Plant Syst. Evol. 240: 83–89 (2003)
DOI 10.1007/s00606-003-0017-y

Plant Systematics and Evolution
Printed in Austria

Centothecoid grasses and the evolution of panicoid spikelets

G. H. Rua[1,2]

[1]Cátedra de Botánica Agrícola, Facultad de Agronomía, Universidad de Buenos Aires, Buenos Aires, Argentina
[2]Investigador Asistente, Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina

Received September 10, 2002; accepted February 25, 2003
Published online: September 17, 2003

Abstract. An evolutionary pathway leading to acrotonous, 2-flowered spikelets of Panicoideae has been suggested elsewhere, which involves apical reduction of many-flowered mesotonic spikelets. Current phylogenies of the grass family show a sister relationship between Panicoideae and Centothecoideae. A survey of spikelet structures occurring among centothecoid grasses shows that some representatives of this group have intermediate morphologies which are consistent with that hypothesis. *Chasmanthium* and *Bromuniola* have many-flowered spikelets with a barren proximal floret, whereas *Thysanolaena*, *Gouldochloa* and *Gynerium* represent a series of apical reductions leading to 2-flowered spikelets. Moreover, many-flowered spikelets with 1-3 proximal male flowers followed by several female-fertile ones occur in Puelioideae, one of the early-diverging clades of the Poaceae. This fact suggests that some "panicoid" characters may have evolved long before the radiation of the Panicoideae took place.

Key words: Morphology, Poaceae, Panicoideae, Centothecoideae, spikelet evolution.

The subfamily Panicoideae A. Br. constitutes a well supported monophyletic taxon (GPWG 2001). Spikelets of most species belonging to this subfamily are strikingly homogeneous: they bear two glumes (the first of which may be reduced or completely absent) followed by two florets (Clayton and Renvoize 1986; Cialdella and Vega 1996; Le Roux and Kellogg 1999; Kellogg 2000a, b). The distal floret is usually perfect, whereas the proximal may be either male or sterile, and then usually reduced to an empty lemma. Because panicoid male florets arise from an early abortion of the gynoecium (Butzin 1965, Moncur 1981, Cheng et al. 1983, Le Roux and Kellogg 1999), both male and sterile flowers can be regarded as "incomplete" ones. Thus, the panicoid spikelets are acrotonic, i.e. the development of their distal lateral meristems are favoured over the remaining ones (cf. Rua 1999).

A plausible evolutionary pathway leading to the 2-flowered acrotonic spikelets of the Panicoideae has been suggested by Cámara-Hernández and Rua (1991), which involves racemization of the distal portion of many-flowered spikelets followed by apical reduction, in such a way that only two florets remain (Fig. 1).

In the last years several phylogenetic analyses of the grass family were carried out (GPWG 2000, 2001, and references therein), which provide a tool to test evolutionary pathways by mapping character transformation

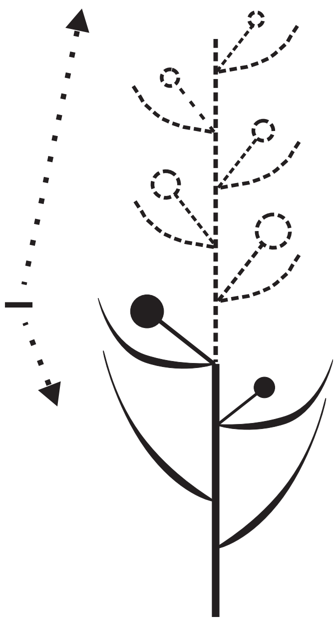

Fig. 1. Diagram representing the two-flowered acrotonic spikelet of Panicoideae (solid lines) and its ancestral condition (dashed lines) as hypothesized by Cámara-Hernández and Rua (1991). The arrows indicate the hypothetic plesiomorphic sequence of flowering

upon the cladogram(s) reflecting the more plausible phylogenetic hypothesis. In recent analyses the 'core' Panicoideae group together with *Danthoniopsis* and *Gynerium* (GPWG 2001) and consistently appears as sister group of a Centothecoid clade which comprises the genera originally assigned to the subfamily Centothecoideae (Soderstrom 1981) plus some genera seggregated from other subfamilies (*Cyperochloa*, *Gouldochloa*, *Spartochloa*, and *Thysanolaena*) (Sánchez-Ken and Clark 2000). Nevertheless, new analyses are in progress which throw doubts on the monophyly of Centothecoids as well as on the position of *Danthoniopsis* (J. G. Sánchez-Ken, pers. comm.).

A survey of spikelet structures within representants of Centothecoideae was carried out in order to look for intermediate morphologies supporting or rejecting the hypothesis about panicoid spikelets proposed by Cámara-Hernández and Rua (1991).

Material and methods

Spikelets of all available species belonging to centothecoid (s. l.) genera (Appendix 1) were dissected with aid of a current stereoscopic microscope, and diagrams were drawn in order to compare them easily. No specimens of *Chevalierella*, *Cyperochloa*, *Gouldochloa*, *Pohlidium*, and *Spartochloa* were available, thus information about spikelet structure was extracted in these cases from literature (Clayton and Renvoize 1986, Nicora and Rúgolo de Agrasar 1987, Valdés et al. 1986, Watson and Dallwitz 1992).

Results

There is a considerable variation in spikelet structure among centothecoid genera. Many-flowered spikelets occur in *Bromuniola* (Fig. 2C), *Centotheca*, *Chasmanthium* (Fig. 2A, B), *Gouldochloa*, *Megastachya*, *Orthoclada*, and *Spartochloa*. Spikelets can sometimes be 2-flowered in *Chasmanthium*, *Gouldochloa*, and *Orthoclada*, and are 1-flowered in *Chevalierella dewildemanii* (Vand.) Van der Veken, *Centotheca uniflora* Swallen, and some specimens of *Chasmanthium laxum* (L.) Yates (Yates 1966). Incomplete distal florets and/or a prolongation of the main axis beyond the distal floret occur in most genera; this feature indicates that racemization is a general condition among Centothecoids. An extreme condition occurs in *Lophatherum*, in which the only fertile floret is distally followed by several empty lemmas.

Spikelets with a proximal female floret distally followed by a variable number of male florets occur in *Zeugites* and *Calderonella*, whereas species of *Pohlidium* are diclino-dioecious. In all these cases, female-fertile florets are proximal. Dioecy also occurs in *Gynerium*, a genus of doubtful position within the Panicoid-Centothecoid clade (see below). The female spikelets of *Gynerium* are 2-flowered (Fig. 2H), whereas the male spikelets bear 2–4 florets (Fig. 2I), and no obvious developmental difference is noticeable between the proximal and the distal florets.

Female-sterile proximal flowers occur in several genera. They can be represented either

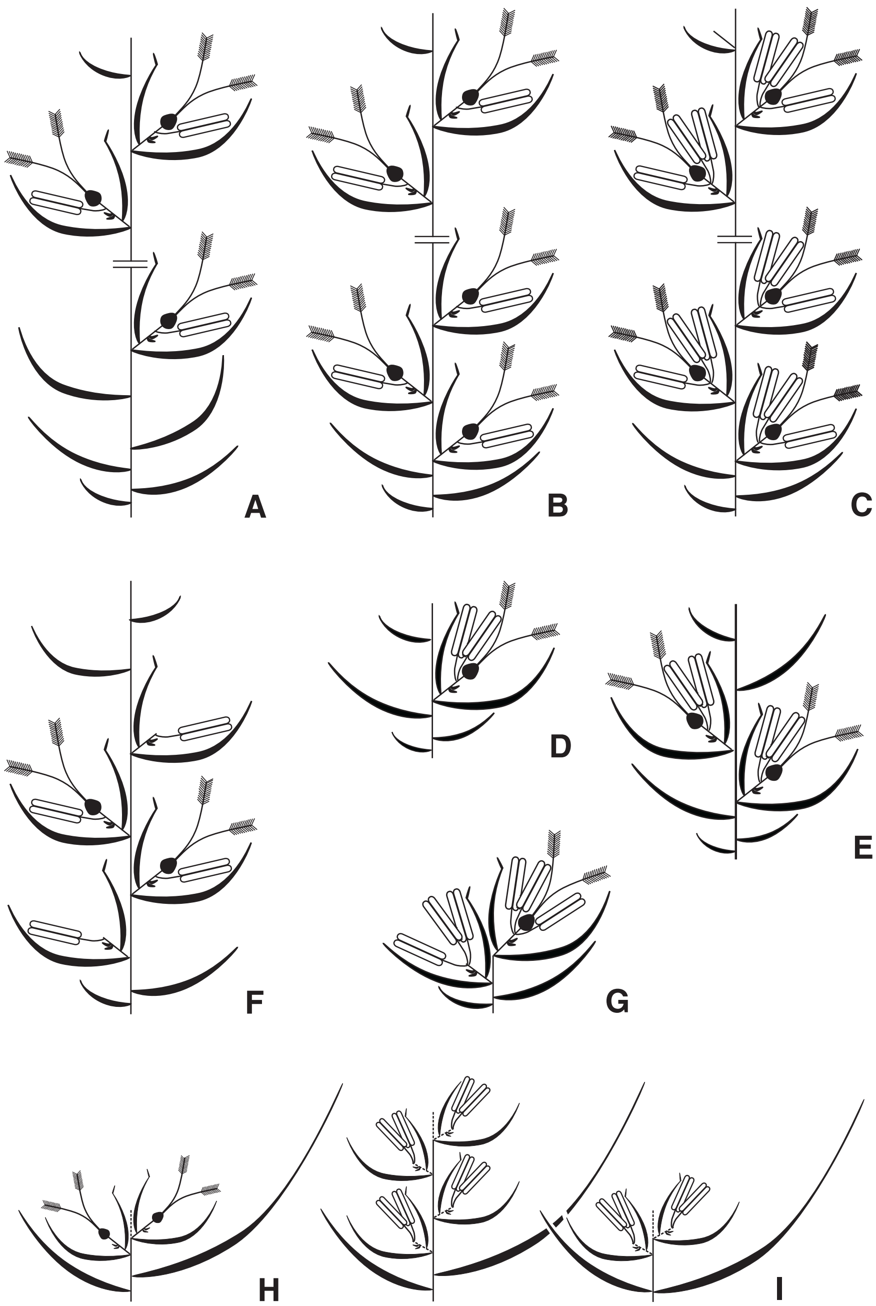

Fig. 2. Spikelet diagrams of some cases in which abortion or reduction of the proximal flower[s] occurs. **A** *Chasmanthium ornithorhynchum*; **B** *Chasmanthium latifolium*; **C** *Bromuniola gossweileri*; **D–E** *Thysanolaena maxima*, normal and anomalous spikelets respectively; **F** *Gouldochloa curvifolia*; **G** *Danthoniopsis* sp.; **H–I** *Gynerium sagittatum* (female and male spikelets respectively)

by male flowers as in the case of *Gouldochloa* (Fig. 2F), or by empty lemmas, as occurring in *Bromuniola* (Fig. 2C), *Chasmanthium* (Fig. 2A–B), and *Thysanolaena* (Fig. 2D-E). The case of *Thysanolaena* is remarkable in that the only fertile floret is accompanied by 2 empty lemmas, one of which proximal and the other distal (Fig. 2D). Anomalous spikelets were observed in the specimen BAA 24608, corresponding to a plant with inflorescence prolification (Beetle 1980, Bell 1991), in which 2 fertile florets were preceded by an empty lemma, and followed by 2 empty ones (Fig. 2E). In all these cases, spikelets are mesotonic, i.e. the more developed florets are located at a middle position. Reduction or abortion of proximal florets is a feature shared by the mentioned centothecoid genera, *Danthoniopsis* and the 'core' Panicoideae. In fact, all examined species of *Danthoniopsis* bear a proximal male flower (Fig. 2G), whereas among the 'core' Panicoideae both male and barren florets can occur at the proximal position.

Discussion

Spikelet structures were found among Centothecoid genera which are compatible with the hypotheses enunciated above. A hypothetical series of reductions could be traced out which can be illustrated by structures actually present in extant genera (Fig. 3). Thus, panicoid spikelets could be derived from multiflowered spikelets such as those occurring in *Chasmanthium* and *Bromuniola*, in which the proximal floret is barren and the following ones develop acropetally. Reduction of the floret number has been reported within *Chasmanthium* (Yates 1966, Clayton and Renvoize 1986), so that spikelets with only one fertile floret preceded and followed by empty lemmas sometimes occur. The same spikelet structure occurs regularly in *Thysanolaena* (Fig. 2D, see above), and mesotonic anomalous spikelets with more than one fertile floret have been observed in this genus (Fig. 2E). Therefore, acrotonic spikelets could have been derived from mesotonic ones by evolutionary loss of the portion just above the more developed floret. The occurrence of a prolongation of the rhachilla beyond the distal floret in some panicoid spikelets (Butzin 1965) also supports this hypothesis.

Apical reduction of axes seems to be a widespread evolutionary trend among Poaceae (Butzin 1979).The hypothetical evolutionary pathway depicted above coincides with that proposed by Cámara-Hernández and Rua (1991) on morphological grounds, and is also consistent with current phyloge-

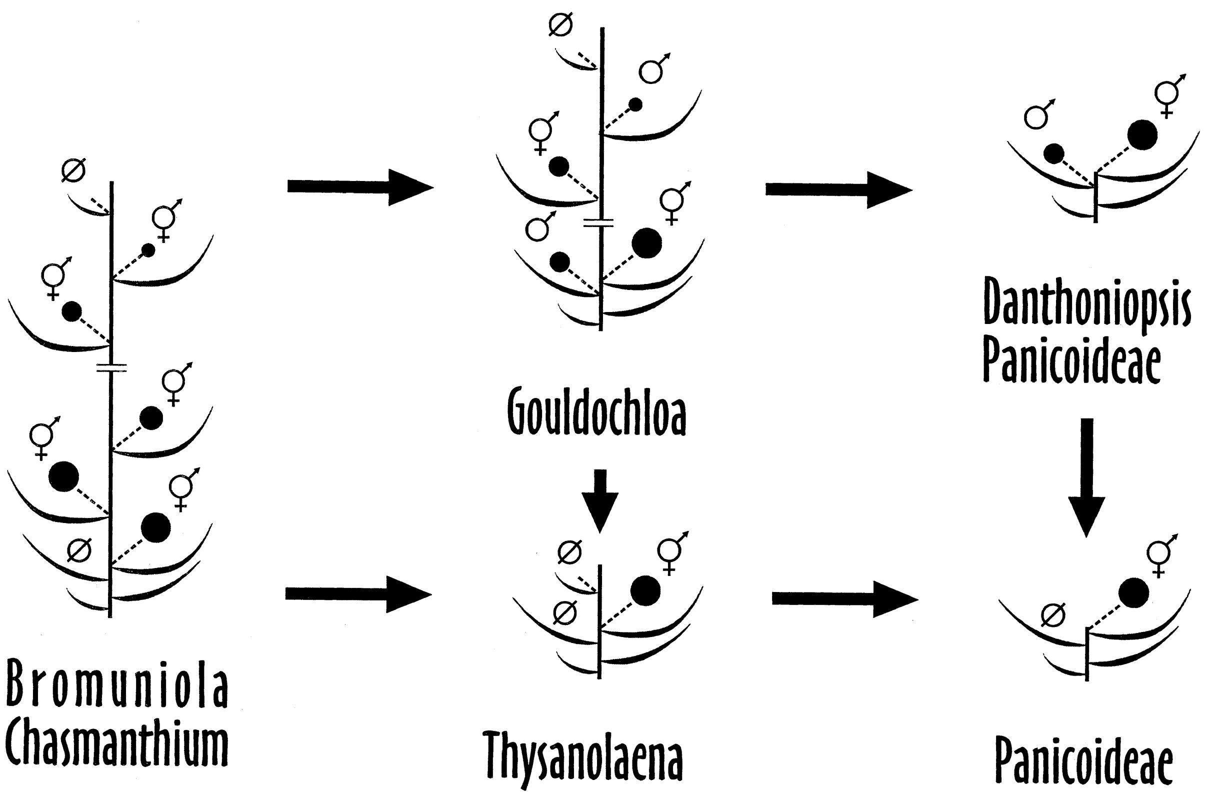

Fig. 3. Diagram showing the hypothesized evolutionary reduction from multiflowered mesotonic spikelets (as exemplified by *Bromuniola* and *Chasmanthium* p.p.) to 2-flowered acrotonic spikelets as occurring in Panicoideae. Intermediate steps are illustrated by *Chasmanthium* p.p., *Thysanolaena*, and *Gouldochloa*

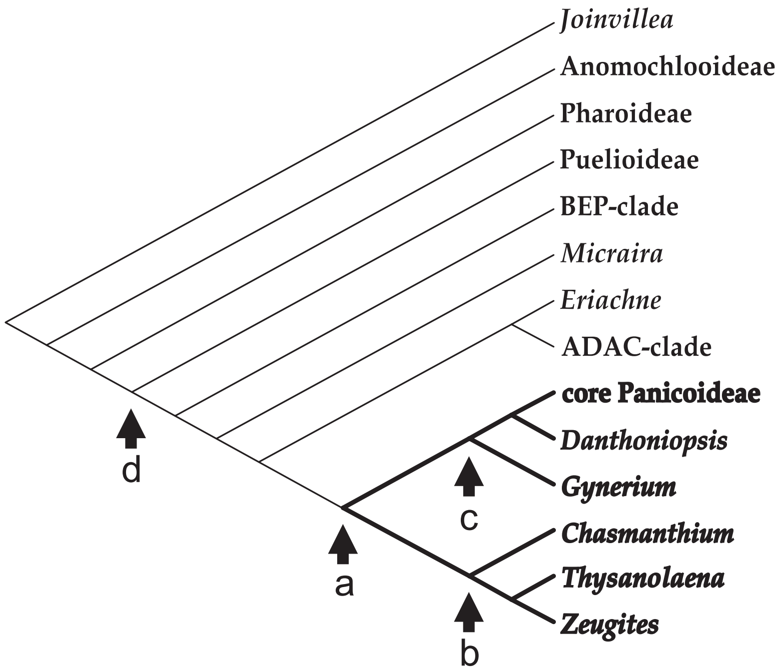

Fig. 4. Current cladogram of Poaceae (redrawn from GPWG 2001), showing the relationships of Panicoids and Centothecoids. Arrows: *a* Panicoid-Centothecoid clade; *b* Centothecoids; *c* Panicoids sensu lato; *d* early divergence of Puelioideae. BEP-clade = Bambusoideae + Ehrhartoideae + Pooideae; ADAC-clade = Aristidoideae + Danthonioideae + Arundinoideae + Chloridoideae

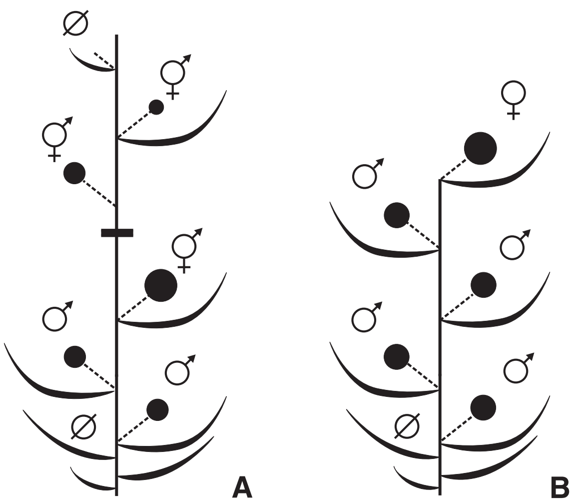

Fig. 5. Spikelet diagrams of Puelioideae; in both cases a proximal empty lemma followed by several male flowers occurs. **A** *Guaduella*, note the racemized distal portion of the spikelet; **B** *Puelia*, the acrotonic spikelets bear only one female-fertile flower at the distal position

netic hypotheses (GPWG 2000, 2001, see Fig. 4). The sister relationship between Panicoideae and Centothecoideae is relatively well supported by current data, although the monophyly of Centothecoideae itself is weekly supported (GPWG 2001, J. G. Sánchez-Ken, pers. comm.). The position of *Gynerium* and *Danthoniopsis* remain unstable within the Panicoideae + Centothecoideae clade (GPWG 2001, Sánchez-Ken and Clark 2001). Although *Danthoniopsis* does not substantially differ from panicoid grasses in spikelet morphology (Fig. 2G), resemblance could be an outcome of convergent evolution (J. G. Sánchez-Ken, pers. comm.). *Gynerium*, on its turn, possesses unisexual spikelets, the plants being dioecious. Whereas female spikelets are 2-flowered (Fig. 2H), male spikelets vary from 2- to 4-flowered (Fig. 2I), and no obvious acrotony is shown.

Although the evolutionary pathway depicted seems plausible, it could have taken place in a more complex way. In fact, some analyses are in progress which suggest the occurrence of several independent events of apical reduction and gain/loss of a female-fertile flower in the axil of the proximal lemma within the Panicoid-Centothecoid clade (J. G. Sánchez-Ken, pers. comm.). Further work on Centothecoid phylogeny would provide a more accurate framework for testing hypotheses about evolution of the panicoid spikelet.

Moreover, the occurrence of many-flowered spikelets with 1-3 proximal male flowers followed by several female-fertile ones (Fig. 5) in Puelioideae (Clark et al. 2000), one of the early-diverging clades of the Poaceae, suggests that some "panicoid" characters may have evolved long before the radiation of the Panicoideae took place.

I am grateful to J. G. Sánchez-Ken for valuable comments on the manuscript, and to J. Cámara-Hernández and R. D. Tortosa for critical review. I am also indebted to the curators of BAA, K, and SI for making the herbarium material available. This research was supported by the grant UBACyT AG-027, from the Buenos Aires University.

Appendix 1. Examined specimens

Bromuniola gossweileri Stapf & C. E. Hubbard: Chisumpa 139 (K), Callens 3999 (K)

Calderonella sylvatica Soderstrom & H. F. Decker: Calderón & Dressler 2141 (SI)

Centotheca lappacea Desv.: Smith 8832 (BAA)

Centotheca latifolia Trin.: E. D. Merrill 137 (SI), 763 (SI)

Chasmanthium latifolium (Michx.) H. O. Yates: R. Manning 20051 (BAA), G. H. Rua s.n. (BAA 24592), R. Taylor 15 (BAA), B. Wooten 80 (BAA),

Chasmanthium laxum (L.) H. O. Yates: Weatherwax s.n. (BAA)

Chasmanthium sessiliflorum (Poir.) H. O. Yates: Fenald & Long 10526 (BAA)

Danthoniopsis barbata (Nees) C. E. Hubbard: Collenette 4427

Danthoniopsis dinteri (Pilger) C. E. Hubbard: Davidse 5940 (K)

Danthoniopsis petiolata (Phipps) W.D.Clayt.: Simon & Hill (K)

Danthoniopsis pruinosa C. E. Hubbard: Biegel 1042 (K), Verboom B (K)

Danthoniopsis ramosa (Stapf) W.D.Clayt.: Engler 6507 (K)

Danthoniopsis stocksii (Boiss.) C. E. Hubbard: Charif 1049 (K)

Danthoniopsis viridis (Rendle) C. E. Hubbard: Astle 1526 (K), Hinds? 246 (K)

Gynerium sagittatum (Aubl.) P. Beauv.: T. Rojas 4653 (BAA), Joly s.n. (BAA)

Lophatherum gracile Brongn.: colector desc. 3962 (SI)

Megastachya mucronata P. Beauv.: H. C. Dowshire 845 (SI)

Orthoclada laxa (Rich.) P. Beauv.: M. Vázquez Ávila 442 (SI)

Puelia ciliata Franch.: G. Zenker 159 (SI)

Thysanolaena maxima Kuntze: J. J. Valla s.n. (BAA 21576), s.n. (BAA 24607)

Zeugites latifolia (Fourn.) Hemsl.: C. G. Pringle 11765 (SI)

Zeugites mexicana (Kunth) Trin. ex Steud.: Davidse & D'Arcy 10175 (BAA)

References

Beetle A. A. (1980) Vivipary, proliferation, and phyllody in grasses. J. Range Managem. 33: 256–261.

Bell A. D. (1991) Plant form: An illustrated guide to flowering plant morphology. Oxford University Press, Oxford.

Butzin F. (1965) Neue Untersuchungen über die Blüte der Gramineae. Unpublished D. Thesis, Freie Universität Berlin.

Butzin F. (1979) Apikale Reduktionen im Infloreszenzbereich der Gramineae. Willdenowia 9: 161–167.

Cámara-Hernández J., Rua G. H. (1991) The synflorescence of Poaceae. Beitr. Biol. Pflanzen 66: 297–311.

Cheng P. C., Greyson R. I., Walden D. B. (1983) Organ initiation and the development of unisexual flowers in the tassel and ear of *Zea mays*. Amer. J. Bot. 70: 450–462.

Cialdella A. M., Vega A. S. (1996) Estudios sobre la variación estructural de las espiguillas en géneros de la tribu Paniceae (Poaceae). Darwiniana 34: 173–182.

Clark L. G., Kobayashi M., Mathews S., Spangler R. E., Kellogg E. A. (2000) The Puelioideae, a new subfamily of Poaceae. Syst. Bot. 25: 181–187.

Clayton W. D., Renvoize S. A. (1986) Genera Graminum, Grasses of the World. Kew Bull., add. ser. 13: 1–389.

GPWG (Grass Phylogeny Working Group) (2000) A phylogeny of the grass family (Poaceae), as inferred from eight character sets. In: Jacobs S. W., Everett J. E. (eds.) Grass systematics and evolution. CSIRO, Melbourne, pp. 3–7.

GPWG (Grass Phylogeny Working Group) (2001) Phylogeny and subfamilial classification of the grasses (Poaceae). Ann. Missouri Bot. Gard. 88: 373–457.

Kellogg E. A. (2000a) The grasses: a case study in macroevolution. Annual Rev. Ecol. Syst. 31: 217–238.

Kellogg E. A. (2000b) Molecular and morphological evolution in the Andropogoneae. In: Jacobs S. W., Everett J. E. (eds.) Grass systematics and evolution. CSIRO, Melbourne, pp.149–158.

Le Roux L. G., Kellogg E. A. (1999) Floral development and the formation of unisexual spikelets in the Andropogoneae (Poaceae). Amer. J. Bot. 86: 354–366.

Moncur M. W. (1981) Floral initiation in field crops: An atlas of scanning electron micrographs. CSIRO, Canberra.

Nicora E. G., Rúgolo de Agrasar Z. E. (1987) Los géneros de Gramíneas de América Austral. Hemisferio Sur, Buenos Aires.

Rua G. H. (1999) Inflorescencias, bases teóricas para su análisis. Sociedad Argentina de Botánica, Buenos Aires.

Sánchez-Ken J. G., Clark L. G. (2000) Overview of the subfamily Centothecoideae. (Poaceae). Abstracts of Botany 2000!, Portland.

Sánchez-Ken J. G., Clark L. G. (2001) Gynerieae, a New Neotropical tribe of grasses (Poaceae). Novon 11: 350–352.

Soderstrom T. R. (1981) The grass subfamily Centostecoideae. Taxon 30: 614–616.

Valdés J., Morden C. W., Hatch S. L. (1986) *Gouldochloa*, a new genus of Centothecoid grasses from Tamaulipas, Mexico. Syst. Bot. 11: 112–119.

Watson L., Dallwitz M. J. (1992 onwards) 'Grass Genera of the World: Descriptions, Illustrations, Identification, and Information Retrieval; including Synonyms, Morphology, Anatomy, Physiology, Phytochemistry, Cytology, Classification, Pathogens, World and Local Distribution, and References.' http://biodiversity.uno.edu/delta/. Version: 18th August 1999.

Yates H. O. (1966) Revision of grasses traditionally referred to *Uniola* II. *Chasmanthium*. Southw. Naturalist 11: 415–455.

Address of the author: Dr. Gabriel H. Rua (e-mail: ruagabri@mail.agro.uba.ar), Facultad de Agronomía, Universidad de Buenos Aires, Cátedra de Botánica Agrícola, Av. San Martín 4453, RA-1417 Buenos Aires, Argentina.