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Growth forms, branching patterns, and inflorescence structure in *Digitaria* sect. *Trichachne* (Poaceae, Paniceae)

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Summary

A survey of branching patterns occurring within *Digitaria* sect. *Trichachne* is presented. The general growth form type can be characterized as 'lax tuft'. The proximal portion of the tillers is typically plagiotropous and bears short internodia. It is usually thickened and corm-like. Nevertheless, in *D. swalleniana* and *D. catamarcensis* the internodia are elongated and form a well-developed rhizome. In all cases this region of the culm bears cataphylls and behaves as an innovation zone. The culms grow upright to form synflorescences composed of a main flowering unit which can be accompanied by proximal enrichment shoots.

As usual among grasses, the synflorescences are polytelic, and comprise a distal portion bearing short paraclades composed each of two spikelets, and a proximal portion bearing long paraclades, each reproducing the structure of the distal portion. All axes bear terminal spikelets. The number of long paraclades shows a wide range of variation within the section, ranging from a 1 or 2 paraclades in *D. tenuis* and *D. brownii* to about 50 in *D. insularis* and *D. laxa*. Second order long paraclades only were observed in *D. laxa*. The short paraclades occur always in two rows along inflorescence axes, but the arrangement of long paraclades is usually polystichous. Some controversial issues related to branching patterns are discussed on the basis of SEM-observations.

Key words: Poaceae, Paniceae, *Digitaria*, growth form, inflorescence

Introduction

The genus *Digitaria* Haller emend A. S. Vega et Rúgolo comprises 200–300 species distributed in tropical, subtropical and temperated areas worldwide (Veldkamp 1973; Rúgolo de Agrasar 1974; Clayton & Renvoize 1986; Nicora & Rúgolo de Agrasar 1987; Watson & Dallwitz 1999). It includes forage species, minor cereals, turf plants, and soil binders, as well as some weeds (Henrard 1950; Veldkamp 1973; Rúgolo de Agrasar 1974; Clayton & Renvoize 1986; Nicora & Rúgolo de Agrasar 1987; Guzmán et al. 1989; Molina Sánchez 1989; Watson & Dallwitz 1999).

The section *Trichachne* (Nees) Henrard comprises (putatively) 11 species: *D. brownii* (Roem. et Schult.) Hughes, *D. californica* (Benth.) Henrard, *D. hitchcockii* (Chase) Stuck., *D. insularis* (L.) Fedde, *D. laxa* (Rchb.) Parodi, *D. patens* (Swallen) Henrard, *D. sacchariflora* (Nees) Henrard, *D. swalleniana* Henrard, *D. tenuis* (Nees) Henrard, *D. catamarcensis* Rúgolo, and *D. similis* Gould (Henrard 1950; Rúgolo de Agrasar 1974, 1976, 1992, 1994; Webster 1983). They are perennial grasses mostly distributed in America, from southern U.S. to central Argentina (Chase 1906; Henrard 1950), with the exception of the Australian species *D. brownii* (Webster 1983). *Digitaria insularis* was introduced elsewhere (e.g. Hawaii, Malesia) as a weed (Veldkamp 1973). The species belonging to this section are characterized by possessing spikelets with conspicuous rhachilla internodes in such a way that the upper floret appears "stipitate" (Henrard 1950; Rúgolo de Agrasar 1974), although this character is somewhat variable within the group. This section was treated by some authors as an independent genus either under *Valota* Adans. (Chase 1906) or

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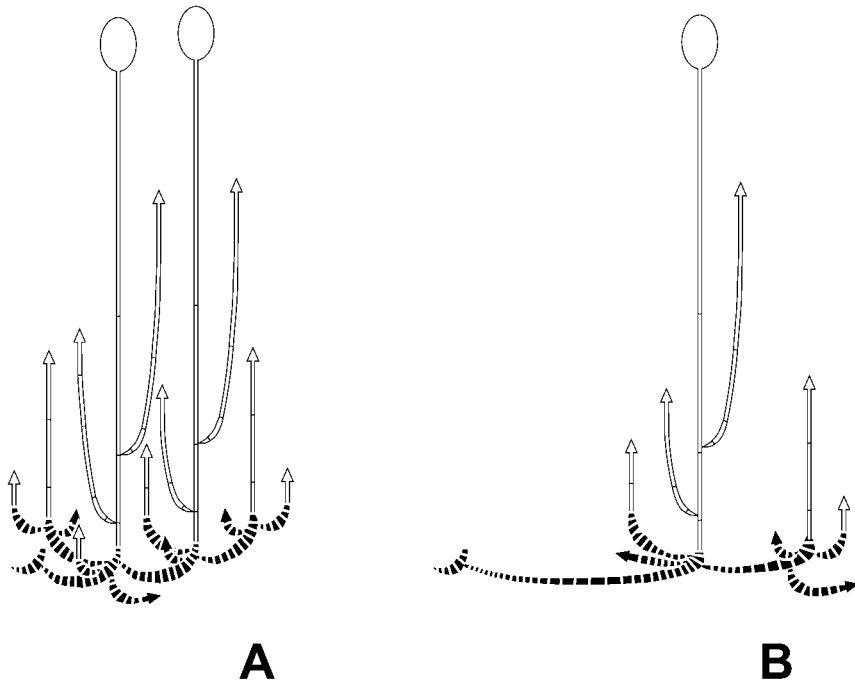
Fig. 1. Schematic representation of shoot branching patterns occurring in *Digitaria* sect. *Trichachne*. **A,** general pattern with short rhizomes; **B,** variant with spreading rhizomes, as occurring in *D. catamarcensis* and *D. swalleniana*. Ellipses represent flowering units, transversal lines represent nodes, arrows indicate direction of growth, leaves and roots were not depicted.

Trichachne Nees (e.g. Hitchcock 1927; Correll & Johnston 1970). Henrard (1950) discussed the systematic position of this group and decided to place it as a section of *Digitaria*, since no character or character combination was found to discriminate unequivocally *Trichachne* from *Digitaria*.

A cladistic analysis is being currently carried out in order to assess the monophyly of *Digitaria* sect. *Trichachne* (Vega et al., in preparation). As a preliminary contribution to this analysis, a survey of growth form features and inflorescence structures occurring in the putative members of this section was carried out. The results of this investigation are communicated in the present paper.

Materials and methods

Herbarium specimens of the 11 species putatively belonging to the sect. *Trichachne* (see above) were examined (BAA, CANB, CTES, SI, US, acronyms after Holmgren et al. (1990), see Appendix 1 for references). A collection of features related to both growth form and inflorescence structure were scored. Observations were also made on living plants cultivated in the "Lucien Hauman" Botanical Garden at the Buenos Aires University (Buenos Aires, Argentina). Description of growth form models and inflorescence were made according to Rua & Gróttola (1997) and Rua & Weberling (1998). Inflorescences in different developmental stages were collected, fixed in FAA (formalin-acetic acid-70 per cent ethanol, 10:5:85 v/v), dehydrated using an ethanol-acetone series,

desiccated in critical point, coated by Au-sputtering, and observed with a scanning electron microscope (SEM) Philips 515 EDAX SW9100.

Results

Growth form

The species belonging to *Digitaria* sect. *Trichachne* have been characterized elsewhere as "perennial grasses with a rhizomatous knotty base and pubescent cataphylls" (Veldkamp 1973). Though this description summarized the general pattern of vegetative growth within the section, some specific variations become apparent.

Each clump is composed of several tillers linked together sympodially, as is the general pattern among grasses and other monocots (Holttum 1955; Mühlberg 1967; Rua & Gróttola 1997). Among species belonging to the sect. *Trichachne* the proximal portion of each tiller is typically plagiotropous and bears short internodia (Fig. 1 A, B), is coated with pubescent cataphylls and bears innovation buds. It usually appears more or less thickened and corm-like, forming a short rhizomatous base (Fig. 2 A, B). Therefore the plants look somewhat loose, without forming tussocks as frequently occurs in many other grasses, including species of *Digitaria* such as *D. phaeotrix* (Trin.) Parodi, and other genera of Paniceae R. Br. (e.g. species of *Paspalum* L., *Leptocoryphium* Nees, *Anthaenantiopsis* Mez ex Pilger).
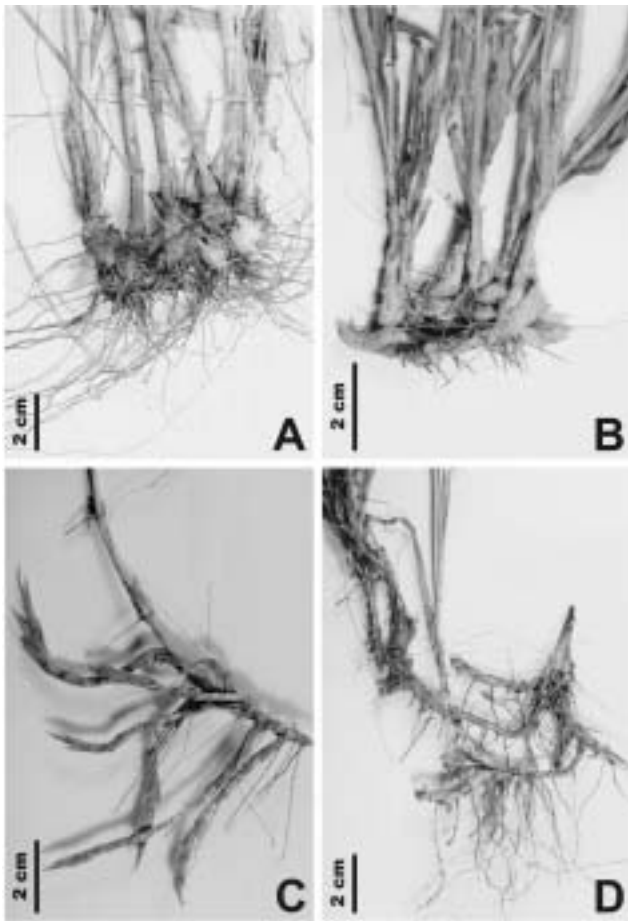
ter of the rhizomatous axis increases, and caulogenous roots develop. The innovation buds are usually located at the distal half of each rhizome segment, i.e. near the transition zone from rhizome to culm. The products of innovation meristems are new tillers which reproduce the structure of their mother axes. Nevertheless, the extent of their proximal rhizomatous portion can vary along the innovation zone, especially in the species with elongated rhizomes. So, the innovation shoots of *D. swalleniana* show a gradient from new rhizomes at the proximal nodes to orthotropous culms at the distal ones (Fig. 3C), whereas in *D. catamarcensis* new rhizomes and orthotropous axes are generally separated by about 6–7 rhizome internodia, along which branching does not occur.

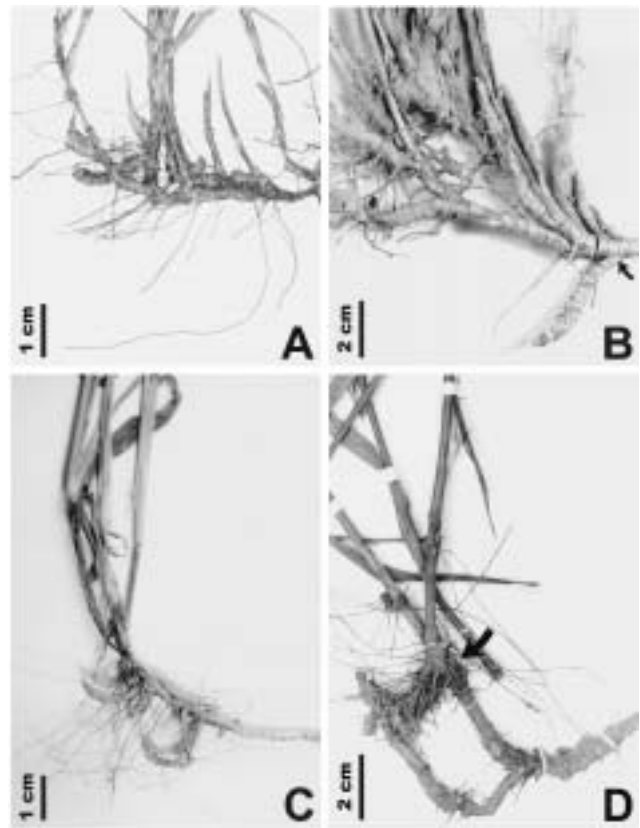A somewhat different case occurs in *D. laxa*. In contrast with the remaining species of the section *Trichach-*

Fig. 2. Rhizome variation within *Digitaria* sect. *Trichachne*. **A,** *D. insularis* (RUA et al. 116); **B,** *D. californica* var. *villosissima* (CABRERA et al. 13688); **C,** *D. swalleniana* (BURKART 24061); **D,** *D. catamarcensis* (RUA & DIOS 498). Note the short knotty rhizomes in **A** and **B,** and the slender spreading rhizomes in **C** and **D**.

Fig. 3. **A,** *D. insularis* (RÚGOLO 1751a); **B,** *D. californica* var. *californica* (BURKART 23934); **C,** *D. swalleniana* (SCHULZ 3875); **D,** *D. laxa* (SCHULZ 3475). Plants in **A** and **B** are vigorous specimens with extraordinarily developed rhizomes (arrow in **B**: rhizome neck). The innovation shoots in **C** show a gradient from new rhizomes at the proximal nodes to orthotropous culms at the distal ones. The strong rhizomes in **D** are buried in the bed mud, and innovation shoots arise from them and also from the lower nodes of the culm (arrow).

In *D. swalleniana* and *D. catamarcensis* the proximal portion of the tillers form profusely spreading rhizomes (Fig. 2C, D). Although relatively slender, such rhizomes do not differ in structure from those of the remaining species. Thus, the spreading condition is achieved in these species because of the relatively high number of internodia (more than 80 in some specimens of *D. swalleniana*), and only secondarily as an outcome of some internode elongation. On the other way, vigorous specimens of *D. insularis* (remarkably RÚGOLO et al. 1751) and *D. californica* (e.g. BURKART 23934; 24099; PARODI 14472) can show extraordinarily expanded rhizomes, which, however, are rather thick (Fig. 3A, B).

The proximal portion of each rhizome segment represents the so-called 'neck' (MCCLURE 1966; JUDZIEWICZ et al. 1999); it is usually quite slender and bears no lateral buds and roots. Beyond the neck, the diame-
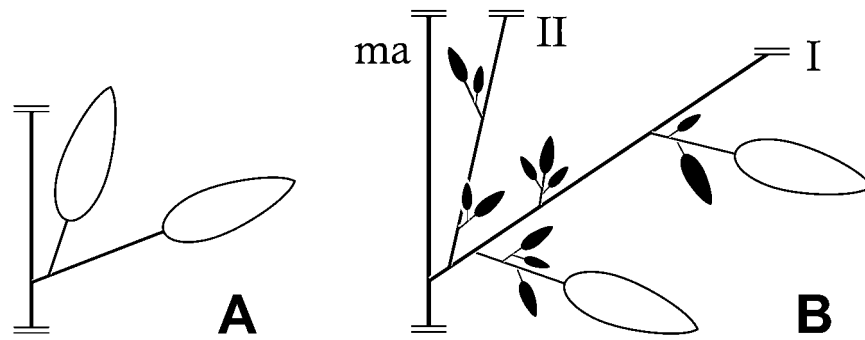
Fig. 4. **A,** Diagram of a normal 2-spikelet short paraclade, as occurring in all species of *Digitaria* sect. *Trichachne*. **B,** Diagrammatic representation of the proximal portion of a basal long paraclade of *D. insularis* showing a second order long paraclade and 3 short paraclades composed each of 3–4 spikelets (from specimen RUA et al. 116). Hollow ovoids represent fertile spikelets, solid ovoids represent abortive spikelets; **ma,** main axis; **I,** first order long paraclade; **II,** second order long paraclade.

ne, *D. laxa* grows in hygrophytic habitats, where periodic overflow occurs. The strong rhizomes are buried in the bed mud, and innovation shoots arise not only from them but also from the lower nodes of the culm, which in addition bear a whorl of adventitious roots (Fig. 3D).

In all cases the culms grow upright to form synflorescences. In contrast with the rhizome internodia, which are always solid, culm internodia are hollow, and the upper one is usually longer than the remaining internodia altogether. Axillary enrichment shoots usually develop from the lower nodes. Each of them normally bears a well developed trophotagma (cf. HAGEMANN 1990) and ends in a flowering unit (*sensu* SELL & CREMERS 1994, see also RUA 1999 and references therein), as well as the main axis. Thus, the whole synflorescence follows a paniculate branching pattern (see next section).

Inflorescence structure

The overall structure of the synflorescence follows a paniculate design, with flowering units ending the main axis and all enrichment shoots.

In the general pattern the flowering units of the species belonging to sect. *Trichachne* conform to those occurring in other sections of *Digitaria*, i.e. a main axis bearing a proximal portion along which a variable number of long paraclades develop, followed by a distal portion bearing short paraclades (cf. RUA & BOCCALONI 1996; CÁMARA-HERNÁNDEZ 2001a). As common among such inflorescences, the transition between both zones bearing respectively long and short paraclades is abrupt, and each long paraclade bears short paraclades reproducing the structure of the distal portion of the main axis (CÁMARA-HERNÁNDEZ & RUA 1991; WEBERLING et al. 1993).

The short paraclades are arranged in 2 rows along the long paraclade axes and the distal portion of the main axis, following a quasi-distichous, dorsiventral pattern (cf. CÁMARA-HERNÁNDEZ & BELLÓN 1992; RUA & WEBERLING 1998). They are typically composed of a primary and a secondary axis, each one ending in a spikelet (Fig. 4A). Nevertheless, in the proximal nodes of the lower long paraclades some secondary paraclades can be observed composed of 3 or 4 spikelets arranged in a paniculate way (Fig. 4B).

The number of long paraclades varies from 1 or 2 (*D. brownii, D. tenuis*) to about 50 (*D. insularis, D. laxa*). They are scattered along the main axis, so the inflorescences among species of *Digitaria* sect. *Trichachne* look like a panicle and never achieve the distinctive digitate appearance of those of *Digitaria* sect. *Digitaria*. In most cases only primary long paraclades develop, with the exception of *D. laxa,* in which long paraclades of higher branching order regularly occur (see below); otherwise they only can be found occasionally at the proximal nodes of basal primary long paraclades (e.g. *D. insularis*, Fig. 4B).

The long paraclades are arranged along multiple orthostichies, at least in the basal and middle portion of the inflorescence (Fig. 5A, B). The number of orthostichies seems to be related to the number of long paraclades along the inflorescence axis: inflorescences with many long paraclades, that occur in *D. insularis* and *D. laxa*, show also a higher number of orthostichies. Nevertheless, some orthostichies "vanish" towards the apex of the inflorescence, in such a way that the number of orthostichies decreases until a trigonous axis with 2 orthostichies just remain (Fig. 6). Thus the quasi-distichous, dorsiventral arrangement characteristic of the short paraclade-bearing distal portion takes place (Fig. 5B). As commonly observed among polystichous
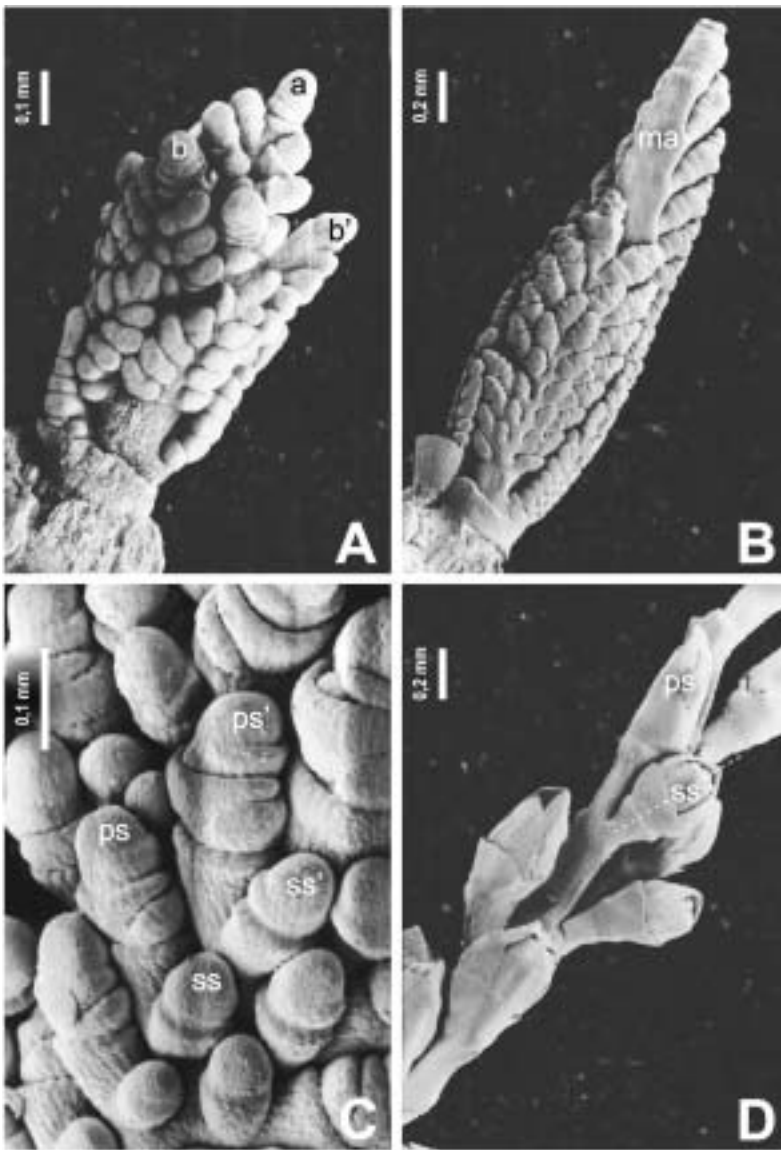
Fig. 5. SEM-micrographs. **A,** young inflorescence of *D. catamarcensis;* note the polystichous arrangement of long paraclades, and the terminal spikelets of main axis (**a**) and long paraclades (**b, b'**) at a more advanced developmental stage than the remaining ones. **B,** young inflorescence of *D. sacchariflora*, showing the polystichous arrangement of long paraclades, and the dorsiventral pattern of the distal portion of the main axis (ma). **C,** portion of a inflorescence of *D. insularis* showing 2-spikelet short paraclades; note the "pedicellate" spikelets at primary axes (**ps, ps'**) more developed than the "subsessile" ones at secondary axes (**ss, ss'**). **D,** portion of other inflorescence of the specimen represented in B, at a more advanced developmental stage; note the median plane (dashed line) of the subsessile spikelet (**ss**) at approximately 90° to that of the pedicellate spikelet (**ps**). A from Rua & Dios 498, B and D from Rua et al. 34, C from Rua & Vega s. n.

grass inflorescences (cf. Cámara-Hernández 2001b), the position of long paraclades along different orthostichies sometimes is (nearly) coincident at a same node, and thus a verticillate or quasi-verticillate arrangement results. In the case of *D. laxa* the verticillate appearance is further reinforced by the basal branching of long paraclades, in such a way that a bunch of long paraclades of different branching order arise at each node. The branching pattern of such long paraclade bunches, however, is obscured in dried herbarium specimens. No living material of this species was available.

Pulvini at the base of long paraclade axes are inconspicuous. This fact could be associated with the position of long paraclades, which are nearly adpressed in all species of the sect. *Trichachne* but *D. patens*.

Discussion

Growth form

Growth forms within *Digitaria* sect. *Trichachne* are quite homogeneous. The growth form type of most species can be assigned to the "lockere Horste" of the German authors (cf. Mühlberg 1965, 1967; Kästner & Karrer 1995) or the PB2 model (PB = perennial branched) coined for *Paspalum* by Rua & Gróttola (1997). Beyond continuous-quantitative traits such as plant height, leaf blade width, etc., the only growth form-related feature that conspicuously varies among species is the type of rhizome (Fig. 1 and 2). Grass rhizomes usually comprise the proximal portions of tillers,
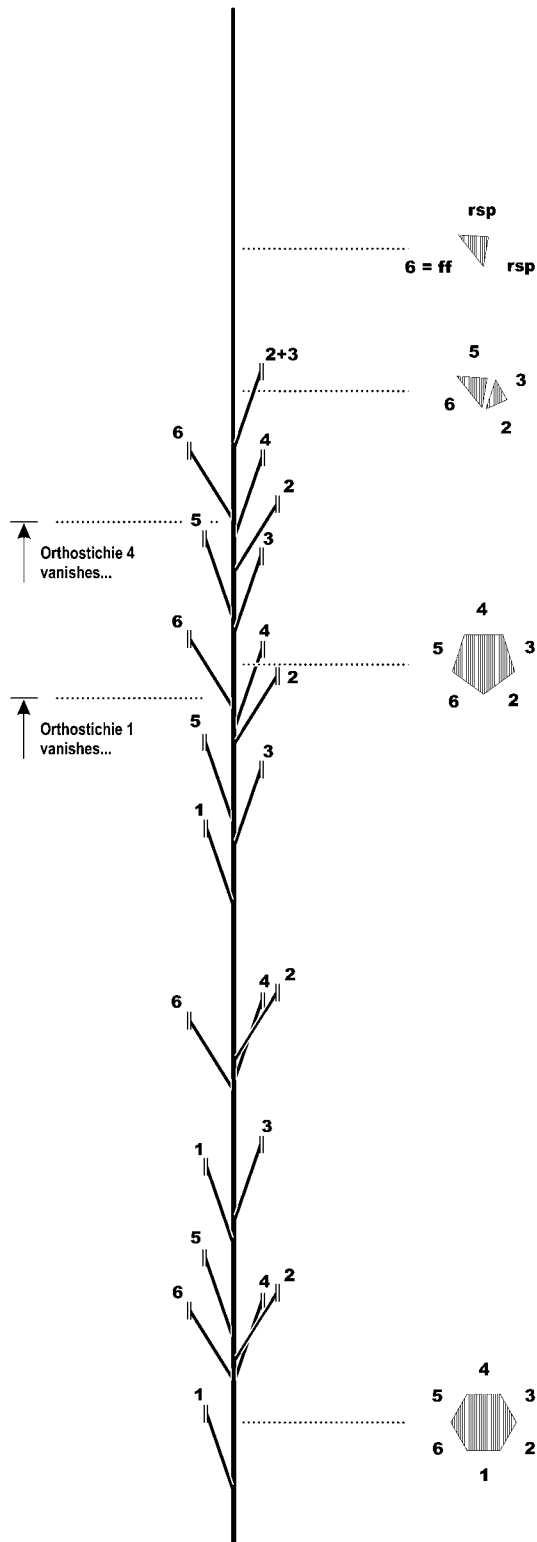
Fig. 6. Diagram of an inflorescence showing the distribution of long paraclades along the main axis. Numbers indicate orthostichies, numbered counterclockwise from the orthostichie corresponding to the first long paraclade. ff, flat face; rsp, row of spikelet pairs.

which display to some extent a plagiotropic growth before turning upwards to form a culm and producing an inflorescence. Thus, rhizome and culm are respectively the proximal and the distal portion of a same shoot unit (in the sense of Bell 1994), and different shoot units are connected with one another in a sympodial way. In spite of their different relative length, rhizomes of *Digitaria* sect. *Trichachne* conform in their main features with the pachymorph type (McClure 1966; Judziewicz et al. 1999), because of their relatively short and thick, solid internodia, and their strictly sympodial mode of branching.

Length of rhizomes determines spacing of the culms. Species with short rhizomes form more or less dense clumps, whereas species with elongated rhizomes grow dispersedly. Thus short and long rhizomes could represent different ecological strategies in relation with space occupation (cf. Bell & Tomlinson 1980; Huber 1997). The value of such traits as phylogenetic characters is probably limited, because it seems to be scarcely conservative evolutionarily. Remarkably, pairs of morphologically similar species differing in rhizome development can be found not only in *Digitaria* (*D. swalleniana* – *D. similis*) but also in *Paspalum* (e.g. *P. nicorae* Parodi – *P. plicatulum* Michx., *P. paucifolium* Swallen – *P. erianthum* Nees) and probably in other grass genera. This fact suggests that similar rhizome types could be achieved independently several times.

Among species of *Digitaria* sect. *Trichachne*, rhizome and culm buds behave typically in different ways. Rhizome buds form innovation shoots, i.e. new complete tillers composed of a proximal rhizome and a distal culm, no matter if they are cataleptic or sylleptic ('iterative innovation', Troll 1964: 325–331). On the other hand, culm buds behave as enrichment buds, originating paraclades which are always sylleptic and never bear a proximal rhizome. Such differentiation of bud behavior seems to be a general feature of grasses with orthotropous culms, whereas species with plagiotropous, stoloniferous culms (e.g. *D. fuscescens* (J. Presl) Henrard, a representative of the sect. *Atrofuscae* Henrard) can develop innovation buds at the culm nodes.

In *Digitaria* sect. *Trichachne*, and probably in the whole genus *Digitaria*, enrichment shoots follow a paniculate branching pattern. The bud subtended by the 'flag leaf' (the most distal foliage leaf) is usually completely repressed in *Digitaria*, with exception of some species belonging to sect. *Aequiglumae* Henrard, in which an axillary paraclade bearing cleistogamous spikelets develops (Rosengurtt & Arrillaga de Maffei 1961; Rosengurtt et al. 1970). Cymosely branched paraclades, as described for other panicoid genera (Rua & Weberling 1998 and references therein), were not observed within *Digitaria*.

Inflorescence structure

Although in agreement with the general inflorescence pattern in the genus, the inflorescences of the species belonging to *Digitaria* sect. *Trichachne* are distinctive because of the relative elongation of the main axis internodia. Long paraclades appear scattered along the main axis and – with the exception of *D. patens* – they are usually shorter than the main axis, so that the inflorescence does not show the typical digitate appearance of other species of *Digitaria*. Moreover, the distal portion of the main axis is always well developed, bears short paraclades, and ends in a terminal spikelet. On the contrary to that occurring in other major genera of *Paniceae* (e.g. *Paspalum, Axonopus* P. Beauv.), reduction of the distal, short paraclade-bearing portion of the main axis is rare within *Digitaria*. Nevertheless, such a case has been recently reported in some specimens of *D. sanguinalis* (L.) Scop. (Cámara Hernández 2001a).

Short paraclades bearing 2 spikelets (usually referred to as 'paired spikelets') are widespread within the subfamily *Panicoideae* A. Br. (Clayton & Renvoize 1986; Nicora & Rúgolo de Agrasar 1987; Watson & Dallwitz 1999). The structure of such paraclades is somewhat controversial. Cámara-Hernández & Gambino (1990) postulated the 2-spikelet short paraclades of *Zea diploperennis* H. H. Iltis, Doebley & R. Guzmán to be diplostachyous, cymosely branched structures composed of 2 successive axes, each ending in a spikelet (Fig. 7A). This model was generalized by Cámara-Hernández & Rua (1991), and supported by SEM observations on young inflorescences of *Paspalum* spp. (Rua 1996; Rua & Weberling 1998) and *Digitaria phaeotrix* (Trin.) Parodi (Rua & Boccaloni 1996). In a later paper, however, Cámara-Hernández et al. (1995) revised this interpretation and proposed an alternative one, on the base of positional observations: 2-spikelet short paraclades would be composed of truncate primary axes bearing 2 lateral spikelets placed each on a secondary axis (Fig. 7B). This new interpretation was then applied to all members of *Andropogoneae* Dumort., and associated with considerations about the prophyllar origin of the lower glume in this group. In a recent paper on inflorescences of *Digitaria sanguinalis*, Cámara-Hernández (2001a) assumes the latter to be the accurate interpretation, without further considerations. In the same paper, and presumably based on identical positional considerations, this author postulated a quite strange position for the distal spikelet of each long paraclade: it would be homologous to the subsessile spikelet of a 2-spikelet short paraclades. Such interpretation requires to hypothesize 2 levels of truncation, affecting the inflorescence main axis and the short paraclade axis (Fig. 7C).
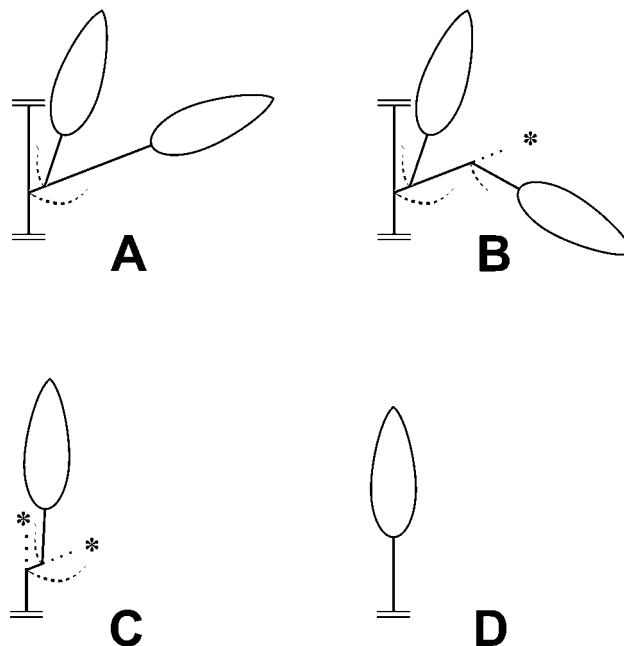

Fig. 7. **A–B,** Diagrams representing two alternative hypotheses about the structure of the 2-spikelet short paraclades: **A,** two axes of successive branching order, each ending in a spikelet; **B,** a truncate axis bearing two lateral spikelets. **C–D,** Diagrams representing two alternative hypotheses about the position of the distal spikelet of main axis and long paraclades: **C,** pseudoterminal on a second-order branch of the main axis; **D,** truly terminal. Asterisks indicate hypothesized truncation events, dashed lines indicate axes and leaves hypothetically lost during evolution.

Nevertheless, SEM observations on young inflorescences in *Digitaria* sect. *Trichachne* do no support such assumptions (Fig. 5C, D). In all cases the pedicellate spikelet differentiates early (Fig. 5C), no prolongation of the short paraclade axis is insinuated, and the position of the subsessile spikelet corresponds exactly to that expected for a prophyllar branch, i.e. the median planes of the subsessile and the pedicellate spikelet form an angle of 90°, with the lower glume abaxial (Fig. 5D). On the other hand, no evidence was found to reject the terminal position of the distal spikelet of each long paraclade, inasmuch as terminal spikelets seem to be always the first ones to develop (cf. Fig 5A). As far as the spikelet orientation is consistent with both interpretations, and no further evidence supporting the hypothesis of Cámara-Hernández was found, I prefer to interpret it provisionally in the most parsimonious way, ie as a true terminal spikelet (Fig. 7D). The same considerations are applied to the terminal spikelet of the main axis.

Short paraclades composed of more than two spikelets do not usually occur within *Digitaria* sect. *Trich-*

achne. Three-spikelet short paraclades regularly occur among the species belonging to the HACKEL's series *Ternata* (cf. HENRARD, 1950: XVII–XVIII). Such paraclades were described for *D. phaeotrix* (RUA & BOCCALONI 1996) as "constituted of 2–4 spikelet-bearing axes of successive branching order", so they follow a cymose branching pattern (cf. RUA 1999); this description probably accounts for the entire group. In *Digitaria* sect. *Trichachne* grouplets of more than two spikelets sometimes occur at the base of the proximal long paraclades (see above). Nevertheless, they follow a paniculate pattern (Fig. 4B), similar to that reported by CÁMARA-HERNÁNDEZ (2001a) for *D. sanguinalis*. Thus, such paraclades do not follow neither the regular (also homogeneous) 2-spikelet pattern of the group, nor that of the series *Ternatae*. They would be better grasped as proximal non-homogeneous branches of otherwise homogenized inflorescences (cf. RUA 1996 for a similar case in *Paspalum*).

The structure and arrangement of short paraclades in *Panicoideae* merits further exploration, in order to assess their whole variation, and to investigate whether a unique pattern occurs throughout the entire subfamily – so "spikelet pairing [would be] potentially synapomorphic for a large group of *Paniceae* including *Andropogoneae*" (KELLOGG 2000) – or spikelet pairs with dissimilar branching patterns characterize different groups within *Panicoideae*.

Acknowledgements

Appendix 1

Reference material. Specimens marked by * are vouchers for living plants cultivated in the "Lucien Hauman" Botanical Garden at the Buenos Aires University (Buenos Aires, Argentine).

D. brownii

Hartley 35 (CANB), Jessup & Gray 2992 (CANB), Prober s.n. (CANB), Pullen & Galore 4688 (CANB), Roe 502, 515 (CANB).

D. californica var. californica

Burkart 17479, 23934, 24099 (BAA), Cáceres 103 (BAA), Cano & Cámara 358 (BAA), Castellanos 573 (BAA), Dawson 3329 (BAA), Fabris 5497 (BAA), Hampton s.n. (BAA 17061), Hunziker 8690 (BAA), León 3101, 3102 (BAA), Nicora 6840 (BAA), Otamendi s.n. (BAA 17176), Parodi 4872, 7423, 7812, 14105, 14448, 15486 (BAA), Rua & Dios 502* (BAA), Rúgolo s.n. (BAA 5012), s.n. (BAA 5013), s.n. (BAA 24821*), Sánchez 4 (BAA).

D. californica var. villosissima

Cabrera et al. 13688, 15559 (BAA), Hunziker 10558 (BAA), Ibarrola 206 (BAA), Parodi 7828 (BAA col. typus 561), 13560, 13982, 14057, 14451, 14472 (BAA), Rojas 2766 (BAA).

D. catamarcensis

Chávez de Michel 2736 (SI), Killeen 1571 (SI), Parodi 14356 (BAA col. typus 4190), Rua & Dios 498*, 500* (BAA).

D. hitchcockii

Cleavenworth 66 (US), Hitchcock 5329 (BAA col. typus 644), 5730 (US), Martínez Martínez & Borja Luyando F-2369 (US), Roybal 48 (US), Sohns 1353 (US).

D. insularis

Adamoli et al. 91 (BAA), Boccaloni s.n. (BAA 22435), Boelcke 13428, 13483 (BAA), Cabrera & Fabris 16163 (BAA), Cabrera et al. 27506 (BAA), Ciuffi 66 (BAA), Eggers 13084 (BAA), Fabris & Zuloaga 7652 (BAA), Macedo 1406 (BAA), Molina 118 (BAA), Parodi 4349, 8397, 14476, 14481 (BAA), Piccinini & Cirino 2177 (BAA), Roitman & Tourn s.n. (BAA 24805), Rua & Caponio 509*, 516* (BAA, CTES), Rua & Dios 499* (BAA), Rua et al. 25, 116, 142, 231* (BAA), Rúgolo s.n. (BAA), Rúgolo et al. 1409,1751 (SI), Vega & Rua s.n. (BAA 24647*).

D. laxa

Meyer 94, 2592 (BAA), Pavetti & Rojas 10294 (BAA), Rojas 2765, 9124 (BAA), Schulz 3745 (CTES), Zardini & Velázquez 27524 (SI).

D. patens

Bogusch (?) S-214 (US), Gould 11361 (US), Hitchcock 5328 (BAA col. typus 645), Runyon 1542, 1867 (US), Silveus 517 (US).

D. sacchariflora

Anderson 2080 (BAA), Anderson et al. 2206 (BAA), Araujo 136 (BAA), Boelcke 1325 (BAA), Bridarolli s.n. (BAA 15132), Buchtien 31, 8043 (BAA), Burkart & Crespo 22921 (BAA), Burkart et al. 23619 (BAA), Cabrera et al. 27508 (BAA), Hatschbach 3864 (BAA), Jorgensen 3530 (BAA), Nicora 7658 (BAA), Parodi 4656, 8472, 13635 (BAA), Pedersen 5862 (BAA), Quarín et al. 158 (BAA), Rosengurtt B-3198 (BAA), Rua et al. 34, 195, 329 (BAA), Schulz 11550 (BAA), Spegazzini 168b (BAA), Türpe 4221 (BAA)

D. similis

Articó & Luti 3885 (BAA), Cano & Cámara Hernández 584, 662, 841 (BAA), Krapovickas et al. 24769 (BAA), Parodi 8373 (BAA), Pedersen 6379 (BAA), Ramírez 45 (BAA),

Roitman & Tourn s.n. (BAA 24804*), Rojas 2776 (BAA), Rua & Caponio 513* (BAA, CTES), Sacco 86, 283, 902 (BAA), Schulz 3282, 3312, 3841, 3901, 11550$^1/_2$ (BAA)

D. swalleniana

Boelcke 1383, 1567 (BAA), Burkart 732, 24061 (BAA), Burkart & Crespo 22869 (BAA), Calderón 1392 (BAA), Cano & Cámara Hernández 868 (BAA), Chebataroff 10992 (BAA), Galli 58 bis (BAA), Gallinal et al. PE-5169 (BAA), García s.n. (BAA 3632), Meyer 2296 (BAA), Parodi 12502, 14443, 14456, 14462, 14464, 14482 (BAA), Peirano s.n. (BAA 17891), Ragonese 366 (BAA), Rojas 8700 (BAA), Romano s.n. (BAA 15793), Rosengurtt B-919, B-4902$^1/_2$, B-4968 (BAA), Rua & Caponio 514* (BAA, CTES), Sacco 22, 282 (BAA), Schulz 3875, 4013 (BAA), Soriano 1657 (BAA), Suero s.n. (BAA 13194)

D. tenuis

Harley 16615 (US), Nees 196? (BAA col. typus 648), Pickel 3830 (US), Sarmento 59-207 (BAA), Steyermark 88559 (US), Swallen 4312 (US).

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