states within Paniceae. Based on Giussani et al. (2001).

to the basalmost bud of *A. suffultus* (by early initiation before the elongation of the apical meristem, and the presence of prophyll-like primordia); (3) the scales at the base of the primary branch of *P. stellatum* (only present in paired inflorescences) are homologous to the prophyll primordia of the first basalmost primary branch in *A. suffultus*; and (4) solitary spikelets of *A. suffultus* are homologous to the subsessile spikelets of *P. simplex*, and solitary spikelets of *P. stellatum* are homologous to the pedicellate spikelet of *P. simplex* (Fig. 46).

Concerning spikelets, our results support the homology between the pedicellate spikelet of *P. simplex* and the solitary spikelet of *P. stellatum*. Kellogg (2000) has suggested that development does not support a clear homology between the solitary spikelet of species of *Paspalum* with two rows of solitary spikelets and any of the spikelets of species with two rows of spikelet pairs. That statement was based on the common origin of the spikelet meristems in paired spikelet species, which arise by the division of a primordium of a secondary branch (Kellogg, 2000). Our observations in *P. simplex* show that there is a hierarchy between the outer larger primordium (corresponding to the pedicellate spikelet) and the inner, smaller one (corresponding to the subsessile spikelet), which is congruent with the meristem of the secondary branch (larger) and the meristem of the third order branch (smaller). That hierarchy also agrees with the nonsimultaneous differentiation of spikelets: the differentiation of the pedicellate, outer spikelet is clearly more advanced than the differentiation of the subsessile inner one. Based on these facts, and assuming that spikelets of the same pair arise from different branches of consecutive order, the pedicellate spikelet of *P. simplex* should be homologous to the solitary spikelet of *P. stellatum* because both are born by the differentiation of the meristem of a secondary branch. This hypothesis is also supported by other developmental studies of inflorescences of Poaceae, particularly of Paniceae (Orr et al., 2002; Orr and Sundberg, 2004, R. Reinheimer, Universidad Nacional del Litoral, unpublished data), as well as by genetic studies (Kellogg, 2006) and spikelet orientation.

Spikelet orientation concerning the bearing axis is a distinctive character among genera of Paniceae (Webster, 1988; Zuloaga et al., 2000), and it is the only difference between *Paspalum* and its morphologically closest genus *Axonopus* (Webster, 1988; Giraldo-Cañas, 2000). However, spikelet orientation is not always easy to assess (Zuloaga et al., 2000), particularly in species with long pedicels (Webster, 1988). Typically, *Paspalum* has pedicellate spikelets with the lower lemma in abaxial position respect to the bearing (primary) branch and, in species with paired spikelets, the subsessile spikelet with its lower lemma toward (adaxial position) the pedicel of the pedicellate spikelet. *Paspalum simplex* shows this morphology (Fig. 16), whereas *P. stellatum* has nonpaired spikelets that are always abaxial (Fig. 24), a fact that supports the homology with the pedicellate spikelet of *P. simplex*. The nonpaired spikelets of *Axonopus* are adaxial and supposed to be homologous to the pedicellate spikelets of *Paspalum* (because of their position on a secondary branch = pedicel), but with a 180° rotation in the pedicel (Clifford, 1987; Crins, 1991). However, there are no external or internal evidence of a rotation (O. Morrone, personal observation). The inflorescence development of *A. suffultus* showed a meristem on the adaxial side in some spikelets of the primary branch (Fig. 42) resembling (by position) the meristem of the pedicellate spikelet of *Paspalum*. This interpretation agrees with that of typological analyses (Cámara-Hernández and Rua, 1991; Rua, 1993) suggesting that the change in orientation in solitary spikelets between *Axonopus* and *Paspalum* is derived by truncation of the terminal pedicellate spikelet in *Axonopus* (see also Giraldo-Cañas, 2000). On the basis of our results, we suggest that the solitary adaxial spikelet of *Axonopus* is homologous to the subsessile adaxial spikelet of *Paspalum* and that the pedicellate abaxial spikelet of *Paspalum* is absent in *Axonopus* (Fig. 46). Some species of *Paspalum* have different degrees of reduction of the subsessile spikelet (Webster, 1988; Rua and Weberling, 1995), a phenomenon that is supposed to have arisen from the possible heterochronic origin of pedicellate and susbsessile spikelets (Rua and Weberling, 1995). However, our observations in *P. simplex* show that both spikelet primordia arise simultaneoulsy, and therefore, some cases of reduction of the subssesile spikelet in *P. simplex* are the result of a delayed development respect to paired pecidellate spikelet. A heterochronic development does exist in most apical secondary branch primordia, where the subsessile spikelet primordia do not arise, and the most apical secondary branch primordia differentiate bracts when the basal ones differentiate the pedicellate and subsessile spikelet primordia (Fig. 14).

Although we suggest two origins for the single spikelet condition in Paniceae, starting from the paired spikelet state, this does not mean that the paired spikelet state is plesiomorphic. Even though the phylogeny of Paniceae is not well understood yet, published phylogenies (e.g., Aliscioni et al., 2003) suggest multiple origins of both paired spikelets and the derived single spikelet condition.

Possible functional background—On the basis of the close phylogenetic relationship between Andropogoneae and the $x = 10$ clade of Paniceae (Fig. 47) (Giussani et al., 2001), we could suppose that the RAMOSA pathway, which controls spikelet pair differentiation in maize (Wu et al., 2009, and references therein), works in a similar way within the Paniceae clade to which *Axonopus* and *Paspalum* belong. Although the RAMOSA and polar auxin transport pathways seem to be linked (Wu et al., 2009), the connection has not been demonstrated, and we must consider that *SOS1*, *bif1*, *bif2* and *ba1* could also be involved in the development of the single abaxial spikelet of *P. stellatum* by sessile spikelet (lateral meristem) suppression (Wu and McSteen, 2007; Barazesh and McSteen, 2008). Because the single spikelet state has appeared several times in Paniceae (Fig. 47), it would be interesting to test whether the single spikelet condition derived from different genetic controls. The reduction in the number of primary branches in the inflorescence is a widespread phenomenon within *Paspalum* (Rua and Weberling, 1995). *Paspalum stellatum* is an extreme example of reduced inflorescence by inhibition of the development of primary branches (reduction of the enrichment zone, according to Troll's conception). In that sense, *ba1* could be involved in the inhibition of primary branch development (Vollbrecht et al., 2005) and may have played an important role in the evolution of *Paspalum* inflorescences.

In *P. simplex* with paired spikelets, both the terminal spikelet and distal lateral spikelet pairs of the main axis and apical primary branches can be eventually suppressed (truncation). As that truncation has been seldom observed in *P. simplex*, we suppose that it is the consequence of enviromental conditions and not a fixed developmental character. The case of *A. suffultus*, where the single spikelet state has been developed by suppression of the pedicellate, terminal spikelet, suggests a very different genetic control affecting only the (apical) spikelet-pair meristem and not affecting other apical meristems (suppressing the terminal spikelet of the main axis and primary branches) still active or undifferentiated by the time lateral spikes initiate on the basal branches. Just as only the third order apical meristems are inhibited in *A. suffultus* (producing single spikelets from spikelet pairs), only apical meristems of first and second order (and not the third order apical meristems, which produce the single spikelets) are inhibited in *P. stellatum*, suggesting that apical meristem inhibition is sensitive to branching order.

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Appendix 1. Vouchers of studied species; all are housed at SI (Instituto de Botánica Darwinion). Those marked with an asterisk (*) are the reference vouchers of the cultivated material used for the developmental study.

Taxon—**Collection site:** *vouchers*.

Paspalum simplex Morong ex Britton—**Argentina:** *Guaglianone, E. R. et al. 281*; *Lewis, P. J. 639*; *Morrone, O. and Giussani, L. M. 5794**; *Pedersen, T. M. 8283*; *Quarín, C. 2955; Rotman, A. D. et al. 245*; *Schinini, A. and Martínez Crovetto, R. 12310; Schulz, A. G. 11729*. **Bolivia:** *Killeen, T. 1722*. **Paraguay:** *Burkart, A. 18302*; *Burkart, A. 18404*; *Mereles, F. and Ramella, L. 2611*; *Zuloaga, F. O. and Morrone*, *O. 7328*. **Uruguay:** *Rosengurtt, B. B-7142*.

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Axonopus suffultus (J.C. Mikan ex Trin.) Parodi—**Argentina:** *Morrone, O. 5800*; Morrone, O. s.n. **