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RESISTANCE OF SORGHUM VARIETIES AND HYBRIDS TO THE EUROPEAN CORN BORER (OSTRINIA NUBILALIS HBN.)

F.F. Dicke, R.E. Atkins, and G.R. Pesho

ABSTRACT. Investigations were conducted in Iowa over a 3-year period to compare several methods for evaluating the resistance of sorghum varieties and hybrids to infestation by the second brood of the European corn borer. Evaluation of the relative resistance to second-brood corn borer infestation exhibited within a group of sorghum varieties and hybrids of diverse parentage also was accomplished.

Application of egg masses to the underside of the top leaves of sorghum plants at the early to active pollen-shedding stage, followed by splitting the stem from the seed head to the top node after the surviving larvae were full grown, and counting the cavities in the peduncle area was determined to be an expedient method for evaluating the degree of infestation. Number of leaf-sheath lesions, number of internode cavities, and number of surviving larvae generally gave comparable, but less expedient evaluations of infestation.

The basic kafir and feterita varieties of sorghums exhibited low to moderately low levels of infestation in all tests. The variety Shantung Brown kaoliang showed low to moderate infestation throughout the 3-year period. Conversely, the basic milo varieties generally were among the more heavily infested entries in all tests. Infestation of the durra, shrock, and hegari varieties was heavy to moderately heavy. Hybrids derived from kafir and milo varieties generally exhibited a level of infestation intermediate to that observed for the Kafir and milo parent varieties.

Sorghum has been observed as a host of the European corn borer, Ostrinia nubilalis Hübner, in widely scattered parts of the world. It has been postulated that broomcorn was the source through which this insect

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4 The authors recognize the assistance given by D. B. Lucek in collecting data in 1957 and 1958.
was introduced into the United States and Canada (Smith 1920). Although
not a preferred host, broomcorn has been known to be commonly infested
in Europe (Thompson and Parker 1928). In the Orient, in Manchuria and
Korea (Chosen), Clark (1934) found 15 to 30% of the plants of grain sor
ghum infested. Sorghum in this area served as a source for extensive
collections of larvae for parasite rearing and distribution in the United
States. In Massachusetts, Hodgson (1928) reported that sorghums rarely
were infested by the first generation, and the number of second-generation
larvae was low on an infested-plant basis. According to his observations,
feeding on the grain was negligible and the reduction in yield was believed
to be slight. Milo, feterita, and hegari varieties yielded the most larvae
per infested plant, and kafir the least. Under single-generation condi-
tions in Michigan, egg masses, and later in the season infested plants
were found in sorghum and sudangrass (Dicke 1932). Painter and Weibel
(1951) reported on second-generation infestations in Kansas and described
the feeding habits of the larvae on the grain and stem. Most of the holes
in the stalk were found in the upper third of the plant, and stalk breakage
occurred mostly above the flag leaf and in or just below the head. Basing
their opinion on weight of larvae in November, they concluded that the
larvae thrived as well or better on the sorghum tested than on corn.

Records obtained in Iowa in recent years are in agreement with Hodg-
son (1928) and Painter and Weibel (1951) with respect to the economic
importance of the first generation on sorghum.

Newly hatched larvae of the first generation do some feeding in the
whorl, which results in small lesions on a few leaves, similar to the
early leaf injury on corn. Seldom have larvae of the first generation been
found to develop beyond the fifth instar.

In years of high moth populations of the second generation, substantial
infestations have developed in some grain-sorghum varieties and hybrids.
In view of the expansion of sorghum production and research in areas
where the European corn borer is an important pest, biological studies
were begun in 1957 to provide information on procedures for evaluating
resistance of genotypes of varying maturity which would be suitable for
evaluating lines in a sorghum-breeding program. The primary objective
was to find sorghum genotypes having resistance to second-generation
borer infestation.

**METHODS AND MATERIALS**

The sorghum seed was assembled from several sources and consisted
of representative types of grain, forage, and sweet varieties or hybrids.
The origin and parentage of many of the varieties and hybrids have been
discussed by Quinby et al. (1958). Most of the entries were tested for the
3-year period, 1958-60. In 1958 and 1959 single-row plots were planted
on each of two dates, the first late in May and the second about 10 days
later. In 1960 the tests consisted of a single planting in late May with
3-fold replication of each entry. Stands were thinned to 3 to 5 inches
between plants. In order to have the culms reasonably uniform in matur-
ity at the time of the application of egg masses, the delayed tillers were
removed.
Information available on the low rate of plant infestation and survival of larvae of the first generation on whorl-stage sorghum, and the incidence of substantial infestations during the second-generation period, indicated that, as with corn, exposure of the inflorescence was associated with increased establishment and survival of larvae. Preliminary tests under artificial infestation in 1957, conducted from the late-whorl to active pollen-shedding stages of growth, showed that reasonably stable and higher rates of infestation occurred from the time heads emerged from the flag leaf until active pollen shedding. Additional tests in 1960 confirmed these results.

Egg masses near hatching were pinned through the midrib under the top leaves at the early to active pollen-shedding stage. In 1958 two applications of two average masses, or a total of about 80 eggs, were made per culm. In 1959 and 1960 a single application of three masses, or a total of about 60 eggs, was made. The range in maturity represented among varieties and hybrids required egg applications from the first to third week in August. It was recognized that variability was introduced by applying egg masses over a period of time under varying weather conditions. However, it was deemed more essential to apply egg masses at a comparable stage of morphological development than at a constant environment.

Records on plant infestation were taken in October, after the surviving larvae were full grown. Criteria for determining the degree of infestation followed a pattern similar to that used for evaluating plant injury in corn (Dicke 1954, Guthrie et al. 1960). Figure 1A shows a typical feeding lesion on the leaf sheath and collar, which to a large extent was produced by the early larval instars. Typical cavities in the upper part of the stem (peduncle) and seed head, caused by late larval instars, are shown in Figure 1B. Externally visible feeding lesions at the base of the midrib and on the sheath of the top four leaves were counted. Then the culms were split from the seed head through the top four nodes, and the numbers of cavities and larvae in the peduncle and in the top three internodes were recorded.

EVALUATION OF VARIETIES AND HYBRIDS FOR RESISTANCE

Plant-infestation data obtained from 1958-60 for the evaluation of resistance of varieties and hybrids are summarized in Tables 1-3. Entries are arranged in sequence according to the total number of cavities observed.

The test in 1958 (summarized in Table 1) was based on a single sample of 35 culms for each genotype from the first planting and regarded primarily as a preliminary test, both for evaluation of resistance and comparison of methods. The data show a general trend for kafir varieties to be low in sheath lesions, culm cavities, and curviving larvae; whereas the milo varieties usually exhibited much higher infestation indices. For the entire test, 76% of the cavities observed occurred in the peduncle. Of the total surviving larvae, 63% were in the peduncle. When the number

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Unpublished notes.
### Table 1. Summary of sheath and culm infestation for 34 sorghum genotypes

Ankeny, Iowa, 1958.

<table>
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<th>Variety or hybrid</th>
<th>Sheath lesions</th>
<th>Number of larvae</th>
<th>Number of cavities</th>
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<td>Internode Peduncle</td>
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<tr>
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<tr>
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</tr>
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^a Total for a sample of 35 plants.
Table 2. Summary of sheath and culm second-brood corn borer infestation for 38 sorghum genotypes. Ankeny, Iowa, 1959.

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<thead>
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<th>Variety or hybrid</th>
<th>Mean sheath lesions</th>
<th>Number of larvae</th>
<th>Number of cavities</th>
<th>Total cavities mean</th>
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<td>Internode Peduncle</td>
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Mean 33.3 1.3 8.0 3.2 33.7 18.8

a Mean of two replicates.

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<th>Variety or hybrid</th>
<th>Mean sheath lesions&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Number of larvae</th>
<th>Number of cavities</th>
<th>Total cavities mean&lt;sup&gt;a&lt;/sup&gt;</th>
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<tbody>
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<tr>
<td>Westland</td>
<td>38.7</td>
<td>4</td>
<td>17</td>
<td>7</td>
</tr>
<tr>
<td>Rox</td>
<td>18.3</td>
<td>3</td>
<td>20</td>
<td>6</td>
</tr>
<tr>
<td>Tx 660</td>
<td>36.0</td>
<td>1</td>
<td>17</td>
<td>5</td>
</tr>
<tr>
<td>Redbine 66</td>
<td>49.7</td>
<td>2</td>
<td>20</td>
<td>5</td>
</tr>
<tr>
<td>Early Hegari</td>
<td>22.7</td>
<td>3</td>
<td>1</td>
<td>8</td>
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<tr>
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<td>43.7</td>
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<td>KS 603</td>
<td>40.3</td>
<td>3</td>
<td>18</td>
<td>9</td>
</tr>
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<td>18</td>
<td>5</td>
</tr>
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<td>KS 701</td>
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</tr>
<tr>
<td>KS 602</td>
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<td>1</td>
<td>18</td>
<td>7</td>
</tr>
<tr>
<td>Tx 620</td>
<td>26.7</td>
<td>1</td>
<td>18</td>
<td>8</td>
</tr>
<tr>
<td>Shant. Br. Kaol.</td>
<td>9.3</td>
<td>3</td>
<td>1</td>
<td>24</td>
</tr>
<tr>
<td>RS 610</td>
<td>38.0</td>
<td>1</td>
<td>28</td>
<td>3</td>
</tr>
<tr>
<td>Redbine 60</td>
<td>38.3</td>
<td>2</td>
<td>22</td>
<td>9</td>
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Table 3. (cont.)

<table>
<thead>
<tr>
<th>Variety or hybrid</th>
<th>Mean sheath lesions</th>
<th>Number of larvae</th>
<th>Number of cavities</th>
<th>Total cavities mean</th>
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<tr>
<td></td>
<td></td>
<td>Internode Peduncle</td>
<td>Internode Peduncle</td>
<td></td>
</tr>
<tr>
<td>Martin</td>
<td>44.7</td>
<td>10</td>
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<td>18</td>
</tr>
<tr>
<td>RS 650</td>
<td>38.7</td>
<td>4</td>
<td>34</td>
<td>14</td>
</tr>
<tr>
<td>Tex. Milo</td>
<td>30.7</td>
<td>6</td>
<td>26</td>
<td>11</td>
</tr>
<tr>
<td>RS 608</td>
<td>40.3</td>
<td>7</td>
<td>37</td>
<td>15</td>
</tr>
<tr>
<td>DeKalb E56a</td>
<td>50.0</td>
<td>8</td>
<td>31</td>
<td>16</td>
</tr>
<tr>
<td>Tx 7078</td>
<td>41.7</td>
<td>8</td>
<td>45</td>
<td>13</td>
</tr>
<tr>
<td>RS 661</td>
<td>48.7</td>
<td>3</td>
<td>45</td>
<td>14</td>
</tr>
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<td>Sooner</td>
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<td>20</td>
<td>23</td>
</tr>
<tr>
<td>Combine Hegari</td>
<td>39.3</td>
<td>3</td>
<td>40</td>
<td>15</td>
</tr>
<tr>
<td>Tx '04</td>
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<td>3</td>
<td>49</td>
<td>13</td>
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<tr>
<td>Plainsman</td>
<td>51.0</td>
<td>8</td>
<td>45</td>
<td>28</td>
</tr>
<tr>
<td>N. Dak. M. S. 323</td>
<td>33.0</td>
<td>21</td>
<td>22</td>
<td>44</td>
</tr>
<tr>
<td>Tx 07</td>
<td>46.3</td>
<td>8</td>
<td>48</td>
<td>17</td>
</tr>
<tr>
<td>Res. D. D. Y. Milo</td>
<td>30.0</td>
<td>9</td>
<td>22</td>
<td>22</td>
</tr>
<tr>
<td>Dwf. Wh. Durra</td>
<td>27.3</td>
<td>8</td>
<td>10</td>
<td>33</td>
</tr>
<tr>
<td>Caprock</td>
<td>54.3</td>
<td>12</td>
<td>67</td>
<td>22</td>
</tr>
<tr>
<td>N. Dak. M. S. 405</td>
<td>41.7</td>
<td>17</td>
<td>38</td>
<td>42</td>
</tr>
<tr>
<td>D. D. Y. Sooner</td>
<td>41.0</td>
<td>11</td>
<td>12</td>
<td>39</td>
</tr>
<tr>
<td>Mean</td>
<td>29.8</td>
<td>4.4</td>
<td>19.8</td>
<td>12.7</td>
</tr>
</tbody>
</table>

*Mean number of peduncle and stalk cavities for three replicates.*
of eggs placed on the plants in relation to the number of cavities observed was considered, the recovery of full-grown larvae appeared to be low.

In 1959 the test sorghums were grown in two adjoining randomized blocks, planted on May 27 and June 4. There was little difference in maturity in the two blocks by pollen-shedding time. The egg masses were applied between July 31 and August 16 on the first and between July 31 and August 20 on the second planting. Thirty culms of each genotype were infested in each block. Since the varieties and hybrids in the two blocks were similar in maturity, results from the two blocks were treated as replicates in the variance analysis. Data obtained in 1959 for the different infestation indices are shown in Table 2. When means for the various infestation criteria were compared with those from the 1958 test, it was apparent that the level of infestation was higher in 1959, even though the number of eggs applied was somewhat less. Means for the 1959 test showed that the peduncles contained 91% of the cavities and 86% of the larvae. With a high percentage of the culm cavities located in the peduncle, where lodging stress is most pronounced, breakage in the peduncle area was high for the milo varieties. Figure 1B illustrates the most common type of stem breakage. Frequently the heads had fallen to the ground. Differences in the susceptibility of certain entries in each of the 2 years were evident. Reliance exhibited a markedly higher number of total cavities in 1958 than in 1959. The hybrids RS 590, Tx 611, Tx 620, and RS 630 were low in total cavities in 1958, but exhibited moderate to high infestations in 1959. The kafir varieties were most prevalent among the lightly infested entries in 1959, and the milo varieties again were most heavily infested. A low infestation was observed for feterita in both seasons.

Results for the 1960 tests are summarized in Table 3. The sample consisted of 20 culms from each of three replicates. Means for the entire test showed that the peduncles contained 82% of the larvae and 75% of the cavities. On a per-plant basis the infestation was considerably higher in 1960 than in the previous 2 years. This result was consistent with the results from nearby tests on inbred lines of corn, an indication of a higher larval survival or vitality index in 1960. Kafir varieties again predominated at the resistant end, and milo varieties at the susceptible end of the infestation indices. An analysis of variance of the total number of cavities per plot, summarized in Table 4, indicated there were highly significant differences among the genotypes tested. The great similarity of infestation for entries common to the 1959 and 1960 tests is substantiated by a significant r value of 0.881 (31df) for the association of total cavities in the 2 seasons.

Several conclusions may be drawn from observations of the evaluations obtained over the 3-year period. The basic kafir varieties (Blackhull Kafir, Pink Kafir, Red Kafir, etc.) were consistently low to moderately low for the various criteria of infestation. Conversely, the basic milo varieties (Double Dwarf Yellow Milo, Texas Milo, Sooner Milo, etc.) generally were among the more heavily infested entries in all tests. Feterita, another basic sorghum variety, consistently exhibited low infestation ratings in all tests, and Shantung Brown kaoliang showed low to moderate infestation throughout the 3-year period. Infestation readings for the durra, shrock, and hegari varieties usually were heavy to moder-
Figure 1. Typical external and internal corn borer injury in sorghum.

A. Leaf sheath injury resulting in leaf breakage.

B. Cavity in peduncle and seed head resulting in head breakage.
Table 4. Summary of analysis of variance for comparisons of infestation as measured by cavities in sorghum varieties and hybrids.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom</th>
<th>Mean square</th>
<th>F value ( ^a )</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>1959</td>
<td>1960</td>
</tr>
<tr>
<td>Genotype</td>
<td>37</td>
<td>353.1</td>
<td>349.6</td>
</tr>
<tr>
<td>Blocks</td>
<td>1</td>
<td>31.6</td>
<td>23.5</td>
</tr>
<tr>
<td>Error</td>
<td>37</td>
<td>20.1</td>
<td>38.6</td>
</tr>
<tr>
<td>Total</td>
<td>75</td>
<td></td>
<td>137</td>
</tr>
</tbody>
</table>

\( ^a \) ** Exceeds the 1\% level of probability

\( ^{ns} \) Nonsignificant

atly heavy for all tests. The other varieties or hybrids have most al- ways been derived from combinations of the basic sorghum types, largely kafir x milo combinations. As might be expected, infestation observed among kafir x milo combinations generally was intermediate to the levels of infestation exhibited by the kafir and milo parent varieties. The in- festation and relative resistance rankings from season to season were somewhat more variable among this intermediate group than among the basic sorghum varieties. The respective low and high infestation ratings observed in this investigation for the kafir and milo varieties were in agreement with results reported by Hodgson (1928). Levels of infesta- tion obtained for other basic sorghum varieties were not in complete accord with Hodgson's ratings, particularly for the feterita variety.

INFESTATION AND RESISTANCE INDICES

The evaluation of relative resistance among varieties and hybrids was arrived at by observing the pattern of larval feeding on the plant. The early larval instars feed on structures associated with the inflorescence, premature grain, or the leaf sheath. The late instars burrow primarily in the stem (peduncle), and very often just below or in the seed head, as shown by the high percentage of cavities and larvae found in the peduncle.

Correlation coefficients for the relationship between the different infestation indices are given in Table 5. In each of the 3 years highly significant \( r \) values were obtained for the association of sheath lesions with total cavities, sheath lesions with peduncle cavities, and between
Table 5. Summary of correlation coefficients among criteria used to evaluate the degree of second-brood corn borer infestation.

<table>
<thead>
<tr>
<th>Criteria</th>
<th>1958a</th>
<th>1959</th>
<th>1960</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sheath lesions vs. total culm cavities</td>
<td>0.900**</td>
<td>0.595**</td>
<td>0.696**</td>
</tr>
<tr>
<td>Sheath lesions vs. peduncle cavities</td>
<td>.941**</td>
<td>.667**</td>
<td>.764**</td>
</tr>
<tr>
<td>Total culm cavities vs. peduncle cavities</td>
<td>.960**</td>
<td>.985**</td>
<td>.970**</td>
</tr>
</tbody>
</table>

** Exceeds the 1% level of probability

total cavities and peduncle cavities. The different r values were moderately to extremely high in all tests, an indication that any one of the indices should give a reliable index of the total infestation.

Because of the disappearance of many of the larvae from cavities, the number of surviving larvae would be a poor index of relative resistance. Sheath lesions may be counted readily but sometimes are difficult to identify after the leaves are dried and broken. Studies on the pattern of plant infestation as well as factors involved in taking records showed that the most expedient and practical method of obtaining an infestation index for evaluating resistance in sorghums was to split the stem from the seed head to the top node and count the cavities in the peduncle area.

REFERENCES

ABSTRACT. This paper is a taxonomic revision of the genus Cenchrus (Gramineae), together with descriptions of species, synonyms, illustrations and distribution maps.

A study of geographic variation in three species is based on population samples from the southern United States and Mexico. Data thus obtained provide evidence for merging the widely distributed C. pauciflorus Benth. and the recently described C. parviceps Shinners with C. incertus M. C. Curtis.

Cytological studies and chromosome counts were made on ten species. The chromosome numbers of C. biflorus Roxb., C. gracillimus Nash, C. palmeri Vasey, and C. pilosus H. B. K., all previously unknown, were determined as N=17.

Leaf anatomy and morphology in the genus are compared with those of other members of the panicoid grass tribe. Suggestions are made concerning the possible phylogeny, intergeneric relationships, and origin of the genus.

INTRODUCTION

The genus Cenchrus (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 cohabitants. A few species, with less spiny inflorescences and more luxuriant 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.

1 Journal Paper No. J-4459 of the Iowa Agricultural and Home Economics Experiment Station, Ames, Iowa. Project No. 1136. The facilities of the Iowa State Herbarium, supported by the Industrial Science Research Institute, were used in the preparation of this paper.

2 Present address: Simpson College, Indianola, Iowa.
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 delimit more accurately the genus Cenchrus and its species and to present a more nearly complete picture of their natural variation and geographic distribution. Recent cytological and morphological data are correlated with traditional taxonomic criteria and suggestions are made regarding possible intra and extra-generic relationships.

MATERIALS AND METHODS

Field collections and herbarium specimens provided the bulk of material used in this study. I wish to express my sincere appreciation to the curators of the following herbaria for their loan of material:

F Chicago Natural History Museum
DAO Canada, Department of Agriculture, Ottawa
ISC Iowa State University, Ames
MA Instituto "Antonio Jose Cavanilles," Madrid
MO Missouri Botanical Garden
SMU Southern Methodist University
NY New York Botanical Garden
SUI State University of Iowa
UC University of California, Berkeley
AHUC University of California, Davis
US United States National Herbarium
TEX University of Texas

Additional herbarium specimens were examined at the University of Colorado and at the Rocky Mountain Herbarium.

During the summer of 1960, field collections and population studies were made in Missouri, Kansas, Oklahoma, Texas, New Mexico, Colorado, Wyoming, Nebraska, and Iowa. Population samples and specimens were also obtained in late summer of 1961 in Oklahoma, Texas, Louisiana, Mississippi, and Alabama. Specimens for population studies and material for seed were air-dried and placed in special envelopes.

The measurement of small structures such as spikelets and florets was facilitated by the use of an ocular micrometer fitted to a wide-field binocular microscope. The internode length represents a measure of the average distance between burs in a two-centimeter length of the central region of the inflorescence.

Leaf epidermal studies were based on dried material from herbarium collections. The leaves were first treated with a special softening agent (Pohl 1954), after which the upper epidermis and mesophyll were removed with a razor blade. The remaining lower epidermis was dehydrated in absolute alcohol, placed abaxial side up on a microscope slide and made permanent with the addition of diaphane and a cover slip.
Chromosome counts were obtained from pollen mother cells of plants grown from seed. All plants were grown under uniform greenhouse conditions in six-inch pots containing a mixture of three-fourths sand and one-fourth soil. Voucher specimens for all counts obtained by me are deposited in the herbarium of Iowa State University.

Drawings of chromosomes, leaf cross sections and epidermal preparations were made with a Zeiss Microscope Drawing Apparatus. Those of spikelets, florets and caryopses were obtained by the use of a camera lucida attached to a stereo binocular microscope.

Distribution maps indicate the locations of specimens examined by me. A selected list of specimens is included following the discussion of each species. The complete list is deposited in the herbarium of Iowa State University.

In the treatment of synonyms, a method suggested by Isely has been followed. Criteria used for the synonymy are listed below:

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.

The basis for the inclusion of each synonym is indicated by one or more of the above numbers in parentheses after the name. This procedure is also used for the excluded and unidentified names in the appendix.

MORPHOLOGY

Cenchrus 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 one or more spikelets are enclosed.

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 Cenchrus. 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 Cenchrus, Sohns (1955) found that the spikelets of Cenchrus 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 branches have become sterile. Sohns (1955), further suggested that the prolonged awn-like

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1 Isely, Duane, Iowa State University, Ames, Iowa. Personal communication, 1962.
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 *Cenchrus*. However, this feature (prolonged bristle) occurs widely in both genera and is highly variable in such species as *C. caliculatus* and *C. multiflorus*. It therefore does not appear to be a useful taxonomic trait except possibly on an interspecific basis.

Many species of *Cenchrus* have burs in which the spines are dark purple, probably because of the presence of anthocyanin pigments. This character I have observed to be highly variable, even in inflorescences of the same plant, and therefore is 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" (*C. 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 *C. 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 burs 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 soldiers' 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 that solid stems in such forms as *C. pauciflorus* 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 (1895) 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 *Cenchrus* (Fig. 1) illustrate the panicoid features common to members of the genus. These drawings also show that the guard cells are typically rhombic, and the siliceous cells are all "dumbbell or cross-shaped." Bicellular hairs of all species of *Cenchrus* studied had typically long terminal cells. Size of the stomata appears to be fairly uniform in the four species illustrated.
Figure 1. Leaf anatomy in *Cenchrus*.

A. Leaf cross section of *C. longispinus*, (DeLisle 240).
B - E. Lower leaf epidermis.
B. *C. setigerus* (ISC 216333); C. *C. longispinus* (ISC 141746);
D. *C. elymoides* (Perry 2616; E. *C. echinatus* (ISC 140161).
A cross-section of the leaf of *C. longispinus* (Fig.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 described 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 subfamily Eragrostoideae.

I myself made no morphological studies on embryos of *Cenchrus*, 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 scutellum and the coleorhiza. The embryonic leaf of this species contains numerous vascular bundles, and the leaf margins slightly overlap.

**FLORAL BIOLOGY**

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" lacks an ovary but usually produces functional stamens with apparently viable pollen, based on staining results with lactophenol and cotton-blue. In 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.

All twelve species studied during the cytological work were markedly protogynous. The stigmas become exserted 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 exsertion, 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 not completely known. Anthesis of the stamens in fertile florets occurs about two days following exsertion 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 are receptive.

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). I also failed to find 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 C. ciliaris and C. setigerus (Fisher, Bashaw and 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 and Emery (1958) for C. pauciflorus and C. myosuroides.

Tests of germination indicate that the seeds of all species of Cenchrus require a dormancy of about five or six months. I have tried several methods to break the dormancy of seeds harvested in the fall, but most of them 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 C. biflorus.

CYTOLOGY

Using pollen mother cell smears, cytological studies were made on ten species of Cenchrus. The results of these chromosome counts, together with those made by other workers, are presented in Table 1. Reports published by many early authors make no mention of voucher specimens. For this reason, it is not always possible to attest to the validity of their counts with reference to certain species. Meiotic figures of those species counted by me are shown in Figure 2. Detailed cytological discussions are 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 of species 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=0 or X=10. Two exceptions to this old-world group include C. prieurii, reputedly having a basic number of X=17, and a recent count I obtained suggesting a basic number of X=17 for C. biflorus.

Avdulov (1931) claimed 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 in a diploid form, followed by immediate reduplication. According to Nunez (1952) the basic number of Cenchrus is X=17. Brown (1948, 1950) obtained a basic number of X=9 in two species, i.e., C. myosuroides and C. longispinus. Nunez attributes the secondary basic number of X=17 to factors of intragenic differentiation. Stebbins and Love (1941) reported a similar condition in the aneuploid genus Stipa, suggesting that the 2n=34 number in this genus could have been derived
Table 1. Summary of chromosome numbers reported in the genus *Cenchrus*.

<table>
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<tr>
<th>Species</th>
<th>Somatic number</th>
<th>Reference</th>
</tr>
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<tbody>
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<td><em>C. biflorus</em> Roxb.</td>
<td>34 present author.</td>
<td>present author.</td>
</tr>
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<td><em>C. brownii</em> R. &amp; S.</td>
<td>34 Avdulov (1931), present author.</td>
<td>Avdulov (1931)</td>
</tr>
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<td><em>C. echinatus</em> L.</td>
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</tr>
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<td>34 present author.</td>
<td>present author.</td>
</tr>
<tr>
<td><em>C. palmeri</em> Vasey</td>
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</tr>
<tr>
<td><em>C. pilosus</em> H.B.K.</td>
<td>34 present author.</td>
<td>present author.</td>
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<tr>
<td><em>C. tribuloides</em> L.</td>
<td>34 Avdulov (1931), Hunter (1934), present author.</td>
<td>Avdulov (1931), Hunter (1934), present author.</td>
</tr>
</tbody>
</table>

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*a* Gould, F.W., College Station, Texas. Data on chromosome numbers of *Cenchrus*. Private communication. 1962.
Figure 2. Meiotic chromosomes in the genus Cenchrus.

A, B. C. brownii (Weatherwax 3338)
C. C. echinatus (Pohl 8105)
D. C. echinatus (Weatherwax 3336)
E. C. pilosus (Weatherwax 3337)
F. C. longispinus (DeLisle 362)
G. C. longispinus (DeLisle 429)
H. C. gracillimus (Birdsey 677)
I. C. palmeri (Weatherwax 3339)
J, K. C. incertus (Pohl 8182)
L. C. tribuloides (Fairbrothers 486)
M. C. setigerus (USPI 216374)
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, by Tateoka, and by myself, however, do not substantiate those made by Brown, but rather indicate that the basic number, at least of the American species of Cenchrus, is 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 to fusion and loss of part of a chromosome containing a centromere. He further suggests that this characteristic change is because 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. I have not obtained chromosome numbers for C. myosuroides, but Avdulov (1931) and Gould (1962, see footnote, Table 1) reported a number of 2n=70. Brown (1950, 1951), on the other hand, reported 2n=54 for this species. 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 Cenchrus and in Pennisetum.

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 expressed as coalescence of inflorescence branches. The trends in such a fusion and subsequent reduction in number of inflorescence branches may be traced in various genera in the Paniceae. For example, members of the subgenus Paurochetium of the genus Panicum have spikelets subtended by one or a few very fine bristles. In Setaria, where there are more numerous bristles, disarticulation occurs between the bristles and the spikelets. In Pennisetum, the accumulation of bristles becomes more pronounced, but there is little evidence of fusion. In Cenchrus, the most highly specialized members of the genus appear to have almost complete fusion of the branches into a compact bur.

Bews (1929) also suggested a number of genera in the Paniceae which 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*. According to Reeder (1960) *Anthephora* appears to be closely related to *Cenchrus* on the basis of its floret characters. The florets of *Pennisetum* are also morphologically quite similar to those of *Cenchrus*.

There has been considerable confusion as to the actual generic limits of *Cenchrus* 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 in the other, depending upon the interpretation of the worker. In recent years there has been a tendency to place in the genus *Cenchrus* all those species that 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 *Cenchrus*, 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 *Cenchrus*. It is quite possible that further morphological and anatomical studies may indicate the need for a revision and possible merging of the two genera. The present treatment of the genus, however, is based in large part on traditional criteria with some refinement.

**PHYLOGENY**

To arrive at a somewhat more objective idea of the possible phylogenetic relationships of species within the genus *Cenchrus*, 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, a specialization for a given trait. The following ten characteristics, each designated by a letter, were chosen for twenty species of *Cenchrus*.

A. **Prolonged Bristle**: Absence of this feature is probably an advancement. Many species of *Cenchrus* 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 that 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 of specialization of *Cenchrus* is apparently from terete to flattened spines. This may usually be correlated 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 *Cenchrus* 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, whorls of bristles tend to become fewer in number and may be completely lost in some species.

I. Spine Number: There appears to be a tendency in the more specialized species of *Cenchrus* toward a reduction in total number of spines per bur. There are, however, a few exceptions in which decrease in number of burs per inflorescence is accompanied by an increase in the 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 *Cenchrus*, 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 *Cenchrus* 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 *Cenchrus* are shown in Table 2. By transposing these index values on a series of concentric circles (Hardin 1957), it is possible to graphically 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 (Fig. 3) by its position relative to the concentric circles. Those taxa showing the most apparent specialization in several traits occupy positions on the graph farthest 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 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. Intermediate characters 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.

Figure 3 shows that the species of *Cenchrus* fall into two basic groups. Those in the upper, and presumably more specialized group, include
Figure 3. Suggested phylogenetic relationships of twenty species of *Cenchrus*. 
<table>
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<th>Species</th>
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<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
<th>F</th>
<th>G</th>
<th>H</th>
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<th>J</th>
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</table>
C. 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 with the exception of C. mitis of East Africa, all are native to the western hemisphere. Cenchrus pilosus, brownii, mitis, and echinatus appear somewhat less specialized 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 C. mitis, have rather dense inflorescences with numerous burs. C. echinatus probably represents a derived tetraploid from the basic number of X=17. Two perennial species, C. gracillimus and C. distichophyllus, show considerable specialization 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. Cenchrus platyacanthus, however, 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 C. myosuroides from Central America, all are restricted to Africa, India, Southeast Asia, or 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 lends 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 surmises that the Paniceae alone among 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. The existence of large numbers of apomictic species, according to Hartley, suggests that the Paniceae 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, if it is assumed that polyploidy provides the best genetic environment for apomixis (Stebbins 1950). Stebbins places differentiation of the grass genera during late Cretaceous. However, Bor (1960) contends that there is little or no evidence that would support these ideas concerning apomixis and time of grass development.

A second hypothesis, that of origin of Cenchrus in the Afro-Asian regions, is suggested by the preponderance of primitive species in those areas. Several species of Cenchrus 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 in new areas than their diploid ancestors 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 that 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 subequal, 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 none or abortive; stamens 3, 1—3 mm long; styles 2, 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 antrosely or retrosely 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-Linnaean 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 C. 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 panicis," 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 in Stapf and 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 Cenchrus

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

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

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. C. brownii

5. Bristles at least twice as long as the body of the bur, the burs densely crowded in the inflorescence. 3. C. pilosus

6. Leaves narrow, usually less than 3 mm wide; plants perennial.

7. 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. C. echinatus

2. Bur consisting of several whorls of flattened spines, the spines emerging at irregular intervals throughout the body of the bur.

6. Leaves narrow, usually less than 3 mm wide; plants perennial.
7. Leaf blades involute, crowded and markedly distichous, about 2 cm long.  
5. *C. distichophyllus*

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

6. Leaves wider, 3m 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.  
7. *C. longispinus*

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

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—1.4 mm long.  
9. *C. platyacanthus*

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

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

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

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—3 meters tall, leaves broad, to 20 mm, rachis velvety-pubescent.  
12. *C. caliculatus*

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 8 mm wide, bur about 2 mm wide, spine-margins densely ciliate-pubescent. 14. C. ciliaris

15. Plants from 1-2 meters tall, leaves 8-20 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 2.5-4.5 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 0.9-2.2 mm long, glabrous. 18. C. biflorus

18. Spines antrorsely barbed. 20

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

20. Spines short, 2-4 mm long, margins glabrous. 20. C. setigerus

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

Cenchrus brownii Roem. and Schult. Syst. Veg. 2:258. (1817).
(Based on C. inflexus R. Br.)
Cenchrus inflexus R. Br. Prodr. 1:195. (1810) (Non C. inflexus Poir. 1804) (Type in BM, fragment of type in US)
Cenchrus viridis Spreng. Syst. 1:301. (1825) (Type in B, fragment of type in US) (1)


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

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

Cenchrus echinatus Steud. ex Doell in Mart. Fl. Bras. 2, 2:309. (1877) (Non C. echinatus L.) (4)

Cenchrus rigidus Willd. ex Doell in Mart. Fl. Bras. 2, 2:310. (1877) (A herbarium name given as a synonym of C. 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; 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**

*Cenchrus brownii* has many morphological affinities with *C. echinatus* L., but differs from the latter species in having smaller, globose burs with narrower peduncles, and a more densely compact inflorescence. The tawny color of the mature burs of *C. brownii*, as contrasted with the purple-tipped spines of *C. echinatus*, may often aid in delimiting these two taxa. In *C. brownii* the outer bristles are more numerous and usually surpass the inner spines, while in *C. 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.

*Cenchrus brownii* R. and 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. 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. and S. Doell, in Martius (1877), apparently based *C. viridis* var. *macrocephalus* on a form with slightly longer bristles. However, Doell’s description of this variety 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. and S., (reported as *C. viridis* Spreng.). The 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 *C. brownii* R. and S.**

<table>
<thead>
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<th>Chromosome No.</th>
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<tr>
<td>Weatherwax no. 3338</td>
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</tr>
<tr>
<td>DeLisle voucher no. 471</td>
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</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 United States. 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).

**BRASIL:** Miras (MO); Vicinity of Maceio, Alagoas, A. Chase 7843, Dec. 5, 1924 (MO).

**BRITISH GUIANA:** Upper Demeara 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).

**CAROLINES:** Saipan, R. Kanehira 961, 1930 (NY); Truk, F.R. Fosberg 24412, May 23, 1946 (NY).
Figure 4. Geographic distribution of *Cenchrus Brownii*
2. *Cenchrus echinatus* (Figure 6, F–J; map, Figure 5)

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

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


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

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

*Cenchrus echinatus* A. Rich. Tent. Fl. Abyss. 2:389. (1847) (C. echinatus A. Rich. of various authors, Richard attributes this species to L.) (2)


*Cenchrus hexaflorus* Blanco. Fl. Filip. Ed. I. 36. (1877) (4)
TAXONOMY OF THE GENUS CENCHRUS

Cenchrus brevisetus Fourn. Mex. Pl. 2:50. (1886) (Holotype in P, fragment of type in US) (1)
Cenchrus echinatus var. morisonii O. Ktze. Rev. Gen. 2:765. (1891) (2)
Cenchrus brevisetus Scribn. ex Millsp. Field Mus. Bot. Ser. II. 26. (1900) (Based on C. brevisetus Fourn.) (2)
Cenchrus insularis Scribn. ex Millsp. Field Mus. Bot. Ser. II. 26. (1900) (Holotype in F) (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 that 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 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 subglabrous 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. brevisetum* 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. I also obtained a count of 2n=68 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 I examined.

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

<table>
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<tr>
<th>Collection</th>
<th>Location</th>
<th>Chromosome number</th>
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<tbody>
<tr>
<td>Pohl no. 8105</td>
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</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); Carrients prov., W. Lossen 548 (UC).
AUSTRALIA: Arnhem land, R. L. Specht 149 (US); Strand-Townsville, D. A. Goy 357 (MO).
BRASIL: Brasilia, C. Orth 861 (MO); Rio Grande do Sul, A. A. Beetle 1487 (UC, AHUC).
BRITISH GUIANA: A. S. Hitchcock 16741 (NY, UC, MO).
BRITISH HONDURAS: Stann Creek, W. A. Schipp 893 (NY, UC, MO).
BOLIVIA: Dept. Santa Cruz, Buena Vista, J. Steinbach 5576 (NY, MO).
CHILE: Azapa, E. Werdermann 703 (NY, MO).
COLUMBIA: Santa Marta, H. H. Smith 159 (MO); Boca Grande near Cartagena, E. P. Killip and A. C. Smith 14096 (NY, US).
ECUADOR: Cobundo 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, P. Jorgensen 3532 (NY, MO).
UNITED STATES: East Brewton, Alabama, D.J. Banks 775 (ISC);
Tucson, Arizona, J.J. Thornber 2140 (DAO, SUI); Imperial Co., Calif.,
D.W. Ragsdale 21 (AHUC); Washington, D.C., W.P. Conant, 1884 (MO);
Jacksonville, Florida, A.H. Curtiss 5152 (F, UC, ISC); Lake Co.,
Florida, G.V. Nash 189 (UC, MO); Waycross, Georgia, D.J. Banks 980
(ISC); Oahu, Hawaii, A.S. Hitchcock 14068 (NY, UC, US, 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. Silveus 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);
WEST INDIES: Bahamas, P. Wilson 7350 (NY); Cuba, Distr. of Cien-
fuegos, 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. Cenchrus pilosus (Figure 6, K—O; map, Figure 7)

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

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

_Cenchrus 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 antorserly 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 3.0—6.0 mm long, 3 to 5-nerved;
Figure 6. *Cenchrus brownii*, *Cenchrus echinatus*, and *Cenchrus pilosus*.

A—E. *Cenchrus brownii* (Weatherwax 3338); A. spikelet, B. floret, C. caryopsis, D. bur, E. inflorescence
F—J. *Cenchrus echinatus* (DeLisle 662); F. inflorescence, G. bur, H. spikelet, I. floret, J. caryopsis.
K—O. *Cenchrus pilosus* (Svenson 11298); K. Bur, L. spikelet, M. caryopsis, N. floret, O. inflorescence
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 C. mitis, the latter species having bristles only slightly surpassing the inner spines in length. The peduncle of C. pilosus is densely ciliate-pubescent in contrast to that of C. mitis which is scabrous to only short-pubescent. The density of the inflorescence of C. pilosus, with internode lengths of 1.0—2.5 mm as contrasted with 2.8—5.0 mm for C. mitis, also serves as a means of distinguishing these two taxa.

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

Cytology

Results of my cytological investigations on C. pilosus are shown in Table 6. There have been no counts reported by other authors for this species.

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Distribution

Cenchrus pilosus 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).
GUATEMALA: Department Santa Rosa, P.C. Standley 77737, Nov. 21, 1940 (F); near ruins of Quirigua, Weatherwax 1590, March 1, 1932 (US).
NICARAGUA: Chichigalpa, P.C. Standley 11322, July 1947 (F).
NICARAGUA: Jinotepe, A.S. Htchcock 8667, Nov. 3-7, 1911 (US); Managua, Bro. A. Garnier 12 and 827 (US).
PERU: Dept. of Lima, O. Haught F-76, 1928 (F); Dept. Piura, Prov. Paita, O.B. Horton 11591, June 9, 1942 (F, MO, UC).
VENEZUELA: Cubaqua Island, F. Elmore Q4, April 14, 1939 (F); Llanos de Nuva Barcellona, Bonpland (P) (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. Cenchrus mitis (Figure 9, A—E; map, Figure 7)

*Cenchrus 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; bur 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 antrorsely 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 their apparent centers of distribution are 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 *C. mitis*, any notions concerning its evolution or place of origin may be conjectural.

*Cenchrus mitis* is based on specimens collected by Peters on Querimba [Kerimba] Island, Portuguese East Africa. I have not examined the isotype at Kew. Andersson's original description and the more recent treatment by Stapf and Hubbard (1934) leave little 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 EAST AFRICA: Changamwe, 14 mi. from Mombasa, E.A. Mearns 2155, Nov. 21-30, 1909 (US).

DUTCH EAST 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).

5. **Cenchrus distichophyllus** (Figure 9, J—O; map, Figure 8)

*Cenchrus distichophyllus* Griseb. Cat. Pl. Cuba 234. (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 minute rim of hairs, less than 0.5 mm long; blades glabrous, strongly inrolled, tapering to a sharp point, 2.6—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,
Figure 7. Geographic distribution of *Cenchrus pilosus* and *C. mitis*. 
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 me. 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 I have seen indicate that this taxon is endemic to the Pinar del Rio province of Western Cuba, occurring in the sandy pinelands 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. *Cenchrus gracillimus* (Figure 9, F—I; map, Figure 8)

(Holotype in NY) (1)

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, 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 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 my count, shown in Table 7, no chromosome numbers have been reported for this species.

Table 7. Chromosome count from pollen mother cells of *Cenchrus 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
*Cenchrus gracillimus* occurs in sandy soil of the open pine woods of Georgia, Alabama, Florida, and the West Indies.

Selected specimens examined
BAHAMAS: Fortune Islands, A.S. Hitchcock, Nov. 1880 (MO).
Figure 8. Geographic distribution of Cenchrus gracillimus and Cenchrus distichophyllus.


JAMAICA: St. Elizabeth, G. R. Proctor 7748, March 14, 1953 (US); Southern Manchester, Wm. Harris 12690, Nov. 20, 1917 (US, MO).


FLORIDA: Miami, A. S. Hitchcock 617, March 1903 (F, US, UC, MO); Miami, near subtropical lab., A. Chase 3847, Sept. 6, 1907 (US, ISC); 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); Lake County, Florida, G. V. Nash 1766 Lake County, Florida, Nash 288, April 1-15, 1894 (DAO, UC); Lake County, Florida, Nash 188, 1894 (NY) (Lectotype); Orange County, Florida, J. K. Small, July 1894 (F); Marion County, Florida, R. L. Wilbur, G. L. Webster 2669, Aug. 17, 1950 (SMU); John's Pass, S. M. Tracy 7181, May 28, 1901 (F, ISC, US, MO).

GEORGIA: McIntosh County, W. H. Duncan, June 26, 1956 (ISC).

7. Cenchrus longispinus (Figure 11, A — E; map, Figure 10)

Cenchrus longispinus (Hackel in Kneucker) Fern. Rhodora 45:388. (1943) (Type in ISC) (1)
Figure 9. *Cenchrus mitis*, *C. gracillimus*, and *C. distichophyllus*.

A—E. *Cenchrus mitis* (Hitchcock 24410); A. inflorescence, B. bur, C. spikelet, D. floret, E. caryopsis.

F—I. *Cenchrus gracillimus* (from the type, Nash 188); F. inflorescence, G. spikelet, H. caryopsis, I. floret.

J—O. *Cenchrus distichophyllus* (from the type, Wright 3475); J. floret, K. spikelet, L. caryopsis, M. bur, N. inflorescence, O. portion of culm.
Nastus carolinianus (Walt.) Lunell. Amer. Midl. Nat. 4:214. (1915) (Based on C. carolinianus Walt.) (2)

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 a 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 cm 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. C. 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 C. longispinus, C. tribuloides, and C. incertus, a number of characters are shown in Table 8. The data shown in the table represent measurements from several hundred collections each of C. longispinus and C. incertus, and from 90 collections of C. tribuloides.
Table 8. Comparison of some morphological characters of _C. incertus_, _C. longispinus_, and _C. tribuloides_.

<table>
<thead>
<tr>
<th>Character</th>
<th><em>C. longispinus</em></th>
<th><em>C. incertus</em></th>
<th><em>C. tribuloides</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Floret length</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>in mm</td>
<td><strong>R</strong>ₐ</td>
<td><strong>M</strong> emo</td>
<td><strong>b</strong></td>
</tr>
<tr>
<td></td>
<td>5.8—7.6</td>
<td>3.4—5.8</td>
<td>6.8—8.7</td>
</tr>
<tr>
<td>Floret width</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>in mm</td>
<td><strong>R</strong></td>
<td><strong>M</strong></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2.1—3.3</td>
<td>1.0—2.2</td>
<td>2.2—3.5</td>
</tr>
<tr>
<td>Bur width</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>in mm</td>
<td><strong>R</strong></td>
<td><strong>M</strong></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3.5—6.0</td>
<td>2.5—5.0</td>
<td>4.0—8.0</td>
</tr>
<tr>
<td>Spine length</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>in mm</td>
<td><strong>R</strong></td>
<td><strong>M</strong></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3.5—7.0</td>
<td>2.0—5.8</td>
<td>4.1—8.0</td>
</tr>
<tr>
<td>Spine width</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>in mm</td>
<td><strong>R</strong></td>
<td><strong>M</strong></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.7—1.4</td>
<td>0.7—2.0</td>
<td>1.2—3.0</td>
</tr>
<tr>
<td>Fruit width</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>in mm</td>
<td><strong>R</strong></td>
<td><strong>M</strong></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1.5—2.6</td>
<td>1.0—2.0</td>
<td>2.2—3.1</td>
</tr>
<tr>
<td>Spine number</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>R</strong></td>
<td><strong>M</strong></td>
<td></td>
</tr>
<tr>
<td></td>
<td>45—75</td>
<td>8—40</td>
<td>15—43</td>
</tr>
<tr>
<td>Pubescence, bur</td>
<td>medium</td>
<td>short to medium</td>
<td>long, dense</td>
</tr>
</tbody>
</table>

---

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 latter 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 \textit{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 tend to approach \textit{C. longispinus}, but in all other features these plants can readily be referred to \textit{C. incertus}. These forms will be discussed in the section dealing with \textit{C. incertus}.

The first valid name applied to \textit{C. longispinus} was apparently that of \textit{C. echinatus} forma \textit{longispina} by Hackel in Kneucker (1903). Previous to that time the species had erroneously been identified either as \textit{C. tribuloides} L., or \textit{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, \textit{Nastus}, based on Walter's \textit{C. carolinianus}, and retained Walter's species as the type of the genus. Although I have not examined the type of \textit{Nastus}, it is certain from Lunell's description, and his citation of specimens from North Dakota, that he was referring to \textit{C. longispinus}, since no other species of \textit{Cenchrus} occurs in that region.

Fernald (1943) elevated Hackel's form to specific status, naming it \textit{C. longispinus}, and basing the name on Kneucker's \textit{Gramineae Esxiccatae} no.426. Since a number of these duplicate collections are in existence, the type specimen of \textit{C. longispinus} is hereby designated as Kneucker no.426, in the Herbarium of Iowa State University (ISC 227735). In his description of \textit{C. longispinus}, Fernald indicated his disdain for the genus with these remarks:

As a diagnosis of a form of \textit{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 \textit{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, \textit{C. longispinus} has also been confused with \textit{C. pauciflorus}, herein treated as a synonym under \textit{C. incertus}. Jansen and Wachter (1949), apparently also confusing \textit{C. longispinus} with \textit{C. pauciflorus} Benth., relegated the former species to varietal status, naming it \textit{C. pauciflorus} variety \textit{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 and Wachter, and Fernald, as synonyms under \textit{C. pauciflorus} Benth.

**Cytology**

Brown (1948) published a chromosome number of $2n=36$ for \textit{C. longispinus} (reported by him as \textit{C. pauciflorus} from northern U.S.). A chromosome number of $2n=34$ has been reported by Gould (1958) and was obtained by me on a number of collections of \textit{C. longispinus} as shown in Table 9. Meiosis was normal in all material examined.
Table 9. Chromosome counts from pollen mother cells of *Cenchrus longispinus* (Hack. in Kneuck.) Fern.

<table>
<thead>
<tr>
<th>Collection</th>
<th>Location</th>
<th>Chromosome number</th>
</tr>
</thead>
<tbody>
<tr>
<td>De Lisle voucher no. 362</td>
<td>Ford Co., Kansas</td>
<td>n=17</td>
</tr>
<tr>
<td>De Lisle voucher no. 391</td>
<td>Guadeloupe Co., New Mexico</td>
<td>n=17</td>
</tr>
<tr>
<td>De Lisle voucher no. 395</td>
<td>Guadeloupe Co., New Mexico</td>
<td>n=17</td>
</tr>
<tr>
<td>De Lisle voucher no. 405</td>
<td>Las Animas Co., Colorado</td>
<td>n=17</td>
</tr>
<tr>
<td>De Lisle voucher no. 429</td>
<td>Morrill Co., Nebraska</td>
<td>n=17</td>
</tr>
<tr>
<td>B. Crampton</td>
<td>Merced Co., California</td>
<td></td>
</tr>
<tr>
<td>De Lisle voucher no. 467</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Distribution

*Cenchrus 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 farther 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. *Cenchrus longispinus* often occurs in localized areas 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, Prescott, Peebles 2654 (MO); California, Riverside County, H.S. Yates 6734, June 28, 1937 (UC, AHUC); Riverside County, M.A. Nobs and S.G. Smith 493, Sept. 3, 1948 (ISC); Colorado, Fremont County, Canon City, T.S. Brandegee 845, 1873 (MO, UC); Las Animas County, D. De Lisle 405, Aug. 1, 1960 (ISC); Connecticut, Hartford County, F. Wilson 1266 (F); Oxford, A. Kneuwer 426, 1903, (Holotype ISC) (US, UC); Florida, Pinellas County, R.W. Pohl 8104, July 18, 1960 (ISC); Monroe County, W.C. Muenscher 18160, March 12, 1947 (UC); Georgia, University of Georgia, D.J. Banks 1051, Aug. 30, 1961 (ISC); Illinois, Carroll County, L.H.A. Pammel 1212, Aug. 9, 1925 (MO, ISC); Peoria, V.H. Chase 3207, July 23, 1919 (F, UC, MO, SUI); Indiana, 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,
Figure 10. Geographic distribution of *Cenchrus longispinus*.

July 14, 1897 (ISC); Story County, L.H. Pammel, Sept. 1904 (ISC); Palo Alto County, S. Hayden 8227, Aug. 7, 1940 (ISC); Webster County, C.E. Bessey, Aug. 3, 1872 (ISC); Linn County, D. DeLisle 459, Sept. 23, 1960 (ISC); Kansas, 13 mi. s.w. of Lakin, P.A. Rydberg and R. Imler 937, July 13, 1929 (MO); Greeley County, M. 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, Hampden County, F.C. Seymour 266, Sept. 8, 1914 (DAO, SMU); Michigan, Chelsea, R. McVaugh 7594 (F); Van Buren County, South Haven, O.E. Lansing Jr. 3332, Sept. 3, 1911 (F, SUI); Minnesota, Crow Wing County, Brainerd, E.B. Watson, Aug. 4, 1902 (ISC); Missouri, Douglas County, J. Steyermark 23593, July 23, 1937 (MO); Nebraska, Sheridan County, R.E. Buchanan, Aug. 2, 1905 (ISC); Brown County, D. DeLisle 444, Aug. 6, 1960 (ISC); Nevada, Clark County, I.W. Clokey 8262, July 13, 1939 (UC); New Mexico, Lea County, G.L. Fisher 40105, Aug. 23, 1940 (DAO, ISC); Guadaloupe County, D. DeLisle 395, July 30, 1960 (ISC); New Jersey, Monmouth County, R.F. Thorne, Aug. 25, 1940 (SUI); New York, Charlotte, D.M. White, Aug. 16, 1930 (ISC); Brooklyn, J. Monachina 103, July 21, 1936 (SMU, ISC); North Carolina, Beaufort, H.L. Bloomquist (AHUC); Mitchell County, H.E. Ahles 49708, Sept. 25, 1958 (SMU); North Dakota, Fargo, O.A. Stevens 660, Aug. 24, 1942 (MO, UC); Ohio, Cuyahoga County, J.R. Watson, 1897 (F); Oklahoma, Payne County, R.W. Pohl 8160, Aug. 27, 1960 (ISC); Oregon, Morrow County, A.N. Steward 7341, Sept. 7, 1956 (ISC);
Cenchrus palmeri (Figure 11, F—I; map, Figure 12)


Description
Small annuals; culms usually solitary, glabrous, 9.0—35 cm tall; sheaths slightly compressed, puberulent, the 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, 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 a black-purple color which often extends down
into the body of the bur. However, infrequent variants occur in which the entire bur may have a yellowish color.

The type specimen of *C. palmeri* is in the U.S. National Herbarium and was examined by me. 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 I obtained for *C. palmeri* is shown in Table 10. Meiosis appeared normal in this material.

Table 10. Chromosome count from pollen mother cells of *Cenchrus 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 Alemán, 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 mi. s.w. of Sonoyta, I.L. Wiggins 8360, March 14, 1936 (UC); Sonora, between Tastiota and Hermosillo, I.S. Wiggins and R.W. Rollins 267, Sept. 3, 1941 (NY, UC, MO).

9. *Cenchrus platyacanthus* (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;
Figure 11. *Cenchrus longispinus*, *C. palmeri*, and *C. platyacanthus*.

A—E. *C. longispinus* (from the type, Kneucker 426); A. inflorescence, B. bur, C. caryopsis, D. spikelet, E. floret.

F—I. *C. palmeri* (Weatherwax 3339); F. spikelet, G. floret, H. caryopsis, I. bur.

J—N. *C. platyacanthus* (Stewart 1246); J. spikelet, K. caryopsis, L. floret, M. bur, N. inflorescence.
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 or 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

Cenchrus platyacanthus has a distinctly compact inflorescence with small burs and few, usually short, spines. The 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. platyacanthus have from 30 to 90 burs per inflorescence, in contrast to 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 pedunculate burs over 4.0 mm long, he assigned the name C. platyacanthus. Other forms having smaller burs with little or no peduncle, and that were variously pubescent, were assigned the name C. granularis. The bur size differences are not significant and overlap in the collections I have observed. 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 C. granularis is a later homonym, C. platyacanthus remains as the valid name for this species.

Cytology

No chromosome numbers have been reported for C. platyacanthus.

Distribution

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

Selected specimens examined


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

Cenchrus tribuloides L. Sp. Pl. 1050. (1753) (Holotype in L) (1)

Cenchrus vaginatus Steud. Syn. Pl. Glum. 1:110. (1855) (2)

Cenchrus tribuloides macrocarpus Steud. Syn. Pl. Glum. 1:110. (1855) (A garden name given as a synonym for C. vaginatus Steud.) (2)

Cenchrus tribuloides var. macrocephalus Doell in Mart. 2, part 2:312. (1877) (2)


Cenchrus 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--10.0 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 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 extend 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 semineis globosis muricato-spinosis hirsutis." The holotype is in the Linnaean Herbarium and I have examined a photograph of the type.
The type specimen collected in Virginia by Peter Kalm was marked by Linnaeus with a small "K" (Hitchcock 1908).

Torrey (1824) gave the name *C. echinatus tribuloides* to this species, apparently in the belief that it was a pubescent and large-burred form of *C. echinatus*. However, only *C. tribuloides* and *C. longispinus* occur in the New Jersey pine barrens where Torrey's plant was collected.

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 of Martius' herbarium.

**Cytology**

A chromosome number of 2n=34 has been reported for *C. tribuloides* by Avdulov (1928) and by Hunter (1934). Counts determined by the writer for this species are shown in Table 11. In the material studied, meiotic divisions appeared normal.

<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 no. 486</td>
<td></td>
<td></td>
</tr>
<tr>
<td>D.E. Fairbrothers</td>
<td>Cape May County, N.J.,</td>
<td>n=17</td>
</tr>
<tr>
<td>DeLisle voucher no. 487</td>
<td>Stone Harbor beach</td>
<td></td>
</tr>
</tbody>
</table>

**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.

**Selected specimens examined**

**BAHAMAS:** Andros Island, J.K. Small, J.J. Carter, Feb. 4-5, 1910 (NY).

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

**UNITED STATES:** Delaware, Ocean City, A. Chase 12670, Aug. 19, 1952 (DAO); Newcastle, Wm. M. Canby (MO); Florida, Palm Beach, June 7, 1896 (MO); Soldier Key, J.K. Small 3300, Feb. 20, 1911 (US); Navarre, D.J. Banks 838, Aug. 1, 1961 (ISC); Georgia, Beachhead Island, W.L. McAtee 3334, Oct. 16, 1923 (US); Maryland, Calvert County, Scientists Cliffs, F.C. Seymour 17275, Aug. 6, 1957 (SMU, ISC); Mouth of Patuxent River, A. Chase 12667, Aug. 20, 1948 (DAO); Mississippi, Biloxi, S.M. Tracy 4526, Aug. 19, 1899 (F, MO); Harrison County, Beach at Biloxi, D. DeLisle 660, Aug. 28, 1961 (ISC); Jackson County, Pount Aux Chenes, R.B. Channell 775, July 17, 1952 (SMU); New Jersey, Camden, F.L. Scribner 122, 1881 (F); Pine Barrens, C.F. Rafinesque (MO); Cape May, C.F. Parker, 1871 (F, US); South Amboy, A.P. Kelley, Oct. 4, 1927 (SU); Wildwood, A. Chase 3506, July 25, 1906 (US, ISC); New York, Long Island, T.H. Kearney,
Figure 12. Geographic distribution of Cenchrus palmeri, Cenchrus tribuloides, and Cenchrus platyacanthus.
Aug. 27, 1894 (F, US); North Carolina, Dare County, P. O. Schallert 5077,
Aug. 20, 1957 (SMU); 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. Hitchcock, Aug. 22, 1905 (US); Beaufort County, Godfrey and Tryon
1533, Aug. 14, 1939 (US, UC); Virginia, Colonial Beach, L. Tidestrom 7834,
Aug. 19, 1916 (DAO); Cape Henry, A. S. Hitchcock 621, June 27, 1905 (F,
UC); Southampton County, Franklin, A. Heller 1170, July 22-29, 1893 (F,
MO, UC).

11. Cenchrus incertus (Figure 16, F—J; map, Figure 15)

(Holotype in NY) (1)

Cenchrus pauciflorus Benth. Bot. Voy. Sulph. 56. (1844) (Holotype
in BM, fragment of type in US) (1)

Cenchrus muricatus Phil. Sert. Mend. Atl. 44. (1870) (non C. muri-
catus L. 1771) (Holotype in BM, fragment of type in US) (1)


Cenchrus roseus Fourn. Mex. Pl. 50. (1885) (Holotype in P, frag-
ment of type in US) (1)

Herb. 18:356. (1917) (Holotype in NY) (1)

(Holotype in US) (1)

(Type in US, cotypes in FHKSC) (1)

Cenchrus parviceps Shinners. Field and Lab. 24:73. (1956)
(Holotype in SMU) (1)

Description

Plant annual, often biennial or over-wintering; culms decumbent or
erect, sometimes with many branches from the base, glabrous, 5.0—80
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 cm 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 7-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, 1.3—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 inflorescence 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 over-all lower stature, shorter leaves, and narrower bur width. 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 my experience that it is difficult, if not impossible, to separate the three species on the basis of these traits, 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 represent more accurately 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.
Figure 13. Scatter diagram showing the relationships of four morphological characters in *Cenchrus incertus*. 
throughout the range of *C. incertus* in 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 (Fig. 14) at the approximate locations where the samples were collected. Population samples I collected 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 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 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 (Fig. 14), it will be 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 (Fig. 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 variable 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 approaching those plants in the northern parts of the range.

Many plants from the West Indies possess somewhat more robust culms and the often purple-colored burs have more numerous spines (generally around 35 to 40). These forms are commonly identified with C. tribuloides, probably because of culm size and slightly larger burs, but they lack the dense pubescence of the former species, possess 2 to 3 spikelets per bur, and the spikelet length is usually 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 that I observed can with little difficulty be 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 I have examined, 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. However, 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 Millsap in 1905. The inflorescence of the type specimen, in the New York Botanical Garden herbarium appears to be immature.

_Cenchrus humilis_ from Peru, was described by Hitchcock (1927) as a small plant with long-pubescent, purple burs having short, broad spines. Hitchcock apparently based the name on the small stature and pubescent nature of the burs. However, many collections of _C. incertus_ closely matching the former species have been observed from the southern United States, Mexico, the West Indies, and Brazil. The type specimen of _C. humilis_ also bears a striking resemblance to the short-statured plants of _C. incertus_ of the Rio Grande Plain.

_Cenchrus albertsonii_ Runyon (1939) was based on a long-spined form of _C. incertus_ from the northern edge of its range in Oklahoma.

_Cenchrus spinifex_ (Cavanilles 1799), collected in Chile, was discussed by Chase (1920) who rejected the name because she had not seen the type and because of inadequate description by Cavanilles. A specimen reputed to be an isotype of _C. spinifex_ was examined by me at the Chicago Natural History Museum. This specimen labeled "type fide Parodi," closely resembles _C. incertus_ of the southern United States and Mexico. As such it may represent an earlier name for _C. incertus_. The name _C. spinifex_, however, I am rejecting until further studies can be made on the isotype and holotype. The latter was unavailable for examination and the correctness of the isotype label has not been 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_. My counts, shown in Table 13, were all 2n=34. Gould's single count 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 as a possible explanation for the extreme variability shown by this taxon throughout its range.
Table 13. Chromosome counts from pollen mother cells of *Cenchrus incertus* M. A. Curtis.

<table>
<thead>
<tr>
<th>Collection</th>
<th>Location</th>
<th>Chromosome number</th>
</tr>
</thead>
<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 Co., N. Mex.</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></td>
<td>n=17</td>
</tr>
<tr>
<td>Pohl no. 8181</td>
<td>Tulsa County, Oklahoma</td>
<td>n=17</td>
</tr>
<tr>
<td>DeLisle voucher no. 483</td>
<td></td>
<td>n=17</td>
</tr>
<tr>
<td>Pohl no. 8185</td>
<td>Mayes County, Oklahoma</td>
<td>n=17</td>
</tr>
<tr>
<td>DeLisle voucher no. 485</td>
<td></td>
<td>n=17</td>
</tr>
</tbody>
</table>

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."

Selected specimens examined
BOLIVIA: San Pedro, G. Mandon 1267 (NY).
HONDURAS: Tela, T. G. Yuncker 4678, 7-20-34 (UC); Puerto Sierra, P. Wilson 21, Jan. 15, 1923 (NY).
PARAGUAY: Balausa 151 (US).
Figure 15. Geographic distribution of *Cenchrus incertus*. 
PERU: La Merced Junin, A.S. Hitchcock 22134, Oct. 23, 1923 (US);

URUGUAY: Montevideo, L. Barattini, 1920 (MO, SMU); Dept. Durazno;
Río Yi, W. Herter 2713, 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);
Arizona, Pima County, F. Ginter, Sept. 22, 1941 (UC); Nogales, M.E.
Jones 22798, Oct. 23, 1926 (MO); Arkansas, Izard County, D. Demaree
3319, June 11, 1927 (F, SMU); California, Santa Barbara, H.M. Pollard,
July 11, 1958 (DAO, AHUC); Florida, Bennet, D.J. Banks 898, Aug. 2,
1961 (ISC); Key Largo, A. Chase 3937, Sept. 10, 1907 (US, ISC); Gadsden
County, G. V. Nash 2580, Sept. 5, 1895 (US, F, MO); Duval County, A.H.
Curtiss 6020, Oct. 11, 1897 (MO, UC, ISC); Sarasota, R. W. Pohl 7653,
June 20, 1957 (ISC); Georgia, Wayne County, D. J. Banks 725, July 28,
1961 (ISC); 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); Mississippi,
Jackson County, D.G. DeLisle 677, Aug. 28, 1961 (ISC); Ocean Springs,
S. M. Tracy, Sept. 2, 1889 (US, 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); Harnett
County, H. Laing 267, Sept. 29, 1956 (UC); Oklahoma, Payne County, R. W.
Pohl 8158, Aug. 27, 1960 (ISC); South Carolina, Columbia, H. Eggert,
Aug. 10, 1898 (MO); Georgetown, R. K. Godfrey and R. M. Tryon 217,
June 30, 1939 (F, DAO, UC, US, MO); Texas, Bexar County, D.G. DeLisle
625, Aug. 25, 1961 (ISC); Mason County, D.G. DeLisle 617, Aug. 25, 1961
(ISC); Harris County, E. Boon 323, July 12, 1946 (US, MO, TEX); Wise
County, L.H. Shinners 18843, May 30, 1954 (SMU, ISC); 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); Cameron County,
D. Isely 7563, April 14, 1961 (ISC); Kenedy County, B. 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); 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. and E. G. Heller 4211, Sept. 3, 1898 (MO, ISC); 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); Virginia, Southampton County, M. L. Fer-

WEST INDIES: Bahamas, Jamaica, Pigeon Island, Maxon and Killip
1569, April 6-7, 1920 (NY); Bahamas, Bimini Islands, R. A. and E.S.
Howard 10094, May 1948 (UC, US, SMU, NY); Trinidad, W. E. Broadway
8016, April 24, 1932 (MO); Porto Rico, J. A. Shafer 2751, Feb. 7, 1914 (NY);
Dominican Republic, J. Jimenez 2862, March 19, 1955 (US); Santo Domingo,
E. L. Ekman 13167, July 12, 1929 (US); Haiti, E. and G. Leonard 13938,
March 21, 1929 (US); Guadeloupe, H. Stehle 197, July 1935 (US).

SOUTH AFRICA: Bloemfontein, Praetoria, Dec. 1918 (US); Pretoria,
J. J. Lindegue 16433, March 1934 (US).
12. *Cenchrus caliculatus* (Figure 16, A—E; map, Figure 17)

*Cenchrus caliculatus* Cav. Icones. 5:40. t.463. (1799) (Type in MA, fragment of type in ISC) (1)

*Cenchrus australis* R. Br. Prod. 1:196. (1810) (Fragment of type in US) (1)


*Cenchrus australis* var. *latifolius* Drake Fl. Polyn. 252. (1892) (not of Sprengel 1827) (2)

*Cenchrus taitensis* Steud. Syn. Pl. Glum. 1:419. (1855) (Type in P., fragment of type in US) (1)

**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.

*Cenchrus 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 those of *C. caliculatus*, are otherwise a close match to the Cavanilles type.
Figure 16. *Cenchrus incertus*, *C. caliculatus*, and *C. tribuloides*.

A—E. *Cenchrus caliculatus* (Smith 4292); A. spikelet, B. floret, C. caryopsis, D. bur, E. inflorescence.

F—J. *Cenchrus incertus* (De Lisle 618); F. burs, G. inflorescences, H. floret, I. caryopsis, J. spikelet.

K—N. *Cenchrus tribuloides* (Chase 12667); K. spikelet, L. caryopsis, M. floret, N. bur.
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 Cenchrus australen 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, Gloucester, W. Heron, 1909 (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); Mangareva Islands, H. St. John 14890, June 6, 1934 (US, UC); Aukena Island, H. St. John 14597, May 28, 1934 (F, US); Nouvelle Caledonie, M. Hennecart, 1879 (NY); New Hebrides, F. S. Kajewski 358, June 4, 1958 (NY); New Zealand, North Island, T. F. Cheese- man 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); Tona, Nomuka Island, T. G. Yuncker 15827, April 30, 1953 (US); Philippines, Mindanao, M. Ramos and G. Edano 85197, April 1932 (US).

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

**Cenchrus elymoides** F. v. Muell. Frangm. 8:107. (1873) Type in MEL)

**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; inflorescence 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 C.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.

Cytology
No cytological work has been reported on this species.

Distribution
Cenchrus 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. Cenchrus 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)
Cenchrus lappaceus Tausch in Flora. 20:57. (1837) (non C. lappaceus L. 1763) (4)
Cenchrus bulbosus Fresen. ex Steud. Nom. ed. II. 1:317. (1840) (2)
Cenchrus echinoides Wight ex Steud. Nom. ed. II. 1:317. (1840) (2)
Cenchrus pennisetiformis Hochst. and Steud. ex Steud. Nom. ed. II. 1:317. (1840) (2)
Cenchrus ciliaris Fig. and DeNot. Mem. Acc. Torin. Ser. 2. 14:383. (1854) (non C. ciliaris L. 1771) (2)
Cenchrus ciliaris var. nubicus Fig. and DeNot. Mem. Acc. Sci. Torino. Ser. 2. 14:392. (1854) (2)
Cenchrus ciliaris var. villiferus Fig. and DeNot. Mem. Acc. Sci. Torino. Ser. 2. 14:386. (1854) (2)
Cenchrus rigidifolius Fig. and 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 ciliarius var. nubicus Durand and Schinz. Conspr.Fl. Afr. 5:776. (1894) (non var. nubicus Fig. and DeNot. 1854) (2)
Cenchrus ciliarius var. villiferus Durand and Schinz. Conspr.Fl. Afr. 5:776. (1894) (non var. villiferus Fig. and 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)
Cenchrus pubescens L. ex Jackson. Index Linn. Herb. 53. (1912) (name only) (4)
Cenchrus 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)
Cenchrus ciliaris var. genuinus (Leeke) Maire and Weiller in Maire. Fl. Afr. du Nord. 1: 342. (1952) (2)

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

Cenchrus ciliaris var. pallens (Fenzl ex Leeke) Maire and 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 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 mm long, 0.2—0.6 mm wide, long-ciliate pubescent on the inner margins, connate only at the base or slightly above, antrorsely 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 and Hubbard (1934), suggest the presence of putative hybrids between this species and C. setigerus wherever their ranges meet or overlap. Apomixis has been reported in both C. ciliaris and C. setigerus by Brown (1948), Fisher et al. (1954), and Snyder et al. (1955). The latter authors reported from 1 to 8 embryo sacs per ovule in Pennisetum ciliare (C. 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.

I have observed about 40 collections each of \textit{C. ciliaris} and \textit{C. setigerus} throughout their ranges, and have seen only a few specimens which could be considered intermediates, although these were all more similar, morphologically, to \textit{C. ciliaris} than to \textit{C. setigerus}. Since these two species are quite distinct, morphologically, I am of the opinion 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.

\textit{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 "\textit{ciliaris}," apparently written by Sir James Smith (Jackson 1912). This collection is hereby designated as the type. The other collections of \textit{C. ciliaris} in the Linnean herbarium are represented by sheet no. 1217.10 from "Horto Upsaliensi," and no. 1217.11, which has no inscription.

**Cytology**

Chromosome numbers of \(2n=38\) were reported by Krishnaswamy (1940), \(2n=34\) by Darlington and Wylie (1955), and \(2n=40\) and 52 by Nath and Swaminathan (1957). The number \(2n=36\) has been observed by several authors including DeWett (1958), Fisher et al. (1954), and Moffett and Hurcombe (1949). Fisher et al. (1954) studied eighteen different introductions of \textit{Pennisetum ciliare} (\textit{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 types. The apparent meiotic irregularities in many of the aneuploids lends further support to the presence of widespread apomixis in this taxon.

**Distribution**

\textit{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 North 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, Rauindi, Lebrun 8366, Nov. 1937 (US); British Somaliland, A. S. McKinnon S221, Nov. 1958 (US); Eritrea-Amasen, 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. 1962 (UC); Senegal, Meisner Herbarium, 1835 (NY); So. Rhodesia, H. Wild 3395, 8-6-50 (MO); Sudan, Blue Nile Province, F. W. Andrews A206, March 18, 1936 (US); Tanganyika, Tanga Prov., Oct. 1946 (MO); Biskra, Algeria (F).
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• = C. ciliaris
• = C. setigerus

Figure 18. Geographic distribution of Cenchrus ciliaris and Cenchrus setigerus.


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 PRC) (2, 3)

Pennisetum karwinskyi Schrad. Linnaea. 12:431. (1838) (type in LE) (3)

Pennisetum multiflorum Fourn. Mex. Pl. 2:49. (1886) (type in C) (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 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, 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, 5.5–6.1 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 mm long.

Observations and nomenclature

*Cenchrus multiflorus* is readily distinguished from *C. 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 *Cenchrus*, and applied the earlier name of *C. multiflorus*. The type specimen of *C. 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

*Cenchrus multiflorus* is apparently restricted to rocky uplands and moist slopes in Mexico and Costa Rica.

Selected specimens examined

MEXICO: State of Jalisco near Guadalajara, C.G. Pringle 3849, Sept. 15, 1891 (F); 4 miles north of Acapulco, F.A. Barkley 31, Aug. 20, 1947 (US); Oaxaca, San Augustin, Liebman 341, 1841-43 (isotype of Fournier's *Pennisetum multiflorum*); Chihuahua, Rio Mayo, H.S. Gentry 1568, Aug. 5, 1935 (F); Guadalajara, C.G. Pringle 11327, July 28, 1902 (US); Jalisco, A.S. Hitchcock 7364 and 7342, Sept. 28, 1910 (US); Sonora, H.S. Gentry 7955, April 11, 1948 (US); Sonora, 8 miles east of Matape, I.L. Wiggins
and R. Rollins 429, Sept. 9, 1941 (US); Sonora, 15 miles north of Ures, I. L. Wiggins 7367, Sept. 21, 1934 (US).
NICARAGUA: Managua, H. A. Garnier, 1930 (F).

16. Cenchrus myosuroides (Figure 19, M—P; map, Figure 20)

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

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

(non P. cenchroides Rich. 1792) (type in CHARL) (1)

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

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

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

Cenchrus alopecuroides Presl. Rel. Haenk. 1:317. (1835) (non C.
aloepecuroides Thunb. 1794) (type in PRC, fragment of type in US)
(1)

Cenchrus setoides Buckley, Prel. Rept. Geol. and Agric. Surv. Tex.
App. 1:2. (1866) (type in PH) (1)


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

243:361. (1936) (type in US) (1)

Description
Plants perennial, culms from 0.5—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 inflores-
cence. 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 C. myosuroides H.B.K. is in the herbarium of the Mu-
seum National d'Histoire Naturelle in Paris. I examined a fragment
of the type in the U.S. National Herbarium. Nuttall's description of
Pennisetum pungens (1818) was based on 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 C. myosuroides, i.e. Cen-
chropsis myosuroides by Nash in Small (1903), appears to have little or
no justification on morphological grounds, and the genus has been re-
jected by subsequent workers. A large-burred form, having two or three
spikelets per bur, was described from Santo Domingo in 1936 by Hitch-
cock, and was given the name C. ekmanianus. An examination of the
type in the U.S. National Herbarium reveals a variation in one inflo-
rescence of from one to three spikelets per bur. I have observed occasional
plants from Mexico and Central America with two spikelets per bur. It
would appear that C. ekmanianus was based on sporadic forms which
may occur throughout the range of the species. In all other character-
istics, the type specimen falls within the range of variation of C. myo-
suroides.

Cytology

A chromosome number of 2n=54 has been reported by Brown (1950,
1951). Avdulov (1931) reported a number of 2n=70, which was later also
obtained by Gould (F. W. Gould, College Station, Texas, 1962, personal
communication). These counts indicate that C. myosuroides is a poly-
ploid that has probably originated from some form with a basic number
of X=9 or 10 (see discussion in chapter on cytology).

Distribution

Cenchrus 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: Bei Cordoba, T. Stuckert, Jan.-Mar. 1902 (ISC);
Estancia St. Teresa, T. M. Petersen 1403, Dec. 21, 1951 (NY, MO); Bei
Cordoba, A. Kneucker 428, Jan.-March 1902 (US, UC, MO); Dept. Andal-
gala, P. Jorgensen 1144, 10-11-1915 (UC, MO); Buenos Aires, A. T. Hun-
ziker 3489, April 8, 1942 (NY, MO).

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); Tacna, J. G. Hosmann, April 19, 1918 (AHUC).


ECUADOR: Prov. Azuay, C.G. Pringle 429, May 25, 1885 (NY, F); Durango, E. Palmer 866, 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 Puebla, A.S. Hitchcock 619, Aug. 9, 1910 (NY, UC, 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).

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, ISC).

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


17. Cenchrus agrimonioides. (Figure 21, A—D; Map, Figure 17)

Cenchrus agrimonioides Trin. Diss. Gram. Panic. 72. (1826) (Type in B, fragment of type in US) (1)
Cenchrus calyculatus var. uniflorus Hillebr. Fl. Haw. Isl. 505. (1888) (2)
Cenchrus pedunculata Degener and 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-keel ed, 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 mm wide, tapering to a point; inflorescence open, spike-like, 7.8—28 cm long, 1.6—2.2 cm wide; rachis angled, usually not flexuons, 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

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Figure 19. *Cenchrus elymoides*, *C. ciliaris*, *C. multiflorus*, and *C. myosuroides*.

A—D. *Cenchrus elymoides* (Perry 2616); A. spikelet, B. caryopsis, C. bur, D. floret.

E—H. *Cenchrus ciliaris* (Stewart 17267B); E. floret, F. caryopsis, G. spikelet, H. bur.

I—L. *Cenchrus multiflorus* (Hitchcock 7364); I. bur, J. caryopsis, K. spikelet, L. floret.

M—P. *Cenchrus myosuroides* (Hitchcock 619); M. floret, N. bur with spikelet, O. caryopsis, P. inflorescence.
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Figure 20. Geographic distribution of *Cenchrus myosuroides* and *Cenchrus multiflorus*.
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 mm wide, the tips retrogressively 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. caliculatus* 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. *laysanensis* 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. *laysanensis* and *C. pedunculata* are in the U.S. National Herbarium and were examined.

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 Ekanehoa, Oahu, Degener and Whitney 12, 800, May 1, 1940 (MO, NY, US); Ocean Island, E.L. Caum, April 18, 1923 (NY); Oahu, Kau-mokunui 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. *Cenchrus biflorus* (Figure 21, I—L; map, Figure 22)


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


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

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

*Cenchrus echinatus* Benth. in *Hook. Niger Fl.* 564. (1849) (of authors, non *C. echinatus* L. 1753) (2)

*Cenchrus niloticus* Fig. and DeNot. *Mem. Acc. Torin.* 14:380., *Pl.* 33. (1854) (2)

*Cenchrus annularis* Anderss. in *Peters. Reise Mossamb. Bot.* 553. (1863) (2)

*Cenchrus biflorus* of authors, non *Hook. f.* *Fl. Brit. Ind.* 7:89. (1896) (Attributed by Hooker to Roxburgh) (2)


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

**Description**

Plants annual, 5.0—85 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, bursv 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 affinities with *C. prieurii* and *C. myosuroides*, 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 me. However, Roxburgh's reference to the grooved spines with hairy margins and slightly hooked spines 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 and DeNotarisi's 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 (*C. annularis*), 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 me. This seems 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 perinvolucratus* was collected on Zanzibar and described by Stapf and 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 me, is shown in Table 14. Meiosis was normal in the material examined.

<table>
<thead>
<tr>
<th>Collection</th>
<th>Location</th>
<th>Chromosome number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Th. Monod Dakar, North Africa</td>
<td>n=17</td>
<td></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-Amasen, A. Pappi 238, Nov. 29, 1902 (US, MO); Timbuktu, French Sudan, C. H. Sweeney 40, Dec. 11, 1953 (US); Gold Coast (Ghana), C. Vagre 143, July, 1938 (US); Kimbinbi, 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. Oulfsen 460, Oct. 7, 1927 (US); Tanganyika, R. E. S. Tanner 2053, Aug. 10, 1955 (UC).

19. Cenchrus prieurii (Figure 21, E—H; map, Figure 22)


*Cenchrus hystrix* Fig. and 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 antrorsely 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.

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

The figure accompanying the description of *C. hystrix* (Fig. and 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 and Leelamma (1956). No other cytological investigations have been noted for this species.

**Distribution**

*Cenchrus prieurii* is of rather localized occurrence in northern Africa, Arabia and India.
Figure 21. *Cenchrus agrimonioides*, *C. prieurii*, *C. biflorus*, and *C. setigerus*.

A—D. *Cenchrus agrimonioides* (from the type fragment); A. bur, B. spikelet, C. floret, D. caryopsis.

E—H. *Cenchrus prieurii* (Hagerup 611a); E. bur, F. caryopsis, G. spikelet, H. floret.

I—L. *Cenchrus biflorus* (Rodin 4187); I. bur, J. caryopsis, K. floret, L. spikelet.

M—Q. *Cenchrus setigerus* (Stewart 15119); M. bur, N. spikelet, O. floret, P. caryopsis, Q. inflorescence.
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. Ilustr. Bot. Himal. 416 (1839) (nomen nudum) (2, 4)
- *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. (1869) (2, 4)
- *Cenchrus bulbifer* Hochst. ex Boiss. Fl. Orient. 5:448. (1884) (2)
- *Cenchrus uniflorus* Ehrenb. ex Boiss. Fl. Orient. 5:448. (1884) (2)
Cenchrus ciliaris var. setigerus (Vahl.) Maire and Weiller in Maire. 1:342. (1952) (2)

Description
Plants perennial, forming clumps from somewhat bulbous bases; culms 5.0—80.0 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 antorosely 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—0.8 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 antosely 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 takes place in a manner similar to that of C. ciliaris, from enlarged nucellar cells following the four-nucleate stage of megsaprogenesis. The multiple embryo sacs observed were usually crowded in the central part of the ovule and by the time they reached maturity often 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. Vahl'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. I have examined a fragment of the type of the latter species in the U.S. National Herbarium. 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 and 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 me 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 no. 216374</td>
<td>Origin unknown</td>
<td>n=18</td>
</tr>
<tr>
<td>DeLisle voucher 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-Amasen, 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).

**AUSTRALIA:** 7 miles no. of Tennant Creek Twp. N.T., R.A. Perry 540, April 24, 1948 (US); Queensland, 2 miles no. of Malabon Twp. M. Lazarides 4405, March 16, 1954 (US); Tasmania, J. Ehrenberg 235 (US); Kimberley Research Sta. W.A., M.L. 3167, Aug. 8, 1952 (US); Brisbane, D.A. Goy 355 (cultivated) July 25, 1938 (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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DONALD G. DE LISLE


TAXONOMY OF THE GENUS CENCHRUS

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ACKNOWLEDGEMENTS

I wish to express my sincere gratitude and appreciation to Dr. R.W. Pohl for his aid in selection of the problem and in obtaining seeds and collections, and for his advice and encouragement throughout the course of this study.

A number of suggestions on nomenclatorial procedure were provided by Dr. Duane Isely. Dr. C.E. Hubbard, of Kew, graciously sent information concerning the locations of some type specimens.

A special note of thanks is due each of the following individuals who...
kindly furnished seeds of various species of Cenchrus: Dr. Wilbur Duncan and Mr. D. J. Banks, University of Georgia; Dr. M. R. Birdsey, University of Miami, Florida; Dr. Beecher Crampton, University of California, Davis; Dr. D. E. Fairbrothers, Rutgers University; Dr. F. W. Gould, Texas A. and M., College Station; Prof. Th. Monod, University of Dakar, North Africa; Dr. Wallace C. Mitchell, University of Hawaii; Dr. L. H. Shinners, Southern Methodist University; Dr. W. H. Skrdla, U. S. Plant Introduction Station, Ames, Iowa; Dr. Paul Weatherwax, Indiana University; and Dr. Daniel Zohary, Hebrew University, Jerusalem, Israel.

Finally, for their patient efforts in the search for rare journals and botanical volumes, I am grateful to the reference librarians at Iowa State University and to Dr. G. B. Van Schaack of the Missouri Botanical Garden.

APPENDIX

The following list contains names which have at some time been included in the genus Cenchrus. The criteria for treatment of each name herein are the same as those followed in the body of the work and explained in Methods and Materials.

Cenchrus aegyptium Beauv. Agrost. 157. (1812) = Dactyloctenium aegyptium (L.) Richt. (1890) (2)
Cenchrus anomoplexis Desf. Fl. Atlant. 2:388. (1799) = ? (no reference to this name in Desfontaines, may be the same as C. anomoplexis Labill. 1824).
Cenchrus asperifolius Desf. Fl. Atlant. 2:388. (1799) = Pennisetum orientale. (2)
Cenchrus biflorus Broun and Massey (non C. biflorus Roxb. 1820) = (original description not seen; cited as synonym of C. setigerus in Andrews (1956) (4)
Cenchrus carolinianus Walt. Fl. Carol. 79. (1788) = nomen nudum. (See discussion under C. longispinus) (2)
Cenchrus echinatus laevigatus Trin. Fund. Agrost. 172. (1820) = Anthephora elegans (2)


Cenchrus frutescens Sieber. Flora 9:14. (1822) = Phragmites communis (2)

Cenchrus geniculatus Thunb. Prod. Pl. Cap. 24. (1794b) = Pennisetum thunbergii (2)

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

Cenchrus granularis L. Mant. 2: App. 575. (1771) = Manisuris granularis (2)


Cenchrus hilarii Raspail Ann. Sci. Nat. 5:309. (1825) = Hilaria chenchoideas (2)

Cenchrus hirsutus Spreng. Neue Entdeck. 3:15. (1822) = Scleria hirtella (2)

Cenchrus hordeiformis Pers. Syn. Pl. 1:71. (1805) = Pennisetum orientale (2)


Cenchrus hordeiformis Thunb. Prod. Pl. Cap. 24. (1794b) = Pennisetum compressum (2)

Cenchrus inflexus Poir. Encycl. 6:50. (1804) = Echinolaena hirta (2)

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

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

Cenchrus lappaceus L. Sp. Pl. ed. II. 1488. (1763) = Centotheca lappacea (2)

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

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

Cenchrus marginalis Rudge. Pl. Guian. 2:20. (1805) = Panicum marginale (2)


Cenchrus mucronatus Pers. ex Steud. Nom. Ed. 2. 1:172. (1840) = C. muricatus (2)

Cenchrus mucraticus L. Mant. 302. (1771) = Trachys mucronata (2)


Cenchrus ovatus Lam. ex Poir. Encycl. 6:51. (1804) = ? (Lagurus) illustration does not resemble any known species of Cenchrus.
TAXONOMY OF THE GENUS CENCHRUS

Cenchrus panicus Heyne ex Wall. Cat. No. 8650. (1828) nomen nudum = Pennisetum typhoideum (4)

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

Cenchrus pubescens Steud. Nom. ed. 2. 1:317. (1840) = Anthephora pubescens (2, 4)

Cenchrus purpurascens Thunb. in Trans. Linn. Soc. 2:329. (1794a) = Gymnothrix japonica (2, 4)


Cenchrus racemosus L. Sp. Pl. 1049. (1753) = Tragus racemosus (2)

Cenchrus ramosissimus Poir. Encycl. 6:51. (1804) = Pennisetum dichotomum (2)

Cenchrus setosus Sw. Prod. Veg. Ind. Occ. 26. (1778) = Pennisetum polystachyon (2)

Cenchrus spicatus Cav. Descr. 5:304, 614. (1802) = Pennisetum spicatum (2)


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

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

Cenchrus tripsaceus L. ex Munro. Journ. Linn. Soc. 6:55. (1862) = Trachys mucronata (2)

Cenchrus tripsacoides Cav. Elench. Pl. Hort. Matrit. 9. (1803) = ?

Original description not seen; cited in Chase, 1920, may refer to Anthephora hermaphroditia.

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


Cenchrus villosus Spreng. Syst. 1:301. (1825) = Anthephora elegans (2)

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