Taxonomy and distribution of the genus Cenchrus

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TAXONOMY AND DISTRIBUTION OF THE GENUS CENCHRUS

by

Donald Gordon DeLisle

A Dissertation Submitted to the
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Approved:

Signature was redacted for privacy.

In Charge of Major Work

Signature was redacted for privacy.

Head of Major Department

Signature was redacted for privacy.

Dean of Graduate College

Iowa State University
Of Science and Technology
Ames, Iowa
1962
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INTRODUCTION

The genus *Oenchrus* (Gramineae) comprises an ubiquitous group of grasses inhabiting disturbed areas and sandy soils in the warmer regions of both hemispheres. Because of the spiny nature of their inflorescences, members of the genus have, whenever possible, been avoided by their human co-habitants. A few species, with less spiny inflorescences and more luxurious foliage, have been introduced as forage grasses in some areas, especially in Africa, India, and South America, and are regularly consumed by livestock. The seeds of species in both Africa and Central America are used as food, made into cooling beverages or brewed as a palliative tea. The roots are used as an ingredient in some native aphrodisiac prescriptions.

Previous monographic works on the genus, published more than a century ago, provide only fragmentary descriptions, disagree markedly in their various taxonomic treatments, and give little information regarding distributions of the various taxa. More recent studies in the genus deal only with one or a few species or are confined to specific geographic areas.

This study is an attempt to more accurately delimit the genus *Oenchrus* and its species and to present a more complete picture of their natural variation and geographic distribution. Recent cytological, and morphological data are
correlated with traditional taxonomic criteria, and sugges-
tions are made regarding possible intra and extra-generic relationships.
METHODS AND MATERIALS

Field collections and herbarium specimens provided the bulk of the material used in this study. Measurements on those portions of the plants which were larger than 1 centimeter were made to the nearest 0.2 centimeter using a small metric ruler. Leaf length, whenever possible, was taken on the second leaf below the inflorescence, and leaf width was measured at the widest point of the leaf. Plant height was taken from the point of root emergence to the top of the uppermost inflorescence. For structures smaller than one centimeter, critical measurements were made to the nearest one-tenth millimeter by the use of an ocular micrometer fitted to a Spencer binocular microscope, equipped with 1X objectives and 9X oculars. Bur length was taken from the base of the pedicel to the tip of the longest erect spine; bur width, exclusive of spines, was made at the widest point of the bur, usually near its base. Because of compression of the spikelets within the bur, the largest and usually central spikelet was measured. Length of the spikelet, first and second glumes, and sterile lemma was taken from their respective bases or points of attachment to the tip of each structure. Width of each of these floral members was obtained at their widest point. The average distance between burs in the inflorescence (internode length) was obtained by counting the nodes within a length of two centimeters at the center of
the inflorescence, and dividing this length by the total number of nodes counted.

In addition to critical measurements, other important characters such as number of spines, nodes, amount of pubescence, and bur color were noted.

All measurements and observations, field data, location and date of collection and collector's name were recorded on 3 x 5 cards for each herbarium specimen as well as for the writer's own collections and population samples.

Leaf epidermal studies were made using dried material from herbarium collections. The leaves were first softened with methyl alcohol-detergent preparation (Pohl 1954), after which the upper epidermis and mesophyll were scraped away using a razor blade. The remaining lower epidermis was then dehydrated in absolute alcohol and placed abaxial side up on a clean microscope slide. Slides were made permanent by adding a drop of diaphane and a cover slip. Cross sections of fresh leaves were fixed in Craf III, imbedded, sectioned, and stained with safranin and fast-green.

Seeds of a number of species were obtained from various sources for which appreciation is expressed in the acknowledgements. Seedlings and mature plants were grown in 8-inch pots in the greenhouse, in a soil mixture consisting of three-fourths sand and one-fourth soil. Inflorescences were picked for cytological study as they emerged from the sheaths or shortly thereafter, and were immediately fixed in 3:1
alcohol-acetic acid. The specimen bottles were aspirated to insure complete fixation. Plants from which inflorescences had been removed were tagged, and voucher specimens were made from these plants whenever successful chromosome counts were obtained from the original inflorescences. Voucher specimens for all counts made by the writer are deposited in the herbarium of Iowa State University.

Herbarium specimens used in this study were kindly furnished by the following institutions, and the writer takes this opportunity to express his grateful thanks to the curators whose loan of material helped make the study possible. Abbreviations used for the various herbaria are those of Lanjouw and Stafleu (1959).

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Institution</th>
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<tbody>
<tr>
<td>F</td>
<td>Chicago Natural History Museum</td>
</tr>
<tr>
<td>DAO</td>
<td>Canada, Department of Agriculture, Ottawa</td>
</tr>
<tr>
<td>ISC</td>
<td>Iowa State University</td>
</tr>
<tr>
<td>MA</td>
<td>Instituto &quot;Antonio Jose Cavanilles,&quot; Madrid</td>
</tr>
<tr>
<td>MO</td>
<td>Missouri Botanical Garden</td>
</tr>
<tr>
<td>SMU</td>
<td>Southern Methodist University</td>
</tr>
<tr>
<td>NY</td>
<td>New York Botanical Garden</td>
</tr>
<tr>
<td>SUI</td>
<td>State University of Iowa</td>
</tr>
<tr>
<td>UC</td>
<td>University of California, Berkeley</td>
</tr>
<tr>
<td>AHUC</td>
<td>University of California, Davis</td>
</tr>
<tr>
<td>US</td>
<td>United States National Herbarium</td>
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<td>TEX</td>
<td>University of Texas</td>
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Specimens were also examined at the University of Colorado and at the Rocky Mountain Herbarium.

In addition to herbarium specimens, field collections and population studies were made during the summer of 1960 in the states of Missouri, Kansas, Oklahoma, Texas, New Mexico, Colorado, Wyoming, Nebraska, and Iowa. During the summer of 1961 extensive collections and population samples were made in Oklahoma, Texas, Louisiana, Mississippi, and Alabama.

Specimens for population studies and material for seed were air-dried and placed in special envelopes marked with the collection number, date, location, and other pertinent data.

Drawings of chromosomes were made using a 97X oil-immersion objective, 10X ocular and a Zeiss microscope drawing apparatus. A 43X objective was used for the leaf cross-section drawing. Drawings of inflorescences and burs were obtained from herbarium collections, type specimens, or from fresh material. Those of spikelets, florets, and caryopses were made with the aid of a camera lucida attached to a stereo binocular microscope.

Distribution maps indicate the locations of specimens examined by the writer. A selected list of specimens is included following the discussion of each species. The complete list of specimens examined by the writer is deposited in the herbarium of Iowa State University.
Appropriate synonyms are included for each species where applicable. Criteria for the inclusion of each name are indicated by a number or numbers in parenthesis after each. The same designation is followed in the list of excluded or unidentified names appearing in the appendix. The following numbers indicate the criteria used in the treatment of each name.

1. Type specimen, fragment of the type, or a photograph of the type examined.
2. Inclusion of name based on original description.
3. Follows usage of another author who has seen the type.
4. Follows present accepted usage.

This procedure for the treatment of synonyms is one suggested by Isely (Isely, Duane, Iowa State University, Ames, Iowa, Private communication, 1962).
MORPHOLOGY

*Oenchrus* is a genus of Panicoid grasses with terete, solid culms and somewhat fibrous roots. The annual plants are usually solitary or may occasionally form large clumps, whereas the perennials, some of which have bulbous bases, may produce large tussocks or mats. The inflorescence of members of this genus is a spike-like panicle consisting of a few to numerous fascicles (burs or involucres), within which are enclosed one or more spikelets.

Doell in Martius (1877), was the first to suggest the nature of these burs, believing that they were derived from leaves. This may have been suggested to him by the appearance of the bracts which often appear at the base of inflorescences, or perhaps by the abortive lowermost bur, often found in most species of *Oenchrus*. Goebel (1882), disagreed with Doell, and concluded that the involucre was derived from cohesion of the members of a complex system of branches, a suggestion also later concurred in by Arber (1931). In a recent morphological study of the fascicles (burs) in *Pennisetum* and *Oenchrus*, Sohns (1955) found that the spikelets of *Oenchrus* are terminal in the fascicles, and that the spines represent sterile first-order axes whose branches have become fused laterally. The now-fused branches are part of an elongated inflorescence whose axis has become shortened and whose lateral branches have become sterile. Sohns
(1955), further suggested that the prolonged awn-like bristles, found in a number of species of *Pennisetum*, represent a continuation of the stem axis, that the spikelets in these forms are lateral instead of terminal, and that this character might prove useful in separating the genus *Pennisetum* from that of *Oenchrus*. However, this feature, (prolonged bristle), occurs widely in both genera, and is highly variable in such species as *O. caliculatus* and *O. multiflorus*. It therefore does not appear to be a useful taxonomic trait except possibly on an inter-specific basis.

Many species of *Oenchrus* have burs in which the spines are dark purple in color, probably because of the presence of anthocyanin pigments. This character has been observed by the writer to be highly variable, even in inflorescences of the same individual plant, and therefore too unreliable to serve as a taxonomic trait for delimiting species.

Gayle (1892) first pointed out that the barbs on the spines of this "vile weed" (*O. tribuloides*) were somewhat tube-like and contained a light purple substance which he assumed was of a highly irritating nature. In an anatomical and chemical study of *O. tribuloides* L., Youngken and La Wall (1922) found that the lumina of the barbs of young spines contained a formate-like substance, which apparently is lacking in the mature spines. It was thought that this substance intensified the pain of puncture wounds from the sand-burs. These same authors also suggested a rather interesting theory
regarding the distribution of this species (probably *C. incertus*).

It appears that few lay citizens of the United States made the acquaintance of sand spurs until the battle of Palo Alto, during the Mexican War, when according to Meehan, they were quite as annoying to our soldiers as the bullets of the Mexicans. The bur-like fruits attached themselves to the soldier's clothing and in this way the plants became widely distributed after the Mexican War.

The culms of members of the genus *Cenchrus* are, for the most part, solid with a large central pith area. In ecological studies of range grasses, Canfield (1934) observed solid stems in such forms as *C. nauciflorus* Benth. were characteristic of grasses which are apparently best able to survive under semi-arid conditions.

Leaf epidermises of almost all the species of *Cenchrus* were studied by the author and, without exception, have the typical appearance of grasses of the tribe Paniceae, (Prat 1932, 1936). Grob (1896) studied the epidermis of grass leaves, and on the basis of epidermal morphology, placed *C. tribuloides* L. in the tribe Paniceae. Additional studies on the relation of leaf anatomy and taxonomy of the grasses have been made by Brown (1958a), Tateoka, Inoue, and Kawano (1959), and Reeder (1960). These authors point out the diamond-shaped guard cells, bicellular hairs, and certain other features of both external and internal leaf anatomy which provide evidence for placing *Cenchrus* in the tribe Paniceae. Drawings of epidermal cells of a number of species
of *Oenohrus*, (Figure 1), illustrate the panicoid features common to members of the genus. In Figure 1 it will be noted that the guard cells are typically rhombic, and the siliceous cells are all "dumbbell or cross-shaped." Bicellular hairs of all species of *Oenohrus* studied had typically long terminal cells. Size of the stomata appears to be fairly uniform in the four species illustrated.

A cross-section of the leaf of *C. longispinus*, (Figure 1), reveals a number of features which also indicate the panicoid relationship of the genus. The drawing shows little or no evidence of an endodermis around the major vascular bundle. Just outside the vascular bundle region, and surrounding it, is a somewhat ill-defined parenchyma sheath. A similar arrangement of the parenchyma sheath as well as the presence of conspicuous bulliform cells was pointed out by Britton (1903), who also noted that stomata were more numerous on the abaxial leaf surface. Brown (1960) mentions that the mesophyll of *C. pauciflorus* and *C. myosuroides* has the plastids centrifugally arranged, and Reeder (1960) reported a similar type of organization in leaf cross-sections of *C. echinatus* L. The mesophyll surrounding the bundle is not radially oriented as is that of members of the sub-family *Eragrostoideae*.

Morphological studies were not made by the writer on embryos of *Oenohrus*, but Reeder (1957) has noted the panicoid features of the embryo of *C. pauciflorus* Benth. In his
Illustration of the embryo of this species, there is a distinct elongation between the point of divergence of the scutellum bundle and the coleoptile, there is no epiblast present, and there is a distinct cleft between the scutellum and the coleorhiza. The embryonic leaf of this species contains numerous vascular bundles, and the leaf margins slightly overlap.
Figure 1. Leaf anatomy in Cenchrus

A. Leaf cross section of *C. longispinus*
B. Lower leaf epidermis of *C. setigerus*
C. Lower leaf epidermis of *C. longispinus*
D. Lower leaf epidermis of *C. elymoides*
E. Lower leaf epidermis of *C. echinatus*
The spikelets of members of the genus *Cenchrus* consist of a first and second glume, sterile lemma and palea, and a fertile floret. The so-called "sterile lemma" always lacks an ovary, but usually produces functional stamens with apparently viable pollen, based on staining results with lacto-phenol and cotton-blue. In those species of *Cenchrus* grown from seed, the anthers produced by the sterile lemmas were about twice the length of those borne in the adjoining fertile florets.

Of the twelve species studied during the course of cytological work, it was noted that all were markedly protogynous, the stigmas being exerted at about the same time that the inflorescence is just beginning to emerge from its surrounding sheath. Emergence of the stigmas proceeds in basipetal succession; i.e., beginning at the apex of the inflorescence and proceeding toward its base. The anthers in fertile florets, at the time of stigma exertion, are mature, but those of the sterile lemmas are often at the beginning of first meiotic division. The time of meiosis is highly variable in species of *Cenchrus*, but emergence of stigmas is a fairly reliable indication of meiotic activity in the male florets.

Self-fertilization is apparently common in most species of *Cenchrus*, but cross fertilization probably also occurs...
normally, as evidenced by the amount of variation in populations observed in the field. The degree to which self-fertilization occurs in the various species is, as yet, incompletely known. Anthesis of the stamens in fertile florets occurs about two days following exertion of the stigmas of that particular floret. This would allow self-pollination to occur within an inflorescence since anthers at the tip of the inflorescence are dehiscing at the same time as stigmas in the lower portions of the inflorescence are receptive. Cross pollination undoubtedly takes place in those areas where there are many individual plants in a population.

The absence of lodicules has been reported in the florets of Anthoxanthum and Pennisetum by Arber (1934), and in Cenchrus by Bor (1960), and Arber (1934). The writer has also failed to find or observe the presence of lodicules in the species of Cenchrus examined. Arber (1934) assumes that the absence of lodicules and the state of protogyny, which is prevalent in the genus, are in some way connected. She also attributes the absence or suppression of the first glume in some species of Cenchrus to pressure exerted by the bur upon the developing spikelets. In many species the first glume may continue to develop even though it may be quite small. Pressure of the developing bur also results in distortion during early growth of the spikelets, resulting in one larger central spikelet, with some suppression of those spikelets
surrounding it. For this reason the reliability of spikelet characters in taxonomic treatments, with the possible exception of size, is questionable.

Apomixis and pseudogamy are reported to be prevalent in *O. ciliaris* and *O. setigerus*, (Fisher, Bashaw & Holt 1954), and will be discussed fully in the taxonomic treatment of these two taxa. Normal embryo development, without apomixis, has been reported by Brown & Emery (1958) for *O. pauciflorus* and *O. myosuroides*.

Tests of germination indicate that the seeds of all species of *Cenchrus* require a period of dormancy of about five or six months. Several methods have been tried by the writer to break the dormancy of seeds harvested in the fall, but most of these methods were unsuccessful. Cold treatment was the most promising, but the results were highly erratic. Scarification had little or no effect upon germination, although Akamine (1944) reported that this method was successful in stimulating germination of the seeds of *O. biflorus*. 
CYTOLOGY

Cytological studies, using pollen mother cell smears, were made on ten species of Cenchrus by the writer. The results of these chromosome counts, along with those made by other workers, are presented in Table 1. Many early counts made by other workers give no indication as to whether voucher specimens were designated or retained; therefore it is not possible to attest to the reliability of their reports. Meiotic figures of those species counted by the writer are included in Figure 2. Detailed cytological discussions of species for which such information is available is included in the taxonomic treatment.

There are evidently two major groupings in the genus Cenchrus, with respect to the basic chromosome number. In that group largely confined to the western hemisphere, the basic number appears to be $X=17$, while those plants largely confined to Africa and Asia have a basic number of $X=9$ or $X=10$. To this second group, however, there are two exceptions, in that C. prieterii reputedly has a basic number of $X=17$, and a recent count obtained by the writer would also indicate a possible basic number of $X=17$ for C. biflorus. Avdulov (1931) suggested that the genus Cenchrus has a basic number of $X=17$, which may have been derived from a basic number of $X=9$, either through loss of one pair of chromosomes in a tetraploid form, or by loss of one chromosome.
Table 1. Summary of chromosome numbers reported in the genus Oenchrus

<table>
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<tr>
<th>Species</th>
<th>Somatic number</th>
<th>Reference</th>
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<tbody>
<tr>
<td>C. ciliaris L.</td>
<td>32 Fisher, Bashaw &amp; Holt (1954)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>34 E. K. J. (unpublished, cited in Darlington &amp; Wylie, 1955)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>35 Krishnaswamy (1940)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>40 Fisher, Bashaw &amp; Holt (1954)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>43 Snyder, Hernandez &amp; Warmke (1955)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>44 Nath &amp; Swaminathan (1957)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>48 Snyder, Hernandez &amp; Warmke (1955)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>52 Nath &amp; Swaminathan (1957)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>54 Fisher, Bashaw &amp; Holt (1954), Hernandez (1953)</td>
<td></td>
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<tr>
<td>C. biflorus Roxb.</td>
<td>34 present author</td>
<td></td>
</tr>
<tr>
<td>C. brownii R. &amp; S.</td>
<td>34 Avdulov (1931), present author</td>
<td></td>
</tr>
<tr>
<td>C. echinatus L.</td>
<td>34 Avdulov (1931)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>68 Nunez (1952), Tateoka (1955), present author</td>
<td></td>
</tr>
<tr>
<td>C. gracillimus Nash</td>
<td>34 present author</td>
<td></td>
</tr>
<tr>
<td>C. incertus M. A. Curtis</td>
<td>32 Gould (1958)</td>
<td></td>
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Table 1. (Continued)

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<tr>
<th>Species</th>
<th>Somatic number</th>
<th>Reference</th>
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<tbody>
<tr>
<td>C. longispinus (Hack. in Kneuck.) Fernald</td>
<td>34</td>
<td>Gould (1958), (1960, as C. parviceps), Tateoka (1955), present author</td>
</tr>
<tr>
<td></td>
<td>36</td>
<td>Brown (1948, as C. pauciflorus from northern U. S.)</td>
</tr>
<tr>
<td>C. myosuroides H. B. K.</td>
<td>54</td>
<td>Brown (1950, 1951)</td>
</tr>
<tr>
<td></td>
<td>70</td>
<td>Avdulov (1931), Gould (1962)&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>C. palmeri Vasey</td>
<td>34</td>
<td>present author</td>
</tr>
<tr>
<td>C. pilosus H. B. K.</td>
<td>34</td>
<td>present author</td>
</tr>
<tr>
<td>C. prieurii (Kunth) Maire</td>
<td>34</td>
<td>Mulay &amp; Leelamma (1956)</td>
</tr>
<tr>
<td>C. tribuloides L.</td>
<td>34</td>
<td>Avdulov (1931), Hunter (1934), present author</td>
</tr>
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<sup>a</sup>Gould, F. W., College Station, Texas. Data on chromosome numbers of Cenchrus. Private communication. 1962.

In a diploid form, followed by immediate reduplication. Thus, according to Nunez (1952), even though the basic number of Cenchrus is X=17, the fact that Brown (1948, 1950) obtained a basic number of X=9 in two species, i.e., C. myosuroides and C. longispinus, permits the assumption that the genus originated directly from those forms characterized by the
most prevalent number in the tribe, X=9. Nunez attributes the secondary basic number of X=17 to factors of intrageneric differentiation. Stebbins and Love (1941) reported a similar condition in the aneuploid genus Stina, suggesting that the 2n=34 number in this genus could have been derived from a 2n=36 form with a basic number of X=6 or X=12, by loss of a single pair of chromosomes. Brown (1948) concluded that in Cenchrus the basic number is X=9, basing this on the results of only one count, 2n=36, which he obtained from a specimen of C. longispinus. Counts made by Gould, Tateoka, and the writer, however, do not appear to substantiate those made by Brown, and indicate that the basic number, at least of the American species of Cenchrus, is more probably X=17.

Darlington (1956) states that a secondary polyploid with change in basic number may arise when the number is doubled or trebled and one chromosome is dropped. Then the original diploid, or its tetraploid or hexaploid derivative, has often disappeared. Such a change may be due to a direct loss of a whole chromosome, or by fusion and loss of part of a chromosome containing a centromere. He further suggests that this characteristic change is due to the fact that the polyploid is better able to afford such a loss than is the diploid, and that such a loss is often an evolutionary advantage.

The second group of species, having a basic number of X=9 or X=10, includes C. ciliaris, C. setigerus, and C.
myosuroides. Chromosome numbers have not been obtained by the writer for O. myosuroides, but Avdulov (1931) and Gould (1962, see footnote, Table 1, page 20) reported a number of 2n=70. Brown (1950, 1951), on the other hand, reported 2n=54. Avdulov (1931) suggested that the 2n=70 form could have arisen as the result of a backcross of a tetraploid species of Cenchrus with a basic number of X=9, followed by reduplication in the zygote. Brown (1950) offered no suggestion regarding the possible origin of his reported 2n=54 form.

The presence of a basic number of X=9 in at least two species of Cenchrus does, however, lend some support to the origin of present-day species of Cenchrus from an ancestral form with this basic number. There still remain a number of species of Cenchrus upon which cytological studies have not been made. Such future cytological and genetic work as may be done in the genus will give us a clearer picture of the relationships and evolutionary patterns in both Cenchrus and Pennisetum.
Figure 2. Meiotic chromosomes in the genus *Oenchrus*

A, B. *C. brownii*
C, D. *C. echinatus*
E. *C. pilosus*
F, G. *C. longispinus*
H. *C. gracillimus*
I. *C. palmeri*
J, K. *C. incertus*
L. *C. tribuloides*
M. *C. setigerus*
GENERIC RELATIONSHIPS AND LIMITS

In the discussion of *Cenchrus* morphology, it was pointed out that the involucre (bur) of many species in the genus represents a rather high degree of specialization as shown by the coalescence of inflorescence branches to form a spiny bur. The trends in such a coalescence of inflorescence branches may be traced in a number of genera in the Paniceae. For example, members of the sub-genus *Paurochetium* of the genus *Panicum* have spikelets subtended by one or a few very fine bristles. In *Setaria* there are more numerous bristles; in *Pennisetum* the accumulation of bristles has become much more pronounced, and in *Cenchrus* there is almost complete fusion of many of the spines or bristles.

Bews (1929) also suggested that a number of genera in the Paniceae could be sequentially arranged on the basis of involucral complexity. Beginning with *Anthephora*, having an involucre composed of large, indurated first glumes, the series continues through *Odontelytrum*, *Setaria*, and *Pennisetum*, reaching its culmination in the genus *Cenchrus*. Because of its floret characteristics, *Anthephora*, according to Reeder (1960), appears to be most closely related to *Cenchrus*. The florets of *Pennisetum* are also morphologically quite similar to those of members of the genus *Cenchrus*.

There has been considerable confusion on the part of many workers with respect to the actual generic limits of
Oenchrus and Pennisetum. The primary problem concerns interpretation of presence or absence of union at the base of the spines or bristles. Because of past difficulty in resolving this question, a number of species have been treated first in one genus, and then the other, depending upon the interpretation of the worker. In recent years there has been a tendency to place in the genus Oenchrus all those species which have at least some union of spines or bristles at the base, resulting in a more or less definite disc, cup, or involucre (Henrard 1935). In species of Pennisetum the bristles seldom are more than 0.2—0.4 mm wide, and the base of the involucre rarely exceeds 0.5 mm in width. In species of Oenchrus, on the other hand, the spines tend to be quite wide, usually 0.5 mm or more, and are generally united for a considerable distance above the base of the bur, with the base itself usually at least 1.5 mm in diameter. These characteristics, although admittedly arbitrary, are used in the present treatment of the genus Oenchrus. It is possible that further morphological and anatomical studies may indicate the need for a revision and possible merging of the two genera, but until such time, the treatment of the genus Oenchrus is based on traditional criteria with some refinement.
In order to arrive at a somewhat more objective idea of the possible phylogenetic relationships of species within the genus *Oenchrus*, a number of morphological characters were examined, which tend to indicate the degree of advancement. Each character was assigned a value of 0, 1, or 2, with 0 denoting a probable primitive condition, 1, an intermediate condition, and 2, representing an advanced stage for a given trait. The following ten characteristics, each designated by a letter, were chosen for twenty species of *Oenchrus*.

A. **Prolonged Bristle**: Absence of this feature is probably an advancement. Many species of *Oenchrus* which approach *Pennisetum* morphologically usually also have long bristles, one of which is much prolonged. These forms are considered less specialized than those which lack prolonged bristles.

B. **Union of Spines**: Union of spines (connation) above the base of the bur is considered a more specialized condition.

C. **Grooved Outer Spine Surface**: This character is found in many species which also have free spines. The presence of this trait is therefore correlated with other primitive features of the genus.

D. **Inflorescence Internode Length**: The distance between burs in the inflorescence is a measure of the
compactness of the inflorescence. The general trend in the
genus appears to be toward reduction in the number of burs
and wider spacing of burs in the inflorescence.

E. *Spine Shape:* The trend in *Oenchrus* is apparently
from terete to flattened spines. This may usually be corre­
lated with reduction in spine number or coalescence of
several spines to form a broad single spine.

F. *Ciliate Spine Margins:* This characteristic is
usually present in those forms which have terete spines not
united above the base. In the genus *Oenchrus* there are a
number of intermediate species, and in a few taxa with flat
spines this trait persists to some degree.

G. *Spine Length:* In general, longer more slender
spines are associated with those less specialized forms
having the spines free to the base. The trend appears to be
toward a progressive shortening of the spines as the latter
become coalesced into the bur.

H. *Number of Whorls of Bristles:* In the more primitive
forms with free spines there are usually present from one to
several whorls of bristles at the base of the bur. As the
spines become progressively more connate, the number of whorls
of bristles tends to become reduced and may be completely
lost in some species.

I. *Spine Number:* There appears to be a tendency in the
more specialized species of *Oenchrus* toward a reduction in
total number of spines per bur. There are, however, a few
exceptions in which decrease in the number of burs per inflorescence is accompanied by an increase in number of spines.

J. Perennial or Annual Growth: According to Stebbins (1950), perennial habit of growth is generally thought to be more primitive, with annual habit a derived condition. Again, there are a few exceptions to this in Centaurea, although most of the species which possess numerous advanced traits are also annuals.

The values for each of the above traits assigned to each species of Centaurea are totaled, giving a specialization index number. This number is an indication of the relative degree of advancement for that species. The index values thus obtained for twenty species of Centaurea are shown in Table 2. By transposing these index values on a graph consisting of concentric circles (Hardin 1957), it is possible to more objectively suggest phylogenetic relationships within the genus. Such an arrangement is shown in Figure 3.

The degree of advancement or specialization of each species is represented on the graph (Figure 3) by its position relative to the concentric circles, those showing the most apparent advancement in several traits occupying positions on the graph furthest from the circles at zero. The degree of relationship is indicated by connections of one or more species with each other or with the open circles, the latter representing hypothetical ancestors of the species.
Table 2. Specialization index values for twenty species of Cenchrus

<table>
<thead>
<tr>
<th>Species</th>
<th>Prolonged bristles</th>
<th>Union of spines</th>
<th>Outer spine grooves</th>
<th>Inf. internode length</th>
<th>Spine shape</th>
<th>Spine margins ciliate</th>
<th>Spine length</th>
<th>Number of whorls</th>
<th>Perennial or annual</th>
<th>Total advancement index</th>
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<td>C. agrimonioides</td>
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<td>C. tribuloides</td>
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</table>
connected above them. Letters under each circle or species indicate the morphological characters (Table 2) which all the taxa attached above that point have in common. Characters which are intermediate in nature are indicated by underlined letters. The positions and angles of the connecting lines between species are merely diagrammatic and for convenience in arrangement and are not intended to denote the amount or rate of evolutionary divergence between them. The probable basic chromosome number, when available, is indicated in parenthesis after the name of each species.

Referring to Figure 3, it will be noted that the species of *Oenchrus* fall into two basic groups. Those in the upper and presumably more specialized group include *O. pilosus*, *brownii*, *mitis*, *echinatus*, *distichophyllus*, *gracillimus*, *longispinus*, *tribuloides*, *palmeri*, *incertus*, and *platyacanthus*. The second and somewhat more primitive group consists of *C. ciliaris*, *setigerus*, *multiflorus*, *elymoides*, *caliculatus*, *agrimonioides*, *prieurii*, *myosuroides*, and *biflorus*.

The first group, a rather homogeneous assemblage of species, is united by a number of similar characteristics. These include presence of a definite bur resulting from more or less complete fusion of the spines, the presence of flattened and broad spines, and the absence of prolonged bristles. In addition, members of this group have apparent basic chromosome numbers of $X=17$, and all are native to the
Figure 3. Suggested phylogenetic relationships of twenty species of *Oenchrus*
western hemisphere, with the exception of *Oenchrus mitis* from eastern Africa. *Oenchrus pilosus, brownii, mitis,* and *echinatus* show somewhat less advancement than other members of the group, since they all possess definite whorls of bristles at the base of the bur, and with the exception of *O. mitis,* have rather dense inflorescences with numerous burs. *Oenchrus echinatus* probably represents a derived tetraploid from the basic number of $X=17$. Two perennial species, *O. gracillimus* and *O. distichophyllus,* show considerable advancement over the previously discussed forms in having a reduced number of burs, fewer spines, and loss of most of the basal bristles. Additional advancement is indicated in the remaining five species by progressive reduction in the number of spines and by a reduced number of burs in the inflorescence, with the exception of *O. platvacanthis.* This species, while showing extreme specialization by drastic reduction of spine number, retains the more primitive feature of a dense inflorescence with large numbers of burs.

The second basic group shown in the lower part of the graph represents a rather heterogeneous assemblage of species. All are characterized by having the spines free to the base of the bur, but there is wide variation as to shape, length, and number of spines within the members of this group. Three species have an apparent basic chromosome number of $X=9, 10,$ and two species have a basic number of $X=17$. With the exception of *O. myosuroides* from Central America, all are
restricted to Africa, India, Southeast Asia, and Australia. Many of these forms have apparent closer affinities with members of the genus *Pennisetum* than do their relatives in tropical America. The fact that the latter genus is more abundantly represented in Africa and India than is the genus *Cenchrus* would tend to lend some support to the origin of *Cenchrus* in those areas.

There seems little doubt that members of both *Cenchrus* and *Pennisetum* originated from common ancestral stock, but because of the paucity of fossil records in the grasses generally, one can only speculate as to the place of origin of present-day forms. Two possibilities are suggested: origin of the genus in tropical America, or development of the group from ancestors inhabiting a once-larger land mass in the southern hemisphere.

The first suggestion, that of origin in tropical America, has been discussed by Hartley (1950), who feels that the Paniceae alone among the major grass tribes has predominantly a New World distribution, being especially abundant in a well-defined region from the Bahamas to southeastern Brazil. Higher percentages of the Paniceae occur in regions of relatively high annual rainfall, with the numbers decreasing from this primary center of frequency. Hartley implies that distribution of the Paniceae is consistent with the view that they are monophyletic and probably originated in eastern tropical America and have spread widely throughout the moist
tropical regions of the world. Because of large numbers of apomictic species, according to Hartley, it is possible that the Panicoideae is a very old group that has been established in both hemispheres for a long time. Brown (1958b) claims that apomixis has been a characteristic feature in the Panicoideae for at least 100 million years, and he suggests that the tribe had genes widely distributed for apomixis. Hybridization among carrier species would occasionally bring together, in polyploid hybrids, all necessary genes for apomictic systems, it being assumed that polyploidy provides the best genetic environment for apomixis (Stebbins 1950). Stebbins places differentiation of the grass genera during late Cretaceous, but Bor (1960) contends that there is little or no evidence which would support these ideas concerning apomixis and time of grass development.

A second hypothesis, that of origin of *Oenchrus* in the Afro-Asian regions, is suggested by the preponderance of primitive species in those areas. Several species of *Oenchrus* in Africa and India have apparent lower basic chromosome number (X=9, 10) and are perennials. Stebbins (1950) says that the trend in many groups of plants is from long-lived perennials which are slow in establishing themselves in new regions to short-lived annuals that become established easily and more quickly. New polyploid forms, especially amphiploids, are probably better able to establish themselves than their diploid ancestors in new areas because of their greater
supply of potential new gene combinations.

In a discussion of distribution patterns, Camp (1947) suggests the possibility of a southern hemisphere origin for many Angiosperms and the presence of a larger, more continuous land mass in the south than now exists. Under such conditions the ancestors of Cenchrus and Pennisetum could have been quite widespread with several centers of dispersal rather than one as proposed by Hartley.

Regardless of the place of origin of Cenchrus, it appears that the modern-day species are quite adaptive, and with the recent activities of man in dispersal and the disturbance of large areas of land, many species are becoming much more widespread. Under such conditions it is possible that new forms may emerge and some of the present species may be eliminated through competition.
THE GENUS CENCHRUS


Nazia Adans. Fam. Pl. 2:31, 581. (1763)
Raram Adans. Fam. Pl. 2:35, 597. (1763)
Echinaria Desf. Fl. Atlant. 2:385. (1799)

Generic description

Plants annual or perennial; culms terete, solid; leaf sheaths compressed-keeled; ligule reduced to a ciliate rim, 1--3 mm long; leaf blades flat, sometimes folded or involute; spikelets lanceolate-oblong, usually acute, dorsally compressed, solitary or in groups of two to eight, sessile, enclosed by an involucre or bur of more or less connate, rigid spines or bristles (modified axes); florets 2, the lower staminate or sterile, the upper hermaphroditic; glumes lanceolate to ovate-oblong, acute or obtuse, membranous or hyaline, the glumes sub-equal, the first about one-half the length of the second or sometimes suppressed; first glume 1 to 3-nerved, second glume 1 to 7-nerved; lower floret about equal to upper floret in length; sterile lemma 3 to 7-nerved; sterile palea 2-nerved, equaling sterile lemma; fertile lemma as long as the spikelet, membranous, 5 to 7-nerved, palea as
long as the lemma, 2-nerved; lodicules non or abortive; stamens 3, 1 to 3 mm long; styles two, terminal, free or united only at base; stigmas plumose; grain elliptic to ovoid, dorsally flattened, lying free between the lemma and palea when mature; hilum basal; burs sessile or nearly so on a slender, compressed or angled rachis of the solitary spike-like panicle (false spike); tip of the rachis usually prolonged into a short point beyond the uppermost bur; bristles connate only at the base or more often above the base, forming a cup-like receptacle; spines antrorsely or retrorsely scabrid or barbed, usually flattened towards the base; spikelets permanently enclosed within the bur or with the tips projecting.

Type of the genus: *Cenchrus echinatus* L. (Chase 1920).

**History of the genus**

Sandburs were undoubtedly known to early botanists and gardeners but there are few references to them before the time of Linnaeus. A detailed discussion of the pre-Linnean names applied to this genus is found in Chase (1920). Linnaeus described the genus in 1742, the name *Cenchrus* presumably being derived from the Greek word Kenchros which referred to some form of millet (Gunther 1934). According to the *International Rules*, (Lanjouw 1961), however, the valid name (*Cenchrus*) dates from Linnaeus' *Species Plantarum* (1753). The five species described by Linnaeus were 0.
racemosus, C. capitatus, C. echinatus, C. tribuloides, and C. frutescens. The first two names were subsequently made the types of the genera Nazia and Echinaria respectively. The fifth species, C. frutescens, does not apply to any known grass, according to Chase (1920).

Poiret (1804) discussed 18 species of Cenchrus in his work on the Gramineae, followed by Persoon (1805), who described eleven species. Trinius (1833) treated eight species in his "De graminibus paniceis," of which only four are still retained in the genus. Kunth (1833), in his "Agrostographia," listed forty-five species of Cenchrus in the index. However, only eleven of these were considered valid species by him, and seven others were included under "species mihi dubiae." Roemer and Schultes described 21 species of Cenchrus in their Systema vegetabilium in 1817. The last of the general "enumerations of gramineae" were those of Steudel (1840, 1855). In the former work are listed sixty species which at some time had been associated with the genus Cenchrus, whereas in the latter work Steudel listed and described thirty species of Cenchrus.

Since 1855 no monographic treatments have dealt with the genus Cenchrus, although a number of regional works have appeared during the past century. These include Nash's North American Cenchrus (1895), Hitchcock and Chase's Grasses of the West Indies (1917), Hitchcock's work on Central American species (1930), Chase's monograph of the North American
species (1920), and the excellent treatment of African species by Stapf & Hubbard (1934). More recent regional works dealing with the genus include Chippindall's work on South African grasses (1955) and Bor's Grasses of Burma, India, Ceylon, and Pakistan (1960).

Key to the species of \textit{Oenchrus}

1. Spines connate for a considerable distance (more than halfway above the base) forming a globose bur or involucre, the bur enclosing one or more spikelets . . 2

2. Bur consisting of one whorl of united, flattened spines, subtended by one to several whorls of smaller and finer bristles . . . . . . . . . . . 3

3. Spines and bristles retrorsely barbed, the bristles usually not much exceeding the spines . . 4

4. Burs closely crowded in the inflorescence, outer bristles equal to or slightly exceeding the inner spines of the bur, peduncle about 2.0 mm wide . . . . . . . . . . . 1. \textit{O. brownii}

4. Burs loosely spaced in the inflorescence, outer bristles mostly about one-half the length of inner spines of the bur, peduncle more than 2.0 mm wide . . . . . 2. \textit{O. echinatus}

3. Spines and bristles antrorsely barbed, the bristles much exceeding the inner spines . . . . . 5

5. Bristles at least twice as long as the body of the bur, the burs densely crowded in the inflorescence . . . . . . . . . . . 3. \textit{O. pilosus}

5. Bristles only slightly longer than the body of the bur, burs loosely spaced in the inflorescence . . . . . . . . . . . 4. \textit{O. mitis}

2. Bur consisting of several whorls of flattened spines, the spines emerging at irregular intervals throughout the body of the bur . . . . . . . . . . . 6
6. Leaves narrow, usually less than 3 mm wide; plants perennial 7

7. Leaf blades involute, crowded and markedly distichous, about 2 cm long. C. distichophyllus 5

7. Leaf blades not involute, crowded or markedly distichous, 4 to 16 cm long. C. gracillimus 6

6. Leaves wider, 3 mm or more wide, plants annual 8

8. Spines slender, numerous, usually more than 50. 9

9. Inflorescence of 6 to 18 burs, spines usually not over 7 mm long, with 2 to 4 spikelets per bur. C. longispinus 7

9. Inflorescence of 1 to 3 burs, spines 9 to 14 mm long, 5 to 8 spikelets per bur, plants of Baja California and Mexico. C. palmeri 8

8. Spines broader at the base, fewer, less than 45. 10

10. Burs minute with from 5 to 10 spines, the burs crowded in the inflorescence, rachis internodes from 0.6 to 1.4 mm long. C. platvacanthus 9

10. Burs large, spines more numerous, usually more than 10, burs not crowded in the inflorescence, rachis internodes from 2.0 to 10.0 mm long. C. tribuloides 11

11. Burs densely pubescent, the usually solitary spikelet from 6 to 9 mm long, plants of coastal sand dunes. C. incertus 10

11. Burs glabrous to short-pubescent, the two to four spikelets from 3.5 to 5.8 mm long. C. incertus 11

1. Spines connate only at the base, forming a small disc or shallow cup at least 1.5 mm in diameter 12

12. One of the spines prolonged beyond the bur forming a distinct bristle. 13
13. Spines retrorsely barbed, robust plants
   1 to 3 meters tall, leaves broad, to 20 mm,
   rachis velvety-pubescent...12. C. caliculatus

13. Spines antrorsely barbed...14

14. Bristles at base of bur reduced to 6 or 8,
   spines few, 5 to 15, broad and flat, about
   1.0 mm wide, only slightly ciliate on the
   margins, peduncle glabrous...13. C. elymoides

14. Bristles at base of bur numerous, 20 or
   more, spines numerous, 20 to 30, narrow,
   less than 0.5 mm wide, peduncle ciliate
   to short-pubescent...15

15. Plants 30 to 90 cm tall, leaves up to
    eight mm wide, bur about 2 mm wide,
    spine-margins densely ciliate-pubescent...14. C. ciliaris

15. Plants from 1 to 2 meters tall, leaves
    8 to 20 mm wide, bur about 3 mm wide,
    spine-margins sparsely ciliate-pubescent...15. C. multiflorus

12. None of the spines prolonged beyond the bur
    to form distinct bristles...16

16. Spines rounded or terete throughout their length. 17

17. Spines densely ciliate for one-half their
    length, burs not crowded on inflorescence...12. C. caliculatus

17. Spines glabrous throughout, burs densely
    crowded in the inflorescence. 16. C. myosuroides

16. Spines broad, flattened at least at the base...18

18. Spines retrorsely barbed. . . . . . . . . . . . . 19

19. Burs fusiform, spines few, 6 to 10, terete
    and not grooved on the outer surface,
    peduncle 2.5 to 4.5 mm long, densely
    short-pubescent...17. C. agrimonioides

19. Burs not fusiform, somewhat globose, spines
    numerous with a definite groove on the outer
    surface, peduncle 0.9 to 2.2 mm long,
    glabrous...18. C. biflorus
18. Spines antorsely barbed. ... 20

20. Spines long, plumose, up to 10 to 20 mm long, lower one-third of the spine margins densely ciliate ... 19. O. pruriest

20. Spines short, 2 to 4 mm long, margins glabrous. ... 20. O. setigerus

1. Oenchrus brownii (Figure 6, A--E; map, Figure 4)

Oenchrus brownii Roem. & Schult. Syst. Veg. 2:258. (1817). (Based on O. inflexus R. Br.)

Oenchrus inflexus R. Br. Prodr. 1:195. (1810) (Non O. inflexus Poir. 1804) (Type in BM, fragment of type in US) (1)

Oenchrus viridis Spreng. Syst. 1:301. (1825) (Type in B, fragment of type in US) (1)


Oenchrus echinatus var. viridis Spreng. ex Griseb. Fl. Brit. W. Ind. 556. (1864) (Based on O. viridis Spreng.) (2)

Oenchrus viridis var. macrocephalus Doell in Mart. Fl. Bras. 2, 2:310. (1877) (2)

Oenchrus echinatus Steud. ex Doell in Mart; Fl. Bras. 2, 2:309. (1877) (Non O. echinatus L.) (4)

Oenchrus rigidus Willd. ex Doell in Mart. Fl. Bras. 2, 2:310. (1877) (A herbarium name given as a synonym of O. viridis var. macrocephalus Doell in Mart.) (4)

Description

Small annual; culms 25--95 cm tall; sheaths slightly compressed, the margins sometimes sparsely pilose; ligule ciliate, 0.6--1.3 mm long; leaves 8.0--30 cm long, 4.0--11.0 mm wide, glabrous or sometimes with sparsely pilose upper surface and margins; inflorescence compact, 3--12 cm
long, about 1.5 cm wide; rachis slightly angled, minutely pubescent; internodes 0.8—1.7 mm long; bur globose, 2.0—4.5 mm wide, 5—8 mm long including outer bristles, villous at peduncle and lower part of bur, the bur tawny in color; inner spines connate forming a cup, erect or interlocking at maturity, 2—4 mm long, 0.6—1.8 mm wide; outer spines numerous, bristle-like, arising from a whorl at the base of the bur, sometimes surpassing the inner spines; spines and bristles retrorsely barbed; spikelets 2 or 3 per bur, sessile, 4—6 mm long; first glume 0.5—2.5 mm long, 1-nerved, 0.2—1.0 mm wide; second glume 2.2—4.9 mm long, 3 to 5-nerved; sterile lemma 3.5—5.5 mm long, enclosing a narrow, scabrous palea of equal length; fertile floret 3.6—5.4 mm long, 1.3—2.1 mm wide; anthers 0.8—2.3 mm long; fruit ovoid, 1.9—2.6 mm long, 0.8—1.9 mm wide; somatic chromosome number 2n=34.

Observations and nomenclature

Oenchrus brownii has many morphological affinities with O. echinatus L., but differs from the latter species in the smaller, globose burs with narrower peduncles, and in the more densely compact inflorescence. The tawny color of the mature burs of O. brownii, as contrasted with the purple-tipped spines of O. echinatus, also aids in delimiting these two taxa. In O. brownii the outer bristles are more numerous and usually surpass the inner spines, while in O. echinatus
the bristles are fewer, and shorter than the inner spines.
Table 3 gives a comparison of significant taxonomic characters which separate these two species.

Table 3. Comparison of *C. brownii* R. & S. and *C. echinatus* L.

<table>
<thead>
<tr>
<th>Character</th>
<th><em>C. brownii</em></th>
<th><em>C. echinatus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Peduncle width</td>
<td>0.6—2.0 mm</td>
<td>2.2—3.6 mm</td>
</tr>
<tr>
<td>Bur width</td>
<td>2.0—4.5 mm</td>
<td>3.5—6.0 mm</td>
</tr>
<tr>
<td>Rachis internode L.</td>
<td>0.8—1.7 mm</td>
<td>2.0—3.0 mm</td>
</tr>
<tr>
<td>Floret length</td>
<td>3.6—5.4 mm</td>
<td>5.0—7.6 mm</td>
</tr>
</tbody>
</table>

*Cenchrus brownii* R. & S. was based on the name *C. inflexus* R. Br., which had previously been assigned by Poiret (1804) to a species of *Echinolaena*. The name was accordingly changed to *C. brownii* by Roemer and Schultes (1817). A fragment of the holotype of *C. inflexus* R. Br., in the U. S. National Herbarium, was examined by the writer. This taxon was given the name *C. viridis* by Sprengel (1825), but the type in the Krug and Urban Herbarium, Berlin, of which a fragment was examined, identifies it as the earlier-named *C. brownii* R. & S. Doell, in Martius (1877), apparently based *C. viridis* var. *macrocephalus* on a form with slightly longer bristles. However, the description of this character
indicates that it falls within the normal range of variation of the species.

Cytology

Avdulov (1931) reported a chromosome number of 2n=34 for *C. brownii* R. & S., (reported as *C. viridis* Spreng). The writer's count obtained for this species is indicated in Table 4. Meiotic figures appeared normal in the material from which the count was made.

Table 4. Chromosome count from pollen mother cells of *Cenchrus brownii* R. & S.

<table>
<thead>
<tr>
<th>Collection</th>
<th>Location</th>
<th>Chromosome number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Weatherwax no. 3338</td>
<td>Florida</td>
<td>n=17</td>
</tr>
<tr>
<td>DeLisle voucher no. 471</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Distribution

*Cenchrus brownii* is found in sandy waste places and forest borders throughout the West Indies, Mexico, Central and South America, and infrequently in the southern U. S. This species was apparently introduced into Australia at an early date and more recently has become adventive in the Philippines, Guam, Indochina, the Pacific Islands, and South Africa.
Selected specimens examined

AUSTRALIA: Arnheim, South Bay, Brown 6140, 1803 (Holotype BM); Port Darwin, Schultz (US).
BOLIVIA: Lara Santa Cruz, J. Steinbach 6838, Dec. 28, 1924 (MO); Guayaquil, H. H. Rusby 190, May 1886 (NY).
BRASIL: Miras (MO); Vicinity of Maceio, Alagoas, A. Chase 7843, Dec. 5, 1924 (MO).
BRITISH GUIANA: Upper Demera River, Jenman 4011, Sept. 1887 (US); New Amsterdam, A. S. Hitchcock 16820, Nov. 21, 1919 (NY, UC, US, MO).
BRITISH HONDURAS: West of Salt Creek, H. O'Neill 8490, Sept. 15, 1936 (NY); El Cayo District, C. L. Lundell 6142, (F, NY, US).
COLUMBIA: Rio Frio, F. Walker, June 1, 1925 (MO); Medellin Valley, C. Allen 251, Aug. 3, 1924 (MO).
COSTA RICA: Puerto Limon, B. Lehmann 1290 (US).
ECUADOR: Milagro, A. S. Hitchcock 20188 (NY).
EL SALVADOR: San Vicente, F. C. Standley & E. Padilla 3752, Feb. 1947 (F); South of Lago de Zapotitlan, M. O. Carlson 306, Jan. 27, 1946 (UC).
GUATEMALA: Huehuetenango, Steyermark 51144, Aug. 28, 1942 (F); Quirigua, P. Weatherwax, Feb. 24, 1932 (SUI);
INDOCHINA: Annan, J. & M. S. Clemens 4469 (NY, UC).
MARIANAS: Agrigan, F. R. Fosberg 31587, Feb. 17, 1950 (NY);
MARSHALL ISLANDS: Eniwetok, H. St. John 23711, Aug. 6, 1949 (UC, MO).
MEXICO: Vera Cruz, (MO); Manzanillo, E. Palmer 1086, Dec. 1890 (NY); Yucatan, Tuxpena, C. L. Lundell 911, Nov. 6, 1931 (NY, DAO, MO, UC).
PHILIPPINES: Sulu province, Tawitawi, M. Ramos & G. Edano 44273, 1924 (NY, UC); Luzon, Manila, E. D. Merrill 811, Feb. 1915 (MO).
SOUTH AFRICA: Natal, Durban Point, C. Kent 32229, April 1940 (US).
UNITED STATES: Del Rio, Texas (MO); Florida, Key Largo, H. N. Moldenke 781, March 18, 1930 (MO).
VENEZUELA: Lara, Saer 153 (NY); Island of Margarita, O. O. Miller & J. R. Johnston 186, July 30, 1901 (NY, MO).
WEST INDIES: Bahamas, Fortune Island, A. S. Hitchcock, Nov. 1890 (MO); Cuba, Santiago City, Palmer 284, Feb. 14, 1902 (NY, MO); St. Croix, D. W. I., A. Ricksecker 124,
Figure 4. Geographic distribution of *Cenchrus brownii*.
Nov. 28, 1895 (U.O); Haiti, Gonave Island, E. C. Leonard
3084, March 1920 (NY); Jamaica, St. Andrew Parish, T. G.
Yuncker 17026, Oct. 11, 1957 (MO); Martinique, Pere Duss 790
(NY); Porto Rico, Rio Piedras, J. A. Stevenson, Dec. 18, 1914
(NY); Cayo Muertos, N. L. Britton, J. F. Cowlfull, & S. Brown
4986, March 1915 (NY, MO). Santo Domingo, Azui, N. Taylor
295, Nov. 25, 1919 (NY).

2. Oenchrus echinatus (Figure 6, F—J; map, Figure 5)

Oenchrus echinatus L. Sp. Pl. 1050. (1753) (Holotype
in L) (1)

Oenchrus echinatus Cav. Ic. 5:39. t. 462. (1799)
(C. echinatus Cav. of various authors, Cavanilles
attributes this species to L.) (2)

(1815) (Holotype in P, fragment of type in US) (1)

Oenchrus cavanillesii Tausch. Flora. 20:97. (1837)
(Based on C. echinatus Cav.) (2)

Oenchrus macrocarpus Ledeb. ex Steud. Nom. Ed. II.
2:317. (1840) (A garden name given as a synonym of
C. echinatus L.) (2)

(1847) (C. echinatus A. Rich. of various authors,
Richard attributes this species to L.) (2)

(1857) (Holotype in P, fragment of type in US) (1)

(1877) (4)

Oenchrus brevisetus Fourn. Mex. Pl. 2:50. (1886)
(Holotype in P, fragment of type in US) (1)

2:765. (1891) (2)

Ser. II. 26. (1900) (Based on O. brevisetus Fourn.)
(2)

Ser. II. 26. (1900) (Holotype in F) (1)

(1917) (Holotype in B, fragment of type in US) (1)
Cenchrus hillebrandianus Hitch. in Mem. Bern. P. Bishop Mus. 8:211. (1922) (Holotype in US) (1)


Description

Plant annual; culms terete, ascending from a geniculate base, 15–85 cm long; pubescence highly variable; sheaths compressed, pilose on the margins near the summit; ligule ciliate, 0.7–1.7 mm long; leaves glabrous to pubescent, 4–26 cm long, 3.5–11 mm wide; inflorescence open, 2.0–10.0 cm long, 0.8–1.8 cm wide; rachis strongly flexuous, scabrous, the internodes 2.0–3.0 mm long; burs truncate at the base, globose, 5.0–10.0 mm long, 3.5–6.0 mm wide; the spine tips usually turning purple with age; outer bristles fewer than in C. brownii, and shorter than the body of the bur; inner spines mostly erect, sometimes interlocking at maturity, 2.0–5.0 mm long, 0.6–1.5 mm wide, retrorsely scabrid; body of bur short-pubescent; peduncle pubescent, 2.2–3.6 mm wide, 1.0–3.0 mm long; spikelets 2 or 3 per bur, sessile, 5.0–7.0 mm long; first glume 1.3–3.4 mm long, 0.6–1.8 mm wide; second glume 3.8–5.7 mm long, 3 to 6 nerved; sterile lemma 4.5–6.4 mm long, enclosing a slightly longer, scabrous palea; fertile floret 4.7–7.0 mm long, 1.2–2.3 mm wide;
anthers 0.8—2.4 mm long; fruit ovoid, 1.6—3.2 mm long; 
1.3—2.2 mm wide; somatic chromosome number 2n=34, 68.

Observations and nomenclature

_Cenchrus echinatus_, commonly referred to as "hedgehog
grass," is an annual with large burs which are widely spaced
on the inflorescence. The spine-tips in mature burs of most
collections examined tend to assume a purple tinge, a trait
which is apparently lacking in the closely-related _C. brownii_.
Characters which serve to distinguish these two species have
been summarized in Table 3. Pubescence is highly variable
in _C. echinatus_. Some plants are completely glabrous while
others may possess rather densely villous sheaths and blades.
This trait was the basis for establishment of the species
_C. hillebrandianus_ by Hitchcock (1922). However, there is
wide variation in pubescence of collections observed by the
writer, and there does not appear to be any correlation of
this character with the geographic distribution of the
species. Brown (1931) reported that seedlings of Hawaiian
pubescent forms of _C. echinatus_ varied from sub-glabrous to
pubescent, according to the conditions under which they were
grown.

Linnaeus (1753) included five species in the genus
_Cenchrus_, of which _C. echinatus_ and _C. tribuloides_ are the
only two still retained. In his generic description,
Linnaeus (1742) described the bur as follows:
Cal. Involucra plura, laciniata, echinata, in capitulum congesta: singulis sessilibus tres calyces includentibus.

It appears that he was referring to a specimen of *C. echinatus*, which usually has three spikelets per bur. In *C. tribuloides* the calyx (involucre) is not laciniate and there is generally only one spikelet in each bur. *Cenchrus echinatus* L. is, therefore, taken as the type of the genus. The holotype in the Linnaean Herbarium is a specimen marked by Linnaeus with no indication as to its origin. In his description of the species, however, he cites a specimen collected by Sloane in Jamaica. A photograph of the holotype on microfiches (Linnean Society of London, 1959) was examined by the writer.

The holotype of *C. brevisetus* Fourn. (1886) is in Paris. Fragments of the type specimen, in the U. S. National Herbarium, show a marked resemblance to depauperate or immature specimens of *C. echinatus* L. Occasional variant forms with slightly longer and more erect spines have provided the bases for establishment of *C. insularis* Scribn. (1900), and *C. echinatus* var. *morisonii* Kuntze (1891), but this trait appears to be highly variable and has no apparent geographic correlation.

**Cytology**

A chromosome number of 2n=34 has been reported by Avdulov (1931). However, Nunez (1942) and Tateoka (1955)
both reported a somatic number of 2n=68. This same count was obtained by the writer, as shown in Table 5. It appears that *C. echinatus* L. is probably a tetraploid form derived from some ancestor with a basic number of x=17. Meiosis was normal in the specimens examined by the writer.

Table 5. Chromosome counts from pollen mother cells of *Cenchrus echinatus* L.

<table>
<thead>
<tr>
<th>Collection</th>
<th>Location</th>
<th>Chromosome number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pohl no. 8105</td>
<td>Tampa, Florida</td>
<td>n=34</td>
</tr>
<tr>
<td>DeLisle voucher no. 468</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weatherwax no. 3336</td>
<td>Florida</td>
<td>n=34</td>
</tr>
<tr>
<td>DeLisle voucher no. 472</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Distribution**

*Cenchrus echinatus* L. is distributed throughout the warmer regions of southern United States, Central and South America and the West Indies. It is adventive and widely distributed on most of the Pacific Islands, the Philippines, and Australia, probably as a result of man's activities. The species has also been introduced into Africa, and in the last four to six years has begun to spread over the coastal plain of Israel (Dr. D. Zohary, Hebrew University, Jerusalem, 1961, personal communication).
Selected specimens examined

ARGENTINA: Province de Salta, S. Venturi 5509, Nov. 10, 1927 (NY, MO); Carriientes prov., W. Lossen 548 (UC).
AUSTRALIA: Arnheim land, R. L. Specht 149 (US); Strand-Townsville, D. A. Goy 357 (MO).
BRASIL: Brasilia, G. Orth 861 (MO); Rio Grande do Sul, A. A. Beetle 1487 (UC, AHS).
BRITISH GUIANA: A. S. Hitchcock 16741 (NY, UC, MO).
BRITISH HONDURAS: Stann Creek, W. A. Schipp 893 (NY, UC, MO).
BOLIVIA: Dept. Santa Cruz, Buela Vista, J. Steinbach 5576 (NY, MO).
CHILE: Azapa, E. Werdermann 703 (NY, MO).
ECUADOR: Cuboendo el Ambi, M. Acosta Solis 18120 (US); Rio Guano, H. J. F. Schimpff 918 (MO).
GUATEMALA: Culico, J. Steyermark 50868 (F); Guatemala City, P. C. Standley 3480 (ISC).
HONDURAS: Along Aguan River below Coyoles, T. G. Yuncker 8126 (NY, UC, MO).
MEXICO: Vera Cruz, J. R. Swallen 35355 (DAO, SMU); Oaxaca City, C. L. Smith 954 (MO, SUI); Tampico, E. Palmer 155 (F, NY, MO); Victoria, E. Palmer 83 (NY, UC, MO); San Luis Potosi, A. S. Hitchcock 616 (NY, UC, MO); Baja California, San Jose del Cabo, C. A. Purpus 320 (UC, MO).
PARAGUAY: Villa Rian, F. Jorgensen 3532 (NY, MO).
UNITED STATES: East Brewton, Alabama, D. J. Banks 775 (ISC); Lee Co., Alabama, F. S. Earle (MO); Tucson, Arizona, J. J. Thorner 2140 (DAO, SUI); Imperial Co., Calif., D. W. Ragsdale 21 (AHU); Washington, D. C., W. P. Conant, 1884 (MO); Jacksonville, Florida, A. H. Curtiss 5152 (F, UC, ISO); Key West, Florida, J. M. Gillett 7414 (DAO); Lake Co., Florida, G. V. Nash 139 (UC, MO); Waycross, Georgia, D. J. Banks 980 (ISC); Oahu, Hawaii, A. S. Hitchcock 14068 (NY, UC, MO); Waikiki, Hawaii, A. S. Hitchcock 13801 (NY, UC, MO); Honolulu, Hawaii, O. Degener 12255 (NY, US); Ouachita Parish Louisiana, D. S. Correll 10357 (F, MO); Biloxi, Miss.; DeLisle 662 (ISC); New Mexico, Thornber, 1908 (ISC); Bentonville, N. C., A. E. Radford 27812 (UC, SMU); Beaufort, S. C., R. K. Godfrey 1530 (DAO); Cameron Co., Texas, E. U. Clover 1219 (SMU, TEX); Valverde Co. Texas, H. Eggert Sept. 11, 1900 (MO); Hidalgo Co., Texas, W. Sileveus 2568 (SMU, TEX); Galveston Co., Texas, B. C. Tharp 43178 (TEX, MO); Willacy Co., Texas, Tharp, Dec. 1948 (ISC, TEX).
VENEZUELA: H. Gines 3659 (DAO).
PACIFIC ISLANDS: Polynesia, Taumoto, G. P. Wilder, Sept. 1932 (NY); Tahiti, Setchell, May 1922 (US, UC); Rurutu Island, F. R. Fosberg, Aug. 1934 (US); Mangareva Island, H. St. John 14647 (US); New Caledonia, Loyalty Island, I. Franc 1073 (NY); Easter Island, F. Fuertes, April 1911 (US); Carolines, R. Kanehira, June 1929 (NY); Marshall Islands, Ujae atoll, F. R. Fosberg 34310 (NY); Einewetok, H. St. John 23844 (UC, MO); Bikini Atoll, W. R. Taylor 1173 (UC, US).

WEST INDIES: Bahamas, P. Wilson 7350 (NY); Cuba, Distr. of Cienfuegos, R. Combs 597 (NY, MO, ISC); Haiti, L. R. Holdridge 1709 (NY, UC, MO); Martinique, Pere Duss 791 (NY, MO); Porto Rico, Guanica, N. L. Britton 4916 (NY, MO).

3. Oenchrus pilosus (Figure 6, K--0; map, Figure 7)


Oenchrus pallidus Fourn. Mex. Pl. 2:50. (1886) (Holotype in C, fragment of type in US) (1)

Oenchrus pallidus Millsp. Field Mus. Bot. 1:351. (1896) (pro parte, non C. pallidus Fourn. 1886) (2)

Description

Plants annual; culms tufted, 30--60 cm tall; sheaths compressed-keeled, glabrous or sometimes scabrous; ligule ciliate, 0.5--1.6 mm long; blades glabrous or slightly pilose near the base, 6.0--30.0 cm long, 4.0--11.0 mm wide; inflorescence compact, 2.0--13.0 cm long, 0.8--2.7 cm wide; rachis strongly angled, scabrous, the internodes 1.0--2.5 mm long; burs globose, 5.0--8.0 mm long, 3.0--5.5 mm wide, stramineous or sometimes purple; peduncle and body of bur pubescent; inner spines 3.0--6.0 mm long, 0.6--2.0 mm wide, erect or interlocking; outer whorl of bristles numerous with many twice as long as the body of the bur; spines and bristles
Figure 5. Geographic distribution of *Cenchrus echinatus*
C. echinatus

HAWAIIAN ISLANDS
antrorsely barbed; spikelets 2 to 3 per bur, sessile, 6.0--7.5 mm long; first glume 1.0--4.0 mm long, 0.6--1.4 mm wide; second glume 3.1--6.0 mm long, 3 to 5-nerved; sterile lemma 4.0--7.0 mm long, enclosing a slightly shorter, minutely scabrous palea; fertile floret 5.0--7.5 mm long, 1.0--2.2 mm wide; lemma 3-nerved; anthers 0.9--1.8 mm long; fruit ovoid, 2.2--3.0 mm long, 1.0--2.2 mm wide; chromosome number 2n=34.

Observations and nomenclature

This species is characterized by its plumose outer bristles, which are at least twice as long as the body of the bur, including the inner spines. In this respect, it can be readily distinguished from O. mitis, the latter species having bristles which only slightly surpass the inner spines in length. The peduncle of O. pilosus is densely ciliate-pubescent in contrast to that of O. mitis which is scabrous to only short-pubescent. The density of the inflorescence of O. pilosus, with internode lengths of 1.0--2.5 mm as contrasted with 2.8--5.0 mm for O. mitis, also serves as a means of distinguishing these two taxa.

Oenchrus pilosus was described by Humboldt, Bonpland & Kunth (1815) from a specimen labeled "Llanos de Neuva Barcellona," apparently referring to a location in Venezuela. The holotype is in the Humboldt & Bonpland Herbarium, Paris. A fragment of the holotype in the U. S. National Herbarium was examined by the writer. The holotype of O. pallidus
Fourn. was collected near Tehauntepec, Mexico, (Liebmann no. 465). A fragment of this specimen in the U. S. National Herbarium was examined by the writer and matches closely the type of *Oenchrus pilosus* H. B. K.

**Cytology**

Results of the writer's cytological investigations on *Oenchrus pilosus* are shown in Table 6. There have been no counts reported by other authors for this species.

Table 6. Chromosome count from pollen mother cells of *Oenchrus pilosus* H. B. K.

<table>
<thead>
<tr>
<th>Collection</th>
<th>Location</th>
<th>Chromosome number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Weatherwax no. 3337</td>
<td>Guatemala</td>
<td>n=17</td>
</tr>
<tr>
<td>DeLisle voucher no. 473</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Distribution**

This species is restricted to central Mexico, south through central America to northern South America.

**Selected specimens examined**

- **ECUADOR**: Province of Guayas, H. K. Svenson 11298, March 7, 1941 (F, NY, MO, UC).
- **EL SALVADOR**: Department of La Libertad, Playa del Paz, N. C. Fasset 28264, Oct. 8, 1950 (F).
Figure 6. *Cenchrus brownii*, *Cenchrus echinatus*, and *Cenchrus pilosus*

A--E. *Cenchrus brownii*: A. spikelet, B. floret, C. caryopsis, D. bur, E. inflorescence

F--J. *Cenchrus echinatus*: F. inflorescence, G. bur, H. spikelet, I. floret, J. caryopsis

K--O. *Cenchrus pilosus*: K. bur, L. spikelet, M. caryopsis, N. floret, O. inflorescence
GUATEMALA: Department Santa Rosa, P. C. Standley 77737, Nov. 21, 1940 (F); near ruins of Quirigua, Weatherwax 1590, March 1, 1932 (US); Dept. of Santa Rosa, So. of Guazacapan, P. C. Standley 79492, Dec. 6, 1940 (UC).


HONDURAS: Amapala, J. V. Rodriguez 3355, Sept. 11, 1945 (F); San Lorenzo, J. V. Rodriguez 3316, Sept. 9, 1945 (F); Dept. of Choluteca, P. C. Standley, Oct. - Nov. 1949 (NY, F).


PERU: Dept. of Lima, O. Haught F-76, 1928 (F); Dept. Piura, Prov. Piata, O. B. Horton 11591, June 9, 1942 (F, MO, UC).


VENEZUELA: Cubagua Island, F. Elmore Q4, April 14, 1939 (F); Llanos de Neuvu Barcellona, Bonpland (F) (Holotype of C. pilosus); La Victoria, Aragua, L. Williams 10877, Nov. 29, 1938 (F, US); vicinity of Maracaibo, H. Pittier 10681, Nov. 10, 1922 (NY); Island of Margarita, O. O. Miller 179, 8-2-1901 (NY, US, MO).


4. *Oenchrus mitis* (Figure 9, A--E; map, Figure 7)

*Oenchrus mitis* Anderss. in Peters Reise Mossamb. Bot. 2:553 (1864) (Holotype in B, isotype in K) (2, 3)

**Description**

Plants annual; culms geniculate, decumbent or ascending, 30--80 cm high; sheaths compressed-keeled, glabrous; ligule ciliate, about 1.5 mm long; blades glabrous, sometimes sparsely pilose, 2.0--5.5 mm wide, 8--20 cm long; inflorescence open, 8--12 cm long, 1--2 cm wide; rachis flexuous, scaberulous, the nodes 2.8--5.0 mm long; burs somewhat
fusiform, minutely pubescent, 6.5—9.0 mm long, 3.5—5.4 mm wide; peduncle 1.0—1.6 mm long, 1.0—2.0 mm wide; inner spines connate for at least one-third to one-half their length, pubescent on the outside; spine tips erect, tapering, 4.0—5.0 mm long, 1.0—1.3 mm wide; tips of spines and bristles antroserly barbed, the outer whorl of bristles narrow, 5.5—9.0 mm long, slightly surpassing the inner spines in length; two, rarely three spikelets per bur, the spikelets 4.0—5.8 mm long; first glume 1-nerved, 2.0—3.0 mm long, 0.6—1.3 mm wide; second glume 6-nerved, 3.6—4.6 mm long; sterile lemma 4.2—5.7 mm long, 5-nerved, the enclosed palea slightly shorter; fertile floret 4.0—5.8 mm long, 1.4—2.0 mm wide, glabrous, 3 to 5-nerved; fruit elliptic-oblong, 1.9—2.7 mm long, 1.2—1.8 mm wide.

Observations and nomenclature

The long internodes and shorter bristles distinguish C. mitis from C. pilosus. Morphologically, C. mitis appears to have its strongest affinities with C. pilosus, C. echinatus and C. brownii, although the general appearance of the bur places it closest to C. echinatus. C. mitis has a rather restricted geographic range in East Africa, while C. echinatus and C. brownii are found widely distributed in both hemispheres, although having their apparent centers of distribution in Central America. In view of its restricted range, it is possible that C. mitis is a relict species which
formerly had a much wider distribution than at present. Since there is no information regarding the cytology and genetics of *O. mitis*, any notions concerning its evolution or place of origin can only be conjectural.

*Cenchrus mitis* is based on specimens collected by Peters on Querimba Kerimba Island, Portuguese East Africa. The isotype at Kew has not been examined by the writer. Anderson's original description and the more recent treatment by Stapf and Hubbard (1934) leaves no doubt as to the identity of this taxon.

**Cytology**

No cytological work or chromosome numbers have been published for *Cenchrus mitis*.

**Distribution**

This species has a rather restricted geographic range in Eastern Africa, from Kenya south to Mozambique, and the island of Zanzibar.

**Selected specimens examined**

BRITISH E. AFRICA: Changamwe, 14 mi. from Mombasa, E. A. Mearns 2155, Nov. 21-30, 1909 (US).
DUTCH E. AFRICA: Stuhlmann 765-4, July 1894 (US).
MOZAMBIQUE: O. Kuntze, 8-10-94 (NY).
UGANDA: Setchell, June 10, 1927 (UC).
ZANZIBAR: J. T. Last, 1908 (NY, F); Zanzibar Island, A. S. Hitchcock 24455, Aug. 27, 1929 (US).
Figure 7. Geographic distribution of *Cenchrus pilosus* and *Cenchrus mitis*.
5. *Oenchrus distichophyllus* (Figure 9, J—0; map, Figure 8)

(1866) (Holotype in GOET, isotypes in NY and HABA) (1)

**Description**

Plants perennial, culms erect, arising from a knotted base; nodes numerous, short, 0.5—3.0 cm, mostly 0.5—1.0 cm long; culms appressed-pubescent; sheaths appressed-pubescent, long-ciliate at upper margins and throat; ligule reduced to a minute rim of hairs, less than 0.5 mm long; blades glabrous, strongly inrolled (involute), tapering to a sharp point, 2.5--3.0 cm long; about 1.5 mm wide; rachis flexuous, short-pubescent, the nodes 2.0--6.0 mm long; inflorescence 2.5--4.0 cm long, 0.6--1.6 cm wide; burs stramineous, ovoid, 3.5--6.5 mm long, 1.5--3.0 mm wide, glabrous to short-pubescent; peduncle pilose, 1.0--2.0 mm long, about 1.5 mm wide; spines numerous, 35 to 50, the upper ones 2.0--3.0 mm long, 0.5 mm wide, retrorsely barbed; spines at the base of bur small, bristle-like; spikelets one per bur, about 2.5--3.6 mm long; first glume 1.0--1.9 mm long, 0.6--0.9 mm wide, 1-nerved; second glume 2.2--3.1 mm long, 3 to 4-nerved; sterile lemma 2.9--3.3 mm long, 3-nerved, enclosing a slightly shorter palea; fertile floret 2.4--3.6 mm long, 0.8--1.1 mm wide, 3 to 5-nerved, surrounding the equally long palea; mature fruit ovoid, turgid, about 2.0 mm long, 1.6 mm wide.
Observations and nomenclature

The numerous, extremely short culm internodes and the short, involute, and sharp-pointed leaves readily distinguish *C. distichophyllus* from all other species of the genus. This taxon also has characteristically small, ovoid burs with minute spines which appear to always be stramineous, no purple coloration being found in any of the collections examined.

The holotype of *C. distichophyllus* was collected in Cuba, (Wright no. 3475, 1863), and is in the Grisebach Herbarium, Goettingen, Germany. Isotypes are deposited in the New York Botanical Garden and the U. S. National Herbarium, and were examined by the writer. Labels on the specimen from the U. S. National Herbarium indicate that an isotype is also deposited in the Academia de Ciencias de la Habana, Cuba.

Cytology

Seeds of this species were unavailable for germination; therefore no chromosome counts were obtained, and none have been reported by other authors.

Distribution

*Cenchrus distichophyllus* is confined to the island of Cuba. The type specimens and other collections observed by the writer indicate that this taxon is endemic to the Pinar del Rio province of Western Cuba, occurring in the sandy pine-lands of that region. Leon (1946), however, reports it from
other regions of Cuba.

Selected specimens examined

CUBA: San Julian, Province of Pinar del Rio, R. Lamas, Aug. 1917 (F, NY, DAO, UC, MO); Cuba, occ., Wright 3475, 1863 (GOET, holotype; NY, US, HABA, isotypes); near Santa Catalina, E. L. Ekman 18102, Nov. 17, 1923 (NY); Pinar del Rio, E. L. Ekman 11166, June 9, 1920 (NY); Pinar del Rio, E. L. Ekman 17270, Aug. 23, 1923 (NY); Pinar del Rio, E. L. Ekman 11264 (NY); Pinar del Rio, Laguna Jovero, J. A. Shafer 10717, Dec. 5-7, 1911 (NY); Pinar del Rio, E. L. Ekman 11250, June 14, 1920 (NY, F); Cuba, C. Wright 3475, 1860-64 (MO).

6. Oenchrus gracillimus (Figure 9, F—I; map, Figure 8)


Description

Plants perennial, in time forming rather dense clumps, sometimes flowering the first year; culms 15--60 cm tall; sheaths keeled, very slender, glabrous or rarely sparsely pilose; ligule minute, 0.2--0.6 mm long; blades slender and stiff, usually folded, glabrous or sometimes scabrous, 4.5--17.0 cm long; 1.1--3.3 mm wide; inflorescence 2.0--6.8 cm long, 0.8--1.9 cm wide, the burs not crowded; rachis flexuous, scabrous, the internodes 4.0--10.0 mm long; burs ovoid, tapering toward the base, glabrous, 5.2--12.9 mm long, 2.1--3.9 mm wide; peduncle glabrous, 1.0--2.0 mm long, 1.4--2.6 mm wide; spines slender, spreading, 3.2--6.0 mm long, 0.2--1.0 mm wide, the tips retrorsely barbed, and often with purple coloration; spikelets 1 to 3 per bur, sessile, 4.0--6.5 mm long; first glume 1.4--3.1 mm long, 0.6--1.8 mm wide,
1-nerved; second glume 3.2—5.4 mm long, 3 to 5-nerved; sterile lemma 4.1—6.0 mm long, 3 to 5-nerved, enclosing a narrow, scabrous palea of equal length; fertile floret 3.9—6.5 mm long, 1.1—2.2 mm wide, glabrous, 3-nerved; anthers 0.9—1.9 mm long; fruit ovoid-elliptic, 1.8—3.0 mm long, 1.0—1.5 mm wide; somatic chromosome number 2n=34.

Observations and nomenclature

The long, narrow leaf blades and the matted, perennial nature of this species aid in delimiting it from other members of the genus Cenchrus. The burs, which are widely spaced on the inflorescence, are marked by being almost completely glabrous, and by the appearance of their extremely long and narrow spines. Plants of this species begin forming clumps during their first year of growth, and in some instances may flower the first year.

Nash (1895) in his description of C. gracillimus cited his collection numbers 188 and 288 which were taken in the vicinity of Eustis in Lake County, Florida, in 1894. He did not, however, indicate which of these collections was the holotype. Chase (1920) therefore designated Nash No. 188 as the lectotype. This specimen is in the Herbarium of New York Botanical Garden, and was examined by the writer.

Cytology

Aside from the count obtained by the writer and shown in Table 7, no chromosome numbers have been reported by other
authors for this species.

Table 7. Chromosome count from pollen mother cells of *Oenchrus gracillimus* Nash

<table>
<thead>
<tr>
<th>Collection</th>
<th>Location</th>
<th>Chromosome number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Birdsey no. 677</td>
<td>Coral Gables, Florida</td>
<td>n=17</td>
</tr>
<tr>
<td>DeLisle voucher no. 477</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Distribution

*Oenchrus gracillimus* occurs in sandy soil of open pine woods of Georgia, Alabama, Florida, and the West Indies.

Selected specimens examined

**BAHAMAS**: Fortune Islands, A. S. Hitchcock, Nov. 1880 (MO); Bimini's Island, H. C. Beardslee Jr., Nov. 1934 (UC).


**DOMINICAN REPUBLIC**: Puerto Plata, Jose de JS. Jiminez 2724, Sept. 16, 1954 (US).

**HAITI**: Ile La Tortue, E. L. Ekman 9760, March 22, 1928 (US).

**JAMAICA**: St. Elizabeth, G. R. Proctor 7748, March 14, 1953 (US); Southern Manchester, Wm. Harris 12590, Nov. 20, 1917 (US, MO).


**FLORIDA**: Miami, A. S. Hitchcock 617, March 1903 (F, US, UC, MO); Miami, near sub-tropical lab., A. Chase 3847, Sept. 6, 1907 (US, ISO); Tampa, Campo 1363, 10-6-1898 (US); Levy County, Fla., R. Kral 4631, April 8, 1957 (SMU); Suwanee County, Florida, A. S. Hitchcock, June-July 1898 (MO); Hernando County, Florida, J. D. Ray 9499, Oct. 14, 1959, (US);
Figure 8. Geographic distribution of *Cenchrus gracillimus* and *Cenchrus distichophyllus*
Figure 9. *Cenchrus mitis*, *Cenchrus gracillimus*, and *Cenchrus distichophyllus*

A--E. *Cenchrus mitis*: A. inflorescence, B. bur, C. spikelet, D. floret, E. caryopsis

F--I. *Cenchrus gracillimus*: F. inflorescence, G. spikelet, H. caryopsis, I. floret

J--O. *Cenchrus distichophyllus*: J. floret, K. spikelet, L. caryopsis, M. bur, N. inflorescence, O. portion of culm showing distichous arrangement of leaves
Description

Plants annual, often forming large clumps with many branches arising from a sometimes decumbent and geniculate base; culms terete, 10--90 cm tall; sheaths strongly compressed-keeled, pilose on the margins and at the throat; ligule at rim of ciliate hairs, 0.7--1.7 mm long; blades scabrous to sparsely pilose, 6.3--18.7 cm long, 3.0--7.2 mm wide; inflorescence compact, 4.1--10.2 cm long, 1.2--2.2 mm wide; rachis angled, flexuous, and glabrous or more often minutely scabrous, the internodes 2.0--5.0 mm long; burs somewhat globose, medium to short-pubescent, 8.3--11.9 mm long, 3.5--6.0 mm wide; peduncle short-pubescent, 1.1--3.0 mm long, 2.2--4.2 mm wide; spines slender, retrorsely barbed and
often purple-tinged, 3.5—7.0 mm long, 0.7—1.4 mm wide, the margins often narrowly grooved, the lower margins sometimes long pubescent, but not densely so as in C. tribuloides; spines at the base of bur numerous and pointing downward, shorter than those on body of bur; spikelets sessile, 2 to 3 per bur, rarely 4, 6.0—7.8 mm long; first glume 1.5—3.8 mm long, 0.6—2.2 mm wide, 1-nerved; second glume 4.4—6.0 mm long, 3 to 5-nerved; sterile lemma 5.0—6.5 mm long, 3 to 7-nerved, enclosing a slightly longer, scabrid palea; fertile floret 5.8—7.6 mm long, 2.1—3.3 mm wide, 3-nerved, both lemma and palea smooth, enclosing the turgid, ovoid fruit which is 2.2—3.8 mm long, 1.5—2.6 mm wide; anthers 0.8—2.1 mm long; somatic chromosome number 2n=34 and 36.

Observations and nomenclature

Cenchrus longispinus, which is distributed throughout most of the United States, has often been identified as, and confused with, both C. tribuloides and C. incertus. This taxon is a pioneer plant characteristic of sandy, waste places, abandoned fields and recently disturbed soils. Its appearance and subsequent development in over-grazed fields has been recently studied by Thomson, (1943), who reported that Cenchrus was one of the first plants to appear in disturbed areas but that it was replaced in two or three years by more stable species. Cenchrus longispinus exhibits a wide tolerance with respect to soil types, moisture content, and
plant associates throughout its range. Although exhibiting wide variation in most vegetative characters, it maintains a marked stability in several traits, such as spine number and floret length. In order to compare the morphological features of *O. longispinus*, *O. tribuloides*, and *O. incertus*, a number of characters are shown in Table 8. The data shown in the table represent measurements from several hundred collections, each of *O. longispinus* and *O. incertus*, and from 90 collections of *O. tribuloides*.

Table 8. Comparison of some morphological characters of *O. longispinus*, *O. incertus*, and *O. tribuloides*

<table>
<thead>
<tr>
<th>Character</th>
<th><em>O. longispinus</em></th>
<th><em>O. incertus</em></th>
<th><em>O. tribuloides</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Floret length</td>
<td>R.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>in mm</td>
<td>5.8—7.6</td>
<td>3.4—5.8</td>
<td>6.0—8.7</td>
</tr>
<tr>
<td>M.</td>
<td>6.7</td>
<td>4.7</td>
<td>7.4</td>
</tr>
<tr>
<td>Floret width</td>
<td>R.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>in mm</td>
<td>2.1—3.3</td>
<td>1.0—2.2</td>
<td>2.2—3.5</td>
</tr>
<tr>
<td>M.</td>
<td>2.5</td>
<td>1.5</td>
<td>2.9</td>
</tr>
<tr>
<td>Bur width</td>
<td>R.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>in mm</td>
<td>3.5—6.0</td>
<td>2.5—5.0</td>
<td>4.0—8.0</td>
</tr>
<tr>
<td>M.</td>
<td>4.6</td>
<td>3.5</td>
<td>5.5</td>
</tr>
<tr>
<td>Spine length</td>
<td>R.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>in mm</td>
<td>3.5—7.0</td>
<td>2.0—5.8</td>
<td>4.1—8.0</td>
</tr>
<tr>
<td>M.</td>
<td>4.8</td>
<td>3.9</td>
<td>6.8</td>
</tr>
<tr>
<td>Spine width</td>
<td>R.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>in mm</td>
<td>0.7—1.4</td>
<td>0.7—2.0</td>
<td>1.2—3.0</td>
</tr>
<tr>
<td>M.</td>
<td>1.1</td>
<td>1.4</td>
<td>2.3</td>
</tr>
<tr>
<td>Fruit width</td>
<td>R.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>in mm</td>
<td>1.5—2.6</td>
<td>1.0—2.0</td>
<td>2.2—3.1</td>
</tr>
<tr>
<td>M.</td>
<td>2.1</td>
<td>1.5</td>
<td>2.6</td>
</tr>
<tr>
<td>Spine number</td>
<td>R.</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>45—75</td>
<td>.8—40</td>
<td>15—43</td>
</tr>
<tr>
<td>M.</td>
<td>56</td>
<td>28</td>
<td>32</td>
</tr>
<tr>
<td>Pubescence, bur</td>
<td>medium</td>
<td>short to</td>
<td>long, dense</td>
</tr>
<tr>
<td></td>
<td></td>
<td>medium</td>
<td></td>
</tr>
</tbody>
</table>

\( a^R = \text{Range.} \)

\( b^M = \text{Mean.} \)
As shown in the table, *C. longispinus* is most readily distinguished from *C. incertus* and *C. tribuloides* by the greater number of spines. *C. longispinus* and *C. incertus* may also be delimited by floret length, since only rarely does the length of a floret of the latter approach that of the former, and in such instances, the two species may almost always be separated on the basis of spine number. Those features which appear to best delimit *C. longispinus* from *C. tribuloides* are the larger, more densely pubescent burs with fewer, but broader spines of the latter species, and the presence of but one spikelet per bur in *C. tribuloides* as contrasted with two or three per bur in *C. longispinus*. *Cenchrus incertus* can, most obviously, be distinguished from *C. tribuloides* on the basis of floret width and length and fruit width.

Spine width has often been suggested and used as a means of separating these three taxa. Data from Table 8, however, indicate that this trait is highly variable and extremely unreliable as a taxonomic character. In general, the spines of *C. longispinus* appear somewhat longer and more slender than do those of the other two species, possibly due to their slightly lower width-to-length ratios.

In the course of field work, little difficulty was experienced in distinguishing between these three species. No specimens were observed in the field which could be considered intermediate between *C. longispinus* and either of the
other two taxa. However, a number of herbarium collections have been observed in which the spine number and floret length tends to approach that of *C. longispinus*, but in all other features, these plants can readily be referred to as *C. incertus*. These forms will be discussed in the section dealing with *C. incertus*.

The first valid name applied to *C. longispinus* was apparently that of *C. echinatus* forma *longispina* by Hackel in Kneucker (1903). Previous to that time the species had erroneously been identified either as *C. tribuloides* L., or *C. carolinianus* Walt. This latter name, because of inadequate description by Walter, and the absence of any known type specimen (Hitchcock 1905, 1908), is included in the appendix under rejected or excluded names.

More recently Lunell (1915) established a separate genus, *Nastus*, based on Walter's *C. carolinianus*, and retained Walter's species as the type of the genus. Although the type of *Nastus* has not been examined by the writer, it is certain from Lunell's description, and his citation of specimens from North Dakota, that he was referring to *C. longispinus*, since no other species of *Cenchrus* occurs in that region.

Fernald (1943) elevated Hackel's form to specific status, naming it *C. longispinus*, and basing the name on Kneucker's Gramineae Exsiccateae no. 426. Since a number of these duplicate collections are in existence, and since Fernald apparently did not specify which was the holotype, the type specimen
of *C. longispinus* is hereby designated as Kneucker no. 426, in the Herbarium of Iowa State University (ISC 227735). In his description of *C. longispinus*, Fernald indicated his disdain for the genus with these remarks.

As a diagnosis of a form of *C. echinatus*, in the loose sense, Hackel's brief description was sufficient. Treated as a species the plant demands a fuller account. It is fortunate that Hackel has supplied the basionym and type. Even so, I take no comfort in having even my name intimately associated with a *Cenchrus* and the keen taxonomist who called it to my attention would not care to have the species named for him.

During the past century, *C. longispinus* has also been confused with *C. pauciflorus*, herein treated as a synonym under *C. incertus*. Jansen & Wachter (1949), apparently also confusing *C. longispinus* with *C. pauciflorus* Benth., relegated the former species to varietal status, naming it *C. pauciflorus* variety *longispinus*. Not recognizing the taxon of the northern United States as a distinct entity, Hitchcock (1950) included the names given to it by Hackel, Jansen & Wachter, and Fernald, as synonyms under *C. pauciflorus* Benth.

**Cytology**

Brown (1948) published a chromosome number of 2n=36 for *C. longispinus* (reported by him as *C. pauciflorus* from northern U. S.). Chromosome numbers of 2n=34 have been reported by Gould (1958) and were obtained by the writer on a number of collections of *C. longispinus* as shown in Table 9. Meiosis was normal in all specimens examined.
Table 9. Chromosome counts from pollen mother cells of *Oenchrus longispinus* (Hack. in Kneuck.) Fern

<table>
<thead>
<tr>
<th>Collection</th>
<th>Location</th>
<th>Chromosome number</th>
</tr>
</thead>
<tbody>
<tr>
<td>DeLisle voucher no. 362</td>
<td>Ford County, Kansas</td>
<td>n=17</td>
</tr>
<tr>
<td>DeLisle voucher no. 391</td>
<td>Guadeloupe County, New Mexico</td>
<td>n=17</td>
</tr>
<tr>
<td>DeLisle voucher no. 395</td>
<td>Guadeloupe County, New Mexico</td>
<td>n=17</td>
</tr>
<tr>
<td>DeLisle voucher no. 405</td>
<td>Las Animas County, Colorado</td>
<td>n=17</td>
</tr>
<tr>
<td>DeLisle voucher no. 429</td>
<td>Morrill County, Nebraska</td>
<td>n=17</td>
</tr>
<tr>
<td>B. Crampton DeLisle voucher no. 457</td>
<td>Merced County, California</td>
<td>n=17</td>
</tr>
</tbody>
</table>

**Distribution**

*Oenchrus longispinus* occurs in sandy or recently disturbed soils, abandoned fields, roadsides, and borders. It is an ubiquitous weed in the eastern and central portions of the United States, and more recently has invaded the western portions of this country. In the eastern part of North America, it grows as far north as Ontario, Canada, but has not been reported further west in Canada. This species also occurs rarely in Mexico, Central America, and the West Indies, and has become naturalized locally in Western Europe, South Africa, and Australia. *Oenchrus longispinus* appears to occur
sporadically throughout its range in the United States.

Selected specimens examined


UNITED STATES: Arkansas, Craighead County, D. Demaree 3364 (MO); Muskogee County, C. S. Wallis 5456, Sept. 8, 1957 (SMU); Arizona, Fort Apache, F. S. Mayerhoff 41, 1901 (F); Prescott, Peebles 2654 (MO); California, Riverside County, H. S. Yates 6734, June 28, 1937 (UC, AHUC); Riverside County, M. A. Nobs, & S. G. Smith 493, Sept. 3, 1948 (ISO); Colorado, Plum Creek, H. L. Zobel, Sept. 10, 1935 (DAO); Fremont County, Canon City, T. S. Brandegee 845, 1873 (MO, UC); Las Animas County, D. DeLisle 405, Aug. 1, 1960 (ISC); Connecticut, Hartford County, F. Wilson 1266 (F); Oxford, A. Knucker 426, 1903. (Holotype ISC) (US, UC); Florida, Pinellas County, R. W. Pohl 8104, July 18, 1960 (ISO); Monroe County, W. C. Muenscher 18160, March 12, 1947 (UC); Georgia, University of Georgia, D. J. Banks 1051, Aug. 30, 1961 (ISO); Illinois, Cook County, J. W. Thieret 2503 (F); Carroll County, L. H. Pammel 1212, Aug. 9, 1925 (MO, UC); Champaign, I. W. Clokey 378, 1898 (UC, MO); Peoria, V. H. Chase 3207, July 23, 1919 (F, UC, MO, SUI); Indiana, Howard County, C. M. Ek 8278, July 29, 1939 (SMU); Howard County, C. M. Ek, July 20, 1942 (UC, MO); Iowa, Muscatine County, B. Shimek, July 14, 1911 (ISC); Montgomery County, R. W. Pohl 7053, Sept. 22, 1950 (ISC); Fremont County, R. W. Pohl 6752, Aug. 12, 1949 (ISC); Polk County, L. H. Pammel 657, July 14, 1897 (ISC); Story County, L. H. Pammel, Sept. 1904 (ISC); Palo Alto County, A. Hayden 8227, Aug. 7, 1940 (ISO); Webster County, C. E. Bessey, Aug. 3, 1872 (ISC); Linn County, D. DeLisle 459, Sept. 23, 1960 (ISO); Kansas, 13 m. s.w. of Lakin, P. A. Rydberg & R. Imler 937, July 13, 1929 (MO); Greeley County, N. Reed, July, 1892 (UC); Ford County, near Dodge City, D. G. DeLisle 362, July 29, 1960 (ISC); Kentucky, Corn Island, Ohio River, C. W. Short, 1840 (MO); Maryland, Calvert County, F. C. Seymour 16615, July 17, 1956 (SMU); Massachusetts, Fitchburg, A. B. Simonds, ca 1901 (UC); Hampden County, F. C. Seymour 266, Sept. 8, 1914 (DAO, SMU); Michigan, Chelsea, R. McVaugh 7594 (F); Muskegon County, L. H. Pammel, Aug. 13, 1920 (ISC); Van Buren County, South Haven, C. E. Lansing Jr. 3332, Sept. 3, 1911 (F, SUI); Minnesota, Grow Wing County, Brauner, E. B. Watson, Aug. 4, 1902 (ISC); Missouri, Pemiscot County, E. J. Palmer 61572 (F); Douglas County, J. Steyermark 23593, July 23, 1937 (MO); St. Louis County, J. Steyermark 8837, Aug. 5, 1933 (MO); Nebraska, Adams County, L. H. Pammel, July 20, 1895 (ISC); Sheridan County, R. E. Buchanan, Aug. 2, 1905 (ISC); Brown County, D. DeLisle 444, Aug. 6, 1960 (ISO);
8. *Oenchrus palmeri* (Figure 11, F—1; map, Figure 12)


**Description**

Small annuals; culms usually solitary, glabrous, 9.0--35 cm tall; sheaths slightly compressed, puberulent, the
Figure 10. Geographic distribution of *Canthurus longispinus*
margins and throat variously pilose; ligule 1.3--2.3 mm long, ciliate; blades puberulent, 4.4--10.0 cm long, 3.8--6.8 mm wide; inflorescence with 1 to 4 burs, usually 3; rachis 2.0--4.2 cm long, slightly flexuous, scabrous; bur closely pubescent, 11.5--18.5 mm long, 4.6--9.5 mm wide; spines numerous, 40 to 65, dark purple or sometimes yellowish in color, retrorsely barbed, 5.8--11.0 mm long, 0.6--1.8 mm wide, the enlarged, rounded bases close-pubescent; spikelets 4 to 8 per bur, sessile, 5.2--7.3 mm long; first glume reduced or abortive; second glume 4.5--6.4 mm long, 5-nerved; sterile lemma 4.5--6.5 mm long, 5 to 6-nerved, the palea 5.0--6.0 mm long, slightly scabrous; fertile floret 5.2--7.1 mm long, 1.5--2.5 mm wide; fruit turgid, ovoid, 2.2--3.4 mm long, 1.5--2.2 mm wide; anthers 1.7--2.1 mm long; somatic chromosome number 2n=34.

**Observations and nomenclature**

The extremely large burs with their long, slender, and usually dark-colored spines are characteristics which single out *C. palmeri* from all other members of the genus. This species is an inhabitant of dry and bare, rocky or sandy bottoms and lower slopes in those regions where annual rainfall is sparse. Plants grown from seed were observed in the greenhouse, and, in contrast to most other species of *Cenchrus*, it was noted that they reach maturity in a matter of three or four weeks, often producing mature inflorescences
before the culms had attained more than a few inches in height. This growth habit is undoubtedly a response of the species to its normally harsh growing conditions in the arid regions of western Mexico and Baja California. In most of the collections observed, the spines are of a black-purple color which often extends down into the body of the bur, but infrequent variants occur in which the entire bur may have a yellowish color.

The type specimen of *Oenchrus palmeri* is in the U. S. National Herbarium and was examined by the writer. This specimen was collected by Dr. E. Palmer, no. 689, near Guaymas, Mexico, in 1887 along with specimens of the yellow-colored form.

**Cytology**

A chromosome count obtained by the writer for *Oenchrus palmeri* is shown in Table 10. Meiosis appeared normal in this material.

**Table 10. Chromosome count from pollen mother cells of Oenchrus palmeri Vasey**

<table>
<thead>
<tr>
<th>Collection</th>
<th>Location</th>
<th>Chromosome number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Weatherwax no. 3339</td>
<td>San Felipe, Baja</td>
<td>n=17</td>
</tr>
<tr>
<td>DeLisle voucher no. 469</td>
<td>California</td>
<td></td>
</tr>
</tbody>
</table>
Distribution

_Cenchrus palmeri_ is restricted to arid, sandy regions of Baja California and the adjacent western coastal regions of Mexico.

**Selected specimens examined**

BAJA CALIFORNIA: Punta de Conejo, I. L. Wiggins 5559, April 30, 1931 (NY, US, UC); Pescadero, T. S. Brandegee, Sept. 23, 1893 (NY, UC); Magdalena Bay, T. S. Brandegee, Jan. 13, 1889 (UC); District Del Norte, A. Carter 1905, Nov. 10, 1947 (F, US, UC); Santa Catarina Landing, R. L. Dressler 601, April 16, 1949 (MO); San Felipe, E. A. Goldman 1611, June 20, 1905 (US); San Jose del Cabo, M. E. Jones, Jan. 23, 1928 (MO); Carmen Island, E. Palmer, July 14, 1870 (US); 27.4 mi. so. of Pozo Aleman, I. L. Wiggins 7866, March 4, 1935 (F, UC); Los Desiertos de Los Chinos, S. Galen Smith 350, Jan. 4, 1948 (UC); Santa Margarita Island, W. E. Bryant, March 1888 (UC).

MEXICO: Guaymas, E. Palmer 689, 1887 (US) (Holotype); (F, UC); Sonora, near Adair Bay, G. Sykes, Nov. 20, 1907 (US); Sonora, 32 miles s.w. of Sonoyta, I. L. Wiggins 8360, March 14, 1936 (UC); Sonora, between Tastiota & Hermosillo, I. L. Wiggins & R. W. Rollins 267, Sept. 3, 1941 (NY, UC, MO).

9. _Cenchrus platvacanthus_ (Figure 11, J—N; map, Figure 12)


**Description**

Plants annual; culms 20--90 cm tall; sheaths slightly pubescent, the margins and throat variously pilose; ligule ciliate, 1.4--2.3 mm long; blades glabrous, 4.0--24.0 cm long, 2.0--8.0 mm wide, tapering to an acute tip; inflorescence very dense, 3.8--8.6 cm long, 0.6--2.0 cm wide;
rachis angled, scabrid, the internodes only 0.6—1.4 mm long; burs small, glabrous to very short-pubescent, purple of stramineous, 2.8—6.0 mm long, 1.5—3.5 mm wide; spines few in number, 6 to 22, short and broad, retrorsely barbed near the tips, 1.8—3.0 mm long, 0.6—1.3 mm wide; spikelets sessile, only one per bur, 2.4—5.8 mm long; first glume 0.3—1.1 mm long, about 0.6 mm wide; second glume 1.9—3.4 mm long, 3-nerved; sterile lemma 2.4—3.7 mm long, 3-nerved, enclosing a slightly shorter palea; fertile floret 2.2—5.8 mm long, 0.5—2.0 mm wide; fruit about 1.4 mm long, 1.0—1.2 mm wide; anthers 0.5—1.0 mm long.

Observations and nomenclature

*Oenchrus platvacanthus* has a distinctly compact inflorescence with small burs and few, usually short spines. The rachis internode length of this species ranges from 0.6 to 1.4 mm, compared with a length of 2.0—5.0 mm in *C. incertus*. Plants of *C. platvacanthus* have from 30 to 90 burs per inflorescence, in contrast with 5 to 20 burs per inflorescence for *C. incertus*. This trait thus serves as an excellent means of distinguishing between the two taxa.

Andersson (1854) named and described two species of *Cenchrus* from the Galapagos Islands. To those plants with somewhat glabrous sheaths and blades, and with pedicellate burs over 4.0 mm long, he assigned the name *C. platvacanthus*. Other forms having smaller burs with little or no pedicel,
Figure 11. *Cenchrus longispinus*, *Cenchrus palmeri*, and *Cenchrus platvacanthus*

A–E. *Cenchrus longispinus*: A. inflorescence, B. bur, C. caryopsis, D. spikelet, E. floret

F–I. *Cenchrus palmeri*: F. spikelet, G. floret, H. caryopsis, I. bur

J–N. *Cenchrus platvacanthus*: J. spikelet, K. caryopsis, L. floret, M. bur, N. inflorescence
and which were variously pubescent, were assigned the name of *C. granularis*. The bur size differences are not significant and overlap in the collections observed by the writer. Likewise, pubescence in these forms is highly variable. It appears that Andersson was dealing with two extremes of the same taxon, and since the name *O. granularis* is a later homonym, *C. platvacanthus* remains as the valid name for this species.

**Cytology**

No chromosome numbers have been reported for this species.

**Distribution**

This species is endemic to the Galapagos Islands, where it grows in open, gravelly or sandy soil near the shore line (Svenson 1935).

**Selected specimens examined**


10. *Cenchrus tribuloides* (Figure 16, K--N; map, Figure 12)

*Cenchrus tribuloides* L. Sp. Pl. 1050. (1753)

(Holotype in LIMN) (1)
Oenchrus mlnatas
96
Oenchrus tribuloides macrocarpus Steud. Syn. Pl. Glum. 1:110. (1855) (A garden name given as a synonym for C. vaginatus Steud.) (2)
Oenchrus tribuloides var. macrocephalus Doell in Mart. 2, part 2:312. (1877) (2)
Oenchrus tribuloides of Authors, non Millsp. Field Mus. Bot. 2:27. (1900) (Millspaugh attributes this name to L.) (2)

Description
Plants annual, usually robust, the culms 10.0—70 cm tall; sheaths compressed, the margins and throat softly pilose; ligule a ciliate rim, 1.0—2.1 mm; blades glabrous, 2.0—14.0 cm long, 3.0—14.2 mm wide, tapering to a point; inflorescence compact or sometimes open, 2.0—8.2 cm long, 1.5—3.0 cm wide; rachis flexuous, glabrous or slightly scabrous, the internodes 3.0—10.00 mm long; burs large, ovoid, densely long-pubescent, 9.0—16.0 mm long, 4.0—8.0 mm wide, stramineous or often purple; spines not as numerous as in C. longispinus, from 15 to 43, usually about 30, 4.1—8.0 mm long, 1.2—3.0 mm wide, retrorsely barbed near the tips; peduncle glabrous, 1.5—3.5 mm long, 2.6—5.5 mm wide; spikelets sessile, 1 per bur, rarely two, 6.0—8.8 mm long; first glume 1.0—4.0 mm long, 0.6—2.2 mm wide, usually
1-nerved; second glume 4.9–6.8 mm long, 3 to 7-nerved; sterile lemma 5.5–7.5 mm long, 3 to 6-nerved, the palea exceeding the lemma, 6.0–8.0 mm long, scabrous; fertile floret 6.0–8.7 mm long, 2.2–3.5 mm wide, 3-nerved; fruit smooth, ovoid-elliptic, 2.6–4.0 mm long, 2.2–3.1 mm wide; anthers 0.8–2.8 mm long; somatic chromosome number 2n=34.

Observations and nomenclature

The "dune sandbur," *C. tribuloides*, has the most heavily pubescent burs and largest spikelets of any species in the genus. While the pubescent nature of the bur is somewhat variable in nature, it is usually always possible to identify this species on the basis of spikelet size and spine number. Plants of the West Indies, with very short-pubescent burs, and with considerably smaller spikelets, have often been included with *C. tribuloides*. The affinities of this nearly glabrous form, however, appear to be with *C. incertus* rather than with the former species, and will be taken up in the discussion of *C. incertus*.

Plants observed in the field were growing in somewhat moist sand just above high tidal zone along the Gulf coastal regions, and did not appear to extend for any great distance inland. This species in that region flowers relatively late in August and through September, producing large amounts of vegetative growth before initiation of flowering.

*Cenchrus tribuloides* was described by Linnaeus (1753) as
"Cenchrus glumis seminis globosis muricato-spinosis hirsutis." The holotype is in the Linnaean Herbarium and a photograph of the type was examined by the writer. The type specimen collected in Virginia by Peter Kalm was marked by Linnaeus with a small "K" (Hitchcock 1908).

Torrey, in giving the name *C. echinatus tribuloides* (1824) to this species, apparently believed it was a pubescent and large-burred form of *C. echinatus*. However, he was probably referring to *C. longispinus*, since it and *C. tribuloides* are the only two species of *Cenchrus* which occur in the New Jersey pine barrens.

In his description of *C. tribuloides* var. *macrocephalus* Doell in Martius (1877) referred to a somewhat less villous bur with only one spikelet from a collection in Martius's herbarium.

**Cytology**

Chromosome numbers of 2n=34 have been reported for *C. tribuloides* by Avdulov (1928) and Hunter (1934). Counts made by the writer are shown in Table 11. In the material examined, meiotic activity appears normal.

**Distribution**

This species is restricted to the immediate coastal sand dune areas from New York south to Florida and along the Gulf coast to Texas. It is rarely found in Bermuda, the West Indies, and the coast of South America to Brazil.
Table 11. Chromosome counts from pollen mother cells of *Oenchrus tribuloides* L.

<table>
<thead>
<tr>
<th>Collection</th>
<th>Location</th>
<th>Chromosome number</th>
</tr>
</thead>
<tbody>
<tr>
<td>D. E. Fairbrothers</td>
<td>Cape May, New Jersey</td>
<td>n=17</td>
</tr>
<tr>
<td>DeLisle voucher</td>
<td></td>
<td></td>
</tr>
<tr>
<td>no. 486</td>
<td></td>
<td></td>
</tr>
<tr>
<td>D. E. Fairbrothers</td>
<td>Cape May County, New Jersey, Stone</td>
<td>n=17</td>
</tr>
<tr>
<td>DeLisle voucher</td>
<td>Harbor beach</td>
<td></td>
</tr>
<tr>
<td>no. 487</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Selected specimens examined**

**BERMUDA:** Tucker's Town, Brown & Britton 871, Aug. 26, 1912 (NY).

**UNITED STATES:** Delaware, Cape Henlopen & Rehoboth Beach, L. M. Snow, 1902 (F); Wilmington, W. M. Canby, Sept. 1885 (F); Ocean City, A. Chase 12670, Aug. 19, 1952 (DAO); Newcastle, Wm. M. Canby (MO); Florida, Palm Beach, June 7, 1896 (MO); Miami, J. K. Small & G. K. Small, Nov. 26, 1913 (MO); Soldier Key, J. K. Small 3300, Feb. 20, 1911 (US); Navarre, D. J. Banks 838, Aug. 1, 1961 (ISO); Georgia, Beachhead Island, W. L. McAtee 3334, Oct. 16, 1923 (US); Maryland, Point Lookout, E. H. Walker 3905, Aug. 29, 1945 (F); Calvert County, Scientists Cliffs, F. O. Seymour 17275, Aug. 6, 1957 (SMU, ISO); Mouth of Patuxent River, A. Chase 12667, Aug. 20, 1948 (DAO); Mississippi, Biloxi, S. M. Tracy 4526, Aug. 19, 1899 (F, MO); Harrison County, Cat Island, A. E. Seymour 215, Sept. 5, 1891 (AHUC); Harrison County, Beach at Biloxi, D. DeLisle 660, Aug. 28, 1961 (ISO); Jackson County, Point Aux Chenes, R. E. Channell 775, July 17, 1952 (SMU); New Jersey, Camden, F. L. Scribner 122, 1881 (F); Atlantic City, F. L. Scribner, Aug. 29, 1885 (US); Pine Barrens, C. F. Rafinesque (MO); Cape May, C. F. Parker, 1871 (F, US); South Amboy, A. P. Kelley, Oct. 4, 1927 (SUI); Wildwood, A. Chase 3506, July 25, 1906 (US, ISO); Ocean County, J. Bright 17902, Aug. 17, 1940 (UC); New York, Albany (MO); Coney Island, J. A. and H. F. Ruth, Sept. 5, 1886 (UC); Long Island, T. H. Kearney, Aug. 27, 1894 (F, US); North Carolina, Dare County, P. O. Schalpert, 5077, Aug. 20, 1957 (SMU); Craven County, T. H. Kearney, 1948, July 31, 1898 (US); Kitty Hawk, R. K. Godfrey 5261, July 18, 1938 (US); South Carolina, Myrtle Beach, O. Schallert, 8-3-33 (DAO); Isle of Palms, A. S.
Figure 12. Geographic distribution of *Oenchrus palmeri*, *Oenchrus tribuloides*, and *Oenchrus platyacanthus*
C. tribuloides

C. palmeri

C. platyacanthus

GALAPAGOS ISLANDS
11. *Oenchrus incertus* (Figure 16, F--J; map, Figure 15)


*Oenchrus muricatus* Phil. *Sert. Mend. Atl.* 44. (1870) (non *O. muricatus* L. 1771) (Holotype in BM, fragment of type in US) (1)


*Oenchrus roseus* Fourn. *Mex. Fl.* 50. (1885) (Holotype in P, fragment of type in US); (1)


*Oenchrus parviceps* Shinners. *Field & Lab.* 24:73. (1956) (Holotype in SMU) (1)

**Description**

Plant annual, sometimes biennial or over-wintering; culms decumbent or erect, sometimes with many branches from the base, glabrous, 5.0--80.0 cm tall; sheaths compressed, glabrous or sparsely pilose, the margins and throat glabrous
to pilose; ligule ciliate, 0.5--1.5 mm long; blades glabrous, the margins scabrous, 2.0--18.0 cm long, 2.0--6.0 mm wide, gradually tapering to a point; inflorescence open or compact, 2.0--8.5 cm long, 0.8--2.0 mm wide; rachis angled and flexuous, glabrous or scabrous, the internodes 2.0--5.0 mm long; burs highly variable, ovoid to globose with clefts on two sides, short to medium pubescent, rarely glabrous or long-pubescent, 5.5--10.2 mm long, 2.5--5.0 mm wide; peduncle glabrous to short-pilose, 0.5--2.0 mm long, 1.0--3.3 mm wide; spines 8 to 40, rarely more, highly variable in shape from long, slender to short and broad, retrorsely barbed, 2.0--5.0 mm long, 0.7--2.0 mm wide at base; body of bur and spines stramineous to mauve or purple; spikelets sessile, glabrous, 3.5--5.8 mm long, 2 to 4 per bur; usually three; first glume 1.0--3.3 mm long, 0.6--1.4 mm wide, 1-nerved; second glume 2.8--5.0 mm long, 5 to 6-nerved; sterile lemma 3.0--5.9 mm long, 4 to 7-nerved, enclosing the scabrous palea, 3.5--6.2 mm long; fertile floret 3.4--5.8 mm long, rarely to 6.0 mm, 1.0--2.2 mm wide, 3-nerved; fruit ovoid, smooth, 1.4--3.0 mm long, 1.0--2.0 mm wide; anthers 0.5--2.0 mm long; somatic chromosome number 2n=34.

Observations and nomenclature

Because of its wide geographic range and highly variable inflorescences and burs, *Cenchrus incertus* poses a number of taxonomic problems. For the past one hundred years the
western American and Mexican plants of this taxon have gone under the name *C. pauciflorus*, while those occurring in the southeastern United States have generally been identified as *C. incertus*. Chase (1920) and Silveus (1933) included the northern *C. longispinus* in *C. pauciflorus* and the eastern and southern plants in *C. incertus*. Shinners (1954) followed Fernald's (1943) treatment of *C. longispinus*, but separated *C. incertus* and *C. pauciflorus* largely on the basis of rachis internode length. A third species from the Rio Grande Plain, *C. parviceps*, was named and described by Shinners in 1956. He distinguished this species from *C. incertus* by its overall lower stature, shorter leaves, and narrower diameter of the bur. A summary of the criteria used by Hitchcock, Chase, and Shinners for separating these three taxa is presented in Table 12.

Table 12. Criteria used for delimiting *C. incertus*, *C. parviceps*, and *C. pauciflorus*

<table>
<thead>
<tr>
<th>Character</th>
<th><em>C. incertus</em></th>
<th><em>C. parviceps</em></th>
<th><em>C. pauciflorus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Bur width (including spines) mm</td>
<td>7--12</td>
<td>6--10</td>
<td>7--12</td>
</tr>
<tr>
<td>Rachis internode length, mm</td>
<td>2.5--9</td>
<td>2.5--9</td>
<td>1.5--3</td>
</tr>
<tr>
<td>Leaf length, cm</td>
<td>4--14</td>
<td>2--6</td>
<td>3--15</td>
</tr>
<tr>
<td>Plant height, cm</td>
<td>15--100</td>
<td>6--35</td>
<td>20--90</td>
</tr>
</tbody>
</table>
Data from the table indicate considerable overlap between species for each of the characters shown. It has been the experience of the writer that it is difficult, if not impossible, to separate the three species on the basis of these characters, either in the field or from herbarium collections.

In order to determine if a combination of several of the above traits might be used to define two or more taxa, a scatter diagram (Figure 13) was constructed. Bur width was plotted against spine number on the two axes of the graph. The diverging rays arising from each dot indicate, respectively, leaf length on the left and rachis internode length on the right. The data given for bur width by Shinners (1956) represents the total width, including the spines, but the differences in this trait (Table 12) among the three species hardly appear significant. Bur length shown in Figure 13 represents only the solid portion of the bur, since this is considered to more accurately represent the bur size.

Relative positions of the type specimens of *C. incertus*, *C. parviceps*, and *C. pauciflorus* are indicated on the graph by open circles. The dots on the graph represent data from 160 collections taken at random throughout the range of *C. incertus* in the southern United States, Mexico, and the West Indies.

Examination of the scatter diagram indicates a random distribution of all four characters portrayed, with little or no apparent correlation between two or more of these traits.
The type specimens all readily fall within the range of variability, and there does not appear to be any significant gap or gaps which would segregate two or more morphological entities. The data thus suggest the existence of but one highly variable taxon, with no evidence which would support the existence of two or more species or varieties.

As a further aid in understanding the nature of the wide variability of this species, a study of its geographic variation in the southern United States and northern Mexico was undertaken.

A number of data obtained from population samples were superimposed upon a map (Figure 14) at the approximate locations where the samples were collected. Population samples collected by the writer are indicated by a number from 1 to 10 at the lower right of each circle on the map. The data from these samples were obtained from twenty to thirty individuals in each such population. Additional circles indicate composite samples of from 6 to 15 herbarium collections within an area of approximately 100 miles square for each location. These composite sample locations are designated by the letters A through O respectively.

Spikelet length is represented by the relative amount of darkened area in a circle, those with shorter spikelets being indicated by larger black areas. Spine length is designated by the length of the ray diverging to the left, spine number by the ray diverging to the right, and plant height by the
Figure 13. Scatter diagram showing the relationship of four morphological characters in *Cenchrus incertus*.
RACHIS INTERNODE LENGTH
- 2.1 - 3.0 mm.
- 3.1 - 4.0 mm.
- 4.1 - 5.0 mm.

LEAF LENGTH
- 1.0 - 6.9 cm.
- 7.0 - 12.9 cm.
- 13.0 - 19.0 cm.

TYPE SPECIMENS
- C. parviceps
- C. incertus
- C. pauclflorus

SPINE NUMBER
BUR WIDTH, mm.

Graph showing data points for spine number, bur width, and leaf length.
relative length of the vertical ray. All data represented on the map are averages of the four characters for each population portrayed.

Referring to the map (Figure 14), it is observed that there is very little correlation of spine length and number or of plant height with distribution. However, there appears to be some tendency for taller plants to occur in the northern portions of the range of this species as indicated by the length of the vertical rays in plant populations from New Mexico, Oklahoma and Arkansas. Shorter plants occur primarily in the central Texas and Rio Grande regions, the shortest being those of populations in northern Mexico.

Spikelet length, on the other hand, exhibits a definite decrease as the plants range southward into Mexico. That the variation in spikelet length is gradual or clinal in nature, and not discontinuous, is indicated by the separate graph to the left of the map (Figure 14). The sample locations represent a north-south transect through New Mexico, Texas, and northern Mexico. The horizontal bar indicates the range of variation in spikelet length for each population, while the vertical bar denotes the mean length for that population. The graph thus illustrates a very definite clinal variation in this trait with considerable overlap between adjoining populations. The factors contributing to this variation are incompletely known. Amounts and periods of precipitation, for instance, are highly varied within the general area of the
transect. Rainfall amounts range from 10 inches annually in western Texas and adjacent parts of Mexico, to 30 inches or more along the Texas coastal plain. The sparse rainfall and relatively short and infrequent growing seasons in western Texas and Mexico may possibly be contributing factors to the shorter plants and smaller spikelets in that area. Such environmental conditions do not, however, account for the short spikelets of those plants farther east where precipitation is greater. Further studies of variation and its correlation with genetic, ecological and geographic factors in this species are needed in order to arrive at a more complete idea of the nature of its variation.

Sufficient samples were not available to show graphically the trend of variation farther south in Mexico, Central America, the West Indies and South America. Enough collections from these areas have been examined, however, to indicate a gradual increase in plant stature and spikelet length to the south of the areas shown in Figure 14, and continuing on through South America.

Many collections from the West Indies have somewhat more robust culms, the burs have more numerous spines (generally around 35 to 40), and the burs themselves are often purple colored. These forms have often been identified with C. triploides, probably because of their more robust culms and slightly larger burs, but they lack the dense pubescence of the former species, possess 2 to 3 spikelets per bur, and the
Figure 14. Geographic variation of spikelet length, spine length, plant height, and spine number in populations of *Oenchrus incertus* in the southern United States and Mexico.
SPIKELET LENGTH

<table>
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<th>35</th>
<th>40</th>
<th>45</th>
<th>50</th>
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</tbody>
</table>

VERTICAL BAR = MEAN

HORIZONTAL BAR = RANGE

SPIKELET LENGTH

- 40-46 mm
- 47-52 mm
- 53-58 mm

SPINE LENGTH

- 20-32 mm
- 33-45 mm
- 46-58 mm

PLANT HEIGHT

- 5-20 cm
- 21-40 cm
- 41-60 cm

SPINE NUMBER

- 10-20
- 21-30
- 31-40

1-10 = POPULATION SAMPLES
A-O = COMPOSITE SAMPLES

SAMPLE LOCATION

E F
spikelet length is usually always less than 5.8 mm. Chase (1920) suggests that these two species approach one another morphologically in the West Indies, intimating the possibility of hybridization. However, most of the collections from this area observed by the writer can usually be definitely assigned to C. incertus. More detailed study of the West Indian populations may, however, reveal the existence of hybrids between these two species.

The earliest apparent name assigned this taxon was that of C. incertus in 1837 by M. A. Curtis. His description was of a few-spined form from Cape Fear, North Carolina. The type specimen, which was examined by the writer, is in the herbarium of the New York Botanical Garden. Seven years later, Bentham (1844) described a plant with small burs and numerous spines from Magdalena Bay, Baja California, and assigned it the name C. pauciflorus. It is this species which has often been confused with C. longispinus of the central and northern United States. The type specimen of C. pauciflorus, in the British Museum, does not approach C. longispinus, either in number of spines, or in spikelet size. Cenchrus roseus Fourn. (1885) is a narrow-spined plant with short spikelets, collected at Vera Cruz, Mexico. It resembles closely the type of C. pauciflorus. Cenchrus microcephalus Nash (1917) is a depauperate form of C. incertus. It was collected on Berry Island in the Bahamas by Britton and Millspaugh in 1905. The inflorescence of the type specimen,
in the New York Botanical Garden, appears to be immature. Hitchcock (1927) described a small plant with a few, long-pubescent and purple-colored burs, having short, broad spines, which he collected in Peru, and named *C. humilis*. The type specimens are all short plants, from fifteen to twenty cm tall. Hitchcock based the name on the small stature and pubescent burs of this form. However many collections closely approaching it in appearance have been observed by the writer from southern United States, Mexico, the West Indies, and Brasil, and it also resembles many of the plants found in the Rio Grande Plain. It is thus considered to be an occasional variant throughout the range of the species. *Oenchrus albertsonii* Runyon (1939) was based on a long-spined form of *C. incertus* from the northern edge of its range in Oklahoma.

*Oenchrus spinifex* was named and described by Cavanilles in 1799 from a plant collected in Chile. Chase (1920) mentioned this species, but because she had not seen the type, and since the description by Cavanilles was inadequate, she rejected the name. A specimen reputed to be an isotype of *C. spinifex* was examined at the Chicago Natural History Museum. This specimen was labeled "type fide Parodi." The plant on the sheet closely resembles *C. incertus* of the southern United States and Mexico. As such it represents an earlier name for *C. incertus*. I am rejecting the name *C. spinifex* until further studies can be made on the isotype and
holotype, since the latter has not been seen by the writer, and the correctness of the isotype label could not be verified.

Cytology

Tateoka (1955) reported a chromosome number of 2n=34 for *C. incertus*. In 1958, Gould published numbers of 2n=34 and 32 for this species, and again (Gould 1960) a number of 2n=34, which he reported for the species *C. parviceps*. The writer's counts, shown in Table 13, were all 2n=34, with no other numbers observed. The single count of Gould's indicating a number of 2n=32 may denote the presence of occasional aneuploids in this species, and may represent an apomictic form. However, Brown and Emery (1958) in a study of 28 ovules of *C. pauciflorus* from the southern United States, reported that all the embryo sacs were normal with no evidence of apomixis. Further studies on this wide-ranging species may possibly reveal the presence of apomictic forms, and reveal a possible explanation for the wide variability shown by this taxon throughout its range.

Distribution

This species occurs throughout the southern United States from North Carolina west to California, and south through Mexico, Central and South America, and in the West Indies. In recent years, according to Chippindall (1955), it has become a noxious weed in South Africa where it has been given the name
"fine-bristled burgrass."

Table 13. Chromosome counts from pollen mother cells of *Oenchrus incertus* M. A. Curtis

<table>
<thead>
<tr>
<th>Collection</th>
<th>Location</th>
<th>Chromosome number</th>
</tr>
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<tbody>
<tr>
<td>DeLisle voucher no. 387-A</td>
<td>Quay County, New Mexico</td>
<td>n=17</td>
</tr>
<tr>
<td>DeLisle voucher no. 396</td>
<td>Guadeloupe County, New Mexico</td>
<td>n=17</td>
</tr>
<tr>
<td>Pohl no. 8182</td>
<td>Tulsa County, Oklahoma</td>
<td>n=17</td>
</tr>
<tr>
<td>DeLisle voucher no. 479</td>
<td>Tulsa County, Oklahoma</td>
<td>n=17</td>
</tr>
<tr>
<td>Pohl no. 8181</td>
<td>Tulsa County, Oklahoma</td>
<td>n=17</td>
</tr>
<tr>
<td>Pohl no. 8185</td>
<td>Mayes County, Oklahoma</td>
<td>n=17</td>
</tr>
</tbody>
</table>

Selected specimens examined


BAJA CALIFORNIA: Cape St. Lucas, L. J. Xantus 115, August 1859 (NY, US); Punta de Conejo, L. L. Wiggins 5560, April 30, 1931 (NY, US, UC); Primera Agua near Loreto, M. E. Jones 27644, Oct. 19, 1930 (UC, MO).

BOLIVIA: San Pedro, G. Mandon 1267 (NY).

BRAZIL: Santa Catarina, R. Klein 397, 5-3-1953 (NY, US, UC); Leblon, near Lagoa de Freitas, A. Chace 8212, 13-14 Jan. 1925 (NY, US, MO).
COLUMBIA: Dept. del Valle: Isla del Guayabel, J.
Cuatrecasas 16222, Feb. 12, 1944 (US).
CUBA: Havana, H. A. Van Hermann 54 (UC); Camaguey, Cayo
HONDURAS: Tela, T. G. Yunker 4678, 7-20-34 (UC); Puerto
Sierra, P. Wilson 21, Jan. 15, 1923 (NY).
MEXICO: Charcas, San Luis Potosi, A. Whiting 849, July-
Aug. 1934 (UC, MO); Chihuahua, H. LeSueur, Sept. 3-4, 1935
(SMU, UC); Oaxaca, W. H. Camp 2579, Feb. 9-11, 1937 (NY);
Guaymas, E. Palmer 349, 1887 (NY); Sonora, near Alamos, J. N.
Rose 12837, March 14, 1910 (NY, US); Acapulco, E. Palmer 290,
Oct. 1894 (NY, MO); Durango, E. Palmer 196, April-Nov. 1896
(NY, MO, UC); Tamaulipas, J. Graham 4130, Sept. 29, 1959
(TEX); Tamaulipas, 24 km. south of Nuevo Laredo, R. M. King
2214, Nov. 28, 1959 (SMU, TEX); Monterrey, Bro. G. Arsene
6150, July 1911 (US, MO); Muzquiz, Wynd & Mueller 444, July
3, 1936 (NY, US, MO).
PARAGUAY: Balaura 151 (US).
PERU: La Merced Junin, A. S. Hitchcock 22134, Oct. 23,
1923 (US); Dept. Arequipa, Camana, R. Ferreyra 2540, Nov. 9,
1947 (US); Mollendo, Arequipa, A. S. Hitchcock 22349, Nov.
17, 1923 (NY, US).
URUGUAY: Montevideo, L. Barattini, 1920 (MO, SMU);
Dept. Durazno: Rio Y1, W. Herter 2712, April 1907 (US).
UNITED STATES: Alabama, Mobile, T. H. Kearney 59, July
8, 1895 (US); 3.3 miles s.w. of Eufaula, D. J. Banks 768,
July 31, 1961 (ISC); Spring Mill, E. F. Bush 273, Aug. 5,
1897 (US, MO); Arizona, Pima County, F. Ginter, Sept. 22,
1941 (UC); Nogales, E. E. Jones 22798, Oct. 23, 1926 (MO);
Tucson, E. E. Sherff, 29-7-1908 (F); Arkansas, Izard County, D.
Demaree 3319, June 11, 1927 (F, SMU); Pulaski County, H.
Eggert, July 3, 1894 (MO); California, Santa Barbara, H. M.
Pollard, July 11, 1958 (DAO, AHUC); Florida, Bennett, D. J.
Banks 898, Aug. 2, 1961 (ISC); Key Largo, A. Chase 3937, Sept.
10, 1907 (US, ISC); Lee County, A. S. Hitchcock, July-Aug.
1900 (MO); Gadsden County, G. V. Nash 2530, Sept. 5, 1895 (US,
F, MO); Kays, W. A. Silveus 4061, April 25, 1939 (SMU, UC);
Duval County, A. H. Curtiss 6020, Oct. 11, 1897 (MO, UC, ISC);
Sarasota, R. W. Pohl 7563, June 20, 1957 (ISC); Georgia, Wayne
County, D. J. Banks 725, July 28, 1961 (ISC); Dougherty
County, R. F. Thorne 4356, June 2, 1947 (SUI); Dooley County,
R. M. Harper 570, Sept. 3, 1900 (F, US, MO); McIntosh County,
W. H. Duncan 20651, Oct. 15, 1956 (SMU, US, SUI, ISC);
Louisiana, Alexandria, C. R. Ball 533, June 3, 1899 (US, UC,
MO); St. Tammany Parish, D. G. DeLisle 657, Aug. 28, 1961
(ISC); Natchitoches Parish, L. H. Shinners 22001, Oct. 8, 1955
(SMU); Mississippi, Jackson County, D. G. DeLisle 677, Aug.
28, 1961 (ISC); Ocean Springs, S. M. Tracy, Sept. 2, 1889
(US, MO); Chaneleur Island, S. M. Tracy 4525, May 30, 1898 (F,
MO); New Mexico, DeBaca County, L. H. Shinners 20911, Aug. 5, 1955 (SMU); Guadalupe County, D. G. DeLisle 396, July 30, 1960 (ISC); Quay County, D. G. DeLisle 387, July 30, 1960 (ISC); North Carolina, Cape Fear R., M. A. Curtis, 1837 (NY, Holotype); Greene County, A. E. Radford 40449, Sept. 13, 1958 (DAO); Harnett County, H. Laing 267, Sept. 29, 1956 (UC); Brunswick County, R. Iltis 4118, Aug. 23, 1949 (SMU); Oklahoma, Muskogee County, U. T. Waterfall 10085, July 3, 1951 (SMU); Payne County, R. W. Pohl 8158, Aug. 27, 1960 (ISC); Woods County, G. W. Stevens 768, May 29, 1913 (MO); South Carolina, Columbia, H. Eggert, Aug. 10, 1898 (MO); Georgetown, R. K. Godfrey & R. M. Tryon 217, June 30, 1939 (F, DAO, UC, US, MO); Orangeburg, A. S. Hitchcock 618, Aug. 18, 1905 (F, US, MO); Texas, Bexar County, D. G. DeLisle 525, Aug. 25, 1961 (ISC); Mason County, D. G. DeLisle 617, Aug. 25, 1961 (ISC); Goliad County, L. H. Shinners 2582, Oct. 13, 1956 (SMU); Harris County, E. Boon 323, July 12, 1946 (US, MO, TEX); Polk County, E. R. Girvin, Nov. 1, 1940 (UC, TEX); Wise County, L. H. Shinners 18843, May 30, 1954 (SMU, ISC); Shackelford County, V. L. Cory 58426, Sept. 29, 1950 (SMU); Baylor County, D. G. DeLisle 588, Aug. 23, 1961 (ISC); Stephen County, F. W. Gould 7597, June 5, 1957 (SMU); Taylor County, W. L. Tolstead 7413, June 12, 1943 (SMU, MO, UC); Nueces County, D. Isely 7527, April 13, 1961 (ISC); Howard County, D. G. DeLisle 605, Aug. 24, 1961 (ISC); Brooks County, D. Isely 7599, April 15, 1961 (ISC); Cameron County, D. Isely 7563, April 14, 1961 (ISC); Kleberg County, M. C. Johnston; Kenedy County, D. Isely 7551, April 13, 1961 (ISC); Kenedy County, E. C. Tharp 49046, June 16, 1949 (MO, UC, ISC, TEX); Mitchell County, R. W. Pohl 4404, Oct. 2, 1942 (SMU, ISC); Kerr County, F. W. Gould 8280, July 15, 1958 (UC, SMU); Dallas County, C. L. Lundell 12031, Sept. 19, 1942 (SMU); Morris County, D. S. and H. B. Correll 12457, June 6, 1946 (SMU); Upshur County, R. M. King 2177, Sept. 27, 1959 (SMU, TEX); Smith County, H. E. Moore Jr. 990, Aug. 1-20, 1945 (ISC, SUI, UC, SMU); Bowie County, A. E. & E. G. Heller 4211, Sept. 3, 1898 (MO, ISC); Brewster County, E. H. Warnock 21077, Aug. 8, 1940 (UC, TEX); Galveston County, D. G. DeLisle 638, Aug. 27, 1961 (ISC); Colorado County, L. H. Shinners 14643, May 16, 1953 (SMU, TEX); Edwards County, V. L. Cory 52457, Oct. 5, 1946 (SMU, UC); Brazos County, F. W. Gould 7807, Oct. 8, 1957 (UC, SMU, TEX); Bell County, C. L. York 54251, May 8, 1954 (SMU, TEX); Hidalgo County, D. Isely 7597, April 15, 1961 (ISC); Dimmit County, L. H. Shinners 17320, Nov. 8, 1953 (SMU); Virginia, Southampton County, M. L. Fernald and B. Long 6025, July 27, 1956 (US).

WEST INDIES: Bahamas, Turk's Island, Millspaugh 9374, March 22, 1911 (NY); Jamaica, Pigeon Island, Mason & Killip 1569, April 6-7, 1920 (NY); Bahamas, Bimini Islands, R. A. & E. S. Howard 10094, May, 1948 (UC, US, SMU, NY); Trinidad, W. E. Broadway 8016, April 24, 1932 (MO); Porto Rico, J. A.
Figure 15. Geographic distribution of *Cenchrus incertus*
SOUTH AFRICA: Bloemfontein, Praetoria, Dec. 1918 (US); Pretoria, J. J. Lindegue 16435, March 1934 (US).

12. Oenchrus callculatus (Figure 16, A—E; map, Figure 17)

Oenchrus callculatus Cav. Icones. 5:40. t. 463. (1799) (Type in MA, fragment of type in ISC) (1)
Oenchrus australis R. Br. Prod. 1:196. (1810) (Fragment of type in US) (1)
Oenchrus australis var. latifolius Drake Fl. Polyn. 252. (1892) (not of Sprengel 1827) (2)

Description

Plants perennial, robust, 1 to 2 meters tall, often reaching 3 meters; sheaths compressed, open at the throat, glabrous; ligule ciliate, 1.0—1.6 mm; blades scabrous, 14.0—56.0 cm long, 3.0—19.0 mm wide; inflorescence lax, 8.2—23.5 cm long, 1.0—2.8 cm wide, the burs often on long peduncles at right angles to the axis; rachis slightly flexuous, short-pubescent, the internodes 1.0—3.2 mm long; burs ovate to globose, 6.0—10.8 mm long, 2.0—4.5 mm wide; peduncle short-pubescent, tapering, 1.0—3.0 mm long; 0.8—2.9 mm wide at base of bur; spines terete, erect, rarely flattened, connate only at their bases, retrorsely barbed, the margins densely
pubescent except at the tips; outer whorl of spines at the base shorter and bristle-like; one inner spine often prolonged beyond the others; spikelets sessile, glabrous, one, rarely two or three, per bur, 3.8—6.5 mm long; first glume 1.2—3.5 mm long, 0.6—1.5 mm wide, 1-nerved; second glume 2.4—4.8 mm long, 3 to 5-nerved; sterile lemma 3.5—6.5 mm long, 5-nerved, enclosing the slightly shorter palea; fertile floret 3.8—6.1 mm long, 1.0—1.7 mm wide, 3-nerved; fruit ovoid, 1.8—2.8 mm long, 1.0—2.0 mm wide; anthers about 2.0 mm long.

Observations and nomenclature

This species occurs commonly in Australia where it is referred to as "tall bur grass." It usually grows in low scrub land and on the poor soil of hillsides. According to Turner (1893), the plants may form large tussocks, and when established along river banks, the tough, fibrous roots aid in maintaining the soil, affording protection against erosion by heavy rains and flood waters. The burs are a source of annoyance to sheep ranchers as they are difficult to remove from the wool.

Oenchrus caliculatus was described by Cavanilles in 1799, from a plant collected in "Amicorum insula Babae," presumably in reference to one of the "Friendly Islands." The holotype is in the Instituto "Antonio Jose Cavanilles" in Madrid. Photographs and a fragment of the type were furnished by that institution and are deposited in the
herbarium of Iowa State University.

A fragment of the type of *C. australis*, in the U. S. National Herbarium, was examined, and the burs, although slightly smaller than usual, are otherwise a close match to the Cavanille type. Drake (1892) listed *C. australis* var. *latifolius* as a synonym under *C. caliculatus* Cav., citing Sprengel (1827) as the author of this variety. However, Sprengel's treatment of the name in volume 4., Curae posteriores p. 33, was as follows, "Ad Oenchrum australem R. Br. *C. anomoplexis* Labill. in nov. Caledon. var. foliis latioribus." It thus appears that Sprengel was only referring to *C. anomoplexis* Labill. as a wide-leaved variety of *C. australis*.

Cytology

No chromosome counts have been reported for this species.

Distribution

Tall bur grass is common in Australia, being most abundant in the Northern Territory. It also occurs widely scattered in New Zealand, New Caledonia, Cook and Mangareva Islands, Tahiti, New Hebrides, and many other islands of the south pacific. It is apparently a rare adventive in the Philippines.

Selected specimens examined

AUSTRALIA: Queensland, Moreton Bay, F. Mueller, Aug. 1855 (US); S. E. Queensland, Gympie, F. H. Kenny, 1842 (US); Queensland, Cooranga North, via Bell, V. R. Cummings 6, 5-2-1937 (NY); New South Wales, Glaucaster, W. Heron, 1909
Figure 16. *Genchrus incertus*, *Genchrus caliculatus*, and *Genchrus tribuloides*

A--E. *Genchrus caliculatus*; A. spikelet, B. floret, C. caryopsis, D. bur, E. inflorescence

F--J. *Genchrus incertus*; F. burs, G. inflorescences, H. floret, I. caryopsis, J. spikelet

K--N. *Genchrus tribuloides*; K. spikelet, L. caryopsis, M. floret, N. bur
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(F); Sydney, Cape Byron, March 1896 (UC); Richmond River
District (US); Burnett District, Coalstoun Lakes, C. T. White
7709, May 16, 1931 (NY); New South Wales, Macleay's River,
Beckler (US).

SOUTH PACIFIC ISLANDS: Cook Islands, Rarotonga (UC);
Fiji: Viti Levu, A. C. Smith 4292, May 9-12, 1947 (US); Fiji,
Koro, A. C. Smith 1104, Feb. 1-8, 1934 (NY, US, UC); Mangar-
eva Islands, H. St. John 14890, June 6, 1934 (US, UC); Aukena
Island, H. St. John 14597, May 28, 1934 (US, UC); Nouvelle
Caledonie, M. Hennecart, 1879 (NY); New Hebrides, F. S.
Kajewski 358, June 4, 1958 (NY); New Zealand, North Island,
T. F. Cheeseman 1013, Aug. 1884 (US); Niue Island, T. G.
Yuncker 10213, Feb. 16, 1940 (US, UC); Pitcairn Island, H. St.
John 15024, June 14, 1934 (US); Pitcairn, J. P. Chapin 990,
Dec. 31, 1934 (NY, US); Tahiti, W. A. Setchell 88, May 23,
1922 (US, UC); Tonga, Nomuka Island, T. G. Yuncker 15827,
April 30, 1953 (US); Philippines, Mindanao, M. Ramos & G.
Edano 85197, April 1932 (US).

13. *Oenchrus elymoides* (Figure 19, A—D; map, Figure 17)

(1873) (Type in MEL) (2)

Description

Plants perennial, robust, culms terete, 60—150 cm tall;
sheaths slightly pubescent, open at the throat; ligule
ciliate, 1.0—2.0 mm long; blades sparsely pilose, 14.0—34.0
cm long, 3.3—10.2 mm wide, tapering to a point; inflores-
cence dense, 10.5—16.0 cm long, 1.1—1.5 cm wide; rachis
angled, glabrous, the internodes 1.2—2.8 mm long; burs
elongate, glabrous, sometimes scabrous, 9.8—14.0 mm long,
2.4—3.7 mm wide, with from 5 to 15 broad, thin spines 6.2—
11.4 mm long, 0.7—1.2 mm wide, antrorsely barbed and united
only at their bases, lower margins often pilose; the spines
prolonged into short awn-like tips, one spine prolonged
beyond the others 8—25 mm; spines subtended by 6 to 8
bristles, 5.0--7.5 mm long; peduncle rotund, smooth, 0.5--0.8 mm long, 0.9--1.6 mm wide; spikelets 1 to 3 per bur, sessile, elongate and narrow, 5.0--7.5 mm long; first glume 1.0--1.5 mm long, 0.8--1.2 mm wide; second glume 5.0--7.4 mm long, 3 to 5-nerved; sterile lemma 5.5--7.0 mm long, 3 to 5-nerved, the partially enclosed palea only slightly shorter; fertile floret 4.9--6.1 mm long, 1.0--1.7 mm wide; fruit elongate, 3.7--4.0 mm long, 1.0--1.5 mm wide; anthers 1.0--2.0 mm long.

Observations and nomenclature

Superficially this plant, with its spike-like inflorescence and burs with a prolonged bristle, has a striking resemblance to Elymus and other members of the Hordeae. Its spikelet structure, however, places it in the Paniceae, and the broad base of the bur makes it easily referable to the genus Cenchrus. The presence of one extremely prolonged bristle in each bur, the thin, flat spines and elongate shape of the fruit make this species one of the most distinctive in the genus.

Cenchrus elymoides was based on collections from Sturt's creek in Northwest Australia. The type, which has not been seen, is presumably in the National Herbarium of Victoria, Melbourne. In the Kew Herbarium, according to Hubbard (O. E. Hubbard, Kew, Surrey, England, 1962, personal communication), is a specimen collected by E. Damel on Cape York, and labeled "Cenchrus elymoides" in F. von Mueller's handwriting.
Figure 17. Geographic distribution of *Genchrus caliculatus*, *Genchrus elymoides*, and *Genchrus agrimonicide*. 
Cytology

No cytological work has been reported on this species.

Distribution

*Oenchrus elymoides* is apparently endemic to northern Australia where it is known from the Kimberley Division, the Northern Territory, and Queensland.

Selected specimens examined

AUSTRALIA: Northern Territory, 70 mi. e. of Carlton Sta., R. A. Perry 2616, July 27, 1949 (US); Kunmanga, West Australia, Rev. G. Holmes 1270, Feb. 1914 (US); Thursday Island, G. Palmer, 1883 (US); 15 miles south of Darwin, F. W. Heley, Jan. 1943 (US); 36 miles s.w. of Dorisvale Station, M. L. 2794, May 18, 1952 (US); 44 miles s.w. of Katherine Twp., R. A. Perry 2004, 3-6-49 (US).

14. *Oenchrus ciliaris* (Figure 19, E--H; map, Figure 18)

*Cenchrus ciliaris* L. Mant. 302. (1771) (Holotype in LINN) (1)

*Cenchrus rufescens* Desf. Fl. Atlant. 2:388. (1799) (4)


*Setaria vulpina* Beauv. Agrost. 51. (1812) (4)

*Pennisetum rufescens* Spreng. Syst. 1:303. (1825) (2)

*Pennisetum ciliare* Link. Hort. Berol. 1:213. (1827) (2)

*Cenchrus anjana* Ham. ex Wall. Cat. no. 8649-B. (1828) (name only) (4)

Oenchrus lappaceus Tausch in Flora. 20:57. (1837) (non O. lappaceus L. 1763) (4)

Oenchrus bulbosus Fresen. ex Steud. Nom. ed. II. 1:317. (1840) (2)

Oenchrus echinoides Wight ex Steud. Nom. ed. II. 1:317. (1840) (2)

Oenchrus pennisetiformis Hochst. & Steud. ex Steud. Nom. ed. II. 1:317. (1840) (2)

Oenchrus ciliaris Fig. & DeNot. Mem. Acc. Torin. Ser. 2. 14:383. (1854) (non O. ciliaris L. 1771) (2)

Oenchrus ciliaris var. pubicus Fig. & DeNot. Mem. Acc. Sci. Torino. Ser. 2. 14:392. (1854) (2)

Oenchrus ciliaris var. viliferus Fig. & DeNot. Mem. Acc. Sci. Torino. Ser. 2. 14:396. (1854) (2)

Oenchrus rigidifolius Fig. & DeNot. Mem. Acc. Sci. Torino. Ser. 2. 14:386. (1854) (2)


Cenchrus digynus Ehrenb. ex Boiss. Fl. Orient. 5:449. (1884) (in synonymy) (2)


Cenchrus ciliaris var. pubicus Durand & Schinz. Consp. Fl. Afr. 5:776. (1894) (non var. pubicus Fig. & DeNot. 1854) (2)

Cenchrus ciliaris var. viliferus Durand & Schinz. Consp. Fl. Afr. 5:776. (1894) (non var. viliferus
Fig. & DeNot. (1854) (2)


Cenchrus mutabilis Wight ex Hook. f. Fl. Brit. Ind. 7:88. (1896) (2)

Pennisetum cenchroides var. echinoides Hook. f. Fl. Brit. Ind. 7:88. (1896) (2)


Pennisetum ciliare var. pallens Fenzl ex Leeke. Zeitschr. Naturwiss. 79:22. (1907) (2)


Oenchrus pubescens L. ex Jackson. Index Linn. Herb. 53. (1912) (name only) (4)


Oenchrus aequiglumis Chiov. Agric. Colon. 20:108. (1926) (2)

Pennisetum ciliare forma brachystachys Peter. Fedde Repert. 40:71. (1930) (2)

Pennisetum ciliare forma longifolium Peter. Fedde Repert. 40:71. (1930) (2)

Oenchrus ciliaris var. genuinus (Leeke) Maire & Weiller in Maire. Fl. Afr. du Nord. 1:342. (1952) (2)

Oenchrus ciliaris var. leptostachys (Leeke) Maire & Weiller in Maire. Fl. Afr. du Nord. 1:342. (1952) (2)

Oenchrus ciliaris var. pallens (Penzl ex Leeke) Maire & Weiller in Maire. Fl. Afr. du Nord. 1:342. (1952) (2)


Description

Plants perennial, often forming mats or tussocks, 25--100 cm tall; sheaths compressed, glabrous to sparsely pilose; ligule ciliate, minute, 0.5--1.3 mm long; blades scabrous, sometimes slightly pilose, 2.8--24.0 cm long, 2.2--8.5 mm wide, tapering to a point; inflorescence dense, cylindric, 2.0--12.0 cm long, 1.0--2.6 cm wide; rachis flexuous, scabrous, the internodes 0.8--2.0 mm long, usually about 1.0 mm long; burs elongate, variously pubescent, 6.0--15.0 mm long, 1.5--3.5 mm wide; peduncle minute, densely pilose, 0.5--1.5 mm long, 1.0--2.0 mm wide; spines erect or spreading, 4.3--
10.0 mm long, 0.2--0.6 mm wide, long-ciliate pubescent on the inner margins, connate only at the base or slightly above, antorosely barbed, often with plumose tips; lower whorl of spines bristle-like, shorter than inner spines; spikelets 2 to 4 per bur, 2.0--5.6 mm long; first glume 1.0--3.0 mm long, 0.7--1.4 mm wide, thin and membranous, 1-nerved; second glume 1.3--3.4 mm long, 1 to 3-nerved; sterile lemma 2.5--5.0 mm long, 5 to 6-nerved, the partially enclosed palea 2.5--5.0 mm long; fertile floret 2.2--5.4 mm long, 1.0--1.5 mm wide, enclosing the turgid, ovoid fruit, 1.4--1.9 mm long, about 1.0 mm wide; anthers 2.0--2.5 mm long; chromosome numbers 2n=32, 34, 35, 36, 40, 44, 52, and 54.

Observations and nomenclature

Some notion of the wide morphological variability exhibited by this taxon is suggested by the many specific names which have been applied to it by various authors. Several reports in the literature, including those of Maire (1952), Tackholm (1941), and Stapf & Hubbard (1934), suggest the presence of putative hybrids between this species and *O. setigerus* wherever their ranges meet or overlap. Apomixis has been reported in both *O. ciliaris* and *O. setigerus* by Brown (1948), Fisher, Bashaw, & Holt (1954), and Snyder, Hernandez, & Warmke (1955). The latter authors reported from 1 to 8 embryo sacs per ovule in *Pennisetum ciliare* (*O. ciliaris*). Fisher et al. (1954), in a study of the embryo sacs of
Pennisetum ciliare (C. ciliaris), observed that these were normal up to the four-nucleate stage. At that time adventitious embryo sacs were aposporously produced from enlarged nucellar cells. Normal embryo sacs appeared to have been crowded out by the developing adventitious embryo sacs. Inflorescences were bagged before stigmas appeared, and seed set approached that of normal open-pollinated inflorescences, according to the authors. Apomixis was suggested by the fact that the parents and their progeny from seeds of bagged inflorescences appeared similar. These same authors suggest that the evidence from apomixis in both C. ciliaris and C. setigerus, as well as the presence of intermediates between these two taxa, may be indications that both are members of a single agamic complex.

The writer has observed about 40 collections each of C. ciliaris and C. setigerus throughout their ranges, and has seen only a few specimens which could be considered intermediates, although these all were more similar, morphologically, to C. ciliaris than to C. setigerus. Since these two species are quite distinct, morphologically, it is felt that they should be retained as separate taxonomic entities. Further genetic, cytological, and anatomical studies are needed on both species before their true relationships can be adequately assessed.

Cenchrus ciliaris was described by Linnaeus (1771) from a collection taken at the Cape of Good Hope. In the Linnean
herbarium is a sheet (no. 1217.9) with the name "ciliaris," apparently written by Sir James Smith (Jackson 1912). This collection is hereby designated as the type. Two other collections of C. ciliaris in the Linnean herbarium are represented by sheets number 1217.10 from "Horto Upsaliensi," and number 1217.11, which has no inscription.

Cytology

Chromosome numbers of $2n=38$ were reported by Krishnaswamy (1940), $2n=34$ by Darlington & Wylie (1955), and $2n=40$ and 52 by Nath & Swaminathan (1957). The number $2n=36$ has been observed by several authors including DeWett (1958), Fisher et al. (1954), and Moffett & Hurcombe (1949). Fisher et al. (1954) studied eighteen different introductions of Pennisetum ciliare (C. ciliaris). Of these, thirteen plants had a chromosome number of $2n=36$, three had $2n=54$, one had $2n=40$, and one $2n=32$. Behavior of chromosomes at meiosis appeared normal in all plants having a number of $2n=36$, but lagging chromosomes were common in meiotic anaphase-I in those plants having $2n=32$, 40, and 54. The number of laggards ranged from two to eight bivalents in the 32 and 40 chromosome types, to as many as eighteen univalents in the 54 chromosome type. The apparent meiotic irregularities in many of the aneuploids lends further support to the presence of widespread apomixis in this taxon.
Figure 18. Geographic distribution of *Oenchrus ciliaris* and *Oenchrus setigerus*
• = C. ciliaris
△ = C. setigerus
Distribution

Cenchrus ciliaris ("buffel grass," "anjan grass") is an inhabitant of dry, sandy areas throughout Africa, the Canary Islands, Madagascar, and eastward to India where it occurs largely in the northern territories. The species is also reported as adventive in South America, Australia and America. It is considered a good fodder grass in dry regions. In Puerto Rico it is now a major component of the flora in savanna areas of the semi-arid southern coastal regions (Snyder et al. 1955).

Selected specimens examined

AFRICA: Congo Belgica, Bauindi, Lebrun 8366, Nov. 1937 (US); British Somaliland, A. S. McKinnon S221, Nov. 1958 (US); Eritrea-Asamena, A. Pappi 4008, March 2-10, 1902 (MO, UC); Kalahiri Desert, South Africa, R. J. Rodin 3569, Feb. 8, 1948 (F, UC); Transvaal, 10 miles E. of Punda Maria, R. K. Godfrey SH-1716, Jan. 1953 (UC); Senegal, Melserner Herbarium, 1835 (NY); So. Rhodesia, H. Wild 3395, 8-6-50 (MO); Sudan, Blue Nile Province, E. W. Andrews A206, March 18, 1936 (US); Tanganyika, Tanga Prov., Oct. 1946 (MO); Fiskra, Algeria (F).


SOUTHERN ASIA: Red Sea, I. K. Lord (F).


15. Cenchrus multiflorus (Figure 19, I--L; map, Figure 20)

Cenchrus multiflorus Presl. Rel. Haenk. 1:318. (1830) (type in PRO) (2, 3)
Pennisetum karwinskyl Schrad. Linnaea. 12:431. (1838) (type in LE) (3)

Pennisetum multiflorum Fourn. Mex. Pl. 2:49. (1886) (type in O) (3)

Description

Plants perennial, the culms often arising from basal scaly buds, 60--140 cm tall; sheaths slightly keeled, glabrous, to slightly pilose at the margins and throat; ligule ciliate, 1.3--1.8 mm long; blades scabrous to slightly pilose, long and tapering to a point, 16.0--25.0 cm long, 7.8--20.0 mm wide at the base; inflorescence dense, spike-like, 7.0--18.0 cm long, 1.3--1.6 cm wide; rachis flexuous, scabrous to short-pubescent, the internodes 0.8--1.7 mm long; burs elongate, glabrous to slightly pilose, 6.8--9.6 mm long, 2.8--4.5 mm wide; spines erect, slightly rounded and connate at the base, glabrous, the lower margins sometimes slightly pilose, 6.0--7.0 mm long, 0.5--0.7 mm wide, antrorsely barbed at the tips; outer whorl of spines bristle-like, rarely exceeding one-half the length of the inner spines; one inner spine usually prolonged, 16--30 mm long; spikelets two to four per bur, sessile, 5.5--6.8 mm long; first glume 2.2--2.9 mm long, 1.0--1.5 mm wide, 1-nerved; second glume 3.5--5.2 mm long, 5-nerved; sterile lemma 5.0--6.1 mm long, 5 to 6-nerved; palea equaling the lemma and partially enclosed by it; fertile floret 5.2--6.6 mm long, 1.0--1.5 mm wide, 5-nerved; fruit ovoid, about 3.0 mm long, 1.5--2.0 mm wide; anthers 1.9--2.4
Observations and nomenclature

Oenchrus multiflorus is readily distinguished from O. ciliaris, by its glabrous, connate spines, and the wider burs and leaves. The prolonged spines are also a distinctive feature of this species, but the length of these is somewhat variable, being longest in those burs at the base of the inflorescence and gradually becoming shorter toward the tip of the inflorescence.

This taxon has long been considered a member of the genus Pennisetum and was so treated by Chase (1921) as P. karwinskyi. Because of the connation of spines at the base and the larger diameter of the burs, Henrard (1935) considered this a member of the genus Oenchrus, and applied the earlier name of O. multiflorus. The type specimen of O. multiflorus is in the herbarium of the German University at Prague, and was examined by Chase (1921). The types of Pennisetum karwinskyi and Pennisetum multiflorum have also been examined by the same author.

Cytology

No cytological work has been done on this species.

Distribution

Oenchrus multiflorus is apparently restricted to rocky uplands and moist slopes in Mexico and Costa Rica.
Selected specimens examined


NICARAGUA: Managua, H. A. Garnier, 1930 (F).

16. Cenchrous myosuroides (Figure 19, M--P; map, Figure 20)


Pennisetum pungens Nutt. Gen. N. Am. Pl. 54. (1818) (based on Panicum cenchroides Ell.) (2)


Setaria elliottiana Roem. & Schult. Mant. 2:279. (1824) (Based on Panicum cenchroides Ell.) (2)

Pennisetum myosuroides Spreng. Syst. 1:303. (1825) (Based on C. myosuroides) (2)

Cenchrous elliottii Kunth. Rev. Gram. 1:51. (1829) (Based on Panicum cenchroides Ell.) (2)


Cenchropsis myosuroides Nash in Small. Fl. S. E. U. S. 109. (1903) (Based on C. myosuroides H. B. K.) (2)

Description
Plants perennial, culms from 0.5 to 2.0 meters tall; sheaths open, glabrous; ligule ciliate, 1.5--3.4 mm long; blades glabrous to slightly pilose, 12.0--38.0 cm long, 4.0--13.0 mm wide; inflorescence compact, spike-like, 6.5--23.0 cm long, 0.6--1.5 cm in diameter; rachis angled, puberulent, the internodes 0.6--1.7 mm long, usually less than 1 mm between nodes; burs scabrous, often glabrous, 3.8--8.1 mm long, 1.2--2.6 mm wide; peduncle glabrous, 0.5--1.5 mm long, 1.1--2.3 mm wide; spine erect or spreading, terete, connate only at base, retrorsely barbed and glabrous, 3.0--5.8 mm long, 0.2--0.6 mm wide; one spikelet per bur, rarely two or three, 3.8--5.6 mm long; first glume 1.5--3.0 mm long, 0.6--1.8 mm wide, 1-nerved; second glume 3.1--5.0 mm long, 3 to 5-nerved; sterile lemma 3.1--5.5 mm long, partially enclosing the slightly shorter palea; fertile floret 3.8--5.4 mm long, 1.0--2.1 mm wide, 3 to 5-nerved; fruit ovoid, 1.5--2.6 mm long, 1.0--1.5 mm wide; anthers 1.2--2.2 mm long; chromosome numbers 2n=70, 54.

Observations and nomenclature
Those morphological features which best distinguish this species from others in the genus include its terete, glabrous spines which are only slightly longer than the spikelets, and
the extremely compact inflorescence. The plants are perennial, producing new shoots from the bases of older culms, and rarely produce inflorescences the first year when grown from seed. The spines are quite narrow and somewhat more widely spaced than most other species of Cenchrus, giving the bur an "open appearance."

The type of \textit{C. myosuroides} H. B. K. is in the herbarium of the Museum National d'Histoire Naturelle in Paris. A fragment of the type in the U. S. National Herbarium was examined by the writer. Nuttall's description of \textit{Pennisetum pungens} (1818) was based on \textit{Panicum cenchroides} of Elliott (1821), which is a later homonym. Since Elliott's name was apparently published three years after that of Nuttall, it is possible that Nuttall referred to herbarium collections of Elliott for his source of information. The establishment of a separate genus for \textit{C. myosuroides}, i.e., \textit{Cenchropsis myosuroides} by Nash in Small (1903), appears to have little or no justification on morphological grounds, and the genus has been rejected by subsequent workers. A large-burred form, having two or three spikelets per bur, was described from Santo Domingo in 1936 by Hitchcock, and was given the name \textit{C. ekmanianus}. An examination of the type in the U. S. National Herbarium reveals a variation in one inflorescence of from one to three spikelets per bur. Occasional plants from Mexico and Central America have been observed by the writer with two spikelets per bur. It would appear that
O. ekmanianus was based on such sporadic forms which may occur throughout the range of the species. In all other characteristics, the type specimen falls within the range of variation of the species.

**Cytology**

A chromosome number of 2n=54 has been reported by Brown (1950, 1951). Avdulov (1931) indicated a number of 2n=70, and this same count has been obtained by Gould (F. W. Gould, College Station, Texas, 1962, personal communication). These counts indicate that O. myosuroides is a polyploid that has probably originated from some form with a basic number of \( X=9 \) or 10 (see discussion in chapter on cytology).

**Distribution**

*Chencherus myosuroides* occurs in the southern United States, but is more common in Mexico, the Caribbean, and throughout South America. This grass apparently is of little or no economic importance.

**Selected specimens examined**

ARGENTINA: Prov. Cordoba (MO); Bel Cordoba, T. Stuckert, Jan.-March, 1902 (ISO); Chaco, O. Spegazzini 11870, April 21, 1883 (NY); Tucuman, Capria, Rodriguez 252, Dec. 29, 1911 (MO); Estancia St. Teresa, T. M. Petersen 1403, Dec. 21, 1951 (NY, MO); Bel Cordoba, A. Kneucker 428, Jan.-March 1902 (US, UC, MO); Dept. Andalgala, P. Jorgensen 1144, 10-11-1915 (UC, MO); Buenos Aires, A. T. Hunziker 3489, April 8, 1942 (NY, MO); San Juan, Pocito, A. R. Ouezzo 2201, Dec. 27, 1945 (DAO); Prov. San Luis, Bruch, Feb. 1914 (NY).

BOLIVIA: Cochabamba, H. A. Senn 4087, May 14, 1949 (DAO); Prov. Larecaja, G. Mandon 1266, March-April, 1868 (NY).
BRAZIL: Rio Grande do Sul, S. Leopoldo 1066, 7-10-34 (MO); Rio de Janeiro, A. Chase 9808, May 18, 1925 (MO).

CHILE: Prov. Tacna, Azapa, E. Werdermann 713, Aug. 1925 (NY, UC, MO); Tacua, J. G. Hosmann, April 19, 1918 (AHUC).


CUBA: Morro Castle, Bro. Leon 1589, Jan. 10, 1910 (NY); Guantanamo, Ekman 10153, Dec. 16, 1919 (NY); Oriente, H. Batiste & B. Hirram 1279, Nov. 15, 1917 (NY).


MEXICO: Sonora, Hermosillo, J. N. Rose, Standley, P. C. & P. G. Russell 12484, March 7, 1910 (NY); Coahuilla, Reeves and Morrow PI-216375, Oct. 5, 1954 (SMU); El Riego Puebla, C. A. Purpus 1218, July 1905 (UC); Chihuahua, O. G. Pringle 429, May 25, 1885 (NY, F); Durango, E. Palmer 868, April-Nov. 1896 (F, NY, UC, MO); Guadalajara, E. Palmer 765, July-Oct. 1886 (F, NY, MO); Durango, R. Q. Landers PI-216381, Sept. 21, 1954 (SMU); Tehuacan, State of Pueblo, A. S. Hitchcock 619, Aug. 9, 1910 (NY, UC, MO); Ojo de San Fernando, J. Gregg, May 6, 1847 (MO); Baja California, T. S. Brandegee, Feb. 12, 1889 (AHUC); Revillagigedo Islands, San Benedicto, H. L. Mason 1682, May 11, 1925 (MO); Socorro Island, J. T. Howell 8401, March 23, 1932 (NY, UC, MO); Socorro Island, S. Carlquist 379, May 5, 1955 (F, UC).

PARAGUAY: P. Jorgensen 3567, Dec. 20, 1928 (NY, MO); E. Hassler, 1885-1895 (NY).

FLORIDA: Florida Keys (MO); Indian Key, A. H. Curtiss, 5643, April 29, 1896 (MO, UC, ISO).

TEXAS: Laredo, Feb. 1828 (MO); Webb County, H. R. Reed, July 19, 1947 (SMU); Val Verde County, B. H. Warnock & J. O. Parks 350, May 31, 1949 (SMU); Dimmit County, B. C. Tharp 47442, July 28, 1947 (ISO); Atascosa County, L. H. Shinners 16942, Nov. 5, 1953 (SMU, UC); Dimmit County, F. W. Gould 5790, Aug. 24, 1950 (SMU, UC).


17. Cenchrus agrimonicoides (Figure 21, A--D; map, Figure 17)

(1826) (Type in B, fragment of type in US) (1)
Figure 19. *Cenchrus elymoides*, *Cenchrus ciliaris*, *Cenchrus multiflorus*, and *Cenchrus myosuroides*

A--D. *Cenchrus elymoides*: A. spikelet, B. caryopsis, C. bur, D. floret

E--H. *Cenchrus ciliaris*: E. floret, F. caryopsis, G. spikelet, H. bur

I--L. *Cenchrus multiflorus*: I. bur, J. caryopsis, K. spikelet, L. floret

M--P. *Cenchrus myosuroides*: M. floret, N. bur with spikelet, O. caryopsis, P. inflorescence
Figure 20. Geographic distribution of *Cenchrus myosuroides* and *Cenchrus multiflorus*
C. myosuroides

C. multiflorus

Cenchrus calyculatus var. uniflorus Hillebr. Fl. Haw. Isl. 505. (1888) (2)


Cenchrus pedunculata Degener & Whitney in Degener. Fl. Haw. 1:Fam. 47. (1936) (Type in US, cotype in NY, MO) (1)

Description

Plants perennial; culms robust, 35--200 cm tall, glabrous; sheaths compressed-keeled, glabrous, sometimes short-pubescent; ligule ciliate, about 2.5 mm long; blades scabrous to short-pubescent, 16.0--41.2 cm long, 6.0--16.0 mm wide, tapering to a point; inflorescence open, spike-like, 7.8--28.0 cm long, 1.6--2.2 cm wide; rachis angled, usually not flexuous, pubescent, the internodes 1.7--3.3 mm long, usually about 2.5 mm between the nodes; burs fusiform to turbinate, puberulent, 10.0--14.2 mm long, 3.0--4.2 mm wide; peduncle 2.5--4.5 mm long, 2.5--3.5 mm wide; inner spines few, somewhat flattened, erect, connate at the base or often for some distance above the base, the inner margins ciliate-pubescent, 5.7--7.0 mm long, 0.6--1.4 wide, the tips retrorsely barbed and often curving outwards; outer whorl of spines numerous, short and bristle-like; spikelets sessile, one or two per bur, about 6.0--7.0 mm long; first glume 1.5--3.5 mm long, 0.8--1.6 mm wide; second glume 4.5--6.3 mm long, often ending in a
short awn-like tip; sterile lemma 5.9–6.6 mm long, 5-nerved, the palea 4.5–5.5 mm long; fertile floret 5.8–7.0 mm long, 1.1–2.0 mm wide, 3-nerved; fruit ovoid, about 2.6 mm long, 1.0 mm wide.

Observations and nomenclature

Morphologically this species appears to have close affinities with *C. caliculatus* of the south pacific regions. It is most easily distinguished from the latter species, however, by its turbinate burs with fewer spines (6 to 10), which are flattened and often connate for some distance above the base. The spines of *C. caliculatus*, on the other hand, are more numerous (12 to 20), are terete throughout their length, and are connate only at the base. Most specimens of *C. agrimonioides* have the long-peduncled burs extending at right angles to the rachis.

Trinius (1826) based his description of *C. agrimonioides* on a specimen collected in the Sandwich Islands by A. Chamiso. A fragment of the type from the Berlin-Dahlem Herbarium, and collected by Chamiso, is in the U. S. National Herbarium. It is not known if the original type specimen is still in existence.

Hillebrand (1888) based *C. calyculatus* var. *uniflorus* on robust plants with slightly larger burs. The type has not been seen but Hitchcock (1922) treated this name as a synonym of *C. agrimonioides* Trin. Occasional plants from Laysan
Island are taller with slightly wider leaves. These forms were the basis for *C. agrimonioides* var. *layasanensis* F. Brown (1931). In all other characteristics, however, these plants fall within the range of variation of *C. agrimonioides*. Degener's *C. pedunculata*, described in 1936, was apparently based on specimens with slightly villous-pubescent leaves and more conspicuously tomentose burs. These characters are quite variable throughout the range of the species, however, and therefore do not seem sufficiently distinct to warrant varietal status. The types of both *C. agrimonioides* var. *layasanensis* and *C. pedunculata* are in the U. S. National Herbarium and were examined by the writer.

**Distribution**

*Cenchrus agrimonioides* is largely restricted to Hawaii and Midway. Collections have also been reported from New Caledonia and the Loyalty Islands. Further exploration and collections in the Pacific may reveal a somewhat wider distribution for the species than is at present indicated.

**Selected specimens examined**

**HAWAIIAN ISLANDS:** Laysan Island, J. O. Snyder, May 1902 (NY, US, MO); Pahu, Wilder, 1912 (US); Maui, J. F. Rock (US); Lanai, G. C. Munro 404 (US); Pua Ekanaehoa, Oahu, Degener & Whitney 12,800, May 1, 1940 (MO, NY, US); Ocean Island, E. L. Caum, April 18, 1923 (NY); Oahu, Kaumokunui Gulch, Degener 12264, April 13, 1936 (NY, US); Oahu, Makua Valley, Degener 12265, June 26, 1932 (NY, MO, US).

**MIDWAY:** Eastern Island, W. A. Bryan, Aug. 22, 1902 (NY).
18. *Oenchrus biflorus* (Figure 21, I—L; map, Figure 22)

*Oenchrus biflorus* Roxb. *Flora Ind.* 1:238. (1820)  
Hort. Beng. 1:81. (1814) (nomen nudum.) (Type in BM) (2)

*Elymus canut medusae* Forsk. *Fl. Aeg.-Arab.* 25. (1775)  
(non L.) (2)

Guin. Fl.* 63. (1828) (Type in Mus. Bot. Hauniense,  
fragment of type in US) (1)

*Oenchrus catharticus* Schlect. *Linnaea.* 4:78. (1829)  
(non *O. catharticus* Delile, 1839) (2)

*Oenchrus catharticus* Delile. *Cat. Hort. Monsp.* (1838)  
(4)

(1849) (of authors, non *O. echinatus* L. 1753) (2)

*Oenchrus piloticus* Fig. & DeNot. *Mem. Acc. Torin.*  
14:380., Pl. 33. (1854) (2)

Bot.* 553. (1863) (2)

Ind.* 7:89. (1896) (Attributed by Hooker to Roxburgh)  
(2)

80:774. (1933) (Type in P, fragment of type in US) (1)

*Oenchrus perinvolucratus* Stapf & Hubbard. *Kew Bull.*  
No. 6:299. (1933) (Type in K) (2)

**Description**

Plants annual, 5.0—85.0 cm tall; sheaths compressed-  
keeled, scabrous to slightly pubescent; ligule ciliate, about  
1.4 mm long; blades usually glabrous, sometimes loosely  
pilose, 2.0—24.0 cm long, 2.6—7.0 mm wide, tapering to a  
point; inflorescence spike-like, 2.5—14.3 cm long, 0.8—1.6
cm wide; rachis angled, usually flexuous, scabrous, the internodes 1.2--4.0 mm long, normally about 2.0 mm between nodes; burs ovoid, 3.8--11.1 mm long, 2.0--4.5 mm wide; peduncle glabrous, 0.9--2.2 mm long, 1.0--3.5 mm wide, forming a somewhat ovoid disc at the base of bur; inner spines flattened, erect, more often spreading, connate only at the base, 2.9--7.0 mm long, 0.2--1.1 mm wide, the outer surfaces with one to three shallow grooves, the inner margins long-ciliate pubescent; spine tips retrorsely barbed and often variously hooked or bent; lower or outer whorl of spines numerous, bristle-like, less than one-half the length of the inner spines; spikelets 3.5--6.0 mm long, sessile, from one to three per bur; first glume 0.5--2.5 mm long, 0.6--1.4 mm wide, 1-nerved; second glume 2.5--4.9 mm long, 3 to 5-nerved; sterile lemma 3.2--5.5 mm long, 4 to 5-nerved, partially enclosing the palea of equal or slightly shorter length; fertile floret 3.4--5.9 mm long, 1.0--2.0 mm wide, 3 to 5-nerved; fruit ovoid, 2.0--3.4 mm long, 1.0--3.5 mm wide; anthers about 1.5 mm long.

Observations and nomenclature

The distinctive ovoid or often diamond-shaped disc at the base of the bur, and the flattened, grooved spines are characters which readily distinguish this species. While it has many apparent affinities with C. prieurii and C. myosurus-oides, it lacks the long plumose, antrorsely barbed spines of
the former, and the terete, glabrous spines of the latter species.

The type specimen of *C. biflorus*, collected on the Coromandel coast of India, and in the British Museum, has not been seen by the writer. However, Roxburgh's reference to the grooved spines with hairy margins and slightly hooked apices could pertain to no other species of *Cenchrus* in that region.

*Cenchrus barbatus* Schum. represents a form with small burs, but since this characteristic exhibits considerable variation over the range of the species, the collection from which he made his description undoubtedly represents such a small-burred form of *C. biflorus*. The figure which accompanies Figari & DeNotaris' description of *C. niloticus* from North Africa identifies it as the earlier-named *C. biflorus*. Andersson's (1863) mention of deeply laciniate spines with pilose margins, likewise, appears to be in reference to *C. biflorus*. The type specimen of *C. leptacanthus* A. Camus is in the Museum National d'Histoire Naturelle, Laboratoire de Phanerogamie, Paris, and a fragment, in the U. S. National Herbarium, was examined by the writer. This appears to be a form of *C. biflorus* in which the spines are rounded at the tips, a condition observed in many specimens, particularly of those burs near the base of the inflorescence. *Cenchrus perinvolutatus* was collected on Zanzibar and described by Stapf & Hubbard (1933). The description apparently refers to
a form of *C. biflorus* with robust burs which have straighter spines.

**Cytology**

A chromosome count for *C. biflorus*, obtained by the writer, is shown in Table 14. Meiosis was normal in the material examined.

**Table 14. Chromosome count from pollen mother cells of *Cenchrus biflorus* Roxb.**

<table>
<thead>
<tr>
<th>Collection</th>
<th>Location</th>
<th>Chromosome number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Th. Monod Dakar</td>
<td>Dakar, North Africa</td>
<td>n=17</td>
</tr>
<tr>
<td>DeLisle voucher no. 684</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Distribution**

*Cenchrus biflorus* is widely distributed throughout northern and eastern Africa, Madagascar, Arabia, and India.

**Selected specimens examined**

AFRICA: Abyssinia, W. Schimper 2019, 1852 (US); Belgian Congo, Albertville, L. Shantz 662, Feb. 12, 1920 (US); British Somaliland, R. E. Glover 342, Nov. 21, 1944 (US); Eritrea-Somaliland, A. Pappi 238, Nov. 29, 1902 (US, MO); Timbuktu, French Sudan, O. H. Sweeney 40, Dec. 11, 1953 (US); Gold Coast (Ghana), C. Vagre 143, July, 1938 (US); Kimbimbi, H. Vanderyst, Nov. 24, 1913 (US); Mozambique, R. J. Rodin 4187, March 29, 1948 (US, UC, MO); South Nigeria, Lagos, July 22, 1952 (MO); Niger Colony, O. Olufsen 460, Oct. 7, 1927 (US); Tanganyika, R. E. S. Tanner 2053, Aug. 10, 1955 (UC).

19. Oenchrus prieurii (Figure 21, E--H; map, Figure 22)


Pennisetum prieurii Kunth. Rev. Gram. 2:411. (1831) (2)

Oenchrus hystrix Fig. & DeNot. Mem. Acc. Torin. Ser. 2. 14:382. (1854) (2)


Description

Annual, culms 12.0--33.0 cm tall; sheaths glabrous to scabrous, compressed; ligule ciliate, about 1.6 mm long; blades scabrous, 5.0--7.0 cm long, 3.4--4.8 mm wide, tapering to a point; inflorescence 5.0--9.1 cm long; rachis flexuous, scabrous, the internodes 2.5--3.3 mm long; burs 15.0--26.6 mm long including the plumose spines, 2.0--3.0 mm wide; spines numerous, erect or spreading, flattened and connate only at base, prolonged into long plumose bristles which are antorse-ly barbed; lower margins of the spines densely pilose-pubescent, outer surfaces with one or two shallow grooves; base of bur short-peduncled, glabrous, forming a shallow oval
or diamond-shaped disc; spikelets one or two per bur, sessile, about 4.3 mm long; first glume about 0.8 mm long, 0.6 mm wide, sometimes absent or reduced; second glume 2.9–3.5 mm long, sterile lemma 3.3–3.8 mm long, fertile floret about 4.2 mm long, 1.1–1.3 mm wide; chromosome number 2n=34.

Observations and nomenclature

The long, antrorsely barbed and plumose spines of this species distinguish it from C. biflorus of the same general area of distribution.

Genchrus prieurii was based on Pennisetum prieurii Kunth. The type, which may have been in Berlin, has not been seen by the writer, but the illustration in Kunth (tab. 19, 1831) identifies this species as C. prieurii.

The figure accompanying the description of C. hystrix (Fig. & DeNot., 1854) agrees closely with that of C. prieurii. Steudel's treatments of C. macrostachyus and Pennisetum breviflorum indicate bur size and color variants of C. prieurii.

Cytology

A chromosome number of 2n=34 has been reported for C. prieurii by Mulay & Leelamma (1956). No other reports of cytological investigations have been noted for this species.
Figure 21. *Oenchrus agrimonioides*, *Oenchrus prieurii*, *Oenchrus biflorus*, and *Oenchrus setigerus*

A--D. *Oenchrus agrimonioides*: A. bur, B. spikelet, C. floret, D. caryopsis

E--H. *Oenchrus prieurii*: E. bur, F. caryopsis, G. spikelet, H. floret

I--L. *Oenchrus biflorus*: I. bur, J. caryopsis, K. floret, L. spikelet

M--Q. *Oenchrus setigerus*: M. bur, N. spikelet, O. floret, P. caryopsis, Q. inflorescence
Figure 22. Geographic distribution of *Cenchrus biflorus* and *Cenchrus prieurii*.
Distribution

*Cenchrus prieurii* is of rather localized occurrence in northern Africa, Arabia and India.

**Selected specimens examined**

Colonie du Niger, Zinder, O. Hagerup 611a, Nov. 15, 1927 (US); Timbuktu, Soudan Francais, O. Hagerup 195, July 17, 1927 (US); Abyssinia, Tacaze, M. W. Schimper 1777, 1856 (US); Central India, Rajputana (US).

20. *Cenchrus setigerus* (Figure 21, M—Q; map, Figure 18)

*Cenchrus setigerus* Vahl. Enum. Pl. 2:395. (1806) (Type in C) (2, 3)


*Cenchrus echinatus* Wall. Cat. no. 8854. (1828) (nomen nudum) (non *C. echinatus* L. 1753) (2, 4)

*Cenchrus quinquevalvis* Ham. ex Wall. Cat. no. 8854-B. (1828) (nomen nudum) (4)

*Pennisetum vahlii* Kunth Rev. Gram. 1:49. (1829) (2, 4)

*Cenchrus montanus* Nees in Royle. Illustr. Bot. Himal. 4:16. (1839) (nomen nudum) (2, 4)

*Cenchrus schimperi* Hochst. & Steud. ex Steud. Nom. ed. 2. 1:317. (1840) (Isotype in MO) (1)

*Cenchrus setigerus* Spreng. ex Steud. Nom. ed. 2. 1:317. (1840) (of various authors, non *C. setigerus* Vahl., 1806) (2)

*Cenchrus triflorus* Roxb. in Aitch. Panjab Pl. 163. (1839) (2, 4)

*Cenchrus bulbifer* Hochst. ex Boiss. Fl. Orient. 5:448. (1834) (2)

*Cenchrus uniflorus* Ehrenb. ex Boiss. Fl. Orient. 5:448. (1834) (2)
**Oenchrus ciliaris** var. *setigerus* (Vahl.) Maire & Weiller in Maire. 1:342. (1952) (2)

**Description**

Plants perennial, forming clumps from somewhat bulbous bases; culms 5.0—8.0 cm tall; sheaths compressed, glabrous or scabrous, the margins often short-ciliate; ligule reduced, ciliate, 0.6—1.1 mm long; blades glabrous, sometimes slightly pilose on upper surfaces near the base, tapering to a point, 2.0—20.0 cm long, 1.8—6.9 mm wide; inflorescence compact, spike-like, 2.0—12.0 cm long, 0.4—1.0 cm wide; rachis angled, often flexuous, scaberulous, the internodes 0.6—1.6 mm long, usually about 1.0 mm between the nodes; burs cup-shaped, glabrous, often slightly puberulent, 3.0—7.0 mm long, 1.5—4.0 mm wide; inner spines erect, short, connate for one-third to one-half their length, 2.0—4.2 mm long, 0.6—1.0 mm wide, grooved on the outer surface, the tips antrorsely barbed; outer spines fewer in number than inner, short, often directed outward; burs and spines varying in color from stramineous to purple; spikelets one to three per bur, sessile, 3.5—5.2 mm long; first glume chartaceous, 1.0—2.5 mm long, 0.6—1.2 mm wide, 1-nerved; second glume chartaceous, 1.9—3.4 mm long, 1 to 3-nerved; sterile lemma 3.4—4.6 mm long, 3 to 5-nerved, the slightly shorter palea narrow and partially enclosed by the lemma; fertile floret 3.4—5.0 mm long, 0.8—1.5 mm wide, 3 to 5-nerved; fruit ovoid, 1.2—1.8 mm long, 0.4—1.0 mm wide; anthers 1.6—2.4 mm long;
chromosome number 2n=36.

**Observations and nomenclature**

The short, broad spines with antorsely barbed tips distinguish this species from others in the genus.

The presence of apomixis in *C. setigerus* was indicated by Fisher *et al.* (1954) and by Snyder *et al.* (1955). The latter authors observed from one to four embryo sacs per ovule in this species. Aposporous formation of embryo sacs in *C. setigerus* took place in a manner similar to that of *C. ciliaris*, from enlarged nucellar cells following the four-nucleate stage of megasporogenesis. The multiple embryo sacs observed were usually crowded in the central part of the ovule and by the time they reached maturity might occupy most of the region formerly held by the nucellus. Removal of stigmas of *C. setigerus*, before anthesis, or within 2½ hours after anthesis, was found by Snyder *et al.* to prevent seed production, presumably because their removal prevented growth of the pollen tubes into the ovule. Removal of stigmas 3 to 3½ hours after anthesis had an intermediate effect on seed set (26 to 30%), while removal of stigmas 4 hours or more after anthesis had no appreciable effect on normal seed set of from 80 to 95%. Quite similar results were noted in tests on both *C. setigerus* and *Pennisetum ciliare* (*C. ciliaris*), by Snyder *et al.* (1955), indicating that both species are not only apomictic but also pseudogamous, since normal seed set does
not occur unless pollination and fertilization of the endosperm takes place. Division of the aposporously produced eggs are apparently stimulated by development of the endosperm.

The type of *C. setigerus* is in the Botanical Museum of Copenhagen, and was collected by Forskal in Arabia. Wahl's reference to the multifid, glabrous bur would seem to apply only to *C. setigerus* in that area. The type has been examined by Hubbard (C. E. Hubbard, Kew, Surrey, England, 1962, personal communication) and was matched with a collection by Schweinfurth, no. 581, from the Sudan.

The isotype of *C. schimperi* is in the herbarium of Missouri Botanical Garden, and was examined by the writer. This collection represents *C. setigerus* as treated by present-day workers, as does that of the type of *C. tripsacoides* R. Br., in the British Museum. A fragment of the type of the latter species in the U. S. National Herbarium has been examined by the writer. Bossier's description of *C. bulbifer* (1884) makes mention of eight to ten short, scabrid, erect spines, seemingly applying to *C. setigerus*. Bossier includes *C. uniflorus* as a synonym of *C. bulbifer*.

**Cytology**

A chromosome number of 2n=36 has been reported for *C. setigerus* by Darlington & Wylie (1955), Fisher et al. (1954), and Snyder et al. (1955). In their discussion of
meiosis in this species, Fisher et al. (1954) noted only normal meiotic divisions with no apparent lagging. Snyder et al. (1955), however, reported lagging chromosomes with some univalents in from 10 to 14% of the first meiotic anaphase cells examined. The chromosome count obtained by the present writer is indicated in Table 15. No aberrant meiosis was noted in the material studied.

Table 15. Chromosome count from pollen mother cells of *Cenchrus setigerus* Vahl.

<table>
<thead>
<tr>
<th>Collection</th>
<th>Location</th>
<th>Chromosome number</th>
</tr>
</thead>
<tbody>
<tr>
<td>U. S. Plant Introduction</td>
<td>Origin unknown</td>
<td>n=18</td>
</tr>
<tr>
<td>No. 216374</td>
<td></td>
<td></td>
</tr>
<tr>
<td>DeLisle voucher</td>
<td></td>
<td></td>
</tr>
<tr>
<td>no. 480</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Distribution

*Cenchrus setigerus*, commonly referred to as "birdwood grass," occurs throughout Africa, Arabia and India. It is an adventive in the southern United States, Australia and South America, where it has been introduced as an experimental forage grass.

Selected specimens examined

AFRICA: Kenya Colony, Archer Post, H. L. Shantz 852, June 14, 1920 (US); Eritrea-Asmara, March 2-10, 1902 (US); Ethiopia, A. T. Semple, Sept. 15, 1944 (US); Libysche Wuste,
P. Ascherson, March 24, 1874 (MO); Arabia, C. G. Ehrenberg, 1825 (US); Arabia, Schimper 797 (US); Arabia (Shrenbey?) (MO).


SOUTH AMERICA: Paraguay, E. Anderson 1176, March 22, 1950 (US); Uruguay (cultivated, introduced), March 12, 1943 (US).

UNITED STATES: Starkville, Miss., S. M. Tracy, 8-5-1891 (NY); Gainesville, Florida, Experiment Station, W. A. Silveus 4013, 4-22-39 (SMU); Angleton, Texas, P. B. Kennedy, 7-31-1920 (AHUC).
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Finally, for their patient efforts in the search for rare journals and botanical volumes, the writer is grateful to the reference librarians at Iowa State University and to Dr. G. B. Van Schaack of the Missouri Botanical Garden.
The following list contains names which have at some time been included in the genus Oenchrus. The criteria for treatment of each name herein are the same as that followed in the body of the work and explained in Methods and Materials, pages 3 to 7.


*Oenchrus anomoplexis* Desf. *Fl. Atlant.* 2:388. (1799) = ? (no reference to this name in Desfontaines, may be the same as *O. anomoplexis* Labill. 1824).


*Oenchrus biflorus* Broun & Massey (non *O. biflorus* Roxb. 1820) = (original description not seen; cited as synonym of *O. setigerus* in Andrews (1956) (4).


*Oenchrus carolinianus* Walt. *Fl. Carol.* 79. (1788) = nomen nudum. (See discussion under *O. longispinus*) (2).


Oenchrus gracilis Beauv. Agrost. 157 (1812) = ? (a name only for a specimen sent by Bosc., presumably from the Carolinas, Chase, 1920) (2).

Oenchrus granularis L. Mant. 2: App. 575. (1771) = Mansuris granularis (2).


Oenchrus inflexus Poir. Encycl. 6:50. (1804) = Echinochaena hirta (2).

Oenchrus laniflorus Steud. Syn. Pl. Glum. 1:110. (1855) = ? (may refer to O. caliculatus, described from Tahiti) (2).

Oenchrus lapeta Ham. ex Wall. Cat. No. 8654-D. (1828) nomen nudum = ?

Oenchrus limensis Mейен, Reise. 2:71. (1834) = ?
(Original description not seen; cited in Index Kewensis).

Oenchrus linearus Lam. Fl. Fr. 3:631. (1805) = Tragus racemosus (2).


Oenchrus muricatus L. Mant. 302. (1771) = Trachys mucronata (2).


Oenchrus ovatus Lam. ex Poir. Encyc. 6:51. (1804) = ? (Lagurus) illustration does not resemble any known species of Oenchrus.

Oenchrus paniceus Heyne ex Wall. Cat. no. 8650. (1828) nomen nudum = Pennisetum typhoidesum. (4).

Oenchrus parviflorus Poir. Encyc. 6:52. (1804) = ? possibly Setaria geniculata (4).


Oenchrus purpurascens Thumb. in Trans. Linn. Soc. 2:329. (1794a) = ? Gymnothrix japonica (2, 4).


**Oenchrus spinifex** Cav. *Icones* 5:38. (1799) = ? may refer to *O. incertus*, see discussion under that species. (2).

**Oenchrus tomentosus** Poir. *Encycl.* 6:51. (1804) = ?


**Oenchrus tripsacoides** L. ex Jackson. *Index Linn. Herb.* 53. (1912) nomen nudum = ?


**Oenchrus villosus** Sprang. *Syst.* 1:301. (1825) = *Anthephora elegans* (2).