American Journal of Botany

American Journal of Botany 99(8): 1276–1288. 2012.

# MULTIPLE ORIGINS OF CONGESTED INFLORESCENCES IN *CYPERUS* S.S. (CYPERACEAE): DEVELOPMENTAL AND STRUCTURAL EVIDENCE[1]

NICOLÁS J. GUARISE[2,4], ABELARDO C. VEGETTI[2] AND RAÚL POZNER[3]

[2]Morfología Vegetal, Facultad de Ciencias Agrarias, Universidad Nacional del Litoral; Kreder 2805, S3080HOF Esperanza, Santa Fe, Argentina; and [3]Instituto de Botánica Darwinion, C. C. 22, B1642HYD San Isidro, Buenos Aires, Argentina

- *Premise of the study:* The understanding of homoplasic structures becomes more relevant when they are complex and define large angiosperm taxa. Inflorescence architecture usually fulfills both features, as happens with *Cyperus*, a genus with two taxonomical subdivisions characterized either by alternative expressions of Kranz anatomy ($C_3$ or $C_4$) or inflorescence shape (condensed or lax). Those subdivisions are not completely congruent because at least one of these presumed characters has evolved several times. We focused a SEM study on the inflorescence development in species with condensed inflorescences and different photosynthetic anatomy to test the possibility that condensed inflorescences of subgen. *Anosporum* ($C_3$ anatomy) have evolved independently from those of subgen. *Cyperus* ($C_4$ anatomy).
- *Methods:* Freshly collected inflorescences of *C. entrerianus*, *C. eragrostis*, *C. oxylepis*, and *C. incomtus* were studied using stereoscopic and scanning electron microscopy.
- *Key results:* Condensed inflorescences of *Cyperus* species with $C_3$ and $C_4$ anatomy had differences in structure and development: (1) mature structure, (2) position of second-order branching initiation in the first developmental stage of the inflorescence, (3) main axis development and elongation, and branching development, (4) types of ramifications, (5) phyllotaxis and symmetry.
- *Conclusions:* Results support multiple origins of condensed inflorescences in *Cyperus*, based especially on differences in timing during development and elongation of the main axis and branches, branching pattern and phyllotaxis. Structure and development may be the key to using inflorescence morphology as an external feature to distinguish large natural groups within *Cyperus* based on vegetative anatomy.

**Key words:** branching pattern; Cyperaceae; *Cyperus* $C_3$-$C_4$ anatomy; development; homology; inflorescence; phyllotaxis; prophyll; spikelet.

Plant molecular phylogenetics is helping to focus plant morphologists' attention on complex plant structures that need to be re-evaluated because of their high probability of homoplasic origin. The understanding of homoplasic structures becomes more relevant when they are complex and define large angiosperm taxa. In many taxonomical groups, the inflorescence structure and development have been used as an important source of diagnostic characters with phylogenetic value (Doust et al., 2005; Friedman and Harder, 2005; Liu et al., 2005, 2007; Reinheimer et al., 2005, 2009, 2010). In Cyperaceae, the understanding of the structure and homologies of inflorescences is one of the main concerns among cyperologists (Raynal, 1971; Kukkonen, 1994), because the inflorescence has proved to be a source of reliable diagnostic traits and indications for phylogenetic pathways (Bruhl, 1995; Goetghebeur, 1998; Tucker and Grimes, 1999; Guarise and Vegetti, 2007, 2008). In Cyperaceae, inflorescence architecture is known to be variable among taxa, but its development is not well known, as happens in *Cyperus* L., a large genus (more than 550 species) with no general consensus about its circumscription and infrageneric division (Muasya et al., 1998, 2000, 2002, 2009). In its wide circumscription (Muasya et al., 1998, 2000, 2002), *Cyperus* L. s.l. is the second largest genus in the Cyperaceae (Tucker, 1994; Goetghebeur, 1998), and even in its more restricted circumscription, *Cyperus* s.s. appears to be polyphyletic (Muasya et al., 2009). *Cyperus* s.s. has considerable morphological variation, and numerous attempts have been made to organize its infrageneric division, based on different and varied features such as chemical characters, types of dispersal unit, shape of the spikelets, number of style branches, fruit shape and orientation, inflorescence form, and leaf or culm anatomy (Kükenthal, 1935–1936; Barros, 1938; Haines and Lye, 1983; Tucker, 1983, 1994; Goetghebeur, 1989, 1998; Bruhl, 1995; Muasya et al., 2000, 2002, 2009). In these infrageneric proposals, *Cyperus* s.s. is usually subdivided into two units characterized by the alternative stages of two character sets: either (1) the vegetative anatomy is eucyperoid ($C_3$) or chlorocyperoid ($C_4$) (Bruhl, 1995) or (2) the inflorescence is composed of digitately arranged or head-like condensed spikelets (subgenus *Pycnostachys* C. B. Clarke), or it has spicately arranged spikelets (subgenus *Choristachys* C. B. Clarke) (see Kükenthal, 1935–1936 and Goetghebeur, 1989). There seems to be congruence between vegetative anatomy and inflorescence structure in *Cyperus*: $C_3$ taxa have inflorescences with the spikelets arranged in digitate clusters or head-like condensed clusters, while $C_4$ taxa have spikelets spicately arranged (Muasya et al., 2009). However, these characters sets are not completely congruent because some $C_4$ sections include species with head-like

---

[1] Manuscript received 2 November 2011; revision accepted 26 June 2012.

The authors thank to Lic. Leandro Lucero for the contribution in the drawing of the figure and thank Dr. Rosa Guaglianone for critical reading of the manuscript.

[4] Author for correspondence (e-mail: nguarise@fca.unl.edu.ar)

doi:10.3732/ajb.1100528

condensed inflorescences (Goetghebeur, 1989, 1998); this means that at least one or perhaps both of these presumed apomorphic character stages ($C_4$ anatomy and head-like condensed inflorescence) has had a multiple origin (Goetghebeur, 1989). Raynal (1973) and Goetghebeur (1989) considered a multiple origin of the head-like condensed type of inflorescence much more probable than a multiple origin of the $C_4$ anatomy within *Cyperus*. Although multiple origins of $C_4$ anatomy are recorded in several lineages in Cypereae, including *Cyperus* (Raynal, 1973; Goetghebeur, 1998, Soros and Bruhl, 2000; Muasya et al., 2009), $C_4$ anatomy has evolved only once in the *Cyperus* clade (Muasya et al., 2009).

The incongruence between vegetative anatomy and inflorescence structure is observed in sections *Luzuloidei* Kunth and *Glutinosi* (Boeckeler) Kük. Because of the condensed head-like inflorescences of both sections, Kükenthal (1935–1936) placed them in subgenus *Eucyperus* Griseb. [= subgen. *Anosporum* (Nees) Clarke, $C_3$ anatomy]. However, species of section *Glutinosi* have $C_4$ anatomy (Tucker, 1983; Goetghebeur, 1989; Wilson, 1991) and should be positioned within the subgenus *Cyperus* (Tucker, 1983, 1994; Goetghebeur, 1989; Wilson, 1991) with noncondensed, spicately arranged inflorescences.

Our study is a first step toward a re-evaluation of inflorescence structure in *Cyperus* systematics. We focused our study on inflorescence development in four problematic species with condensed inflorescences and $C_3$ or $C_4$ anatomy to test the possibility that condensed inflorescences of subgen. *Anosporum* ($C_3$ anatomy) have evolved independently from those of subgen. *Cyperus* ($C_4$ anatomy). We also studied the value of inflorescence characters to determine the taxonomic position of *C. incomtus* Kunth, a species of ambiguous classification in either section *Luzuloidei* (subgen. *Anosporum*) and section *Glutinosi* (subgen. *Cyperus*).

## MATERIALS AND METHODS

We studied the inflorescence development of four species of *Cyperus* with condensed inflorescences (Table 1): *C. entrerianus* Boeck. and *C. eragrostis* Boeck., both with $C_3$ anatomy (Denton, 1983; Araujo and Longhi-Wagner, 1997), from section *Luzuloidei* (subgen. *Anosporum*); *C. oxylepis* Nees ex Steud., with $C_4$ anatomy, from section *Glutinosi* (subgen. *Cyperus*), and *C. incomtus*, which was placed by Kükenthal (1935–1936) in section *Luzuloidei* for its condensed inflorescence, but Denton (1978) excluded it from that section and suggested it belonged to section *Glutinosi* for its scales with many nerves and winged rachilla. However, *C. incomtus* has $C_3$ anatomy (Araujo and Longhi-Wagner, 1997), like species that belong to subgen. *Anosporum.*

Fresh inflorescences of the four species of *Cyperus*, covering from the earliest stages of development up to the differentiation of stamens and carpels, were collected from wild populations in Santa Fe Province, Argentina (Table 1) between September 2004 and March 2005. Thirty plants were studied per accession and a total of 240 samples of inflorescences (60 samples per species) were fixed in FAA (formalin–acetic acid–70% ethanol, 10 : 5 : 85, v/v). Of the latter, 120 samples (30 samples per species) were selected from the original stock for scanning electron microscopy (SEM) observation. Fixed inflorescences were dissected with the aid of a stereoscopic microscope and classified according to their different stages of development. Those samples were dehydrated with a graded ethanol series plus two final changes of 100% acetone. The dehydrated material was critical-point dried with $CO_2$ as transitional fluid and coated with gold-palladium. All samples of inflorescences, spikelets, and flowers were observed and photographed using a PHILIPS XL 30 scanning electron microscope from the Electron Microscopy Service of Bernardino Rivadavia Museum, Buenos Aires. The terminology used here follows that of Troll's school as used in Guarise and Vegetti (2007, 2008).

TABLE 1. Material studied. Vouchers are housed in Arturo Ragonese Herbarium (SF), Facultad de Ciencias Agrarias, Universidad Nacional del Litoral, Argentina.

| Taxa | Origin (Argentina) | Voucher |
|---|---|---|
| *Cyperus entrerianus* Boeck. | Santa Fe | Guarise N. J. 58 (SF) |
| *Cyperus eragrostis* Lam. | Santa Fe | Guarise N. J. 60 (SF) |
| *Cyperus incomtus* Kunth | Santa Fe | Guarise N. J. 122 (SF) |
| *Cyperus oxylepis* Nees ex Steud. | Santa Fe | Guarise N. J. 39 (SF) |

## RESULTS

***Structure of the mature inflorescence***—The structure of the mature inflorescence of *C. entrerianus*, *C. eragrostis*, and *C. incomtus* has been previously described by Tucker (1987, 1994) and Guarise and Vegetti (2008).

The structure of mature inflorescences is compared in Table 2and Fig. 1. The inflorescence of *C. incomtus* (Fig. 1C) is a contracted head, like a capitulum, while in *C. entrerianus* (Fig. 1A), *C. eragrostis* (Fig. 1B) and *C. oxylepis* (Fig. 1D), generally the inflorescence is an anthela (a cyme with the lateral branches overtopping the central one) and has a congested form. Along the main axis of the four species studied, two zones can be recognized (Fig. 1): (1) the basal-middle zone of the inflorescence with complex branches (bmz) and (2) a distal zone with branches reduced to a single spikelet in *C. incomtus* and *C. oxylepis* or with fascicles of spikelets in *C. entrerianus* and *C. eragrostis* (dz). There are differences among the species in the highest order of branching (Table 2). The order, number, and length of the branches decreased acropetally in all species (Fig. 1). Sometimes, in *C. incomtus*, the inflorescence can be reduced to its distal zone, a dense spike of spikelets. Generally, *C. entrerianus* has up to second-order branches with an elongated epipodium (a compound anthela), while *C. eragrostis* and *C. oxylepis* have only first-order branches with an elongated epipodium (a simple anthela). In the distal region of these elongated branches, there are clusters of spikelets (glomerules; glm); such glomerules are composed of branches with a reduced epipodium each bearing a terminal spikelet (Fig. 1). The glomerules in *C. oxylepis* are made up of short and dense spikes of spikelets (racemose pattern, Fig. 1D), while in *C. entrerianus* and *C. eragrostis*, they are composed of fascicles of spikelets (cymose pattern, Figs. 1A, 1B, 22–27).

The four species have different branching patterns (Table 2; Fig. 1). In accessory serial branches, there is only one bract, and each branch has its own prophyll (Figs. 1A, 17). These branches have a basipetal development and maturation (Fig. 23). The accessory serial branches are spikelets, which are aggregated in a fascicle, termed a serial fascicle (Figs. 22, 23). In *C. entrerianus*, in a serial fascicle, one (Figs. 24, 25) or two (Figs. 26, 27) branches can be produced in the axils of a spikelet prophyll; this fascicle is called a mixed fascicle (developmental details explained below). In *C. eragrostis*, there are no mixed fascicles. *C. incomtus* does not have accessory serial branches, but can have a prophyllar branch (Figs. 12, 13). *Cyperus oxylepis* does not have either accessory serial or prophyllar branches.

The phyllotaxis of mature inflorescences is the same in all studied species, but the number of orthostichies varies (Table 2). The arrangement of the vegetative leaves is spiro-tristichous, whereas in the inflorescence zone, the bracts and their branches have a spiral arrangement. On branches, except for the spikelets, the arrangement of bracts and branches follow either a right-handed or left-handed spiral, and the symmetry differs between the species (Table 2).

TABLE 2. Developmental features of the branching system of the inflorescences of *Cyperus entrerianus*, *C. eragrostis*, *C. incomtus*, and *C. oxylepis*.

| Characters | *C. entrerianus* | *C. eragrostis* | *C. incomtus* | *C. oxylepis* |
|---|---|---|---|---|
| Inflorescence shape | simple or compound anthela, rarely contracted head | simple anthela, rarely contracted head | contracted head or spike of spikelets | simple anthela |
| Maximum order of branching | 5th | 4th | 3rd | 4th |
| Branching pattern | normal, prophyllarm and accessory-serial | normal and accessory-serial | normal and prophyllar | normal |
| Fascicles | serial and mixed | serial | prophyllar | — |
| Phyllotaxis [a] | spiro-tristichous | spiro-tristichous | spiro-tristichous | spiral |
| Orthostichies [a] | 3 | 3 | 3 | 0 |
| Orthostichies torsion | Yes | Yes | yes | not |
| Symmetry of the complex branching [b] | Radiate | Radiate | dorsiventral | radiate |

[a] In early development stages.

[b] Over the prophyll; this is not considered the spikelet's phyllotaxis. See text for explanation of terms.

***Inflorescence development****—Transition to flowering*—During the vegetative growth phase of all examined species, the apical meristem of the shoot elongates and produces leaf primordia, which early cover the apical meristem (Fig. 3). Morphologically, the transition from the vegetative to flowering phase is evident when the apical meristem elongates beyond the first formed bract primordium and its axillary first-order branch primordium (Figs. 10, 11). Bract primordia cover the apical meristem later in development.

After the transition to flowering and during development of the inflorescence branch system, four main differences were found among the studied species. Three differences belong to the main axis and branching development: (1) position of second-order branching initiation in the first developmental stage of the inflorescence, (2) development and elongation of the main axis and branching development, (3) types of branches; the fourth one includes phyllotaxis and symmetry.

*Main axis and branching development*—The apical meristem continues with the production of bracts and first-order branch primordia along the main axis in acropetal succession (Figs. 5–8, 10, 11, 16–20). While the apical meristem is still elongating and producing primary branches, second-order branches are produced in acropetal succession in both the whole inflorescence and on the primary branches (Figs. 7, 8, 10, 11, 16–19). During the first stage of development in *C. entrerianus* and *C. eragrostis*, second-order branches are produced at the base of first-order branches along the inflorescence (Figs. 7, 8), while in *C. incomtus* and *C. oxylepis*, second-order branches are produced only in the proximal region of the inflorescence (Figs. 10, 11, 16–18).

Differences in diameter increase and lengthening of the internodes of the main axis and lengthening of the branches were observed between species of subg. *Anosporum* and subg. *Cyperus* (Fig. 2). In *C. entrerianus*, *C. eragrostis*, and *C. incomtus*, throughout most of the inflorescence development, the main axis diameter increases, but no notable elongation of the internodes is observed (Figs. 3, 4, 6–8). In *C. entrerianus* and *C. eragrostis*, once the highest order (fourth- or fifth-order) branch primordia have formed and developed, the internodes of the proximal and middle regions of the main axis begin to elongate; this does not happened in *C. incomtus*. Development is different in *C. oxylepis*. In the early stages, the main axis grows beyond the proximal first-order branches (Figs. 2, 16). Then, the most proximal branch begins to develop quickly, produces a higher number of secondary branches and increases its length, becoming almost as long as the main axis (Fig. 17); at this point, this proximal branch stops elongating, and the branch on the next node, going acropetally, takes up its growth until it becomes as tall as the main axis (Fig. 18). As each activity shift from one branch to another occurs, the internode between the two branches lengthens and thickens (Figs. 16–18). This type of development is not observed in the distal branches at an advanced developmental stage: these barely elongate (Figs. 19–21). The proximal and median branches that stopped elongating in the early stages resume their growth, becoming longer and more complex, and the proximal internodes lengthen (Figs. 19–21).

In *C. entrerianus*, *C. eragrostis*, and *C. oxylepis*, in advanced developmental stages, the inflorescence main axis is finally surpassed by the lengthening of the inflorescence branches in the proximal and middle regions. In *C. incomtus*, there is no lengthening of the main axis and branch internodes so the inflorescence becomes capitulum-like.

Different types of branching in mature inflorescences (Table 2) were observed. Prophyllar branches arise from the middle plane of the prophyll, between the two keels (*C. entrerianus* and *C. incomtus*) (Figs. 12, 13, 24, 25). In serial branches (*C. entrerianus* and *C. eragrostis*), one or more buds per node are produced between a primordium or developing branch and its bract (Figs. 22, 23); these serial buds develop basipetally (Figs. 22, 23). Each branch that grows from a serial bud has a prophyll but lacks its own bract (Figs. 22, 23). In *C. entrerianus*, serial branches may occur in the axil of a prophyll (Figs. 24, 25), and both prophyllar and serial branches may develop in a single ramification (Figs. 26, 27). In *C. entrerianus* and *C. eragrostis*, serial buds produce spikelets whose location in the inflorescence depends on the branching order and the species. In both species, first-order serial spikelets are restricted to the distal region of the inflorescence, and their emergence is topologically correlated with the zone of scarce branching (Figs. 8 white arrow, 9). In *C. eragrostis*, second-order serial branches are distributed along the subtending branch (Fig. 36), whereas in *C. entrerianus*, second-order serial spikelets occur only in the distal region of the branch (Fig. 35). In both species, spikelets produced by serial buds usually occur as fascicles (Figs. 22–25).

*Spikelet development*—There are no differences in spikelet development in the species studied. The apical spikelet meristem has a conical form (dome) (Figs. 9, 11, 21). The spikelet consists of an indeterminate rachilla, with many distichous glumes (Figs. 9, 11–15, 21).

In all four species, spikelets are initiated at every branching order and also at the apex of the main axis; however, the

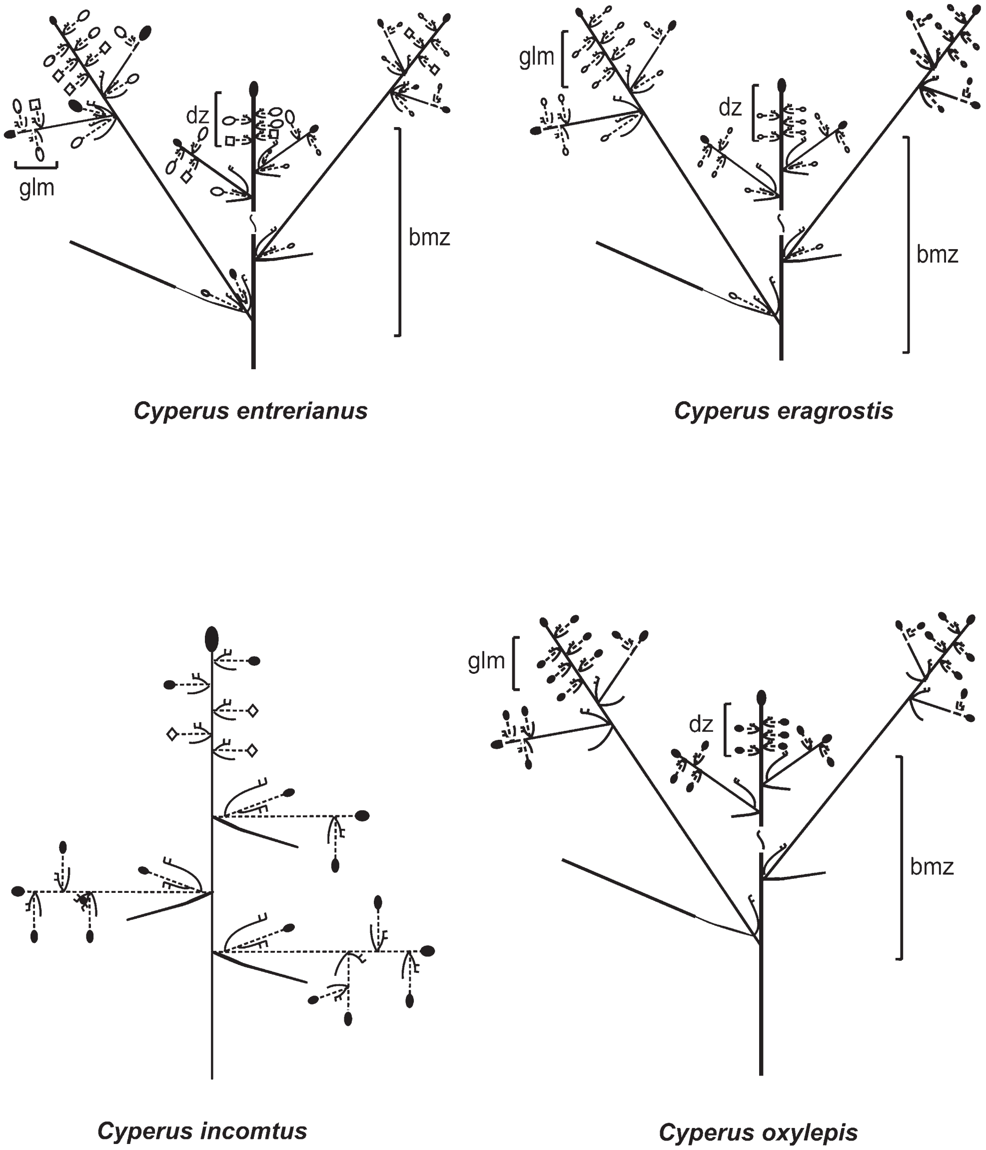


Fig. 1. Comparison of the mature inflorescence structure of *Cyperus* species. *Figure abbreviations:* ◇, prophyllar fascicle; □, mixed fascicle; ⬭, serial fascicle; ⬬, spikelet; b-ac, accessory serial branch; bmz, basal-middle zone of the inflorescence; dz, distal zone of the inflorescence; fl, flower; b-pr, prophyllar branch; br, bract; en, internode; ep, main axis; esp: normal spikelet; esp-ac: accessory spikelet; esp-pr: prophyllar spikelet; gl, glume; glm, glomerule; lp, leaf primordium; ma, apical meristem; n, node; pr, prophyll; ra, rachilla; $r^1$, primary branch; $r^2$, branch of second order, $r^3$, branch of third order; sp, terminal spikelet; $sp^1$, spikelet of first order; $sp^2$, spikelet of second order.

differentiation sequence (basipetal or acropetal) depends on the branching orders considered. During the first stages of spike development, the differentiation sequence is basipetal when comparing spikelets of different branching orders: i.e., the terminal spikelet of the main axis develops before the first-order spikelets, and the terminal spikelet of a first-order branch develops before the second-order spikelets (Figs. 9, 10, 11, 14, 15, 21, 37, 38). On the other hand, first-order spikelets differentiate acropetally along the main axis, and second-order spikelets differentiate acropetally along each first-order branch (Figs. 9, 11, 21, 37, 38). Developmental differences among spikelets are not discernable at later and mature stages of development. Spikelets originated by accessory buds differentiate basipetally in a single node (Figs. 22, 23, 36, 37). Acropetal differentiation is also observed in prophyllar spikelets (Figs. 12, 13). In *C. incomtus*, second-order spikelets may (1) not develop (so the inflorescence is a spike of spikelets), (b) remain as reduced spikelets (Figs. 14, 15), or (3) develop completely. In *C. incomtus* and *C. oxylepis*, some spikelets show at their base one or two spikelet primordia of the second or third order, covered by their prophylls and glumaceous bracts.

***Symmetry, phyllotaxis, and prophyll development****—Main axis*—Changes in phyllotaxis and symmetry are related to the developmental stage of the inflorescence, torsion of primordia and bracts on the main axis, and the shape of the apical meristem.

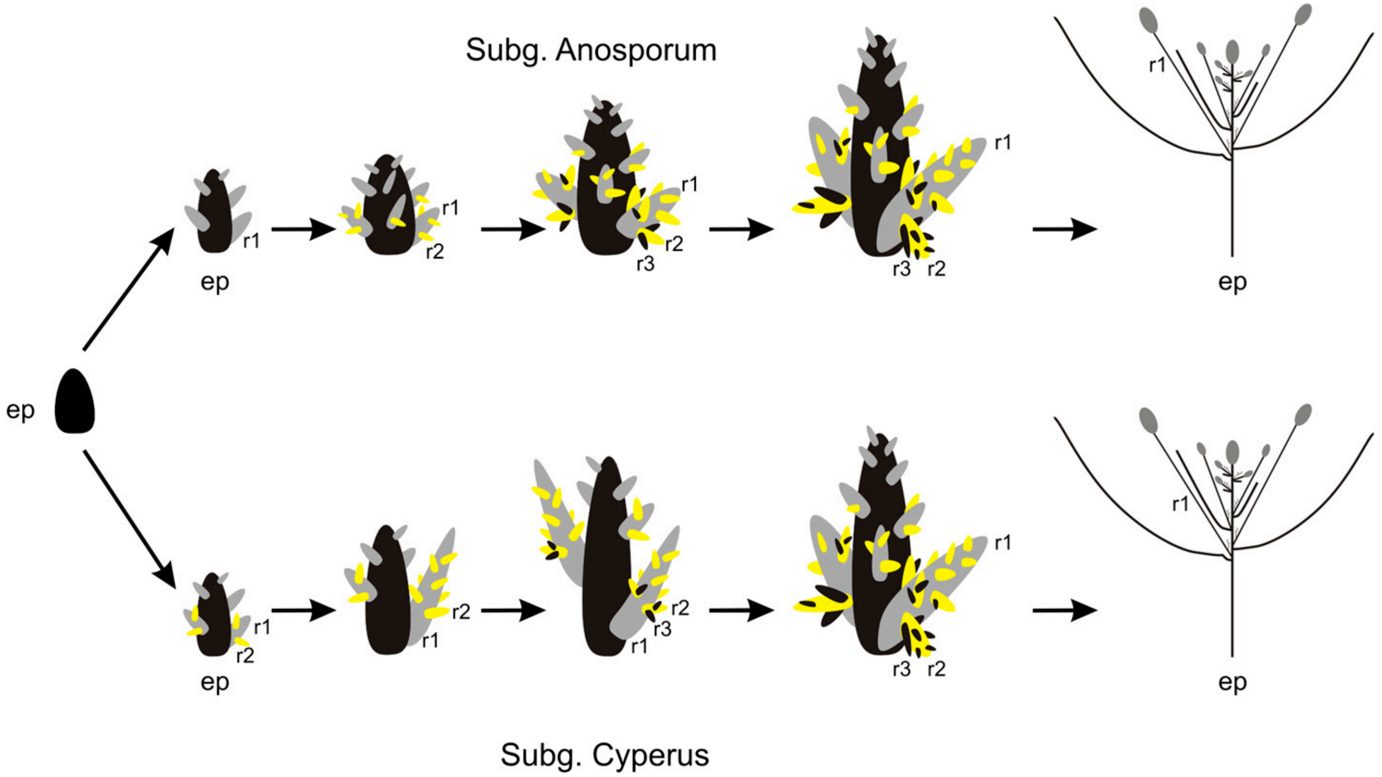


Fig. 2. Development patterns of inflorescences in *Cyperus* subg. *Anosporum* and *Cyperus* subg. *Cyperus* showing differences in the lengthening of the internodes of the main axis and lengthening of the branches during development, but final mature structures are superficially similar.

Differences in phyllotaxis development and numbers of orthostichies were observed (Table 2). The symmetry of the main axis is always radiate, while the phyllotaxis can be modified or not during inflorescence development. During vegetative growth, the apical meristem of the shoot, with a more or less three-faced shape, produces leaf primordia in a spiro-tristichous array (Fig. 3). In the transition from the vegetative to the reproductive stage, the apical meristem maintains its three-faced shape (Figs. 4, 5), but in an advanced stage of inflorescence development, the apical meristem becomes dome-shaped.

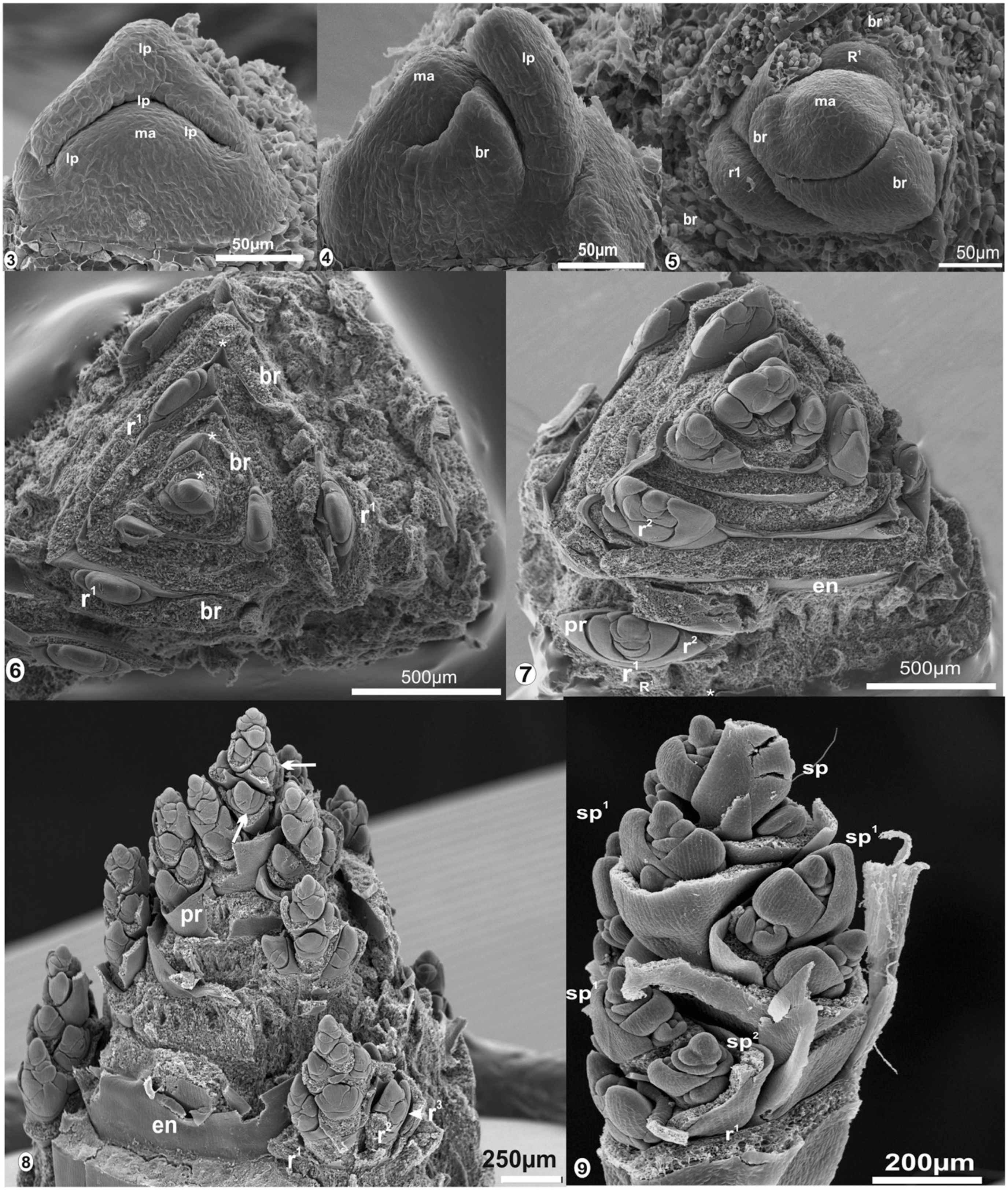
In *C. entrerianus*, *C. eragrostis*, and *C. incomtus*, bracts and first-order branch primordia arise in a spiro-tristichous array (Fig. 5), in three orthostichies (Figs. 6, 10), while *C. oxylepis* shows a deviance from tristichous orthostichies very close to the shoot apical meristem (Figs. 16–18). In *C. entrerianus*, *C. eragrostis*, and *C. incomtus*, in the first stages of inflorescence development, while the apical meristem is still producing primary branches in a tristichous array, torsion of orthostichies is occurs (Figs. 6–8, 11). In *C. entrerianus* and *C. eragrostis*, a branch primordium is displaced relative to the middle nerve of the subtending bract, which is still in a tristichous array (Fig. 6; white asterisks); such displacement takes place in the branches of the proximal and middle regions of the main axis. In *C. incomtus*, displacement of the bract and its branch also occurs; however, unlike the above described displacements, it takes place simultaneously (Fig. 11; white asterisk). In *C. oxylepis*, there is no displacement of either the bract or the branch primordium (Figs. 16–21).

In *C. entrerianus*, *C. eragrostis*, and *C. oxylepis*, the change of the apical meristem shape (dome-like) is correlated with the production of poorly developed first-order branches in the distal region of the inflorescence (Figs. 8, 19, 20; white arrows). In this stage, the apical meristem of the inflorescence in *C. entrerianus* and *C. eragrostis* produces spirally arranged primary branches that do not form orthostichies (Fig. 8), which involves a change in the production of branches in both species. There is no displacement of the branch and its bract in this region (Figs. 5, 9).

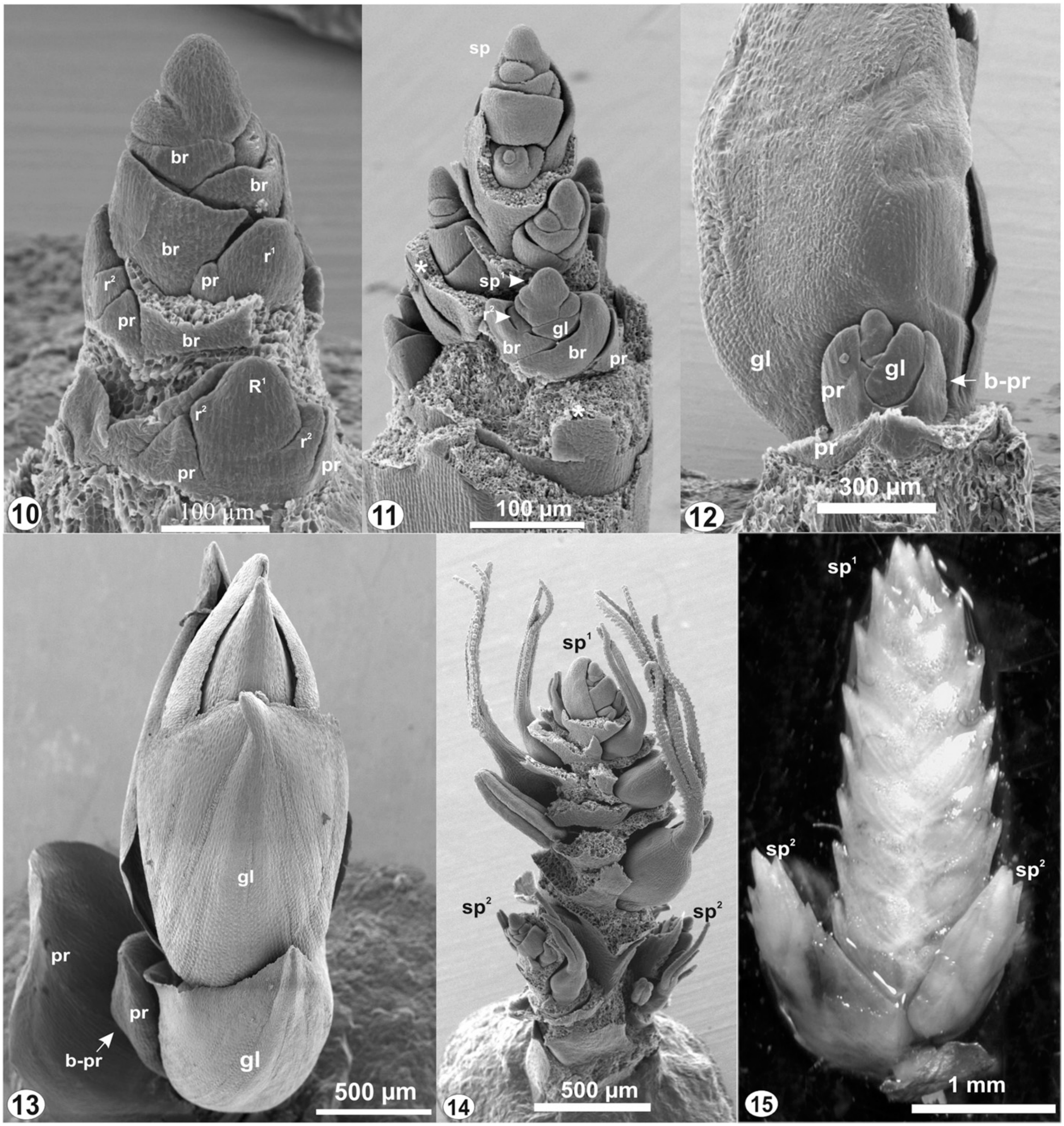
*Branches*—Symmetry and phyllotaxis development is similar in all species studied. Branch symmetry and phyllotaxis vary according to: (1) different stages of branch development, (2) development of new branches, (3) development of the prophyll, (4) development of bracts, and (5) whether the branch has many ramifications, only two ramifications, or is reduced to one spikelet.

In terms of symmetry, every branch is more or less planar when it first starts forming, and shows a bilateral symmetry (Figs. 5, 10, 16). This symmetry becomes dorsiventral due to the prophyll formation on the adaxial face of the primordium (Fig. 28). Then, as the prophyll expands laterally, the branch symmetry becomes bilateral again (Figs. 29, 30). The branch symmetry may remain bilateral or change back to dorsiventral, either because of pressure on the adaxial face of the primordium exerted by the upper branches or the main axis changing the branch primordium shape (Figs. 7, 10–12, 32) or due to the adaxial growth of the prophyll (Fig. 31).

The prophyll continues growing on its adaxial face and the keels (Fig. 33), then on the adaxial and abaxial faces and the keels (Fig. 34) and, finally, only on its adaxial face and margins. The prophyll gradually acquires its final, two-keeled form until it covers the developing branch completely. At this stage,



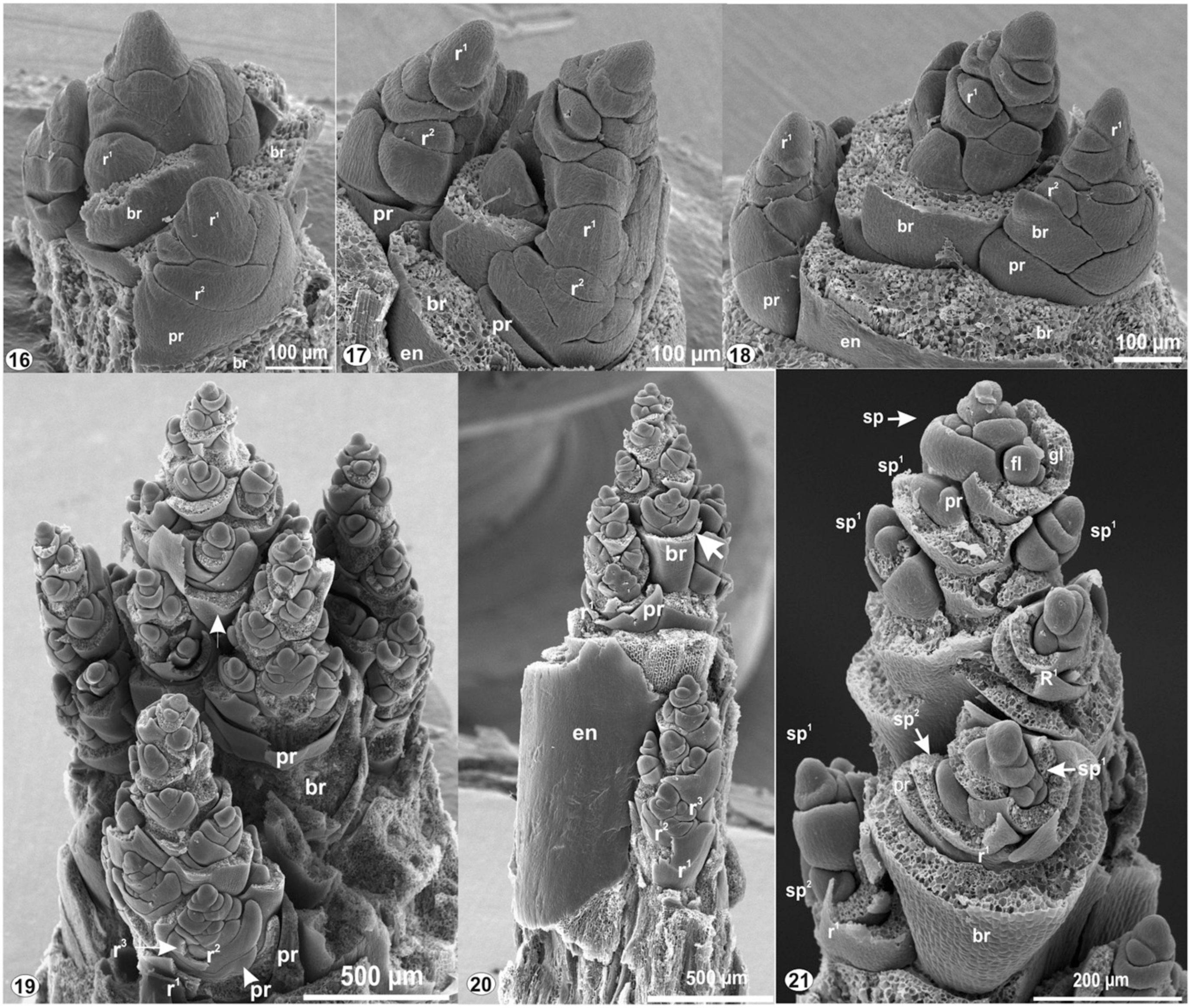
Figs. 3–9. Scanning electron micrographs of inflorescence development in *Cyperus eragrostis* (Figs. 3, 9) and *C. entrerianus* (Figs. 4–8). **3.** Vegetative state with main apical meristem and three-ranked leaf primordia. **4.** Transition from the vegetative to the flowering phase where the apical meristem elongates beyond the first formed bract primordium. **5–8.** Development and elongation of main axis and branches, showing changes in phyllotaxis during development (white asterisks and white arrows). **9.** Each spikelet has an indeterminate rachilla, with many distichous glumes; its differentiation on the whole inflorescence is basipetal on different-order branches and acropetal on same-order branches.



Figs. 10–15. Scanning electron micrographs of inflorescence development of *Cyperus incomtus.* **10.** Development and elongation of the main axis and branches. **11.** In the inflorescences, the terminal spikelet and spikelets of the first order are differentiated. **12, 13.** Prophyllar branch (in this case reduced to a spikelet). **14, 15.** Second-order spikelets have scarcely developed and remain as reduced spikelets.

the prophyll margins are only fused at its base. In *C. incomtus*, the prophyll mostly develops on the adaxial face and margins (Figs. 11, 12). In this species, the prophyll growth does not cover the developing branch entirely. The lateral position of the prophyll causes a dorsiventral symmetry at the base of the adult branch in all species studied.

Phyllotaxis varies based on the development of new bracts and branches. The first two bracts above a branch prophyll follow a distichous arrangement (Fig. 30). The following bracts and branches are spirally arranged (Fig. 34). While the apical meristem continues producing spirally arranged bracts, the branch thickens and causes the displacement



Figs. 16–21. Scanning electron micrographs of inflorescence development in *Cyperus oxylepis.* **16–20.** Development and elongation of the main axis and branches, always with a spiral phyllotaxis. White arrow indicates production of scarcely developed first-order branches in distal region of the inflorescence. **21.** Each spikelet has an indeterminate rachilla, with many distichous glumes; spikelet differentiation in the whole inflorescence is basipetal on different-order branches and acropetal on same-order branches.

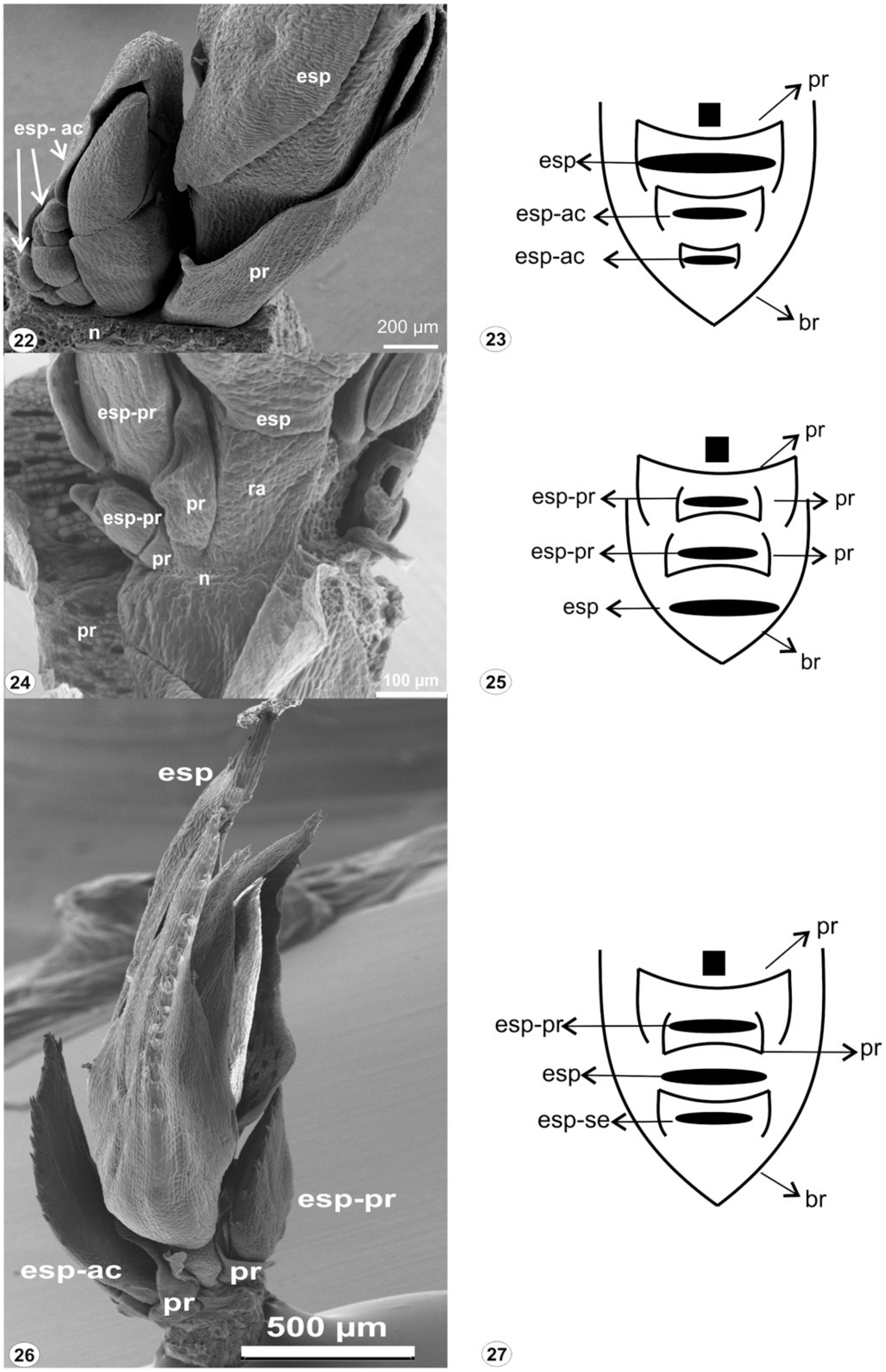
of the first two bracts, which were originally distichous, so they follow the spiral direction of the upper bracts (Figs. 35–38).

By the end of the development of a complex branch with many ramifications, the lateral position of the prophyll causes a dorsiventral symmetry at the base of the adult branch, while the spiral phyllotaxis determines a radial symmetry above the prophyll. When a branch does not produce more than two ramifications, the two basal bracts are located at an angle of less than 180° (Fig. 15); in such cases, the phyllotaxis is spiral, but the symmetry is dorsiventral (Fig. 15).

The first stages of spikelet development are similar to the early stages of a complex branch, except that all glumes are distichously produced and the two proximal glumes do not change their position at maturity (Figs. 9, 13–15). As in a complex branch, the symmetry of a spikelet during its first development stages may be bilateral or dorsiventral, depending on the prophyll position. By the end of its development, the spikelet shows a dorsiventral symmetry at its base due to the prophyll position and a bilateral symmetry in the region above the prophyll.

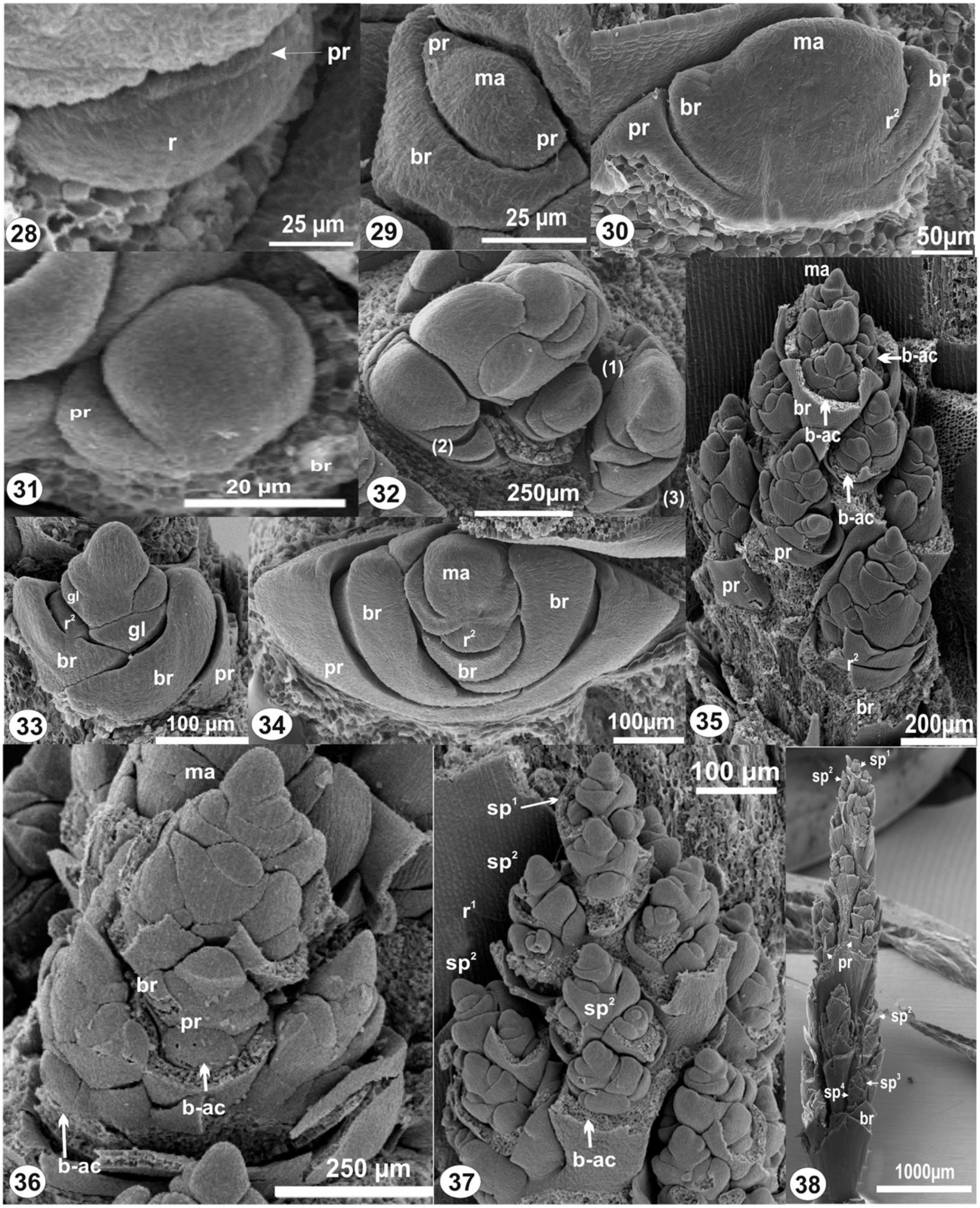
## DISCUSSION

***Multiple origins of congested inflorescences in Cyperus***—*Cyperus entrerianus*, *C. eragrostis*, and *C. incomtus* present $C_3$ anatomy (Araujo and Longhi-Wagner, 1997) and generally have compound or decompound anthelic inflorescences, or sometimes a contracted, capitulum-like head (Kükenthal, 1935–1936; Denton, 1978; Tucker, 1994; Guarise and Vegetti, 2008)



Figs. 22–27. Scanning electron micrographs and diagrams of the different branching patterns. The branches can be complex or reduced to a single spikelet. **22, 23.** Serial branches of *Cyperus eragrostis*. One or more branches per node can be produced between a branch and its bract. Figs. 24–27. *C. entrerianus*. **24, 25.** Prophyllar branches. One branch originates from the axillary bud of a bract and in the prophyll one or more than one axillary buds can origínate a branch in a serial sequence. **26, 27.** Both prophyllar and serial branches may develop in a single ramification.

with spikelets arranged in clusters. *Cyperus oxylepis* has $C_4$ anatomy, and the spikes are short and dense and appear glomerulate (Tucker, 1987), although they are not densely capitate (Wilson, 1991) like in the others three species studied by us (Guarise and Vegetti, 2008). The inflorescence shape in *C. oxylepis* (subgenus *Cyperus*) led Kükenthal (1935–1936) to believe



Figs. 28–38. Successive developmental stages of first-order branching in *Cyperus entrerianus* and *C. eragrostis*, showing prophyll development and changes in the symmetry and phyllotaxis branch. Figs. 28–34, 37, 38: *C. entrerianus*; Figs. 35, 36: *C. eragrostis*. **28–34.** At the first development stage of a branch, the prophyll appears on the adaxial face. Due to the growth of the prophyll and the pressure on the adaxial face of the branch primordium (Fig. 32, nos. 1–3), the symmetry of the branch may change. The first two bracts above a prophyll are distichousy arranged (Fig. 30). The following bracts and branches are spirally arranged (Figs. 33, 34). **35–38.** Advanced stages of development. Branches of second and third order are developed. The first-and second-order branches have a terminal spikelet with flower differentiation (Figs. 37, 38).

that this section was most closely related to section *Luzuloidei* in the subgenus *Pyncnostachys* (Tucker, 1987) subgenus *Anosporum*. In spite of the similar form observed in mature inflorescences, our findings regarding differences in mature and developing inflorescences of specimens of the subgenus *Anosporum* and *Cyperus* support the hypothesis of multiple origins of the condensed type of inflorescence due to the differences in (1) differences in timing in the development and elongation of the main axis and branches, (2) branching pattern, (3) presence of fascicles of spikelets, and (4) phyllotaxis development. Among the features described, developmental timing differences and changes in phyllotaxis cannot be discerned in mature inflorescences. The four characteristics mentioned above are potentially useful in future cladistic analysis, helping determine the origins of complex inflorescences in this genus.

***Inflorescence and branching pattern development***—In the transition to reproductive growth, the apical meristem elongates beyond the first formed bract primordium and becomes broader in transverse section. This change in the apical meristem was also observed in inflorescences of Poaceae (Doust and Kellogg, 2002; Reinheimer et al., 2005). Later, during inflorescence development, the apical meristem changes to a dome shape. The apical meristem of an inflorescence undergoes changes, which tend to be successional, and is capable of a marked shift during the course of its activity (Doust and Kellogg, 2002). These apical meristem changes can be mapped onto a cladistic analysis (Doust and Kellogg, 2002).

Although the bracts and branch primordia are produced in acropetal succession in the whole inflorescence, there are differences between the species of *Cyperus* subgenus *Anosporum* and *Cyperus* subgenus *Cyperus* in the timing of production, elongation, and position of the new branches and elongation of the main axis.

Three types of branching patterns were observed: normal branching (produced by an axillary bud of a bract), prophyllar branching (produced by a prophyllar bud), and accessory-axillary branching (produced by serial buds). The two subgenera differ in the branching patterns; *C. oxylepis* only has normal branching, while the species studied of subgenus *Anosporum* can also have prophyllar or accessory-axillary branches, which can form groups of spikelets named fascicles of spikelets, a distinctive characteristic of section *Luzuloidei* (Guarise and Vegetti, 2008).

The interpretation of the origin, structure, and classification of the branching pattern is controversial. Meert and Goetghebeur (1979) set out three branching patterns for Cyperaceae, based on the ideas of Haines (1966); these are applicable to both the main axis and the lateral branches (Goetghebeur, 1986; Bruhl, 1995). The three types of patterns are: normal, prophyllar, and tandem branching. According to Haines (1966), tandem branching is constituted by serial branches, but Meert and Goetghebeur (1979) did not recognize the serial buds and considered tandem branching as a variant of the prophyllar pattern, where branches originate in the axil of the opposing keel of successive prophylls, thus appearing zig-zagged. This latter interpretation is recognized by Bruhl (1995). However, four features support the serial buds interpretation, at least in the four species that we studied: (1) they arise at the same node, (2) they arise and differentiate basipetally, (3) they arise from the middle of the prophyll, not on an opposite keel, and (4) the branches do not have an antidromic arrangement. The antidromic arrangement, as the change from of a clockwise to a counter- clockwise spiral phyllotaxis and vice versa between branches of different order of ramification, is typical of successive ramification (Mora-Osejo, 1960), and it was not observed in the accessory branching present in the inflorescences studied (Guarise and Vegetti, 2008). In the prophyllar branching pattern of the species that we studied, the prophyll and the main nerve of the bract are all in the same plane; this disposition is not the most generalized for this branching pattern (Meert and Goetghebeur 1979) and is considered a primitive characteristic by Haines (1966).

***Phyllotaxis and symmetry***—Inflorescence phyllotaxis and symmetry have not been used as taxonomic and systematic characters in Cyperaceae and particularly in *Cyperus*; however, differences in phyllotaxis and symmetry were observed in both mature (number of orthostichies) and developing inflorescences.

It should be noted that the transition from a spiro-tristichous disposition, characteristic for the leaves of the vegetative region, to a spiral arrangement of bracts and branching in the inflorescence, and the variation within the inflorescence, is a feature of the adult plant in *Cyperus* (Mora-Osejo, 1960; Guarise and Vegetti, 2008). Variation in phyllotaxis along the inflorescence and its ramification has also been observed in grasses (Vegetti and Anton, 1995; Cámara-Hernández, 2001a, b; Reinheimer and Vegetti, 2004; Kern et al., 2008; Reinheimer et al., 2005).

Phyllotaxis and shoot symmetry are evident during development (Diggle and Endress, 1999). Many factors cause modifications in phyllotaxis and symmetry during development (Dengler, 1999; Kwiatkowska, 1999). Some of those factors were observed in the four species of *Cyperus*: elongation of internodes, primary circumferential growth of the stem, abrupt diminution in size of parts, change of the leaf position, asymmetric relationships of the leaf-axis, changes in the apical meristem form, contact with preceding parts, unequal pressure over the bud and influence on the meristem leading to change in leaf position. The combination of two or more of these factors varies in time and space among the species.

The apical meristem form often correlates with the phyllotaxis pattern and symmetry of the axis (Dengler, 1999). In all species that we studied, modifications in the apical meristem of an inflorescence do not produce changes either in the (radial) symmetry or in the overall (spiral) arrangement of the branches on the main axis of the inflorescence, but they do lead to changes in the number of orthostichies in *C. entrerianus*, *C. eragrostis*, and *C. incomtus*. In these three species, secondary alterations produce a spiral arrangement of the branches with the formation of more than three orthostichies in the mature inflorescence. In the last stage of development, each of these orthostichies is constituted by branches from the basal and distal regions of the inflorescences, whereas the branches of the middle region are not positioned over any orthostichies (Guarise and Vegetti, 2008). If the number of primary branches on the main axis is not nine or more than nine, there are no orthostichies (e.g., *C. incomtus* var. *incomtus*) (Guarise and Vegetti, 2008).

Although all four species present a spiral phyllotaxis and a radial symmetry on the main axis in their adult stage, *C. oxylepis* is different from the three species of subgenus *Anosporum* in that, on the main axis, first-order branch primordia deviate from tristichous orthostichies very close to the shoot apical meristem, and no displacements of the branch are observed relative to its bract during any developmental stage of the inflorescence. There are no differences in phyllotaxis and symmetry during branch development of the four species studied, that is, distinctive and significant differences occur only on the main axis.

***Systematic position of* C. incomtus**—*Cyperus incomtus* was placed by Kükenthal (1935–1936) in section *Luzuloidei*, but Denton (1978) excluded it from that section and considered *C. incomtus* to be related to section *Glutinosi*. Due to its inflorescence structure, *C. incomtus* is the most distinctive species in section *Luzuloidei* sensu Kükenthal (Guarise and Vegetti, 2008). Similarities in the inflorescence structure of *C. incomtus* and *C. ochraceus* Vahl (section *Luzuloidei*) (Guarise and Vegetti, 2008), shared anatomical characters with other species of the section *Luzuloidei* (especially as regards $C_3$ anatomy) (Araujo and Longhi-Wagner, 1997) and more shared development features with *C. entrerianus* and *C. eragrostis* than with *C. oxylepis* do not support the exclusion proposed by Denton (1978). During development, *C. incomtus* shows similarities to *C. entrerianus* and *C. eragrostis* in the elongation of the main axis internodes and the phyllotaxis development (formation of orthostichies followed by branch displacement), two important features that distinguish it from *C. oxylepis*. Therefore, we regard *C. incomtus* as best placed in section *Luzuloidei*.

***Conclusion***—Our results support the multiple origins of congested inflorescences in the genus *Cyperus*, based especially on differences in the timing during development and elongation of the main axis and branches, branching pattern, and phyllotaxis.

Inflorescence development in *C. entrerianus*, *C eragrostis*, and *C. incomtus* is similar in early stages. *Cyperus incomtus* is different from *C. entrerianus* and *C eragrostis* in that its mature form retains configuration acquired in an early stage of development, with no later internode elongation. *Cyperus oxylepis* is different from the other three species in the following aspects: lack of serial or prophyllar branches, absence of fascicles of spikelets, phyllotaxis, and relationship between the formation of new branch primordia and the lengthening of those primordia and the main axis. However, as we only studied a single representative of the subgenus *Cyperus*, we do not know how generalizable these results are to the entire subgenus.

Inflorescence morphology in Cyperaceae is elaborate at mature stages, and even more complicated when development is analyzed. Only a few comparative developmental studies have been performed on complete inflorescences of *Cyperus* (Mora Osejo, 1960). Developmental studies on spikelets and flowers of Cyperaceae (Nijalingappa and Goetghebeur, 1989; Bruhl, 1991; Vrijdaghs et al., 2004, 2005a, b, 2006; Richards et al., 2006; Vrijdaghs, 2006) showed that either only a few changes in the pattern of development account for the variation seen at maturity or that similar mature inflorescences are the result of different development programs. Our work is the first comparative study in the family that analyzes the whole process of inflorescence development and shows that developing inflorescences are even more diverse than mature stages. Because a general inflorescence morphology can be reached by multiple origins in the Cyperaceae, the systematic value of inflorescence morphology deserves re-evaluation based on typological and developmental studies (cf. Vegetti, 1992, 1994; Heinzen and Vegetti, 1994; Perreta and Vegetti, 2002; Guarise and Vegetti, 2008).

## LITERATURE CITED

ARAÚJO, A. C., AND H. M. LONGHI-WAGNER. 1997. Anatomia foliar e micromorfologia da superficie do fruto na taxonomia de *Cyperus* L. (Cyperaceae). *Iheringia, série Botanica* 48: 103–120.

BARROS, M. 1938. Ciperaceas argentinas III, géneros *Androtrichum, Lipocarpha, Ascolepis* y *Cyperus. Anales del Museo de Ciencias Naturales de Buenos Aires* 39: 253–381.

BRUHL, J. J. 1991. Comparative development of some taxonomically critical floral/inflorescence features in Cyperaceae. *Australian Journal of Botany* 39: 119–127.

BRUHL, J. J. 1995. Sedge genera of the world: Relationships and a new classification of the Cyperaceae. *Australian Journal of Botany* 8: 125–305.

CÁMARA HERNÁNDEZ, J. 2001a. La polistiquia en las inflorescencias de las Poáceaes. *Boletín de la Sociedad Argentina de Botánica* 36 (supplement): 9–10.

CÁMARA HERNÁNDEZ, J. 2001b. Morfología de las inflorescencias de *Diplachne* y *Leptochloa* (Poaceae). *Boletín de la Sociedad Argentina de Botánica* 36: 267–278.

DENGLER, N. G. 1999. Anisophylly and dorsiventral shoot symmetry. *International Journal of Plant Sciences* 160: S67–S80.

DENTON, M. A. 1978. A taxonomic treatment of the Luzulae group of *Cyperus. Contributions from the University of Michigan Herbarium* 11: 197–271.

DENTON, M. A. 1983. Anatomical studies of the Luzulae group of *Cyperus* (Cyperaceae). *Systematic Botany* 8: 250–262.

DIGGLE, P. K., AND P. K. ENDRESS. 1999. Development, function and evolution of symmetry in plants. *International Journal of Plant Sciences* 160: 1–166.

DOUST, A. N., K. M. DEVOS, M. D. GADBERRY, AND E. A. KELLOGG. 2005. The genetic basis for inflorescence variation between foxtail and green millet (Poaceae). *Genetics* 169: 1659–1672.

DOUST, A. N., AND E. A. KELLOGG. 2002. Integrating phylogeny, developmental morphology and genetics: A case study of inflorescence evolution in the ''bristle grass'' clade (Panicoideae: Poaceae). *In* Q. C. B. Cronk, R. M. Bateman, and J. A. Hawkins [eds.], Developmental genetics and plant evolution, 298–314. Taylor and Francis, London, UK.

FRIEDMAN, J., AND L. D. HARDER. 2005. Functional associations of floret and inflorescence traits among grass species. *American Journal of Botany* 92: 1862–1870.

GOETGHEBEUR, P. 1986. Genera Cyperacearum. Ph.D. dissertation, University of Ghent, Belgium, Ghent.

GOETGHEBEUR, P. 1989. Studies in Cyperaceae 9. Problems in the Lectopyfication and Infrageneric Taxonomy of *Cyperus* L. *Bulletin de la Société Royale Botanique de Belgique* 122: 103–114.

GOETGHEBEUR, P. 1998. Cyperaceae. *In* K. Kubitzki, H. Huber, P. J. Rudall, P. S. Stevens, and T. Stützel [eds.], The families and genera of plants, vol. 4, 141–190. Springer Verlag, Berlin, Germany.

GUARISE, N. J., AND A. C. VEGETTI. 2007. Inflorescences structure of *Cyperus* L. section *Luzuloidei* Kunth (Cyperaceae). *Plant Systematics and Evolution* 271: 41–63.

GUARISE, N. J., AND A. C. VEGETTI. 2008. Processes responsible of the structural diversity of the Cyperaceae synflorescence: Hypothetical evolutionary trends. *Flora* 203: 640–647.

HAINES, R. W. 1966. Prophylls and branching in Cyperaceae. *Journal of the East Africa Natural History Society* 26: 51–78.

HAINES, R. W., AND K. A. LYE. 1983. The sedges and rushes of East Africa. East African Natural History Society, Nairobi, Kenya.

HEINZEN, F. A., AND A. C. VEGETTI. 1994. Typology of the inflorescence in *Cyperus corymbosus* var. *subnodosus* and *C. rotundus* (Cyperaceae). *Beiträge zur Biologie der Pflanzen* 68: 263–273.

KERN, V., N. GUARISE, AND A. VEGETTI. 2008. Typology of the inflorescence in *Spartina* (Poaceae: Eragrostoideae). *Plant Systematics and Evolution* 273: 51–61.

KÜKENTHAL, G. 1935–1936. Cyperaceae-Scirpoideae-Cypereae. *In* A. Engler [ed.], Das Pflanzenreich, vol. IV, part 20, fascicle 101, 1–160. W. Englemann, Leipzig, Germany.

KUKKONEN, I. 1994. Definition of descriptive terms for the Cyperaceae. *Annales Botanici Fennici* 31: 37–43.

KWIATKOWSKA, D. 1999. Formation of pseudowhorls in *Peperomia verticillata* (L.) A. Dietr. shoots exhibiting various phyllotactic patterns. *Annals of Botany* 83: 675–685.

LIU, Q., P. M. PETERSON, J. T. COLUMBUS, N. XHAO, G. HAO, AND D. ZHANG. 2007. Inflorescence diversification in the "finger millet clade" (Chloridoideae: Pocaceae): A comparison of molecular phylogeny and developmental morphology. *American Journal of Botany* 94: 1230–1247.

Liu, Q., N. X. Zhao, and G. Hao. 2005. Inflorescence structures and evolution in subfamily Chloridoideae (Gramineae). *Plant Systematics and Evolution* 251: 183–198.

Meert, M., and P. Goetghebeur. 1979. Comparative floral morphology of Bisboeckelereae and Cariceae (Cyperaceae) on the basis of the anthoid concept. *Bulletin de la Société Royale Botanique de Belgique* 112: 128–143.

Mora Osejo, L. E. 1960. Beitträge zur Entwicklungsgeschichte und vergleichenden Morphologie der Cyperaceen. *Beiträge zur Biologie der Pflanzen* 35: 293–341.

Muasya, A. M., D. A. Simpson, M. W. Chase, and A. Culham. 1998. An assessment of suprageneric phylogeny in Cyperaceae using *rcb*L DNA sequences. *Plant Systematics and Evolution* 211: 257–271.

Muasya, A. M., J. J. Bruhl, D. A. Simpson, M. W. Chase, and A. Culham. 2000. Suprageneric phylogeny of Cyperaceae: A combined analysis. *In* K. L. Wilson, and D. A. Morrison [eds.], Monocots: Systematics and evolution, 610–614. CSIRO, Collingwood, Australia.

Muasya, A. M., D. A. Simpson, and M. W. Chase. 2002. Phylogenetic relationships in *Cyperus* L. s.l. (Cyperaceae) inferred from plastid DNA sequence data. *Botanical Journal of the Linnean Society* 138: 145–153.

Muasya, A. M., A. Vrijdaghs, D. A. Simpson, M. W. Chase, P. Goetghebeur, and E. Smets. 2009. What is a genus in Cypereae: Phylogeny, character homology assessment and generic circumscription. *Botanical Review* 75: 52–66.

Nijalingappa, B., and P. Goetghebeur. 1989. Morphology and ontogeny of the spikelet in *Ascopholis* C.E.C. Fisher (Cyperaceae). *Biologisch Jaarboek Dodonaea* 57: 81–86.

Perreta, M. G., and A. C. Vegetti. 2002. The inflorescence of *Cyperus giganteus* Vahl (Cyperaceae). *Feddes Repertorium* 113: 256–260.

Raynal, A. 1971. Quelques notes morphologiques sur les Cypéracées. *Mitteilungen der Botanischen Staatssammlung München* 10: 589–603.

Raynal, J. 1973. Notes cypérologiques: 19. Contribution à la classification de la sous-famille des Cyperoideae. *Adansonia série* 13: 145–171.

Reinheimer, R., R. Pozner, and A. C. Vegetti. 2005. Inflorescence, spikelet and floral development in *Panicum maximum* and *Urochloa plantaginea* (Poaceae). *American Journal of Botany* 92: 565–575.

Reinheimer, R., and A. C. Vegetti. 2004. The inflorescence of South American species of *Panicum* subg. *Phanopyrum* sect. *Laxa* (Poaceae: Panicoideae: Paniceae). *Beiträge zur Biologie der Pflanzen* 73: 185–199.

Reinheimer, R., F. O. Zuloaga, A. C. Vegetti, and R. Pozner. 2009. Diversification of inflorescence development in the PCK clade (Poaceae: Panicoideae: Paniceae). *American Journal of Botany* 96: 549–564.

Reinheimer, R., F. O. Zuloaga, A. C. Vegetti, and R. Pozner. 2010. Changes in floret development patterns that may correlate with sex determination in the PCK clade (Poaceae). *International Journal of Plant Sciences* 171: 24–33.

Richards, J. H., J. J. Bruhl, and K. L. Wilson. 2006. Flower or spikelet? Understanding the morphology and development of reproductive structures in *Exocarya* (Cyperaceae, Mapanioideae, Chrysitricheae). *American Journal of Botany* 93: 1241–1250.

Soros, C. L., and J. J. Bruhl. 2000. Multiple evolutionary origins of $C_4$ photosynthesis in Cyperaceae. *In* K. L. Wilson and D. A. Morrison [eds.], Monocots: Systematic and evolution, 629–636. CSIRO Publishing, Melbourne, Australia.

Tucker, G. C. 1983. The taxonomy of *Cyperus* (Cyperaceae) in Costa Rica and Panama. *Systematic Botany Monographs* 2: 1–85.

Tucker, G. C. 1987. The genera of Cyperaceae in the SE United States. *Journal of the Arnold Arboretum.* 68: 361–445.

Tucker, G. C. 1994. Revision of the Mexican species of *Cyperus* (Cyperaceae). *Systematic Botany Monographs* 43: 1–213.

Tucker, C. S., and J. Grimes. 1999. The inflorescence: Introduction. *Botanical Review* 65: 303–316.

Vegetti, A. C. 1992. Typology of the inflorescence in species *Schoenoplectus* (Cyperaceae) in Austral America. *Beiträge zur Biologie der Pflanzen* 67: 241–249.

Vegetti, A. C. 1994. Typology of the inflorescence of *Isolepis. Beiträge zur Biologie der Pflanzen* 68: 21–26.

Vegetti, A. C., and A. M. Anton. 1995. Some evolution trends in the inflorescences of Poaceae. *Flora* 190: 225–228.

Vrijdaghs, A. 2006. A floral ontogenetic approach to homology questions in non-mapanioid Cyperaceae. Ph.D. thesis, Laboratory of Plant Systematics, K.U. Leuven, Leuven, Belgium.

Vrijdaghs, A., P. Caris, P. Goetghebeur, and E. Smets. 2005a. Floral ontogeny in *Scirpus, Eriophorum* and *Dulichium* (Cyperaceae), with special reference to the perianth. *Annals of Botany* 95: 1199–1209.

Vrijdaghs, A., P. Goetghebeur, M. A. Muasya, P. Caris, and E. Smets. 2005b. Floral ontogeny in *Ficinia* and *Isolepis* (Cyperaceae), with focus on the nature and origin of the gynophore. *Annals of Botany* 96: 1247–1264.

Vrijdaghs, A., P. Goetghebeur, M. A. Muasya, E. Smets, and P. Caris. 2004. The nature of the perianth in *Fuirena* (Cyperaceae). *South African Journal of Botany* 70: 587–594.

Vrijdaghs, A., P. Goetghebeur, E. Smets, and M. A. Muasya. 2006. The floral scales in *Hellmuthia* (Cyperaceae, Cyperoideae) and *Paramapania* (Cyperaceae, Mapanioideae), a floral ontogenetic study. *Annals of Botany* 98: 619–630.

Wilson, K. L. 1991. Systematic studies in *Cyperus* section *Pinnati* (Cyperaceae). *Telopea* 4: 361–496.