TAXONOMY

Hopia, a new monotypic genus segregated from *Panicum* (Poaceae)

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Taxonomic features of *Panicum obtusum*, a species ranging from Southern United States to Central Mexico and previously classified in subg. *Agrostoides*, sect. *Obtusa* of *Panicum*, are reviewed and compared with other taxa in the tribe Paniceae. The species is transferred to the new genus *Hopia* on the basis of morphological and molecular characters. Affinities of the new genus with other genera of Paniceae are discussed.

KEYWORDS: *Hopia,* Paniceae, Panicoideae, *Panicum,* phylogeny, Poaceae, taxonomy

INTRODUCTION

Panicum L., as traditionally circumscribed, was one of the largest genera of the Poaceae (Webster, 1988). It included approximately 450 species distributed worldwide in tropical and subtropical regions from different habitats, such as savannas, grasslands in dry or wet areas, streamsides, or forest edges, from sea level to approximately 2,500 m (Zuloaga, 1987). *Panicum* was established by Linnaeus (1753), who described 20 species and three forms for the genus. Of these, species of the Paniculata group currently are considered within *Panicum* subg. *Panicum; Panicum patens* L. has been transferred to *Cyrtococcum* Stapf, and *Panicum dactylon* L. to *Cynodon* Rich. The members of the Spicata group are referable to *Setaria* P. Beauv., *Pennisetum* Rich., *Echinochloa* P. Beauv., *Stenotaphrum* Trin., *Digitaria* Haller, and *Oplismenus* P. Beauv. Other treatments of the genus, which tended to be very inclusive, retained the paniculate species as members of *Panicum* and have often included *Echinochloa* and *Digitaria* as sections (e.g., Bentham, 1881; Bentham & Hooker, 1883; Hackel, 1887). Hooker (1897) transferred several species of *Panicum* to *Digitaria*, *Tricholaena* Schrad. ex Schult. & Schult. f., *Axonopus* P. Beauv., and *Ichnanthus* P. Beauv., and recognized nine sections in *Panicum: Paspaloideae* Nees, *Echinochloa* (P. Beauv.) Nees, *Brachiaria* Trin., *Hymenachne* (P. Beauv.) Hack., *Breviglumae* Hook. f., *Effusae* Hook. f., *Ptycophyllum* (A. Braun) Döll, *Gibbosae* Hook. f., and *Pseudechinolaena* Hook. f. Chase (1906, 1908a, b, 1911) made a significant contribution to the delimitation of the genus and related genera, indicating several characters to exclude outlying species from *Panicum*. On the basis of inflorescence and spikelet characters Hitchcock & Chase (1910) recognized two subgenera and 13 informal groups for species of *Panicum* in North America. Zuloaga (1987) provided an infrageneric classification of the New World species of *Panicum,* using morphological characters including ornamentation of the upper anthecium, photosynthetic type, spikelet characters, and chromosome base number, and recognized six New World subgenera: *Panicum*, *Agrostoides* (Hitchc.) Zuloaga, *Megathyrsus* Pilg., *Phanopyrum* (Raf.) Pilg., *Dichanthelium* Hitchc. & Chase, and *Steinchisma* (Raf.) Zuloaga. Spikelets of *Panicum* are somewhat uniform, a feature which contrasts with the variation in vegetative characters and preferential habitat of the different species (Crins, 1991). This infrageneric variation in vegetative characters is related to the presence of all known photosynthetic types found in grasses. *Panicum* includes species with non-Kranz and Kranz physiology with all Kranz subtypes, including NADP-me, NAD-me, and PEP-ck (Brown, 1977; Hattersley, 1987; Ellis, 1988). These photosynthetic types are correlated with particular anatomical characters, e.g., number of vascular bundles, and presence of specialized chloroplasts in the parenchymatic or mestomatic bundles (Brown, 1977; Ellis, 1977).

Recent phylogenetic studies based on morphological and molecular characters have questioned the monophyly of *Panicum* (Zuloaga & al., 2000; Gómez-Martínez & Culham, 2000; Giussani & al., 2001; Duvall & al., 2001; Aliscioni & al., 2003). These studies allowed new delimitations in the Paniceae, such as the recognition of four genera, previously treated by Zuloaga (1987) at the subgeneric level: *Dichanthelium, Phanopyrum, Steinchisma,* and *Megathyrsus* (Zuloaga & al. 1998, 2003; Aliscioni & al., 2003; Freckmann & Lelong, 2003; Simon & Jacobs, 2003; Barkworth, 2004).

In a phylogenetic study based on the *ndhF* chloroplast gene, Aliscioni & al. (2003) restricted *Panicum*, in a strict sense, to the typical subgenus, and characterized it by including cespitose plants with ciliate or membra-

nous-ciliate ligules, spikelets arranged in an open and lax inflorescence, with the upper glume and lower lemma (5–)7–13 nerved, the upper anthecium indurated, and the palea with simple or compound papillae toward the apex. Species of subgenus *Panicum* are C_4, of the NAD-me subtype, and have a basic chromosome number of $x = 9$. In the treatment of Aliscioni & al. (2003) the subgenus is strongly supported as a monophyletic group, with a 97% bootstrap support and a decay value of six. Five sections were included in *Panicum* subg. *Panicum* for the New World: sect. *Panicum*, sect. *Virgata* Hitchc. & Chase ex Pilg., sect. *Dichotomiflora* (Hitchc.) Honda, sect. *Rudgeana* (Hitchc.) Zuloaga, and sect. *Urvilleana* (Hitchc.) Pilg. Previously, Hsu (1965), Brown (1977), and Zuloaga (1987) treated subgenus *Panicum* as a homogeneous group clearly distinguishable from other elements of the genus. Consequently, if *Panicum* is restricted to subgenus *Panicum* and other remaining sections are recognized as genera, such as *Dichanthelium, Phanopyrum, Steinchisma,* and *Megathyrsus,* the species considered by Zuloaga (1987) as belonging to subgenus *Agrostoides* and sections previously placed in *Phanopyrum* need to be reevaluated and classified within the Paniceae.

Panicum subgenus *Agrostoides* included just 11 species in seven monotypic or small sections (Zuloaga, 1987): sect. *Agrostoidea,* sect. *Bulbosa* Zuloaga, sect. *Discrepantia* Zuloaga, sect. *Obtusa* Pilg., sect. *Prionitia* Zuloaga, sect. *Tenera* Hitchc. & Chase ex Pilg., and sect. *Tuerckheimiana* (Hitchc.) Zuloaga. Later, Zuloaga & al. (1989) established *Panicum* sect. *Valida* Zuloaga & Morrone in subg. *Agrostoides*. Species of *Panicum* subg. *Agrostoides* share a similar Kranz subtype, NADP-me (Brown, 1977; Zuloaga, 1987; Zuloaga & al., 1989; Zuloaga & al., 1993; Zuloaga & al., 2000). Nevertheless, Giussani & al. (2001) postulated that the NADP-me subtype appeared several times in the evolution of the Paniceae. Also, the basic chromosome number is variable among these species, with $x = 9$ in *Panicum* sects. *Agrostoidea* and *Bulbosa*, and $x = 10$ in sects. *Obtusa, Prionitia, Tenera,* and *Valida*. No chromosome counts are available for *Panicum* sects. *Tuerckheimiana* and *Discrepantia*. Zuloaga & al. (2000) indicated that species of *Panicum* sect. *Agrostoidea* are unrelated to other species of *Panicum,* and that the different sections could be segregated into independent genera. This hypothesis was corroborated by Aliscioni & al. (2003), who showed that the subgenus is polyphyletic, i.e., its species are not related to *Panicum* s.str. and should be removed from the genus.

Within *Panicum* subg. *Agrostoides,* sect. *Obtusa* is monotypic containing only *P. obtusum*. Hitchcock & Chase (1910, 1915), noted its similarity with *P. repandum* Nees ex Trin. [= *Thrasyopsis repanda* (Nees ex Trin.) Parodi], and Pilger (1931) placed the two species in *Panicum* sect. *Obtusa,* based on the presence of contracted panicles and spikelets with the lower glume almost as long as the spikelet. Zuloaga (1987) placed *Panicum* sect. *Obtusa,* limited to *P. obtusum,* in subg. *Agrostoides* and characterized the species by its broadly ellipsoid spikelets, lower glumes 7-nerved and ¾ to ⅘ the length of the spikelet, and the upper glume and lower lemma 7–11-nerved. However, based on molecular characters *Panicum* sect. *Obtusa* was grouped with *Paspalum* and *Thrasya* (Giussani & al., 2001; Aliscioni & al., 2003).

The purpose of this contribution is to corroborate the position of *Panicum obtusum* and re-evaluate the relationships of *Panicum* sect. *Obtusa* within tribe Paniceae using the *ndhF* phylogeny, morphological, and anatomical characters.

MATERIALS AND METHODS

Morphological and anatomical analyses. — Morphological data were based on field collections, revision of herbarium collections, and published accounts. Upper anthecia were viewed on a Zeiss 940 A scanning electron microscope at Darwinion Institute, operating at 10–20 kV.

For anatomical studies the second leaf below the inflorescence was selected. Specimens compared were *Garza & Castillo 187, Gould 2889,* and *Zuloaga & al. 7381*. Transverse sections of dried leaf blades were prepared after desilicification in 10% hydrofluoric acid (Breakwell, 1914). Midblade transverse sections were made by hand, dyed with safranin and mounted on semipermanent microscope slides in gelatine-glycerin. Epidermal preparations for light microscope studies were made following the methodology of Metcalfe (1960). The epidermis was stained with safranin. Standardized terminology in Ellis (1976, 1979) was used to describe the leaf anatomical characteristics.

DNA sequencing. — A specimen of *Panicum obtusum* was collected in Puebla, Mexico and stored in silica gel (*Zuloaga & al. 7381*). This voucher was added to the data matrix in order to corroborate the position of another specimen of *Panicum obtusum* (*Ortiz & Gomez, 16K*), and to discuss its relationship with other species of *Panicum* s.l. and genera of the tribe Paniceae.

DNA extraction was conducted using a modified CTAB protocol similar to that used by Giussani & al. (2001). The *ndhF* gene was amplified via the polymerase chain reaction (PCR) using two pairs of primers specified by Olmstead & Sweere (1994): 5F/972R, and 972F/2110R. These primers, and F536, R536, F1318, and R1821 were used for the sequencing reactions in order to get forward and reverse strands with a minimum overlap of 90%. Cleaning of PCR products and sequencing reactions were performed by Macrogen, Inc. To edit and assemble the sequences, we used the program Chromas Pro version 1.22

(Technelysium Pty, Ltd). The sequences were translated to check for stop codons and then manually aligned using the program BioEdit version 5.0.9 (Hall, 1999). The complete sequence was submitted to Genebank, # DQ415281.

Outgroup selection. — We added the sequence of the *ndhF* corresponding to *Panicum obtusum* into a larger sample that includes all available sequences of *Panicum* (Aliscioni & al. 2003), and a broad sample of the Paniceae representing 35% of the genera of the tribe as selected from Giussani & al. (2001). Sampled taxa of the tribes Andropogoneae, Centotheceae, Paniceae, and Thysanolaeneae (Panicoideae) were similar to that used in Aliscioni & al. (2003), with the exception of *Paspalum* and *Thrasya* (= *Paspalum*). A total of 122 taxa comprise the matrix used in the molecular phylogenetic analyses (Appendix 1). The aligned matrix was submitted to TreeBASE (http://www.treebase.org/treebase/).

Phylogenetic analyses. — A maximum parsimony analysis was performed using Nona version 2.0 (Goloboff, 1997) with all characters equally weighted with respect to codon position and gaps scored as missing data. Overall, 3.5% of the data matrix cells were scored as gaps. Winclada version 1.00.08 (Nixon, 2002) was used as the interphase to construct trees. All informative characters were considered unordered. Searches were performed using "mult*1000". It stores one most-parsimonious tree in memory per replicate, and repeats the process 1,000 times. The shortest trees retained from the subsearches were then TBR swapped with the "max*" command and terminated when it found more than 20,000 trees. A consensus tree was generated from the most parsimonious trees. To assess the relative support for clades, bootstrap analyses were performed: a total of 1,000 replicates of heuristic searches were done using random taxon entry followed by tree bisection-reconnection (TBR).

RESULTS

Leaf blade anatomy

Panicum obtusum is a C_4 species, with Kranz anatomy of the MS (XYMS-) subtype (Hattersley & Watson, 1976; Brown, 1977; Ellis, 1977) characterized by having a single mestome sheath surrounding the vascular bundles and in contact with the metaxylem vessels. This mestome sheath presents specialized chloroplasts, and the mesophyll is characterized by the presence of three chlorenchyma cells between consecutive vascular bundles (Hattersley & Watson, 1975).

Leaf blade in transverse section. — *Outline:* open, broadly V-shaped, with the margins slightly recurved; leaf thickness at mid-lamina 185–235 μm, arms of the lamina symmetrical. *Ribs and furrows:* slightly flat-topped or rounded adaxial ribs, abaxial ribs and furrows indistinguishable; ribs associated with first- and second-order vascular bundles; furrows ⅙–⅛ deep in relation to the width of the lamina. *Keel:* developed, variable in side, flattened on the abaxial side and rounded on the abaxial side, associated with adaxial colorless parenchyma and 1 first-order and 2–4 third-order vascular bundles. *Vascular bundle arrangement:* 6–7 first-order, 8–10 second-order, and 30–36 third-order vascular bundles in the entire blade; 1 second-order vascular bundle and 5–6 third-order vascular bundles between consecutive first-order vascular bundles; first- and second-order vascular bundles centrally located in the blade, although third-order vascular bundles are slightly abaxially displaced. First-order vascular bundles elliptical in outline; phloem adjoined to the Kranz vascular bundle sheath; angular metaxylem vessels in contact with the Kranz cells. Second-order vascular bundles elliptical in outline, with xylem and phloem tissue distinguishable. Third-order vascular bundles angular in outline, located below the bullifom cells, with xylem and phloem tissue indistinguishable. *Vascular bundle sheath:* mestome Kranz cells sheath of the first-order vascular bundles entire or with abaxial interruption of sclerenchyma girders, consisting of 20–25 rounded and inflated cells; with uniformly thickened walls; mestome Kranz sheath of second-order vascular bundles elliptical in outline, entire, without extensions, formed by 12–17 cells rounded and inflated cells; mestome Kranz sheath of the third-order vascular bundles circular in outline, complete, without extensions, formed by 6–10 cells similar to the ones of the second vascular bundles. *Sclerenchyma:* small, adaxial and abaxial girders associated with the first-order vascular bundles, absent on the second-order and third-order vascular bundles or associated as abaxial strands; fiber lignified; small, rounded sclerenchyma caps located in leaf margins. *Mesophyll:* chlorenchyma not radiately arranged; three chlorenchyma cells between consecutive vascular bundles. *Adaxial epidermal cells:* bulliform cells fan-shaped, in restricted groups of 3–6 cells, occupying up to ½ the leaf thickness in the adaxial furrows. Epidermal cells small, regular in outline, papillae, macrohairs or prickles absent. *Abaxial epidermal cells:* bulliform cells absent, cuticle thickened; macrohairs, prickles, and papillae absent (Fig. 1 A, B).

Abaxial epidermis in surface view. — *Zonation:* costal and intercostal zones distinguishable; costal zone formed by 3 to 5 rows of long cells; intercostal zone consisting of 5 to 7 rows of long cells. *Intercostal cells:* elongated rectangularly, more than 3 times longer than wide; side walls parallel, end walls vertical, and anticlinal walls slightly thickened; rectangular cells with moderately undulated anticlinal walls. *Stomata complex:* triangular, 1 to 2 rows of stomata in each intercostal zone. *Intercostal short cells:* absent or present, solitary, trans-

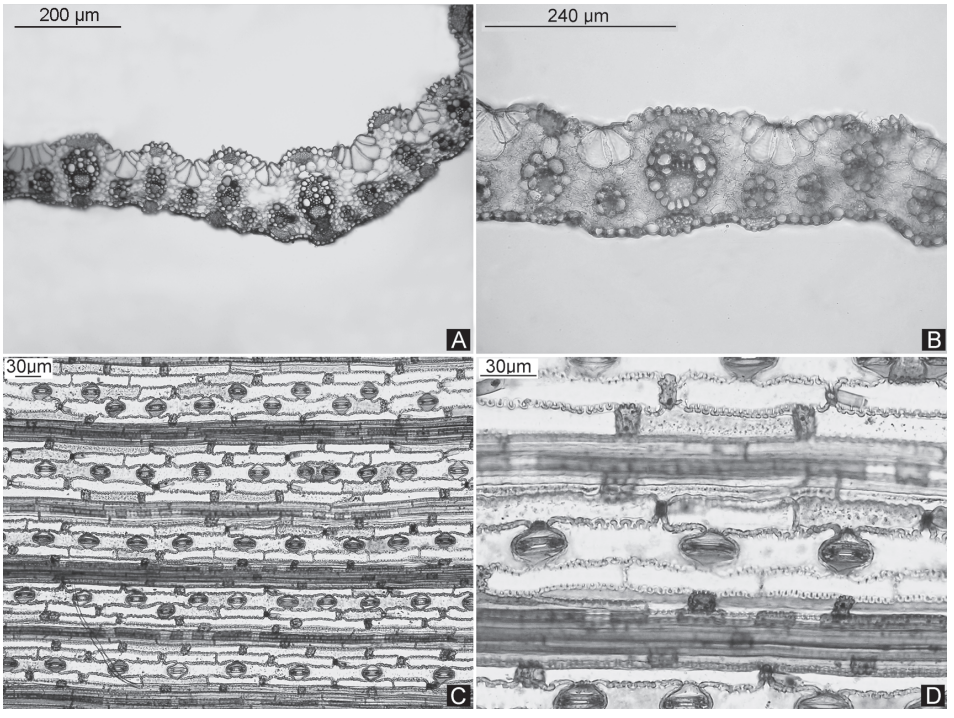

Fig. 1. Leaf blade anatomy of *Hopia obtusa* (= *Panicum obtusum*). A–B, transverse leaf section. A, general aspect of the keel, with portions of the leaf blade; B, portion of the leaf blade showing first-, second-, and third-order vascular bundles. C–D, abaxial epidermis. C, epidermal zonation with narrow intercostal zones; D, detail of stomata, with triangular subsidiary cells, rectangular long cells with moderately undulating anticlinal walls, bicellular microhairs, and short cells. (A–D, based on *Zuloaga & al. 7381*.)

versely elongated when present. *Microhairs:* bicellular, finger-like, with basal cell slightly longer than the distal cells. *Macrohairs:* absent. *Papillae:* absent. *Prickles:* absent or present, in the costal zone when present. *Silica bodies:* transversely elongated, present over the first- and second-order vascular bundles; intercostal silica bodies irregular in outline, transversely elongated (Fig. 1 C, D).

Adaxial epidermis in surface view. — Epidermal cells similar to the abaxial surface, except for the presence of a central band of rectangular cells, 2 to 4 cells wide, in the intercostal zones.

Molecular phylogeny

The dataset has 122 taxa and 2,061 base pairs, including indels. A total of 432 characters were phylogenetically informative and used in the analyses. The cladistic analyses found more than 20,000 most parsimonious trees of 1,464 steps (CI = 0.43, RI = 0.79). The high number of trees are found because there is no resolution among species or taxa of well supported clades such as the *Paspalum* clade.

Both specimens of *Panicum obtusum* form a well-supported clade with a 99% bootstrap (BS) value (Fig. 2). *Panicum obtusum* was included in the Paniceae with $x = 10$, within a highly supported clade (BS = 99%) that includes *Panicum tuerckheimii* Hack. and *Panicum validum* Mez, both from *Panicum* sections *Tuerckheimiana* and *Valida* respectively, *Anthaenantiopsis rojasiana* Parodi, and *Paspalum* spp. (Fig. 2). In the consensus tree, *Panicum obtusum* is the sister group to the *Paspalum* clade although not well supported (BS = 59%, Fig. 2). *Panicum tuerckheimii, Panicum validum,* and *Anthaenantiopsis rojasiana* form a third clade with 89% of bootstrap value and constitute the sister group to the *P. obtusum-Paspalum* clade. The relationships among these three clades are variable depending on the taxon sampling. When adding new sequences of *Panicum* sect. *Lorea* Zuloaga to the analysis, the *Panicum tuerckheimii-P. validum-Anthaenantiopsis* clade is the sister group to *Paspalum* clade (Giussani, pers. comm.). Other relationships among the subfamily Panicoideae and *Panicum* species were similar to the results obtained by Giussani & al. (2001) and Aliscioni & al. (2003).

DISCUSSION

Comparison of *Panicum obtusum* with other Paniceae. — *Panicum obtusum* was grouped in the molecular analysis with *Panicum* "incertae sedis" species and

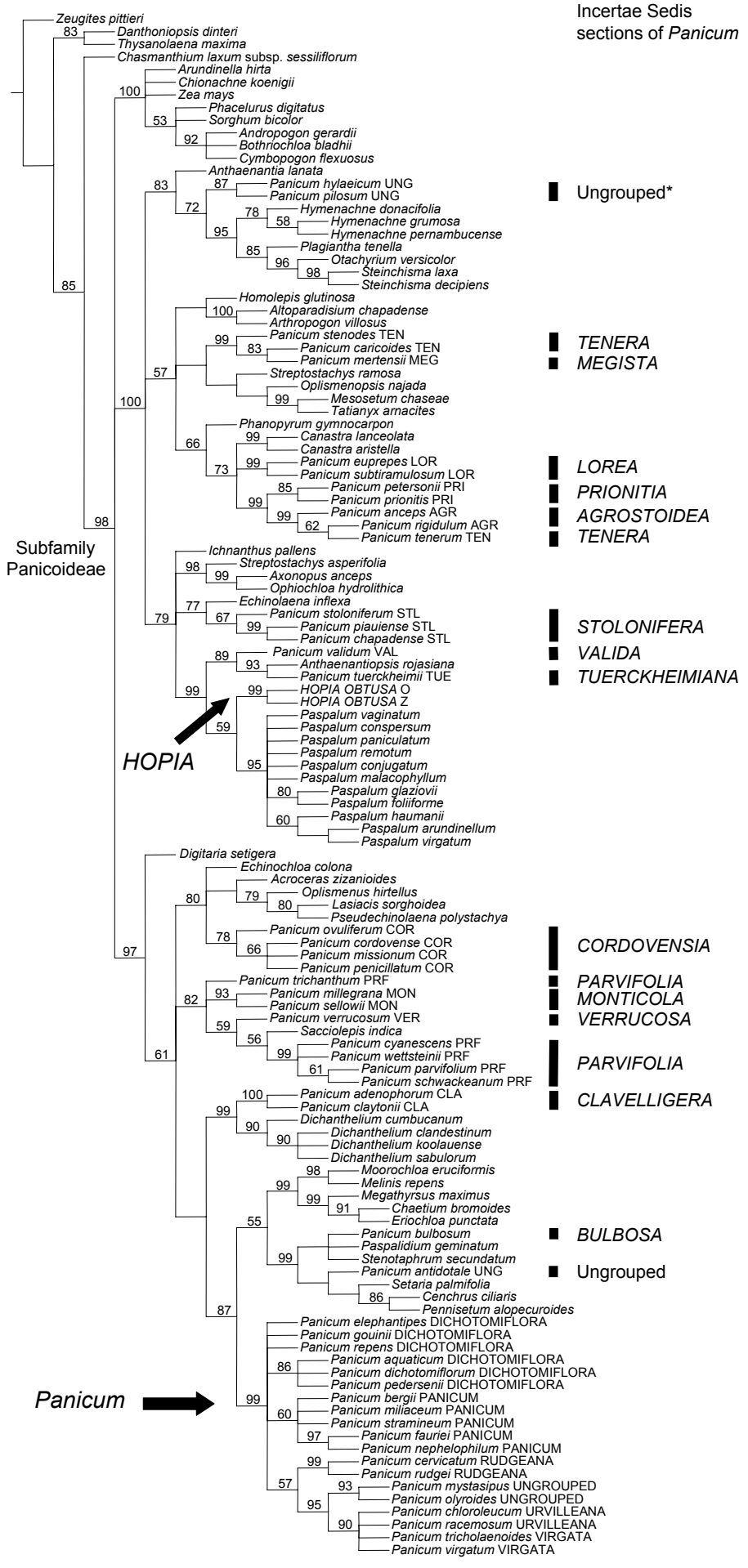

Fig. 2. Strict consensus tree of the Panicoid grasses using the *ndhF* chloroplast gene. Values above branches represent bootstrap values. The phylogeny shows the relationship between two specimens of *Hopia obtusa (= Panicum obtusum)* (O = *Ortiz & Gómez 16K*, AY029659; Z = *Zuloaga & al. 7381*, DQ415281) and related taxa of Paniceae. Sections of *Panicum*, including incertae sedis and ungrouped species are shown on the right side. The first three letters of each sections or ungrouped taxa follow the species names.

****Panicum hylaeicum* and *P. pilosum*, previously treated within sect. *Laxa*, are here considered ungrouped species.**

genera of the Paniceae $x = 10$ clade, therefore departing from species of *Panicum* s.str. Based on shared *ndhF* sequences both accessions of *Panicum obtusum* form a monophyletic clade with 99% bootstrap support. *Panicum obtusum* appears as the sister group to *Paspalum* (Fig. 2), in agreement with results previously found by Giussani & al. (2001) and Aliscioni & al. (2003).

Panicum obtusum is clearly distinguished from *Paspalum* by the shape of the spikelet, the presence and size of the lower glume, the number of nerves of the upper glume and lower lemma, the type of branches (unilateral or not) of the inflorescence, the shape of the rachis, the presence of a lower flower and a lower palea, and the ornamentation of the upper anthecium (Table 1). In *Panicum obtusum* the lower glume is always present and isomorphic, while the glume is usually absent in *Paspalum;* a dimorphic lower glume is only present in species of subgenus *Harpostachys* of *Paspalum* (Denham, 2005, including species previously considered in *Thrasya*). The lower palea and the lower flower are always present in *Panicum obtusum* and usually absent in *Paspalum,* but again occasionally present in species of *Paspalum* subg. *Harpostachys*. *Panicum obtusum* is also characterized by having an upper anthecium with multicellular microhairs and simple papillae present at the apex and bottom of the lemma and palea; this particular arrangement is absent in *Paspalum;* in the latter genus the papillae, when present, are all over the anthecium surface while multicellular microhairs are absent.

As previously mentioned, *Panicum obtusum* has often been considered related to the genus *Thrasyopsis* Parodi (Hitchcock & Chase, 1910; Pilger, 1931). Both differ by the inflorescence type, rachis of the inflorescences, upper glume and lower lemma nervation, and upper anthecium ornamentation (differences summarized in Table 1). Unfortunately, it was not possible to include material of *Thrasyopsis* in the molecular analyses. *Panicum obtusum* has also been considered within the genera *Oplismenus* and *Brachiaria* (= *Moorochloa*) (see synonymy of the species given below); *Oplismenus* is a non-Kranz species with a basic chromosome number of $x = 9$, with glumes awned, and lower lemma usually awned. *Moorochloa* is a Kranz genus, of the PEP-CK subtype, with a basic chromosome number of $x = 9$; it includes species with lower glume reduced, enerved, and upper glume and lower lemma 5-nerved.

Although the *Panicum obtusum*-*Paspalum* clade was present in the consensus tree of all shortest trees, with a low bootstrap value (BS 59%), this relationship is not supported when including species of *Panicum* sect. *Lorea* in the analysis (Giussani, pers. comm.). As a consequence, *Panicum obtusum* and the *Paspalum* clade share common ancestors with *Anthaenantiopsis* Mez ex Pilg. and *Panicum* sections *Tuerckheimiana* and *Valida*, previously classified in *Panicum* subg. *Agrostoides,* and presently considered as "incertae sedis" within the Paniceae. All of these taxa form a well supported clade in our analysis (BS = 99%).

Anthaenantiopsis is a genus of four South American species, ranging from eastern Bolivia, Paraguay and southern Brazil to northern Argentina. The genus is distinguished by having pilose spikelets, spicifom to racemose panicles, scale-like lower glumes, staminate lower flowers, upper lemmas with membranous margins, and the upper palea gaping at anthesis (Morrone & al., 1993).

Panicum sect. *Tuerckheimiana* is monotypic and includes *P. tuerckheimii*, a species restricted to forests, rivers, and margins of trails in southern Mexico (Chiapas and Veracruz), Belize, Guatemala, and Nicaragua. The species is characterized by having an open panicle, pubescent to glabrous spikelets, a scale-like lower glume, lower palea reduced or absent, lower flower absent, and the upper anthecium cartilaginous with the lemma margins closed, not exposing the tip of the palea.

Panicum sect. *Valida* is also monotypic and includes *P. validum,* which grows near rivers and streams in eastern Argentina and western Uruguay. This species is characterized by having a caespitose habit, with blades conspicuously keeled, open panicles, glabrous spikelets, with the lower glume ¾ the length of the spikelet, 1- or 3-nerved, and the lower palea and lower flower present. The upper anthecium also has multicellular microhairs at the apex, a character already reported by Zuloaga & al. (1989). Similar microhairs were previously reported on the leaf blade epidermis (Türpe, 1967) or upper anthecium (Denham, 2005) in *Paspalum,* and were also described in *Guaduella* Franch. (subfamily Bambusoideae) (Jacques-Félix, 1955; Metcalfe, 1960).

Panicum obtusum is unrelated to *Panicum* s.str., as defined by Aliscioni & al. (2003). *Panicum,* as presently circunscribed, includes species with membranous-ciliate or ciliate ligules, open and lax inflorescences, spikelets ellipsoid to long-ellipsoid, with the upper anthecium indurated, with simple or compound papillae at the top of the palea and without multicellular microhairs. In addition, all species of *Panicum* s.str. differ by C_4 carbon fixation, by having the NAD-me subtype, and a basic chromosome number of $x = 9$.

Based on its distinctive morphology and the results of the molecular-phylogenetic analysis, *Panicum obtusum* is transferred here to the new, monotypic genus *Hopia*.

TAXONOMIC TREATMENT

Hopia Zuloaga & Morrone, **gen. nov.** – Type: *Panicum obtusum* Kunth, Nov. Gen. Sp. 1: 98. 1815 [1816] ≡ *Hopia obtusa* (Kunth) Zuloaga & Morrone.

Table 1. Comparison of *Hopia obtusa* with related taxa.

Character	*Hopia*	*Paspalum*	*Thrasyopsis*	*Anthaenantiopsis*	*Panicum* s. str.	*Panicum tuerckheimii*	*Panicum validum*
Spikelets	Biconvex	Plano-convex or concavo-convex	Biconvex	Biconvex	Biconvex	Plano-convex	Plano-convex
Lower glume	Present, isomorph, 4/5–1/1 the length of the spikelet	Usually absent, when present dimorphic	Present, squamiform or up to 4/5 the length of the spikelet, not dimorphic	Present, squamiform	Present (1/3)1/2–3/4(4/5), (1–)5–7(–11), isomorphic	Present 1/3–1/5, neverless, isomorphic	Present, 3/4, (1–)3, isomorphic
Upper glume nervation	7–11	3–5(–7)	11–17	5–7(–9)	7–9(–13)	5	5(–7)
Lower lemma nervation	7–9	3–5	7–9	5–7(–9)	7–9(–13)	3–5	5(–7)
Rachis	Triquetrous	Narrow to broad foliaceous or membranous	Narrow to broad foliaceous	Triquetrous	Triquetrous to filiform	Triquetrous	Triquetrous
Rachis	Ending in a spikelet	Ending in a spikelet	Ending in a naked point	Ending in a spikelet	Ending in a spikelet	Ending in a spikelet	Ending in a spikelet
Branches of the inflorescence	Not unilateral	Unilateral	Unilateral	Not unilateral	Not unilateral	Not unilateral	Not unilateral
Lower palea	Present	Usually absent	Present	Present	Present or absent	Absent to reduced	Present
Lower flower	Present	Absent	Present	Present	Present or absent	Absent	Present
Upper anthecium	Multicellular microhairs present, and simple papillae at the apex and base	Multicellular microhairs absent, simple papillae all over surface or absent	Multicellular microhairs absent, strong simple papillae all over surface present	Multicellular microhairs absent; macrohairs and prickle toward the apex; simple papillae all over surface or up 2/3	Multicellular microhairs absent; simple papillae or compound papillae toward the apex	Multicellular microhairs absent; simple papillae all over surface; macrohairs and pickles present toward the apex	Multicellular microhair present, simple papillae all over surface
Distribution	Southwestern USA and Mexico	Central USA to Argentina	Southern Brazil	Southern Brazil, Paraguay, Bolivia, and northern Argentina	Pantropical	Southern Mexico to Nicaragua	Southern Brazil to eastern Argentina

= *Panicum* unranked *Obtusa* Hitchc., N. Amer. Fl. 3(2): 200, 209. 1915

= *Panicum* sect. *Obtusa* Pilg., Notizbl. Bot. Gard. Berlin-Dahlem 11(104): 243. 1931.

Gramina perennia, rhizomatosa, rhizomatibus brevibus, validis, stolonibus reptantibus late efferentibus; culmi simplices. Ligulae membranaceae. Laminae lineari-lanceolatae. Inflorescentiae contractae, spiculae ellipsoideae ad ovoideas, biconvexae, glabrae. Gluma infera 3/4–4/5 quam spicula longior, 3–7-nervia. Gluma supera 7–11 nervia, lemmate infero aequans, lemma inferum 7–11 nervium. Flos inferus praesens. Anthoecium superum ovoideum, induratum, micro pilis et papillis simplicibus apicem versus et basin ornato.

Rhizomatous perennial, with short and strong rhizomes and producing widely creeping stolons; culms simple. Ligules membranous. Blades linear-lanceolate. Inflorescences contracted, spikelets ellipsoid to obovoid, biconvex, glabrous. Lower glume 3/4–4/5 the length of the spikelet, 3–7-nerved. Upper glume and lower lemma subequal, upper glume 7–11-nerved. Lower flower present. Upper anthecium obovoid, indurate, with microhairs and simple papillae toward the apex and base.

Hopia obtusa (Kunth) Zuloaga & Morrone, **comb. nov**.
≡ *Panicum obtusum* Kunth, Nov. Gen. Sp. 1: 98. 1815 [1816] ≡ *Oplismenus obtusum* (Kunth) Smyth, Trans. Kansas Acad. Sci. 16: 164. 1899 ≡ *Brachi-*

aria obtusa (Kunth) Nash, Man. Fl. N. States 77. 1901 – Type: Mexico: "In planitie montana Regni Mexicani, prope Guanaxuato, 1080 hexap N 4204," *F.W.H.A. Humboldt & A.J.A. Bonpland s.n.* (holotype: P!; isotypes: B, not seen, LE!, P!, US-808888!, fragment and photo ex P, US-2907466!, fragment ex B). Figs. 3–4.

= *Panicum polygonoides* Müll. Hal., Bot. Zeitung (Berlin) 19(44): 323. 1861, *nom. illeg.* – Type: United States of America. Texas: without locality, *T. Drummond 371* (isotype: US-80927!, fragm. ex B).

Description. — Rhizomatous perennial, with short and strong rhizomes and producing widely creeping stolons, up to 2 m long, with long internodes; cataphylls densely villous; erect *culms* 15–80 cm tall, geniculate or not at the base, simple; internodes cylindrical, hollow, glabrous; nodes pale, glabrous or covered with long whitish hairs. *Sheaths* striate, usually shorter than the inter-

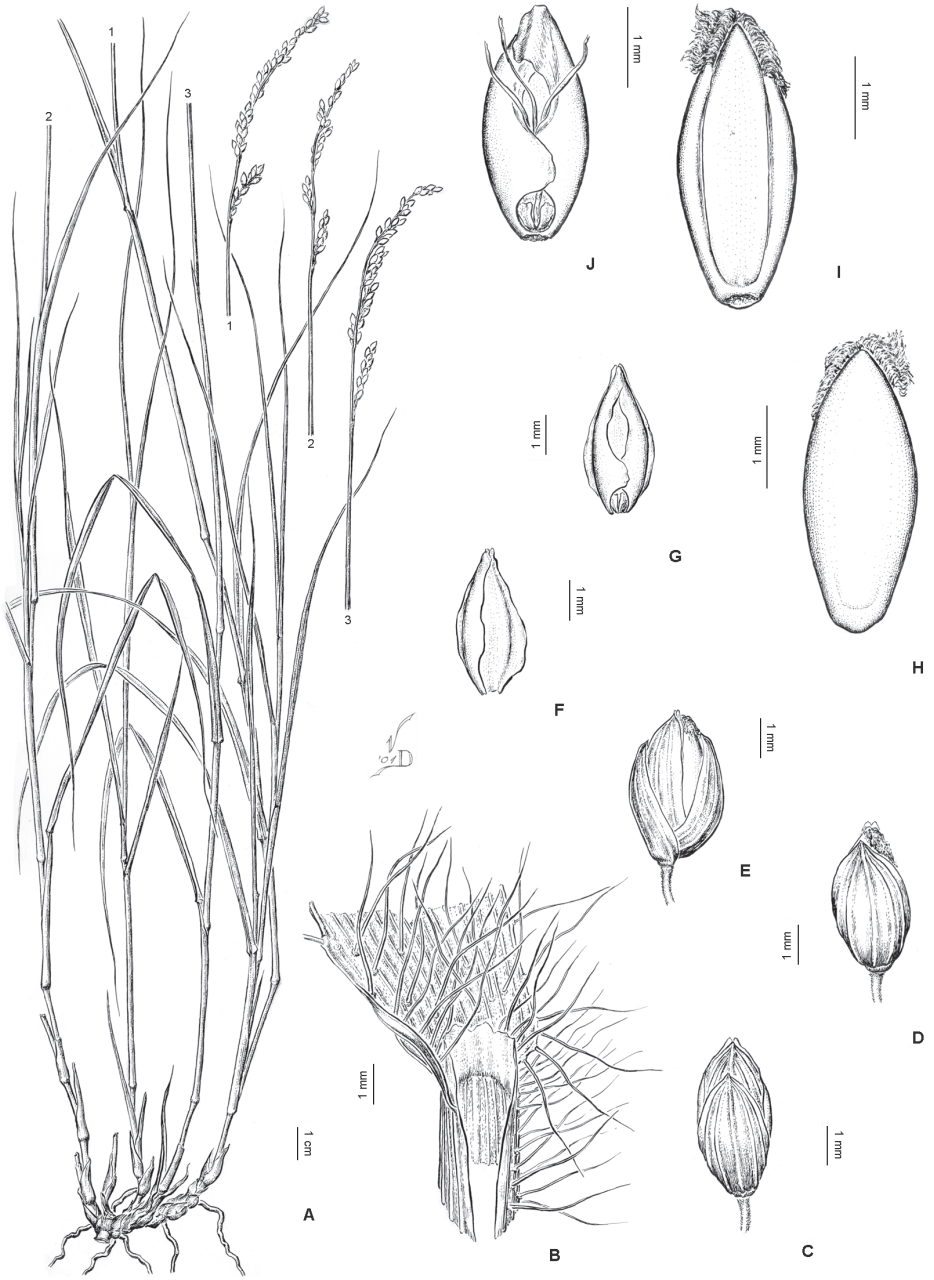

Fig. 3. *Hopia obtusa*. A, habit; B, detail of ligule; C, spikelet, dorsal view; D, spikelet, ventral view; E, spikelet, lateral view; F, lower palea, dorsal view; G, lower palea, ventral view; H, upper anthecium, dorsal view; I, upper anthecium, ventral view; J, upper palea, lodicules, filaments and gynoecium (from *Zuloaga & al. 7381*).

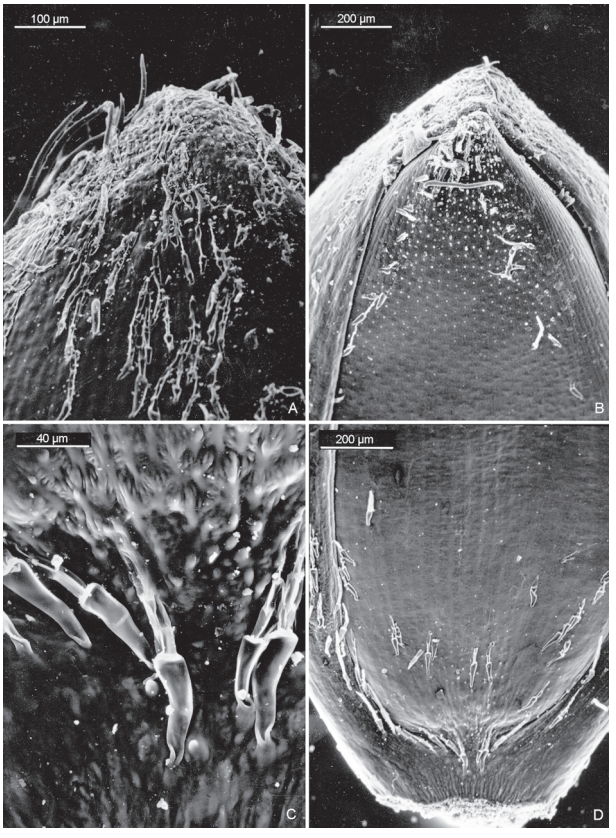

Fig. 4. Scanning electron micrographs of the upper anthecia of *Hopia obtusa*. A, apex of the upper lemma with multicellular microhairs, macrohairs, and simple papillae; B, apex of the upper palea; C, upper lemma with simple papillae and multicellular micohairs; D, base of the upper palea with multicellular microhairs and simple papillae (from *Hitchcock 7563*).

nodes, the lower ones hirsute, with short papillose-pilose hairs, the upper ones glabrous, the margins membranous. *Ligules* 1–2 mm long, membranous, with sparse papillose-pilose hairs beneath at the base of the blade; collar brown, glabrous. *Blades* 3.5–20 cm long, 0.2–0.4 cm wide, linear-lanceolate, flat or with slightly involute margins, narrow at the base, the apex attenuate, glabrous on both surfaces or the adaxial surface with long papillose-pilose, whitish hairs at the lower portion. *Inflorescences* 3–20 cm long, 1–2 cm wide, terminal, exserted and contracted; peduncles 5–30 cm long, flattened, smooth and glabrous; main axis flattened, smooth, glabrous; pulvini short-pilose, first-order branches ascendent, appressed to the main axis, alternate, axis of the branches triquetrous, scabrous; pedicels in pairs, claviform, short, the lower spikelet usually aborted. *Spikelets* 3–3.8 mm long, 1.4–1.7 mm wide, ellipsoid to obovoid, biconvex, pale brown or tinged with purple, glabrous, glumes and lower lemma rigid. *Lower glume* ¾–⅘ the length of the spikelet, 3–7-nerved, the nerves anastomosed toward the apex, acute, glabrous. *Upper glume* and *lower lemma* subequal, the upper glume 7–11-nerved, obtuse, lower lemma 7–9-nerved, obtuse or acute. *Lower palea* elliptic, membranous, pale, glabrous; lower flower staminate, stamens 3, lodicules 2. *Upper anthecium* 2.9–3.7 mm long, 1.3–1.6 mm wide, obovoid, pale, with multicellular microhairs and simple papillae toward the apex and base, and unicellular macrohairs at the apex of the lemma; stamens 3, anthers 1.4–1.5 mm long; stigma 2, styles free at the base; lodicules 2, conduplicate, 7–9-nerved. *Caryopsis* not seen.

Phenology. — Flowering between April and October.

Chromosome number. — $2n = 20$, 40 (Brown, 1950; Gould, 1966, 1968). Brown (1948) reported a chromosome count of $2n = 36$, although omitting the reference. This is most likely a mistaken count.

Common names. — "Zacate guía", "zacate gramilla", "panizo mesquite", "purga de paridas" (Mexico, Beetle & al., 1999).

Etymology. — The generic epithet makes reference to the Hopi Native Americans ("the peacable people"), a tribe native to, as the new genus, the southwestern United States.

Distribution and habitat. — *Hopia obtusa* is found in the southwestern United States, northern and central Mexico (Fig. 5), in open areas on sandy, and gravelly soils; it is frequent along roadsides and in cultivated fields, streambanks, ditches, also present in edge of forests, between sea level and 2,850 m elevation. According to Beetle & al. (1999) it is a good source of forage, remaining green throughout the winter.

For the examined specimens see Appendix 2.

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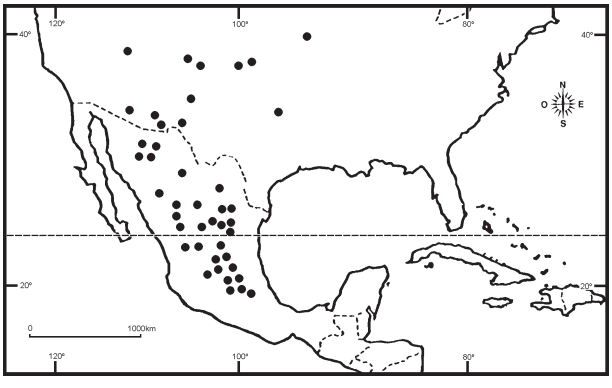

Fig. 5. Map of western North America showing the distribution of *Hopia obtusa*.

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LITERATURE CITED

Aliscioni, S.S., Giussani, L.M., Zuloaga, F.O. & Kellogg, E.A. 2003. A molecular phylogeny of *Panicum* (Poaceae: Paniceae). Tests of monophyly and phylogenetic placement within the Panicoideae. *Amer. J. Bot.* 90: 796–821.

Barkworth, M.E. 2004. *Manual of Grasses for North America and North of Mexico.* University of Utah, Logan. (http://herbarium.usu.edu/webmanual/)

Beetle, A.A., Villegas Durán, G., Bolaños Medina, A., Miranda Sánches, J.A., Aragón Melchor, L., Vergara Batalla, M.A., Chimal Hernández, A., Castillo Badillo, M.M., Galván García, O.M., Villalpando Prieto, J.L., Lizama Manrique, M., Valdés-Reyna, J., Manrique de Skendzic, E., & Rodríguez-Rodríguez, A.M. 1999. *Las Gramíneas de México.* V. Secretaria de Agricultura, Ganadería y Desarrollo Rural, y Recursos Hidraulícos: COTECOCA-SAGAR, México.

Bentham, G. 1881. Notes on Gramineae. *J. Linn. Soc. Bot.* 19: 14–134.

Bentham, G. & Hooker, J.D. 1883. Gramineae. *Genera Plantarum* 3: 1074–1215. L. Reeve & Co., London.

Breakwell, E. 1914. A study of the leaf anatomy of some native species of the genus *Andropogon* (Gramineae). *Proc. Linn. Soc. New South Wales* ser. 2, 39: 385–394.

Brown, W.V. 1948. A cytological study in the Gramineae. *Amer. J. Bot.* 35: 382–395.

Brown, W.V. 1950. Chromosome numbers of some Texas grasses. *Bull. Torrey Bot. Club.* 78: 63–76.

Brown, W.V. 1977. The Kranz syndrome and its subtype in grass systematics. *Mem. Torrey Bot. Club* 23: 1–97.

Chase, A. 1906. Notes on genera of the Paniceae I. *Proc. Biol. Soc. Wash*. 19: 183–192.

Chase, A. 1908a. Notes on genera of the Paniceae II. *Proc. Biol. Soc. Wash*. 21: 1–10.

Chase, A. 1908b. Notes on genera of the Paniceae III. *Proc. Biol. Soc. Wash*. 21: 175–188.

Chase, A. 1911. Notes on genera of the Paniceae IV. *Proc. Biol. Soc. Wash.* 24: 103–160.

Crins, W.J. 1991. The genera of Paniceae (Gramineae: Panicoideae) in the Southeastern United States. *J. Arnold Arbor. Suppl. Ser.* 1: 171–312.

Denham, S.S. 2005. Revisión sistemática del subgénero *Harpostachys* de *Paspalum* (Poaceae: Panicodieae: Paniceae). *Ann. Missouri Bot. Gard.* 92: 463–532.

Duvall, M.R., Noll, J.D. & Minn, A.H. 2001. Phylogenetics of Paniceae (Poaceae). *Amer. J. Bot.* 88: 1988–1992.

Ellis, R.P. 1976. A procedure for standardizing comparative leaf blade anatomy in the Poaceae. I. The leaf blade as viewed in transverse section. *Bothalia* 12: 65–109.

Ellis, R.P. 1977. Distribution of the Kranz syndrome in the southern African Eragrostoideae and Panicoideae according to bundle sheath anatomy and cytology. *Agroplantae* 9: 73–110.

Ellis, R.P. 1979. A procedure for standardizing comparative leaf blade anatomy in the Poaceae. II. The epidermis as seen in surface view. *Bothalia* 12: 641–672.

Ellis, R.P. 1988. Leaf anatomy and systematics of *Panicum* (Poaceae: Panicoideae) in southern Africa. *Monogr. Syst. Bot. Missouri Bot. Gard.* 25: 129–156.

Freckmann, R.W. & Lelong, M.G. 2003. Nomenclatural changes and innovations in *Panicum* and *Dichanthelium* (Poaceae: Paniceae). *Sida* 20: 161–174.

Giussani, L.M., Cota-Sánchez, J.H., Zuloaga, F.O. & Kellogg, E.A. 2001. A molecular phylogeny of the grass subfamily Panicoideae (Poaceae) shows multiple origins of C_4 photosynthesis. *Amer. J. Bot.* 88: 1993–2012.

Goloboff, P.A. 1997. *NONA* version 2.0 for windows. Computer program and documentation distributed by the author, http://www.cladistics.com.

Gómez-Martínez, R. & Culham, A. 2000. Phylogeny of the subfamily Panicoideae with emphasis on the tribe Paniceae: evidence from the *trnL-F* cpDNA region. Pp. 136–140 in: Jacobs, S.W.L. & Everett, J.E. (eds.), *Grasses: Systematics and Evolution*. Commonwealth Scientific and Industrial Research Organization (CSIRO) Publishing, Collingwood.

Gould, F.W. 1966. Chromosome numbers of some Mexican grasses. *Canad. J. Bot.* 44: 1683–1696.

Gould, F.W. 1968. Chomosome number of Texas grasses. *Canad. J. Bot.* 46: 1315–1325.

Hackel, E. 1887. Gramineae. Pp. 1–97 in: Engler, A. & Prantl, K. (eds.), *Natürliche Pflanzenfamilien* II, 2. Engelmann, Leipzig.

Hall, T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucl. Acids Symp. Ser.* 41: 95–98.

Hattersley, P.W. 1987. Variation in photosynthetic pathway. Pp. 49–64 in: Soderstrom, T.R., Hilu, K.W., Campbell, C.S. & Barkworth, M.E. (eds.), *Grass Systematics and Evolution*. Smithsonian Institution Press, Washington, D.C.

Hattersley, P.W. & Watson, L. 1975. Anatomical parameters for predicting photosynthetic pathways of grasses leaves: The "maximum lateral cell count" and the "maximum cells distans count". *Phytomorphology* 25: 325–326.

Hattersley, P.W. & Watson, L. 1976. C_4 grasses: An anatomical criterion for distinguishing between NADP-Malic enzyme species and PCK or NAD-Malic enzyme species. *Austral. J. Bot.* 24: 297–308.

Hitchcock, A.S. & Chase, A. 1910. The North American species of *Panicum*. *Contr. U.S. Natl. Herb.* 15: 1–396.

Hitchcock, A.S. & Chase, A. 1915. Tropical North American species of *Panicum*. *Contr. U.S. Natl. Herb.* 17: 459–539.

Hooker, J.D. 1897. Gramineae. *Flora of British India,* vol. 7: 1–422. L. Reeve & Co., London.

Hsu, C.C. 1965. The classification of *Panicum* (Gramineae) and its allies, with special reference to the characters of lodicule, style-base and lemma. *J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot.* 9: 43–150.

Jacques-Félix, H. 1955. VI. Notes sur les graminées D'Afrique Tropicale. *J. Agric. Trop. Bot. Appl.* 2: 423–430.

Linnaeus, C. 1753. Panicum. *Species Plantarum,* vol. 1: 55–59. Stockholm, Salvius. (Fascimile edition: London, 1957)

Metcalfe, C. R. 1960. *Anatomy of the Monocotyledons.* Clarendon Press, Oxford.

Morrone, O., Filgueiras, T.S., Zuloaga, F.O. & Dubcovsky, J. 1993. Revision of *Anthaenantiopsis* (Poaceae: Panicoideae: Paniceae). *Syst. Bot.* 18: 434–453.

Nixon, K.C. 2002. *WinClada* ver. 1.00.08. Published by the author, Ithaca (http://www.cladistics.com).

Olmstead, R.G. & Sweere, J.A. 1994. Combining data in phylogenetic systematics: an empirical approach using three molecular data sets in the Solanaceae. *Syst. Biol.* 43: 467–481.

Pilger, R. 1931. Bemerkungen zu *Panicum* und verwandten Gattungen. *Notizbl. Bot. Gart. Berlin-Dahlem* 11: 240–245.

Simon, B.K. & Jacobs, S.W.L. 2003. *Megathyrsus,* a new generic name for *Panicum* subgenus *Megathyrsus*. *Austrobaileya* 6: 571–574.

Türpe, A.M. 1967. Histotaxonomía de las especies argentinas del género *Paspalum*. *Lilloa* 32: 35–299, 497–498.

Webster, R.D. 1988. Genera of the North American Paniceae (Poaceae: Panicoideae). *Syst. Bot.* 13: 576–609.

Zuloaga, F.O. 1987. Systematics of New World Species of *Panicum* (Poaceae: Paniceae). Pp. 287–306 in: Soderstrom, T.R., Hilu, K.W., Campbell, C.S. & Barkworth, M.E. (eds.), *Grass Systematics and Evolution*. Smithsonian Institution Press, Washington, D.C.

Zuloaga, F.O., Dubcovsky, J. & Morrone, O. 1993. Infrageneric phenetic relations in New World *Panicum* (Poaceae: Panicoideae: Paniceae): a numerical analysis. *Canad. J. Bot.* 71: 1312–1327.

Zuloaga, F.O., Morrone, O., Davidse, G., Filgueiras, T.S, Peterson, P.M., Soreng, R.J. & Judziewicz, E.J. 2003. Catalogue of New World Grasses (Poaceae): III. Subfamilies Panicoideae. Aristidoideae, Arundinoideae, and Danthonioideae. *Contr. U.S. Natl. Herb.* 46: 7–662.

Zuloaga, F.O., Morrone, O. & Dubcovsky, J. 1989. Exomorphological, anatomical, and cytological studies in *Panicum validum* (Poaceae: Panicoideae: Paniceae): its systematic position within the genus. *Syst. Bot.* 14: 220–230.

Zuloaga, F.O., Morrone, O. & Giussani, L.M. 2000. A cladistic analysis of the Paniceae: a preliminary approach. Pp. 123–135 in: Jacobs S.W.L. & Everett, J.E. (eds.), *Grasses: Systematics and Evolution*. Commonwealth Scientific and Industrial Research Organization (CSIRO) Publishing, Collingwood.

Zuloaga, F.O., Morrone, O., Vega, A.S. & Giussani, L.M. 1998. Revisión y análisis cladístico de *Steinchisma* (Poaceae: Panicoideae: Paniceae). *Ann. Missouri Bot. Gard.* 85: 631–656.

Appendix 1. List of taxa used in the molecular analysis, voucher information of the new sequence, and GenBank accession numbers.

Tribe Centotheceae. *Chasmanthium laxum* (L.) H.O. Yates subsp. *sessiliflorum* (Poir.) L.G. Clark, U27296; *Danthoniopsis dinteri* (Pilg.) C.E. Hubb., AY029695; **Tribe Thysanolaenae**. *Thysanolaena maxima* (Roxb.) Kuntze, U21984; *Zeugites pittieri* Hack., U21987. **Tribe Andropogoneae**. *Andropogon gerardii* Vitman, AF117391; *Bothriochloa bladhii* (Retz.) S.T. Blake, AF117395; *Chionachne koenigii* (Spreng.) Thwaites, AF117397; *Cymbopogon flexuosus* (Nees ex Steud.) Will. Watson, AF117404; *Phacelurus digitatus* (Sibth. & Sm.) Griseb., AF117418; *Sorghum bicolor* (L.) Moench, U21981; *Zea mays* L., U21985. **Tribe Arundinelleae.** *Arundinella hirta* (Thunb.) Tanaka, AF117393. **Tribe Paniceae** (not *Panicum*). *Acroceras zizanioides* (Kunth) Dandy, AY029618; *Altoparadisium chapadense* Filg. & al., AY029619; *Anthaenantia lanata* (Kunth) Benth., AY029640; *Anthaenantiopsis rojasiana* Parodi, AY029620; *Arthropogon villosus* Nees, AY029622; *Axonopus anceps* (Mez) Hitchc., AY029623; *Canastra aristella* (Döll) Zuloaga & Morrone, *Longhi 9659,* DQ355988; *C. lanceolata* (Filg.) Morrone & al., AY029621; *Cenchrus ciliaris* L., AY029625; *Chaetium bromoides* (J. Presl) Benth. ex Hemsl., AY029626; *Dichanthelium clandestinum* (L.) Gould, AY188461; *D. cumbucana* (Renvoize) Zuloaga, AY188464; *D. koolauense* (H. St. John & Hosaka) C.A. Clark & Gould, AY029627; *D. sabulorum* (Lam.) Gould & C.A. Clark, AY029654; *Digitaria setigera* Roth ex Roem. & Schult., AY029629; *Echinochloa colona* (L.) Link, AY029631; *Echinolaena inflexa* (Poir.) Chase, AY029633; *Eriochloa punctata* (L.) Desv., AY029634; *Homolepis glutinosa* (Sw.) Zuloaga & Soderstr., AY029637; *Hopia obtusa* (Kunth) Zuloaga & Morrone, *Ortiz & Gómez 16K,* AY029659; *Zuloaga & al. 7381,* DQ415281; *Hymenachne donacifolia* (Raddi) Chase, AY029635; *H. grumosum* (Nees) Zuloaga, AY188468; *H. pernambucense* (Spreng.) Zuloaga, AY188478; *Ichnanthus pallens* (Sw.) Munro ex Benth., AY029638; *Lasiacis sorghoidea* (Desv.) Hitchc. & Chase, AY029639; *Melinis repens* (Willd.) Zizka, AY029675; *Megathyrsus maximus* (Jacq.) B.K. Simon & S.W.L. Jacobs, AY029649; *Mesosetum chaseae* Luces, AY029641; *Moorochloa eruciformis* (Sm.) Veldkamp., AY188452; *Ophiochloa hydrolithica* Filg. & al., AY029642; *Oplismenopsis najada* (Hack. & Arechav.) Parodi, AY188453; *Oplismenus hirtellus* (L.) P. Beauv., AY029644; *Otachyrium versicolor* (Döll) Henrard, AY029643; *Paspalidium geminatum* (Forssk.) Stapf, AY029662; *Paspalum arundinellum* Mez, AY029663; *P. conjugatum* Bergius, AY029669; *P. conspersum* Schrad. ex Schult., AY029666*; P. foliiforme* S. Denham, AY029690; *P. glaziovii* (A.G. Burm.) S. Denham, AY029689; *P. haumanii* Parodi, AY029664; *P. malacophyllum* Trin., AY029671; *P. paniculatum* L., AY029667; *P. remotum* J. Remy, AY029668; *P. vaginatum* Sw., AY029665; *P. virgatum* L., AY029670; *Pennisetum alopecuroides* (L.) Spreng., AY029672; *Phanopyrum gymnocarpon* (Elliott) Nash, AY188469; *Plagiantha tenella* Renvoize, AY029674; *Pseudechinolaena polystachya* (Kunth) Stapf, AY029676; *Sacciolepis indica* (L.) Chase, AY029677; *Setaria palmifolia* (J. König) Stapf, AY029680; *Steinchisma decipiens* (Nees ex Trin.) W.V. Br., AY188499; *S. laxa* (Sw.) Zuloaga, AY029655; *Stenotaphrum secundatum* (Walter) Kuntze, AY029684; *Streptostachys asperifolia* Desv., AY029687; *S. ramosa* Zuloaga & Soderstr., AY029686; *Tatianyx arnacites* (Trin.) Zuloaga & Soderstr., AY029688.

Panicum* sect. *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. & Chase, AY188489. **Section *Rudgeana*** (Hitchc.) Zuloaga. *P. cervicatum* Chase, AY188459; *P. rudgei* Roem. & Schult., AY029661. **Section *Urvilleana*** (Hitchc.) Pilg. *P. chloroleucum* Griseb., AY188460; *P. racemosum* (P. Beauv.) Spreng., AY188481. **Section *Virgata*** Hitchc. & Chase ex Pilg. *P. tricholaenoides* Steud., AY188493; *P. virgatum* L., U21986. **Ungrouped.** *P. mistasypus* Zuloaga & Morrone, AY188474; *P. olyroides* Kunth, AY188475.

Appendix 1. Continued.

Panicum incertae sedis. **Section *Agrostoidea*** Hitchc. & Chase ex C.C. Hsu. *Panicum anceps* Michx., AY188455; *P. rigidulum* Bosc ex Nees, AY188482. **Section *Bulbosa*** Zuloaga. *P. bulbosum* Kunth; AY029648. **Section *Clavelligera*** Stapf. *P. adenophorum* K. Schum., AY188454; *P. claytonii* Renvoize, AY188462. **Section *Cordovensia*** Parodi. *P. cordovense* E. Fourn., AY188463; *P. missionum* Ekman, AY188473; *P. ovuliferum* Trin., AY029653; *P. penicillatum* Nees ex Trin., AY188477. **Section *Lorea*** Zuloaga. *P. euprepes* Renvoize, AY029657; *P. subtiramulosum* Renvoize & Zuloaga, AY188490. **Section *Megista*** Pilg. *P. mertensii* Roth, AY188471. **Section *Monticola*** Stapf. *P. millegrana* Poir., AY029660; *P. sellowii* Nees, AY188484. **Section *Parvifolia*** Hitchc. & Chase ex Pilg. *P. cyanescens* Nees ex Trin., AY188465, *P. parvifolium* Lam., AY188476; *P. schwackeanum* Mez, AY188483; *P. trichanthum* Nees, AY188492; *P. wettsteinii* Hack., AY188497; **Section *Prionitia*** Zuloaga. *P. petersonii* Hitchc. & Ekman, AY188479; *P. prionitis* Nees, AY029652. **Section *Stolonifera*** Hitchc. & Chase ex Pilg. *P. piauiense* Swallen, AY029656; *P. stoloniferum* Poir., AY188488; *P. chapadense* Swallen, AY188486. **Section *Tenera*** Hitchc. & Chase ex Pilg. *P. caricoides* Nees ex Trin., AY188458. *P. stenodes* Griseb., AY188487; *P. tenerum* Beyr. ex Trin., AY188491. **Section *Tuerckheimiana*** (Hitchc.) Zuloaga. *P. tuerckheimii* Hack., AY188494. **Section *Valida*** Zuloaga & Morrone. *P. validum* Mez, AY188495. **Section *Verrucosa*** Hitchc. & Chase ex C.C. Hsu. *P. verrucosum* Muhl., AY188496. **Ungrouped.** *P. antidotale* Retz., AY188456; *P. hylaeicum* Mez, AY188470; *P. pilosum* Sw., AY188480.

Appendix 2. Representative specimens examined: COUNTRY. STATE: Location, Collector (Herbarium Acronym).

MEXICO. AGUASCALIENTES: 11 mi N of Rincon de Romos, *Shreve 9244* (US); Aguascalientes, *Hitchcock 7456* (US); Valladolid, Municipio Pabellón, *Martínez Guerra s.n.* (MEXU 266681); Rancho Tres Elenas, *Morones s.n.* (MEXU 266971); near city of Aguascalientes, *Rose & Hay 6231* (MEXU). CHIHUAHUA: 10 km E of Ciudad Jiménez, *Harvey 1349* (US); Majalca, *Harvey 1480* (US); 40 km W of Chihuahua, 1,735 m, *Harvey 1551* (US); valley near Chihuahua, *Pringle 476* (F, MEXU, US); 2 mi W of Pozo de Villa, *Johnston 8164* (MEXU, MO); on flood plain of small river about 2 mi N of Natachic, *Reeder & al. 1241* (MEXU); La Campana, *Almeida 132* (MEXU); 10 mi W of General Trias off Hwy. 16, *Ellis & al. 937* (MEXU). COAHUILA: 2 mi W of Saltillo, road to Torreón, *Harvey 1095* (US); 3 km W of Santa Elena, *Stewart 834* (MO, US); Torreón, along ditch, *Hitchcock 7563* (US); 50 km S of Monclova, 585 m, *Harvey 1124* (US); Torreón, *Palmer 504* (MEXU, MO); La Ventura, *Nelson 3908* (F, US); Saltillo, *Palmer 394* (F, MO, US), *Hitchcock 5582* (US); 41 mi W of Saltillo, *Gould 11542* (US); Santa Rosa mountains, *Marsh 1535* (F); about 5 mi S of Saltillo, *Barkley 16049* (F); in dry steep walled canyon, 5 km NE of Jimulco, *Stanford & al. 125* (MO); open country between Rancho Santo Domingo and Hacienda Piedra Blanca, *Wynd & Mueller 486* (MO). DURANGO: Road from Gómez Palacio to Fresnillo, 39 km SE of Cuencame, *Koch 74158* (MEXU, US); 25 mi NW of La Zarca, *Soderstrom 827* (US); Tepehuanes, *Fisher 44195* (MO, US); about 8 mi S of Matamoros along Highway 7, *Reeder & al. 1269* (MEXU); city of Durango and vicinity, *Palmer 175* (F, MEXU, MO, RB); km 3 de la carretera Santiago Papasquiaro-Los Altares, *Benítez 1809* (MEXU). GUANAJUATO: Irapuato, *Hitchcock 7407* (US); Obregón, *Hitchcock 5801* (US); about 6 kms N of San Francisco del Rincón, *Sohns 365* (US); 5 km al NE de Salvatierra, sobre la carretera a Celaya, *Rzedowski 38563a* (MEXU). HIDALGO: Tailings dam from Loreto Mill, Santa Julia near Venta Prieta, *Moore Jr. 3087* (US); near Tula, along railroad, *Rose & al. 8356* (US); Mun. Huichapán, km 30.7 al E de carr. 57, sobre carr. 45, *Cowan 4008* (MEXU, MO); 5 km al este de Huichapán, desvío a Chichimequillas, *Hernández Magaña 4539* (MEXU); Chapantongo, *Finney & al. s.n.* (MEXU). JALISCO: Ojuelos, *Díaz Luna 14533* (MO); Rancho Ledesma, Lagos de Moreno, 1950 m, *Melgoza & Martín 208* (MEXU). MEXICO: San Juan de Teotihuacán, *Vera Santos 2196* (MO); Tepexpán, *Matuda 19017* (MO). NUEVO LEÓN: Mun. Galeana, *Chase 7749* (MO, US); Monterrey, *Hitchcock 5533* (US); Hacienda Pablillo, Galeana, *Taylor 150* (F); El Jarro, localizado a 14 km de la cabecera municipal de Dr. Arroyo, por la carretera Dr. Arroyo-Matehula, *Garza & Castillo 187* (SI). PUEBLA: Tehuacán, along railway ditch, *Hitchcock 6060* (US); vicinity of Puebla, *Arséne 1595* (US); cerros al N de San Antonio Texcala, *Chiang & al. 2072* (MO); Tehuacán, *Purpus 1464* (LA); autopista de Puebla a Tehuacán, 11 km N de Tehuacán, *Zuloaga & al. 7381* (SI). QUERÉTARO: without locality, *Arséne 10263* (F, MO, US); Querétaro, *Hitchcock 5813* (US); near San Juan del Río, *Rose & al. 9552* (MEXU, US). SAN LUIS POTOSÍ: San Luis Potosí, *Hitchcock 5657* (US), *Schaffner 148* (F, P, US); Mun. Charcas, Laguna Seca, *Rzedowski 6528* (US); Charcas, *Whiting 583* (MO); near San Juan del Río, *Rose & al. 9594* (MEXU); Santo Domingo, km 30 carretera San Luis-Valles, *Bravo 10* (MEXU). SONORA: Nogales to Cocospora ranch, *Griffiths 6800* (US); Colonia Morelos, *Vera Santos 1882* (MEXU, MO), *2065* (US); 3 mi E of Agua Prieta, road to Colonia Morelos, *Vera Santos 1752* (F, MEXU, MO); rocky south-facing slope, 27 km NE of Cananea, *Reeder & Felger 8101* (MEXU); San Pedro, *Hartman 820* (MO). ZACATECAS: near Concepción del Oro, *Palmer 266* (F, MO, US); on mountain 18 km W of Concepción del Oro, *Stanford & al. 582* (MO, US); 6 mi S of Sierra Hermosa, *Johnston 7419* (F, US); on Hacienda de Zaragosa, Llano de Zaragosa, *Gentry 8502* (US); along Hwy. 45, 9.3 mi NW of state line of Zacatecas, *Dunn & al. 22572* (MO); 50 km N of Escondida junction on Mex. 54, *Brunken & Perino 473* (MO); about 3 mi from San Alto in thorn forest of Mesquite, *Reeder & al. 1314A* (MEXU). UNITED STATES OF AMERICA. ARIZONA: Pima County, near Box Canyon road just off of Highway 83, *Gould 2889* (SI); Cochise, *Gardner 213* (MO); Santa Cruz, *Gould & al. 2401* (MO). COLORADO: El Paso, *Christ 1104* (MO); Otero, *Williams 2496* (MO). KANSAS: Clark, *Palmer 41865* (MO); Seward, *Goodman 2219* (MO); Stanton, *Hitchcock 572* (MO). MISSOURI: Boone, *Planchuelo 413* (MO). NEW MEXICO: Socorro, *Vasey s.n.* (P). OKLAHOMA: Fort Sill, *Clemens 11453* (P); Major, *Stevens 1732* (MO). TEXAS: El Paso, *Jones 4168* (MO, P); Brown, *Palmer 13033* (MO). UTAH: San Juan, *Holmgren 3808* (MO).