Ophiochloa, a New Endemic Serpentine Grass Genus (Poaceae: Paniceae) from the Brazilian Cerrado Vegetation

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ABSTRACT. *Ophiochloa* is described and illustrated as a new, monotypic genus and new species of the Digitariinae, Paniceae, from Goiás, Brazil, characterized by ligules a row of hairs, solitary, unilateral, winged racemes that end in a sterile projection, adaxial spikelets, specialized, narrow 2-nerved lower lemma with 2 prominent setae, and hyaline, free, upper lemma and palea tips. It is a C_4 grass with Kranz anatomy. Its putative relationships are discussed. The new species is a narrow, serpentine endemic that grows on rocks along intermittent or permanent streams in the ultramafic rock belt of the cerrado of central Brazil.

Serpentine soils occur in many parts of the world, and they often support a flora that is generally poorly diversified but highly endemic (Brooks, 1987). These soils are derived from ultramafic rocks and because they are characterized by high concentrations of magnesium, iron, nickel, chromium, and cobalt plus abnormally low levels of some plant macronutrients such as potassium, calcium, and phosphorus, they provide an unusual environment for plants (Brooks, 1987).

During a recent botanical survey carried out in the municipality of Niquelândia in the Brazilian state of Goiás, where previous fieldwork had detected serpentine soil and the presence of a serpentinic adapted flora (Brooks et al. 1990; Davidse & Filgueiras, 1993; Filgueiras & Davidse, in prep.), an interesting grass was collected that could not be placed in any described genera of the Poaceae (Clayton & Renvoize, 1986; Webster et al., 1989; Watson & Dallwitz, 1992). This plant is here described as a new genus and a new species.

Ophiochloa hydrolithica Filgueiras, Davidse & Zuloaga, gen. et sp. nov. TYPE: Brazil. Goiás: Município de Niquelândia, Macedo, (14°18′S–48°23′W), ca. 20 km N da cidade, crescendo dentro dágua, sobre pedras, em pequeno riacho temporário e brejo adjacente, única população vista, 4 Aug. 1992, *T. S. Filgueiras & R. D. Lopes 2438* (holotype, SP; isotypes, CANB, IBGE, ISC, K, L, LE, MO, PRE, RB, SI, UB, UFG, US). Figures 1–3.

Leptocoryphio Nees spiculis membranaceis, flosculo superiore cuprino, lemmate superiore marginibus aplanatis apicem versus, apice hyalino et palea superiore hianti apice similis sed ligula pilis seriatis, inflorescentia racemo solitario ac axillari racemo adjecto, rhachidi alata projectura sterili in extremitate, spiculis sessilibus, gluma superiore 2-nervia, hyalina, spiculae aequanti arcte flosculum superiorem amplectanti, lemmate inferiore 2-nervio, hyalino, dense ciliato-pectinato prompter distinguitur.

Densely caespitose perennial with a dense accumulation of wiry, adventitious roots and old culm bases forming a compact mass. Culms 54–78 cm tall, erect, stiff, unbranched in the vegetative portion, with 7–11 elongated internodes; internodes hollow, glabrous, stramineous; nodes dark, glabrous. Leaves basal and cauline; sheaths rounded on the back, persisting for some time, striate, glabrous, the margins free, hyaline, glabrous, the apex much broader than the base of the blade, without auricles; ligule a minute fringe of hairs, V-shaped and continuous with the hyaline shoulder of the sheath apex, the hairs to 0.5 mm long, the hairs behind the ligule to 6.5 mm long, whitish; collar undifferentiated; blades 10–19.2 cm long, 0.5–1 mm wide, setaceous, glabrous but with a few scattered, whitish hairs to 6.3 mm long, U-shaped in cross section with an adaxial groove, becoming nearly circular toward the apex, the apex subpungent, slightly scaberulous. Inflorescences solitary, unilateral, spike-like racemes, 1 terminal and usually 1 axillary per

Figure 1. *Ophiochloa hydrolithica* Filgueiras, Davidse & Zuloaga. —A. Habit. —B. Portion of the leaf in the ligular area showing the broad, hyaline sheath margins and adaxial groove of the leaf blade. —C. Portion of the winged rachis showing the solitary, adaxial spikelets. —D. Lower portion of the spikelet showing the upper glume and the free, 2-nerved lower lemma. —E. Upper glume, flattened. —F. Lower lemma with 2 prominent setae. —G. Apex of the lower lemma showing the prominent, pectinate-ciliate nerves with the pustulose bases of the setae. —H. Spikelet viewed from the back of the upper glume. —I. Upper floret, viewed from the palea side. J–K. Caryopsis. —J. Embryo view. —K. Hilum view. [Based on *Filgueiras & Lopes 2438* (SI).]

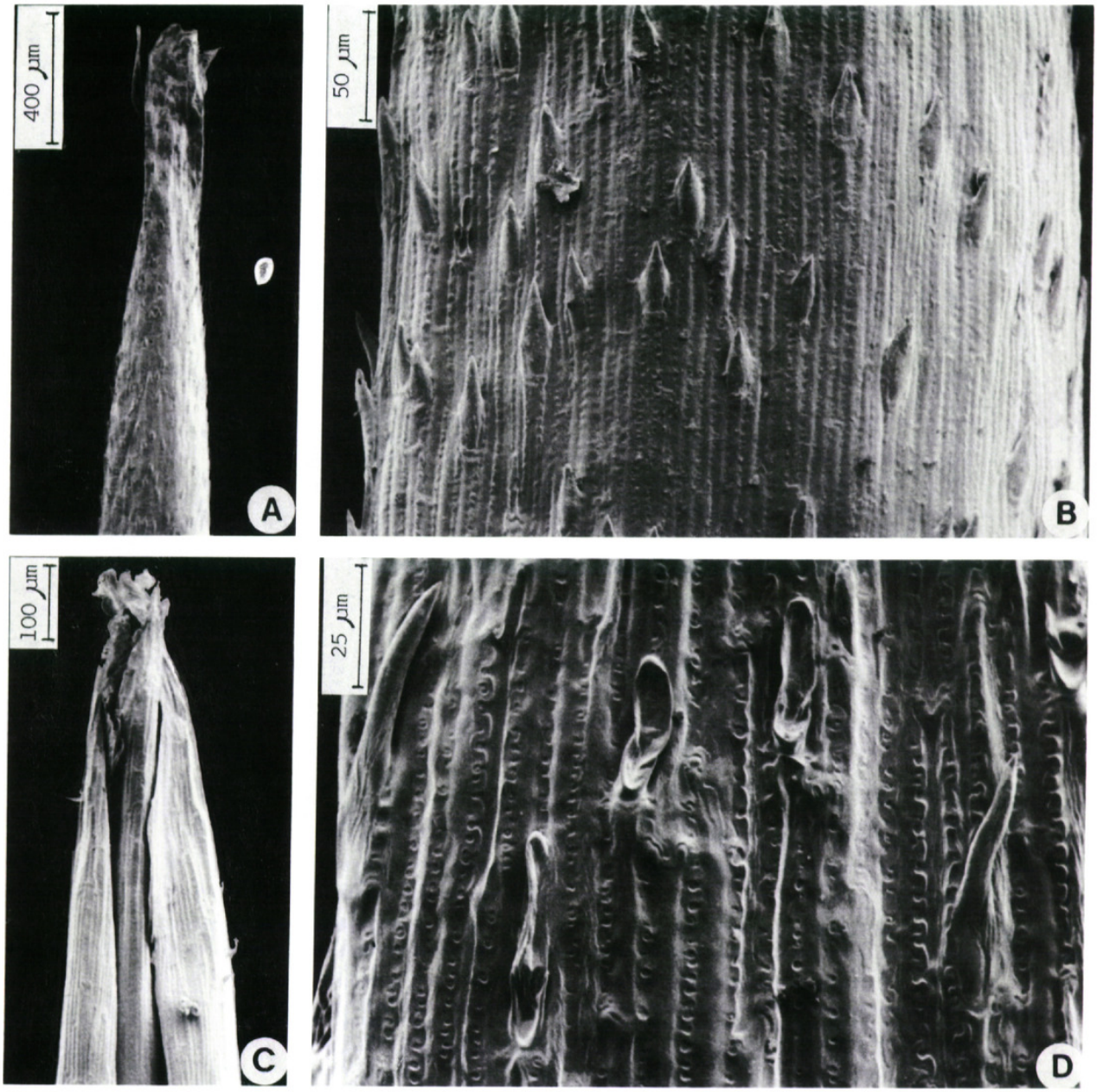

Figure 2. SEM photomicrographs of the spikelet of *Ophiochloa hydrolithica* Filgueiras, Davidse & Zuloaga. —A. Upper glume. —B. Detail of upper glume with prickle hairs and scattered bottlelike microhairs. —C. Apex of the upper floret showing the hyaline, free tips of the upper lemma and palea. —D. Detail of the upper lemma with bottlelike microhairs and prickle hairs. [Based on *Filgueiras & Lopes 2438* (SI).]

culm; peduncles 6–21 cm long, well exserted, delicate; prophyll at the base of the axillary branch 2-keeled, membranous, pale, about half as long as the subtending leaf sheath; racemes 6.6–9.2 cm long, erect to drooping at maturity, acuminate apically; rachis winged, the wings 0.9–1.1 mm wide, membranous, partially enclosing the spikelets, the central portion light green, nerved, the midrib shortly ciliate and narrowly winged with colorless, hyaline tissue, the marginal wings hyaline, colorless, rarely purplish, irregular, glabrous or sparingly ciliate, the rachis apex extending beyond the spikelets as a sterile projection to 5 mm long; pedicels minute, to ca. 0.5 mm long, adnate to the midrib. Spikelets 2.3–3.1 mm long, 0.4–0.5 mm wide, solitary, awnless, all alike, bisexual, alternately arranged on each side of the midrib, dorsally compressed, adaxial, narrowly oblong-lanceolate in outline, disarticulating below the glume and falling as a single unit, with 2 florets; lower glume absent; upper glume as long as the spikelet, 2.3–3.1 mm long, faintly 2-nerved, colorless, hyaline, glabrous, the surface covered by prickle hairs and with scattered bottlelike microhairs, embracing the upper floret but leaving the lower lemma free in mature spikelets, acute apically, the apex irregularly erose and minutely ciliolate; lower

floret sterile, without a lower palea, consisting only of a lower lemma 1.5–2.0 mm long, narrow, hyaline except for the stout nerves, colorless, strongly 2-nerved, the apex acute, ciliolate, the nerves marginal, densely pectinate-ciliate, the cilia to 1.5 mm long, with bulbous bases, whitish, the uppermost cilia on each side of the margins 5–7 mm long, stout, equal to subequal in size, rarely unequal, flexuous, straight or curled; upper floret 1.9–2.2 mm long, copper-colored, bisexual; upper lemma 1.9–2.2 mm long, indistinctly nerved, membranous except at the apex, covered with numerous bottlelike microhairs and a few prickle hairs, a germination flap not evident, the margins undifferentiated, somewhat inrolled in the lower half, flat and free from the palea in the upper $\frac{1}{5}$–$\frac{1}{6}$, the apex acute, colorless, hyaline; upper palea 1.8–2.2 mm long, colorless, hyaline, 2-nerved, the apex minutely 2-notched, gaping; lodicules 2, conduplicate, ca. 0.1 mm long; ovary ca. 0.2–0.3 mm long; styles 2, separate; stigmas 2, plumose, yellow or purple, terminally exserted; stamens 2, rarely 3, terminally exserted, the anthers 1.3–1.7 mm long, purple. Caryopsis narrowly obovate to clavate, 1–1.2 mm long, ca. 0.2 mm wide, with persistent stylar bases, vinaceous; embryo $\frac{4}{10}$–$\frac{5}{10}$ as long as the caryopsis; hilum punctate-oblong, basal, $\frac{1}{10}$–$\frac{2}{10}$ as long as the caryopsis.

Paratypes. BRAZIL. **Goiás:** Niquelândia, Fonte da Bica, ca. 10 km da cidade, 19 May 1993, *T. S. Filgueiras & F. C. de A. Oliveira 2466* (G, IBGE, ICN, MEXU, MO, R, RB, SPF); mata galeria, 19 May 1993, *T. S. Filgueiras & F. C. de A. Oliveira 2460* (IBGE, sterile); Macedo, 19 May 1997, *T. S. Filgueiras & F. C. de A. Oliveira 2452* (IBGE, UEC).

Spikelet interpretation in *Ophiochloa* is not without difficulty, primarily because of the unusual structure of the second bract, which, although certainly not homologous, nevertheless somewhat resembles the pedicel of a *Bothriochloa* Kuntze pedicellate spikelet because of the hyaline central portion, well-developed, marginal, pectinate-ciliate nerves, and lack of tissue to the outside of the nerves. Furthermore, the basal margins of the first bract do not overlap the narrow base of the second bract so that the relative position of these two bracts is somewhat ambiguous. Because it is prominently 2-nerved, there is thus a question whether this bract represents the lemma or palea of the lower floret. However, in very young spikelets still enclosed within the sheaths in which the large cilia are not yet divergent, the margins of the lower bract do embrace the nerves and cilia of the second bract, at least in the upper $\frac{3}{4}$. This is consistent with the relative position of the lower lemma in a Paniceae spikelet. As discussed further below, it also seems homologous to the somewhat similar 2-nerved lower lemma of *Paspalum ceresia* (Kuntze) Chase, a species where this bract clearly represents a lower lemma. Finally, as far as we know, the lower floret of the Paniceae is never reduced to only a palea, whereas it is frequently reduced to only a lemma.

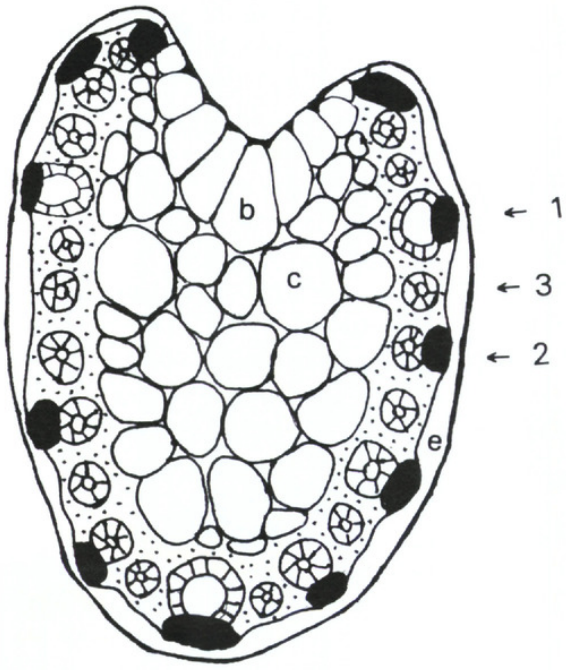

Figure 3. Diagrammatic cross section of leaf blade of *Ophiochloa hydrolithica* Filgueiras, Davidse & Zuloaga. Solid black = sclerenchyma strands; stippled area = chlorenchyma; b = bulliform cells; c = colorless cells; e = epidermis and cuticle; 1 = first-order vascular bundle; 2 = second-order vascular bundle; 3 = third-order vascular bundle. Scale line = 0.1 mm. [Based on *Filgueiras & Lopes 2438* (MO).]

Ophiochloa is tentatively placed in subtribe *Digitariinae* Butzin, sensu Clayton & Renvoize (1986), because of the dorsally compressed spikelets, upper glume as long as the spikelet, lower floret reduced to a membranous sterile lemma, upper lemma membranous with the apex hyaline and not enclosing the palea, and palea hyaline and free at the apex. However, the following combination of characters make it unique in the subtribe: ligule a row of minute hairs without any membrane, solitary racemes that are both terminal and axillary and that end in a sterile projection, adaxial spikelets, hyaline, 2-nerved, colorless upper glume embracing the upper floret but leaving the lower lemma free, 2-nerved, hyaline lower lemma. *Ophiochloa* is an odd member of the subtribe, but homogeneity is not by any measure a characteristic feature of the group (Clayton & Renvoize, 1986).

The relationships of the new genus within subtribe Digitariinae are not readily apparent and therefore merit special remarks. Based primarily on the sim-

ilarity of the morphology of the spikelets, *Ophiochloa* appears to be most similar to *Leptocoryphium* Nees and *Anthaenantia* P. Beauvois. They are alike in lacking a lower glume and in having a membranous or somewhat cartilaginous, copper-colored or dark brown upper floret with hyaline tips, and a palea free from the lemma apex. But *Ophiochloa* is readily distinguished from these because in both genera the inflorescence is an open panicle, the spikelets are long pedicellate, the pedicel apex is cupulate, and the upper glume and lower lemma are similar in size and texture and 5-nerved. Although the texture of the upper lemma in *Anthaenantia* and *Leptocoryphium* is not indurate, it is clearly firmer than that of *Ophiochloa*. [Although both Clayton & Renvoize (1986) and Watson & Dallwitz (1992), describe the spikelets of *Anthaenantia* as laterally compressed, they are clearly dorsally compressed, with the side of the lower lemma somewhat flattened in comparison to the side of the upper glume.] Four other genera in the Digitariinae, *Acritochaete* Pilger, *Baptorhachis* Clayton & Renvoize, *Megaloprotachne* C. E. Hubbard, and *Stereochlaena* Hackel, all African, have racemes with unilateral spikelets. However, all have paired, clearly pedicellate spikelets. *Baptorhachis* is most similar in that it is the only genus of the four with a solitary raceme and a winged rachis, and the lower glume absent. However, *Baptorhachis* differs from *Ophiochloa* by its annual habit, ciliolated membranous ligule, raceme rachis ending in a spikelet, paired spikelets, upper glume and lower lemma awned, 3-nerved, the lateral nerves thickened and bearing a dense tuft of hairs, the upper lemma tightly clasping the upper palea, and stamens 3 (Clayton & Renvoize, 1986; Watson & Dallwitz, 1992).

Ophiochloa also resembles species of *Digitaria* Haller in sect. *Solitaria* Hackel because of the shortly pedicellate, solitary spikelets in two rows on a winged rachis, but in these species the upper glume is never 2-nerved and hyaline and it does not tightly embrace the upper floret, leaving the lower lemma free. Furthermore, the spikelets are abaxial, the racemes are always several to many, the upper floret is indurated, and the tips of the upper lemma and palea are not hyaline.

Outside the Digitariinae, *Ophiochloa* bears the closest resemblance to *Axonopus* P. Beauvois, [Setariinae Dumortier, sensu Clayton & Renvoize (1986)] especially in inflorescence structure and spikelet orientation. They share the following characters: unilateral racemes, axillary inflorescences, adaxial spikelets, lower glume absent, delicate texture of the upper glume and lower lemma, lower floret reduced to a lemma, upper floret frequently brown, and rachis sometimes winged. However, *Axonopus* is quite distinct in the more indurate upper floret in which the upper lemma and palea is never hyaline at the apex and the palea apex is always enclosed by the lemma, the lower lemma is never narrowed and is always enclosed by the margins of overlapping of the upper glume, and the racemes are two to numerous (rarely one in axillary inflorescences).

Two other genera of the Setariinae with unilateral racemes, solitary spikelets, membranous or chartaceous upper florets, and a free palea apex are *Reimarochloa* Hitchcock and *Paratheria* Grisebach. However, both genera have abaxial spikelets. Furthermore, *Reimarochloa* is quite distinct on the basis of its stoloniferous habit and spikelets lacking both glumes. *Paratheria* is very different in having each raceme deciduous and falling as one unit with the single attached spikelet, the basal portion of the raceme rachis forming a pungent callus with the rest of the raceme functioning like an awn.

Another genus of the Setariinae with adaxial, solitary, racemes and sometimes awnless spikelets is *Mesosetum* Steudel. *Ophiochloa* resembles *Mesosetum* by the solitary raceme, the adaxial spikelets, the foliaceous rachis of the species in section *Bifaria* (Hackel) Chase, and the pectinate hairs of the lower lemma (Filgueiras, 1989). However, they differ in that *Mesosetum* typically has terminal inflorescences [except *M. chlorostachyum* (Doell) Chase, an annual with terminal and axillary inflorescences], a well-developed lower glume, coriaceous upper glume, 5–7-nerved lower lemma, indurate upper floret, and a linear hilum.

Ophiochloa is superficially similar to the species of *Paspalum* L. subgen. *Ceresia* (Persoon) Reichenbach because of the winged rachis and the sessile spikelets, but in *Paspalum* the spikelets are always abaxial when solitary, and the upper floret is indurate to chartaceous (except in the anomalous *Paspalum saccharoides* Nees with membranous upper floret, and palea longer than the lemma and free at the apex). However, a striking similarity exists between the lower lemma of *Paspalum ceresia* and that of *O. hydrolithica* because they are both narrower than the upper lemma, 2-nerved, and hyaline between the pectinate-ciliate nerves. However, in *P. ceresia* there is a very narrow strip of hyaline tissue on the outer edge of the nerves, whereas this is not present in *Ophiochloa*, i.e., its nerves are strictly marginal. In *P. ceresia* the lemma bears a tuft of stout cilia at the apex.

A clear relationship to *Thrasya* Kunth, which

also has solitary, frequently winged racemes with unilateral spikelets and the apex of the raceme rachis ending in a sterile projection, is excluded because the genus is characterized by alternately adaxial and abaxial spikelets borne in one row due to the adnation of the pedicels of the spikelet pairs to the rachis (Burman, 1985).

The two stout setae at the tip of the margins of the lower lemma of *O. hydrolithica* are quite remarkable as they are hygroscopic. They seem to be functionally comparable to awns and probably play a role in fruit dispersal or fruit positioning for better seedling establishment. The size of these setae was found to be variable. In the spikelets at the base of the raceme they tend to be unequal, with one sometimes considerably shorter than the other. Stout setae can be found in the upper glume and on the lower lemma of several species of *Paspalum* subgen. *Ceresia*, such as *P. bicilium* Mez, *P. heterotrichon* Trinius, *P. polyphyllum* Nees, *P. setiglume* Chase, and *P. trachycoleon* Steudel.

The relative distance between adjacent spikelets is increasingly shorter from the base to the apex of the raceme; consequently, the basal spikelets are relatively distant from each other and the upper ones are congested.

The great majority of the flowers examined had only two stamens, but occasionally flowers with three stamens were also found. Whereas the color of the anthers was always a deep purple, the color of the stigmas varied from yellow to purple in the same raceme.

Anatomy

Gross cross-sectional leaf anatomy was determined from hand-sectioned blade cross sections on temporary slides. The sections were stained in 0.05% Toluidine Blue O in acetate buffer. A diagrammatic cross section made with the aid of a camera lucida is presented as Figure 3.

The blades are permanently infolded and form a reduced U-shape with a shallow groove on the adaxial surface. Three first-order vascular bundles are present, one in the midrib and one each towards the margins. Second-and third-order vascular alternate between the midrib and the marginal first-order bundle, or sometimes up to three side-to-side third-order bundles may be present. All vascular bundles have a single Kranz bundle sheath with chloroplasts that tend to be centrifugally arranged. However, the chloroplasts are large and fill most of the lumen of the bundle sheath cells so that their position in the cell is not certain. There are no cells between the Kranz cells and the metaxylem elements. The Kranz cells of the third-order vascular bundles are the largest in cross section. Sclerenchyma is present only as abaxial strands below the first-and second-order bundles. The sclerenchyma strands interrupt the bundle sheath of first-order vascular bundles but not that of the second-order vascular bundles. The chlorenchyma is indistinctly radiate with only one or two cells between adjacent vascular bundles. There is also usually one cell between the third-order vascular bundles and the epidermis, and between all vascular bundles and the colorless cells. The central portion of the blade is filled with large colorless cells. These colorless cells abut a single row of prominent inflated bulliform cells that make up the adaxial epidermis.

Following the terminology of Hattersley & Watson (1976), *O. hydrolithica* has Kranz, MS (=XyMS−) anatomy. Because of the well-established correlation in the Kranz syndrome between anatomical and physiological characters (Brown, 1977; Ellis, 1977; Hattersley, 1987), we conclude that *O. hydrolithica* is a C_4 species of the NADP-me physiological type or a malate former (Gutiérrez et al., 1974).

Ecology

Ophiochloa hydrolithica is known from three distinct populations: Macedo (the original population discovered in 1992), Mata Galeria, and Fonte da Bica (discovered in 1993). The Macedo population is about 50 m from a road and is very close to a nickel mining operation. Here *Ophiochloa* grows on rocks in running water in a seasonal rivulet and the adjacent marshy area. The population is about 15 m long and 2–3 m wide. The rather caespitose, wiry looking plants grow only along the drainage line, and where the water from the rivulet sinks into the ground in a nearby campo limpo, plants of *Ophiochloa* can no longer be found. Practically all the plants in this population showed some sign of having being previously burned. Although they grew in wet areas, the rivulet dries out in the dry season (May through September), thus exposing the plants to fires.

The Mata Galeria population is located about 2 km E of the Macedo population. These two populations are separated by two steep hills and belong to two different subwatersheds. This appears to be the healthiest of the three populations. Its size is about the same as the Macedo population, but the plants grow in dense, thick stands, and are lush and green in color. The gallery forest itself is about 200 m long and 3–5 m wide. It is located in a remote

area that is difficult of access because the terrain is rugged and stony. As in the Macedo population, the water stops flowing in the dry season. Here *Ophiochloa* grows on rocks in partial shade of the gallery forest, never in the soil.

The Fonte da Bica population is located about 10 km S of Macedo, and apparently is the least fit of the three populations. There are three reasons for this. First, the plants are less dense, i.e., only about 50 clumps were seen, contrasting to over 100 in the other populations. Second, the entire area is fully exposed without any trees or shrubs. Third, there is some disturbance due to human influence in the area as people stop by to drink and collect water from a spring that originates from the bottom of a steep hill situated just beyond the *Ophiochloa* population. In fact, plants of *Ophiochloa* that grow by the "bica" itself are trampled and display a sickly appearance. Dust from an unpaved road nearby covers most plants during the dry season. In this population water flows throughout the year.

The highly specialized habitat of *Ophiochloa* appears to be rare in the area surveyed, and the species is not likely to be abundant elsewhere, although other populations may eventually be found along the ultramafic rock belt of central Brazil. Like the two sister species of *Paspalum* recently described from the same site (Davidse & Filgueiras, 1993; Filgueiras & Davidse, in press), *O. hydrolithica* faces serious threat of imminent extinction due to the nickel mining and smelting operation now taking place at the type locality (Macedo) of this unique serpentine grass. So far no attempt has been made to bring the plant into cultivation.

The generic name refers to a grass that grows on serpentine (ophiolite) rock and the specific epithet refers to a plant that grows on rock in the water.

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Literature Cited

Brooks, R. R. 1987. Serpentine and Its Vegetation. Dioscorides Press, Portland.

———, R. D. Reeves, A. J. M. Baker, J. A. Rizzo & H. D. Ferreira. 1990. The Brazilian serpentine expedition (Braspex), 1988. Natl. Geogr. Res. 6: 205–219.

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

Burman, A. G. 1985. The genus *Thrasya* H. B. K. (Gramineae). Acta Bot. Venez. 14: 7–93.

Clayton, W. D. & S. A. Renvoize. 1986. Genera graminum. Kew Bull., Addit. Ser. 13: 1–389.

Davidse, G. & T. S. Filgueiras. 1993. *Paspalum longiaristatum* (Poaceae: Paniceae), a new serpentine endemic from Goiás, Brazil, and the first awned species in the genus. Novon 3: 129–132.

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.

Filgueiras, T. S. 1989. Revisão de *Mesosetum* Steudel (Gramineae: Paniceae). Acta Amazon. 19: 47–114.

Gutiérrez, M., V. E. Gracen & G. E. Edwards. 1974. Biochemical and cytological relationships in C_4 plants. Planta 119: 279–300.

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

——— & L. Watson. 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.

Tregunna, E. B., B. N. Smith, J. A. Berry & J. S. Downton. 1970. Some methods for studying the photosynthetic taxonomy of the Angiosperms. Canad. J. Bot. 48: 1209–1214.

Watson, L. & M. J. Dallwitz. 1992. The Grass Genera of the World. C. A. B. International, Wallingford.

Webster, R. D., J. H. Kirkbride & J. Valdes Reyna. 1989. New World genera of the Paniceae (Poaceae: Panicoideae). Sida 13: 393–417.