

A Morphology-Based Cladistic Analysis of *Digitaria* (Poaceae, Panicoideae, Paniceae)

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Abstract—A phylogenetic analysis was performed on 67 species of *Digitaria* belonging to four subgenera and 26 of the 32 sections recognized in Henrard's monograph. The analysis was based on 113 discrete and six continuous morphological characters. In the resulting topologies the genus *Digitaria* was monophyletic. In spite of the low support for most groupings, several clades were recovered. The subdivision of *Digitaria* in the four subgenera proposed by Henrard was not supported since the large subgenus *Digitaria* appears as a paraphyletic assemblage within which the other three subgenera are nested. Nevertheless, the monophyly of some of Henrard's sections was supported. This is the first approach to the phylogeny of *Digitaria*.

Resumen—Se llevó a cabo un análisis cladístico. Se incluyeron 67 especies de *Digitaria* pertenecientes a los 4 subgéneros y a 26 de las 32 secciones reconocidas en la monografía de Henrard. El análisis fue basado en 113 caracteres morfológicos discretos y 6 continuos. En las topologías resultantes el género *Digitaria* resultó monofilético. A pesar del bajo soporte de la mayoría de los grupos, fueron recuperados varios cladogramas. Los resultados no fueron consistentes con la subdivisión de *Digitaria* en 4 subgéneros propuesta por Henrard, ya que el extenso subgénero *Digitaria* aparece como un agregado parafilético dentro del cual se hallan anidados los otros tres subgéneros. Sin embargo, la monofilia de algunas secciones fue confirmada. El presente estudio constituye el primer análisis filogenético de *Digitaria*.

Keywords—Cladistic, *Digitaria*, Paniceae, phylogeny, Poaceae, systematics.

The genus *Digitaria* Haller emend. A. S. Vega & Rúgolo (Vega and Rúgolo de Agrasar 2001) comprises ca. 220 species distributed in tropical, subtropical, and temperate areas worldwide (Watson and Dallwitz 1992 onwards). It includes foraging species, minor cereals, turf plants, and soil binders, as well as some weeds (Henrard 1950; Veldkamp 1973; Rúgolo de Agrasar 1974; Clayton and Renvoize 1986; Nicora and Rúgolo de Agrasar 1987; Guzmán et al. 1989; Molina Sánchez 1990; Watson and Dallwitz 1992 onwards). Species of *Digitaria* can be recognized by their cartilaginous upper florets, with fertile lemmas having noninrolled, membranous margins, scarcely exposing the fertile palea. This character is used to distinguish *Digitaria* from allied genera: *Axonopus* P. Beauv., *Panicum* L. and *Paspalum* L. Another taxonomic character of *Digitaria* is the position of fertile lemmas toward the axis of the inflorescences; lower glumes and lemmas are abaxial, and upper glumes and lemmas are adaxial. This character distinguishes *Digitaria* from *Axonopus*, the latter also without a lower glume (Henrard 1950).

An historical survey of *Digitaria* shows that several authors have considered it as an infrageneric entity (section, series, or subgenus) within *Panicum* and *Paspalum* (Haller 1768; Trinius 1826; Nees von Esenbeck 1829; Steudel 1853; Gray 1856; Bentham 1878 pp. 463–464; Hackel 1901; Camus 1912). Walter (1788) described *Syntherisma* as a new genus, and Nees (1829) described *Trichachne*, including *Acicarpa* Raddi in its synonymy.

Hackel (1901) first divided *Panicum* subg. *Digitaria* into three well-marked, but not quite natural, series: *Solitaria*, *Binata*, and *Ternata*. *Digitaria* ser. *Solitaria* comprises species with single, sessile spikelets along the inflorescence branches; *D.* ser. *Binata* includes species with one spikelet subsessile and the other pedicellate, and in *D.* ser. *Ternata* each short panicle comprises three or more spikelets, one subsessile and the others pedicellate. In her treatment of Paniceae, Chase (1906) recognized three genera, *Valota* Adans. (= *Trichachne* Nees), *Syntherisma* Walter, and *Leptoloma* Chase. According to Chase (1906), *Valota* includes species with lanceolate-acuminate upper florets and upper glumes and lower lemmas clothed

with long hairs exceeding the length of the spikelets; *Syntherisma*, as well as *Leptoloma*, has elliptic upper florets, and upper glumes and lower florets clothed with short hairs or glabrous. *Syntherisma* differed from *Leptoloma* by having "spikelets disposed in 1-sided racemes which are digitate or racemose" rather than "panicles divergent at maturity" (Chase 1906).

According to Stapf (1919) the varied and distinguishable types of hairs in the spikelets, when correlated with other characters, constitute a guide to the main groups of species in *Digitaria*. This author defined two sections of *Digitaria* in Tropical Africa, sect. *Setariopsis* and sect. *Eu-Digitaria*, the latter composed of nine subsections.

Hitchcock (1927, 1950) recognized *Digitaria*, *Leptoloma*, and *Trichachne* as valid genera, and considered *Valota* as a synonym of *Trichachne*.

Parodi (1928) mentioned the necessity of transferring the species of *Valota* (*Trichachne*) to *Digitaria* on the basis of morphological characteristics, and Henrard (1950) formally transferred species in *Valota*, *Syntherisma*, and *Leptoloma* to *Digitaria*, while making some nomenclatural changes.

Even though taxonomic studies on *Digitaria* have been carried out by several authors (Hackel 1901; Chase 1906; Stapf 1919; Rúgolo de Agrasar 1968, 1969, 1970, 1974, 1976, 1990, 1992, 1993, 1994; Veldkamp 1973; Webster 1983; Rúgolo de Agrasar and Sánchez 1989; Wipff and Hatch 1994; Canto-Dorow 2001; Canto-Dorow and Longhi-Wagner 2001; Vega and Rúgolo de Agrasar 2001, 2002a, 2002b, 2003, 2005, 2006a, 2006b, 2007; Renvoize et al. 2006, among others), the only available comprehensive treatment is Henrard's (1950) monograph. He subdivided *Digitaria* into four subgenera: *Leptoloma* (Chase) Henrard, *Setariopsis* (Stapf) Henrard, *Solitaria* (Hack.) Henrard, and *Digitaria*, the latter with 32 sections (Table 1). Nevertheless, Henrard's classification has been partially questioned (Veldkamp 1973; Rúgolo de Agrasar 1974) and the relationships between species and groups of species remain unclear.

Some recent molecular studies on Panicoideae throw some light on the systematic position of *Digitaria* within the sub-

TABLE 1. Classification of *Digitaria* with subgenera and sections recognized by Henrard (1950). The total number of species included in each subgenus or section is mentioned between brackets, including additions (*) from Rùgolo de Agrasar (1976, 1992) and Wipff and Hatch (1994). Taxa considered in this study are listed below.

<i>Digitaria</i>	
Subg. Solitaria (Hack.) Henrard (8 spp.)	<i>D. mariannensis</i> Merr.
Subg. Setariopsis (Stapf) Henrard (9 spp.)	<i>D. diagonalis</i> (Nees) Stapf
	<i>D. minutiflora</i> Stapf
Subg. Leptoloma (Chase) Henrard (4 spp.*)	<i>D. arenicola</i> (Swallen) Beetle
	<i>D. cognata</i> (Schult.) Pilg.
	<i>D. pubiflora</i> (Vasey) Wipff
Subg. Digitaria	
Sect. Aequiglumae Henrard (16 spp.)	<i>D. eriostachya</i> Mez
	<i>D. aequiglumis</i> (Hack. & Arechav.) Parodi
Sect. Atrofuscae Henrard (10 spp.)	<i>D. fuscescens</i> (J. Presl) Henrard
	<i>D. curvinervis</i> (Hack.) Fernald
Sect. Biformes Henrard (2 spp.)	<i>D. bicornis</i> (Lam.) Roem. & Schult.
Sect. Calvulae (Stapf) Henrard (18 spp.)	<i>D. badia</i> (Scribn. & Merr.) Fernald
	<i>D. phaeotrix</i> (Trin.) Parodi var. <i>hackelii</i> (Arechav.) Henrard
Sect. Capitipilae Henrard (4 spp.)	<i>D. maitlandii</i> Stapf & C. E. Hubb.
Sect. Cirripilae (Stapf) Henrard (12 spp.)	<i>D. gazensis</i> Rendle
	<i>D. botryostachya</i> Stapf
Sect. Clavipilae (Stapf) Henrard (22 spp.)	<i>D. balansae</i> Henrard
	<i>D. ternata</i> (A. Rich.) Stapf
	<i>D. thouaresiana</i> (Flüggé) Camus
	<i>D. atra</i> Lucas emend A. S. Vega & Rùgolo
	<i>D. argyrostachya</i> (Steud.) Fernald
	<i>D. melanochila</i> Stapf
Sect. Corynotrichae Henrard (10 spp.)	<i>D. bonplandii</i> Henrard
	<i>D. gerdessii</i> (Hack.) Parodi
	<i>D. chaseae</i> Henrard
Sect. Debiles Henrard (1 spp.)	<i>D. debilis</i> (Desf.) Willd.
Sect. Erianthae Henrard (33 spp.)	<i>D. eriantha</i> Steud.
	<i>D. nodosa</i> Parl.
Sect. Flaccidulae (Stapf) Henrard (4 spp.)	<i>D. nitens</i> Rendle
Sect. Gibbosae Henrard (1 spp.)	not represented
Sect. Glabratae Henrard (9 spp.)	<i>D. abyssinica</i> (Hochst. ex A. Rich.) Stapf
Sect. Heteranthae Henrard (2 spp.)	<i>D. heterantha</i> (Hook. f.) Merr.
Sect. Horizontales Henrard (18 spp.)	<i>D. horizontalis</i> Willd.
	<i>D. pearsonii</i> Stapf
	<i>D. perrottetii</i> (Kunth) Stapf
Sect. Laniflorae Henrard (2 spp.)	<i>D. brownii</i> (Roem. & Schult.) Hughes
Sect. Leianthae Henrard (8 spp.)	<i>D. leiantha</i> (Hack.) Parodi
	<i>D. katangensis</i> Robyns
	not represented
Sect. Leucostachyae Henrard (1 spp.)	<i>D. monodactyla</i> (Nees) Stapf
Sect. Monodactylae (Stapf) Henrard (1 spp.)	<i>D. argillacea</i> (Hitche. & Chase) Fernald
Sect. Orthotrichae Henrard (14 spp.)	<i>D. fragilis</i> (Steud.) Lucas
	<i>D. cayoensis</i> Swallen
	<i>D. lecardii</i> (Pilg.) Stapf
Sect. Parviflorae Henrard (11 spp.)	<i>D. parviflora</i> (R. Br.) Hughes
Sect. Parviglumae Henrard (7 spp.)	<i>D. gymnostachys</i> Pilg.
Sect. Pennatae (Stapf) Henrard (8 spp.)	<i>D. ammophila</i> (F. Muell.) Hughes
	<i>D. coenicola</i> (F. Muell.) Hughes
	<i>D. divaricatissima</i> (R. Br.) Hughes
	<i>D. pennata</i> (Hochst.) T. Cooke
	not represented
Sect. Remotae Henrard (2 spp.)	<i>D. sanguinalis</i> (L.) Scop.
Sect. Sanguinales (Stapf) Henrard (26 spp.)	<i>D. ciliaris</i> (Retz.) Koeler
	<i>D. junghuhniana</i> (Nees ex Steud.) Henrard
	not represented
Sect. Subeffusae Henrard (4 spp.)	<i>D. similis</i> Beetle ex Gould
Sect. Transversales Henrard (1 spp.)	<i>D. californica</i> (Benth.) Henrard
Sect. Trichachne (Nees) Henrard (10 spp.*)	<i>D. swalleniana</i> Henrard
	<i>D. sacchariflora</i> (Nees) Henrard
	<i>D. insularis</i> (L.) Fedde
	<i>D. tenuis</i> (Nees) Henrard
	<i>D. hitchcockii</i> (Chase) Stuck.
	<i>D. laxa</i> (Rchb.) Parodi
	<i>D. patens</i> (Swallen) Henrard
	<i>D. catamarcensis</i> Rùgolo

(Continued)

TABLE 1. Continued

<i>Digitaria</i>	
Sect. Tricholaenoides Henrard (4 spp.)	not represented
Sect. Trichophorae Henrard (3 spp.)	<i>D. pittieri</i> (Hack.) Henrard <i>D. eggersii</i> (Hack.) Henrard
Sect. Verrucipilae (Stapf) Henrard (24 spp.)	<i>D. argyrotricha</i> (Andersson ex Peters) Chiov. <i>D. angolensis</i> Rendle <i>D. violascens</i> Link <i>D. mollicoma</i> (Kunth) Henrard
Sect. Xanthotrichae Henrard (1 spp.)	not represented

family. A DNA sequence data analysis from the chloroplast gene *ndhF* (Giussani et al. 2001) suggests that Panicoideae is divided into three well supported clades: two corresponding to the long-recognized tribe Paniceae and the remainder corresponding to the Andropogoneae. The splitting of Paniceae into two clades correlates with base chromosome numbers $x = 9$ and $x = 10$. *Digitaria* belongs to the $x = 9$ Paniceae, and appears as sister to the remaining genera within this clade. A second analysis using sequences from the *rpoC2* insert (Duvall et al. 2001) also supports the monophyly of *Digitaria* and its relationship with the remaining $x = 9$ Paniceae. Thus, the hypothesis of affinity of *Digitaria* with *Paspalum*, *Axonopus*, and other genera with chromosome base number $x = 10$ proposed by earlier authors (Henrard 1950; Butzin 1970; Rúgolo de Agrasar 1974) would be rejected on the basis of molecular and chromosome base number. However, the position of *Digitaria* is still uncertain, whether sister to all $x = 9$ Paniceae or sister to the *Setaria/Urochloa/Panicum* clade (Giussani et al. 2001).

Since no hypothesis regarding the phylogeny within *Digitaria* is currently available, the aim of the present paper is to explore phylogenetic relationships within the genus, and to test the monophyly of the currently recognized subgeneric entities on the basis of morphological evidence. This analysis will be complementary to an ongoing study based on molecular data (Vega et al. unpubl.).

MATERIALS AND METHODS

Ingroup Taxa—A set of 67 species of *Digitaria* was considered in our analysis, including representatives of subgenera *Leptoloma*, *Setariopsis*, *Solitaria*, and 26 of the 32 sections of subgenus *Digitaria* (Table 1).

Outgroup Taxa—Three further representatives of the $x = 9$ clade of Paniceae were included in our analysis: *Echinochloa pyramidalis* (Lam.) Hitchc. & Chase, *Urochloa brizantha* (Hochst. ex A. Rich.) R. D. Webster, and *Panicum repens* L. *Anthraenantia lanata* (Kunth) Benth., a member of the $x = 10$ Paniceae, was also included and used for the purpose of rooting.

Because “the resolution among multiple outgroup terminals [...] may affect both the position of the ingroup relative to outgroups and the topology of relationships within the ingroup” (Nixon and Carpenter 1993: 422), some characters were included in our analysis to resolve outgroup relationships.

Material—Morphological characters (vegetative, reproductive, and anatomical) were scored from herbarium material. Specimens belonging to the following herbaria were examined (acronyms after Holmgren et al. 1990): AAU, BAA, C, CANB, CTES, G, K, L, LIL, MO, P, PRE, SI, SJ, UB, US, VEN, and WU. Only one or two representative specimens of each taxon are listed in Appendix 1. Whenever possible, morphological data were corroborated with living material, through field observations as well as examination of plants cultivated in the “Lucien Hauman” Botanical Garden, Facultad de Agronomía, Universidad de Buenos Aires, Argentina for *D. aequiglumis*, *D. argyrotricha*, *D. bicornis*, *D. californica*, *D. catamarcensis*, *D. ciliaris*, *D. diagonalis*, *D. eriantha*, *D. fuscescens*, *D. insularis*, *D. laxa*, *D. phaeotrix*, *D. similis*, *D. swalleniana*, *D. ternata*, and *D. sanguinalis*. Morphological characters related to inflorescence structure and growth habit were scored according to Rua (2003).

Anatomical Studies—Segments of the middle portion of the penultimate leaf blade of a fertile innovation were used in anatomical studies. Leaf blades of all studied species were taken from living plants when available, or from herbarium specimens and soaked in a nonionic detergent solution at 70°C for 1 hr. Materials were either hand sectioned and stained with safranin, or embedded in paraffin and cut with a rotary microtome, dehydrated in an ethanol series, and double stained with safranin-fast green (D’Ambrogio de Argüeso 1986). Transverse sections were studied under a Wild M20 light microscope.

Observations and measurements of epidermal cells of the upper lemma were made with an optical microscope (Zeiss Axioplan, Zeiss, Oberkochen, Germany) connected to an image analyzer (Imagenation Px, Imagenation Corp., Beaverton, Oregon). Upper lemmas were dissected from the spikelets and mounted in gelatine-glycerine. Measurements of cell width and relation between the maximum (outer) and minimum (inner) distance of undulations in horizontal anticlinal walls (Ellis 1979) were taken from three cells of each specimen.

Longitudinal sections of the spikelets as well as different types of pilose indumentum were selected, mounted and coated with a gold-palladium (40% - 60%) alloy by a Thermo VGScientific, and observed using a ZEISS DSM 940A Scanning Electron Microscope (SEM) at the Instituto de Botánica Darwinion, Argentina, and a Phillips XL 30 (Phillips, The Netherlands) SEM at the Museo Bernardino Rivadavia, Argentina.

Characters—The matrix included 113 discrete plus six continuous morphological characters (Appendix 2); 105 of these showed variation at the ingroup level. The remaining 14 characters were included either as possible synapomorphies joining the genus *Digitaria* with outgroup terminals, or as informative characters for the outgroups. Autapomorphies were not included in our analysis. Polymorphic characters were scored as such, as recommended when the polarity of the characters are unknown from previous analysis (Kornet and Turner 1999). Missing data (including unavailable as well as inapplicable data) represent 5.7% of the entries in the data matrix. Continuous characters were analyzed as such, using the methodology implemented in TNT (Goloboff et al. 2005).

Data Analysis—The data matrix (Supplemental Appendix 3) was analyzed using TNT (Goloboff et al. 2003a). Data matrix and trees were submitted to TreeBASE (Study number S2186). A heuristic search strategy was adopted, consisting of 100 random addition sequences followed by TBR swapping, using Wagner trees as starting trees and holding a maximum of two trees each time. The trees obtained were submitted to a round of TBR swapping, then to 1,000 iterations of Parsimony Ratchet (Nixon 1999), and then to an additional round of TBR. Branches with ambiguous support (min. length = 0) were collapsed. Group support was quantified through: (1) the decay index of Bremer (BS, Bremer 1994), and (2) the symmetric jackknife group frequency (SJF, Goloboff et al. 2003b).

Because of the high homoplasy of the data set, tree searches were performed using implied weights (Goloboff 1993, Goloboff et al. 2008). When using implied weights, TNT downweights homoplastic characters in proportion to their amount of extra steps (homoplasy), and saves trees that minimize ‘distortion’ (D), which is an increasing function of the homoplasy (Goloboff et al. 2003a). Distortion is quantified with the equation, $D = e / (e + k)$, where e = extra steps, and k = constant of concavity. The strength with which a homoplastic character is downweighted depends on the concavity value (k) of the weighting function: the lower the k value the stronger the weighting function. To explore the stability of the results, analyses were performed under 33 different k values. Since distortion is not a linear function of concavity, k values were selected in such a way that they produce regular distortion increments of 1.25%, within a range of 50–90% related to an average nonhomoplastic character (Mirande 2007). To test tree stability related to variations of k , comparisons between pairs of contiguous trees (i.e. between trees obtained using k_n and k_{n-1})

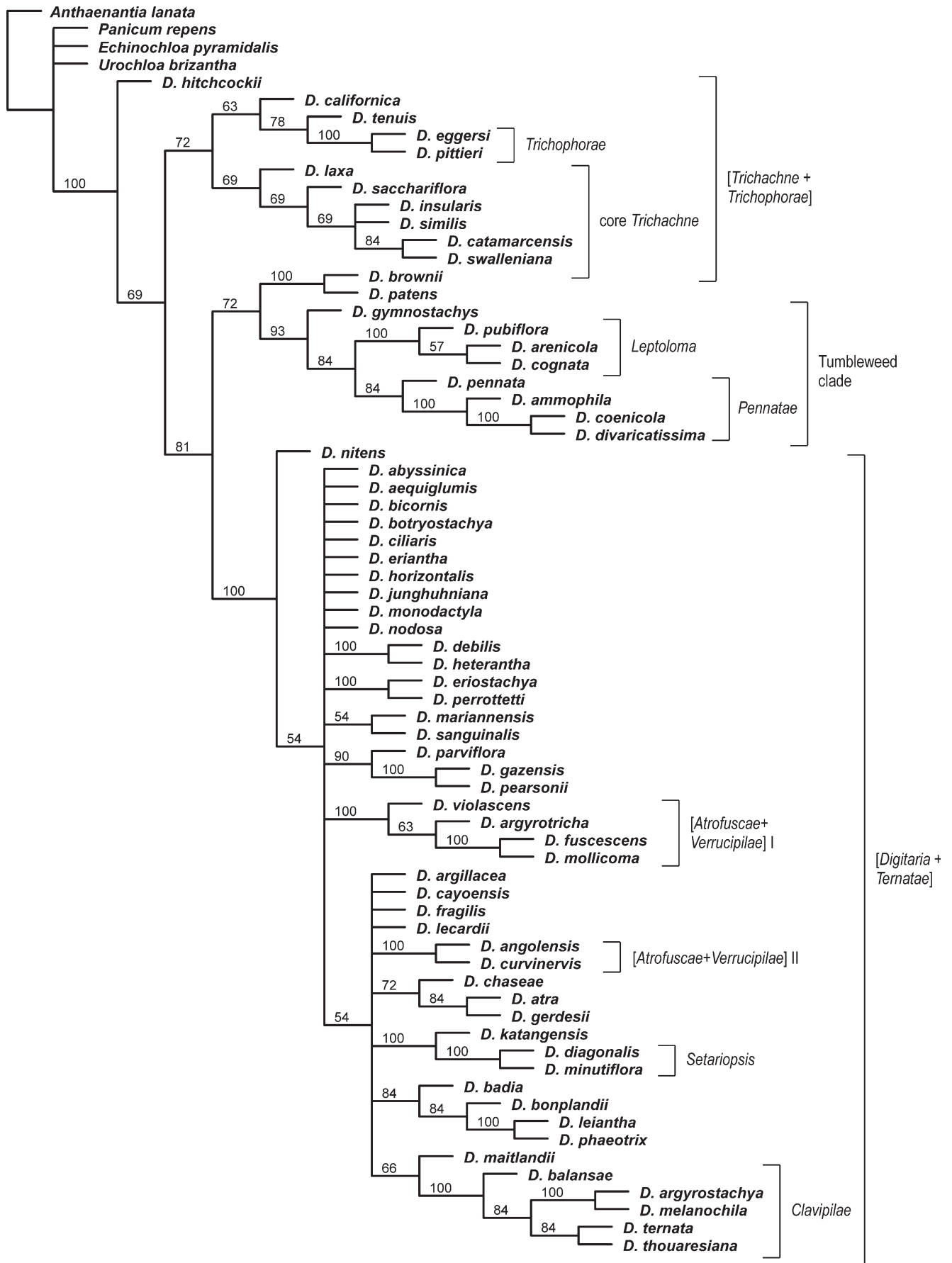


FIG. 1. Majority rule consensus of cladograms resulting from parsimony analysis using implied weighting, with $k = 4.2-37.9$ (for details see text). Numbers above branches indicate the branch frequency (higher than 50%) in all trees.

were performed through calculation of (1) SPR-difference, i.e. the number of SPR-swaps required to convert tree n into tree $n-1$; (2) number of shared taxa (= nodes in agreement subtree), and (3) number of shared groups (= nodes in strict consensus tree). Calculation of k values, tree searches, and calculation of stability measures were all performed using a TNT script written by J. Marcos Miranda (unpublished), who kindly made it available to us. Since support measures are not comparable when using different weighting functions, BS and SJF values were independently calculated for each concavity.

RESULTS

Thirty-three trees were found, using 33 k values ranging between 4.2 and 37.9. These results are summarized in the majority rule consensus tree presented in Fig. 1, which shows the groups being more stable across the range of k values tried. Sixteen of the obtained topologies were different. Values of k ranging between 12 and 17 yielded the more stable topology (Fig. 2). Support measures shown in Fig. 2 were calculated under $k = 15$.

In all trees *Digitaria* was monophyletic (Fig. 1) and relatively well supported by several synapomorphies. In most cases, clades that were more robust in relation to weighting intensity (i.e. having higher frequencies in the majority rule consensus, Fig. 1) were also the better supported (Fig. 2). The following clades (Figs. 1, 2) merit some comments:

1) A clade including representatives of sect. *Trichachne* and *Trichophorae* (hereafter the [*Trichachne* + *Trichophorae*] clade), which splits into two subclades, one of them comprising South American species of the sect. *Trichachne* characterized by large, acuminate spikelets (*D. laxa*, *D. swalleniana*, *D. similis*, *D. catamarcensis*, *D. insularis*, and *D. sacchariflora*, hereafter the 'core-*Trichachne*' clade), the other one including the *Trichophorae* [*D. pittieri* + *D. eggersii*] plus *D. californica* and *D. tenuis*.

2) A clade characterized by 'tumbleweed' inflorescences composed of primary branches with a spikelet-free proximal portion, the basalmost [sub]verticillate (hereafter, the 'tumbleweed' clade); this clade includes *D. gymnostachys* as sister to a subclade which splits into two monophyletic groups: [*D. pubiflora* + *D. arenicola* + *D. cognata*] (i.e. *Digitaria* subg. *Leptoloma*) and [*D. pennata* + *D. ammophila* + *D. divaricatissima* + *D. coenicola*] (*D.* sect. *Pennatae*). In most topologies, the 'tumbleweed' clade is sister to [*D. brownii* + *D. patens*], two "peripheral" members of the sect. *Trichachne* native to Australia and North America respectively.

3) A large clade characterized by having spikelets with glumes and lemmas approximate, i.e. not separated by conspicuous internodes (hereafter, the [*Digitaria* + *Ternatae*] clade). Most topologies favored the splitting of this clade into two subclades, one including species with decumbent to creeping

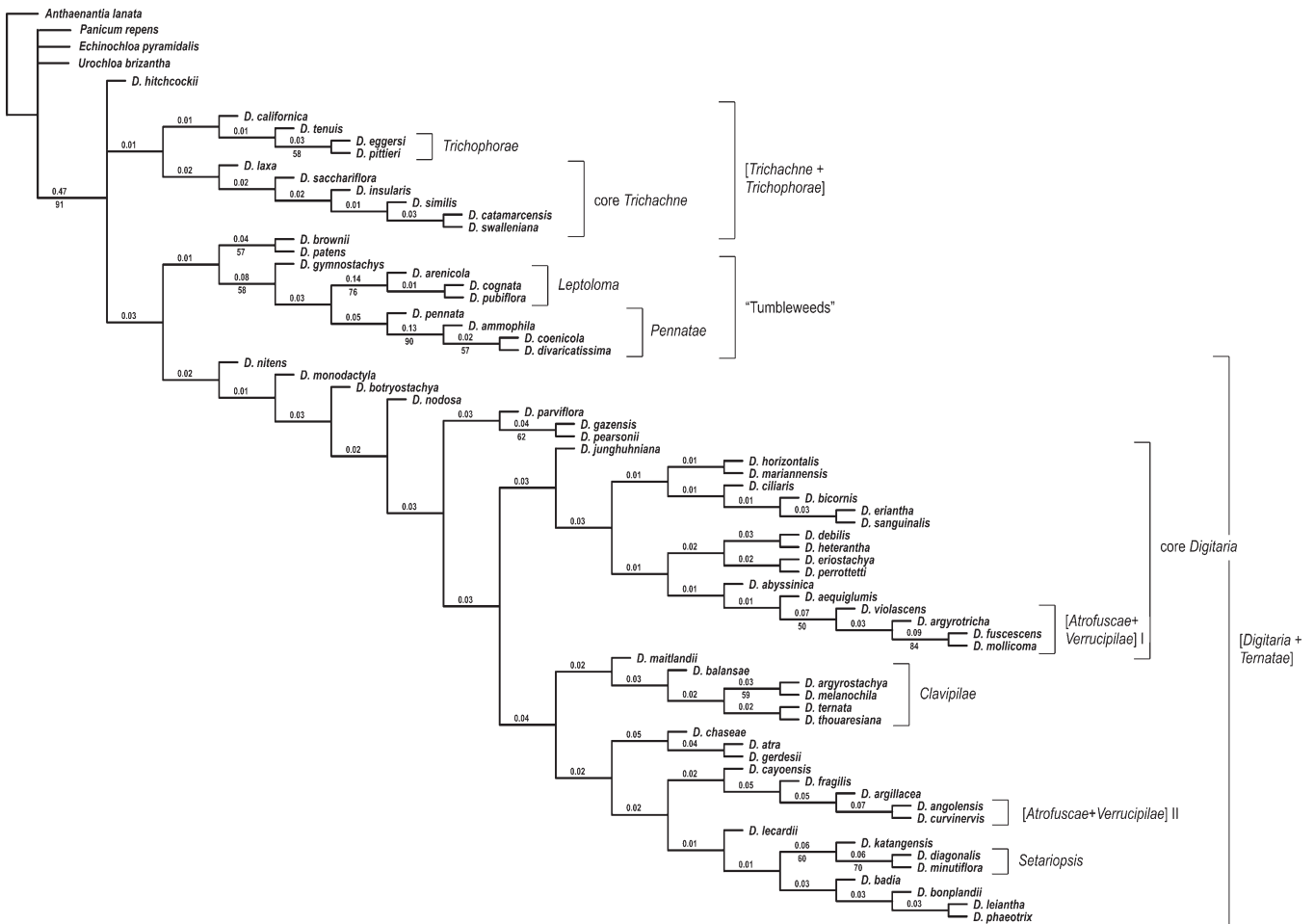


FIG. 2. Most parsimonious tree obtained under $k = 12.6-16.8$. Numbers above branches represent Bremer support, number below branches refer to symmetric jackknife group frequencies; both support measures calculated under $k = 15$.

culms allied to the type species *D. sanguinalis* (hereafter the 'core-*Digitaria*' clade), the other subclade including most species with ternate short paraclades (hereafter the 'Ternata' clade). Species of *Digitaria* sections *Atrofuscus* and *Verrucipilae*, which have ternate short paraclades, were intermingled and separate into two clades, one of them nested within the core-*Digitariae* (*D. fuscescens*, *D. violascens*, *D. argyrotricha*, *D. mollicoma*) and the other one within the *Ternatae* (*D. angolensis*, *D. curvirostris*). *Digitaria mariannensis*, the only species of the subgenus *Solitaria* included in our analysis, was also placed within the core-*Digitaria* clade. *Digitaria* subgenus *Setariopsis* and a clade including most species of the section *Clavipilae* were nested within the *Ternatae*.

DISCUSSION

Monophyly of *Digitaria*—The present analysis supports the monophyly of *Digitaria* which is unambiguously supported by several morphological synapomorphies. Our results are in agreement with previous analyses based on molecular data (Giussani et al. 2001; Duvall et al. 2001).

Subgeneric Classification—Chase distinguished the genera *Trichachne* (sub. nom. *Valota* Adans.) and *Leptoloma* from *Digitaria* (sub. nom. *Syntherisma* Walt.), but her concept was disregarded by Henrard (1950), who defined *Digitaria* in a comprehensive way by including *Leptoloma* and *Trichachne*. Instead, Henrard subdivided *Digitaria* into four subgenera (*Leptoloma*, *Setariopsis*, *Solitaria*, and *Digitaria*). The species of the former genus *Trichachne* were divided by Henrard into two sections, *D. sect. Trichachne* and *sect. Trichophorae*, whereas the Australian species of *Leptoloma* were included in *D. sect. Pennatae*. The North American *Digitaria cognata* was grouped together with the Indian *D. tomentosa* (Schult.) Pilg. into *D. subg. Leptoloma*.

Our analysis is more consistent with Chase's rather than Henrard's concept. Indeed, species of both *Digitaria sect. Trichachne* and *D. subg. Leptoloma* form a clade outside the core *Digitaria* clade. Nevertheless, a clade containing both *Trichachne* and *Leptoloma* species was recovered under $k = 7$ (tree not shown). Henrard's *Digitaria sect. Trichophorae*, formerly placed within *Valota* (Chase 1906), and *D. sect. Laniflorae*, also included by Webster (1983) in the *D. sect. Trichachne*, were also aligned outside the core *Digitaria*, as well as the *D. sect. Pennatae*, which is sister to *Leptoloma*.

According to our data *Digitaria* appears to be composed of a major clade corresponding to a core *Digitaria*, and a doubtfully resolved portion including the *D. subg. Leptoloma* and *D. sections Trichachne, Trichophorae, Laniflorae, and Pennatae*. Clearly, the subgeneric scheme of Henrard must be rejected, since the three minor subgenera *Leptoloma, Setariopsis, and Solitaria* appear nested within a paraphyletic *D. subg. Digitaria*. The validity of some of Henrard's sections will be discussed below.

Our analysis is the first preliminary cladistic contribution to the understanding of the phylogeny within *Digitaria*. Nevertheless, taxonomic decisions seem premature at this time until molecular analyses are completed (A. S. Vega et al. unpubl.).

Evolution of Selected Characters within *Digitaria*—**SPIKELET INDUMENTUM**—Stapf (1919) was the first agrostologist to use the varied nature of the hairs in the spikelets as a guide to the infra-generic taxonomy of *Digitaria*. Henrard

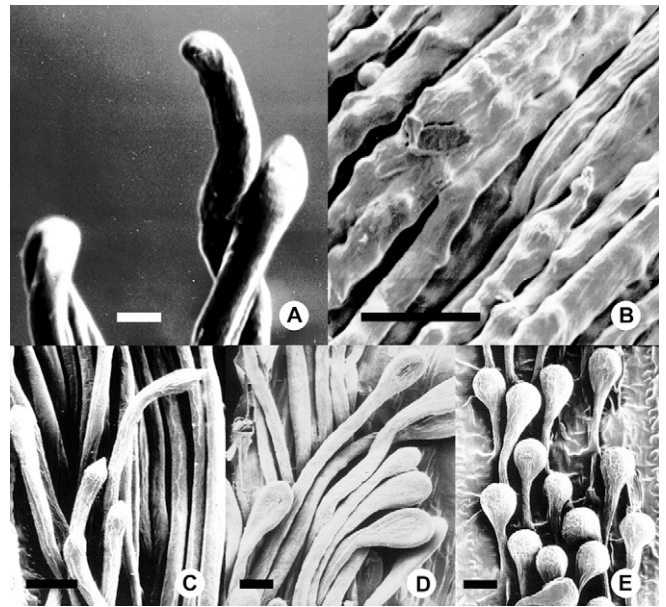


FIG. 3. A–E. Types of pilose indumentum of the spikelets. SEM photographs. A–B. Linear hairs with acute or obtuse apex. A. Smooth walls [*D. aequiglumis*, *Schinini et al. 18993* (CTES)]. Bar = 1 μ m. B. Verrucose walls [*D. violascens*, Klein 11249 (SI)]. Bar = 10 μ m. C. Hairs with a slightly dilated and mucronate apex [*D. phaeotrix* var. *adusta*, *Stuckert 18615* (G)]. Bar = 20 μ m. D–E. Claviform hairs. D. Type *Clavipilae* [*D. filiformis*, *Bittmore 799a* (L)]. Bar = 10 μ m. E. Type *Corynotrichae* [*D. gerdessii*, *Hassler 8384* (G)]. Bar = 20 μ m.

(1950) based several sections on this feature, in combination with other, more general characters. Spikelets of *Digitaria* are typically pilose, although glabrous spikelets occur as well, and a few sections are characterized by glabrous spikelets. Indumentum is varied, usually restricted to upper glume and lower lemma, and occasionally present on the back of the reduced lower palea. Pubescence on the back of a cartilaginous upper lemma had mistakenly been reported in *D. atra* (Lucas 1942); however, the cartilaginous bract corresponds to the lower lemma (Vega and Rúgolo de Agrasar 2001).

The distribution of indumentum on the upper glume and lower lemma has been considered a taxonomically valuable character due to its constancy in each taxon with the exception of *D. ischaemum*, where two types of hair indumentum were reported (Veldkamp 1973). Nevertheless, distribution of the indumentum on the spikelet bracts is highly homoplasious and carries poor phylogenetic information.

Two general types of hairs were recognized in *Digitaria* species: linear hairs, with smooth or verrucose walls with acute or obtuse apices (Fig. 3A, B) and hairs with a dilated apex and smooth walls (Fig. 3C–E). Within this last type, two morphological subtypes can further be recognized: hairs with slightly dilated apices, sometimes provided with an acumen (Fig. 3C), and claviform hairs which are dark at maturity (Fig. 3D, E). Claviform hairs have different forms, which have been used by Henrard (1950) to characterize different sections within the genus: *Clavipilae* (Fig. 3D), *Corynotrichae* (Fig. 3E), and *Capitipilae*.

Hairs with more or less dilated apices are synapomorphic for a large group within the 'Ternatae', and species with plainly dilated hairs form a clade nested within a more general group with slightly dilated hairs (Fig. 4A). Section *Clavipilae*, including species distributed in temperate and tropical regions of both hemispheres, forms a well supported

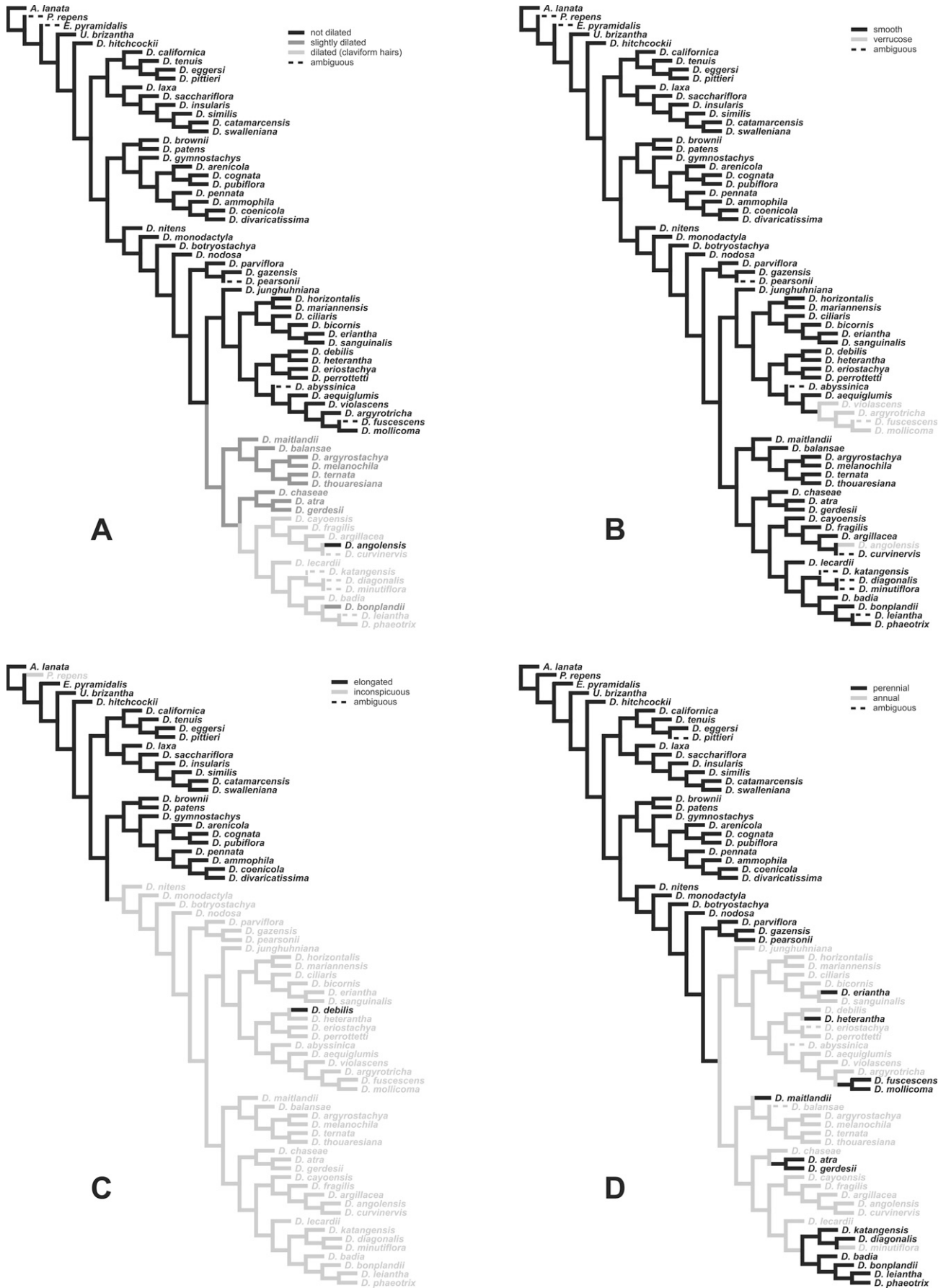


FIG. 4. A–D. Mapping of the apices of spikelet hairs (character (ch.) 6, cladogram (cl.) A), walls of spikelet hairs (ch. 8, cl. B), elongation of the first rachilla internode (ch. 13, cl. C), and life cycle (ch. 79, cl. D) onto the topology of Fig. 2.

clade. Under some concavity values (i.e. 4.2, 6.0, and 6.7), the *Clavipilae* are nested within a clade composed of all species sharing clavate hairs (trees not shown), which also includes species belonging to sections *Capitipilae* and *Corynotrichae*, endemic to tropical Africa and South America respectively, as well as the African *D. monodactyla*, a species with nondilated hairs.

Due to difficulties in placing taxa with glabrous spikelets in the current subgeneric classification, Henrard (1950) created some sections exclusively based on this character, e.g. *D. sect. Atrufuscae* and sect. *Glabratae*. Species with glabrous spikelets occur together with species having pilose spikelets in other sections.

According to our analysis, species of *D. section Atrufuscae* appear intermingled with representatives of *D. sect. Verrucipilae*, characterized by verrucose hairs. Species belonging to *D. sections Verrucipilae* and *Atrufuscae* formed a clade under stronger weighting functions (trees not shown). *Digitaria mollicoma* and *D. fuscescens*, in *D. sect. Verrucipilae* and sect. *Atrufuscae*, respectively, form a highly supported clade under all concavity values explored (Figs. 1, 2). *Digitaria abyssinica*, the only species of *D. sect. Glabratae* included in our analysis, floats across the core *Digitaria* as the weighting constant varies. Spikelet hairs seem to have been lost in several independent lineages during the evolution of this character in *Digitaria*. On the other hand, verrucose hairs could have evolved once or twice (Fig. 4B) within the genus.

RACHILLA INTERNODES—*Digitaria* section *Trichachne* was distinguished from other groups of *Digitaria* based on elongate spikelets with conspicuous internodes (Henrard 1950; Rúgolo de Agrasar 1974) [Fig. 5A]. Elongated rachilla internodes also occur in *D. subg. Leptoloma* and in *D. sections Trichophorae, Laniflorae, and Pennatae*, where at least the first rachilla internode is conspicuously elongated. Elongated rachilla internodes occur frequently among the $x = 9$ Paniceae, and seem to be plesiomorphic for *Digitaria*. Inconspicuous rachilla internodes (Fig. 5B) are synapomorphic for a large clade which includes the typical species *D. sanguinalis* and other common weeds like *D. ciliaris* (Fig. 4C). An elongate first rachilla internode is autapomorphic for *D. debilis* (Fig. 5C, D), a species probably related to *D. heterantha* and clearly nested within the 'core *Digitaria*' clade.

UPPER LEMMA SHAPE AND EPIDERMAL FEATURES—In *Digitaria*, the upper floret is cartilaginous, composed of an upper lemma with membranous flat margins that embrace a similar, subequal upper palea (Fig. 6A). The apex of the upper florets can be obtuse, acute or acuminate (Fig. 6B, C) and both bracts are visibly striate due to the presence of rows of epidermal cells, each one containing an excentric papilla (Fig. 6D). The texture of the upper floret depends on the characteristics of these epidermal cells, which can show differences in length and width as well as in the number and depth of lateral indentations. Although acuminate upper florets seem to have been acquired several times during spikelet diversification in *Digitaria*, they are possibly synapomorphic of a clade including most species of sect. *Trichachne*. On the other hand, width of the epidermal cells and depth of the cell wall indentations, as well as the other continuous characters, were informative at several levels of the tree topologies.

CARYOPSIS DISPERSAL—Many dispersal mechanisms have been described among the Paniceae, including endozoochory, adhesive dispersal by animals, ant dispersal, and wind

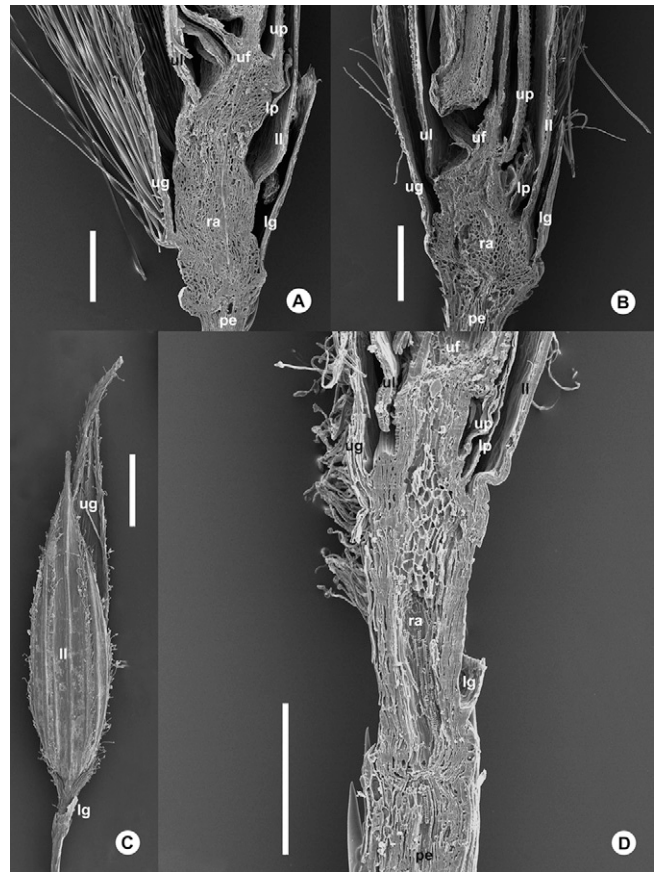


FIG. 5. Spikelets showing rachilla internodes and bract insertion. SEM photographs. A–B, D. Spikelet view in longitudinal section showing rachilla internodes: A. Conspicuous internodes [*D. similis*, Hitchcock 9008 (US)]. Bar = 200 μ m. B. Inconspicuous internodes [*D. ciliaris*, Johnston 683 (US)]. Bar = 200 μ m. C. Spikelet showing bracts distantly inserted [*D. debilis*, Simon & Williamson 1595 (US)]. Bar = 500 μ m. D. Conspicuous internodes [*D. debilis*, Simon & Williamson 1595 (US)]. Bar = 200 μ m. References: lg. Lower glume; ll. Lower lemma; lp. Lower palea; pe. Pedicel; ra. Rachilla; uf. Upper flower; ug. Upper glume; ul. Upper lemma; up. Upper palea.

dispersal (Davidse 1987). One syndrome favoring wind dispersal is the production of tumbleweeds through detachment of the entire inflorescence, as occurring in species of *Digitaria*, *Panicum*, and some less species-rich genera.

Inflorescence tumbleweed species define a well supported clade composed of members of *D. sections Parvoglumae* and *Pennatae*, and *D. subg. Leptoloma*. In the remaining taxa, the unit of dispersal is the spikelet. The small size of *Digitaria* spikelets and the different hair types and hair distribution patterns on the bracts seem to be adaptations for wind and adhesive dispersal (Davidse 1987).

INFLORESCENCE DIVERSITY—The synflorescence of *Digitaria* usually consists of a main axis and a variable number of primary branches ("long paraclades") along the proximal portion (Rua 2003). Both the primary branches and the distal portion of the main axis bear grouplets of two, three or more spikelets or, more rarely, solitary spikelets ('short paraclades', see below). The number of long paraclades and their length relative to that of the main axis is responsible for the overall appearance of the inflorescence, which can vary from a more or less panicle to a typically digitate one. Therefore, the genus is appropriately named. Some evolutionary patterns can be traced upon the tree topologies, e.g. diverse

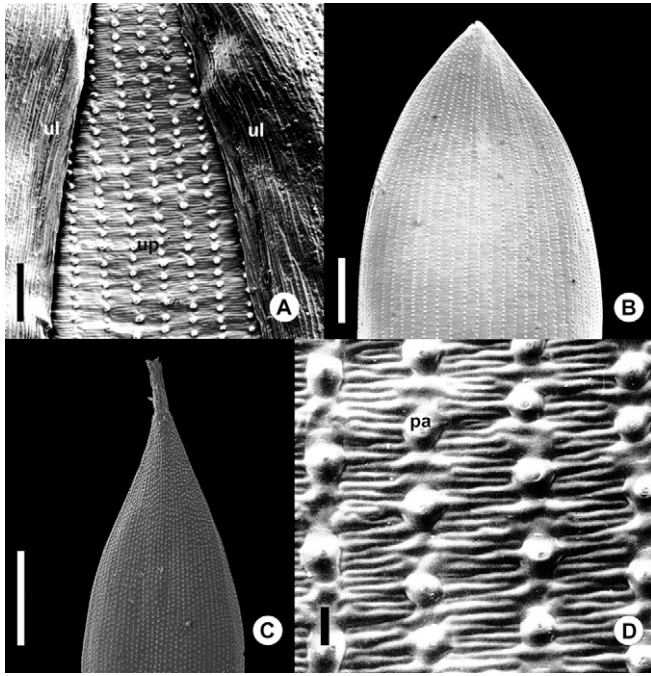


FIG. 6. Upper floret. SEM photographs. A. Middle portion, view from the back of the upper palea. Note membranous and flat margins of the upper lemma. [*D. bonplandii*, Hassler 11927 (G)]. Bar = 100 μ m. B–C. Upper middle, view from the back of the upper lemma: B. Apex acute. [*D. ternata*, Nicora 8746 (SI)]. Bar = 250 μ m. C. Apex acuminate. [*D. californica* var. *villosissima*, Parodi 14052 (BAA)]. Bar = 500 μ m. D. Upper lemma epidermis [*D. violascens*, Dusén 15176 (G)]. Bar = 10 μ m. References: pa. Papilla; ul. Upper lemma; up. Upper palea.

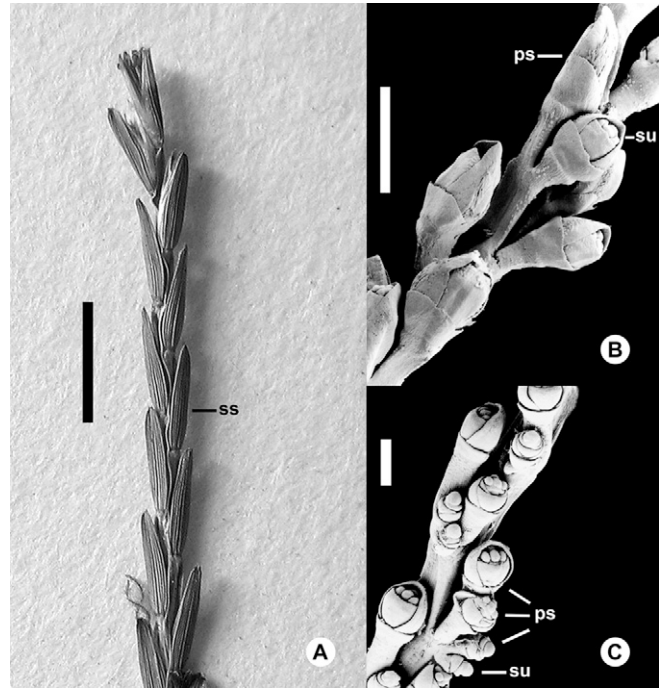


FIG. 7. A–C. Spikelet grouping. Portion of the main axis bearing short paracladia composed of 1–4 axes of successive branching order. SEM photographs. A. Solitary spikelets [*D. mariannensis*, Metzner 45 a (L)]. Bar = 0.3 mm. B. In pairs, composed of one subsessile and other pedicellate young spikelets [*D. sacchariflora*, Rua et al. 34 (BAA)]. Bar = 0.5 mm. C. In triads or more: one subsessile and three pedicellate young spikelets. [*D. phaeotrix*, Rua s.n. (BAA 22205)]. Bar = 0.25 mm. References: ss. Solitary spikelet; su. Subsessile spikelet; ps. Pedicellate spikelet.

degrees of truncation of the main axis occur in the clade of *D. sanguinalis* and relatives, elongation of internodes and pedicels occur among the *Pennatae* and *D.* subg. *Leptoloma*, and solitary as well as ternate spikelets arose from plesiomorphic binate short paraclades. The morphological diversification of inflorescences in *Digitaria* will be extensively revisited in an ongoing paper (G. H. Rua and A. S. Vega, unpubl. results).

SPIKELET GROUPING—The spikelets of *Digitaria* can be solitary (Fig. 7A) or, more usually, grouped in pairs (Fig. 7B) or triads/tetrads (Fig. 7C), arranged as ‘short paraclades’ (Weberling et al. 1993) along the main axis and the primary branches of the inflorescences.

As stated above, Hackel (1901) divided the genus in three series, according to spikelet grouping. Binate spikelets are plesiomorphic within *Digitaria*. Single, sessile spikelets occur in a few species (Henrard’s subgenus *Solitaria*), of which only one species was included in our analysis. They are clearly apomorphic within the genus and they seem to have evolved from binate spikelets through reduction. Short paraclades composed of three or more spikelets are also apomorphic, and they seem to have arisen at least two times during inflorescence diversification, although a unique acquisition of this character was favored under $k = 18.2$ – 19.5 .

LEAF ANATOMY FEATURES—Leaf anatomy has been fragmentarily studied in the genus *Digitaria* (Rúgolo de Agrasar and Sánchez 1989). Anatomical studies have referred to leaf blades in transverse section, epidermis in paradermal view, and features related to the type of photosynthetic pathway (Metcalfé 1960; Ellis 1977; Brown 1977; Webster 1983, 1987; Renvoize 1987; Rúgolo de Agrasar and Sánchez 1989). The typical photosynthetic pathway among *Digitaria* species is C_4 NADP-

ME. Ellis (1977) doubtfully mentioned two African species representative of *D.* sect. *Flaccidulae* as possible PCK species (one, *D. nitens*, was included here), based on the absence of Kranz sheaths in lateral primary bundles and their progressive development toward the median bundle. This characteristic is not typical of PCK type species (Hattersley 1987). The PCK photosynthetic pathway is apparently restricted to a clade of Paniceae containing *Urochloa* and related genera (Giussani et al. 2001), and *Digitaria* sect. *Flaccidulae* is probably not closely related. Other anatomical leaf characters included in our analysis were highly homoplastic.

GROWTH FORM FEATURES—The growth form of a plant is determined by a particular combination of vegetative features (Mühlberg 1967; Meusel 1970; Rua and Gróttola 1997), some of which are frequently underscored in taxonomic treatments. Ancestral growth form reconstruction includes perenniality, short rhizomes sheltered by cataphylls, and erect culms, i.e. a character syndrome for *Digitaria* sect. *Trichachne* (Rua 2003). Annuality is apomorphic in *Digitaria*, and restricted to members of the [*Digitaria* + *Ternatae*] clade (Fig. 4D), as well as lacking cataphylls, whereas decumbent or creeping culms are synapomorphic for the core-*Digitaria*.

Although our analysis allow us to gain some insight into the evolution of morphological characters in *Digitaria*, character evolution hypotheses should be considered cautiously until they can be tested by a phylogeny using molecular data.

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- APPENDIX 1. Taxa of *Digitaria* and outgroups considered in this study including at least one representative specimen used for anatomical observations.
- Anthraenantia lanata* (Kunth) Benth., *G. H. Rua & Boccaloni 151* (BAA 22785). *Echinochloa pyramidalis* (Lam.) Hitchc. & Chase, *G. H. Rua s.n.* (BAA 22207). *Panicum repens* L., *G. H. Rua et al. 270* (BAA 22959). *Urochloa brizantha* (Hochst. ex A. Rich.) R. D. Webster, *G. H. Rua et al. 68* (BAA 22682). *Digitaria abyssinica* (Hochst. ex A. Rich.) Stapf, *R. Pohl 11386* (US). *D. aequiglumis* (Hack. & Arechav.) Parodi, *A. Da Silva 2520* (BAA). *D. ammophila* (F. Muell.) Hughes, *Thompson GAL191* (CANB). *D. angolensis* Rendle, *M. Reekmans 9850* (BAA). *D. arenicola* (Swallen) Beetle, *J. Swallen 10588* (US). *D. argillacea* (Hitchc. & Chase) Fernald, *J. Reeder & C. Reeder 4445* (US). *D. argyrostachya* (Steud.) Fernald, *W. Harris 11413* (US 755154). *D. argyrotricha* (Anderss.) Chiov., *G. H. Rua 526* (BAA). *D. atra* Luces emend A. S. Vega & Rúgolo, *Müller s.n.* (VEN 222492). *D. badia* (Scribn. & Merr.) Fernald, *G. & J. Davidse 9904* (BAA). *D. balansae* Henrard, *G. Davidse et al. 11001* (MO). *D. bicornis* (Lam.) Roem. & Schult., *G. H. Rua et al. 272* (BAA); *G. H. Rua et al. 561* (BAA). *D. bonplandii* Henrard, *Gottsberger 1021-80R-16371* (MO). *D. botriostachya* Stapf, *A. McKinnon S. 65* (UB). *D. brownii* (Roem. & Schult.) Hughes, *R. Roe 502* (CANB); *R. Pullen & Galore 4688* (CANB). *D. californica* (Benth.) Henrard, *L. R. Parodi 13982* (BAA). *D. catamarcensis* Rúgolo, *T. Killeen 1571* (SI). *D. cayoensis* Swallen, *C. L. Lundell 6670* (K, US). *D. chaseae* Henrard, *A. Chase 10764* (US). *D. ciliaris* (Retz.) Koeler, *Vera Santos 7561* (L). *D. coenocola* (F. Muell.) Hughes, *W. Moir s.n.* (CANB). *D. cognata* (Schult.) Pilg., *J. Lerew Kan-2-175* (US). *D. curvirovis* (Hack.) Fernald, *E. Ekman 1049* (AAU, C, K, P). *D. debilis* (Desf.) Willd., *Sampaio s.n.* (WU 2071). *D. diagonalis* (Nees) Stapf, *G. H. Rua 536* (BAA). *D. divaricatissima* (R. Br.) Hughes, *C. Hubbard 5350* (CANB); *C. Hubbard 5071* (CANB). *D. eppersii* (Hack.) Henrard, *Proctor 48361* (SJ, US). *D. eriantha* Steud.,

- Z. Rúgolo 2118* (SI). *D. eriostachya* Mez, *B. Rosengurt 5461* (BAA). *D. fragilis* (Steud.) Luces, *A. Chase 10833* (MO). *D. fuscescens* (J. Presl) Henrard, *Sarmento s.n.* (BAA). *D. gazensis* Rendle, *G. Davidse et al. 6515* (BAA). *D. gerdessii* (Hack.) Parodi, *G. Davidse et al. 11385* (MO). *D. gymnostachys* Pilg., *K. L. Tinley 598* (PRE); *R. P. Ellis 3644* (PRE). *D. heterantha* (Hook. f.) Merr., *Kondo & Edaño s.n.* Phil. Nat. Herb. 36605 (L). *D. hitchcockii* (Chase) Steuck., *J. Roybal 48* (US 1935901). *D. horizontalis* Willd., *G. H. Rua et al. 72* (BAA). *D. insularis* (L.) Fedde, *Krapovickas & Schinini 31450* (BAA). *D. junghuhniana* (Nees ex Steud.) Henrard, *Kievih 1701* (L). *D. katangensis* Robyns, *M. Reekmans 5954* (BAA). *D. laxa* (Rchb.) Parodi, *T. Meyer 2562* (BAA). *D. lecardii* (Pilg.) Stapf, *Meinzingen & Conert 549* (LIL). *D. leiantha* (Hack.) Parodi, *A. Schinini et al. 8322* (BAA, LIL). *D. maitlandii* Stapf & C. E. Hubb., *M. Reekmans 6778* (BAA). *D. mariannensis* Merr., *J. Metzner 45 a* (L). *D. melanochila* Stapf, *H. Schlieben 4644* (UB). *D. minutiflora* Stapf, *J. Lambson 78/234* (BAA). *D. mollicoma* (Kunth) Henrard, *Lugd. Batav. s.n.* (L). *D. monodactyla* (Nees) Stapf, *E. van Jaarsveld 83* (PRE). *D. nitens* Rendle, *R. Davies 2951* (SI). *D. nodosa* Parl., *J. Duvoigneud 77* (BAA). *D. parviflora* (R. Br.) Hughes, *C. Hubbard 5923* (L). *D. patens* (Swallen) Henrard, *E. Bongsch 5-214* (US). *D. pearsonii* Stapf, *P. Ndabaneze 3* (BAA). *D. pennata* (Hochst.) T. Cooke, *M. Gilbert 1649* (UB). *D. perrottetii* (Kunth) Stapf, *P. Ndabaneze 48* (BAA). *D. phaeotrix* (Trin.) Parodi var. *hackelii* (Arechav.) Henrard, *G. H. Rua & I. B. Boccaloni 159* (BAA). *D. pittieri* (Hack.) Henrard, *P. Standley 35968* (US); *O. Jimenez L. 707* (US). *D. pubiflora* (Vasey) Wipff, *A. S. Hitchcock 5157* (US). *D. sacchariflora* (Nees) Henrard, *Seidel 2704* (SI); *G. H. Rua et al. 34* (BAA). *D. sanguinalis* (L.) Scop., *G. H. Rua s.n.* (BAA 24590). *D. similis* Beetle ex Gould, *Seidel & Vargas 2119* (SI). *D. suaillantiana* Henrard, *A. Schulz 4013* (CTES). *D. tenuis* (Nees) Henrard, *R. Smith 5313* (VEN). *D. ternata* (A. Rich.) Stapf, *G. H. Rua 525* (BAA). *D. thouaresiana* (Flügge) Camus, *M. Reekmans 9945* (BAA). *D. violascens* Link, *A. Chase 8520* (BAA).

APPENDIX 2. Morphological characters used for phylogenetic analysis.

1. Inflorescence primary branches.
2. Depth of epidermal cell indentations.
3. Epidermal cell width.
4. Spikelet length [mm].
5. Spikelet-width [mm].
6. Anther length [mm].
7. Spikelet, hair apex: not dilated [0], slightly dilated [1], dilated (claviform hairs) [2].
8. Spikelet, hair apex: acute [0], apiculate-rounded [1], rounded [2].
9. Spikelet, hair walls: smooth [0], verrucose [1].
10. Spikelet, hair apex: straight [0], curved [1].
11. Spikelet, hair length: up to 2 mm [0], 3–5 mm [1].
12. Spikelet, hair pigmentation: silver-white [0], isabelline [1], brownish [2].
13. Spikelet, purple-tinged hairs: wanting [0], present [1].
14. Spikelet, first rachilla internode: elongated [0], inconspicuous [1].
15. Spikelet, second rachilla internode: elongated [0], inconspicuous [1].
16. Spikelet position: Upper lemma abaxial [0], Upper lemma adaxial [1].
17. Spikelet compression: biconvex [0], plano-convex [1], dorsiventrally flattened [2].
18. Lower glume, whether present or not: wanting [0], present [1].
19. Lower glume, shape: truncate, reduced to a rim [0], ovate, acute [1], obtuse [2], bi-lobed, very short and tiny [3].
20. Lower glume, margins: not clasping [0], stem-clasping at the base [1], clasping, with overlapping margins [2].
21. Lower glume texture: membranous [0], hyaline [1].
22. Lower glume, number of nerves: many-nerved [0], 3-nerved [1], without nerves [2].
23. Upper glume, number of lateral veins on each glume half: 0 [0], 1 [1], 2 [2], 3 or more [3].
24. Upper glume, apex: acuminate [0], acute [1], obtuse [2].
25. Upper glume, relative length: obsolete [0], shorter than the lower lemma [1], (sub)equal to the lower lemma [2], longer than the lower lemma [3].
26. Upper glume, relative width: wider than the upper floret, the glume covers the upper floret sides [0], narrower than the upper floret (upper floret laterally visible) [1].
27. Upper glume indumentum: wanting [0], present [1].
28. Upper glume, distribution of indumentum: pilose throughout [0], alternate, inner internervial spaces pilose [1], pilose between margins and outer veins, otherwise glabrous [2], alternate, inner internervial spaces glabrous [3], distal portion pilose [4].
29. Upper glume, scabrousness of nerves: smooth [0], scabrous [1].
30. Upper glume, distribution of nerves: equidistant [0], unequidistant, lateral nerves contiguous [1].
31. Upper glume, distal convergence of lateral nerves: not convergent [0], convergent [1].
32. Lower lemma, number of lateral veins on each lemma half: 1 [0], 2 [1], 3 [2], 4 or more [3].
33. Lower lemma, apex: acuminate [0], acute [1], obtuse [2], apiculate [3].
34. Lower lemma, texture: papyraceous [0], membranous [1], hyaline [2], cartilaginous [3].
35. Lower lemma, indumentum: wanting [0], present [1].
36. Lower lemma, distribution of indumentum: pilose between margins and outer veins, otherwise glabrous [0], alternate, inner internervial space glabrous [1], inner internervial space glabrous, otherwise pilose [2], all internervial spaces fringed with hairs [3], pilose throughout [4].
37. Lower lemma, scabrousness of nerves: smooth [0], scabrous [1].
38. Lower

lemma, pectinate bristles: lacking [0], present in subsessile and pedicellate spikelets [1], present in pedicellate spikelets only [2]. **39.** Lower lemma, vein distribution: equidistant [0], unequidistant, lateral nerves contiguous [1], unequidistant, three central nerves contiguous [2]. **40.** Lower lemma, distal convergence of lateral veins: not convergent [0], convergent [1]. **41.** Lower lemma, axillary flower: lacking [0], reduced to a palea [1], male-fertile [2]. **42.** Upper floret, abscission: not occurring [0], occurring [1]. **43.** Upper floret, lemma apex: closed [0], open [1]. **44.** Upper floret, lemma texture: membranous [0], cartilaginous with membranous margins [1], crustaceous [2]. **45.** Upper floret, lemma and palea surface: smooth [0], papillose [1]. **46.** Upper floret, disposition of lemma margins: enrolled around the palea [0], folded upon the palea [1]. **47.** Upper floret, short, stiff prickles towards lemma apex: wanting [0], present [1]. **48.** Upper floret, pigmentation at maturity: stramineous to ochraceous [0], brown [1], dark purple [2]. **49.** Upper floret, relative length: longer than the lower lemma [0], (sub)equal to the lower lemma [1], shorter than the lower lemma [2]. **50.** Upper floret, apex: acute [0], acuminate [1], obtuse [2], apiculate [3]. **51.** Upper floret, nerves of the upper lemma: 3 nerves distinguishable [0], 5 nerves distinguishable [1], 7 nerves distinguishable [2]. **52.** Flower, pigmentation of anthers: yellow [0], purplish [1]. **53.** Flower, pigmentation of stigmata: pale [0], purplish [1]. **54.** Caryopsis, outline: elliptical/oblong [0], obovate [1], orbicular [2]. **55.** Caryopsis, pigmentation: pale [0], brown [1]. **56.** Reproduction, cleistogamy: none [0], occurring [1]. **57.** Inflorescence, distribution of LPc along the main axis: racemes always alternate [0], proximal racemes (frequently) verticillate [1], distal racemes conjugate, otherwise alternate [2]. **58.** Inflorescence, relative length of primary order branches: decreasing towards apex [0], about the same length throughout [1], longer at the middle, inflorescence fusiform [2]. **59.** Inflorescence, length of racemes relative to main axis: racemes not reaching the apex [0], the lowermost racemes (almost) reaching the apex [1], racemes overtopping the apex [2]. **60.** Inflorescence, orientation of LPc: ascending [0], spreading [1], rigidly horizontal [2]. **61.** Inflorescence abscission as tumbleweed: not occurring [0], occurring [1]. **62.** Inflorescence, homogenization: paniculate [0], proximally paniculate, homogenized distally [1], kPc homogeneous throughout [2]. **63.** Inflorescence, main florescence (= terminal spikelet) and distal kPc: wanting [0], present [1]. **64.** Inflorescence, long paraclades: wanting [0], present [1]. **65.** Inflorescence, phyllotaxis: distichous [0], polystichous [1]. **66.** Inflorescence, second order long paraclades: wanting (occasionally a reduced secondary LPc on the proximal raceme) [0], regularly present [1]. **67.** Inflorescence, pulvini at the base of racemes: inconspicuous (lacking?) [0], conspicuous, bulky [1]. **68.** Inflorescence, pulvini at the base of pedicels: lacking [0], present [1]. **69.** Inflorescence, peduncle indumentum: glabrous [0], distally hirsute [1], hirsute throughout [2]. **70.** Inflorescence, rachis of racemes: trichetrous [0], narrowly winged [1]. **71.** Inflorescence, rachis indumentum: glabrous to scabrous [0], hirsute [1], ventrally pubescent [2]. **72.** Inflorescence, pedicel development: very brief, spikelets subsessile [0], developed, normal [1], extraordinarily developed [2]. **73.** Inflorescence, pedicel indumentum: glabrescent [0], scabrous to antrorse-echinulate (more-than-scabrous) [1], puberulous [2], hirsute/ciliolate [3]. **74.** Inflorescence, pedicel apex (sensu Webster 1983): truncate [0], cupuliform [1], discoid [2]. **75.** Inflorescence, coronula at the apex of pedicels: lacking [0], composed of short hairs [1], composed of long cilia [2]. **76.** Inflorescence, (the more frequent) number of spikelets per node: one [0], two [1], three or more [2]. **77.** Inflorescence, pedicel con-

crease: pedicels free [0], pedicels conrescent with the rachis [1]. **78.** Inflorescence, whether (sub)sessile or pedunculate racemes: (sub)sessile [0], with long peduncles [1]. **79.** Inflorescence, relative length of raceme internodes: short (less than twice the length of the spikelets) [0], long (more than twice the length of the spikelets) [1]. **80.** Growth form, life cycle: annual [0], perennial [1]. **81.** Growth form, branching of culms: unbranched [0], branched [1]. **82.** Growth form, growth direction of culms: orthotropous to geniculate [0], decumbent [1], plainly plagiotropous, stoloniferous [2]. **83.** Growth form, internode indumentum: glabrous [0], distally hirsute [1]. **84.** Growth form, stypochitum: wanting [0], present [1]. **85.** Growth form, leaf sequence along tillers: the prophyll is followed by cataphylls [0], the prophyll if followed by foliage leaves [1]. **86.** Leaves, pubescence of cataphylls: glabrous [0], pubescent [1]. **87.** Growth form, direction of growth in the innovation zone: orthotropous [0], mainly orthotropous, but shortly plagiotropous proximally [1], plainly plagiotropous [2]. **88.** Growth form, rhizome internodes: all internodes short [0], elongated in the plagiotropous portion, distally shortened [1], all elongated [2]. **89.** Growth form, accessory innovation zones along the culm: lacking [0], present [1]. **90.** Growth form, transition from short to long internodes: abrupt [0], gradual [1]. **91.** Growth form, culm internodes: hollow [0], solid [1]. **92.** Leaves, leaf sheath indumentum: glabrous [0], pubescent/pilose [1]. **93.** Leaves, prefoliation: convolute [0], conduplicate [1]. **94.** Leaves, indumentum of the ligular region: glabrous [0], hirsute/pubescent [1]. **95.** Leaves, ligule outline: truncate [0], acute [1], obtuse [2]. **96.** Leaves, ligule margin: entire [0], irregular, erose [1]. **97.** Leaves, type of ligule: entirely membranous [0], membranous with a ciliate margin [1], ciliate, without a conspicuous membranous portion [2]. **98.** Leaves, ligule development: well developed, conspicuous [0], reduced to an inconspicuous ridge [1]. **99.** Leaves, leaf blade outline: narrowly lanceolate, acuminate [0], lanceolate [1], filiform [2]. **100.** Leaves, leaf blade consistence: papiraceous [0], coriaceous [1]. **101.** Leaves, mature leaf blade exposition: plane [0], involute [1]. **102.** Leaf anatomy, midrib: differentiate, distinct [0], undifferentiate [1]. **103.** Leaf anatomy, adaxial papillae: lacking [0], present [1]. **104.** Leaf anatomy, adaxial prickles on rib zones: lacking [0], present [1]. **105.** Leaf anatomy, abaxial prickles on rib zones: lacking [0], present [1]. **106.** Leaf anatomy, differentiation of costal and intercostal adaxial regions: undifferentiate [0], slightly noticeable [1], noteworthy [2]. **107.** Leaf anatomy, differentiation of costal and intercostal abaxial regions: undifferentiate [0], slightly noticeable [1], noteworthy [2]. **108.** Leaf anatomy, location of bulliform cells: only adaxial [0], both adaxial and abaxial [1]. **109.** Leaf anatomy, colorless parenchyma associated to midrib: adaxial [0], both adaxial and abaxial [1], none [2]. **110.** Leaf anatomy, macrohairs: lacking [0], present [1]. **111.** Leaf anatomy, crystals in chlorenchymatous cells: lacking [0], present [1]. **112.** Leaf anatomy, abaxial microhairs: lacking [0], present [1]. **113.** Leaf anatomy, adaxial microhairs: lacking [0], present [1]. **114.** Leaf anatomy, chlorenchyma arrangement: diffuse [0], radiate [1]. **115.** Leaf anatomy, cell layers forming radiate chlorenchyma: one layer [0], more than one [1]. **116.** Leaf anatomy, shape of chlorenchymatous cells: tabular [0], isodiametric [1]. **117.** Leaf anatomy, chlorenchymatous cells between radiate chlorenchyma: lacking, radiate chlorenchyma of contiguous bundles in contact [0], present, separating radiate chlorenchyma of contiguous bundles [1]. **118.** Leaf anatomy, abaxial papillae: lacking [0], present [1]. **119.** Leaf anatomy, photosynthetic pathway: C3 [0], NADPme [1], PCK or PCK-like NADme [2].