A REAPPRAISAL OF *PASPALUM PILOSUM* AND *P. PEREGRINUM* (POACEAE: PANICOIDEAE: PANICEAE)

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ABSTRACT. Paspalum pilosum and P. peregrinum are members of the informal Decumbentes group of Paspalum, and grow from Mexico and Mesoamerica to Brazil and Bolivia in South America. Paspalum pilosum is characterized by its erect to decumbent culms, glabrous to pilose sheaths and blades, one or two racemes in terminal inflorescences, glabrous spikelets arranged in pairs in 2 irregular series on the rachis, dimorphic lower glumes in the pair of spikelets, longitudinally sulcate lower lemmas, and glabrous gynoecium. Paspalum peregrinum has sheaths and blades densely pilose, racemes occasionally branched, hairy spikelets arranged in 1 to 4 series on the rachis, and a hairy gynoecium. These modifications in the morphology of P. peregrinum are due to a fungal infection. Another species, Thrasya venezuelana, known only from the type collection, is the same taxon as P. peregrinum. We conclude that P. peregrinum and T. venezuelana are in fact abnormal specimens of P. pilosum, whose morphology is modified by the fungal infection. Therefore, both species are reduced to the synonymy of P. pilosum. This constitutes two new incidents of erroneous interpretation of abnormal morphology caused by fungi, and the first in the tribe Paniceae.

Key Words: Paspalum, Paniceae, Poaceae, abnormal morphology, fungal infection

Paspalum pilosum Lam. is a member of the informal group Decumbentes of Paspalum L. (Chase 1929). It grows from southern Mexico and Mesoamerica to Bolivia and southern Brazil (Figure 1), inhabiting open fields, savannas, and wooded slopes. It is frequent in grazed places, from 60 to 1700 m elevation.

In a revision of the genus *Thrasya* Kunth, Burman (1987) excluded *T. villosa* Hitchc. from the genus and placed it in *Paspalum*, in the informal group Decumbentes under the new name *P. peregrinum* A. G. Burm. & Filg., since *P. villosum* was pre-occupied by *P. villosum* Thunb. The specimens studied by Burman were from Panama and central Brazil, and the specific epithet *peregrinum* refers to the unusual pattern of disjunction exhibited by the specimens. The type specimen, *Pittier* 5363, is from Panama.

During our revision of the Decumbentes group of *Paspalum*, we found that *Thrasya venezuelana* Chase is the same as *P. peregrinum*. The analysis of new collections from Venezuela and Brazil, in addition

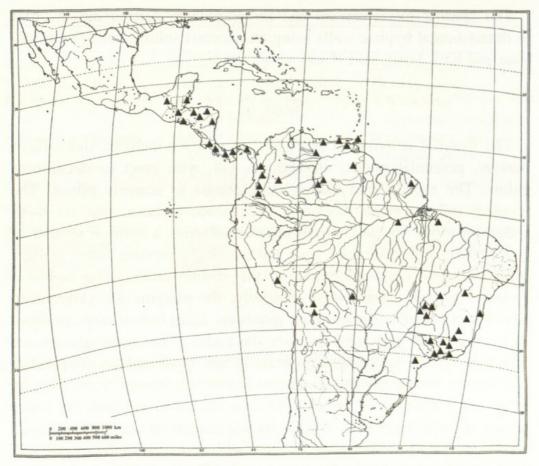


Figure 1. Distribution of Paspalum pilosum.

to field observations made by Dr. O. Morrone (pers. comm.), led us to consider P. peregrinum as a doubtful species, similar to P. pilosum. A detailed morphologic study of both species was performed in order to analyze diagnostic characters and to recircumscribe both species.

MATERIALS AND METHODS

Material studied came from: BM, G, K, LPB, MEXU, MO, P, SI, US, and W (Appendix). Specimens of Paspalum peregrinum included some of the material seen by Burman (Partch 69133 and Hammel 5506) and new material from Venezuela (Trejos 45102) and Brazil (Filgueiras 2219 and Filgueiras & Zuloaga 2101). The type, Pittier 5363, was not seen. The type collection of Thrasya venezuelana, Chase 12407, was examined.

Scanning electron microphotographs of the upper anthecium and gynoecium were prepared following Soderstrom and Zuloaga (1989). The specimens were viewed in a Zeiss 940 A scanning electron microscope at the Darwinion institute, operating at 10-20 kV.

The specific histochemical test for chitin was carried out in order to detect fungal hyphae walls using an aqueous solution of 1% aniline-blue and 85% lactic acid (Clark et al. 1983).

RESULTS

The material determined as Paspalum pilosum includes short-rhizomatous, perennial plants, 40-100 cm tall, with erect to decumbent culms. The sheaths and blades are glabrous to scarcely pilose. The terminal inflorescences have 1-2 unbranched racemes that are 4-15 (-20) cm long. The last sheath usually subtends a cymose system of 1-3 axillary inflorescences, each with a single raceme; other axillary inflorescences commonly occur at the middle nodes. The rachis is glabrous adaxially and hispid abaxially, the margins are glabrous to sparcely pilose. The spikelets are glabrous, 2.2-3.0 mm long, arranged in pairs, in two irregular series on the rachis. The lower glumes are dimorphic when comparing this bract in the upper and lower spikelets of a pair: in the upper spikelet the lower glume is generally reduced, up to 1/6 the length of the spikelet, while in the lower spikelet, the lower glume is well-developed, up to 3/4 the length of the spikelet, and eccentric. The lower lemma is 5-nerved with a longitudinally sulcate and finely papillose back. The lower palea is well-developed and the lower flower is usually absent. The upper anthecium is papillose and glabrous. The gynoecium is glabrous.

The specimens of *Paspalum peregrinum* differ from *P. pilosum* by their shorter culms (25–35 cm tall), sheaths and blades that are densely pilose on both surfaces and margins, shorter racemes (3–6 cm long) that are sometimes branched, and rachis of the racemes that are pilose on both surfaces and margins. The spikelets are pilose, 2.5–3.5 mm long, and irregularly arranged in 1 to 4 series on the rachis. The upper anthecium is papillose and pilose toward the apex. The gynoecium is pilose or rarely glabrous (Table 1). Hairs of the ovary are unicellular, 90–330 µm long, with a rounded or dome-shaped apex and with a basal constriction (Figure 2). Characters shared by the two species are: the terminal inflorescences with 1–2 racemes and the axillary ones with a single raceme; the dimorphic lower glumes in the two spikelets of a pair; the 5-nerved, longitudinally sulcate and finely papillose lower lemma; the well-developed lower palea; and the absence of the lower flower.

The specimen Filgueiras 2219 (MO) presents tillers with the morphology of Paspalum peregrinum and tillers with the morphology

Table 1. Comparison of Paspalum pilosum and P. peregrinum.

Plant part	P. pilosum	P. peregrinum
Culms	40-100 cm tall	25-35 cm tall
Sheaths and blades	Glabrous to scarcely pilose	Densely pilose
Racemes	14–15 (–20) cm long, never branched	3–6 cm long, occasionally branched
Rachis of the racemes	Adaxial surface glabrous, abaxial surface hispid, and margins glabrous to scarcely pilose	Both surfaces and margins pilose
Spikelets	Glabrous, 2.2–3 mm long	Pilose, 2.5-3.5 mm long
Spikelets on the rachis	In 2 irregular series	In 1 to 4 irregular series
Upper anthecium	Glabrous	Pilose toward the apex
Gynoecium	Glabrous	Hairy, rarely glabrous

of *P. pilosum* in the same plant. By using a histochemical reaction to detect chitin, we verified the presence of fungal hyphae on the reproductive structures of the tillers with features of *P. peregrinum*. Fungal hyphae were also detected on reproductive structures of the rest of the specimens of *P. peregrinum*.

Thrasya venezuelana is only known from the type, Chase 12407, from Venezuela. This specimen matches the morphology of Paspalum peregrinum, with sheaths, blades, and rachis of the racemes densely pilose; pilose spikelets, 3.5–3.7 (–4) mm long; the upper anthecium papillose and pilose toward the apex; and the gynoecium densely pilose.

DISCUSSION

The presence of a hairy gynoecium is a frequent feature within the subfamily Pooideae; it can be hairy throughout its surface or only near the top, sometimes as a fleshy hairy appendage (Clayton and Renvoize 1986). A hairy gynoecium is present in some species of *Festuca* L., *Megalachne* Steud., and *Vulpia* C. C. Gmel. of the tribe Poeae; *Avena* L., *Arrhenatherum* P. Beauv., and *Gaudinia* P. Beauv. of the tribe Aveneae; and *Elymus* L. and *Agropyron* Gaertn. of the tribe Triticeae. In contrast, a hairy gynoecium is unusual within the subfamily Panicoideae. Within the tribe Paniceae, Watson and Dallwitz (1992) cited the presence of a hairy ovary only for the African genus *Chaetopoa* C. E. Hubb., although there is no reference of this character in the original description of the genus.

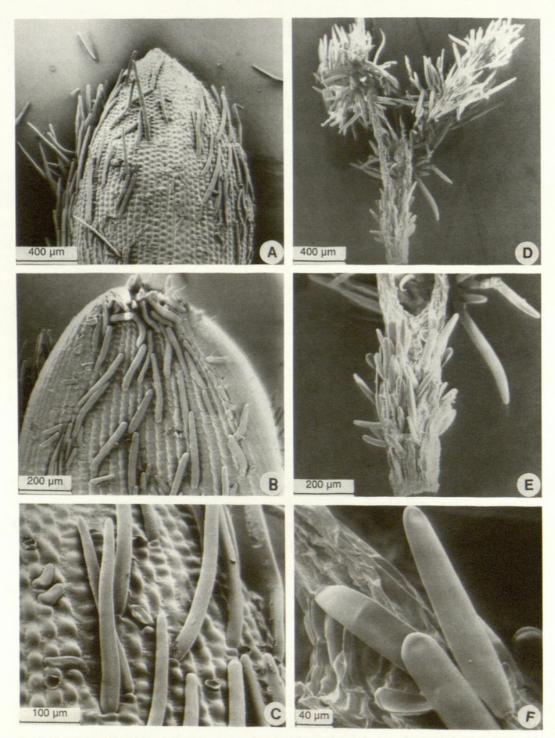


Figure 2. Scanning electron microphotographs of *Paspalum pilosum*. All microphotographs are based on the abnormal specimen *Filgueiras & Zuloaga 2101* (SI). A. Upper anthecium, lemma side. B. Upper anthecium, palea side. C. Detail of lemma of upper anthecium showing hairs. D. Hairy gynoecium. E. Ovary zone. F. Detail of ovary showing hairs.

Structural modifications on vegetative and reproductive parts of the plants, such as culm length, branching at vegetative axes and inflorescences, and proliferation and size of the spikelets, have been cited as malformations caused by fungal infections (Fischer and Holton 1957). Examples of morphological changes caused by fungi in other grass taxa are well documented in Ichnanthus P. Beauv. (Stieber 1982). growing in tropical America, Asia, Africa, and Australia; Streptostachys Desv. (Zuloaga and Soderstrom 1985), which grows from Venezuela to Brazil and Paraguay; and Holcus L. (Menezes de Sequeira and Almaraz 2001), native from Eurasia, but introduced in another areas. Another species of the Decumbentes group of Paspalum, P. unispicatum (Scribn. & Merr.) Nash, which grows from Texas to Argentina, has been reported by Chase (1929) as being frequently affected by a fungus that distorts the inflorescense. The discovery of specimens such as Filgueiras 2219, which presents tillers with normal and abnormal morphology on the same plant, allows us to conclude that the specimens that Burman (1987) recognized as P. peregrinum represent affected plants, constituted only by tillers with the abnormal morphology.

In contrast, we have no evidence that pilosity on sheaths, blades, axis, and bracts of the spikelets may be caused by fungal pathogens. Uphof (1962) reported that it is plausible that mutations can cause glabrous and pubescent varieties of a species. In her treatment of Paspalum pilosum, Chase (unpubl. manuscript) mentioned specimens collected in grazed or trodden places in Brazil, with short culms, blades densely pilose, racemes 4-8 cm long, spikelets densely hispid with glistening hairs, and stamens and gynoecium abnormal. She described these plants as being affected by a fungus, probably belonging to the genus Balansia. Also, she noticed plants with both affected and normal culms. Even though the abnormal morphology of the specimens of P. peregrinum is evidently caused by a fungal infection, we were unable to identify the pathogen due to the lack of living material. However, White (1987), Clay (1988), and Clay and Leuchtmann (1989) have pointed out that the Poaceae are commonly infected by fungal endophytes of the family Clavicipitaceae (Ascomycetes).

Examples of "taxa" based on infected specimens include *Holcus mollis* L. var. *parviflorus* Parn., which was synonymized under *Holcus mollis* L. by Menezes de Sequeira and Almaraz (2001), and *Agrostis pumila* L., which Roemer and Schultes (1817) included as an infraspecific category of *A. vulgaris* With. *Paspalum peregrinum* and *Thrasya venezuelana* represent two new incidents of taxa that are based on characters resulting from a fungal infection, and the first in the

tribe Paniceae. The remaining species of the Decumbentes group of *Paspalum*, approximately 17 species, have been examined for this phenomenon and no infection was detected.

In short, the abnormal morphology observed in the studied specimens of *Paspalum peregrinum* and in *Thrasya venezuelana* represent pathological deformations that cannot be treated as taxonomic differences. For this reason, we propose the reduction of *P. peregrinum* and *T. venezuelana* to synonymy under *P. pilosum*.

The following nomenclatural treatment should be adopted:

- Paspalum pilosum Lam., Tabl. Encycl. 1: 175. 1791. *Dimorphostachys pilosa* (Lam.) E. Fourn., Mexic. Pl. 2: 14. 1886. Type: America Tropical, *Richard s.n.* (HOLOTYPE: P-LA!; ISOTYPE: US!).
 - Thrasya villosa Hitchc., syn. nov., Proc. Biol. Soc. Wash. 40: 84. 1927. Paspalum peregrinum A. G. Burm. & Filg., Acta Bot. Venez. 14(4): 91. 1987. Type: Panamá. Cerro Vaca, eastern Chiriquí, 25–28 Dec 1911, Pittier 5363 (HOLOTYPE: US not seen).
 - Thrasya venezuelana Chase, syn. nov., J. Wash. Acad. Sci. 42(4): 122. 1952, non Paspalum villosum Thunb., 1784. Paspalum venezuelanum (Chase) A. G. Burm., Acta Bot. Venez. 14(4): 90. 1987. Type: venezuela. Federal District, 11 Mar 1940, Chase 12407 (HOLOTYPE: US-1762130!; ISOTYPE: VEN not seen).

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APPENDIX

SPECIMENS EXAMINED.

Specimens previously treated as *Paspalum peregrinum* A. G. Burman & Filg. are identified with an asterisk.

BELIZE. Stann Creek, Possum Point Biological Station, 23 Jun 1993, Vincent et al. 6184 (MO).

BOLIVIA. La Paz: Franz Tamayo, Apolo, 52 km hacia Charasani, 1550 m, 7 Jun 1990, *Beck & Foster 18538* (K, LPB, SI); Nor-Yungas: camino Yolosa-Caranavi, desvío a Coroico, a 9 km de Yolosa, 1 Jun 1993, *Rúgolo & Villavicencio 1936* (SI). Santa Cruz: Velasco, Parque Nacional Noel Kempff M., Catarata Ahlfeld, 300 m, 24 Apr 1993, *Killeen et al. 5451* (MEXU, MO, SI).

BRAZIL. Bahía: 24 km SW of Belmonte on road to Itapebi, 24 Mar 1974, Harley et al. 17387 (K, MO); Serra do Rio de Contas, Harley et al. 15330 (K, MO, P); Mocugé, de Mocugé a Barra de Estiva, 15 Mar 1999, Zuloaga & Morrone 6959 (SI). Distrito Federal: W of Taguatinga, 1200 m, 25 Nov 1965, Irwin et al. 10652 (MO); D.F. 205, entre Sobradinho y Corregom d'Ouro, 15 km W de Sobradinho, 22 Feb 1992, Filgueiras & Zuloaga 2101* (SI). Goiás: Padre Bernardo, entre Padre Bernardo e Curralinho, ca. 20 km N de Curralinho, 28 Feb 1992, Filgueiras 2219* (MO); 15 km N of Corumbá de Goiás on road to Niquelandia, ca. 1150 m, 15 Jan 1968, Irwin et al. 18610 (MO); Chapada dos Veadeiros, 10 km south of Cavalcante, 1000 m, 10 Mar 1969, Irwin et al. 24239 (us); Padre Bernardo, entre Padre Bernardo e Curralinho, ca. 20 km N de Curralinho, 28 Feb 1992, Filgueiras 2219 (MO); Pirinopolis, Pirineus, 17 Feb 1956, without collector 4375 (SI); Serra do Pirineus, 9 km S of Corumbá de Goiás, 1000 m, 1 Dec 1965, Irwin et al. 10892 (us); without locality, 1894-1895, Glaziou 22434 (G, K, P, W). Minas Gerais: 13 Jan 1951, Pires et al. 2907 (US); ca.11 km E of Campanha along Hwy. 267 to Caxabu, 960 m, Davidse & Ramamoorthy 10609 (MO); ca. 22 km S of Padre Paraíso along Hwy. BR-116, 700 m, 29 Mar 1976, Davidse et al. 11516 (MO). Pará: Belém, 10 Nov 1964, Soderstrom & Carvalho 1158 (MO). Paraná: Itararé, 20 Jan 1915, Dusén 13507 (SI); Jaguariaiva, Parque Estadual do Cerrado, 13 Dec 1992, Rúgolo et al. 1725 (MO). Rio de Janeiro: Macieiras, Serra de Itatiaia, 1000 m, 18 Jan 1925, Chase 8346 (US). Sao Paulo: Piracununga, 31 Dec 1964, Clayton 4104 (US); São Paulo, Parque Estadual das Fontes do Ipiranga, 13 Jan 1976, da Silva 235 (MO).

COLOMBIA. Buenaventura: 13 Jun 1923, *Hitchcock 19909* (US). Cauca: Around Calí, western side of Cauca valley, 1000–1200 m, Dec 1905, *Pittier 659* (US); carretera Calipopayan, entre Madomo y Pescador, 1630 m, 26 Jun 1989, *Zuloaga & Londoño 4190* (MO, SI); Cauca Valley, Río Sucio, W of Popayan, 1500–1700 m, 3 Jul 1922, *Pennel et al. 8164* (US); La Esmeralda near Jamundí, Cauca Valley, 1200 m, Jan 1906, *Pittier 1539* (US). Chocó: Hoya del Río San Juan, Andagoya, 12 Apr 1979, *Forero et al. 5117* (MO). Cundinamarca: 4 km SW of Fusagusuga, 1450 m, 8 Jan 1974, *Davidse et al. 5556* (MO). Santander: Mesa de Los Santos, 1500 m, 11–15 Dec 1926, *Killip & Smith 15112* (US). Without locality, 1846, *Moritz 650* (BM, G).

COSTA RICA. Guanacaste: Parque Nacional Rincon de La Vieja, 900–1200 m, 27–28 Jan 1983, *Davidse et al. 23441* (MO). Puntarenas: Buenos Aires, 380 m, 17 Jul 1966, *Pohl & Calderón 10075* (MO). San José: 1 km S of Rivas, 6 km NE of San Isidro del General, 725 m, 14 Jul 1966, *Pohl & Calderón 10050* (MEXU).

EL SALVADOR. Chalatenango: along Hwy. 4, 4 km SSE of La Palma, 950 m, 11 Jun 1970, *Pohl & Davidse 11896* (MO).

FRENCH GUIANA. Cayenne: 1835, Leprieur s.n. (G, P).

GUATEMALA. Chiquimula: 3 km S of Quezaltepeque on CA-10, 8 Dec 1970, Harmon & Dwyer 3690 (MO).

HONDURAS. Comayagua: along new Hwy., 10 km NW of Siguatepeque, 1080 m, 14 Aug 1971, *Pohl 12762* (Mo). Cortes Lago de Yojoa: 60 km SE de San Pedro Sula, 21 Feb 1982, *Izaguirre 148* (Mo). El Paraiso: along Hwy. 4, 25 km E of El Zamorano, 600 m, 14 Jun 1970, *Pohl & Davidse 11921* (Mo); Quebrada Honda, por la carretera entre Manzaragua y San Lucas, 1100 m, 11 Oct 1994, *Linares & Metsger 1805* (MEXU). Morazán: 800 m, Nov 1943, *Rodriguez 1561* (MEXU); ca. 16 km SW of Talanga along the road to Tegucigalpa (Hwy. 3), 750 m, 4 Oct 1986, *Davidse & Pilz 31554* (MEXU, Mo). Olancho: 6 km SW of Dulce Nombre de Culmí, along Hwy. 3, 550 m, 23 Jul 1970, *Pohl & Davidse 12443* (Mo); Vaguada del río de Culmí, 500 m, 17–22 Jul 1978, *Nelson & Romero 4703* (MEXU).

MEXICO. Tabasco: Huimanguillo, 10 Oct 1980, Cowan et al. 3249 (MEXU).

NICARAGUA. Comarca Del Cabo: Puente Pozo Azul, 10 Jul 1972, Seymour 5802 (MO). Zelaya: between Waspan and Ulwas, 12 Jul 1970, Pohl & Davidse 12287 (MO). PANAMÁ. Chiriqui: Alto Boquete, 1125 m, 25 Jan 1969, Partch 69133* (MO); Foothills, vicinity of El Boquete, 1000–1300 m, 28 Sep–7 Oct 1911, Hitchcock 8192 (SI). Panamá: Altos de Campana, a unos 85 km del Moel Sulín, 11 Jun 1977, Méndez 39 (MO); Cerro Campana, 1000 m, 9 Nov 1978, Hammel 5506* (MO); Chorrera, 16 Sep 1911, Hitchcock 8130 (SI); Veraguas, along road to radio tower on Cerro San Cristobla, near Pam. Am. Hwy., 9 km W of bridge over Río Cobre, 450 m, 25 Feb 1974, Nee 10163 (MO). Zona del Canal: Ancón Hill, 26 Nov–9 Dec 1923, Standley 25205 (MO).

PERU. Ayacucho: Aina, between Huanta and Río Apurimac, 750-1000 m, 7-17 May 1929, Killip & Smith 22528 (US).

TRINIDAD Y TOBAGO. Port of Spain, 26 Nov 1912, Hitchcock 9987 (US); Aripo Savanna, northeast of Cumuto Village, 18 Jun 1963, Soderstrom 980 (US); Aripo

Savanna, Cumutu Station, 5 Dec 1912, *Hitchcock 10075* (US); St. Joseph, 23 Dec 1912, *Hitchcock 10189* (US).

VENEZUELA. Amazonas: Rio Negro, Solano, along the Brazo Casiquiare, 75 m, 26 Jun 1984, Davidse & Miller 26655 (MO). Anzoátegui: Bolivar, 1100 m, 24 Nov 1981, Davidse & Gonzalez 19389 (SI). Anzoátegui: Freites, Burro trail between San Durrial and Los Pajaritos, 1200–1400 m, 1 Dec 1981, Davidse & González 19794 (MO, SI). Atures: near Capuana, E bank of the Río Orinoco, 90 m, 27 Apr 1979, Davidse et al. 16795 (MO). Bolivar: a 4 km al N de Santa Elena de Uairen, 900 m, 14 Aug 1989, Zuloaga et al. 4441 (MO); Roscio, Hato La Divina Pastora, approx. 8 km al N de Santa Elena de Uairén, 830 m, 25 Jul 1983, Huber & Alarcon 7831 (MO); Sifontes, sector La Hoyada, 7 km al W de Sta. Elena de Uairén, 850–1100 m, 23 Oct 1986, Aymard 4797 (MO). Distrito Federal: El Avila, 1600 m, Oct 1959, Trejos 45102* (MO). Guárico: Estación Biológica Los Llanos, 10 km SSE of Calabozo, 60 m, 9 Nov 1971, Davidse 2917 (MO). Monagas: via cueva del Guacharo, 19 Aug 1983, Montes 1661 (MO).



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