

Morronea, A New Genus Segregated from Panicum (Paniceae, Poaceae) Based on Morphological and Molecular Data

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Abstract—Taxonomic features of species of *Panicum* section *Parviglumia* are reviewed and compared with those of other taxa in tribe Paniceae. The new genus *Morronea*, including six species ranging from Mexico to Argentina, is proposed on the basis of morphological characters. They are plants growing at forest edges, with membranous-ciliate ligules, lower glume reduced, 1/6 to ¼ the spikelet length, lower palea and lower flower absent, and upper antherium indurate with simple papillae and conspicuous macrohairs all over its surface, and chloroplast *ndhF* sequences to include six species ranging from Mexico to Argentina. The new combinations: *Morronea arundinariae*, *M. cayoensis*, *M. guatemalensis*, *M. incumbens*, *M. parviglumis*, and *M. trichidiachnis* are proposed and the new genus is compared with other genera of the tribe Paniceae.

Keywords—Gramineae, grasses, *Parviglumia*, phylogeny, taxonomy.

Subfamily Panicoideae has been highly supported as a monophyletic natural group (GPWG 2001; Vicentini et al. 2008; Sánchez Ken and Clark 2010; GPWG II 2012). Within the Panicoideae, one of the largest genera, *Panicum* L., as conventionally circumscribed, has ca. 450 species distributed worldwide (Hitchcock and Chase 1910; Clayton and Renvoize 1986; Webster 1988). The history of its classification is complex and different authors have recognized different taxa. Recently, several species of *Panicum* have been transferred to different genera within subfamily Panicoideae on the basis of morphological and molecular characteristics (Gómez-Martínez and Culham 2000; Zuloaga et al. 2000; Duvall et al. 2001, 2003; Giussani et al. 2001; Aliscioni et al. 2003; Simon and Jacobs 2003; Bess et al. 2006; Morrone et al. 2007, 2008; Sede et al. 2008, 2009; Zuloaga et al. 2011; Morrone et al. 2012). These contributions have undoubtedly established the polyphyly of the genus, stressing several exomorphological, anatomical, and physiological differential characters of *Panicum*. Among these characters are differences in the Kranz syndrome, including Kranz and non-Kranz species grouped in subgenera, sections or group of species (Zuloaga 1987), correlation of this character with leaf structures, such as distance between vascular bundles, presence of chloroplasts in the mestome or parenchymatous sheath, inflorescence type, nervation of spikelet bracts, lower glume length, lower flower and palea presence, upper antherium texture and ornamentation, including pilosity, and presence of simple and/or compound papillae. Therefore, *Panicum* has to be restricted to the type subgenus. *Panicum* s.s. is the type genus of tribe Paniceae and subtribe Panicinae (Morrone et al. 2012), where it is related to a few Old World genera, including *Yakirra* Lazarides and R. D. Webster and *Arthragrostis* Lazarides, both from Australia, and the African genus *Louisiella* C. E. Hubb. and J. Léonard. On the other hand, other genera previously considered in tribe Paniceae where segregated (Morrone et al. 2012) to tribe Paspaleae, in coincidence with Bouchenak-Khelladi et al. (2008), authors who stressed that tribe Paniceae was polyphyletic.

Zuloaga (1987) placed non-Kranz species of *Panicum*, with spikelets with the upper glume and lower lemma usually five-nerved in subg. *Phanopyrum* (Raf.) Pilg. Within this subgenus, species were arranged into sections *Laxa* Hitchc. and Chase ex Pilg., *Lorea* Zuloaga, *Megista* Pilg., *Monticola* Stapf, *Parvifolia* Hitchc. and Chase ex Pilg., *Parviglumia* Hitchc. and Chase ex Pilg., *Phanopyrum* Raf., *Stolonifera* (Hitchc. and Chase) Pilg., and *Verrucosa* Hitchc. and Chase ex C. C. Hsu

(Zuloaga 1987). Aliscioni et al. (2003) pointed out that all taxa treated by Zuloaga (1987) in *Phanopyrum* need to be segregated from *Panicum* s.s., either as new genera of within other existing genera of the Paniceae. As a result, and based on molecular and exomorphological characters, several species of section *Laxa* were transferred to *Hymenachne* P. Beauv. and *Steinchisma* Raf. (Aliscioni et al. 2003), those of *Lorea* to *Apochloa* and *Renvoizea* (Sede et al. 2008), *Megista* to *Stephostachys* (Zuloaga et al. 2010), species of *Parvifolia* to the genus *Trichanthecium* (Zuloaga et al. 2011), *Phanopyrum* was treated as a valid genus (Aliscioni et al. 2003), and species of *Stolonifera* were transferred to *Ocellochloa* (Sede et al. 2009). The systematic position of species of sect. *Monticola*, *Parviglumia*, and *Verrucosa* remains uncertain; it should be pointed out that, until now, no molecular studies had been carried out in species of sect. *Parviglumia*.

Historical Background—Hitchcock and Chase (1915) cited *Parviglumia* as an informal group within *Panicum* with three species, *P. parviglume*, *P. schmitzii*, and *P. virgultorum*, all with lanceolate and pseudopetiolate blades, spikelets obovoid, less than 2 mm long, arranged on short, appressed branches, with the lower glume nearly one fifth the length of the spikelet, and upper antherium pilose, exceptionally glabrous in *P. parviglume*. Later, Pilger (1940) established section *Parviglumia* within subg. *Sarmentosum* of *Panicum* with two species, *P. parviglume* and *P. trichidiachne*.

Hsu (1965) and Brown (1977), in their infrageneric treatment of *Panicum*, also classified *Parviglumia* in subg. *Sarmentosum*; Brown (1977) indicated that all species of this section were non-Kranz. Zuloaga (1985) included six species in section *Parviglumia*: *Panicum arundinariae*, *P. cayoense*, *P. guatemalense*, *P. incumbens*, *P. parviglume*, and *P. trichidiachne*, and characterized the section by having spikelets arranged in lax and spreading panicles, with spikelets ellipsoid, glabrous, lower glume 3(5)-nerved, 1/6–1/4 the spikelet length, upper glume and lower lemma 5–7(9)-nerved, lower palea and lower flower absent, upper antherium ellipsoid, pilose, occasionally glabrescent, and papillate, with simple papillae regularly distributed over the lemma and palea, the plants non-Kranz.

The objectives of the present study are: 1) to assess the phylogenetic position of American species of *Panicum* section *Parviglumia*; and 2) to discuss, based on the phylogenetic reconstruction, the taxonomic status of section *Parviglumia* and putative allied genera of the Paniceae. To achieve such purposes, new molecular evidence using the *ndhF* gene, including the

analysis of all species previously considered in this section (Zuloaga 1985) is provided, and the results discussed with related taxa of subtribe Boivinellinae (Morrone et al. 2012).

MATERIALS AND METHODS

Taxon Sampling—The six species assigned to *Parviglumia* by Zuloaga (1985) were analyzed using morphological and molecular data. Six new *ndhF* sequences obtained for the present work, belonging to all species of sect. *Parviglumia*, were included in the Panicoid grass matrix of Aliscioni et al. (2003); also, seven sequences obtained from Morrone et al. (2012) belonging to subtribe Boivinellinae were added to this matrix, giving a total of 132 taxa analyzed. Details of taxa included and GenBank numbers are available in Appendix 1.

The morphological matrix was constructed including the same 132 taxa of the molecular matrix and 57 characters. Data of *Parviglumia* species were coded for the present work, while information of the remaining 126 species was taken from the morphological matrix used by Morrone et al. (2012), which was based on the matrix published by Zuloaga et al. (2000). The list and codification of the 57 characters are shown in Appendix 2.

The combined matrix is available in TreeBASE: Study Accession URL <http://purl.org/phylo/treebase/phyloids/study/TB2:S13995>.

Morphological Data—Morphological studies were based on herbarium specimens from: BAA, F, G, GH, K, LIL, LP, MO, NY, P, SI, US, and VEN (herbarium acronyms follow <http://sciweb.nybg.org/science2/IndexHerbariorum.asp>), and living plants during several fieldtrips within Latin America. Upper antheria were viewed with a Zeiss 940 A scanning electron microscope, operating at 10–20 kV, at the Darwin Institute, San Isidro, Argentina.

Molecular Data—DNA was extracted from herbarium specimens using a DNeasy plant mini kit (QIAGEN Inc., Hilden, Germany) according to the manufacturer's instructions.

The complete *ndhF* gene, coding NADH dehydrogenase subunit F (approx. 2,100 bp), was amplified in three fragments using the following pairs of primers specified by Olmstead and Sweere (1994), Clark et al. (1995), and Aliscioni et al. (2003): 5F-972R, 972F-1666R, and 1666F-2110R.

The PCR amplifications were performed in a 25 μ l final volume with 50–100 ng of template DNA, 0.2 μ M of each primer, 25 μ M of each dNTP, 5 mM MgCl₂, 1x buffer and 1.5 units of Taq polymerase provided by Invitrogen, Brazil. The reaction conditions were: denaturation at 94°C for 5 min, followed by 35 cycles of denaturation at 94°C for 30 sec, annealing at 48°C for 1 min, and extension at 72°C for 1 min. Final extension at 72°C for 6 min terminated the reactions. A negative control with no template was included for each series of amplifications to monitor for contamination. The PCR products were run out on a 1% TBE agarose gel stained with ethidium bromide. Automated sequencing was performed by Macrogen, Inc. Seoul, Korea, using the ABI PRISM BigDye™ Terminator Cycle Sequencing Kits with AmpliTaq DNA polymerase (Applied Biosystems, Seoul, Korea). Both forward and reverse strands were sequenced; single-pass sequencing was performed on each template using selected primers to complete a bidirectional contig of the full sequence.

Sequence alignment was trivial, performed manually, adding gaps to the matrix, using BioEdit ver. 5.0.9 (Hall 1999). Gaps generated by the alignment were treated as missing data. Percentage of missing data, excluding gaps, was 2.99%.

Phylogenetic Analyses—We analyzed the *ndhF* sequence matrix separately (including Bayesian and parsimony approaches) and in combination with the morphological data.

Bayesian analysis was conducted using MrBayes version 3.1.2 (Ronquist and Huelsenbeck 2003). Modeltest 3.7 (Posada and Crandall 1998), using Akaike information criterion, determined the TVM+I+G as the evolution model that best fit the data. We carried out two independent runs of 4,000,000 generations using four Markov chains (one cold and three heated chains), sampling every 1000 generations. The program Tracer v.1.4 (Rambaut and Drummond 2007) was used to examine Bayesian parameters to determine stationarity. Posterior probabilities (PP) were determined after a burn-in of 25% of the trees.

Parsimony analyses were performed using TNT (Goloboff et al. 2008). Search strategy consisted of heuristic searches performed using 10,000 series of random addition sequences followed by TBR branch rearrangements and retaining two trees per series. Trees found were saved in memory and additionally TBR swapped retaining a maximum of 20,000 trees. Branches with ambiguous length of 0 or 1 were collapsed, according to collapsing rule. A strict consensus tree was generated from the most parsimonious trees. Jackknife values (JK) (Farris et al. 1996) were calculated by 10,000 resampling iterations with a removal probability of 36%,

using ten series of random addition sequences, swapped by TBR and holding two optimal trees per series.

The combined data matrix was analyzed only by parsimony; morphological multistate characters were coded as additive, as in Morrone et al. 2012, whenever the states are considered interested (Lipscomb 1992).

RESULTS AND DISCUSSION

The aligned *ndhF* sequences included 2,068 bp of which 452 were phylogenetically informative. The Bayesian analysis yielded a majority-rule consensus tree shown in Fig. 1. F1 Parsimony analysis of the *ndhF* sequences yielded up to 20,000 shortest trees of 1,601 steps (CI = 0.41, RI = 0.77), data not shown. The majority-rule consensus tree of the Bayesian analysis and the strict consensus trees of the parsimony analysis were fully congruent; branches showing posterior probabilities ≤ 0.5 in the Bayesian analysis were collapsed in the parsimony strict consensus tree.

The combined (morphological + molecular) matrix consisted of 132 taxa with 2,125 characters, being 499 informative positions. Parsimony analysis resulted in up to 20,000 trees of 1,970 steps. The combined consensus tree is shown in Fig. 2. F2

Molecular and combined analyses recovered the same major clades for the Paniceae s.l. previously reported by Aliscioni et al. (2003) and Morrone et al. (2012): the $x = 10$ clade, tribe Paspaleae, including subtribes Paspalinae, Otachyriinae and Arthropogoninae (Morrone et al. 2012), and the $x = 9$ clade corresponding to tribe Paniceae (Morrone et al. 2012). Within the Paniceae $x = 9$ clade, the subtribe Boivinellinae resulted monophyletic (PP = 1, JK = 74%) and included all the new accessions sequenced in this study. This clade formed a trichotomy together with B clade sensu Morrone et al. (2012), including *Trichantheicum* Zuloaga and Morrone, *Sacciolepis* Nash and sections *Monticola* Stapf and *Verrucosa* Hitchc. and Chase ex C. C. Hsu of *Panicum* s.l., and a third major group composed of subtribes Melinidinae, Cenchrinae and Panicinae, with section *Clavelligerae* Stapf plus *Dichantheium* (Hitchc. and Chase) Gould as a sister clade. Teerawatananon et al. (2011) treated several genera of Boivinellinae, i.e. *Acroceras*, *Ottochloa*, *Pseudechinolaena*, and *Cyrtococcum* in the forest shade clade, as defined by Giussani et al. (2001), indicating that this clade was moderately supported and ambiguous in their analysis; this study also placed *Alloteropsis* and *Entolasia* in an uncertain position.

Within subtribe Boivinellinae, section *Parviglumia* resulted monophyletic in both molecular and combined analyses (PP = 1, JK = 99%), including all species previously treated by Zuloaga (1985) in this section.

Molecular analyses (Bayesian and parsimony) showed *Amphicarpum* as the sister group of the *Parviglumia* clade, however, in the combined analysis, *Parviglumia* clade is sister to the genus *Entolasia* Stapf and both are sister to *Amphicarpum amphicarpon* (Pursh) Nash.

All species of *Parviglumia* share a similar morphology and habit, with the species growing at forest edges, with culms usually geniculate and rooting at the lower nodes, ligules membranous-ciliate, small, blades ovate-lanceolate to lanceolate, pseudopetiolate, spikelets with the lower glume 1/6 to 1/4 the length of the spikelet, occasionally reaching 1/2 the spikelet length, nerveless to 1–3(-5) nerved, upper glume and lower lemma subequal, 5(-7) nerved, lower palea and lower flower absent, upper antherium ovoid to obovoid, indurate, coriaceous, with long white macrohairs and simple papillae regularly distributed over the lemma and palea, and

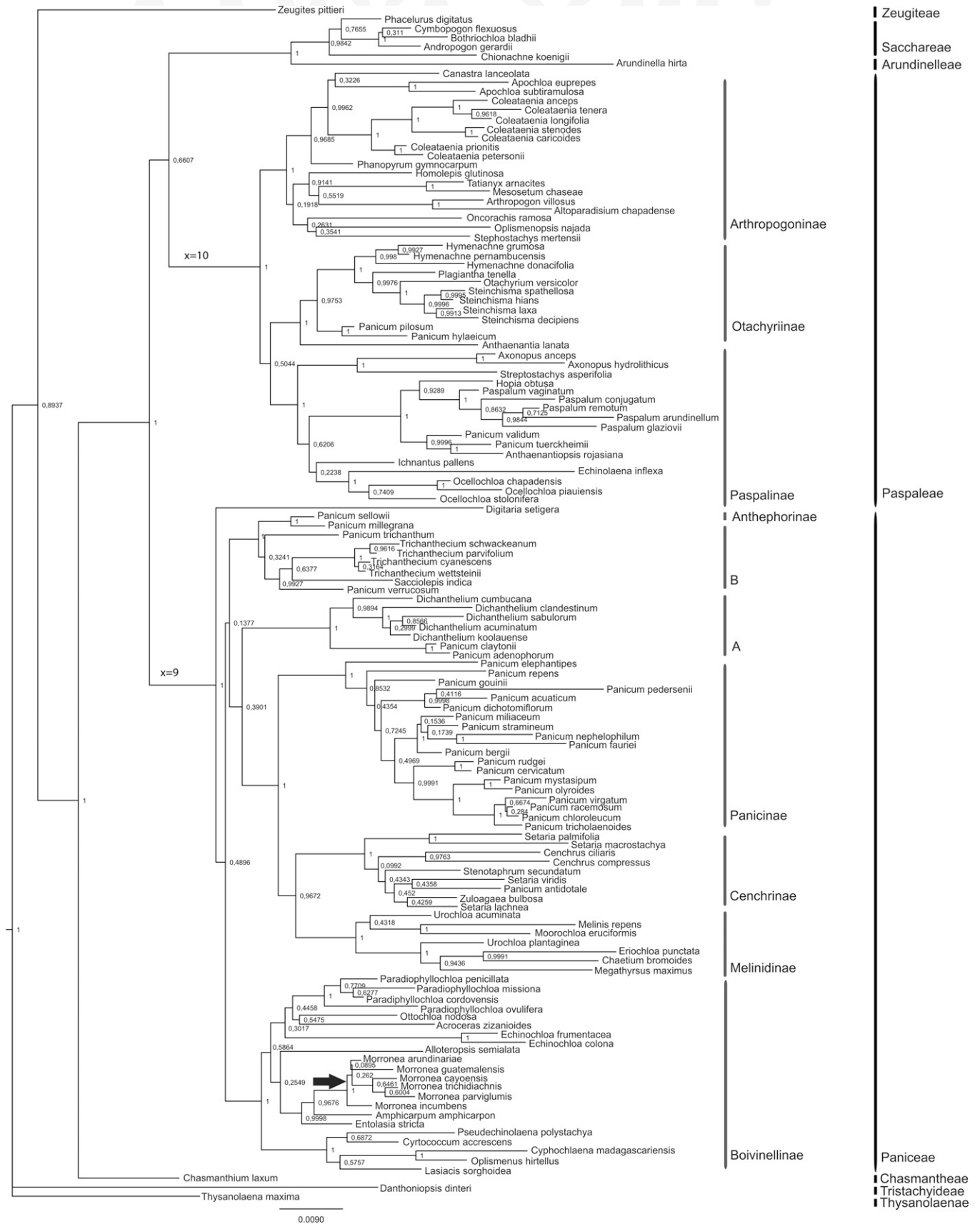


FIG. 1. Majority-rule consensus tree of the Bayesian analysis of the molecular data. Posterior probabilities are shown in the nodes. The position of *Morronea* is indicated with a black arrow. Black and gray bars indicate tribes and subtribes, respectively, as described in Morrone et al. (2012).



FIG. 2. Parsimony strict consensus tree obtained from the analysis of the combined data. Jackknife support values are shown below branches. The position of *Morronea* is indicated with a black arrow. Black and gray bars indicate tribes and subtribes, respectively, as described in Morrone et al. (2012).

caryopsis with a punctiform hilum. *Amphicarpum* Kunth is a small genus, with two species growing in sandy pinewoods of southeastern U. S. A., characterized by including plants with hidden cleistogenes, with short subterranean branches ending in single cleistogamous spikelets, the ascending aerial inflorescences terminating in chasmogamous spikelets, spikelets are 6–9 mm long and dissimilar, those of the aerial inflorescences with the lower glume obsolete or absent, and upper glume and lower lemma subequal, while cleistogamous spikelets do not have a lower glume, and upper glume and lower lemma are strongly and many nerved, exceeded at maturity by an ellipsoid and acuminate upper anthercium which also has a strongly nerved upper lemma with flat margins over the palea; the ligule in this genus is a fringe of hairs. The genus *Entolasia* includes five species in tropical Africa and Australia, which are clearly different from species of *Paroiglumia* by having a ciliate ligule, blades lanceolate, flat or rolled and not pseudopetiolate, inflorescence composed of spiciform racemes, congested along a central axis, with the spikelets lanceolate, appressed, and with the lower glume adaxial.

Other American members of the Boivinellinae include *Echinochloa* P. Beauv., a monophyletic genus with 100% jack-knife support, which differs from *Paroiglumia* by its blades usually lacking ligules, but when present ciliate, spikelets with glumes and lower lemma subulate or shortly-awned, scabrous, lower palea present, lower flower present or absent, and upper anthercium without regularly-distributed simple papillae; additionally, all species of *Echinochloa* are Kranz, and grow in open and humid places. *Acroceras* differs from *Paroiglumia* by having a lower palea, and upper anthercium with the lemma crested, laterally compressed, and the upper

palea with two green areas at the apex similar to the crested lemma. *Parodiophyllochloa* Zuloaga and Morrone differs from species of sect. *Paroiglumia* by the presence of chasmogamous and cleistogamous inflorescences, lower glume one half to four fifth the length of the spikelet, and upper anthercium glabrous and apiculate. Species of *Paroiglumia* departs from *Oplismenus* P. Beauv. by having the latter spikelets arranged in short unilateral racemes, with both glumes awned, or at least the lower glume with a long awn, the awns viscid at maturity, lower palea present or absent, and upper anthercium smooth and glabrous. The genus *Lasiacis* (Griseb.) Hitchc. differs from *Paroiglumia* by including plants with lignified culms, usually arching and climbing on the vegetation, spikelets attached obliquely to the pedicels, glumes pubescent on the apex, the lower glume 5–13-nerved, the upper glume and lower lemma 7–15-nerved, lower palea present, upper anthercium stipitate, dark brown at maturity, with glumes and lower lemma oil-producing. *Pseudechinochloa* Stapf differs from *Paroiglumia* by having ovoid spikelets, and the upper glume gibbous with tubercle-based hooks.

Species of section *Paroiglumia* depart from *Panicum* s.s. by including the latter species usually caespitose and growing in open areas, with ligules membranous-ciliate or ciliate, blades not pseudopetiolate, and spikelets with the upper anthercium with simple or compound papillae at the top of the palea and lemma, without macrohairs all over its surface; also all species of *Panicum* s.s. are C₄, of the NAD-me subtype.

Based on the previously discussed molecular and morphological characters, species of section *Paroiglumia* are here transferred to the new genus *Morronea*. The following key distinguishes *Morronea* from related taxa of subtribe Boivinellinae.

KEY TO MORRONEA AND RELATED GENERA OF SUBTRIBE BOIVINELLINAE

1. Upper anthercium laterally compressed 2
2. Upper glume covered with hooked spines at maturity *Pseudechinochloa*
2. Upper glume without hooked spines at maturity 3
 3. Spikelets arranged in unilateral racemes; glumes awned; upper lemma hyaline *Cyphochlaena*
 3. Spikelets in open to contracted panicles, not in unilateral racemes; glumes awnless; upper lemma papyraceous to crustaceous *Cyrtococcum*
1. Upper anthercium dorsiventrally compressed 4
 4. Plants with hidden cleistogenes, the hidden cleistogenes subterranean *Amphicarpum*
 4. Plants without hidden cleistogenes, all inflorescences aerial 5
 5. Upper lemma crested at the tip, the apex green, laterally compressed *Acroceras*
 5. Upper lemma not crested at the tip, the apex pale 6
 6. Upper anthercium uniformly pilose all over its surface; lower glume obsolete to reduced, the upper glume as long as the spikelet 7
 7. Spikelets adaxial, lanceolate, arranged in unilateral racemes; ligules ciliate. Tropical Africa and Australia *Entolasia*
 7. Spikelets abaxial, ellipsoid, arranged in lax panicles; ligules membranous-ciliate. America *Morronea*
 6. Upper anthercium glabrous or sparsely pilose toward the apex, not covered by macrohairs all over its surface; lower and upper glume subequal or the lower glume shorter but not obsolete or reduced 8
 8. Glumes or lemmas awned 9
 9. Apex of upper lemma awned; glumes ciliate, at least on the margins *Alloteropsis*
 9. Apex of upper lemma awnless, glumes glabrous 10
 10. Spikelets laterally compressed, lower glume awned, the awn often sticky; glumes and lower lemma not scabrous; blades usually ovate-lanceolate, asymmetric at its base; trailing forest grasses *Oplismenus*
 10. Spikelets dorsiventrally compressed, lower glume awnless, glumes and lower lemma conspicuously scabrous, with small hooks or spines, blades usually lanceolate, symmetric at its base; culms herbaceous, species mostly of open habitats *Echinochloa*
 8. Glumes and lemmas awnless 11
 11. Upper lemma with a shallow excavation covered by silky hairs at its apex; spikelets globose, obliquely inserted on the pedicel, black at maturity, culms lignified, species of forest edges, scandent and trailing on the vegetation *Lasiacis*
 11. Upper lemma acuminate to obtuse, without a shallow excavation; spikelets dorsiventrally compressed, ellipsoid, not obliquely inserted on the pedicel; culms herbaceous 12
 12. Blades disarticulating from the sheaths; inflorescences with casmogamous spikelets; glumes shorter than the adjacent lemmas. Africa and Australia *Ottochloa*
 12. Blades not disarticulating from the sheaths; inflorescences with casmogamous and cleistogamous spikelets; upper glume as long as the upper lemma. America *Parodiophyllochloa*

TAXONOMIC TREATMENT

Morronea Zuloaga and Scataglini, gen. nov.—TYPE: *Morronea arundinariae* (Trin. ex E. Fourn.) Zuloaga and Scataglini (*Panicum arundinariae* Trin. ex E. Fourn., Mex. Pl. 2: 25. 1886)

Panicum group *Parviglumia* Hitchc. and Chase, Contr. U.S. Natl. Herb. 15: 29, 124. 1915. *Panicum* sect. *Parviglumia* Hitchc. and Chase ex Pilg, Nat. Pflanzenfam.(ed. 2) 14: 16. 1940.

Perennials with decumbent culms. Ligules membranous-ciliate. Inflorescence a lax and spreading panicle. Spikelets ellipsoid, glabrous. Lower glume 1/6 to

¼(-1/2) the spikelet length, nerveless to 1–3(-5) nerved. Upper glume and lower lemma 5(-7)-nerved. Lower palea and flower absent. Upper antherium ovoid to obovoid, indurate, pilose, occasionally glabrescent, and papillate, with simple papillae regularly distributed over the lemma and palea. Caryopsis with hilum punctiform, embryo ½ or less the length of the caryopsis. Non Kranz species.

Six American species inhabiting humid and shaded places from Mexico to Argentina.

The new genus is named in honor of Dr. Osvaldo Morrone, our dearest friend and an outstanding American agrostologist, author of numerous and valuable publications.

KEY TO THE SPECIES OF MORRONEA

1. Upper antherium glabrous, occasionally sparsely pilose *M. parviglumis*
1. Upper antherium pilose all over its surface 2
 2. Spikelet 2.9–3.3 mm long; inflorescence up to 50 cm long, with sparse spikelets on long pedicels; sheaths with urticant hairs *M. incumbens*
 2. Spikelets 1.5–2.7 mm long; inflorescence up to 20 cm long, with spikelets congested on short pedicels; sheaths without urticant hairs 3
 3. Spikelets 2.4–2.7 mm long 4
 4. Inflorescence a lax and diffuse panicle, 17–20 × 6–12 cm; blades 1.6–1.8 cm wide, the abaxial surface densely hispidulous *M. cayoensis*
 4. Inflorescence a contracted, few flowered panicle, 10 × 1–4 cm; blades 0.9–1 cm wide, the abaxial surface glabrous *M. guatemalensis*
 3. Spikelets 1.6–1.9(2.2) mm long 5
 5. Blades oblong to ovate-lanceolate, asymmetric basally, 1.1–3.1 cm wide; upper antherium with simple papillae evenly distributed all over its surface *M. trichidiachnis*
 5. Blades linear-lanceolate, the base rounded, symmetric, 0.5–0.8 cm wide; upper antherium smooth *M. arundinariae*

1. *Morronea arundinariae* (Trin. ex E. Fourn.) Zuloaga and Scataglini, comb. nov. *Panicum arundinariae* Trin. ex E. Fourn., Mexico. Pl. 2: 25. 1886. —TYPE: MEXICO. Without locality, C.J.W. Schiede s. n. (lectotype: P!, here designated; isolectotype: US-80474!, fragment ex P).

Panicum conchatum E. Fourn., Mexic. Pl. 2: 25. 1886.—TYPE: MEXICO. Sierra de San Cristóbal, Oct, J.G. Schaffner 204 (holotype: P!; isotype: US-80596a!, fragment ex P).

Panicum virgultorum Hack., Oesterr. Bot. Z. 51: 369. 1901. -TYPE: COSTA RICA. San José: in virgultis ad La Verbena prope Alajuelita, 1120 m, Aug 1894, A. Tonduz 8829 (lectotype: US-824021!, designated by Hitchcock and Chase, Contr. U.S. Natl. Herb. 15: 215. 1910; isolectotypes: BM !, CR-8829, G-00099658!, G-00099657!, K!, P !, US-265897!, US-80536!, fragment ex W, US-824021 !, US-973656!, fragment ex CR, US-973658 !, fragment ex CR).

Panicum breviramisum Swallen, Contr. U.S. Natl. Herb. 29(9): 419. 1950. —TYPE: Guatemala. Dept. Huehuetenango: on pine-clad sloop along stream, vicinity of Nucapuxlac, 2500 m, 17 Jul 1942, J.A. Steyermark 48948 (holotype: US-1935038!; isotype: F!). *Panicum conchatum* E. Fourn. ex Hemsl., Biol. Cent.-Amer., Bot. 3: 497. 1885, nom. nud.

Distribution and Habitat—Widely distributed in Mesoamerica, from southern Mexico, Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica, Panama to northern South America, where it is found in Colombia, Venezuela, and Ecuador. This species grows from sea level to 2,000 m elevation.

Representative Specimens Examined—COLOMBIA. Cauca: El Tambo, von Sneidern 1300 (GH). COSTA RICA. San José: Puente Mulas, S de San Rafael, Pohl and Davidse 10802 (F).

ECUADOR. Pichincha: Chaupisacha, Los Reales, Acosta Solís 20356 (US).

EL SALVADOR. Santa Ana: Cerro Verde, Pohl and Gabel 13595 (F, MO, NY). GUATEMALA. Chiquimula: Volcán Quezltepeque, Steyermark 31494 (F). HONDURAS. Ocotepeque: 10 km de Nueva Ocotepeque, Molina 22202 (F, NY).

MEXICO. Veracruz: Jalapa, Hitchcock 6630 (Ny, US).

PANAMA. Chiriquí: El Boquete, Davidse and D'Arcy 10323 (MO).

VENEZUELA. Distrito Federal: Hacienda Sosa, Badillo 57 (US, VEN).

2. *Morronea cayoensis* (Swallen) Zuloaga and Scataglini, comb. nov. *Panicum cayoense* Swallen, Contr. U.S. Natl. Herb. 29(9): 418. 1950. —TYPE: BELIZE. El Cayo: top of limestone hill at San Agustín, Mountain Pine Ridge, Jul-Aug 1936, C.L. Lundell 6809 (holotype: US-1722487!; isotypes: LL!, US-1647559!).

Distribution and Habitat—Forests of southern Mexico, Guatemala, and Belize.

Representative Specimens Examined—GUATEMALA. Petén: Parque Nacional Tikal, sobre la calle Remate, Lundell 17110 (US).

MEXICO. Chiapas: San Quintín, unión del río Perlas con el río Jatafé, Solms 1723 (US).

3. *Morronea guatemalensis* (Swallen) Zuloaga and Scataglini, comb. nov. *Panicum guatemalense* Swallen, J. Wash. Acad. Sci. 23(10): 460. 1933. —TYPE: GUATEMALA. Quezaltenango: in mountains near Santa María, just south of Quezaltenango, 25 Mar 1932, P. Weatherwax 182 (holotype: US-1538064!; isotype: MO!).

Distribution and Habitat—Restricted to the department Quezaltenango in Guatemala, reaching 1800 m elevation.

Representative Specimens Examined—GUATEMALA. Quezaltenango: Retalhuleu, de Koninck 251 (US).

4. *Morronea incumbens* (Swallen) Zuloaga and Scataglini, comb. nov. *Panicum incumbens* Swallen, Contr. U.S. Natl.

Herb. 29(9): 417. 1950. —TYPE: GUATEMALA. Dept. Chiquimula: in cloud forest on top of Cerro Tixixi, 3–5 mi. N of Jocotán, 10 Nov 1939, J.A. Steyermark 31573 (holotype: F-1039524!; isotype: US-2236476!, fragment ex F). Figure 3.

Distribution and Habitat—This species is found in forests of mountain areas of Guatemala and Honduras, between 500 and 1,600 m elevation.

Representative Specimens Examined—HONDURAS. Intibuca: Quebrada del Pelón de Guise, *Molina* 6410 (US); Morazán: Cerro Uyuca, *Molina* 25896 (F, NY, US).

F3

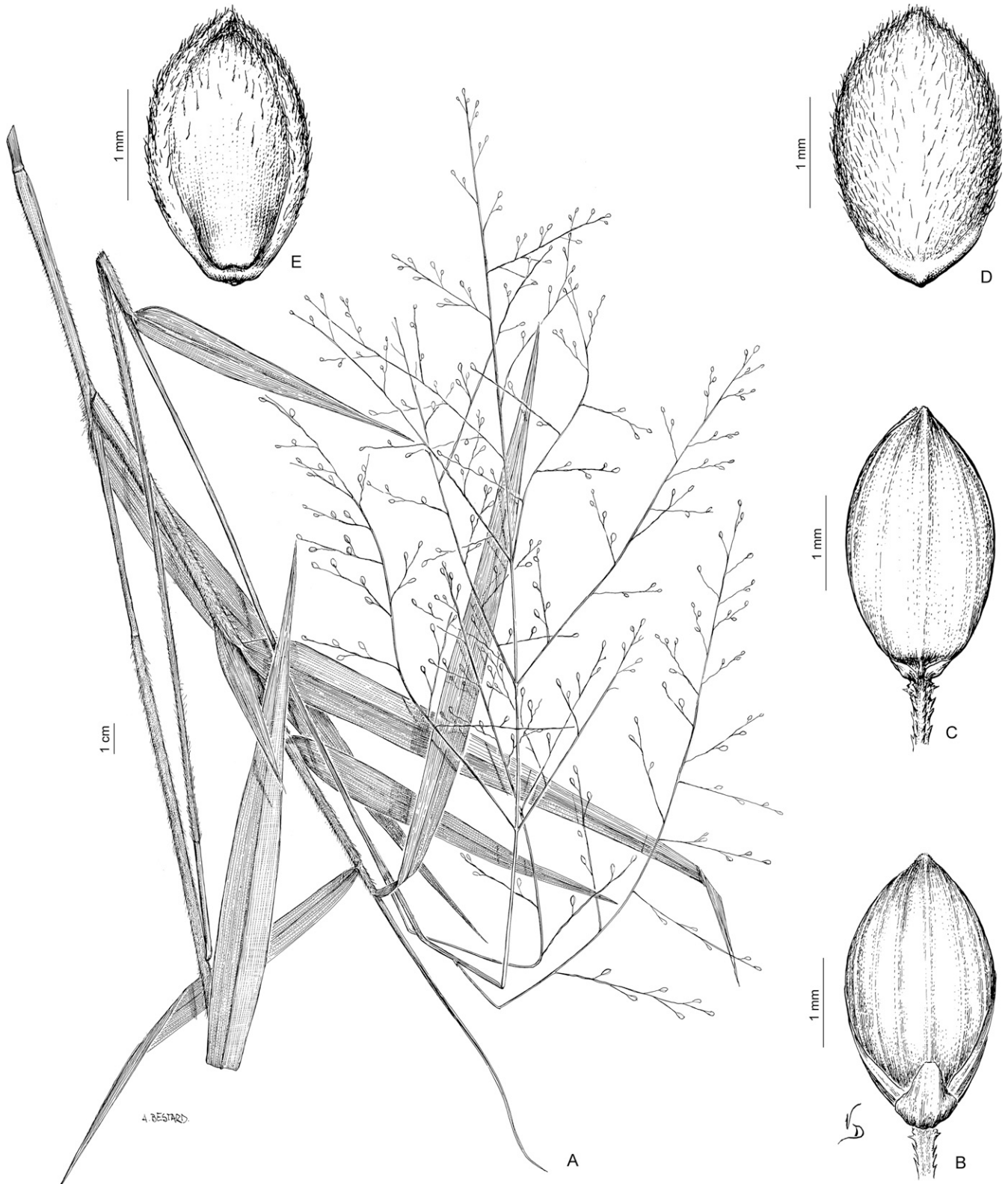


FIG. 3. *Morronea incumbens*. A. Habit. B. Spikelet, ventral view. C. Spikelet, dorsal view. D. Upper antherium, dorsal view. E. Upper antherium, ventral view (based on *Molina* 25896).

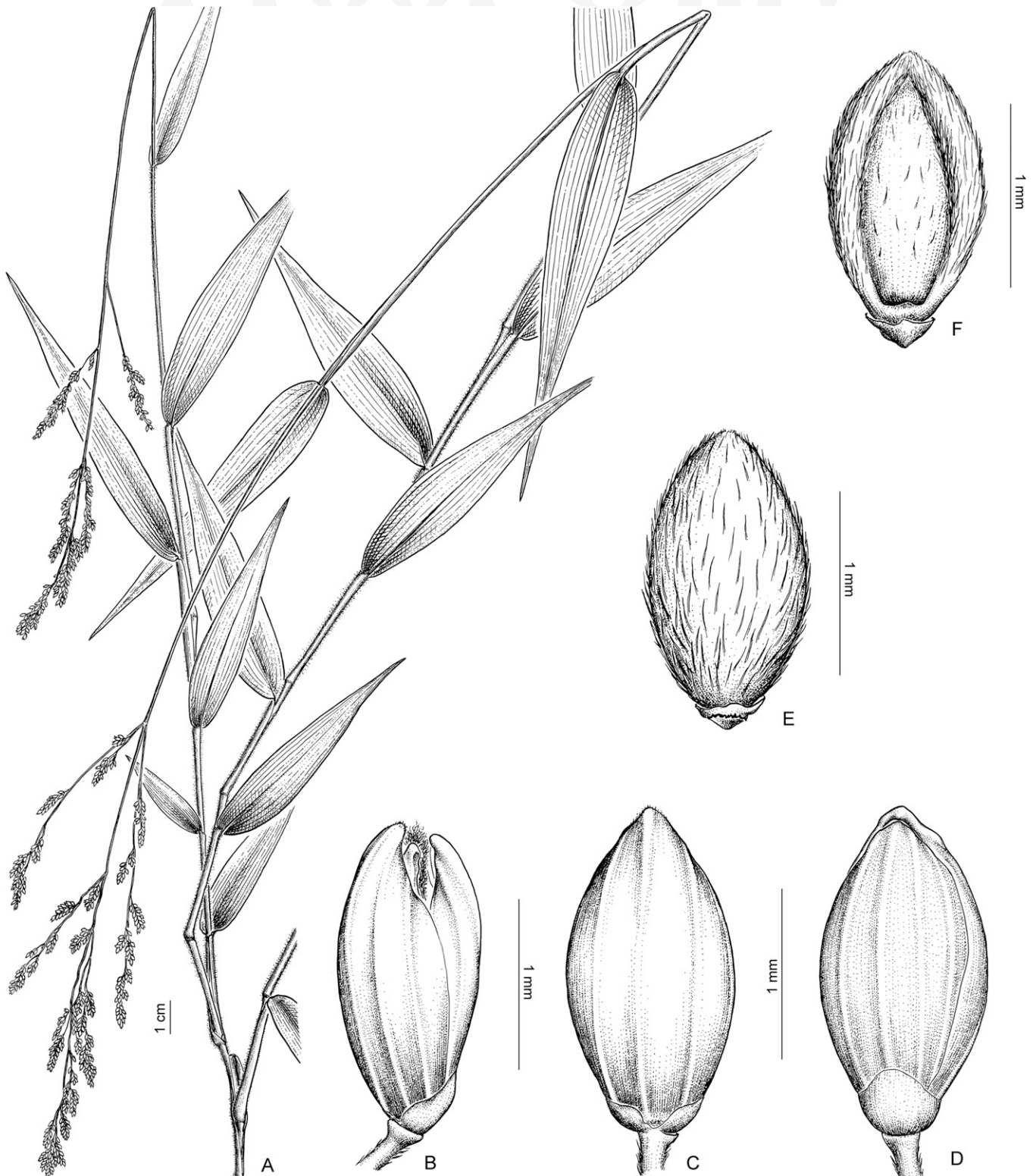


FIG. 4. *Morronea trichidiachnis*. A. Habit. B. Spikelet, lateral view. C. Spikelet, dorsal view. D. Spikelet, ventral view. E. Upper antherium, dorsal view. F. Upper antherium, ventral view (based on Hassler 10014).

5. *Morronea parviglumis* (Hack.) Zuloaga and Scataglini, comb. nov. *Panicum parviglume* Hack., Oesterr. Bot. Z. 51: 429. 1901. —TYPE: COSTA RICA. San José: "in ripis fl. Río Torres prope San José," H. Pittier 9080 (lectotype: W!, designated by Hitchcock and Chase, Contr. U.S.

Natl. Herb. 15: 126. 1910; isolectotype: US-80900, fragment ex W).

Distribution and Habitat—This species grows in humid mountain forests of Mexico, Guatemala, El Salvador, and Costa Rica, between 1,100 and 2,400 m elevation.

Representative Specimens Examined—COSTA RICA. San José: San Miguel, Pohl and Davidse 11431 (F).

EL SALVADOR. Morazán: Montes de Cacaguatique, Tucker 695a (F, US).

GUATEMALA. Quezaltenango: entre San Martín Chile Verde y Colomba, Standley 85519, 85591 (F, US).

MEXICO. Veracruz: Barranca de Teoxolo, Pringle 15604 (GH, MO, US).

6. *Morronea trichidiachnis* (Döll) Zuloaga and Scataglini, comb. nov. *Panicum trichidiachne* Döll, Fl. Bras. 2(2): 339, pl. 49. 1877. —TYPE: BRAZIL. Rio de Janeiro: Rio de Janeiro, 4 Jan 1875, A.F.M. Glaziou 6979 (holotype: P!; isotypes: B!, US-81150!, fragment ex P). Figure 4.

[F4]

Panicum schiffneri Hack., *Ergebn. Bot. Exp. Südbras.* 1: 11. 1906. —TYPE: BRAZIL. São Paulo: prope Fazenda Bella Vista, S. Cruz ad flumen Rio Pardo, ca. 500 m, Jul 1901, R.R. von Wettstein and V.F. Schiffner s.n. (holotype: W!; isotype: US-81102!, fragment ex W).

Panicum schmitzii Hack., *Ann. K. K. Naturhist. Hofmus.* 17: 254. 1902. —TYPE: MEXICO. Without locality, A. Schmitz 837 (holotype: W!; isotype: US-80974!, fragment ex W).

Distribution and Habitat—This is the most widespread species of the genus, growing from the Caribbean and Central America to South America, where it is distributed from Venezuela to northern Argentina; it is found in humid and shady habitats, between sea level and 2,800 m.

Representative Specimens Examined—ARGENTINA. Misiones: Iguazú, Parque Nacional Iguazú, picada al hidrógrafo, detrás del camping El Ñandú, Zuloaga et al. 5213 (SI).

BELIZE. El Cayo: Humming Bird Highway, Gentle 8958 (F, NY, US).

BRAZIL. Minas Gerais: Viçosa, Chase 9440 (F, GH, MO, NY, US).

COSTA RICA. San José: San Miguel de San Ramón, Brenes 19260 (F).

DOMINICAN REPUBLIC. Santiago: Loma Diego de Ocampo, Ekman 16301 (US).

ECUADOR. Chimborazo: entre Hulgra y Naranjapata, Hitchcock 20672 (GH, NY, US).

GUATEMALA. Petén: Parque Nacional Tikal, Molina 15791 (MO, US). HAITI. Massif du Nord, Le Borgne, Ekman 4791 (US).

HONDURAS. 24 km E of Santa Rita de Copán, Harmon and Dwyer 4016 (MO).

MARTINIQUE. Without locality, Hahn 616 (US).

MEXICO. Veracruz: Córdoba, Hitchcock 6459 (MO, NY, US).

NICARAGUA. Managua: Sierra de Managua, Garnier 1246a (F, GH).

PANAMA. Chiriquí: cercanías de El Boquete, Hitchcock 8278, 8305 (US).

PARAGUAY. Amambay: Sierra de Amambay, Hassler 10014 (NY, US).

PUERTO RICO. Alta de Bandera, E de Adjuntas, Chase 6474 (US).

VENEZUELA. Distrito Federal: 7 km SW of Carayaca, Davidse 2894 (MO, NY).

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APPENDIX 1. List of taxa used in the molecular analysis, voucher information of the new sequences (*), and GenBank accession numbers.

Tribe Arundinelleae. *Arundinella hirta* (Thunb.) Tanaka. AF117393.

Tribe Chasmantheae. *Chasmanthium laxum* (L.) H. O. Yates subsp. *sessiliflorum* (Poir.) L.G. Clark. U27296. **Tribe Paniceae.** *Acroceras zizanioides* (Kunth) Dandy. AY029618. *Alloteropsis semialata* (R. Br.) Hitchc. subsp. *eckloniana* (Nees) Pilg. EU159708. *Amphicarpum amphicarpon* (Pursh) Nash. JN604673. *Cenchrus ciliaris* L. AY029625. *C. compressus* (R. Br.) Morrone. AY029672. *Chaetium bromoides* (J. Presl) Benth. ex Hemsl. AY029626. *Cyphochlaena madagascariensis* Hack. JN604683. *Cyrtococcum accrescens* (Trin.) Stapf. JN604684. *Dichanthelium acuminatum* (Sw.) Gould and Clark. AY188485. *D. clandestinum* (L.) Gould. AY188461. *D. cumbucana* (Renvoize) Zuloaga. AY188464. *D. koolauense* (H. St. John and Hosaka) C. A. Clark and Gould. AY029627. *D. sabulorum* (Lam.) Gould and C. A. Clark. AY029654. *Digitaria setigera* Roth ex Roem. and Schult. AY029629. *Echinochloa colona* (L.) Link. AY029631. *E. frumentacea* Link. AY029632. *Echinochloa inflexa* (Poir.) Chase. AY029633. *Etolasia stricta* (R. Br.) Hughes. JN604687. *Eriochloa punctata* (L.) Desv. AY029634. *Lasiacis sorghoidea* (Desv.) Hitchc. and Chase. AY029639. *Megathyrsus maximus* (Jacq.) B. K. Simon and S. W. L. Jacobs var. *maximus*. AY029649. *Melinis repens* (Willd.) Zizka. AY029675. *Moorochloa eruciformis* (Sm.) Veldkamp. AY188452. **Morronea arundinariae* (Trin. ex E. Fourn.) Zuloaga and Scataglini. *Dasa* 4853 (MO), KC701608. **Morronea cayoensis* (Swallen) Zuloaga and Scataglini. *Martinez et al.* 29494 (MO), KC701609. **Morronea guatemalensis* (Swallen) Zuloaga and Scataglini. *Neuling* 2885 (MO), KC701610. **Morronea incumbens* (Swallen) Zuloaga and Scataglini. *Swallen* 11059 (MO), KC701611. **Morronea parvigliumia* (Hack.) Zuloaga and Scataglini. *Morales et al.* 3899 (MO), KC701612. **Morronea trichidiachnis* (Döll) Zuloaga and Scataglini. *Glaziou* 6979 (US), KC701613. *Oplismenopsis najada* (Hack. and Arechav.) Parodi. AY188453. *Ottochloa nodosa* (Kunth) Dandy. JN604696. **Panicum.** Section *Dichotomiflora* (Hitchc.) Honda. *Panicum aquaticum* Poir. AY029658. *P. dichotomiflorum* Michx. AY188466. *P. elephantipes* Nees ex Trin. AY029647. *P. gouinii* E. Fourn. AY188467. *P. pedersenii* Zuloaga. AY029646. *P. repens* L. AY029651. Section *Panicum*. *P. bergii* Arechav. AY188457. *P. fauriei* Hitchc. AY029650. *P. miliaceum* L. AY188472. *P. nephelophilum* Gaudich. AY029645. *P. stramineum* Hitchc. and Chase. AY188489. Section *Rudgeana* (Hitchc.) Zuloaga. *P. cervicatum* Chase. AY188459. *P. rudgei* Roem. and Schult. AY029661. Section *Urvilleana* (Hitchc.) Pilg. *P. chloroleucum* Griseb. AY188460. *P. racemosum* (P. Beauv.) Spreng. AY188481. Section *Virgata* Hitchc. and Chase ex Pilg. *P. tricholaenoides* Steud. AY188493. *P. virgatum* L. U21986. Ungrouped. *P. mystasipum* Zuloaga and Morrone. AY188474. *P. olyroides* Kunth. AY188475. *Panicum* “incertae sedis”. Section *Clavelligera* Stapf. *P. adenophorum* K. Schum. AY188454. *P. claytonii*

Renvoize. AY188462. Section *Monticola* Stapf. *P. millegrana* Poir. AY029660. *P. sellowii* Nees. AY188484. *P. trichanthum* Nees. AY188492. Section *Verrucosa* Hitchc. and Chase ex C. C. Hsu. *P. verrucosum* Muhl. AY188496. Ungrouped. *P. antidotale* Retz. AY188456. *Parodiophyllochloa cordovensis* (E. Fourn.) Zuloaga and Morrone. AY188463. *P. missiona* (Ekman) Zuloaga and Morrone. AY188473. *P. ovulifera* (Trin.) Zuloaga and Morrone. AY029653. *P. penicillata* (Nees ex Trin.) Zuloaga and Morrone. AY18847. *Pseudechinolaena polystachya* (Kunth) Stapf. AY029676. *Sacciolepis indica* (L.) Chase. AY029677. *Setaria lachnea* (Nees) Kunth. AY029683. *S. macrostachya* Kunth. AY029678. *S. palmifolia* (J. König) Stapf. AY029680. *S. viridis* (L.) Beauv. U21976. *Stenotaphrum secundatum* (Walter) Kuntze. AY029684. *Trichanthecium cyanescens* (Lam.) Zuloaga and Morrone. AY188465. *T. parvifolium* (Lam.) Zuloaga and Morrone. AY188476. *T. schwackeanum* (Mez) Zuloaga and Morrone. AY188483. *T. wetsteinii* (Hack.) Zuloaga and Morrone. AY188497. *Urochloa acuminata* (Renvoize) Morrone and Zuloaga. AY029629. *U. plantaginea* (Link) R. D. Webster. AY029693. *Zulogaea bulbosa* (Kunth) Bess. AY029648. **Tribe Paspaleae.** *Altoparadisium chapadense* Filg. et al. AY029619. *Anthraenantia lanata* (Kunth) Benth. AY029640. *Anthraenantiopsis rojasiana* Parodi. AY029620. *Apochloa euprepes* (Renvoize) Zuloaga and Morrone. AY029657. *A. subtramura* (Renvoize and Zuloaga) Zuloaga and Morrone. AY188490. *Arthropogon villosus* Nees. AY029622. *Axonopus anceps* (Mez) Hitchc. AY029623. *Axonopus hydrolithicus* (Filg. et al.) A. López and Morrone. AY029642. *Canastra lanceolata* (Filg.) Morrone et al. AY029621. *Coleataenia anceps* (Michx.) Soreng. AY188455. *C. caricoides* (Nees ex Trin.) Soreng. GU253330. *C. longifolia* (Torr.) Soreng. AY188482. *C. petersonii* (Hitchc. and Ekman) Soreng. AY188479. *C. prionitis* (Nees) Soreng. AY029652. *C. stenodes* (Griseb.) Soreng. GU253333. *C. tenera* (Beyr. ex Trin.) Soreng. AY188491. *Homolepis glutinosa* (Sw.) Zuloaga and Soderstr. AY029637. *Hopia obtusa* (Kunth) Zuloaga and Morrone. AY029659. *Hymenachne donacifolia* (Raddi) Chase. AY029635. *H. grumosa* (Nees) Zuloaga. AY188468. *H. pernambucense* (Spreng.) Zuloaga. AY188478. *Ichnanthus pallens* (Sw.) Munro ex Benth. AY029638. *Mesosetum chaseae* Lucas. AY029641. *Ocellochloa chapadensis* (Swallen) Zuloaga and Morrone. AY188486. *O. piauiensis* (Swallen) Zuloaga and Morrone. AY029656. *O. stolonifera* (Poir.) Zuloaga and Morrone. AY18848. *Oncorachis ramosa* (Kunth) and Soderstr. Morrone and Zuloaga. AY029686. *Otacyrium versicolor* (Döll) Henrard. AY029643. *Panicum incertae sedis*: Section *Tuerckheimiana* (Hitchc.) Zuloaga. *P. tuerckheimii* Hack. AY188494. Section *Valida* Zuloaga and Morrone. *P. validum* Mez. AY188495. Ungrouped. *P. hylaicum* Mez. AY188470. *P. pilosum* Sw. AY188480. *Paspalum arundinellum* Mez. AY029663. *P. conjugatum* Bergius. AY029669. *P. glaziovii* (A. G. Burm.) S. Denham. AY029689. *P. remotum* J. Remy. AY029668. *P. vaginatum* Sw. AY029665. *Phanopyrum gymnocarpon* (Elliott) Nash. AY188469. *Plagiantha tenella* Renvoize. AY029674. *Steinchisma decipiens* (Nees ex Trin.) W. V. Br. AY188499. *S. hians* (Elliott) Nash. AY029685. *S. laxa* (Sw.) Zuloaga. AY029655. *S. spathellosa* (Döll) Renvoize. AY188500. *Stephostachys mertensii* (Roth) Zuloaga and Morrone. AY188471. *Streptostachys asperifolia* Desv. AY029687. *Tatianyx arnatices* (Trin.) Zuloaga and Soderstr. AY029688. **Tribe Sacchareae.** *Andropogon gerardii* Vitman. AF117391. *Bothriochloa bladonii* (Retz.) S. T. Blake. AF117395. *Chionachne koenigii* (Spreng.) Thwaites. AF117397. *Cymbopogon flexuosus* (Nees ex Steud.) Will. Watson. AF117404. *Phacelus digitatus* (Sibth. and Sm.) Griseb. AF117418. **Tribe Thysanolaenae.** *Thysanolaena maxima* (Roxb.) Kuntze. U21984. **Tribe Tristachyidae.** *Danthoniopsis dinteri* (Pilg.) C.E. Hubb. AY029695. **Tribe Zeugiteae.** *Zeugites pittieri* Hack. U21987.

APPENDIX 2. List of characters used in the morphological analysis.

0. Main axis of inflorescences terminating in a spikelet (0), terminating in a bristle (1), terminating in a naked point, without a bristle (2). 1. Rachis terminating in a spikelet (0), terminating in a bristle (1), terminating as a foliaceous axis (2), terminating in a naked point, without a bristle (3). 2. Foliaceous rachis absent (0), present (1). 3. Bracts of the inflorescences absent (0), present (1). 4. Involucral bristles (cauline) absent (0), present (1). 5. Involucral bracts absent (0), present (1). 6. Cleistogenes in leaf axils absent (0), present (1). 7. Apex of the pedicel truncate (0), oblique (1). 8. Disarticulation at the base of the spikelet absent (0), present (1). 9. Disarticulation at the base of the primary branches absent (0), present (1). 10. Disarticulation at the base of the inflorescence absent (0), present (1). 11. Disarticulation between the lower glume and lower lemma absent (0), present (1). 12. Disarticulation at the base of the pedicel absent (0), present (1). 13. Disarticulation at the node of the main axis absent (0), present (1). 14. Disarticulation at the base of the upper antherium absent (0), present (1). 15. Unilateral spikelet absent (0), present (1). 16. Second order branches in the inflorescence multiflowered (0), reduced to a single abaxial

spikelet (1), reduced to a single adaxial spikelet (2). 17. Spikelet shape not gibbous (0), gibbous (1). 18. Presence of incomplete florets distal to fertile florets absent (0), present (1). 19. Breeding system plants with at least with some perfect flowers (0), no perfect flowers, staminate and pistillate flowers on the same plant (1), no perfect flowers, staminate and pistillate flowers on different plants (2). 20. Hairy callus at the base of the spikelet absent (0), present (1). 21. Stipe at the base of the upper floret absent (0), present (1). 22. Lower glume present (0), vestigial (1), absent (2). 23. Lower glume not saccate (0), saccate (1). 24. Lower glume muticous (0), awned (1). 25. Upper glume present (0), absent (1). 26. Lower and upper glume of different size (0), the same size (1). 27. Upper glume as long as or longer than the lower lemma (0), 1/2 or less the length of the lower lemma (1). 28. Upper glume 2 or 4-nerved (0), enerved (1), 1-nerved (2), (1) 3-nerved (3), 3-5-nerved (4), 5-11 nerved (5). 29. Upper glume muticous (0), awned (1). 30. Lower lemma muticous (0), awned (1). 31. Apex of the lower lemma entire (0), bifid (1), trilobite (2). 32. Lower palea absent (0), present, not expanded (1), present and expanded (2). 33. Upper antherium dorsiventrally compressed (0), laterally compressed (1), cylindrical (2). 34. Upper antherium crustaceous (0), cartilaginous (1), hyaline (2), membranous to herbaceous (3). 35. Upper lemma texture smooth (0), transversely rugose (1). 36. Upper lemma with basal scars or

appendages absent (0), present (1). 37. Upper lemma muticous (0), awned (1). 38. Upper lemma not differentiated at the apex (0), differentiated at the apex (1). 39. Upper lemma (margins) tucked in onto the palea (0), lying flat and exposed on the palea (1). 40. Upper palea absent (0), present (1). 41. Upper palea tightly clasped by the lemma (0), gaping (1). 42. Upper palea without simple papillae (0), with simple papillae (1), with compound papillae (2). 43. Distribution of papillae in the upper palea all over surface (0), at apex only (1). 44. Upper palea (presence of microhairs) without bicellular microhairs (0), with bicellular microhairs at the apex and/or base (1), with bicellular microhairs all over its surface (2). 45. Upper palea (presence of macrohairs) without macrohairs (0), with macrohairs at the apex and/or base (1), with macrohairs all over its surface (2). 46. Upper palea (apex) straight (0), recurved (1). 47. Stamen (number) three (0), two (1), one (2). 48. Lodicules present (0), absent (1). 49. Style base free (0), fused (1). 50. Ovary glabrous (0), pilose (1). 51. Caryopsis (hilum) punctiform (0), linear (1). 52. Photosynthetic pathway C3 XyMS+ (0), C4 XyMS- (1), C4 XyMS+ (2). 53. Chloroplasts on the parenchymatous sheath absent (0), centripetal (1), centrifugal (2). 54. Distinctive Kranz cells absent (0), present (1). 55. Fusoid-cells absent (0), present (1). 56. Basic chromosome number (x) 9 (0), 10 (1), 11 (2), 12 (3), 13 (4), 5 (5), 6 (6), 7 (7), 17 (8).