

CARYOPSIS MORPHOLOGY OF *LEPTOCHLOA* SENSU LATO (POACEAE, CHLORIDOIDEAE)

NEIL SNOW¹

Department of Biology
Washington University
Campus Box 1137
St. Louis, MO 63130, U.S.A.

P.O. Box 299
Missouri Botanical Garden
St. Louis, MO 63166, U.S.A.

ABSTRACT

Caryopsis morphology of the grass genus *Leptochloa* was studied regarding the necessity of some authors for segregating *Diplachne*. The data do not support the separation of *Diplachne* from *Leptochloa* based on a putative bimodal distribution of dorsal and lateral cross-sectional compression. The presence or absence of a prominent sulcus and the relative adnation of the pericarp are the only attributes sufficiently distinct to warrant use as phylogenetic markers. However, variations in surface texture and color can be useful regionally as diagnostic characters at the species level.

KEY WORDS: caryopsis, *Leptochloa*, *Diplachne*, morphology, systematics, Poaceae, Chloridoideae.

RESUMEN

Se estudió la morfología del cariósipide del género *Leptochloa* dada la supuesta necesidad de algunos autores de segregar *Diplachne*. Los datos no apoyan la separación de *Diplachne* y *Leptochloa* basada en una supuesta distribución bimodal de la compresión dorsal y en sección transversal lateral. La presencia o ausencia de un surco prominente y la adnación relativa del pericarpo son los únicos atributos suficientemente diferentes para justificar su uso como marcadores filogenéticos. Sin embargo, las variaciones en textura y color de la superficie pueden ser útiles regionalmente como caracteres diagnósticos a nivel específico.

INTRODUCTION

The genus *Leptochloa* P. Beauv. s.l. (including *Diplachne* P. Beauv.) has been the subject of numerous regional systematic studies due to its wide geographic distribution and the relative abundance of herbarium specimens (Hitchcock 1903; Parodi 1927; McNeill 1979; Lazarides 1980; Phillips 1982; Nowack 1994; Nicora 1995). These authors (and others) have disagreed as to whether *Diplachne* should be segregated from *Leptochloa*, thereby mirroring

¹Current Address: Department of Biological Sciences, University of Northern Colorado, Greeley, CO 80639, U.S.A. Email: nsnow@bentley.unco.edu

the differing opinions of two worldwide generic summaries of grasses (Clayton & Renvoize 1986; Watson & Dallwitz 1992). A frequently cited source of evidence to support the segregation of *Diplachne* has been differences in caryopsis features.

Parodi (1927) apparently was the first to examine cross-sectional shapes critically. He partitioned four neotropical species into *Diplachne* or *Leptochloa* based on relative compression (dorsal or lateral) of the caryopsis, and the presence or absence of a hilar groove. He suggested that *Leptochloa chloridiformis* was aberrant in *Leptochloa* because of its lack of a hilar groove (Parodi, l.c.).

Valls (1978) studied the systematic affinities of *Leptochloa dubia* in relation to the generic boundaries of *Leptochloa*. He illustrated cross-sectional profiles and profiles from the embryonic and hilar sides for seven species. The figures revealed a gradation in cross-sectional profile from nearly round in *Diplachne caudata* to somewhat triangular in *Leptochloa virgata* and *L. scabra*, to relatively flattened in *L. fascicularis* (Valls, l.c.: 103). He also concluded that a hilar depression was a tenuous systematic feature. Despite somewhat limited sampling, his results suggested strongly that caryopsis features intergrade too thoroughly to split *Leptochloa* unambiguously into two genera, although he acknowledged that "some grouping of species can be achieved on the basis of caryopsis type" (Valls, l.c.: 105). Unfortunately, his results were never formally published and have not been cited by subsequent authors.

McNeill (1979: 401) and Nicora (1995: 233) repeated almost verbatim the observations of Parodi (1927) without adducing additional data or citing the work of Valls (1978). Lazarides (1980) observed that Australian species generally could be segregated into *Leptochloa* or *Diplachne* on the basis of caryopsis shape, with the exception of *Leptochloa digitata*, with its flattened shape. Phillips (1982: 144) agreed with Parodi (1927) regarding the utility of caryopsis shape for splitting the genera, but noted exceptions in *Diplachne caudata*, *Leptochloa obtusiflora*, and *L. longa*. Nowack (1994) provided a cursory review of caryopsis shapes for Malesian taxa and concluded that the differences set forth by Parodi (1927) were insufficient to permit recognition of segregate genera.

Based on a recent monographic treatment (Snow 1997), *Leptochloa* (including *Diplachne*) represents forty taxa, with one species, *L. monticola* Chase, being of dubious inclusion (Valls 1978; Snow 1996). Prior to this study, relatively few taxa had been examined critically for variation in features of the caryopsis, and much systematic weight had been placed on the meagre observations that existed. In light of lingering debates about generic boundaries between *Leptochloa* and *Diplachne* (Jacobs 1987) and the emphasis previous authors placed on the utility of the caryopsis to segregate these genera, a survey of all currently recognized taxa of *Leptochloa* was undertaken to evaluate whether features of the caryopsis could be useful as phylogenetic markers.

MATERIALS AND METHODS

Caryopses of all currently recognized taxa in *Leptochloa* (Snow 1997) were removed directly from herbarium specimens (Appendix 1), placed under a Nikon SMZ-U dissecting microscope with camera lucida attachment, and the profiles were traced by hand. *Cypholepis yemenicus* was included because it resembles *L. eleusine* and *L. obtusiflora* in several respects (Snow 1996), and was used as an outgroup in preliminary cladistic studies of *Leptochloa* (Snow 1997; see also van den Borre & Watson 1997). In most cases a minimum of three specimens were examined for variation (Appendix 1). The following features were observed: 1) caryopsis shape when viewed from the hilar side ("hilar profile"); 2) caryopsis shape when viewed from a cross-section taken at midpoint with the hilar side oriented above ("cross sectional profile"); 3) the presence or absence of a sulcus or other depression on the hilar side when viewed in cross-section; 4) ornamentation on the outer coat (perisperm); 5) relative adnation of the perisperm to the endosperm, and 6) color of the grain. To standardize the sampled developmental stage, caryopses were selected from spikelets in which florets were beginning to disarticulate, a condition that assures their maturity. In virtually all cases the caryopses from the lowermost floret in the spikelets were selected.

For the sake of precision, descriptive terminology of shapes follows that of the Systematics Association (1962), whereas that of surface ornamentation follows Murley (1951). Given that shape is a continuously varying character, these typologies might not account for the observed and often subtle variations in shape. For example, a caryopsis might have an intermediate elliptic shape of 2.5:1, which is absent from the diagram. Nonetheless, after initial analyses, the diagram shapes appeared adequate to standardize and summarize the majority of both hilar profile and cross-sectional shapes. With respect to cross-sectional shapes, I accounted for the absence of sharp edges by prefixing the terms "obtriangular" (3:2), "shallowly obtriangular" (3:2), and "shallowly obdeltate" with the word "rounded," which more accurately depicts their shapes. To account for concave inflections of the hilar surface (always oriented above, Fig. 2) I used the terms "sulcus" and "depression," depending on the degree of concavity. As used here, a sulcus is a vertical or nearly vertically walled groove; a depression refers to any gradual concavity, and will be further modified by the terms shallow, moderate, deep, narrow, and broad. These subjective terms were deemed necessary to describe the observed variation.

RESULTS

The hilar profile for most species was some variation of obovate or elliptic (Fig. 1; Table 1). Only four taxa had ovate hilar profiles (*L. fusca* subsp.

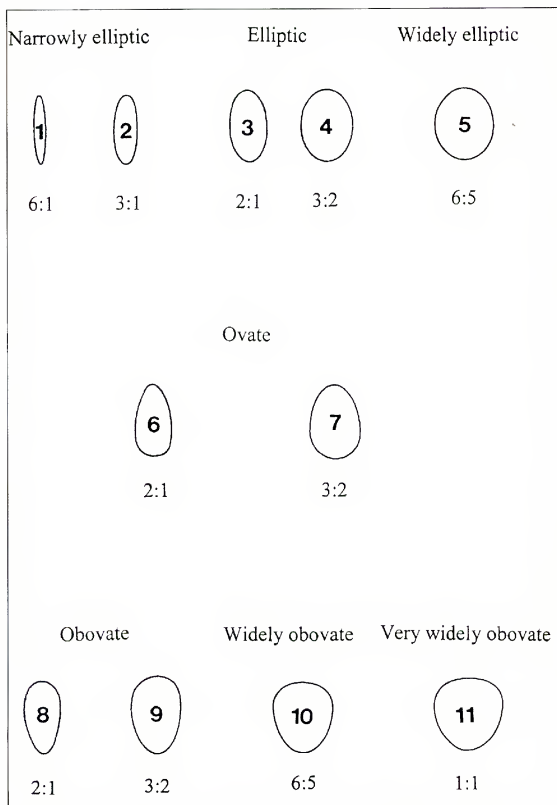


FIG. 1. Hilar profiles of caryopses observed for *Leptochloa*. The apex is oriented above.

TABLE 1. Variation in hilar profiles and cross-sectional shapes of the caryopsis in *Leptochloa* s. l. The numbers following each taxon reflect observed variation: numbers to the left of the double bar (||) indicate hilar profile shapes (see Fig. 1); those to the right of the double bar reflect cross-sectional shapes (Fig. 2). Hence, 2,3,8 || 2,9 would indicate a taxon having narrowly elliptic (3:1), elliptic (2:1), and obovate (2:1) hilar profiles, and oblate and depressed obovate (2:3) cross-sectional shapes. Taxa with an asterisk (*) indicate those previously placed in *Diplachne* by some authors.

<i>Leptochloa aquatica</i> 3,9,10 8,9,12	<i>L. marquisensis</i> 2,3,6 9,10
<i>L. caudata</i> *1,2,8 2	<i>L. monticola</i> * 3,8 4,8
<i>L. chinensis</i> 8,9 2,9	<i>L. nealleyi</i> 4,9 2,9
<i>L. chloridiformis</i> 2 7	<i>L. neesii</i> 5,10 1
<i>L. coerulescens</i> 8,9 2,8	<i>L. obtusiflora</i> 3 8
<i>L. decipiens</i> subsp. <i>asthenes</i> 3,8 2,8,9	<i>L. panicea</i> subsp. <i>brachiata</i> 3,4 10,13
<i>L. decipiens</i> subsp. <i>decipiens</i> 3 9	<i>L. panicea</i> subsp. <i>mucronata</i> 3 1,2,8
<i>L. decipiens</i> subsp. <i>peacockii</i> 3,8 3,9	<i>L. panicea</i> subsp. <i>panicea</i> 7 1,2
<i>L. digitata</i> 2,3,8 8,12	<i>L. panicoides</i> * 3,4 8
<i>L. divaricarissima</i> 3 2,9	<i>L. rupestris</i> 3 10
<i>L. dubia</i> * 2,3,11 8	<i>L. scabra</i> * 2,3 9
<i>L. eleusine</i> * 3,8,9 8,12	<i>L. southwoodii</i> 3,4,8 1,2
<i>L. fusca</i> subsp. <i>fascicularis</i> * 3,8 4	<i>L. squarrosa</i> 2 5,11
<i>L. fusca</i> subsp. <i>fusca</i> * 9 4,8	<i>L. srilankensis</i> 3 9,10,11
<i>L. fusca</i> subsp. <i>muelleri</i> * 3,9 4,8	<i>L. tectoneticola</i> * 2 8
<i>L. fusca</i> subsp. <i>uninervia</i> * 3,7,8 4	<i>L. uniflora</i> 2,6 6,7
<i>L. gigantea</i> * 3,6,8 8	<i>L. virgata</i> 2,3,6 6,7,11,12,13
<i>L. longa</i> 3,8 9	<i>L. viscida</i> * 3,8 4
<i>L. ligulata</i> 3,4 2,7	<i>L. xerophila</i> 3 2
<i>L. malayana</i> * 3 9,11	<i>Cypholepis yemenicus</i> 4 8,9

uninervia, *L. gigantea*, *L. uniflora*, *L. virgata*). The widest was the very widely elliptic shape of a few specimens of *L. dubia*. The thinnest was the narrowly elliptic (3:1) shape expressed by some specimens of *L. caudata*, *L. chloridiformis*, *L. dubia*, *L. digitata*, *L. scabra*, *L. squarrosa*, *L. uniflora*, and *L. virgata* (the lattermost sensu lato, including *L. barbata* and *L. procera* sensu Nicora 1995). Many species were variable, for example having both elliptic (2:1) and obovate (2:1) shapes. Nor surprisingly, the greatest variation in hilar profile shape occurred in widespread species such as *L. dubia* and *L. virgata*.

The cross-sectional shape was considerably more variable than hilar profile shape (Fig. 2). Overall, the observed variation ranged from dorsally compressed through circular (no compression) to laterally compressed (Fig. 2). Most taxa had only slight to moderate degrees of lateral or dorsal compression. As with hilar profiles, many taxa showed infraspecific variation in cross-sectional shapes (Table 1). Some specimens of *L. neesii* appeared circular, whereas others were oblate (Table 1). The greatest degree of dorsal compression was expressed by the depressed obovate (1:2) and transversely elliptic (1:2) shapes. With some modifications, these shapes accounted for some or all of the variation of many species (Table 1). The highest degrees of lateral compression were the obovate (3:2), rounded shallowly obdeltate

(5:6), and rounded shallowly obtriangular shapes. Only *L. squarrosa* was obovate (with a moderate hilar depression), whereas some representatives of *L. virgata* were both rounded shallowly obdeltate (5:6) or rounded shallowly obtriangular (2:3).

A distinct sulcus was present only for *L. rupestris* and *L. uniflora*, although a number of taxa had depressions of varying extent on the hilar surface (see Discussion).

The surface of the pericarp varied from smooth to variously rugose. The following were at least occasionally somewhat rugose: *L. chloridiformis*, *L. decipiens* subsp. *decipiens*, *L. divaricatissima*, *L. gigantea*, *L. longa*, *L. malayana*, *L. monticola*, *L. nealleyi*, *L. neesii*, *L. obtusiflora*, *L. scabra*, *L. southwoodii*, *L. uniflora*. Whereas a smooth pericarp was consistent for many taxa, those that expressed the rugose condition did so irregularly.

Species with a weakly adnate pericarp (detaching soon after placement in water at room temperature) included *L. chloridiformis*, *L. dubia*, *L. eleusine*, *L. fusca* subspecies *fusca*, *fascicularis*, *minervia*, and *L. obtusiflora*.

The color of the caryopsis varied from very light brown to dark reddish or very dark brown, but most were an intermediate shade. *Leptochloa longa*, *L. obtusiflora*, and *L. squarrosa* were usually dark brown. *Leptochloa monticola*, a species of dubious inclusion in the genus (Clayton & Renvoize 1986; Valls 1978; Snow 1996, 1997), was usually a dark reddish brown.

DISCUSSION

This simple study of caryopsis morphology has revealed more variation within and between taxa of *Leptochloa* than previously recognized (Parodi 1927; McNeill 1979; McVaugh 1983; Nowack 1994; Nicora 1995). With two exceptions, features of the caryopsis appear to be of little value in *Leptochloa* as phylogenetic markers, although some are of diagnostic value in keys. These results contrast with those of a recent study in Triticeae, which suggested caryopsis morphology was of systematic value at the tribal level (Terrell & Peterson 1993).

Parodi's (1927) study was limited to four species in *Leptochloa* and one in *Gouinia* Fourn., which represents only ten percent of *Leptochloa* as currently circumscribed (Snow 1997). Another disconcerting aspect was his lack of voucher specimens and uncertain depth of sampling within taxa, although this study does not contradict the profiles of the species he illustrated. Overall, Parodi's sampling underestimated considerably the variation in cross-sectional shape in *Leptochloa*. This study has revealed nearly continuous variation in cross-sectional shape, from dorsally compressed and non-compressed (circular or oblate) to various degrees of lateral compression. The bimodal compression (lateral or dorsal) of caryopses in *Leptochloa* recognized by Parodi

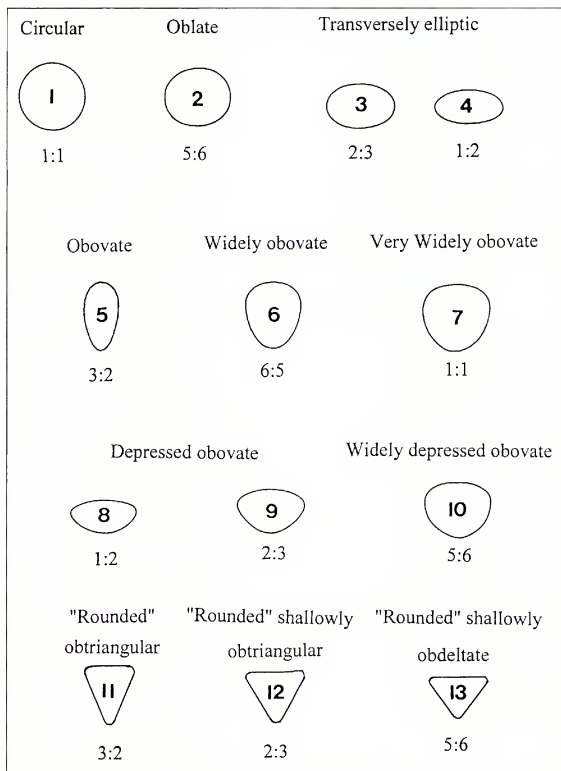


FIG. 2. Cross sectional shapes of caryopses observed for *Leptochloa*. The hilar side is oriented above.

(1927) simply does not exist for the genus as a whole. As such, variation in caryopsis cross-sectional morphology cannot by itself be invoked as a generic-level character to segregate *Diplachne*.

The caryopsis profile as viewed from the hilar side ranges continuously from narrowly elliptic through ovate to obovate and very widely obovate (Fig. 1). Whereas the extremes of variation can be useful as diagnostic features between some taxa, the continuous variation makes the hilar profile useless as a phylogenetic marker (Stevens 1991).

Various degrees of concavity occur on the hilar side. Broad, shallow depressions (not illustrated) characterize certain taxa fairly well, such as *Leptochloa elensine*, *L. longa*, and *L. obtusiflora*. Taxa showing this feature irregularly were *Leptochloa chinensis*, *L. dubia*, and the related *Cypholephbis yemenicus*. Shallow, relatively narrow depressions (not illustrated) occur in other taxa, although less consistently; these included *L. chloridiformis*, *L. decipiens* subsp. *decipiens*, *L. digitata*, *L. squarrosa*, and *L. virgata*. At best, the degree of concavity is useful only as a diagnostic character in regional keys. However, a prominent sulcus, characterized by its vertical or nearly vertical walls, was a consistent character for *L. rupestris* and *L. uniflora*, and is one of only two characters I consider sufficiently distinct and consistent to be phylogenetically useful.

The relative adnation of the pericarp is the second character of the caryopsis useful for phylogenetic inference. It is well known that the pericarp is only weakly adnate to the endosperm in some species of *Leptochloa* (Izaguirre & Laguardia 1987; Watson & Dallwitz 1992) and some related genera, such as *Eragrostis* Wolf (Lazarides 1997). In such taxa the pericarp will dissociate from the endosperm quickly when placed in water at room temperature.

Most species in *Leptochloa* have a smooth outer texture. A few can be rugose, although this feature was unreliable within taxa. For example, a coarse but sparsely rugose surface generally, but not always, characterizes *Leptochloa panicea* subspecies *panicea* and *mucronata* (sensu Snow 1998a, but not sensu Nowack 1994), which helps to distinguish these from the widespread *L. panicea* subsp. *brachiata* (Snow 1998a; formerly known as *L. filiformis* or *L. mucronata* [Snow & Davidse 1993]).

As the color of the caryopsis often varies with the degree of maturity, only mature specimens should be evaluated for this attribute. Except as a diagnostic feature in keys, in which a few species are dark brown, color is of minimal systematic value in *Leptochloa*.

I return now to cross sectional shape, which has been discussed extensively regarding the separation of *Diplachne* from *Leptochloa* (Parodi 1927; McNeill 1979; Phillips 1982; Nicora 1995). As mentioned above, the perceived bimodality of lateral and dorsal compression discussed by Parodi (1927)

has been invoked to segregate *Diplachne* from *Leptochloa*. The results of this study firmly reject such a notion, given the nearly continuous variation of cross-sectional hilar profiles (Fig. 1).

It also has been suggested that the presence or absence of a distinct keel on the lemma is positively correlated with cross-sectional shape, and is a means by which the genera can be separated (Parodi 1927; McNeill 1979; Nicora 1995). It is true that some taxa with a dorsally compressed caryopsis have flat lemmas at maturity, as for example *L. fusca* subsp. *muelleri*. However, others have little or no such positive correlation. Mature fruits of *L. neesii* can be round or nearly so in cross section, yet still be borne within a keeled lemma (e.g., *Langfield 285*, CANB). This is also true for some specimens of *L. ligulata*, *L. nealleyi*, *L. panicca* subsp. *panicca*, and *L. southwoodii*. Preliminary cladistic studies have failed to consistently group together taxa having dorsally flattened caryopses (Snow 1997).

This study upholds and strengthens the unpublished work of Valls (1978), who concluded that variation in caryopsis shape was too great to support the recognition of *Diplachne*. In particular, the data herein have revealed nearly continuous variation in cross-sectional shape, ranging from dorsal compression through circular to various degrees of lateral compression (Table 1; Fig. 2). The lateral/dorsal compression dichotomy of Parodi (1927) simply does not exist for *Leptochloa*. Moreover, a nearly identical range of cross-sectional shapes can exist in closely related genera, as illustrated in a recent revision of Australian *Eragrostis* (Lazarides 1997: 176).

The most general observation to emerge from this and other detailed anatomical and morphological studies of grasses (Dávila & Clark 1990; Ellis & Linder 1992; Snow 1996; Lazarides 1997) is that broader sampling regimes generally reveal additional variation not encountered in narrower surveys. Such variation cannot be ignored. Future studies therefore should seek both breadth and depth of sampling in order to minimize the chances of incompletely characterizing variation. Underestimates of variation leads to errors in the diagnosis of taxon boundaries and in the accuracy of inferring phylogenetic relationships, the latter being the very basis by which we make and support our classifications.

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APPENDIX 1

Voucher specimens and herbarium of origin (acronyms follow Holmgren et al. 1990); those lacking herbarium designation are housed at MO. For new combinations and new species in *Leptochloa* see Snow 1998a, b and Snow and Simon 1997.

- Leptochloa aquatica* Scribn. & Merr.: Hitchcock 7004 (US); Pringle 6664 (US); Soderstrom 650 (US); McVaugh 19124 (US); Snow 6623.
- L. caudata* (K. Schum.) N. Snow: Van Someren AH9575 (US); Snowden 1429 (US); Bogdan 130 (UC).
- L. chinensis* (L.) Nees: Snow et al. 6980; Kasim 254 (K); Poore 440 (K); Davids 7471 (K,MO); Clayton 5644 (K).
- L. chlortidiformis* (Hack. ex Stuck.) Parodi: Birabén 179 (LP); Silveus 622 (MICH); Pedersen 3471 (US); Pedersen 2662 (US).
- L. coerulescens* Steud.: Adam 17175; Adam 14030; Adam 5094.
- L. decipiens* (R. Br.) Stapf ex Maiden subsp. *astibens* (Roem. & Schult.) N. Snow: Snow & Simon 7272; Snow & Simon 7327; Snow & Simon 7335; Crisp et al. 2710 (MEL); Thompson & Sharpe HUG115 (BRI); Hubbard 5098 (K).
- L. decipiens* subsp. *decipiens*: Snow et al. 7247; Snow & Simon 7328; Snow & Simon 7334; Blake 22548 (CANB); Roe s.n. (MEL, accession 234696); Lazarides 5634 (US); Regan s.n. (CANB).
- L. decipiens* subsp. *peacockii* (Maiden & Betche) N. Snow: Snow & Simon 7323; Snow & Simon 7329; Snow & Simon 7330; Snow & Simon 7336; Purdie 315D (BRI); Boorman s.n. (G, accession 8227-86); Johnson 713 (CANB).
- L. digitata* (R. Br.) Domin: Snow et al. 7224; Snow et al. 7235; Snow et al. 7246; Burbidge 5326 (CANB); Blake 11506 (CANB); Blake 6320 (CANB); Walter & Walter 2590 (B).
- L. divaricatissima* S. T. Blake: Snow et al. 7228; Snow et al. 7233; Snow et al. 7236; Snow et al. 7241; Lloyd 979 (CANB); Blake 7747 (BRI).
- L. dubia* (Kunth) Nees: Snow 5865; Warnock 46783 (NCU); Kral 51801; Mearns 1213 (US); Hernández & Mathis N-2066 (GH); Gould 12183 (K); Castillon 43560 (GH).
- L. eleusine* (Nees) T. A. Cope & N. Snow: Snow et al. 6941; Snow & Burgoyne 6954; Snow & Burgoyne 6963; Snow et al. 6982; Schweickert 1896 (PRE); Guy & Ward 7 (PRE); Drège s.n. (S, accession 93/194); Extension Officer 16419 (PRE).
- L. fusca* (L.) Kunth subsp. *fusca*: Snow et al. 7215; Snow et al. 7216; Snow et al. 7222; Snow et al. 7232; Snow et al. 7234; Snow et al. 7237; Tracy 9297 (GH); Fry s.n. (GH).
- L. fusca* subsp. *fascicularis* (Lam.) N. Snow: Snow 5786A; Snow 5800; Snow 5804; Snow 5809H; Snow 5811A; Snow & Koster 5824; Snow & Koster 5840; Snow 5841; Snow 5842; Snow 5896; Snow 5900; Snow 5901-B; Snow 5901-E; Snow 5903; Fraser 631 (MICH); Pringle 9595 (MEXU); Swallen 4265 (BAA); Wooton s.n. (BAA).
- L. fusca* subsp. *muelleri* (Benth.) N. Snow: Latz 11 (BRI); Macconchie 13433 (BRI); Must 487 (CANB).
- L. fusca* subsp. *minerva* (J. Presl) N. Snow: Snow & Prinzie 6484; Snow & Prinzie 6567; Snow & Prinzie 6568; Snow 6598.
- L. gigantea* (Launert) T. A. Cope & N. Snow: Smith 4126 (PRE); Smith 1387 (BRI).
- L. ligulata* Lazarides: Snow & Simon 7324; Snow 7402; Story & Yapp 25 (CANB).
- L. longa* Griseb.: Davids 2612; Soderstrom 1073 (US); Hitchcock 10377 (US).
- L. malayana* (C. E. Hubb.) Jansen ex Veldkamp: Yacob 25883 (P).
- L. marquisensis* (E. Br.) P. M. Peterson & Judw.: Perlman 14919; Perlman 15064.
- L. monticola* Chase: Holdridge 1955 (US); Ekman H11874 (US).
- L. nealleyi* Vasey: Snow 5793B; Snow 5805A; Snow 5920; Cory 20298 (GH); Waller & Banml 3096 (GH); Johnston 4872 (MICH).
- L. neesii* (Thwaites) Benth.: Snow & Simon 7378; Snow & Simon 7384; Davids & Smitbraarabchi 9180 (MO,US); White 8894 (US).
- L. obtusiflora* Hochst.: Milne-Redhead & Taylor 7297 (B); Greenway 10666.
- L. panicea* (Retz.) Ohwi subsp. *panicea*: Reekmans 4982 (B); Ahmad s.n. (B, accession 175193-120); Hitchcock 19474 (US); Field & Loew 6B (US); Baker 35094 (US).
- L. panicea* subsp. *brachiata* (Steud.) N. Snow: Snow 5905; Snow 5910A; Snow & Prinzie 6529C; Snow & Prinzie 6558; Snow 6654; Snow 6672-A.
- L. panicea* subsp. *micronata* (Michx.) Nowack: Snow 5847A

- L. panicoides* (J. Presl) Hitchc.: *Snow* 5792A; *Snow* 5810A; *Snow* 6622; *Jacob* 511 (NCU); *Francoer & Williams* 47 (ENCB); *McDaniel & Rimachi* 18020.
- L. rupestris* C. E. Hubb.: *Wood* 2848 (BM); *Wood s.n.* (K); *Gilbert & Phillips* 8874 (K).
- L. scabra* Nees: *Snow* 5788; *Snow* 5791A; *Snow* 5810A; *McKenzie & Urbatsch* 160 (NY); *Nee* 31921 (NY); *Burger & Liesner* 6938 (NY).
- L. southwoodii* N. Snow & B. K. Simon: *Snow & Simon* 7350; *Snow & Simon* 7362.
- L. squarrosa* Pilg.: *Greenway* 2764 (P); *Schlieben* 6940 (P); *Milne-Redhead & Taylor* 7301 (B).
- L. srilankensis* N. Snow: *Davide & Sumitbraarachchi* 9066 (K); *Fasberg et al.* 50835 (CANB); *Clayton* 5591 (TAES).
- L. tectonicola* (Backer) Jansen ex Veldkamp: *Polane* 15394 (P); *Smitinand* 3418 (CANB); *Kerr* 20633 (K).
- L. uniflora* Hochst. in A. Rich.: *Trimens* 28 (US); *Rains* 67 (US); *Thollon* 4093 (US).
- L. virgata* (L.) P. Beauv.: *Pohl & Davide* 10603 (UC); *Barkart* 22139 (SI); *Meza* 12; *Swallen* 3109 (US); *Brückmann* 18660 (BAA).
- L. viscida* (Scribn.) Beal: *Snow* 6597; *Ruiz s.n.* (ENCB); *Palmer* 1789 (GH); *Gooding & Lusber* 139-45 (NY).
- L. xerophila* P. M. Peterson & Judw.: *Hallé* 2098 (P).
- Cypholepis yemencicus* (Schweinf.) Chiov.: *Bally & Melville* 15783; *Verdcourt* 3275.

REFERENCES

- CLAYTON, W.D. and S.A. RENOUIZE. 1986. Genera graminum: Grasses of the world. Kew Bull. Addit. Ser. 13.
- DÁVILA, P. and L.G. Clark. 1990. Scanning electron microscopy survey of leaf epidermis of *Sorghastrum* (Poaceae: Andropogoneae). *Amer. J. Bot.* 80:1444-1454.
- ELLIS, R.P. and H.P. LINDER. 1992. Atlas of the leaf anatomy in *Pentastichis*. *Mem. Bot. Surv. S. Africa* 60.
- HITCHCOCK, A.S. 1903. North American species of *Leptochloa*. *U.S.D.A. Bull. Pl. Industr. Publ.* 13:1-21.
- HOLMGREN, P.K., N.H. HOLMGREN and L.C. BARNETT. 1990. Index herbariorum. Part I: The herbaria of the world. Eighth Edition. *Regnum Veg.* 120.
- IZAGUIRRE, P. and A. LAGUARDIA. 1987. Un nuevo enfoque hacia la definición del fruto de las gramíneas. *Uruguay Fac. Agron. Bol. Invest.* 3:1-15.
- JACOBS, S.W.L. 1987. Systematics of the chloridoid grasses. In: T.R. Soderstrom, K.W. Hilu, C.S. Campbell, and M.E. Barkworth, eds. *Grass systematics and evolution*. Smithsonian Institution Press, Washington, D.C. Pp. 277-286.
- LAZARIDES, M. 1980. The genus *Leptochloa* Beauv. (Poaceae, Eragrostideae) in Australia and Papua New Guinea. *Brunonia* 3:247-269.
- . 1997 A revision of *Eragrostis* (Eragrostideae, Eleusininae, Poaceae) in Australia. *Aust. Syst. Bot.* 10:77-187.
- MCFEILL, G. 1979. *Diplachne* and *Leptochloa* (Poaceae) in North America. *Brittonia* 31:399-404.
- MCVAUGH, R. 1983. Gramineae. Vol. 14. *Flora Novo-Galaciana: A descriptive account of the vascular plants of western Mexico*, W. R. Anderson, editor. The University of Michigan Press, Ann Arbor.
- MURLEY, M.R. 1951. Seeds of the Cruciferae of northeastern America. *Amer. Midl. Naturalist* 46:1-81.
- NICORA, E.G. 1995. Los géneros *Diplachne* y *Leptochloa* (Gramineae, Eragrostaceae) de la Argentina y países limítrofes. *Darwiniana* 33:233-256.
- NOWACK, R. 1994. Revision of *Leptochloa* Beauv. (incl. *Diplachne* Beauv.) (Poaceae) in Malesia. *Rhedeia* 4:79-92.
- PARODI, L.R. 1927. Revisión de las gramíneas argentinas del género *Diplachne*. *Revista Fac. Agron. Veterin.* 6: 21-43.

- PHILLIPS, S.M. 1982. A numerical analysis of Eragrostideae (Gramineae). Kew Bull. 37:133-168.
- SNOW, N. 1996. The phylogenetic utility of lemmatal micromorphology in *Leptochloa* and related genera in subtribe Eleusininae (Poaceae, Chloridoideae, Eragrostideae). Ann. Missouri Bot. Garden 83:504-529.
- _____. 1997. Phylogeny and Systematics of *Leptochloa* P. Beauv. sensu lato (Poaceae, Chloridoideae). Ph.D. dissertation, Washington University, St. Louis, Missouri.
- _____. 1998a. Nomenclatural changes in *Leptochloa* P. Beauvois sensu lato (Poaceae, Chloridoideae). Novon 8:77-80.
- _____. 1998b. A new species of *Leptochloa* (Poaceae, Chloridoideae) from Sri Lanka. Novon 8:183-186.
- SNOW, N. and G. DAVIDSE. 1993. *Leptochloa mucronata* (Michx.) Kunth is the correct name for *Leptochloa filiformis* (Poaceae). Taxon 42:413-417.
- _____, B.K. SIMON. 1997. *Leptochloa southwoodii* (Poaceae, Chloridoideae), a new species from south-east Queensland. Austrobaileya 5:132-143.
- STEVENS, P.F. 1991. Character states, continuous variation, and phylogenetic analysis: A review. Syst. Bot. 16:553-583.
- SYSTEMATICS ASSOCIATION COMMITTEE FOR DESCRIPTIVE BIOLOGICAL TERMINOLOGY. 1962. I. Terminology of simple symmetrical plane shapes (chart 1). Taxon 11:145-156.
- TERRELL, E.E. and P.M. PETERSON. 1993. Caryopsis morphology and classification in the Triticeae (Pooideae: Poaceae). Smithsonian Contr. Bot. 83.
- VALIS, J.E.M. 1978. A biosystematic study of *Leptochloa* with special emphasis on *Leptochloa dubia* (Gramineae: Chloridoideae). Ph.D. dissertation, Texas A & M University, College Station.
- VAN DEN BORRE, A. and L. WATSON. 1997. On the classification of the Chloridoideae (Poaceae). Australian Syst. Bot. 10:491-531.
- VELDKAMP, J.E. 1971. Notes on Malesian grasses V. New species and combinations in *Pheidochloa*, *Hyparrhenia* and *Leptochloa*. Blumea 19:64.
- WATSON, L. and M.I. DALLWITZ. 1992. The grass genera of the world. C.A.B. International.