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PHYLOGENETIC RELATIONSHIPS OF THE DECUMBENTES GROUP OF *PASPALUM*, *THRASYA*, AND
THRASYOPSIS (POACEAE: PANICOIDEAE: PANICEAE)

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ABSTRACT

Paspalum (Poaceae: Panicoideae: Paniceae) includes 330 species distributed mainly in tropical and subtropical regions of America. Due to the large number of species and convergence in many characters, an adequate infrageneric classification is still needed. Studies on Paniceae based on molecular and morphological data have suggested that *Paspalum* is paraphyletic, including the genus *Thrasya*, but none of these analyses have included a representative sample of these two genera. In this study, phylogenetic relationships among the informal group Decumbentes of *Paspalum*, plus subgenera and other informal groups, and the genera *Thrasya* and *Thrasyopsis* were estimated. A cladistic analysis under parsimony was performed using a matrix of 50 taxa and 77 morphological and anatomical characters. Different analytical parameters were explored, equally weighing characters and employing implied weights by varying the concavity constant, k , from 1 to 12. Almost all analyses showed that species of the Decumbentes group and *Thrasya* form a natural group, supported by the presence of axillary peduncles in the upper foliar sheath, the upper glume slightly shorter than the spikelet, margins of the lower lemma plicate on the upper antherium, and the upper antherium without simple papillae. The position of *Thrasyopsis* is not clear because it varies within the different analyses. The most important clades are discussed as well as diagnostic characters usually employed to distinguish the genera.

Key words: Decumbentes group, Paniceae, Panicoideae, *Paspalum*, phylogeny, Poaceae, *Thrasya*, *Thrasyopsis*.

INTRODUCTION

Poaceae include ca. 650 genera and 10,000 species distributed worldwide (Clayton and Renvoize 1986) and are one of the five largest plant families. Grasses are important ecologically, prominent in many plant communities. Many species are of economic importance in the Americas, e.g., *Zea mays* L., *Sorghum bicolor* (L.) Moench, *Saccharum officinarum* L., *Panicum miliaceum* L., *Pennisetum glaucum* (L.) R. Br., and *Setaria italica* (L.) P. Beauv., all members of subfamily Panicoideae.

Paspalum L. belongs to tribe Paniceae of subfamily Panicoideae. The genus comprises ca. 330 species (Zuloaga and Morrone 2005) of which 308 grow in tropical and subtropical regions in the Americas (Zuloaga et al. 2003). Major centers of species diversity include central and southern Brazil, eastern Paraguay, northeastern Argentina, Mexico, and the Andean region (Chase 1929; Pohl 1980; Nicora and Rúgolo de Agrasar 1987; Zuloaga et al. 2007). Species are found in many different habitats, including savannas, forests, and forest margins, and dry, sandy, saline, or waterlogged soils. Reaching 4500 m in elevation, some species grow in mountainous regions, such as *P. candidum* (Humb. & Bonpl.) Kunth and *P. pygmaeum* Hack. Others grow in cold-temperate regions of Patagonia, e.g., *P. dasyleurum* Kunze ex Desv., *P. distichum* L., and *P. vaginatum*. Several species are considered excellent forage, *P. dilatatum* Poir. (“pasto miel”), *P. guenoarum* Arechav. (“pasto Rojas”), *P. notatum* Flügge (“pasto horqueta”), and *P. urvillei* Steud. (“paja boba”).

Paspalum is characterized by racemose, unilateral inflo-

rescences, plano-convex, solitary or paired spikelets, the lower glume commonly absent, the upper glume and lower lemma herbaceous to membranous, and the upper antherium indurate to membranous. The genus includes small to robust perennial, rarely annual, herbs that are usually cespitose, but may creep via rhizomes or stolons, and have filiform to lanceolate leaf blades, which may be flat, plicate, or involute. Physiologically, all species of *Paspalum* are C₄, of the NADP-ME subtype and anatomically MS (Hattersley and Watson 1976; Brown 1977).

Due to the high number of species and the large morphological variation present within the genus, *Paspalum* has been divided into subgenera, sections, or informal groups, mainly on the basis of morphological characters of the inflorescence and spikelets (Nees von Esenbeck 1829; Döll 1877; Chase 1927, 1929; Pilger 1929, 1940; Clayton and Renvoize 1986; Cialdella et al. 1995; Morrone et al. 1995, 1996, 2000, 2004; Denham et al. 2002; Denham 2005; Zuloaga et al. 2004, 2005). Chase (1929), in her study of *Paspalum* of North America, recognized two subgenera and 27 informal groups of species. According to this classification, the Decumbentes group, the focus of the present paper, is characterized by the upper foliar sheaths having terminal and axillary inflorescences, racemes usually solitary, spikelets paired, the lower glume larger in the lower spikelet of the pair, the lower palea usually present, and the lower flower developed or not. Species in the group have been suggested to be related to other genera of Paniceae, such as *Thrasya* Kunth and *Thrasyopsis* Parodi, on the basis of morphological characters (Chase 1911; Burman 1983, 1987; Davidse and Burman 1987; Burman and Bastos 1988). Recent molecular

phylogenetic studies in Panicoideae (Giussani et al. 2001), Paniceae (Duvall et al. 2001), and the genus *Panicum* L. (Aliscioni et al. 2003), as well as cladistic studies in *Paspalum* based on morphological and anatomical data (Aliscioni 2002), suggest that *Paspalum* is paraphyletic, with species of *Thrasya* embedded within.

The purpose of this work is to estimate phylogenetic relationships among all species of the Decumbentes group, *Thrasya*, and *Thrasypopsis* through a cladistic analysis using morphological and anatomical data. Previous phylogenetic studies lack a complete sample of the Decumbentes group and *Thrasya*, and none of them include *Thrasypopsis*. Characters broadly used in taxonomy are discussed in a phylogenetic context.

Taxonomic Overview

The Decumbentes group includes species that initially were classified in *Panicum* due to the presence of an evident lower glume. Fournier (1875) established the genus *Dimorphostachys* E. Fourn. in which he included species with the lower glume present in the lower spikelet of a spikelet pair and absent or rudimentary in the upper spikelet; i.e., species in which the lower spikelet resembles *Panicum* and the upper spikelet resembles *Paspalum*. Chase (1929) included *Dimorphostachys* in *Paspalum* within the informal Decumbentes group.

The genus *Thrasya* was established by Kunth (1816) based on *T. paspaloides*. However, he misinterpreted the morphology of the spikelet, not observing the first glume and treating the upper glume and lower lemma both as glumes, and the lower flower as having only a developed palea. Trinius (1826, 1834) and Nees von Esenbeck (1829) placed *Thrasya* as a synonym of *Panicum*. Chase (1911) accepted *Thrasya* as a genus and discussed Kunth's (1816) erroneous interpretation of the spikelet. She distinguished *Thrasya* from *Panicum* and *Paspalum* by a set of characters, including the inflorescence strictly racemose, spikelets alternate, the lower lemma indurate, splitting or deeply sulcate, the upper antherium cartilaginous, and the upper lemma with flat margins. She suggested that *T. campylostachya*, *T. cultrata* (Trin.) Nees, and *Paspalum monostachyum* are related and share a common ancestor, but she considered the two *Thrasya* species to be closer to the typical species of *Thrasya*, and *P. monostachyum* to be more closely related to *P. unispicatum*. Later, Burman (1987), in his taxonomic revision of *Thrasya*, divided it into three informal groups based on level of specialization. Group I, with the most specialized species, is characterized by elongate pedicels that are adnate to the rachis, and "back to back," elliptical-lanceolate spikelets, and includes *T. auricoma*, *T. glaziovii*, *T. granitica*, *T. paspaloides*, *T. petrosa*, *T. robusta*, *T. schumannii* (Pilg.) Pilg., *T. seminuda* A. G. Burm., *T. setosa*, *T. stricta*, *T. thrasyooides*, and *T. trinitensis*. Group II includes less specialized species that also have spikelets "back to back" on the rachis, but they differ from Group I species by their elliptical-ovate spikelets and a membranous lower lemma (vs. subindurate); this group includes *T. achlyosphila* Sodrestr., *T. parvula* A. G. Burm., and *T. scandens*. Species in Group III ("unstable species") are *T. campylostachya* and *T. hitchcockii*, which show a combination of long, adnate

pedicels and "back to back" spikelets ("thrasyoide" arrangement) with spikelets having an "in and out" or "paspaloide" arrangement on free and paired pedicels. Burman (1987) stated that the two Group III species should remain in *Thrasya* in spite of these ambiguous features. He also made reference to species with "latent instability," such as *T. robusta*, with specimens that have racemes with both "thrasyoide" and "paspaloide" organization. Davidse and Burman (1987), when describing *T. mosquitiensis*, mentioned that *Thrasya* is a difficult genus to circumscribe due to morphological characters that are intermediate between species of this genus and those of the Decumbentes group of *Paspalum*. Burman and Bastos (1988) suggested that *Dimorphostachys* should be reinstated and expanded to accommodate species with dimorphic lower glumes that were previously treated in *Paspalum* and *Thrasya*, specifically *P. cinerascens*, *P. unispicatum*, *T. cultrata*, and *T. reticulata* Swallen.

Thrasypopsis is a small South American genus with two species, *T. juergensii* and *T. repanda*, both endemic to southern Brazil. *Thrasypopsis* was established by Parodi (1946), who characterized the genus as follows: raceme solitary and unilateral, rachis foliaceous, spikelets paired, obtuse, and arranged in four rows on the rachis, with the back of the antherium positioned against the rachis or towards the center of the rows, lower glume one- to five-nerved, less than half the length of the spikelet to squamiform and nerveless, upper glume rigid, obtuse or truncate, multinerved, the nerves prominent. Parodi (1946) distinguished *Thrasypopsis* from *Panicum* by its obtuse or truncate upper glume (vs. acute or obtuse) and unilateral raceme (vs. a panicle). He also compared his new genus to *Thrasya* and *Paspalum* subgen. *Ceresia* (Pers.) Rchb., all having a membranous raceme rachis, but with *Thrasya* differing by having a three-nerved, membranous upper glume and the lower lemma splitting with maturity, while species of subgen. *Ceresia* differ by having a three-nerved, herbaceous upper glume. Finally, Parodi (1946) mentioned similarities between *Thrasypopsis* and the Decumbentes group of *Paspalum*, in particular with *P. monostachyum* and *P. unispicatum*, both species differing from *Thrasypopsis* in the non-membranous rachis of the racemes, the rudimentary lower flower, and the five-nerved, herbaceous upper glume. Burman (1980) related *Thrasypopsis* to species of the Decumbentes group and *Thrasya* by morphological characters such as dimorphic lower glumes. Later, Burman (1983) revised *Thrasypopsis* and associated the genus with *Thrasya* by the presence of foliaceous racemes, and to *Thrasya*, *Paspalum cinerascens*, *P. pilosum*, and *P. unispicatum* by the prominent lower palea present in all of these taxa.

Phylogenetic Relationship between *Paspalum* and *Thrasya*

Recent phylogenetic studies utilizing molecular data bear out a close relationship between *Paspalum* and *Thrasya*. Giussani et al. (2001) reconstructed the phylogeny of Panicoideae based on the chloroplast gene *ndhF*. For this study, the authors selected two representatives from the genus *Thrasya*, *T. glaziovii*, and *T. petrosa*, and nine species of *Paspalum* from different informal groups, though none belonging to the Decumbentes group. The *ndhF* phylogeny

showed that *Paspalum* is paraphyletic, with *Thrasya* embedded within it in a highly supported clade. Duvall et al. (2001) reached the same conclusion through a phylogenetic analysis of Paniceae using sequences from the chloroplast gene *rpoC2*, including two species of *Thrasya*, *T. glaziovii* and *T. petrosa*, and three species of *Paspalum*, *P. fimbriatum* Kunth, *P. quadrifarium* Lam., and *P. scrobiculatum* L. In addition, Aliscioni et al. (2003) carried out a phylogenetic study of *Panicum* using *ndhF* sequences, and obtained a highly supported *Paspalum* + *Thrasya* clade.

Aliscioni (2002) conducted a phylogenetic study of *Paspalum* based on morphological and anatomical characters. She included representatives of several informal groups of *Paspalum*, and *T. paspaloides* as an outgroup member. Her analysis showed that *Paspalum* is paraphyletic owing to species of *Thrasya* and *Axonopus* P. Beauv. nested within.

MATERIALS AND METHODS

Sampling

Ingroup.—Seventeen species of the Decumbentes group were sampled: *Paspalum adoperiens*, *P. altsonii*, *P. botterii*, *P. cinerascens*, *P. cultratum*, *P. decumbens*, *P. dispar*, *P. hintonii*, *P. inconstans*, *P. monostachyum*, *P. nutans*, *P. peckii*, *P. petilum*, *P. pilosum*, *P. subfalcatum*, *P. unispicatum*, and *P. variabile*. A list of representative specimens studied is given in Table 1.

Outgroup.—Outgroup selection followed Nixon and Carpenter (1993); i.e., taxa sampled share potential synapomorphies with the ingroup. Therefore, the following taxa were sampled:

(1) *Anthaenantiopsis fiebrigii* and *Panicum obtusum*. In the *ndhF* phylogeny an *Anthaenantiopsis* + *Panicum obtusum* clade is sister to *Paspalum* + *Thrasya*, part of a major clade characterized by a base chromosome number of $x = 10$ (Giussani et al. 2001). *Panicum obtusum* shares with *Paspalum* and *Thrasya* the C_4 , NADP-ME photosynthetic type and spikelets unilaterally arranged on the racemes. Morrone et al. (1993) related *Anthaenantiopsis* to some species of *Paspalum* by the contracted or slightly open inflorescences, solitary or paired, pilose spikelets, indurate upper antherium, and the C_4 , NADP-ME photosynthetic type.

(2) Other informal groups or subgenera of *Paspalum*. Sampled were *P. acuminatum* and *P. dissectum* from the Dissecta group; *P. alnum* from the Alma group; *P. cromoerhizon* from the Notata group; *P. flavum* and *P. prostratum* from the Racemosa group; *P. vaginatum* from the Disticha group; and *P. humboldtianum*, *P. polyphyllum*, and *P. stellatum* from subgen. *Ceresia*.

(3) *Thrasyopsis*. This genus has been linked, as previously mentioned, with the Decumbentes group by having an evident lower palea (Burman 1983) and dimorphic lower glumes (Burman 1980). Both species were sampled.

(4) *Thrasya*. Eighteen out of 22 species (Burman 1987; Davidse and Burman 1987; Burman and Bastos 1988; Judziewicz 1990; Killeen 1990) were included in the analysis: *T. auricoma*, *T. axillaris*, *T. campylostachya*, *T. crucensis*, *T. glaziovii*, *T. granitica*, *T. hitchcockii*, *T. longiligulata*, *T. mosquiensis*, *T. oreophila*, *T. paspaloides*, *T. petrosa*, *T. robusta*, *T. scandens*, *T. setosa*, *T. stricta*, *T. thrasyoides*, and *T. trinitensis*. The unsampled species *T. achlysochyla*, *T.*

parvula, and *T. schumannii* are only known from type material, and specimens of the rarely collected *T. seminuda* also were not available. Morphological and anatomical data for these four species were not fully available from the literature. Consequently, with the aim of minimizing the amount of missing data in the matrix, they were not included in the analysis.

(5) *Steinchisma laxa*. This species is a C_3 representative of the $x = 10$ clade of Paniceae (Giussani et al. 2001; Aliscioni et al. 2003), and was selected for rooting the trees.

Representative specimens of the outgroup taxa are provided in Table 1.

Characters

Seventy-seven qualitative characters, 62 exomorphological and 15 anatomical, were used in the cladistic analyses. The data were obtained from herbarium specimens and live plants. For anatomical data, segments were taken from the middle third of the second leaf blade below the inflorescence; hand-cut transverse sections and the epidermis were observed with optical microscopy. Antherium micromorphology was observed using a Zeiss 940 scanning electron microscope following the procedures described by Soderstrom and Zuloaga (1989). The list of characters and character states is provided in Appendix 1. The data matrix is shown in Appendix 2.

Cladistic Analysis

Maximum parsimony analyses (Farris 1983) were performed on the matrix of 50 taxa and 77 characters (the 22 multistate characters were treated as unordered) using TNT vers. 1.0 (Goloboff et al. 2003). Autapomorphies were excluded from the analyses. Analyses with all characters weighted equally detected high levels of homoplasy; consequently, analyses under implied weights were also carried out. Goloboff (1993) stated that because not all characters provide equally strong evidence (some display a lot of homoplasy while others are perfectly hierarchical), trees obtained from properly weighted characters are preferable. His method of implied weights consists of estimating character weights according to their homoplasy. Goloboff (1993) defined "character fit" as a concave function of its homoplasy (i.e., number of extra steps) and trees with maximum total fit are searched for. The "fittest tree" implies that the characters are maximally reliable and, given character conflicts, they are solved in favor of those characters that have less homoplasy. The degree of the concave function can be modified in TNT through the constant k , where higher values of k weight less strongly against characters with homoplasy. When using implied weights it is not clear how much a homoplastic character should be down-weighted; therefore, values of 1–6, 8, 10 and 12 were explored. Using equal weights and implied weights with many concavities is a way of exploring the data under different and independent analytical parameters (Aagesen and Sanso 2003), and the robustness of a group across a range of parameters can be used to confirm monophyly (Wheeler 1995).

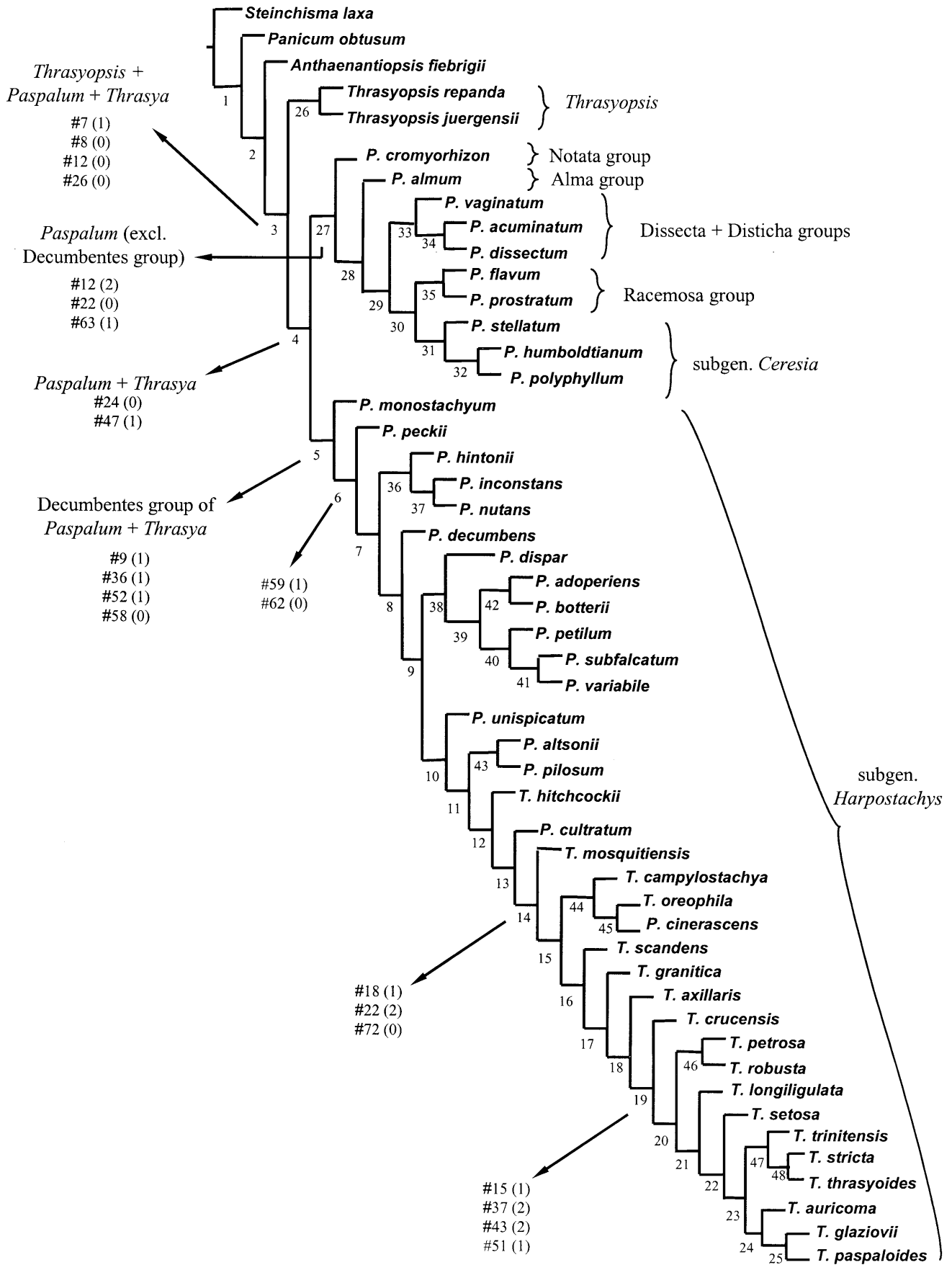
Heuristic searches were performed; in all analyses 1000 initial Wagner trees were constructed using a random-addition sequence, swapping each with tree-bisection-reconnec-

Table 1. Taxa and representative specimens employed in this study. Asterisks designate members of the Decumbentes group of *Paspalum*.

| Taxon | Origin | Voucher |
|-----------------------------------------------------------|---------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------|
| <i>Anthraenantiopsis fiebrigii</i> Parodi | Argentina, Jujuy | <i>Cabrera et al.</i> 32666 (SI) |
| <i>Panicum obtusum</i> Kunth | USA, Arizona | <i>Gould</i> 2889 (SI) |
| <i>Paspalum acuminatum</i> Raddi | Argentina, Tucumán | <i>Venturi</i> 699 (SI), <i>Lillo</i> 38377 (SI) |
| * <i>P. adoperiens</i> (E. Fourn.) Chase | El Salvador, La Paz El Salvador, San Salvador El Salvador, Santa Ana | <i>Pohl & Gabel</i> 13642 (MO) <i>Standley</i> 23596 (US) <i>Pohl</i> 12586 (MO) |
| <i>P. alnum</i> Chase | Paraguay, Central Paraguay, Presidente Hayes | <i>Zardini & Tillería</i> 29180 (SI) <i>Quarín</i> 4049 (SI) |
| * <i>P. altsonii</i> Chase | Guyana, Kaieteur Savannah Guyana, Kanuku Guyana, Nappi-haed | <i>Sandwith</i> 1381 (US) <i>Jansen-Jacobs et al.</i> 1231 (US) <i>Jansen-Jacobs et al.</i> 690 (US) |
| * <i>P. botterii</i> (E. Fourn.) Chase | Belize, Toledo Costa Rica, Guanacaste Venezuela, Lara | <i>Gentle</i> 6882 (US) <i>Pohl & Davidse</i> 10546 (MEXU), <i>Pohl & Lucas</i> 13076 (MO) <i>Burkart</i> 16630 (SI) |
| * <i>P. cinerascens</i> (Döll) A. G. Burm. & C. N. Bastos | Brazil, Distrito Federal Brazil, Mato Grosso Venezuela, Anzoátegui | <i>Irwin et al.</i> 12994 (CTES, MO) <i>Philcox et al.</i> 3085 (MO) <i>Montes</i> 3141 ^a (MO) |
| <i>P. cromyrorhizon</i> Trin. ex Döll | Argentina, Corrientes Brazil, Rio Grande do Sul | <i>Nicora</i> 4629 (SI) <i>Burkart</i> 25051 (SI) |
| * <i>P. cultratum</i> Trin. | Brazil, Minas Gerais | <i>Glaziou</i> 20562 (US), <i>Duarte</i> 5068 (US), <i>Chase</i> 10229 (US) |
| * <i>P. decumbens</i> Sw. | Brazil, São Paulo Colombia, Amazonas Peru, Loreto | <i>Rosengurt et al.</i> 3399 (US) <i>Giraldo-Cañas et al.</i> 2716 (SI), <i>Gasche & Desplats</i> 109 (G) <i>Ferreyra</i> 17178 (US) |
| * <i>P. dispar</i> Chase | Dominican Republic, Costanza Dominican Republic, La Vega Dominican Republic, Santiago | <i>Liogier</i> 15976 (US) <i>Davidse</i> 2626 (MO) <i>Gould & Jimenez</i> 10896 (US) |
| <i>P. dissectum</i> L. | USA, Mississippi | <i>Rogers</i> 2502 (SI) |
| <i>P. flavum</i> J. Presl | Peru, Lima | <i>Ferreyra</i> 8758 (SI), <i>Sullivan</i> 844 (SI) |
| * <i>P. hintonii</i> Chase | Mexico, Jalisco Mexico, Nayarit | <i>Santana & Llorente</i> 3808 (MEXU) <i>Rzedowski</i> 17858 (US), <i>McVaugh</i> 19109 (US) |
| <i>P. humboldtianum</i> Flügge | Argentina, Catamarca Argentina, Córdoba Argentina, Jujuy | <i>Joergensen</i> 1765 (LIL, MO, SI, US) <i>Burkart</i> 10211 (SI), <i>Stuckert</i> 14159 (CORD, G, MO, SI) <i>Burkart & Troncoso</i> 11014 (SI) |
| * <i>P. inconstans</i> Chase | Bolivia, La Paz Brazil, Santa Catarina Colombia, Antioquia | <i>Hitchcock</i> 22609 (US) <i>Smith & Reitz</i> 9659 (US) <i>Barkly et al.</i> 130 (US) |
| * <i>P. monostachyum</i> Vasey | USA, Florida USA, Louisiana USA, Texas | <i>Mosier</i> 250 (US) <i>Rudolph</i> 83 (US) <i>Cory</i> 45679 (US) |
| * <i>P. nutans</i> Lam. | Brazil, São Paulo Colombia, Antioquia Colombia, Chocó | <i>Eiten & Eiten</i> 6066 (MO, P, US) <i>Brant & Betancur</i> 1629 (MO, SI) <i>Gentry et al.</i> 16846 (MO) |
| * <i>P. peckii</i> F. T. Hubb. | Belize, Manatee Lagoon | <i>Peck</i> 71 (isotype US-2942524) |
| * <i>P. petilum</i> Chase | Guyana Venezuela, Amazonas | <i>Cowan & Soderstrom</i> 2215 (US) <i>Steyermark & Holst</i> 130484 (MO), <i>Liesner</i> 24975 (MO, US) |
| * <i>P. pilosum</i> Lam. | Bolivia, Santa Cruz Brazil, Amazonas | <i>Killeen et al.</i> 5451 (MEXU, MO, SI) <i>Spruce</i> 22 (G, US), <i>Harley et al.</i> 17387 (K, MO) |
| <i>P. polyphyllum</i> Nees ex Trin. | Argentina, Chaco Bolivia, La Paz | <i>Meyer</i> 2090 (LIL), <i>Schulz</i> 17275 (G, MO, SI) <i>Cárdenas</i> 3606 (US) |
| <i>P. prostratum</i> Scribn. & Merr. | Mexico, Hidalgo Venezuela, Lara | <i>Pringle</i> 8891 (SI) <i>Davidse & González</i> 21366 (SI) |

Table 1. Continued.

| Taxon | Origin | Voucher |
|---------------------------------------------------------------|-------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------|
| <i>P. stellatum</i> Humb. & Bonpl. ex Flügge | Argentina, Chaco Brazil, Amazonas Brazil, Distrito Federal | Schulz 300 (LIL) Myers 3404 (US) de Jesus 16 (US) |
| * <i>P. subfalcatum</i> (Döll) Tutin | Brazil, Amazonas Venezuela, Amazonas | Baldwin 3564 (US) Liesner 17160 (MO, US), Thomas et al. 3454 (MO) |
| * <i>P. unispicatum</i> (Scribn. & Merr.) Nash | Argentina, Tucumán Bolivia, Chuquisaca | Rodríguez 258 (SI), Venturi 2322 (SI) Saravia Toledo & Joaquín 10536 (SI) |
| <i>P. vaginatum</i> Sw. | Brazil, Paraná Brazil, Rio Grande do Sul | Dusén 13783 (SI) Barreto 73 (SI) |
| * <i>P. variabile</i> (E. Fourn.) Nash | Mexico, Chiapas Mexico, Hidalgo Mexico, Puebla | Breedlove 11035 (US) Moore 3487 (US) Aragón 192 (MEXU) |
| <i>Steinchisma laxa</i> (Sw.) Zuloaga | Costa Rica, Limón Peru, Loreto | Stevens et al. 24680 (SI) Vásquez et al. 3023 (SI) |
| <i>Thrasya auricoma</i> A. G. Burm. | Brazil, Pará | Silva et al. 92 (MO, US) |
| <i>T. axillaris</i> (Swallen) A. G. Burm. ex Judz. | Venezuela, Amazonas | Liesner & Delascio 22186 (SI, US) |
| <i>T. campylostachya</i> (Hack.) Chase | Bolivia, La Paz Colombia, Cauca Guatemala, Alta Verapaz | Hitchcock 22694 (US) Zuloaga & Londoño 4188 (SI) Cook & Griggs 289 (US) |
| <i>T. crucensis</i> Killeen | Bolivia, Santa Cruz | Killeen 1819 (MO, US) |
| <i>T. glaziovii</i> A. G. Burm. | Brazil, Distrito Federal Brazil, Goiás | Filgueiras & Zuloaga 2193 (SI), Irwin et al. 15348 (US) Glaziou 22433 (US) |
| <i>T. granitica</i> A. G. Burm. | Suriname, Voltzberg | Schulz & Donselaar 10581, 10617 (US) |
| <i>T. hitchcockii</i> Chase | Panama, Panamá Venezuela, Distrito Federal | Dwyer 2563A (MO) Chase 12403 (US), Woronow 7408 (US) |
| <i>T. longiligulata</i> C. N. Bastos & A. G. Burm. | Brazil, Pará | Sperling et al. 5583 (MO, US) |
| <i>T. mosquitiensis</i> Davidse & A. G. Burm. | Honduras, Gracias a Dios Nicaragua, Comarca del Cabo | Nelson & Cruz 8621 (MEXU) Seymour 5803 (MO) |
| <i>T. oreophila</i> A. G. Burm. | Brazil, Minas Gerais | Irwin et al. 27989 (MO) |
| <i>T. paspaloides</i> Kunth | Venezuela, Amazonas Venezuela, Bolívar | Davidse 2743 (US) Holst & Werff 2599 (US), Guánchez & Huber 4844 (SI) |
| <i>T. petrosa</i> (Trin.) Chase | Brazil, Pará Venezuela, Bolívar Venezuela, Portuguesa | Anderson 10782 (US) Werff & Holst 7773 (SI) Burkart 17079 (SI) |
| <i>T. robusta</i> Hitchc. & Chase | Costa Rica, Puntarenas French Guiana, Sinnamary-Organabe Venezuela, Bolívar | Pohl & Davidse 10978 (US) Black et al. 17059 (US) Davidse et al. 4754 (MEXU) |
| <i>T. scandens</i> (Tutin) Soderstr. & A. G. Burm. | French Guiana, Oyapocha Guyana, Kaieteur Plateau | Hook 804 (US) Maguire & Fanshawe 23456 (MO, US), Cowan & Soderstrom 1821 (US) |
| <i>T. setosa</i> Swallen | Venezuela, Amazonas Venezuela, Bolívar | Huber 1281, 4752 (MO) Wurdack & Monacino 39984 (US) |
| <i>T. stricta</i> A. G. Burm. | Colombia, Meta Venezuela, Amazonas | Laegaard & Mayorga 17572 (SI) Huber 974 (US) |
| <i>T. thrasyoides</i> (Trin.) Chase | Brazil, Minas Gerais Brazil, Pará | Warming s. n. (US-1125903), Glaziou 20559 (US) Anderson 10909 (US) |
| <i>T. trinitensis</i> Mez | Honduras, Gracias a Dios Nicaragua, Zelaya Trinidad, Piarco Savanna Venezuela, Bolívar | Nelson & Vargas 5039 (MO) Stevens 8589 (US) Soderstrom 981 (US), 997 (SI, US) Zuloaga et al. 4422 (SI) |
| <i>Thrasyopsis juergensii</i> (Hack.) Soderstr. & A. G. Burm. | Brazil, Rio Grande do Sul Brazil, Santa Catarina | Valls et al. 1899 (US), Smith & Klein 15827 (US) Klein 4381 (US) |
| <i>T. repanda</i> (Nees ex Trin.) Parodi | Brazil, Distrito Federal Brazil, Paraná | Glaziou s. n. (US-1061564, Brasilia) Hatschbach 32956 (MO), Dusén 10478 (US) |



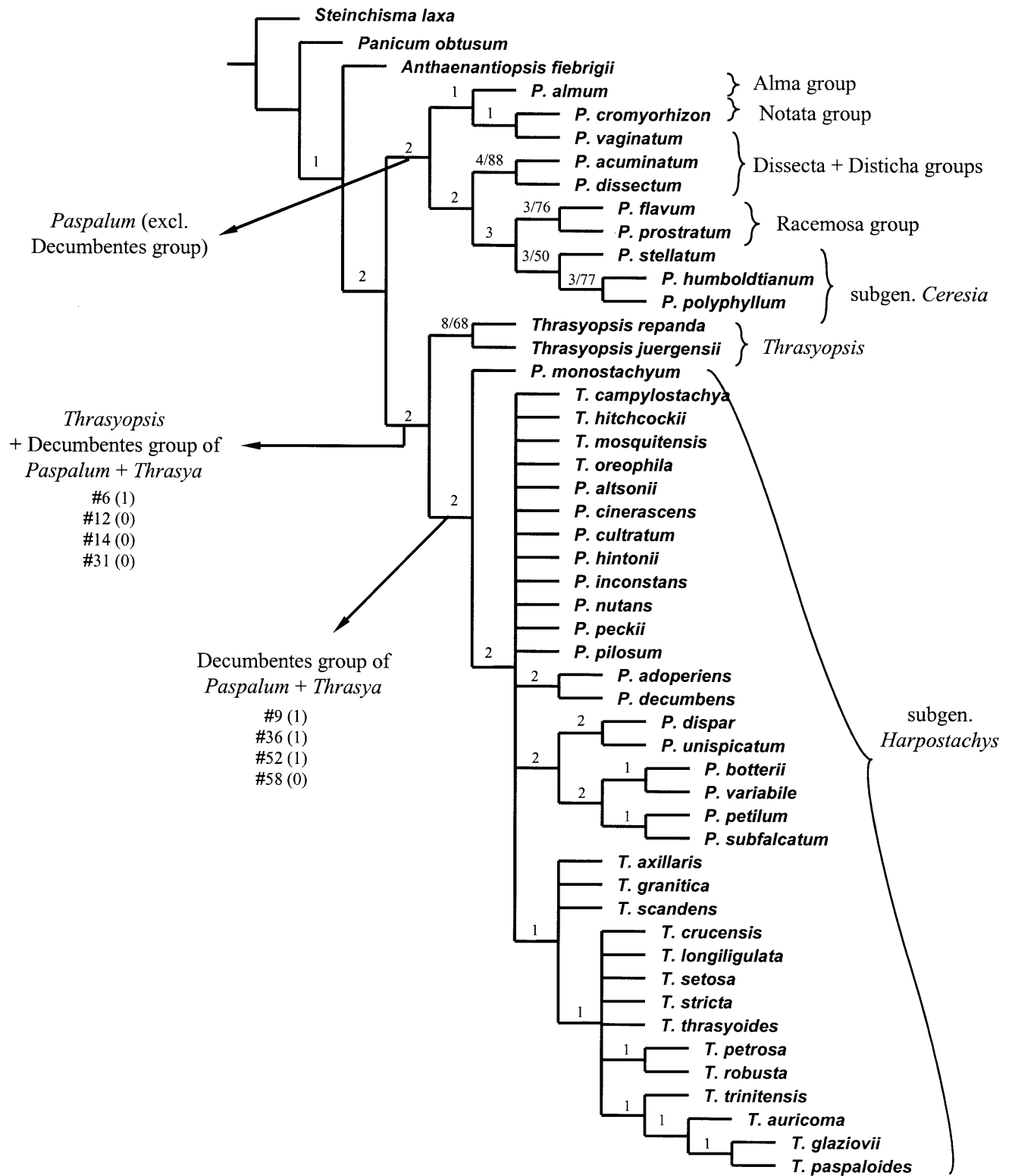


Fig. 2.—Strict consensus of 390 most-parsimonious trees found under equal weighting of characters. Numbers above branches are Bremer support values and jackknife frequencies. Clades and characters discussed in the text are indicated.

←

Fig. 1.—Most-parsimonious cladogram under implied weights with $k = 3$ (Goloboff 1993). Clades are numbered. Clades and characters discussed in the text are indicated. Apomorphies, Bremer support values, and jackknife frequencies are provided in Appendix 3.

tion (TBR), and retaining a maximum of five trees per replicate. In order to expand the tree searches, the resulting trees were swapped using one round of TBR. Bremer support (bs; Bremer 1994) and jackknife frequency values (Farris et al. 1996) were generated to estimate branch support. Bremer support was estimated on the basis of 20,000 trees of 1–20 steps longer and on 20,000 trees of 0.001–5 less fit. For the jackknife analyses, 1000 iterations were performed, randomly deleting 36% of the characters.

RESULTS

We mainly base our interpretations on the implied weights analyses, since this method is preferable in light of our homoplastic data set. Moreover, we highlight the tree obtained from the $k = 3$ analysis, which is the same as the tree obtained using $k = 2$ and 4. The $k = 5$ and 6 analyses produced nearly the same trees, only differing in the positions of *Paspalum dispar* and *Thrasya campylostachya*. Figure 1 displays the unique tree of maximum fit under implied weights with $k = 3$, with total fit = 38.07. Apomorphies for all nodes and taxa in Fig. 1, as well as Bremer support, are listed in Appendix 3.

Figure 1 shows a clade composed of *Paspalum* and *Thrasya* (clade 4). Sister to this clade is *Thrasyopsis*, and basal in the tree are *Panicum obtusum* and *Anthaenantiopsis fiebrigii*. Clade 4 comprises two subclades: clade 27, with *Paspalum* species of groups Notata, Alma, Dissecta, Disticha, Racemosa, and subgen. *Ceresia*, and clade 5 that includes species of the Decumbentes group and *Thrasya*, the latter clade with $bs = 0.06$, meaning that this clade is not present in suboptimal trees with a difference in total fit of 0.06.

Apomorphies shared by *Thrasyopsis* + *Paspalum* + *Thrasya* (Fig. 1, clade 3) are the presence of truncated and homocladic inflorescences (char. #7), nonhelical phyllotaxy of the racemes on the main axis (#8), one raceme per inflorescence (#12), and the lower glume of the upper spikelet of a pair with a wide base and obtuse apex (#26). The clade comprising all species of *Paspalum* and *Thrasya* (clade 4) is supported by plano-convex spikelets (#24) and nerves of the lower lemma not equidistant (#47). The Decumbentes group + *Thrasya* clade (clade 5) is supported by the presence of axillary peduncles in the upper foliar sheath (#9), upper glume slightly shorter than the spikelet (#36), margins of the lower lemma plicate on the upper antherium (#52), and by the absence of simple papillae on the upper antherium surface (#58). The remaining species of *Paspalum* are together in clade 27, based on the presence of three racemes per terminal inflorescence (#12), absence of the upper spikelet of a pair (#22), and by the involute margin of the leaf blade in transverse section (#63). Apomorphies shared by the Decumbentes group and *Thrasya*, excluding *P. monostachyum* (clade 6), are the presence of verrucose papillae (#59) and absence of silica bodies on the upper antherium (#62).

The analysis under equal weighting produced 390 equally parsimonious trees of 462 steps each. The strict consensus tree is shown in Fig. 2. All 390 trees support the monophyly of the Decumbentes group + *Thrasya*, with $bs = 2$ (i.e., suboptimal trees two steps longer do not possess this clade), and synapomorphies for that clade are also characters #9 (1), #36 (1), #52 (1), and #58 (0). However, in contrast to the

Table 2. The effect of character weighting on the monophyly of the Decumbentes group + *Thrasya* and *Thrasyopsis* + Decumbentes group + *Thrasya* in cladistic analyses.

| | Character weighting | Decumbentes group + <i>Thrasya</i> | <i>Thrasyopsis</i> + Decumbentes group + <i>Thrasya</i> |
|---------|---------------------|------------------------------------|---------------------------------------------------------|
| | $k = 1$ | — | — |
| | $k = 2$ | monophyletic | — |
| | $k = 3$ | monophyletic | — |
| | $k = 4$ | monophyletic | — |
| Implied | $k = 5$ | monophyletic | — |
| | $k = 6$ | monophyletic | — |
| | $k = 8$ | monophyletic | monophyletic |
| | $k = 10$ | monophyletic | monophyletic |
| | $k = 12$ | monophyletic | monophyletic |
| Equal | | monophyletic | monophyletic |

implied weights analyses with $k = 2$ –6, *Thrasyopsis*—not the clade comprising the remaining species of *Paspalum*—is sister to Decumbentes + *Thrasya*. The same, (i.e., a *Thrasyopsis* + Decumbentes + *Thrasya* clade), also was obtained from analyses using implied weights with $k = 8, 10,$ and 12 (Table 2).

Synapomorphies of the *Thrasyopsis* + Decumbentes + *Thrasya* clade (Fig. 2) are the presence of pseudogligule (char. #6), one raceme per terminal inflorescence (#12), racemes solitary (#14), and the lower glume of the lower spikelet of a pair with a wide base and obtuse apex (#31).

The analysis with $k = 1$ resulted in one tree of maximum fit, with *Anthaenantiopsis fiebrigii*, *Paspalum humboldtianum*, and *P. polyphyllum* positioned in the Decumbentes group + *Thrasya* clade.

DISCUSSION

Results of the cladistic analyses based on morphological and anatomical data point to a close relationship between *Thrasya* and *Paspalum*, which is consistent with previous findings based on molecular (Duvall et al. 2001; Giussani et al. 2001; Aliscioni et al. 2003) and morphological and anatomical (Aliscioni 2002) data. Specifically, species of *Thrasya* form a clade with species of the Decumbentes group of *Paspalum* (Fig. 1, 2). This confirms the monophyly of subgen. *Harpostachys* (Trin.) S. Denham of *Paspalum* (Denham 2005), which includes species of the Decumbentes group and *Thrasya*. New names and combinations for species of *Thrasya* under *Paspalum* subgen. *Harpostachys* are provided in Denham (2005).

The monophyletic subgen. *Harpostachys* has Bremer support values of 2 under equal weighting of characters and 0.06 under implied weights with $k = 3$, and lacks support based on jackknife frequencies. The relatively poor support of subgen. *Harpostachys* is not surprising since low support values are common when using morphological data. Nevertheless, almost all analytic parameters used in this study (except implied weights with $k = 1$, Table 2) maintained the *Harpostachys* clade, indicating that the clade is robust and well supported by the data (Wheeler 1995).

The following discussion of synapomorphies of the *Harpostachys* clade is based on the implied weights analysis

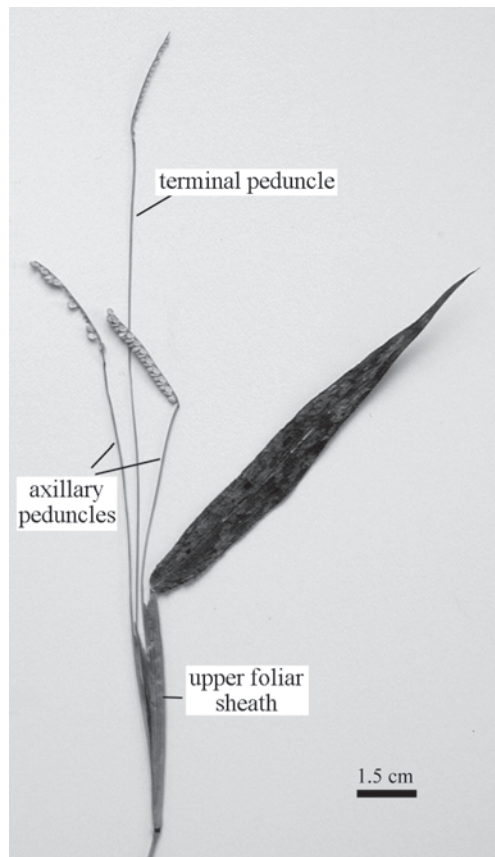


Fig. 3.—*Paspalum decumbens* (Ferreyra 17178). Upper foliar sheath with a terminal and two axillary peduncles and truncate inflorescences, each with a solitary raceme.

with $k = 3$ (Fig. 1, clade 5). The fit of each character is provided, representing the contribution of that character to the total fit of the tree; a character with a higher fit is more reliable and less homoplastic on the tree. Four synapomorphies (chars. #9, #36, #52, and #58) define the *Harpostachys* clade in this analysis:

(1) Presence of axillary peduncles in the upper foliar sheath (char. #9; Fig. 3; fit = 0.75). This character is helpful to identify species of the subgenus. The axillary peduncles form a cymose system of ramification and the prophylls of each peduncle can be observed within the foliar sheath. Nevertheless, axillary peduncles were not observed in *Thrasya stricta* (= *Paspalum huberi* S. Denham) and *T. thrasyoides* (= *P. thrasyoides* (Trin.) S. Denham), species in which a reversal of this character could have taken place.

(2) Upper glume slightly shorter than the spikelet (char. #36; Fig. 8; fit = 0.23). This character is polymorphic in several species and has many extra steps in the tree. Moreover, the reduction of the upper glume to one-half the length of the spikelet (Fig. 4) has occurred independently in *P. decumbens*, *P. hintonii*, *T. axillaris* (= *P. axillare* Swallen), and *T. stricta*.

(3) Margins of the lower lemma plicate on the upper antherium (char. #52; Fig. 4, 8; fit = 0.37). This feature reverses to absent in species of *Thrasya* where the lower palea and flower are present.

(4) Absence of simple papillae on the upper antherium

surface (char. #58; fit = 0.33). This character reverses in *T. axillaris*, *T. granitica* (= *P. graniticum* (A. G. Burm.) S. Denham), and *P. subfalcatum*, all having simple papillae (Fig. 14), and in *P. petilum*, which has no or simple papillae. The absence of simple papillae also occurs within the outgroup in *P. flavum* and *P. stellatum*. Excluding the species above and *P. monostachyum*, in the remaining species of subgen. *Harpostachys* the upper antherium has verrucose papillae (Fig. 11, 12). Indeed, this character (#59) supports clade 6 (Fig. 1), which only excludes *P. monostachyum*, having a smooth upper antherium (Fig. 13). However, the presence of verrucose papillae is not exclusive to subgen. *Harpostachys*, since it also occurs in other groups of *Paspalum*, e.g., in *P. guttatum* Trin. of the Eriantha group, and in *P. delicatum* Swallen, *P. gardnerianum* Nees, *P. nudatum* Luce, and *P. pictum* Ekman of the Gardneriana group (Morrone et al. 2004).

The presence of a lower glume is an attribute widely used to characterize species of the Decumbentes group, and it is also present in several species of *Thrasya*. The size of the lower glume varies intra- and interspecifically and its development can even vary in spikelets of a single raceme. This is reflected in the high degree of homoplasy found for characters #27 and #32. A lower glume occasionally can develop in some species of *Paspalum* outside subgen. *Harpostachys*. In species of the Bonplandiana group the bract is present in isolated spikelets (Cialdella et al. 1995); *P. glabrinode* (Hack.) Morrone & Zuloaga has dimorphic lower glumes in the paired spikelets (Zuloaga and Morrone 2005); *P. ammodes* Trin., *P. erianthoides* Lindm., and *P. erianthum* Nees ex Trin. of the Eriantha group (Morrone et al. 2004), and *P. filifolium* Nees ex Steud., *P. minus* E. Fourn., and *P. subciliatum* Chase of the Notata group (Zuloaga et al. 2004) are species in which the lower glume occasionally can be observed in some spikelets. Characters #27 and #32 do not support monophyly of the *Harpostachys* clade. These characters are more likely symplesiomorphies of subgen. *Harpostachys*, *Thrasyopsis*, *Anthaeantiopsis* Mez ex Pilg., and *Panicum*, while the loss of the lower glume can be explained as an evolutionary novelty for the remaining species of *Paspalum* here analyzed.

The presence of a lower palea (char. #53) has also been used to distinguish species of *Thrasya* and the Decumbentes group from the remaining species of *Paspalum*. The lower palea is present in all species of subgen. *Harpostachys* except for a few, including *P. monostachyum* (however, the character is not a synapomorphy of clade 6 [Fig. 1] because of its ambiguous optimization). As with the presence of a lower glume, the presence of a lower palea also should be considered a symplesiomorphy shared subgen. *Harpostachys* along with *Thrasyopsis*, *Anthaeantiopsis*, and *Panicum*, with the reduction of the palea being an independently derived state in the remaining species of *Paspalum*, *P. monostachyum*, *P. subfalcatum* + *P. variable*, and *T. axillaris*. Character #54, the presence or absence of a lower flower (Fig. 10), displays a similar optimization to that observed for character #53, but it is a synapomorphy for clade 39 (Fig. 1), comprising species in which the lower flower is not developed but the lower palea is sometimes present.

Characters commonly used to distinguish *Thrasya* define subclades in the optimal tree (Fig. 1) that do not include all

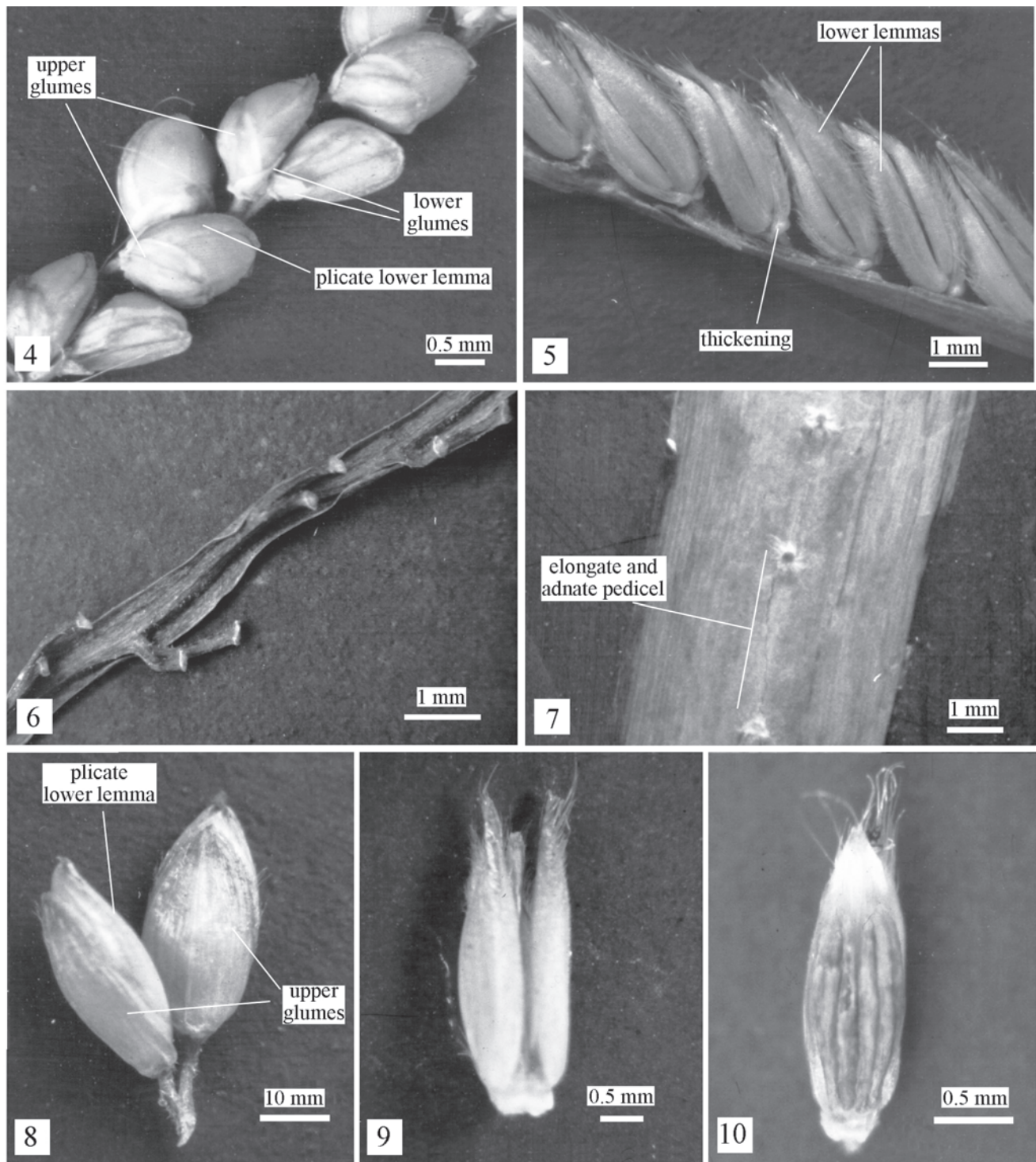


Fig. 4–10.—Spikelets and rachises of *Thrasya* and *Paspalum*.—4. *P. decumbens* (Ferreyra 17247, [US]). Spikelets in the “*Paspalum* type” position on the rachis, with dimorphic lower glumes and the lower lemma with the margins plicate on the upper antherium.—5. *T. trinitensis* (Soderstrom 997). Spikelets in the “*Thrasya*-type” position on the rachis, showing the lower lemma with the margins not plicate on the upper antherium and a thickening at the base of each spikelet (the winged rachis was partially removed).—6. *P. inconstans* (Hitchcock 22609). Rachis with pedicels free and not elongate.—7. *T. petrosa* (Anderson 10782). Foliaceous rachis with elongate pedicels, adnate to the rachis.—8. *P. inconstans* (Barkly et al. 130). Paired spikelets with the upper glume slightly shorter than the spikelet and plicate lower lemma.—9. *T. thrasyoides* (Glaziou 20559). Spikelet with splitting lower lemma.—10. *T. auricoma* (Silva et al. 92). Staminate lower flower.

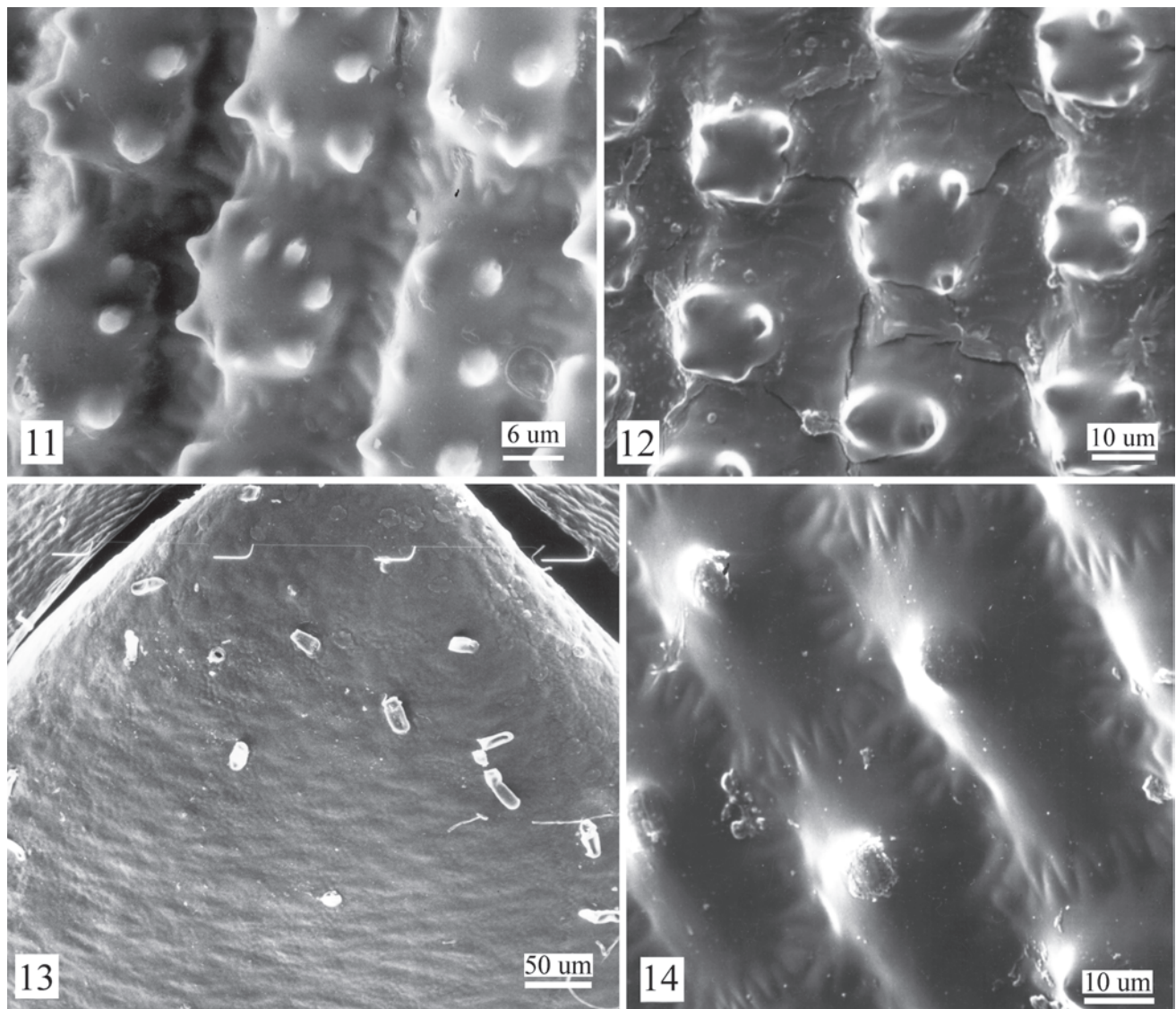


Fig. 11–14.—Upper anthercium. Surface of the palea.—11. *Thrasya trinitensis* (Soderstrom 981) showing verrucose papillae.—12. *Paspalum botterii* (Burkart 16630) showing verrucose papillae.—13. *Paspalum monostachyum* (Lundell & Lundell 14704, [US]) with smooth surface.—14. *P. petilum* (Steiermark 59455, [US]) showing simple papillae.

species of the genus. Thus, the “back to back” position of spikelets on the rachis (#22; Fig. 5) and pedicels adnate to the rachis (#18; Fig. 7) are synapomorphies of clade 14, whereas the lower lemma splitting at maturity (#51; Fig. 9) is a synapomorphy of clade 19. In addition, these are polymorphic or homoplastic characters. In *P. cinerascens*, *T. oreophila* (= *P. oreophilum* (A. G. Burm.) S. Denham), and *T. robusta* (= *P. robustum* (Hitcch. & Chase) S. Denham), the position of the spikelets on the rachis is polymorphic, while the lower lemma splitting at maturity and elongate, adnate pedicels can also be observed in other species of *Paspalum* such as *P. altsonii*, *P. cinerascens*, *P. cultratum*, *P. pilosum*, and *P. unispicatum*. Finally, these characters can be absent in less specialized species of *Thrasya*, such as *T. hitchcockii* (= *P. procerum* S. Denham), *T. mosquitiensis* (= *P. mosquitiense* (Davidse & A. G. Burm.) S. Denham), and *T. scandens* (= *P. scandens* Tutin).

Paspalum altsonii, *P. cinerascens*, *P. cultratum*, *P. pilo-*

sum, *P. unispicatum*, *T. campylostachya*, *T. hitchcockii*, *T. mosquitiensis*, *T. oreophila*, and *T. scandens* constitute species intermediate between *Paspalum* and *Thrasya*, and this is reflected by their positions in the most-parsimonious tree (Fig. 1).

In all optimal trees (except when using $k = 1$), *P. monostachyum* is in a basal position in the *Harpostachys* clade. This species differs from the remaining members of the clade in several features: when the lower glume is present, it is developed only in the upper spikelet of the pair; the lower palea and lower flower are absent; the upper anthercium is smooth, without papillae; and the culms are simple and without inflorescences in the subapical sheaths. In addition, several autapomorphies (not included in the analysis because they are uninformative) distinguish *P. monostachyum*: the leaf blade in transverse section is elliptical, and adaxially grooved; the raceme rachis is solid; and the pedicels are long-ciliate (Denham 2005).

The position of *Thrasypsis* varies among analyses. The genus could be sister to *Paspalum* + *Thrasya* (when using implied weighting with $k = 2-6$; Fig. 1) or sister to *Paspalum* subgen. *Harpstachys* (under equal weighting [Fig. 2] and implied weighting with $k = 8, 10, \text{ and } 12$). In all analyses that result in a *Thrasypsis* + subgen. *Harpstachys* clade synapomorphies are the presence of a pseudoligule (char. #6), one raceme per inflorescence (#12, #14), and the lower glume of the lower spikelet with a wide base and obtuse apex (#31). Inflorescences having a solitary raceme have arisen independently in many species and groups of *Paspalum* with low affinity, as a tendency toward the reduction and simplification of the inflorescence. Vegetti (1987) and Rua and Weberling (1995) considered inflorescences with one or two racemes to have evolved recently within *Paspalum*. *Thrasypsis* and several species of *Thrasya* share a foliaceous raceme rachis (char. #16); this character state appears as a parallelism in *Thrasypsis* and clade 14 of Fig. 1 (the character is not a synapomorphy of clade 14 because of its ambiguous optimization). In both genera, the rachis is usually broad and with conspicuous nerves that extend to the margins. This feature is also present in other species of *Paspalum*: a broad, foliaceous rachis is found in the Bonplandiana, Dissecta, Disticha, and Racemosa groups, while in subgen. *Ceresia* some species have a foliaceous rachis and others a winged rachis, with the margins hyaline and nerveless. The taxonomic value of this character within *Paspalum* has been studied (S. S. Aliscioni and S. S. Denham unpubl. data).

We conclude that species of the Decumbentes group and *Thrasya*, (= *Paspalum* subgen. *Harpstachys*) form a monophyletic group, and this is supported by a range of analytical parameters employed (except $k = 1$, which represents the deepest extreme on the concavity curve). The position of *Thrasypsis* within Paniceae remains unclear.

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APPENDIX 1. Morphological and anatomical characters and character states used in the cladistic analysis.

General

1. Life cycle: perennial (0), annual (1). Most species of *Paspalum* are perennial. Among the species included in the analysis, those of the Racemosa group are annual, as well as *Thrasya axillaris* and *T. longiligulata* (= *P. carajasense* S. Denham). Morrone et al. (1995) considered the annual cycle as a derived character within the genus, according to the evolutionary criteria proposed by Stebbins (1982), Watson and Dallwitz (1982), and Davidse (1987).
2. Decumbent culms: absent (0), present (1). The cespitose habit is most frequent in *Paspalum* (Rua and Weberling 1995), although several species have decumbent or crawling culms.
3. Branched culms: absent (0), present (1).
4. Culms: hollow (0), with spongy pith (1). This character is informative within the outgroup. *Paspalum vaginatum* of the Disticha group and *P. acuminatum* and *P. dissectum* of the Dissecta group have culms with spongy piths as an adaptation to aquatic or subaquatic habitats.
5. Basal internodes: glabrous (0), pilose (1).
6. Pseudoligule: absent (0), present (1).

Inflorescences

7. Truncate and homocladic inflorescences: absent (0), present (1) (Rua and Weberling 1995).
8. Racemes with helical phyllotaxy on the main axis: absent (0), present (1). In *Paspalum*, racemes are usually arranged on two orthostichies with a divergence angle of 180° (Rua and Weberling 1995).
9. Axillary peduncles in the upper foliar sheath: absent (0), present (1). In the Decumbentes group of *Paspalum* and in *Thrasya* it is frequent to observe two or more axillary inflorescences in the upper foliar sheath, forming a cymose system (Fig. 3).
10. Inflorescences in subapical or middle sheaths: absent (0), present (1). Besides the cymose system of peduncles in the apical or upper foliar sheath (char. 9), lateral inflorescences can develop from the subapical or middle sheaths.
11. Peduncles: glabrous (0), pilose (1).
12. Raceme number per terminal inflorescence: one (0), two (1), three (2), four (3), five or more (4). Species of the Decumbentes group and *Thrasya* usually have one raceme per inflorescence (Fig. 3).
13. Rachis disarticulating at maturity: absent (0), present (1). This character is a synapomorphy of the Racemosa group of *Paspalum*, where racemes fall together with spikelets (Morrone et al. 1995).
14. Arrangement of racemes: solitary (0), conjugate (1), subopposite (main axis ≤ 1 cm long between two consecutive racemes) (2),

alternate (main axis >1 cm long between two consecutive racemes) (3).

15. Rachis of the racemes: ending in a spikelet (0), ending in a naked point (1). All species of the Decumbentes group have a developed spikelet at the apex of the rachis, whereas in *Thrasya* this is a variable character.
16. Rachis of the racemes: triquetrous and without lateral extensions (0), with short lateral extensions (1), foliaceous (2). In *Paspalum* the rachis is commonly triquetrous, keeled on the upper surface and with pedicels on both sides of the keel. In certain species, the rachis has lateral extensions varying in development. A foliaceous rachis is predominate in *Thrasya* and *Thrasypopsis*.
17. Rachis of the racemes with densely pilose margins: absent (0), present (1).
18. Upper pedicel: free (0), adnate to the rachis 1/2–4/5 of its length (1), adnate to the rachis >4/5 of its length, except at the apex (2) (Fig. 6, 7).
19. Elongate upper pedicel: absent (0), present (1). The upper pedicel was considered elongate when it was at least four times longer than the lower one.
20. Membranous disc at the tip of the pedicel: absent (0), present (1). Present in *Thrasypopsis*.
21. Arrangement of spikelets at the base of the rachis: solitary (0), paired (1), in groups of three or more (2). Spikelets in *Paspalum* are solitary or paired, but sometimes the raceme bears, at its base, spikelets on ramifications of third or greater order.

Spikelets

22. Upper spikelet of a pair: absent (0), “*Paspalum* type” position (1), “*Thrasya* type” position (2). In *Paspalum*, when spikelets are paired, the upper glume of the upper spikelet faces the lower lemma of the lower spikelet, or it may be laterally located in relation to the lower spikelet (Fig. 4, 8). In *Thrasya* the “back to back” position occurs when the lower lemmas of the paired spikelets face each other (Fig. 5).
23. Shape: ellipsoid (0), widely ellipsoid to slightly obovoid (1), obovoid (2), suborbiculate (3).
24. Compression: plano-convex (0), biconvex (1), concavo-convex (2), biplanar (3).
25. Thickened base: absent (0), present (1). *Thrasya axillaris*, *T. crucensis* (= *P. crucense* (Killeen) S. Denham), *T. glaziovii* (= *P. glaziovii* (A. G. Burm.) S. Denham), *T. longiligulata*, *T. paspaloides* (= *P. orinocense* S. Denham), *T. petrosa* (= *P. foliiforme* S. Denham), *T. robusta*, *T. setosa* (= *P. setosum* (Swallen) S. Denham), *T. stricta*, *T. thrasyooides*, and *T. trinitensis* (= *P. trinitense* (Mez) S. Denham) have a thickening or callus at the base of the spikelet (Fig. 5). Davidse (1987) stated that the thickenings at the base of the spikelets of *T. petrosa* are elaiosomes. This could be related to spikelet dispersal in this species by ants, as occurs in other species in Paniceae (Morrone et al. 2000).

Lower Glume of the Upper Spikelet of the Pair

26. Shape: with a wide base and obtuse apex (0), triangular with an acute apex (1), lanceolate to acuminate (2), ovate (3).
27. Development: absent (0), minute or $\leq 1/6$ spikelet length (1), $1/6$ – $1/2$ spikelet length (2), $>1/2$ or subequal to length of the spikelet (3).
28. Position: concentric (0), excentric (1).
29. Pubescence: glabrous (0), pilose (1).
30. Number of nerves: nerveless (0), one (1), two (2), three (3), five (4).

Lower Glume of the Lower Spikelet of the Pair

Following Zuloaga et al. (2000), solitary spikelets are here considered homologous to the lower (or abaxial) spikelet of a pair, where the upper (or adaxial) one has been aborted.

31. Shape: with a wide base and obtuse apex (0), triangular with an acute apex (1), lanceolate to acuminate (2), ovate (3).
32. Development: absent (0), minute or $\leq 1/6$ spikelet length (1), $1/6$ – $1/2$ spikelet length (2), $>1/2$ or subequal to length of the spikelet (3).
33. Position: concentric (0), excentric (1).
34. Pubescence: glabrous (0), pilose (1).
35. Number of nerves: nerveless (0), one (1), two (2), five (3).

Upper Glume

36. Length: $\leq 1/2$ spikelet length (0), slightly shorter than the spikelet length ($1/2$ – $4/5$) (1), $>4/5$ and subequal to length of the spikelet (2).
37. Pubescence: glabrous (0), with delicate hairs (1), with rigid and conspicuous hairs (2).
38. Papillae: absent (0), present (1).
39. Number of nerves: two (0), three (1), five (2), seven (3), nine (4), more than nine (5), nerveless (6).
40. Arrangement of nerves: equidistant (0), not equidistant (1).
41. Nerves: not prominent (0), prominent (1).
42. Anastomosed veins at the apex: absent (0), present (1).

Lower Lemma

43. Pubescence: glabrous (0), with delicate hairs (1), with rigid and conspicuous hairs (2).
44. Apex with one or two hairs longer than the rest: absent (0), present (1).
45. Papillae: absent (0), finely papillose (papillae not covering the entire outer tangential cell wall) (1), papillose (papillae covering the entire outer tangential cell wall) (2).
46. Number of nerves: two (0), three (1), five (2), seven (3), nine (4).
47. Arrangement of nerves: equidistant (0), not equidistant (1).
48. Nerves: not prominent (0), prominent (1).
49. Anastomosed veins at the apex: absent (0), present (1).
50. Surface: not sulcate (0), sulcate (1).
51. Splitting at maturity: absent (0), present (1) (Fig. 9).
52. Margins plicate on the upper antherium: absent (0), present (1) (Fig. 4, 8).

Lower Palea and Flower

53. Lower palea: absent (0), present (1).
54. Staminate lower flower: absent (0), present (1) (Fig. 10).

Upper Antherium

55. Shape: ellipsoid (0), widely ellipsoid (1), obovoid (2).
56. Texture: membranous to hyaline (0), not membranous to hyaline (1). In *Paspalum* subgen. *Ceresia* and *Anthaeantiopsis* the antherium is membranous to hyaline.
57. Apex of the palea: not enclosed by the lemma (0), enclosed by the lemma (1). In *Paspalum* subgen. *Ceresia* and *Anthaeantiopsis fiebrigii* the antherium is gaping at the apex.
58. Simple papillae: absent (0), present (1) (Fig. 14).
59. Verrucose papillae: absent (0), present (1) (Fig. 11, 12).
60. Microhairs (2–4 cells): absent (0), present (1).
61. Unicellular macrohairs (including prickles): absent (0), present (1).
62. Silica bodies: absent (0), present (1).

Leaf Blade Anatomy

63. Blade margin: flat (0), involute (1), revolute (2).
64. Number of vascular bundles in central keel: one (0), three (1).
65. Carinate bundle in central keel: absent (0), present (1).
66. Distinguishable xylem and phloem in third-order vascular bundles: absent (0), present (1).
67. Position of third-order vascular bundles in transverse section: abaxially located (0), centrally located (1).

68. Complete mestome sheath in first-order vascular bundles: absent (0), present (1).
69. Mestome sheath of second-order vascular bundles with adaxial cells larger than abaxial cells: absent (0), present (1).
70. Bulliform cells in fan-shaped groups: absent (0), present (1).
71. Radiate mesophyll: absent (0), present (1).
72. Colorless parenchyma associated with bulliform cells: absent (0), present (1).
73. Distinctive Kranz cells: absent (0), present (1). Species of the *Racemosa* group of *Paspalum* possess a special anatomy among C₄ plants since the distance between consecutive vascular bundles is greater than four chlorenchyma cells, and groups of two or three distinctive Kranz cells are located among these chlorenchyma cells. The distinctive Kranz cells could be interpreted as highly reduced vascular bundles (Hattersley and Watson 1992). Distinctive Kranz cells also appear in the *Bonplandiana* group.
74. Epidermal cells associated with macrohairs modified in the form of a cushion base: absent (0), present (1).
75. Abaxial epidermis with excentric papillae having a thickened distal wall: absent (0), present (1).
76. Abaxial epidermis with papillae that occupy the entire outer tangential wall, not thickened: absent (0), present (1).
77. Prickles on the abaxial epidermis: absent (0), present (1).

Appendix 3. List of apomorphies for tree of maximum fit under weights with $k = 3$ (Fig. 1). Character state changes are shown for all terminal taxa and nodes. Character and character state descriptions are provided in Appendix 1. Bremer support (bs) and jackknife frequencies $\geq 50\%$ are indicated for each node.

Outgroup Taxa

Anthraenantiopsis fiebrigii: #17: 0→1, #29: 0→1, #34: 0→1, #36: 2→1, #37: 0→2, #43: 0→2, #56: 1→0, #57: 1→0, #66: 1→0, #70: 1→0
Panicum obtusum: #39: 2→3, #68: 0→1, #71: 0→1
Paspalum acuminatum: #66: 1→0
P. alnum: #23: 0→1, #55: 0→1, #60: 1→0
P. cromyrorhizon: #24: 0→3
P. dissectum: no autapomorphies
P. flavum: #38: 0→1, #45: 0→1, #52: 1→0, #58: 1→0, #60: 1→0
P. humboldtianum: no autapomorphies
P. polyphyllum: #10: 0→1, #17: 0→1, #43: 0→1, #61: 0→1
P. prostratum: #10: 0→1
P. stellatum: #3: 1→0, #6: 0→1, #12: 2→0, #14: 3→0, #23: 0→1, #46: 1→0, #55: 0→1, #58: 1→0
P. vaginatum: #12: 2→1, #14: 3→1, #72: 0→1, #77: 0→1
Thrasya auricoma: #25: 1→0, #39: 2→0, #46: 2→1, #52: 0→1, #64: 0→1, #68: 1→0, #70: 0→1, #72: 0→1, #74: 1→0
T. axillaris: #1: 0→1, #16: 2→0, #27: 1→0, #32: 1→0, #36: 1→0, #39: 2→6, #46: 2→1, #53: 1→0, #54: 1→0, #65: 0→1, #70: 1→0, #77: 0→1
T. campylostachya: #15: 0→1, #45: 0→1, #64: 0→1, #70: 1→0, #71: 0→1
T. crucensis: #6: 1→0, #40: 0→1, #46: 2→3, #71: 0→1, #75: 0→1
T. glaziovii: #40: 0→1, #47: 0→1, #69: 0→1, #77: 0→1
T. granitica: #16: 2→1, #38: 0→1, #45: 0→1, #62: 0→1
T. hitchcockii: #6: 1→0, #36: 1→2, #45: 0→1, #60: 1→0
T. longiligulata: #1: 0→1, #6: 1→0, #37: 2→0, #43: 2→0, #45: 0→1, #68: 1→0
T. mosquiensis: #75: 1→0
T. oreophila: #17: 0→1, #60: 1→0
T. paspaloides: #36: 1→2
T. petrosa: #27: 1→0, #63: 0→2, #64: 0→1, #71: 0→1
T. robusta: #35: 0→1, #37: 2→1, #39: 2→3, #43: 2→1, #60: 0→1, #77: 0→1
T. scandens: #52: 0→1, #63: 0→2, #70: 1→0, #71: 0→1
T. setosa: no autapomorphies
T. stricta: #2: 0→1, #6: 1→0, #17: 1→0, #37: 2→0, #46: 2→3, #74: 1→0
T. thrasyoidea: #3: 1→0, #60: 0→1, #64: 0→1, #69: 0→1, #70: 0→1
T. trinitensis: #31: 0→1, #33: 0→1, #54: 1→0, #71: 0→1
Thrasypopsis juergensii: #24: 1→2, #50: 0→1, #62: 1→0, #68: 0→1, #72: 0→1
T. repanda: #26: 0→3, #30: 0→4, #35: 0→3, #42: 0→1, #49: 0→1, #74: 0→1, #77: 0→1

Ingroup Taxa

Paspalum adoperiens: #23: 1→3, #55: 1→2, #65: 0→1, #74: 0→1
P. altsonii: #23: 1→0, #28: 0→1, #54: 1→0, #55: 1→0, #64: 0→1, #66: 1→0, #72: 1→0
P. botterii: #16: 0→1, #70: 0→1, #77: 0→1
P. cinerascens: #5: 0→1, #16: 2→0, #36: 1→2, #45: 0→2, #48: 0→1, #49: 0→1, #55: 0→12, #69: 1→0, #72: 0→1, #77: 0→1
P. cultratum: #2: 1→0, #5: 0→1, #26: 0→1, #27: 1→2, #45: 0→2, #69: 1→0
P. decumbens: #23: 1→2, #36: 1→0, #45: 0→1, #55: 1→2, #60: 1→0, #74: 0→1, #77: 0→1
P. dispar: #2: 1→0, #6: 1→0, #10: 1→0, #11: 0→1, #26: 0→1, #41: 0→1, #48: 0→1, #62: 0→1, #64: 0→1, #71: 0→1, #74: 0→1
P. hintonii: #36: 1→0, #38: 0→1, #45: 0→2, #48: 0→1, #61: 0→1, #71: 0→1, #75: 0→1
P. inconstans: #23: 1→0, #37: 0→1, #55: 1→0

P. monostachyum: #28: 0→1, #39: 2→1, #71: 0→1
P. nutans: #63: 0→2, #69: 1→0
P. peckii: #12: 0→12, #14: 0→2, #16: 0→1, #72: 0→1, #74: 0→1, #75: 0→1, #77: 0→1
P. petilum: #6: 1→0, #10: 1→0, #39: 2→1, #60: 1→0, #68: 0→1
P. pilosum: #38: 0→1, #45: 0→2, #74: 0→1
P. subfalcatum: #23: 1→0, #55: 1→0, #58: 0→1, #61: 0→1, #65: 0→1, #70: 0→1, #74: 0→1
P. unispicatum: #2: 1→0, #10: 1→0, #36: 1→2, #41: 0→1, #60: 1→0, #69: 1→0
P. variabile: #2: 1→0, #12: 0→123, #14: 0→3, #30: 0→2, #35: 1→2, #69: 1→0, #71: 0→1, #77: 0→1

Nodes

Node 2 (bs = 0.17): #19: 1→0, #58: 0→1
Node 3 (bs = 0.39): #7: 0→1, #8: 1→0, #12: 4→0, #26: 1→0
Node 4 (bs = 0.08): #24: 1→0, #47: 0→1
Node 5 (bs = 0.06): #9: 0→1, #36: 2→1, #52: 0→1, #58: 1→0
Node 6 (bs = 0.05): #59: 0→1, #62: 1→0
Node 7 (bs = 0.08): #2: 0→1, #3: 0→1, #23: 0→1, #55: 0→1, #69: 0→1
Node 8 (bs = 0.04): #27: 0→2, #32: 01→3, #33: 0→1
Node 9 (bs = 0.04): #31: 1→2
Node 10 (bs = 0.04): #24: 0→2, #50: 0→1, #72: 0→1
Node 11 (bs = 0.04): #11: 0→1, #27: 2→1, #32: 3→2, #70: 0→1
Node 12 (bs = 0.03): #40: 1→0, #75: 0→1
Node 13 (bs = 0.01): #23: 1→0, #55: 1→0
Node 14 (bs = 0.20): #18: 0→1, #22: 1→2, #72: 1→0
Node 15 (bs = 0.10): #19: 0→1
Node 16 (bs = 0.20): #11: 1→0, #31: 2→0, #32: 2→1, #33: 1→0, #35: 1→0
Node 17 (bs = 0.01): #75: 1→0
Node 18 (bs = 0.04): #2: 1→0, #25: 0→1, #60: 1→0
Node 19 (bs = 0.20, jackknife 50%): #15: 0→1, #37: 0→2, #43: 0→2, #51: 0→1
Node 20 (bs = 0.12): #18: 1→2, #36: 1→2
Node 21 (bs = 0.01): #70: 1→0
Node 22 (bs = 0.22, jackknife 61%): #27: 1→0, #44: 0→1
Node 23 (bs = 0.01): #17: 0→1, #36: 2→1
Node 24 (bs = 0.01): #6: 1→0, #11: 0→1
Node 25 (bs = 0.01): #45: 0→1, #60: 0→1
Node 26 (bs = 0.39): #11: 0→1, #16: 0→2, #20: 0→1, #39: 2→5, #46: 2→4, #48: 0→1, #75: 0→1
Node 27 (bs = 0.14): #12: 0→2, #22: 1→0, #63: 0→1
Node 28 (bs = 0.04): #2: 0→1, #3: 0→1
Node 29 (bs = 0.04): #52: 0→1, #71: 0→1
Node 30 (bs = 0.16): #39: 2→1, #40: 1→0, #46: 2→1, #47: 1→0, #66: 1→0
Node 31 (bs = 0.22): #37: 0→2, #56: 1→0, #57: 1→0, #74: 0→1
Node 32 (bs = 0.27): #21: 0→1, #22: 0→1, #75: 0→1
Node 33 (bs = 0.13, jackknife 50%): #4: 0→1
Node 34 (bs = 0.28, jackknife 91%): #23: 0→1, #24: 0→3, #55: 0→2, #63: 1→0, #76: 0→1
Node 35 (bs = 0.58, jackknife 94%): #1: 0→1, #12: 2→4, #13: 0→1, #63: 1→0, #73: 0→1
Node 36 (bs = 0.04): #31: 1→0
Node 37 (bs = 0.04): #76: 0→1
Node 38: no apomorphies
Node 39 (bs = 0.08): #29: 0→1, #34: 0→1, #37: 0→1, #54: 1→0
Node 40 (bs = 0.05): #43: 0→1
Node 41 (bs = 0.06): #26: 0→1, #53: 1→0
Node 42 (bs = 0.05): #66: 1→0
Node 43 (bs = 0.04): #76: 0→1
Node 44 (bs = 0.01): #2: 1→0, #61: 0→1
Node 45 (bs = 0.20): #10: 1→0, #39: 2→3, #41: 0→1, #42: 0→1, #74: 0→1
Node 46 (bs = 0.04, jackknife 63%): #5: 0→1, #72: 0→1
Node 47 (bs = 0.01): #10: 1→0, #39: 2→1
Node 48 (bs = 0.09): #9: 1→0