Diversification of inflorescence development in the PCK clade (Poaceae: Panicoideae: Paniceae)[1]

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In grasses, inflorescence diversification and its correlation with species evolution are intriguing and not well understood. Part of this problem lies in our lack of comprehension about the inflorescence morphological complexity of grasses. We focused our study on the PCK clade (named for phosphoenol pyruvate carboxykinase), a well-supported monophyletic group for which the relationships among its taxa are not well resolved. Interestingly, the PCK clade has an extensive diversity of adult inflorescence forms. A comparative developmental approach can help us to understand the basis of such morphological differences as well as provide characters that can be used in phylogenetic studies of the group. Using SEM studies, we demonstrate that inflorescence morphology in this clade is even more complex than what is typically observed in adult forms. We describe a number of new characters, and some classical features previously used for taxonomic purposes are redefined on the basis of development. We also define four morphological groups combining adult inflorescence form and development, and we discuss some of the evolutionary aspects of inflorescence diversification in the PCK clade. Taxonomic delimitation among genera in the PCK clade remains confusing and unclear where molecular and morphological studies support different classifications.

Key words: diversity; inflorescence development; Poaceae; PCK clade; SEM.

Grass inflorescence architecture is well known to be extremely variable among taxa, developmentally and genetically complex, and agronomically important; however grass inflorescence diversification and its correlation with species evolution are intriguing and not well understood. Part of this problem lies in our lack of comprehension about the inflorescence morphological complexity of grasses. A study of inflorescence morphology across the entire grass family, which contains about 10 000 species, would be impossible to assess. However, we focused our study on a well-defined group of grasses informally named the PCK clade. This clade is a well-supported monophyletic group within Tribe Paniceae, one of the largest tribes in the grass family. The clade is well known because it contains most of the C_4 grasses that have PEP-ck physiology (phosphoenol pyruvate carboxykinase, PCK) (Gomez-Martínez and Culham, 2000; Zuloaga et al., 2000; Duvall et al., 2001; Giussani et al., 2001). At least six genera (*Moorochloa* Veldkamp [= *Brachiaria* (Trin.) Griseb.], *Chaetium* Nees, *Eriochloa* Kunth, *Megathyrsus* (Jacq.) B. K. Simon and S.W.L. Jacobs, *Melinis* P. Beauv., *Urochloa* P. Beauv.) have been confirmed by molecular data to be members of the PCK clade (Clayton and Renvoize, 1986; Frank, 1998; Gomez-Martínez and Culham, 2000; Zuloaga et al., 2000; Duvall et al., 2001; Giussani et al., 2001;

Torres González and Morton, 2005), while the position of *Eccoptocarpha* Launert, *Thuarea* Pers., and *Yvesia* A. Camus, included in the group on the basis of its PEP-ck physiology by Frank (1998), has yet to be confirmed with molecular markers. Among members of the PCK clade, the *Moorochloa-Urochloa* complex is the most important in terms of number of species and economic value because it includes about 100 species, most of them forage crops as well as aggressive weeds of summer crops like maize, rice, and soy (Frank, 1998).

Although the PCK clade is well supported as monophyletic, its internal resolution is still poorly understood (Frank, 1998; Goméz-Martínez and Culham, 2000; Zuloaga et al., 2000; Duvall et al., 2001; Giussani et al., 2001; Aliscioni et al., 2003; Torres González and Morton, 2005). Moreover, with no evidence to support the monophyly of either genus, the taxonomic delimitation of *Moorochloa* and *Urochloa* is not clear (Palisot de Beauvois, 1812; Trinius, 1826; Grisebach, 1853; Nash, 1903; Stapf, 1920; Hughes, 1923; Henrard, 1941; Clayton and Renvoize, 1982; Webster, 1987, 1988; Morrone and Zuloaga, 1991, 1992, 1993; Davidse, 1993; Veldkamp, 1996a, b, 2004; Frank, 1998; Nelson and Fernández, 1998; López-Ferrari and Espejo Serna, 2000; Giussani et al., 2001; Wunderlin and Hansen, 2001; Sharp and Simon, 2002; Simon and Jacobs, 2003; Zuloaga and Morrone, 2003; Torres González and Morton, 2005). The most recent phylogeny of the PCK clade, based on the nuclear ITS and 5.8S regions, suggests that *Moorochloa* and *Melinis* may be sister taxa and that the *Moorochloa/Melinis* clade may be sister to the rest of the PCK species. *Urochloa* is associated with *Megathyrsus* and *Eriochloa* and appears to be paraphyletic (Fig. 1) (Torres González and Morton, 2005). Nonetheless, the unique molecular phylogeny available for the PCK clade lacks internal resolution (Fig. 1).

Several studies are currently being carried out using different approaches in an effort to understand the evolution and taxonomical delimitation of members of the PCK clade, including molecular systematics as well as an exhaustive revision of morphology. In terms of morphology, the PCK clade has an extensive diversity of adult inflorescence forms previously
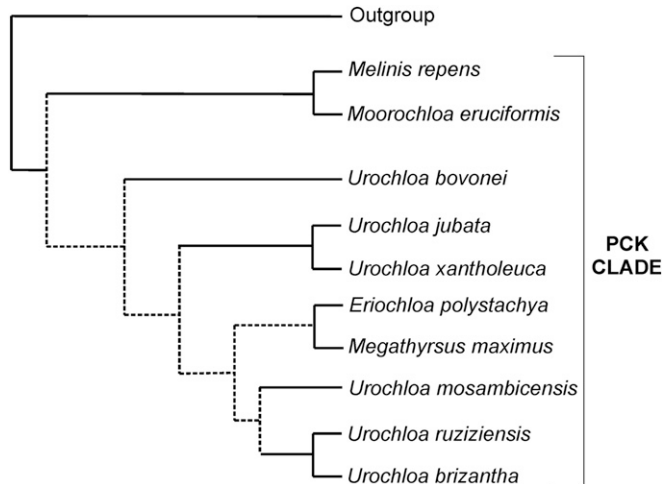
Fig. 1. Simplified PCK clade phylogeny showing relationships among several members of the PCK clade that were included in this work (with the exception of *Eriochloa polystachya* Kunth), based on Torres González and Morton (2005). Heavy black lines indicate bootstrap support values more than >80%. Dashed lines indicate bootstrap support values less than <60%. *Abbreviations for all figures:* AM, apical meristem; B1, primary branch; B2, branch of second order; L, leaf primordium; PA, inflorescence main axis; SL, scale leaf; SP, inflorescence terminal spikelet; sp1, terminal spikelet of the primary branch; sp2, terminal spikelet of the second-order branch; sp3, terminal spikelet of the third-order branch. The asterisk represents the aborted main axis. The black oval represents a spikelet. Bar = 100 μm.

characterized by Reinheimer and Vegetti (2008). Inflorescences in the PCK clade were classified into two main groups: (1) inflorescences with a terminal spikelet (Fig. 2A–C) and (2) inflorescences without a terminal spikelet (Fig. 2D, E). In both groups, the degree of similarity among branches (also called homogenization) identifies three basic types of inflorescences with a terminal spikelet (nonhomogenized, partially homogenized, and completely homogenized, Fig. 2A–C, respectively) and two basic types without a terminal spikelet (partially and completely homogenized, Fig. 2D, E, respectively). Among these five basic inflorescence types, at least 21 different subtypes were described for the PCK clade on the basis of a combination of 14 characters (Reinheimer and Vegetti, 2008).

Studies of inflorescence development have identified even more variation in the inflorescence form in the PCK clade. Developmental studies of *Urochloa decumbens* (Stapf) Webster, *U. plantaginea* (Link) Webster, and *Megathyrsus maximus* (Jacq.) B. K. Simon and S.W.L. Jacobs [= *Panicum maximum* Jacq. or *U. maxima* (Jacq.) R. D. Webster] have shown that inflorescence, spikelet, and floret development differs widely among taxa (Stür, 1986; Reinheimer et al., 2005). For instance, primary branches may arise acropetally (bottom to top) or basipetally (top to bottom) depending on the species (Stür, 1986; Reinheimer et al., 2005). Also, spikelet development shows different sequences and directions of initiation, and floret development may follow one of at least nine different developmental patterns (Reinheimer et al., 2005; Reinheimer, 2007).

The PCK clade is extremely variable in adult inflorescence form, and we believed that comparative developmental studies can help us to understand the basis of such differences as well as provide characters that can be include in future systematic studies of the clade (Rua, 1993, 1996, 2003; Vegetti and Anton, 1995, 2000; Kellogg, 2000; Pensiero and Vegetti, 2001; Doust

and Kellogg, 2002a, b; Doust and Drinnan, 2004; Kellogg, et al., 2004; Bess et al., 2005; Liu, et al., 2005, 2007). Because inflorescence development has not been explored broadly in the group, we investigated the development of the inflorescence branch system in 20 species of the PCK clade as part of a larger project addressing morphological evolution in the group through the study of adult morphology, development, and its genetic bases (Reinheimer, 2007). This paper aims to (1) describe the development of the inflorescence branch system in the PCK clade, (2) identify new characters to include in future phylogenetic studies, and (3) identify changes in developmental patterns that may lead to the inflorescence diversity seen in the clade.

We conclude that the inflorescence branch system in the PCK clade is even more complex than observed in adult forms. New characters are described and some classical features previously used for taxonomic purposes are redefined based on development. We also describe four morphological groups based on adult inflorescence form and development, and we discuss evolutionary aspects of inflorescence diversification observed in the PCK clade. Taxonomic delimitation among genera of the PCK clade remains confusing and unclear because molecular and morphological studies support different classifications.

MATERIALS AND METHODS

Selection of species was based on both availability of material and diversity in adult morphology. A total of 20 species of the PCK clade were selected, including 14 species of *Urochloa*, *Moorochloa eruciformis* (Sm.) Veldkamp, two species of *Eriochloa*, *Megathyrsus maximus*, and two species of *Melinis* (Appendix 1). Developmental aspects of the inflorescences of *U. plantaginea* and *Megathyrsus maximus* were published by Reinheimer et al. (2005); nevertheless, a reanalysis of their development in the context of the PCK clade is presented in this work. *Chaetium*, *Eccoptocarpha*, *Thuarea*, and *Yvesia* are not included due to lack of material. The botanical nomenclature for the species of the PCK clade is highly complex and taxonomically confusing. For details about the taxonomic position and synonymy of species in the PCK clade, see Reinheimer and Vegetti (2008).

Live plants from field collections and seed banks (Centro Internacional de Agricultura Tropical, CIAT), cultivated at the greenhouse of the Agronomy School of the University of Litoral (Argentina), were used for studying inflorescence primordia with scanning electron microscopy (SEM). For SEM observations, inflorescences were collected and fixed in FAA (formalin : acetic acid : 70% ethanol, 10 : 5 : 85, v/v), then dehydrated in an alcohol series plus two final changes of 100% acetone. Dehydrated material was critical point dried using CO_2 as transitional fluid and coated with gold-palladium using a Thermo VG Scientific Polaron SC7620 sputter coater (Zürich, Switzerland). All samples were observed and photographed using a Philips XL30 series (Eindhoven, The Netherlands) scanning electron microscope from the Electron Microscopy Service of the Bernardino Rivadavia Natural Science Museum (Buenos Aires, Argentina).

RESULTS

Transition to flowering—During the vegetative growth phase of all examined species, the apical meristem of the shoot elongates and produces leaf primordia in two distichous rows (Fig. 3). Morphologically, the transition from vegetative to flowering phases is evident when the apical meristem elongates beyond the last-formed leaf primordium (also called the scale leaf by Pizzolato and Sundberg, 1999) to constitute the inflorescence main axis (Fig. 4).

After the transition to flowering and during inflorescence branch system development, several differences are found among the studied species. These include (1) type of main axis development, (2) determination of inflorescence symmetry, (3)
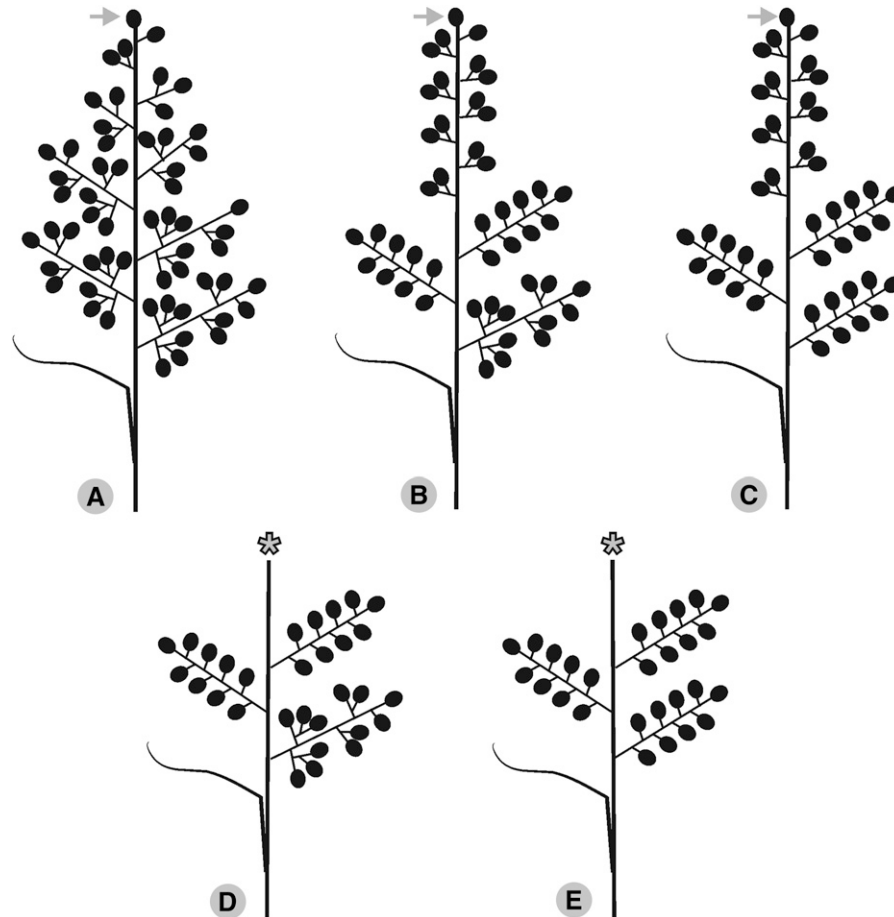
Fig. 2.   Diagrams of the five basic types of inflorescence morphologies in species of the PCK clade previously described by Reinheimer and Vegetti (2008). (A) Inflorescence with terminal spikelet (at arrowhead) and primary branches nonhomogenized. (B) Inflorescence with terminal spikelet (at arrowhead) where some of the primary branches are homogenized. (C) Inflorescence with terminal spikelet (at arrowhead) where all the primary branches are homogenized. (D) Inflorescence without terminal spikelet where some of the primary branches are homogenized. (E) Inflorescence without terminal spikelet where all of the primary branches are homogenized.

direction of primary branch initiation and differentiation, (4) direction of second-order branch initiation along the inflorescence and on the primary branch, and (5) patterns of development and orientation of third-order branches. A summary of these differences is presented in Table 1.

Main axis and primary branch development—After the transition to flowering, the main axis of the inflorescence may follow one of two different patterns of development.

In several species of the PCK clade, the apical meristem elongates above the scale leaf to constitute the inflorescence main axis and gradually produces new primary branches in an acropetal direction (Figs. 5, 6). Late in development and after the formation of primary branches, the apical meristem ends its growth with the formation of a terminal spikelet (Fig. 7). In this case, the first-formed branch (the proximalmost primary branch) initiates in the axil of the scale leaf. Among the species and genera that follow this developmental pattern are *Megathyrsus maximus*, *Melinis*, *Moorochloa eruciformis*, *Urochloa leucacrantha* (Schum.) Stapf, *U. lorentziana* (Mez) Morrone and Zuloaga, *U. mollis* (Sw.) Morrone and Zuloaga, *U. paucispicata* (Morong) Morrone and Zuloaga, and *U. xantholeuca* (Hack. ex Schinz) H. Scholz. In some species examined, the

main axis follows the acropetal pattern of development mentioned, but never ends in a terminal spikelet, as in *Eriochloa* and two species of *Urochloa* [*U. jubata* (Fig. & De Not.) Sosef and *U. lata* (Schumach.) C. E. Hubb.] (Figs. 8–10).

On the contrary, in some species of the clade, the apical meristem of the inflorescence axis does not elongate as much as we observed in the acropetal pattern, and it ceases its activity early in development without forming the terminal spikelet (Figs. 11–13). In this case, the first primary branch initiates above and opposite to the scale leaf (Fig. 11). After the formation of the first primary branch, new primary branches initiate below it in a basipetal direction. In these inflorescences, the primary branch in the axil of the scale leaf is the last formed (Fig. 12). Often, the first primary (distal) branch adopts the position of the main axis (Fig. 13). This pattern is observed in most of the *Urochloa* species examined.

Sometimes, a rudimentary leaf primordium is observed at the base of branches only in inflorescences with acropetal primary branches (Figs. 5, 6, 9, 15, 16). In these cases, the presence of leaves varies depending on species (Figs. 5–6, 9, 14–16) and individual (Figs. 7, 16) as well as the degree of branch ramification and the stage of development. When present, leaf primordia tend to be conspicuous when subtending
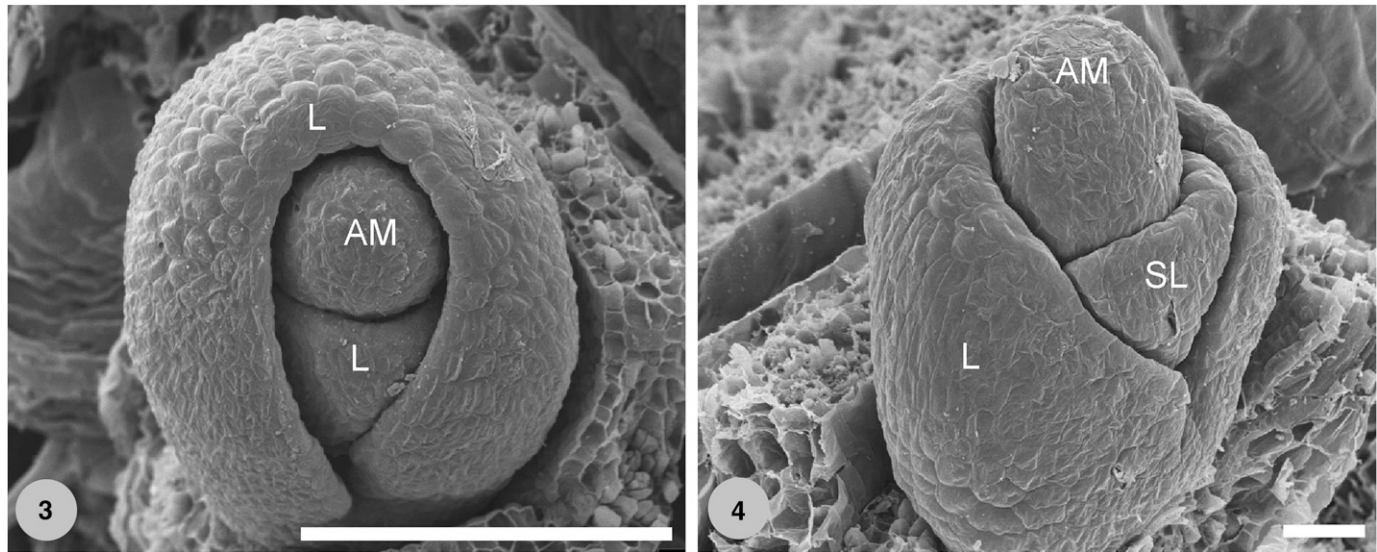
Figs. 3–4. Vegetative stage and transition to flowering in *Moorochloa eruciformis* (scanning electron micrographs). **3.** Apical meristem producing vegetative leaves during the vegetative stage. **4.** Elongation of the apical meristem above the scale leaf during transition to flowering.

primary branches, while they are smaller when subtending second-order branches, and they have the tendency to disappear in higher-order branches (Fig. 16). In general, leaf primordia disappear late in development, when spikelet begins to form (Figs. 7, 10).

Inflorescence symmetry—Three different types of inflorescence symmetry are found in the PCK clade: (1) spiral symmetry, (2) unilateral symmetry, and (3) bilateral symmetry.

When the symmetry is spiral, new primary branch primordia are initiated acropetally on all sides of the main axis (Figs. 15, 17). Several species of the PCK clade show inflorescences with spiral symmetry among all individuals examined. These include *Megathyrsus maximus*, *Eriochloa*, *U. lata*, *U. leucacrantha*, *U. lorentziana*, *U. paucispicata*, and *U. xantholeuca*.

When symmetry is unilateral, primary branch primordia are initiated acropetally in two rows on one side of the main axis (Fig. 18). Examples of this type of inflorescence occur in *Melinis*, *Moorochloa eruciformis*, *U. jubata*, and *U. mollis*.

The inflorescence symmetry of some species of *Urochloa*, such as *U. bovonei* (Chiov.) Torres and Morton, *U. distachya* (L.) T. Q. Nguyen, *U. mosambicensis* (Hack.) Dandy, *U. panicoides* P. Beauv., *U. plantaginea*, *U. platyphylla* (Nash) Webster, and *U. ruziziensis* (R. Germ. and Evrard) Morrone and Zuloaga, is hard to assess because (1) most individuals usually develop few primary branches (i.e., individuals of *U. bovonei* usually produce inflorescences formed by one or two primary branches, Fig. 19), and (2) different individuals of the same species have different inflorescence symmetries because the primary branches do not show a stable pattern of phyllotaxis

TABLE 1. Differences observed during the development of the inflorescence branch system of the PCK clade and the correlation with the adult inflorescence type. B1, branch of first order; B2, branch of second order; I, nontruncated inflorescence; IF, inflorescence; TI, truncated inflorescence.

Species	Direction of B1 initiation	IF symmetry	Direction of B1 differentiation	Direction of B2 initiation along the IF	Direction of B2 initiation on the B1	Type of inflorescence
Moorochloa eruciformis	acropetal	unilateral	acropetal	basipetal	acropetal	I, partial homogenized
Eriochloa montevidensis	acropetal	spiral	basipetal	basipetal	acropetal	TI, partial homogenized
Eriochloa punctata	acropetal	spiral	basipetal	basipetal	acropetal	TI, homogenized
Megathyrsus maximus	acropetal	spiral	acropetal	acropetal	acropetal	I, nonhomogenized
Melinis minutiflora	acropetal	unilateral	acropetal	acropetal	acropetal	I, nonhomogenized
Melinis repens	acropetal	unilateral	acropetal	acropetal	acropetal	I, nonhomogenized
Urochloa bovonei	basipetal	unilateral/bilateral	basipetal	basipetal	acropetal	TI, full-homogenized
Urochloa distachya	basipetal	unilateral/spiral	basipetal	basipetal	acropetal	TI, full-homogenized
Urochloa jubata	acropetal	unilateral	basipetal	basipetal	acropetal	TI, full-homogenized
Urochloa lata	acropetal	spiral	basipetal	basipetal	acropetal	TI, full-homogenized
Urochloa leucacrantha	acropetal	spiral	acropetal	basipetal	acropetal	I, full partial-homogenized
Urochloa lorentziana	acropetal	spiral	acropetal	basipetal	acropetal	I, partial-homogenized
Urochloa mollis	acropetal	unilateral	acropetal	basipetal	acropetal	I, partial-homogenized
Urochloa mosambicensis	basipetal	unilateral/bilateral	basipetal	basipetal	acropetal	TI, full-homogenized
Urochloa panicoides	basipetal	unilateral/bilateral/spiral	basipetal	basipetal	basipetal	TI, full-homogenized
Urochloa paucispicata	acropetal	spiral	acropetal	basipetal	acropetal	I, full-homogenized
Urochloa plantaginea	basipetal	unilateral/bilateral	basipetal	basipetal	amphipetal	TI, partial-homogenized
Urochloa platyphylla	basipetal	unilateral/bilateral	basipetal	basipetal	acropetal	TI, full-homogenized
Urochloa ruziziensis	basipetal	unilateral/bilateral	basipetal	basipetal	acropetal	TI, full-homogenized
Urochloa xantholeuca	acropetal	spiral	acropetal	basipetal	acropetal	I, partial-homogenized

(Figs. 20–22). That is, depending on the specimen studied, some *Urochloa* species have inflorescences that vary from unilateral to bilateral (primary branches are placed on two sides of the main axis), as in *U. mosambicensis*, *U. plantaginea*, *U. platyphylla*, and *U. ruziziensis*, from unilateral to spiral (i.e., *U. distachya*), and some may even have three different types of inflorescence symmetry (i.e., *U. panicoides*, Figs. 20–22). The occurrence of different inflorescence symmetries in a single species was observed only in those species with basipetal initiation of primary branches (Table 1). The total number of individuals examined and a quantification of the distribution of inflorescence symmetry variation are presented in Table 2.

Direction of primary branch differentiation—In the PCK clade, primary branch differentiation consists of the elongation and flattening of primary branches associated with the development of secondary branches. When combining primary branch initiation with differentiation patterns, it is possible to distinguish three different developmental pathways: (1) acropetal initiation and differentiation of primary branches, (2) acropetal initiation and basipetal differentiation of primary branches, and (3) basipetal initiation and differentiation of primary branches.

When initiation and differentiation are both acropetal, primary branch differentiation begins with the proximalmost, first-formed primary branch (Fig. 23). This pattern is observed in *Megathyrsus maximus*, *Melinis*, *Moorochloa eruciformis*, *U. leucacrantha*, *U. lorentziana*, *U. mollis*, *U. paucispicata*, and *U. xantholeuca*. In those species with acropetal primary branch initiation and basipetal differentiation, the first primary branch to differentiate is the distalmost, last-formed primary branch (Fig. 24). This pattern is observed in *Eriochloa* and two species of *Urochloa* (*U. jubata* and *U. lata*). Finally, in those inflorescences with basipetal initiation and basipetal differentiation of primary branches, the first primary branch to differentiate is the distalmost one, that is, the first-formed branch (Fig. 25). This pattern is found in most of examined species of *Urochloa*. In the last two cases, the distalmost primary branch always has a more advanced development and is the first branch in developing spikelets and florets.

Direction of second-order branch initiation—We studied the direction of second-order branch initiation by considering (1) the direction of second-order branch initiation along the whole inflorescence, (2) the direction of second-order branch initiation along the primary branch, and (3) the disposition of second-order branches on primary branches.

All studied species of *Eriochloa, Moorochloa*, and *Urochloa* first develop second-order branches on the distalmost primary branches, independent of the direction of initiation and differentiation of primary branches (Figs. 24–26). On the contrary, in *Megathyrsus maximus* and *Melinis*, the development of second-order branches begins on the primary branches located at the proximal region of the inflorescence (Fig. 27).

The direction of initiation of second-order branches along primary branches may be basipetal, amphipetal, or acropetal. When basipetal, second-order branches develop from the distalmost region to the proximalmost region of primary branches, as in *U. panicoides* (Fig. 28). When amphipetal, second-order branches develop in the middle region of primary branches. Later, new second-order branches develop either from middle to distal and from middle to proximal regions of primary branches. The amphipetal initiation of second-order branch is observed only in *U. plantaginea* (see Reinheimer et al., 2005).

Finally, when the initiation of second-order branches is acropetal, second-order branches develop from proximal to distal regions of primary branches. This pattern is observed in *Moorochloa*, *Eriochloa*, *Megathyrsus*, and *Melinis* and in the remaining species of *Urochloa* examined in this study (Figs. 24–27). In all species, second-order branches develop on the abaxial side of the primary branches (Figs. 24–29).

Development of third- and higher-order branches—Most species of the PCK clade develop third- or higher-order branches, a fact that further complicates the inflorescence ramification system. We studied the development of third- and higher-order branches considering (1) the developmental pattern of third-order branches, (2) the direction of initiation of third- and higher-order branches along the whole inflorescence and on their subtending branches, and (3) the disposition of third- and higher-order branches.

Four different types of third-order branch development are observed in the PCK clade: (1) third-order branches never develop (i.e., *U. bovonei*, *U. dystachya*, *U. mosambicensis*, *U. jubata*, *U. panicoides, U. platyphylla*, *U. plantaginea*, *U. ruziziensis;* Fig. 29), (2) third-order branches may be present without a well-developed terminal spikelet [i.e., *Eriochloa punctata* (L.) Desv. ex Ham., *U. lata*, and sometimes in *U. panicoides*; Fig. 30 and see also Reinheimer and Vegetti (2008)], (3) third-order branches may have a well-developed terminal spikelet (i.e., *Moorochloa eruciformis*, *E. montevidensis*, *U. leucacrantha*, *U. mollis*, *U. paucispicata*, and *U. xantholeuca*; Fig. 31), and (4) third-order branches may develop a terminal spikelet at the tip as well as a fourth-order branch at the base of the branch (i.e., *U. lorentziana* and sometimes *E. montevidensis*; Fig. 32). The first two patterns lead to the formation of solitary spikelets, and in the third pattern, paired spikelets originate along the primary branches. In addition, the last pattern contributes to the formation of spikelet triplets.

Eventually, new branches with well-developed terminal spikelets may develop from the fourth-order branches as have been found in *Megathyrsus* and *Melinis* (Fig. 33). In these two genera, third- or higher-order branches develop preferentially on the proximal region of the inflorescence. That is, the most complex pattern of ramification at maturity always appears in the proximal region of the inflorescence (Figs. 33, 34).

The direction of third- and higher-order branch initiation may be acropetal or basipetal along the whole inflorescence. Development is acropetal in the inflorescence of *Megathyrsus* and *Melinis* (Fig. 35), while it is basipetal in *Moorochloa* and those species of *Eriochloa* and *Urochloa* with third- or higher-order branch development (Fig. 36). In addition, the direction of third- and higher-order branch initiation is always acropetal along the respective subtending branches (Fig. 36).

The disposition of third- and higher-order branches is complex in species when more than third-order branches are present. Third-order branch primordia are organized in two rows on the abaxial side of second-order branches in *Megathyrsus* and *Melinis*; in these genera, the inflorescence becomes more complex when new branches of higher orders are developed: fourth-, fifth- and up to sixth-order branch primordia initiate in two rows on the abaxial side of the branch from which they originate. This disposition creates a false spiral symmetry in *Melinis* (Figs. 37–41) due to the spatial distribution of second- to sixth-order branches that surround the main axis, even though the underlying inflorescence symmetry is clearly unilateral.
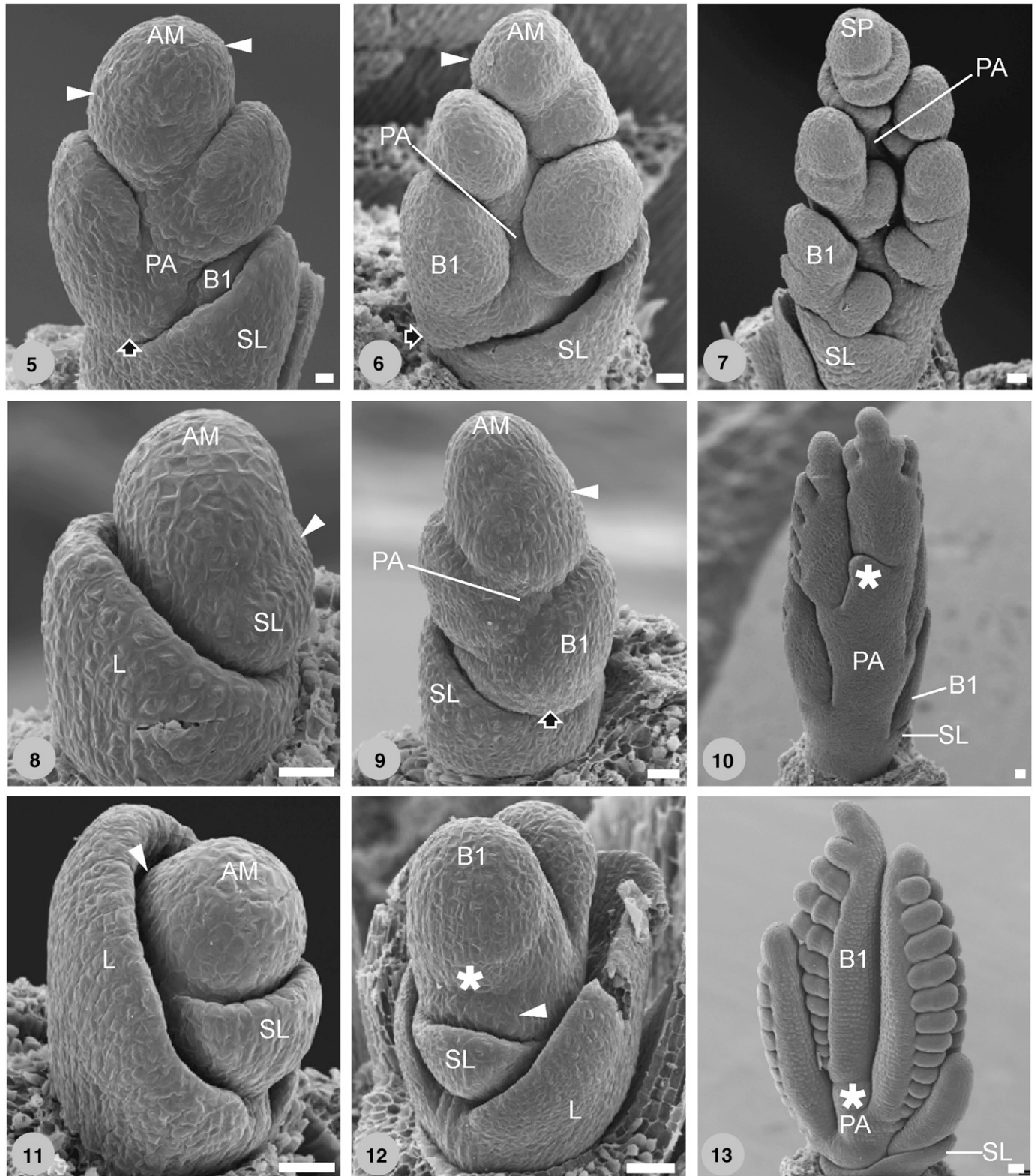
Figs. 5–13.   Patterns of main axis and primary branch development found in species of the PCK clade (scanning electron micrographs). Only the first formed branch (the proximal most primary branch in Figs. 5–10 and the distalmost primary branch in Figs. 12–13) is labeled. Figs. 5–7. Three successive developmental stages of *Urochloa mollis* inflorescence with acropetal initiation of primary branches and terminal spikelet at the tip of the main axis. **5.** The apical meristem of the inflorescence initiates two new primary branch primordia (arrowhead) above the last formed primary branch. Each primary branch is subtended by a leaf primordium (black arrow, only one leaf primordium is labeled). **6.** The acropetal initiation of primary branch primordia continues (arrowhead). Each primary branch is subtended by a leaf primordium (black arrow, only one leaf primordium is labeled). **7.** The main axis ends its development
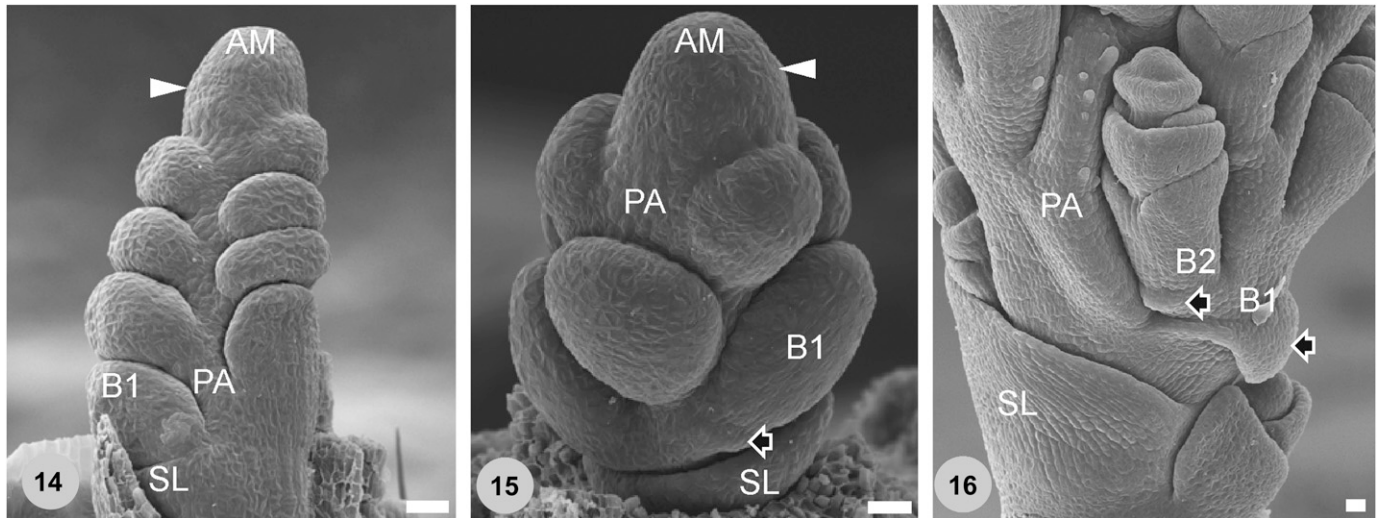
Figs. 14–16.   The presence of leaves in inflorescences with acropetal primary branch development (scanning electron micrographs) in species of the PCK clade. The most proximal, the first-formed, primary branch (in Figs. 15, 16) and the most proximal second-order branch (in Fig. 16) are labeled. The arrowhead indicates the position where the next primary branch primordium will initiate. **14.** Inflorescence of *Moorochloa eruciformis* that lacks leaf primordia at the base of primary branches. **15.** Inflorescence of *Urochloa xantholeuca* where primary branches are subtended by a leaf primordium (black arrow, only one leaf primordium is labeled). **16.** Proximal region of the inflorescence of *Urochloa mollis* where spikelets are already formed. In this case, leaf primordia (black arrows) are still observable even late in development, and they are conspicuous when subtending primary branches while they are smaller when subtending second order branches.

Late inflorescence development—Late inflorescence development is characterized by internode elongation of the main axis, branches, and the basal internode between the flag leaf and the node of the most proximal primary branch. During late inflorescence development after floral organs have initiated and before the emergence of the inflorescence from the sheath, the internodes of the inflorescence main axis may elongate proportionally or differentially relative to each other. Because of differential internode elongation, first-order branches may appear alternate-spiral, subopposite, or pseudoverticillate (i.e., *Eriochloa montevidensis*, some *Urochloa* species, and *Megathyrsus maximus*; see Reinheimer et al., 2005). In addition, during late inflorescence development, internodes of branches may also elongate differentially (i.e., *Moorochloa eruciformis*, *Megathyrsus maximus*, and *Melinis*). In *Melinis*, the basal internode of each branch never elongates, while the internodes of the main axis elongate proportionally (Figs. 40, 41). As a result of this feature, the inflorescence of *Melinis* has false pseudoverticils formed by branches of different orders. Finally, the inflorescence emerges from the sheath by the elongation of the basal inflorescence internode.

DISCUSSION

Inflorescence morphology in grasses is elaborate at mature stages and even more sophisticated when development is analyzed, and the PCK clade is no exception. Our studies of inflorescence development in the PCK clade demonstrated that inflorescences are even more complex than observed in mature stages. Also, we were able to identify numerous developmental characters of the inflorescence that can be used in future systematic studies of the group. Some of these are new characters that allow us to delimitate inflorescence types, and others are classical features previously used to circumscribe taxa of the clade, but redefined here on the basis of development. In addition, we identified developmental pathways that may be associated with the truncation (loss of different inflorescence structures, i.e., the inflorescence terminal spikelet) and homogenization of branches (primary branches having the same ramification pattern) observed in the adult inflorescence. These two evolutionary events have been identified as responsible, at least in part, for the inflorescence diversity observed in the group (Troll, 1964; Weberling, 1989; Vegetti and Weberling, 1996; Rua and Weberling, 1998; Reinheimer and Vegetti, 2008) (Table 1).

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with the formation of a terminal spikelet. This individual lack of leaf primordium at the base of primary branches. Figs. 8–10. Three successive developmental stages of *Urochloa jubata* inflorescence with acropetal initiation of primary branches and without a terminal spikelet at the tip of the main axis. **8.** The apical meristem of the inflorescence initiates the first primary branch primordia (arrowhead) above the scale leaf. **9.** The acropetal initiation of primary branch primordia continues (arrowhead). Each primary branch is subtended by a leaf primordium (black arrow, only one leaf primordium is labeled). **10.** The main axis ends its development without forming a terminal spikelet. Figs. 11–13. Three successive developmental stages of *Urochloa mosambicensis* inflorescence with basipetal initiation of primary branches and without a terminal spikelet at the tip of the main axis. This type of inflorescence lacks leaf primordia at the base of primary branches. **11.** The apical meristem of the inflorescence initiates the first primary branch primordium (arrowhead) above and opposite the scale leaf. **12.** The initiation of primary branches continues with the formation of new primary branches below the first formed branch. The last-formed primary branch is located in the axil of the scale leaf. **13.** Often, the first primary (distal) branch adopts the position of the main axis.
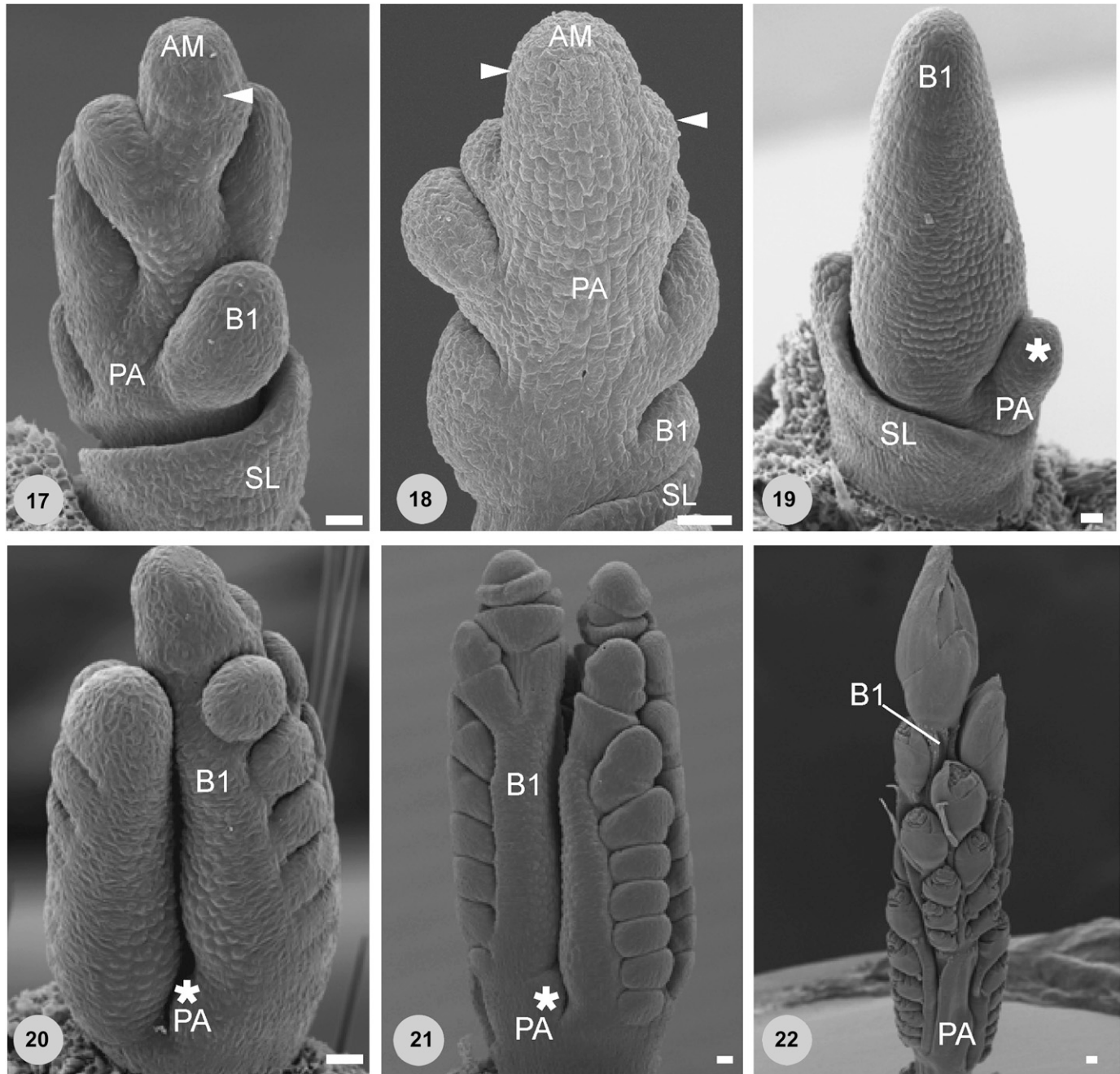
Figs. 17–22.   Inflorescence symmetries found in species of the PCK clade (scanning electron micrographs). The arrowhead indicates the position where the next primary branch primordium will initiate. Only the first-formed branch (the proximal most primary branch in Figs. 17, 18 and the distalmost primary branch in Figs. 20–22) is labeled. **17.** Spiral inflorescence of *Urochloa leucacrantha* where primary branch primordia initiate acropetally on all sides of the main axis. **18.** Unilateral inflorescence of *Moorochloa eruciformis* where primary branch primordia are initiated acropetally in two rows on one side of the main axis. **19.** Inflorescence of *Urochloa bovonei* represented by a single primary branch, where symmetry cannot be assed. Figs. 20–22. Three different individuals of *Urochloa panicoides* with inflorescences showing different symmetries. **20.** One individual with a bilateral inflorescence represented by two primary branches. **21.** A different individual with unilateral inflorescence represented by three primary branches. **22.** A different individual with a spiral inflorescence represented by four primary branches.

Development of inflorescences with terminal spikelet (nontruncated inflorescences) or without terminal spikelet (truncated inflorescences)—Our results show that even when two adult inflorescences look similar they may have originated by different developmental patterns (Table 1). The nontrun-

cated inflorescence is formed when the apical meristem elongates above the scale leaf and finally forms a terminal spikelet late in development, after the initiation of primary branches. In contrast, a truncated inflorescence may be formed by one of two different developmental patterns that differ in the timing when

TABLE 2.   Distribution of the variation of inflorescence symmetry observed in the PCK clade in relation to the total number of individuals examined. N/A: non applicable.

Species	Symmetry			No. individuals examined
	Spiral	Unilateral	Bilateral	
Moorochloa eruciformis	20			20
Eriochloa montevidensis	15			15
Eriochloa punctata	15			15
Megathyrsus maximus	10			10
Melinis minutiflora	2			2
Melinis repens	8			8
Urochloa bovonei	NA	NA	NA	4
Urochloa distachya	3		17	20
Urochloa jubata		10		10
Urochloa lata	7			7
Urochloa leucacrantha	10			10
Urochloa lorentziana	10			10
Urochloa mollis		12		12
Urochloa mosambicensis		6	9	15
Urochloa panicoides	8	3	9	20
Urochloa paucispicata	10			10
Urochloa plantaginea		6	14	20
Urochloa platyphylla		7	13	20
Urochloa ruziziensis		4	4	8
Urochloa xantholeuca	8			8

the apical meristem aborts and when the primary branch initiates. Some truncated inflorescences are formed by the elongation of the apical meristem above the scale leaf, but the main axis ends the development before the formation of a terminal spikelet and after the formation of primary branches; however, truncated inflorescence may also form by an early abortion of the apical meristem before the formation of the terminal spikelet and most of the primary branches.

Primary branch development—Interestingly, we found that primary branch development may be either acropetal or basipetal in the PCK clade, with basipetal development always correlated with an early abortion of the apical meristem. Moreover, both patterns differ in the timing when the primary branch primordia in the axil of the scale leaf initiates. In inflorescences with acropetal initiation of the primary branches, the first-formed primary branch is that one located in the axil of the scale leaf; however, in inflorescences with basipetal development of primary branches, the primary branch in the axil of the scale leaf is formed last.

The acropetal pattern of primary branch development is the most common pattern in grasses (i.e., Bonnett, 1948; Weir and Dale, 1960; Moncur, 1981; Fraser, and Kokko, 1993; Sundberg and Orr, 1996; Pizzolato and Sundberg, 1999, 2001; Doust and Kellogg, 2002a; Kellogg et al., 2004; Bess et al., 2005; Ikeda et al., 2005; Itoh et al., 2005), while the basipetal pattern is well documented only in a few species of *Urochloa* (see also, Stür 1986; Reinheimer et al., 2005). Therefore, it will be important to determine whether this basipetal development of primary branches is unique to *Urochloa* or whether it has arisen more than once in grasses.

Origin of primary branches with basipetal initiation—Stür (1986) hypothesized that basipetal primary branches are adventitious because of the absence of a leaf primordium at their bases. This hypothesis was based on *U. decumbens*, in which it is well documented that only the first primary branch develops in the axil of a leaf primordium, but no sign of a leaf primor-

dium is present at the base of other basipetal primary branches. Therefore, and based on the absence of a leaf primordium, Stür (1986) suggested that primary branches that develop basipetally may arise from meristems formed de novo along the internode of the inflorescence between the insertion node of the flag leaf and the first-formed primary branch. However, the hypothesis about the adventitious origin of basipetal primary branches considers the typical eudicot model of axillary bud development, where a bud forms in the axil of the subtending leaf. In grasses, it is well documented that during leaf development, the proximal portion of the disk of insertion (the transversely expanding segment of the shoot that surrounds the base of leaf primordia) elongates to form the next internode. Such elongation separates the proximal and the distal portions of the disk of insertion (Pizzolato and Sundberg, 1999, 2001 and citations therein). In this context, the distal portion of the disk will always form the sheath and a bud just opposite to its median portion. This phytomer model indicates that the corresponding bud of a leaf is the axillary bud of the leaf above it (Pizzolato and Sundberg, 1999, 2001 and citations therein). Moreover, our study demonstrates that the absence of leaf primordia in the inflorescence is not unique to inflorescences with basipetal primary branch development. The presence or absence of leaf primordia in inflorescences with acropetal development of primary branches varies both among and within species.

A different hypothesis that we propose here is that the meristems, from which primary branches will initiate, arise in an acropetal direction along the main axis. Later activation of those meristems is basipetal, determining the basipetal initiation of primary branches. This hypothesis requires at least one ad hoc assumption: the acropetally initiated meristems are not histologically or morphologically differentiated, although their initial cells are in someway genetically predetermined.

So far, nothing is known about the genetic mechanisms that control the inversion in the direction of primary branch initiation. Further studies are needed to better understand how and why the inversion in primary branch initiation occurs in the context of the bud development complexity of grasses.

Evidence of change in development associated with inflorescence homogenization—Homogenization is the term used to describe an inflorescence in which all primary branches have the same branching pattern and is one feature that contributes to the external appearance of an adult inflorescence in grasses as well as other angiosperms (Troll, 1964; Weberling, 1989; Weberling et al., 1993; Rua, 1999). Studies of homogenized inflorescences are limited to descriptions of the degree of homogenization in adult inflorescences, but we lack data to correlate developmental changes with homogenization of branches.

Our results correlate homogenized inflorescences in the PCK clade with basipetal initiation of second- and third-order branches when the whole inflorescence is analyzed (Table 1). For instance, *Megathyrsus* and *Melinis*, which have nonhomogenized inflorescences, develop second- and third-order branches from the bottom to the top of the inflorescence. In contrast, inflorescences with some degree of homogenization exhibit an inversion in the direction of second- and third-order branch initiation (Table 1). How this correlation may be extrapolated as a general rule for all the homogenized inflorescence in other grasses or angiosperms is still unknown and will be interesting to explore.

Redefinition of characters previously used for taxonomic purposes—The presence of a terminal spikelet on the main
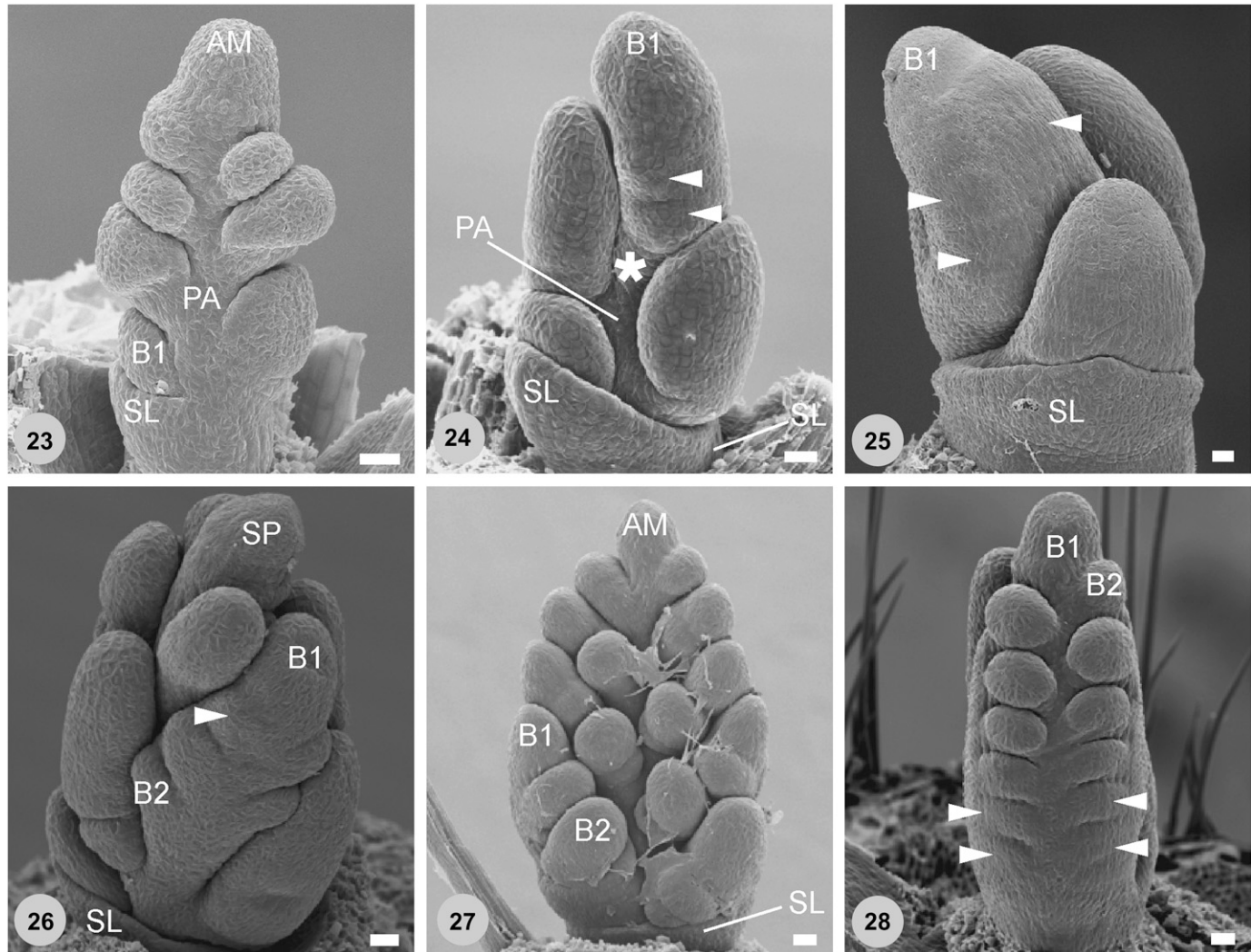
Figs. 23–28.   Patterns of primary branch differentiation and second-order branch development in species of the PCK clade (scanning electron micrographs). Only one primary branch is labeled in each figure. Only one second-order branch is labeled in Figs. 26–28. **23.** Acropetal differentiation of primary branches in *Moorochloa eruciformis*. **24.** Basipetal differentiation of primary branches in *Eriochloa punctata*. In this species, second-order branches (arrowheads) initiate acropetally on the abaxial side of most distal primary branch. **25.** Basipetal differentiation of primary branches in *Urochloa ruziziensis*. In this species, second-order branches initiate acropetally on the abaxial side of most distal primary branch (arrowheads). **26.** Basipetal initiation of second order branches along the inflorescence and acropetal initiation of second order branches on the abaxial side of the primary branch in *Urochloa xantholeuca*. Arrowhead indicates initiation site of new second-order branch primordia. **27.** Acropetal initiation of second-order branches along the inflorescence and on the abaxial side of the primary branch in *Melinis repens*. **28.** Basipetal initiation of second-order branches on the abaxial side of the primary branch in *Urochloa panicoides*. Arrowheads indicate initiation site of new second-order branch primordia.

axis, inflorescence symmetry, disposition of second-order branches, the presence of solitary and paired spikelets, and the presence of pseudoverticils have been used to circumscribe genera and species in the grass family, particularly in the PCK clade. We have already discussed the importance of developmental studies in determining the formation of truncate inflo-

rescence by two different patterns of main axis development. In this context, the developmental study presented here shows that characters such as inflorescence symmetry and the disposition of second-order branches on primary branches should be used with caution in future taxonomic studies when they are based only on adult inflorescences.

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Figs. 29–36.   Scanning electron micrographs of inflorescences in species of the PCK clade showing different patterns of third- and higher-order branches development. **29.** *Urochloa ruziziensis*. Second-order branches end their development with the formation of a terminal spikelet before the formation of a third-order branch. Only one primary branch is labeled. The arrowhead marks a second-order branch ending in a terminal spikelet. **30.** *U. lata*. Second-order branches end in a well-developed terminal spikelet and form a third-order branch at the base. The terminal spikelet of the third-order branch will never become a well-developed spikelet. **31.** *Eriochloa montevidensis*. Third-order branches end in a spikelet that will later develop fully.
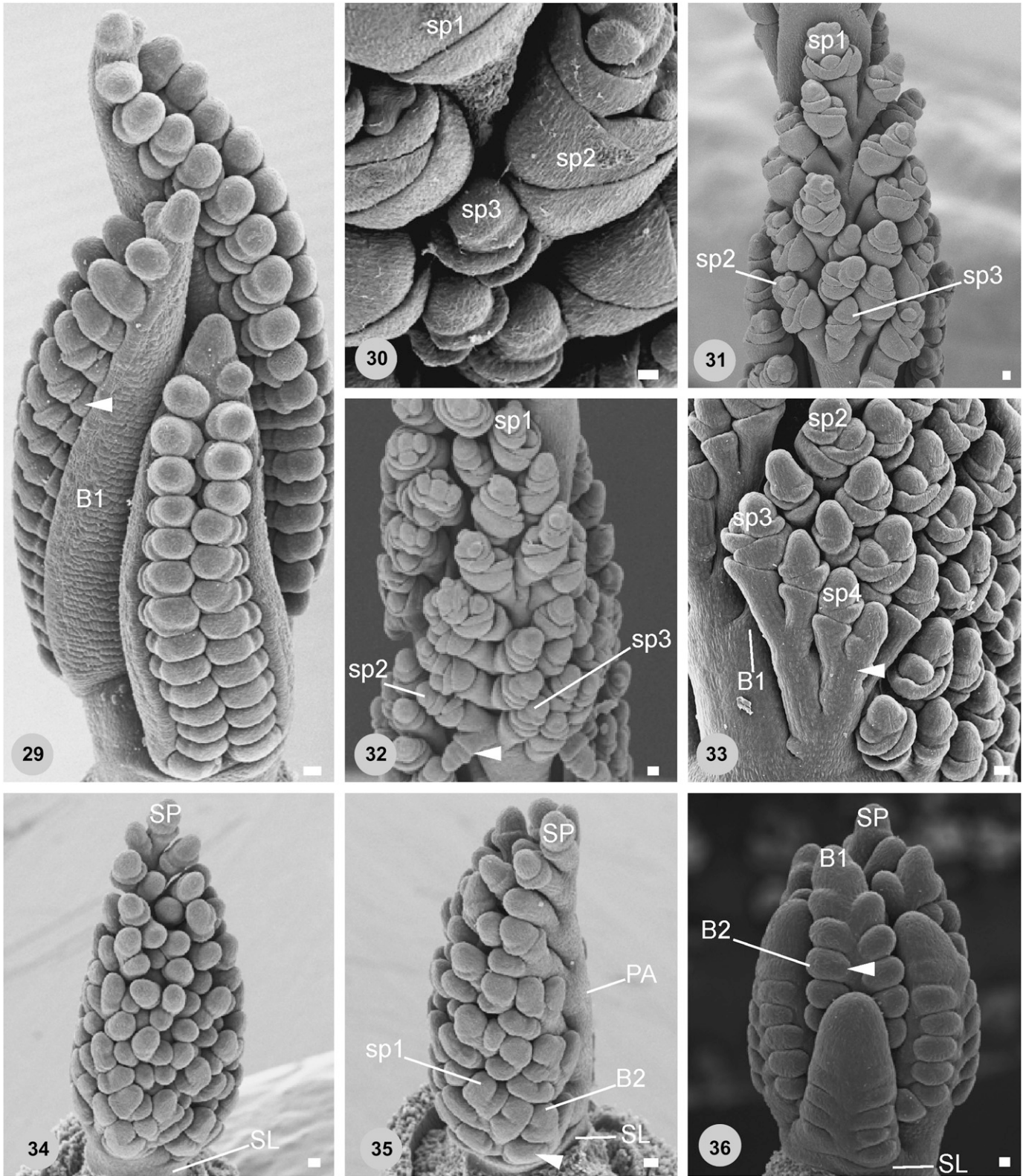
32. *E. montevidensis* where third-order branches may also form a fourth-order branch at the base (arrowhead) that will end its development in a well-developed terminal spikelet. **33.** *Melinis repens*. Proximal region of a primary branch where third- or higher-order (arrowhead) branches have developed. Each branch will develop a terminal spikelet. **34.** *M. repens*. The most complex pattern of ramification always appears in the proximal region of the inflorescence. **35.** *M. repens*. Acropetal initiation of third-order branches (arrowhead) along the whole inflorescence. Only one third-order branch is labeled. **36.** *U. xantholeuca*. Basipetal initiation of third-order branches (arrowhead) along the whole inflorescence; the most proximal primary branches are still forming second-order branches. Only one of the distalmost primary branches is labeled.
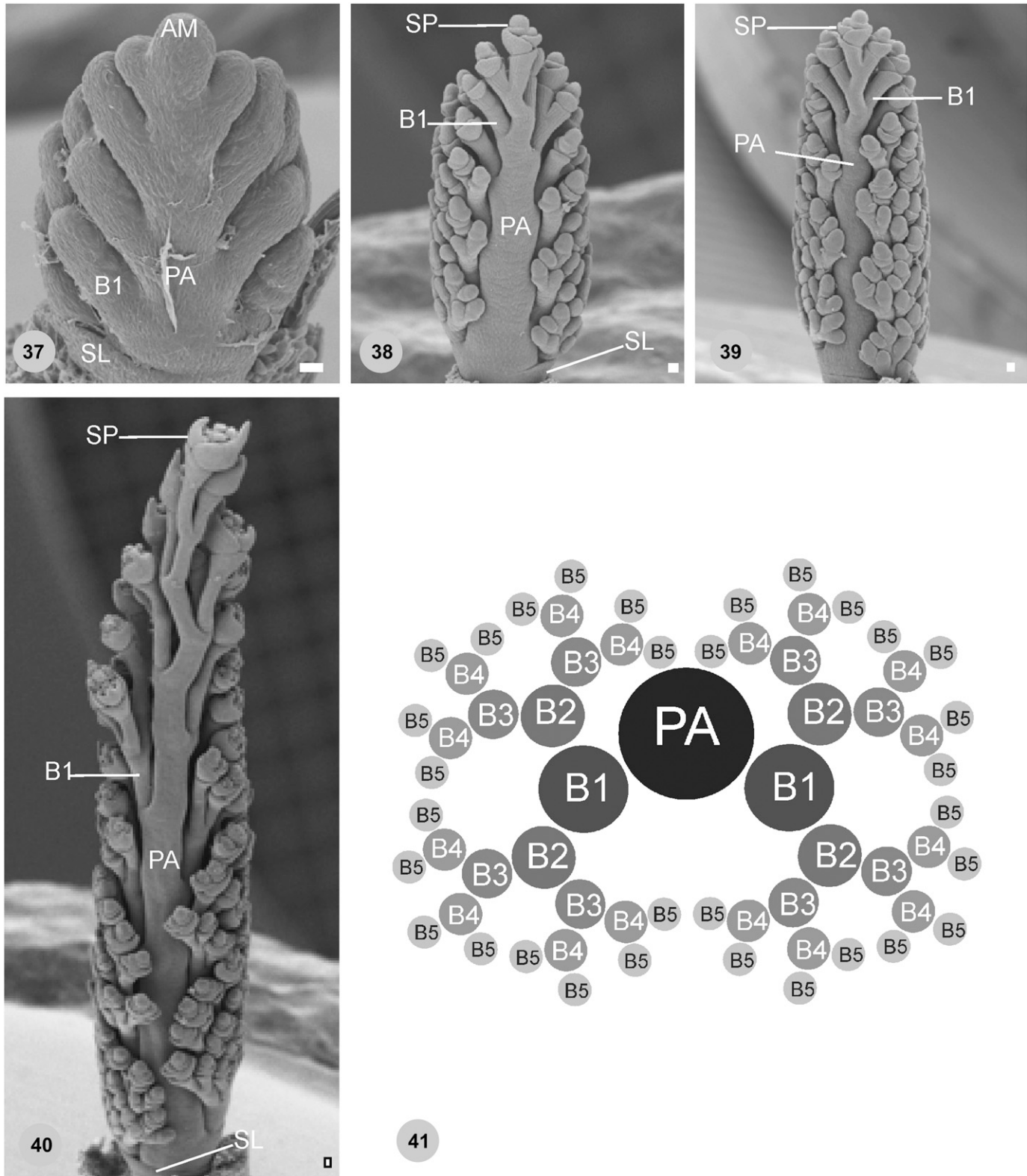
Figs. 37–41. Inflorescence development of *Melinis repens*. Figs. 37–40 are scanning electron micrographs; only one primary branch is labeled in each. **37.** Early inflorescence development where primary branches initiate in one side of the main axis conferring a unilateral symmetry. **38.** The inflorescence becomes more complex when higher-order branch primordia initiate. The branches start to surround the main axis development. **39.** The main axis is partially enclosed by branches with a diverse order of ramification. At the same time, the elongation of the internodes of the main axis begins. **40.** Late in development, the main axis is surrounding by branches, even though the underlying inflorescence symmetry is clearly unilateral. The internodes of the main

Inflorescence symmetry—Inflorescence symmetry is used as one of the most important characters for delineating the American species of *Urochloa* and *Moorochloa* (Morrone and Zuloaga, 1992, 1993). However, determination of symmetry is not simple because (1) a low number of primary branches can make it hard to assess, and (2) in species of *Urochloa* with a basipetal branch initiation, inflorescence symmetry is not stable. For example, we observed that *U. panicoides* has three different inflorescence symmetries depending on the specimen examined. Developmental plasticity is not uncommon in grasses. Our observations suggest that plasticity is present only in species with basipetal primary branch initiation where, in general, one type of symmetry predominates.

Disposition of second-order branches on the primary branches—Many authors use the character "disposition of the second-order branches on the primary ones" as a character with potential taxonomic value (i.e., Clayton and Renvoize, 1986; Webster, 1988; Morrone and Zuloaga, 1991, 1992, 1993; Zuloaga and Morrone, 1995, 1996; Frank, 1998; Arriaga, 2000; Zuloaga et al., 2000; Reinheimer and Vegetti, 2004). Some species are described as having second-order branches placed abaxially, on all sides, or on two sides of the primary branches. Nonetheless, this character is not easy to assess in mature inflorescences with long branches, and it is even a more complex task with herbarium specimens. Long branches and herbarium specimens distort the disposition of second-order branches, leading to incorrect descriptions. Developmental studies are useful for clarifying the position of second-order branches early in development and before the elongation of the internodes. We observed that all studied species have second-order branches on the abaxial side of primary branches, even in those species that were previously described as having second-order branches on all sides of the primary branches (see also Reinheimer and Vegetti, 2008).

Formation of solitary and paired spikelets—In general, inflorescences in the PCK clade develop third- or higher-order branches, complicating the inflorescence structure. The development of third-order branches follow one of four different patterns among the species examined. Due to these patterns, spikelets may be solitary, paired, or in triplets. The organization of spikelets is a feature used to circumscribe and describe the American species of *Moorochloa* and *Urochloa* (Morrone and Zuloaga, 1992, 1993). Here we reported that solitary spikelets may be formed by at least one of two different development patterns, sometimes involving the abortion of the second spikelet. Moreover, we identified more than one pattern of second spikelet abortion that will be treated in a separate paper.

Types of pseudoverticils—*Megathyrsus* and *Melinis* have the most highly branched inflorescences within the PCK clade, and both are characterized by the presence of pseudoverticils along the main axis (Reinheimer et al., 2005; Reinheimer and Vegetti, 2008). The results presented in this study suggest that pseudoverticils of *Megathyrsus* and *Melinis* have different origins. In *Melinis*, pseudoverticils are formed by the proximity of second- or higher-order branches that never elongate their basal internodes,

whereas in *Megathyrsus maximus* they are formed exclusively by primary branches. Moreover, this feature plus the disposition of second- to sixth-order branches obscures the interpretation of symmetry when adult inflorescences of *Melinis* are studied, leading to incorrect descriptions.

Other characters that add more complexity to the inflorescence in the clade—The degree of ramification and the different elongation of the main axis and branch internodes are characteristics that have been widely used to describe adult inflorescences of the PCK Clade as well as other grasses (i.e., Vegetti and Anton, 1995, 2000; Le Roux and Kellogg, 1999; Doust and Kellogg, 2002a; Kellogg et al., 2004; Liu et al., 2005; Reinheimer and Vegetti, 2008). While these features are easily recognized in mature inflorescence, some new features have been identified in this work.

Direction of primary branch differentiation—The direction in which primary branches differentiate is not directly correlated with primary branch initiation in those inflorescences with acropetal initiation because they may have either acropetal or basipetal primary branch differentiation depending on the species studied. In contrast, basipetal initiation of primary branches does appear to correlate with primary branch differentiation; in all these inflorescences, we observed basipetal differentiation of primary branches.

Direction of second-order branch initiation on primary branches—Acropetal initiation of second-order branches along primary branches is the most common pattern observed in the PCK clade. In contrast, amphipetal initiation of second-order branches has only been reported for *U. plantaginea* (Reinheimer et al., 2005), and basipetal initiation of second-order branches on subtending branches was observed only in *U. panicoides*. Nothing is known about the significance of the differences observed in second-order branch initiation on primary branches. The variation in the direction of second-order branches on primary branches is thus an interesting area for future investigations.

Differential elongation of internodes—When mature, the inflorescences of certain species in the PCK clade differ in internode lengths, resulting in diverse and sophisticated inflorescence shapes, as observed in *Moorochloa*, *Megathyrsus*, *Melinis*, and some species of *Urochloa* (Reinheimer and Vegetti, 2008). The final length of internodes in grasses is genetically determined late in development (after spikelet and floret initiation) and may not be under the same genetic control responsible for the formation of inflorescence branch architecture. Evidence supporting this hypothesis includes several previous studies (Fraser and Kokko, 1993; Doust and Kellogg, 2002a, b; Ikeda et al., 2004; Kellogg et al., 2004; Bess et al., 2005; Reinheimer et al., 2005; Malcomber et al., 2006 and citations therein) as well as data reported in this work.

Groups of species based on inflorescences development—Using characters from inflorescence development, we identified four morphological groups:

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axis have elongated; internodes of branches will not extend. **41**. Schematic drawing of transverse section of inflorescence indicating the spatial distribution of second- to sixth-order branches surrounding the main axis.

(1) Nontruncated and nonhomogenized inflorescences with acropetal initiation and differentiation of first-, second-, third-, or higher-order branches. This inflorescence type may or may not have leaves at the base of branches. This group includes *Megathyrsus* and *Melinis*.

(2) Nontruncated and homogenized inflorescences with acropetal initiation and differentiation of primary branches plus basipetal initiation of second- and third- or higher-order branches. This inflorescence type may or may not have leaves at the base of branches. This group includes *Moorochloa* and few species of *Urochloa*.

(3) Truncated and homogenized inflorescences with acropetal initiation of primary branches and basipetal differentiation of primary branches plus basipetal initiation of second- and third- or higher-order branches. This inflorescence type may or may not have leaves at the base of branches. This group is represented by *Eriochloa* and few species of *Urochloa*.

(4) Truncated and homogenized inflorescences with basipetal initiation and differentiation of first-, second-, and third- or higher-order branches. This inflorescence type lost the leaves at the base of branches and inflorescence symmetry showed certain plasticity among individuals. This group is represented by the majority of *Urochloa* species.

These results conflict with the classification proposed on the basis of the current molecular phylogeny of this group. Based on our morphological analysis, *Megathyrsus* and *Melinis* can be segregated from the remaining members of the PCK clade. We found no evidence to support the monophyly of *Moorochloa* and *Urochloa*, instead demonstrating that *Moorochloa*, *Eriochloa*, and *Urochloa* are paraphyletic. *Urochloa* species with inflorescences that fit into morphological group 4 can be segregated into a different group. Taxonomic delimitation among genera in the PCK clade remains confusing and unclear due to molecular and morphological studies support different classifications.

Inflorescence development evolution in the PCK clade—The phylogeny of the PCK clade is currently unresolved, and anything we say about inflorescence evolution in the PCK clade remains speculative. If the phylogeny presented by Torres González and Morton (2005) is correct, then nontruncated inflorescences with acropetal initiation and differentiation of first-, second- or third-order branch initiation may have evolved first and the truncated inflorescence with basipetal initiation and differentiation of primary branches may have developed later in the history of the group. However, the phylogeny of Torres Gonzalez and Morton (2005) is not well supported, and thus a reliable assessment of changes in the inflorescence is still lacking.

The PCK clade is indisputably monophyletic but surprisingly diverse in terms of inflorescence structure and development, even among closely related species. Data presented in this work illustrate the complexity of inflorescence architecture and demonstrate how developmental studies can provide valuable information about that diversity. Previous studies on closely related groups suggest that inflorescence form can easily change over evolutionary time because inflorescence morphologies correlate only partially with the evolution of plastids and nuclear genes (Doust et al., 2007). In this context, it is possible that the diversification of inflorescence form may be random rather than being associated with adaptation. On the other hand, several authors have pointed out the importance of the inflorescence shape in pollination and seed dispersal in the grasses and the congruence with molecular phylogenies (Friedman and Harder, 2005; Liu et al., 2007). So far, we do not have a clear picture about the evolutionary history of the PCK clade to understand the origin of different inflorescence forms. In addition, it is clear that we only partially understand the sophistication of inflorescence morphology. Future work is necessary to clarify the phylogeny of the group and to determine the differences in the genetic control that drive such drastic changes in development patterns.

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APPENDIX 1. Voucher information for the taxa used in this study. *Abbreviations*: CIAT, Centro Internacional de Agricultura Tropical; Prov., province; SF, Herbario E. A. Ragonese; BAA, Herbario Gaspar Xuarez; SI, Herbario del Instituto de Botánica Darwinion.

Taxa; *Voucher specimen*, Collection locale, Herbarium.

Eriochloa montevidensis Griseb.; *Reinheimer et Vegetti 126*, Santa Fe, Argentina, SF. **Eriochloa punctata** (L.) Desv. Ex Ham.; *Reinheimer 127*, Santa Fe, Argentina, SF. **Megathyrsus maximus** (Jacq.) B.K. Simon & S.W.L. Jacobs; *Reinheimer 129*, Santa Fe, Argentina, SF. **Melinis minutiflora** P. Beauv.; *G.H. Rua et al. 23856*, Mato Grosso, Brazil, BAA. **Melinis repens** (Willd.) Zizka; *G.H. Rua, A.I. Honfi and J. Daviña s/n*, Central, Paraguay, BAA; *Reinheimer, Guarise et Marino 4*, Misiones, Argentina, SF; *Reinheimer, Guarise et Marino 9*, Misiones, Argentina, SF; *Reinheimer, Guarise et Marino 101*, Misiones, Argentina, SF; *Reinheimer et Guarise 106*, Misiones, Argentina, SF; *Reinheimer et Vegetti 125*, Santa Fe, Argentina, SF. **Moorochloa eruciformis** (SM.) Veldkamp; *CIAT 26885*, Oman, África, SF; *J. de Dios Muñoz, Reinheimer et Vegetti s/n.*, Entre Ríos, Argentina, SF; *Reinheimer et Vegetti 124*, Entre Ríos, Argentina, SF. **Urochloa bovonei** (Chiov.) A.M. Torres and C.M. Morton; *CIAT 26438*, Iringa, Tanzania, SF. **Urochloa distachya** (L.) T.Q. Nguyen; *CIAT 26893*, Maritime, Tobago, SF; *CIAT 26894*, Maritime, Tobago, SF. **Urochloa jubata** (Fig. and De Not.) Sosef; *CIAT 16514*, Transnzoia, Kenya, SF; *CIAT 16517*, Bungoma, Kenya, SF; *CIAT 16518*, Bungoma, Kenya, SF; *CIAT 16203*, Sidamo, Ethiopia, SF. **Urochloa lata** (Schumach.) C.E. Hubb.; *CIAT 26886*, SF. **Urochloa leucacrantha** (K. Schum.) Stapf; *CIAT 16546*, Kilifi, Kenya, SF. **Urochloa lorentziana** (Mez) Morrone and Zuloaga; *Morrone O. 4653*, Tucumán, Argentina, SI; *Morrone O. 5157*, Córdoba, Argentina, SI; *Zuloaga F.O. 8678*, Salta, Argentina, SI. **Urochloa mollis** (Sw.) Morrone and Zuloaga; *Morrone O. 5048*, Santa Cruz, Bolivia, SI. **Urochloa mosambicensis** (Hack.) Dandy; *CIAT 26084*, Hwange, Zimbabwe, SF; *Morrone O. 4641*, Salta, Argentina, SI. **Urochloa panicoides** P. Beauv.; *Morrone O. 4340*, Tucumán, Argentina, SI; *Morrone O. 5159*, Córdoba, Argentina, SI; *Pensiero J. 7079*, Santiago del Estero, Argentina, SF; *Zuloaga F.O. 8556*, Jujuy, Argentina, SI. **Urochloa paucispicata** (Morong) Morrone and Zuloaga; *Pensiero J. 7055*, Jujuy, Argentina, SF; *Zuloaga F.O. 8576*, Jujuy, Argentina, SI; *Zuloaga F.O. 8677*, Salta, Argentina, SI. **Urochloa plantaginea** (Link) R.D. Webster; *Morrone O. 4349*, Jujuy, Argentina, SI; *Reinheimer et Guarise 104*, Misiones, Argentina, SF; *Reinheimer 128*, Santa Fe, Argentina, SF. **Urochloa platyphylla** (Munro ex C. Wright) R.D. Webster; *Reinheimer 123*, Santa Fe, Argentina, SF. **Urochloa ruziziensis** (R. Germ. and Evrard) Crins; *CIAT 654*, Bujumbura, Burundi, SF; *Reinheimer, Guarise et Marino 8*, Misiones, Argentina, SF; *Reinheimer et Guarise 105*, Misiones, Argentina, SF; *Ramos J. s/n*, Misones Argentina, SF. **Urochloa xantholeuca** (Hack. ex Schinz) H. Scholz; *CIAT 26549*, Centre, Burkina Faso, SF.