Taxonomy and distribution of the genus Phalaris

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TAXONOMY AND DISTRIBUTION OF THE GENUS PHALARIS

by

Dennis Elmo Anderson

A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of
The Requirements for the Degree of
DOCTOR OF PHILOSOPHY

Major Subject: Plant Taxonomy

Approved:

Signature was redacted for privacy.

In Charge of Major Work

Signature was redacted for privacy.

Head of Major Department

Signature was redacted for privacy.

Dean of Graduate College

Iowa State University
Of Science and Technology
Ames, Iowa

1960
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INTRODUCTION

Over a century has passed since the last attempt to monograph the genus *Phalaris* on a world-wide basis.

Members of this genus have been collected on every major land mass excepting Antarctica and Greenland. The habitat ranges of the genus are very broad. Species of *Phalaris* are found at altitudes ranging from well below sea level to several thousands of feet above sea level. Some are dwellers of low, wet, marshy areas; others are found in areas that are dry throughout much of the growing season.

Some members of *Phalaris* have been widely used as forage grasses and as waterway control grasses. Seeds of one species are a commercial source of food for pet birds.

Certain species are dominants in the native vegetation of broad areas; others are ballast waifs and strays that have encircled the globe in their travels. At least three species have become weeds in waste-places in many parts of the world.
MATERIALS AND METHODS

Methods of Investigation

Most of the materials used in this study were herbarium specimens and living plants. Studies of herbarium specimens consisted primarily of measurement of various parts of the plants and critical examination of certain features not amenable to quantitative description. Measurements and observations of structures requiring accuracy to 0.1 millimeter were made with the aid of a Spencer stereoscopic binocular microscope equipped with 1X, 2X, and 3X objectives and 9X wide field oculars. An ocular micrometer was used for measurement of spikelet parts.

Inflorescence length was measured from the point of attachment of the lowermost branch to the apex of the panicle. Panicle width was determined at the widest part of the panicle.

The length of the first glume, second glume, lemma, and palea was measured from the point of insertion on the spikelet axis to the apex of the structure. Width of the spikelet members was determined at the widest point.

Attempts were made to secure chromosome numbers for many of the species. Inflorescences were fixed in Farmer's fluid for one hour. Anthers were then dissected from previously fixed florets under a stereoscopic binocular microscope.
These were placed in a drop of acetocarmine on a clean slide. By using a glass rod that had been filed flat on one end, the anther was crushed and the contents forced out. The anther wall was then removed from the drop by means of two glass needles. Iron necessary for proper staining of the cell contents during the acetocarmine treatment was furnished by placing the end of a rusty nail in the drop on the slide for short intervals. The anther contents were then warmed gently over the flame of an alcohol lamp and a cover slip was applied. A blotter was placed over the slide and pressure applied to flatten the cells.

Observations of the leaf epidermis were made on the abaxial surface of the uppermost culm leaf of a flowering plant. When using fresh material, the other tissues were removed from the epidermis by scraping it with a razor blade. If observations of dried material were necessary, the leaf was soaked in a methyl alcohol-detergent solution (Pohl, 1954) for five minutes. This soaking softened the leaf so that removal of mesophyll tissue could be readily accomplished.

Data supporting taxonomic interpretations are presented in the form of descriptions, tables, pictorialized scatter diagrams, illustrations, and maps. Only those specimens which had been seen and verified by the author were used in compiling distributional data for presentation on maps. Drawings of spikelets were made with the aid of a camera lucida attached
to the binocular microscope previously described.

Complete synonymies are given for each species. Evidence for treatment of the names as synonyms is given by a brief statement. If no explanatory statement is given, then the description accompanying the original publication of the name was used as evidence. Excluded or unidentified names are presented in the Appendix of this paper.

A list of selected specimens examined is provided for each species. Specimens duplicated in several herbaria were used in this listing whenever possible.

Materials

The specimens used in this study were obtained from institutional herbaria and the author's collections. Specimens were obtained from the herbaria listed below. The key letters preceding each institution are the abbreviations given by Lanjouw and Staflou (1956). These abbreviations will be used hereafter whenever reference to a particular herbarium is necessary.

PH Academy of Natural Sciences of Philadelphia
F Chicago Natural History Museum
GH Harvard University, Gray Herbarium
ISC Iowa State University
LINN Linnean Society of London
Field studies and collections of plants for herbarium specimens were made by the author in June and July, 1958, in Iowa, Minnesota, and Oklahoma. Further collections were made in Minnesota and Nebraska in June, 1959. Herbarium specimens were prepared from fresh material. Overnight drying of plants in presses placed on a portable electric dryer produced dry specimens suitable for storage.

The cooperation of the Regional Plant Introduction Station in Ames in providing seeds of many of the species of Phalaris greatly facilitated cytological and morphological studies in the genus. Dr. Beecher Crampton of the University of California, Davis, kindly furnished seeds of several species growing in California.

Collections of inflorescences for cytological studies
commenced as soon as plants in the greenhouse began to bloom. As each inflorescence was removed and fixed, a coded tag was affixed to that particular culm. If cytological studies of florets of this inflorescence were successful, a voucher specimen of this tagged material was made. Any remaining material from the fixed inflorescence was dried and deposited with the voucher. Thus each voucher specimen consists of not only the plant from which an inflorescence was taken but also portions of the actual inflorescence used in cytological studies. A portion of the original seed sample from which any given specimen was grown was placed in an envelope and affixed to the voucher specimen. No chromosome numbers without confirming voucher specimens are presented in this paper. All voucher specimens are deposited in the herbarium of Iowa State University.
THE GENUS PHALARIS

Taxonomic Considerations

**Phalaris** L. *Sp. Pl.* 54. (1753)


*Calamagrostis* Adans. (*sensu* Sibth.) *Fl. Oxon.* 37. (1794) pro parte.


**DESCRIPTION**

Plants annual from fibrous underground roots or perennial from a dense crown or vigorous underground rhizomes; culms erect, terete; uppermost sheaths somewhat dilated distally; ligule up to 12 mm. in height, membranous, truncate; blades linear, flat; panicle ovoid, sub-ovoid, or cylindrical, unbranched or with a few short, closely-appressed branches at base; spikelets 30 to several hundred, laterally compressed, 1-flowered, the single fertile floret subtended by 1 or 2 sterile florets; disarticulation above the glumes; glumes usually glabrous, rarely hirsute, equal or sub-equal, naviculare to acuminate, often keeled, the keel frequently broadened into a wing, wing margin entire, erose, or denticulate; sterile florets 1 or 2 or obsolete, subulate to somewhat swollen...
to chaffy, usually pubescent; fertile lemma coriaceous to in-durate, glabrous or pubescent, often shiny; palea thin and delicate, obscurely 2-nerved, glabrous; stamens 3; stigmas 2, plumose; fruit somewhat flattened and elongated; basic chromosome number 6 or 7; diploids, tetraploids, pentaploids, hexaploids, and aneuploids.

Type of the genus: *Phalaris arundinacea* L. (Britton and Brown, 1913).

**HISTORY OF THE GENUS**

The earliest mention of *Phalaris* is possibly that of Dioscorides in the first century A.D. (see translation by Goodyer, transcribed by Gunther, 1854). Dioscorides refers to a plant with stalks that are knotty, reed-like and much like *Zea* in overall appearance ("Zea", in Dioscorides' terminology, was *Triticum*, perhaps *T. Dicoccon*). On the basis of Dioscorides' description it does not seem possible to assign this plant positively to *Phalaris*. The drawing accompanying the description was made by a Byzantine artist circa 525 A.D. and provides no information as to the identity of Dioscorides' plant.

A description similar to that of Dioscorides' by Matthioli (1554) likewise cannot be positively assigned to *Phalaris*. Bauhin (1623) listed two phrase-names in *Phalaris*. Both of these phrase names were included by Linnaeus (1753) in synonymy under *P. canariensis*. One of Bauhin's names, *Phalaris major semine nigro* was described as "quo Canarios passeres precipitue nutriunt" and was reported as occurring in the
"Canaria insulis".

Rayus (Ray), in 1694, extended the range of the grasses mentioned by Bauhin to include Messina in Sicily, Baiae and Nespolini (Naples) in Italy, and Monspelium in Gallia (France).

Linnaeus (1745) included two species of Phalaris in his treatment of the flora of Sweden. The first of these, identified by the phrase name Phalaris panicula oblonga, was reduced to synonymy under Phalaris arundinacea in later works by the same author. The second species, Phalaris spice cylindrica, was later given as a synonym of Phalaris phleoides by Linnaeus.

In Linnaeus' Materia Medica (1749), a species with the name Phalaris panicula subovata spiciformi, glumis carinatis was listed as providing food (nutriens) for small birds (aviculae) and growing in "Canarise, Hetruriae, Hispaniae". This name was given as a synonym of Phalaris canariensis by Linnaeus in 1753.

The first publication of Phalaris using the binomial system was in the first edition of Linnaeus' Species Plantarum (1753). Five species and one variety were included: P. canariensis, P. arundinacea, P. arundinacea var. picta, P. erucaeformis, P. phleoides, and P. oryzoideae. The last three of the above named, P. erucaeformis, P. phleoides, and P. oryzoideae, were subsequently transferred by other authors to Beckmannia, Phleum, and Leersia, respectively. Phalaris was placed in Triandria, Digynia in Linnaeus' sexual system of classification. Five new species, P. aquatica, P. bulbosa, P. utriculata, P. tuberosa, and P. paradoxa were described by
Linnaeus in later editions of the *Species Plantarum* and in other works before his death in 1778.

Lamarck (1783, p. 92) reviewed *Phalaris* and included twenty-one species. Lamarck's description of the genus is as follows:

> Les fleurs sont glumacées, & ont leur bâle extérieure uniflore, composée de deux valves égales, opposées, concaves, & tranchantes sur leur dos; leur bâle interne, bivalve & plus petite que l'extérieure; trois étamines munies d'anthères oblongues; & un ovaire arrondi, chargé de deux styles capillaires, dont les stigmates sont velus.

> Le fruit est une semence arrondie, un peu en pointe à ses deux bouts, lisse, & recouverte par la bâle interne de la fleur que ne s'ouvre point.

> Les Alpistes different des Fléoles, en ce qu'ils n'ont point leur bâle extérieure tronquée à son sommet, & terminée par deux dents aiguës. On les distingue particulièrement par leur bâle extérieure uniflore, souvent aplatie sur les côtés, & dont deux valves sont tranchantes sur leur dos.

No mention was made of the characteristic sterile florets found in the genus.

Using the above as a basis for delimiting *Phalaris*, it is not surprising that over one-half of the species included by Lamarck were in genera other than *Phalaris*, mostly *Phleum* but possibly also in *Agrostis, Leersia, Beckmannia, Pennisetum, Alopecurus, Koeleria, Polypogon, Helochloa*, and *Panicum*. The circumscription of *Phalaris* without using the sterile florets and coriaceous lemmas was not unique with Lamarck; no author previous to that time had even noted their occurrence.

Trianus (1828) included descriptions and illustrations
of nine species in the genus. All of the species in Trinius' work were members of Phalaris as now delimited. This was the \textit{first taxonomic treatment of the genus to make use of the sterile florets as important generic characters.}

Kunth (1833) included nineteen species in his synopsis of \textit{Phalaris}. Of these species, ten were treated as "species genuinae", two were considered "species anomalaev", and seven listed in "species dubiae". All of the members of the first groups mentioned are species or varieties of \textit{Phalaris} in its present sense while three of the last-mentioned group are in other genera.

The most extensive and critical review of the genus is that of Trinius (1840) in his monograph of the Phalarideae. Trinius treated fifteen species in this work, giving excellent descriptions for the most part, including a short key, and providing brief synonymies.

Steudel (1841) lists one hundred thirty-eight names that had been connected with \textit{Phalaris} prior to that time. Most of the names were treated as synonyms; only twenty species were recognized. In a later work (1855), Steudel listed twenty-five species in the genus and included a short description of each.

Since 1855, no monographic study has been made of \textit{Phalaris} on a world-wide basis. There have been occasional treatments of certain groups of species such as Jansen and
Wachter's treatment of Netherland's species (1916), Parodi's revision of Chilean species (1939), Ruiz' study on the species of Phalaris in Spain (1947), and Hitchcock's work on Phalaris in the United States (1950).

PALEOBOTANY

Brues and Brues (1909, p. 170) described the fossil species Melica primaeve based upon an impression collected by T.D.A. Cockerell in the Miocene shales at Florissant, Colorado. The illustration accompanying the description shows a series of bract-like structures clustered about a short axis. A portion of their original description is as follows:

The specimen shows a detached pair of secund spikelets viewed from the inner, or side nearest the rachis. The spikelet which is best preserved is about 12 millimeters long and shows five glumes; the lower of these, presumably one of the empty glumes, is visible only at the base, its apical portion extending under the shale beneath the lowest flowering glume. The latter is not well preserved at the tip, but the second is visible for its entire length. It is 10 mm. long and about 2 mm. wide, broadly lanceolate in outline, with acutely pointed but unawned apex. Between the second and third flowering glumes can be seen the apex of the second empty glume. The spikelet thus appears to be three flowered, which also appears to be true of the second one . . .

This specimen was identified as a member of the genus Melica by Brues and Brues because of the "secund insertion of the two spikelets as shown in the type, their large size and the form of the glumes, and the apparently very short joints of the rachilla".

MacGinitie (1953), in his review of the fossil plants of
the Florissant beds, rejects *Melica primaeva* Brues and Brues saying that the specimen was too poor for identification.

Beetle (1958) transferred *Melica primaeva* to *Phalaris* as *Phalaris primaeva* (Brues and Brues) Beetle. Beetle lists the following features as a basis for putting this fossil in *Phalaris*: lack of awns, lack of prominent veins, comparatively wide glumes, lemmas, and paleas, comparative size of glume to lemma, comparative size of lemma to palea, and paired grouping of florets.

On the basis of the illustration accompanying Brues and Brues' description the present author can make no attempt at classifying the structure. Certainly two of the reasons that Beetle gave for placing this fossil in *Phalaris*, namely lack of prominent veins and paired grouping of florets, do not seem to be valid. Many species in *Phalaris* have rather prominent veins in the glumes. The paired grouping of florets is not a characteristic of *Phalaris*. One of the characters separating *Phalaris* from many other genera of grasses is that it has only one floret. It would seem that the taxonomic recognition of a fossil species on the basis of such meager evidence is unwarranted.

A second fossil from the Miocene shales of Florissant, Colorado was assigned to *Phalaris* by Cockerell (1913, p. 76). This species, named *Phalaris (?) geometrorum* by Cockerell, is based upon a single structure bearing a nebulous resemblance
to a lemma. A portion of the original description is as follows:

A lemma 19 mm. long, nearly 3 1/4 broad near base; apex narrowly acuminate, but not awned; margin not hispid; median nervure colorless, hardly at all visible; outer nervures (one on each side) thick and dark, reddish-black as preserved, doubtless dark green in life, but pallid apically.

The illustration accompanying this description is that of a lanceolate structure with two lateral nerves and no mid-nerve. Once again, the evidence seems too meager to warrant placing this fossil in any specific genus.

CYTOLOGY AND CYTOGENETICS

A summary of chromosome numbers reported for this genus by previous authors and those reported in this paper by the present author is presented in Table 1. The somatic number is given in all cases. It may have either been directly observed or calculated from observations of meiosis in pollen mother cells. With the exception of the author's counts, no verification of voucher specimens for other reported numbers has been made. No specific voucher specimen citations accompanied the chromosome counts reported by other authors. Pertinent data for the author's chromosome counts are presented under the corresponding species in the taxonomic treatment following.

Referring to Table 1, it will be seen that two basic chromosome numbers have been reported in the genus. One group, including P. angusta, P. arundinacea, P. californica,
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<th>Species</th>
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<td>P. angusta</td>
<td>14</td>
<td>Saura (1943), Ambathsa (1956), present author</td>
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<tr>
<td>P. arundinacea</td>
<td>14</td>
<td>Church (1929)</td>
</tr>
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<td></td>
<td>28</td>
<td>Avdulov (1931), Jenkin and Sethi (1932), Trumble (1935), Parthasarathy (1939), Hutton (1953), Tateoka (1954), Ambathsa (1956), Carnahan and Hill (1955), present author</td>
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<td></td>
<td>27-31,35</td>
<td>Hanson and Hill (1953)</td>
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<td></td>
<td>29</td>
<td>Ambathsa (1956)</td>
</tr>
<tr>
<td></td>
<td>42</td>
<td>Brock (unpublished, cited in Darlington and Wylie, 1955)</td>
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<tr>
<td></td>
<td>56</td>
<td>Carnahan and Hill (1956) (experimentally produced polyploid)</td>
</tr>
<tr>
<td>P. arundinacea x</td>
<td>28</td>
<td>Jenkin and Sethi (1932), Ambathsa (1956)</td>
</tr>
<tr>
<td>P. aquatica</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>35</td>
<td>Ambathsa (1956)</td>
</tr>
<tr>
<td></td>
<td>42</td>
<td>Ambathsa (1956)</td>
</tr>
<tr>
<td>P. brachystachya</td>
<td>12</td>
<td>Miege (1939), Parthasarathy (1939), present author</td>
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<td>P. californica</td>
<td>28</td>
<td>Stebbins and Love (1941), Ambathsa (1956)</td>
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<tr>
<td>P. canariensis</td>
<td>12</td>
<td>Church (1929), Avdulov (1931), Katterman (1931), Parthasarathy (1939), Saura (1943), Hanson and Hill (1953), Ambathsa (1956), present author</td>
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<td><em>P. canariensis</em></td>
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<td>Trumble (1935), Parthasarathy (1939), Saura (1943), Hanson and Hill (1953), Hutton (1953), Ambathsa (1956), present author</td>
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<td><em>P. coerulescens x P. minor</em></td>
<td>21</td>
<td>Hutton (1953) (F₁ hybrid)</td>
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<td></td>
<td>42</td>
<td>Hutton (1953) (experimentally produced allopolyploid)</td>
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<td><em>P. lemmonii</em></td>
<td>14</td>
<td>Parthasarathy (1939), present author</td>
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<td><em>P. minor</em></td>
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<td></td>
<td>28, 29</td>
<td>Hanson and Hill (1953), present author</td>
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<td><em>P. minor x P. aquatice</em></td>
<td>28</td>
<td>Hutton (1953) (F₁ hybrid), Ambathsa (1956)</td>
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<td>56</td>
<td>Hutton (1953) (experimentally produced allopolyploid)</td>
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<td><em>P. paradoxe</em></td>
<td>14</td>
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<tr>
<td><em>P. pityeosis</em></td>
<td>14</td>
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<td><em>P. truncata</em></td>
<td>12</td>
<td>Ambathsa (1956), present author</td>
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<tr>
<td>Species</td>
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<tr>
<td>-----------------</td>
<td>----</td>
<td>---------------------------------------------------------------------------</td>
</tr>
<tr>
<td><em>P. aquatica</em></td>
<td>28</td>
<td>Jenkin and Sethi (1939), Trumble (1935), Miege (1939), Parthasarathy (1939), Hanson and Hill (1953), Hutton (1953), Ambathsa (1956), present author</td>
</tr>
</tbody>
</table>

*P. caroliniana*, *P. coerulescens*, *P. lemmonii*, *P. minor*, *P. paradoxus*, *P. platensis*, and *P. aquatica*, has a basic number of *x*=7; the other group, including *P. brachystachys*, *P. canariensis*, and *P. truncata*, has a basic number of *x*=6.

Avdulov (1931) suggested that the *x*=6 number of *P. canariensis* resulted from the loss of a chromosome in an *x*=7 form. Darlington (1937) demonstrated that conditions favoring loss or gain of a chromosome can be produced by means of unequal translocations. In a study of the cytology of the Phalarideae, Parthasarathy (1939) reported that one pair of chromosomes in the 12-chromosome group is definitely longer than the other pairs. Parthasarathy suggests that the 12-chromosome types are derived from the 14-chromosome types by the fusion of two pairs of chromosomes with sub-terminal constrictions to give one pair with median constrictions. The chromosome complements of *P. truncata*, *P. brachystachys*, and *P. canariensis* (*2n*=12) in material studied by the author did not show much variation in the size of the chromosomes; all
appeared to be about the same size. Ambathsa (1956), in an extensive treatment of the cytology of *Phalaris*, also suggests that the 12-chromosome types were derived from the 14-chromosome types by the fusion of two chromosomes, but proposes that one had a median centromere and the other had a terminal centromere. Ambathsa submits that the terminal-centromere chromosome could fracture, lose its centromere and, subsequently, fuse with a median-centromere chromosome to produce a single chromosome with a sub-median centromere. Stebbins (1950) states that it is impossible to change the basic number through simple transverse fragmentation and end-to-end fusion of single chromosomes. He further states that reduction of basic chromosome number must involve loss of a centromere plus at least a small amount of adjacent chromosomal material. Much evidence seems to indicate that a chromosome with two centromeres cannot function properly. Until experimental evidence can be introduced into the problem of chromosome number reduction in *Phalaris*, the author is unable to suggest which, if any, of the suggested mechanisms have been in operation in this genus.

Ambathsa (1956) divided the n=6 chromosome group into two parts: (1) species with "I" shaped chromosomes, including *P. brachystachya* and *P. canariensis* and (2) species without "I" shaped chromosomes, including *P. truncata*. These groupings do not reflect the morphological relationships
between the species involved. *P. brachystachys* and *P. trun-
cata* are very similar (see Plate 6 and Table 10), the most
obvious difference being that the former is an annual and the
latter a perennial. *P. canariensis* possesses features not
found in either of the other two, the most prominent being
the chaffy sterile florets (Plate 6,c).

Ambathsa proposed two major subdivisions in the $x=7$
group. One subdivision, including *P. angusta*, *P. californica*,
*P. caroliniana*, *P. lemmonii*, *P. paradoxo*, and *P. platensis*,
have a haploid chromosome number of $n=7$; the other subdivision,
including *P. minor* and *P. tuberosa* has a haploid number of
$n=14$. *P. arundinacea* and *P. coerulescens* have both $n=7$ and
$n=14$ as haploid numbers within the population.

Ambathsa further divides the $n=7$ group into two cate-
gories: (1) those species with no "J" or "I" shaped chromo-
somes (*P. coerulescens*) and (2) those species with "J" or "I"
shaped chromosomes (*P. paradoxo*, *P. caroliniana*, *P. angusta*,
and *P. platensis*). These groupings appear to agree only par-
tially with the morphological evidence as to relationships.

*P. paradoxo* and *P. coerulescens*, separated on the basis of
chromosome shapes, are very similar morphologically. The main
difference between these two is that the former is an annual,
the latter a perennial. *P. caroliniana*, *P. angusta*, and *P.
platensis* are somewhat similar to one another but do not seem
to be closely related.
Ambathsa proposed that the n=7 group is the basic stock from which other species in *Phalaris* have been derived. He further suggests three major developmental trends from this stock: (1) a decrease in chromosome number to n=6, resulting in such species as *P. brachystachys*, *P. canariensis*, and *P. truncata*, (2) doubling of chromosome number by autotetraploidy, as in *P. minor*, and (3) doubling of chromosome number by allotetraploidy, as in *P. arundinacea*. Five species, *P. coerulescens*, *P. paradoxa*, *P. caroliniana*, *P. angusta*, and *P. pletenis*, have retained the n=7 number and have undergone specialization at this level.

Stebbins (1950) has suggested that autopolyploidy is not commonly found in nature and states that many of the supposed autopolyploids are actually of hybrid origin. Further work is needed in the polyploid species of *Phalaris* to determine the nature of ploidy in this genus.

The names *P. nodosa*, *P. tuberosa*, and *P. aquatica*, as used by Ambathsa, cannot be identified. Ambathsa did not make any voucher specimens for his chromosome counts and did not cite any references used for the identification of the species studied. Apparently Ambathsa used the names on the seed packets he received from Australian plant introduction services.

Seven of the thirteen species that have been studied cytologically are diploid annuals (*P. angusta*, *P. brachy-
stachys, P. canariensis, P. caroliniana, P. lemmonii, P. paradoxa, and P. platensis); one is a diploid perennial (P. truncata); two were tetraploid perennials (P. californica and P. aquatica). Two of the perennials, P. arundinacea and P. coerulescens, are represented by both diploids and polyploids.

Stebbins (1950, p. 468) states that the annual, specialized species of Phalaris (Stebbins gave P. canariensis and P. paradoxa as examples) have smaller chromosomes than the perennial, generalized species (Stebbins gave no examples). The present author is unable to corroborate this statement. Material of P. canariensis available for study had some of the largest chromosomes of any of the species examined. The chromosomes of P. paradoxa were relatively small, but barely smaller than those of P. arundinacea and P. truncata both of which are perennials. P. paradoxa chromosomes were actually larger than the chromosomes of P. aquatica and P. coerulescens which are also perennials. Ambathsa (1956) likewise found many annual species of Phalaris whose mean chromosome size exceeded that of the perennials.

There have been several successful attempts at producing interspecific hybrids in Phalaris. Of these hybrids, only two have been examined cytologically. These are: P. aquatica x P. arundinacea and P. aquatica x P. minor. The results of these studies are presented in the taxonomic treatment of these species.
Drawings of meiotic figures in species studied by the author are presented in Plate 1.

**PHYLOGENETIC CONSIDERATIONS: GENERIC LEVEL**

The reduction patterns displayed in the spikelets and inflorescences of *Phalaris* have perplexed grass phylogenists for years but have stimulated investigation of the floral anatomy and development in only one species. Holt (1954) made a detailed study of the initiation and development of the inflorescence of *P. arundinacea*. He demonstrated that the fertile floret is ontogenetically lateral and not terminal as commonly interpreted. The two lowermost florets are much reduced; the third floret is fertile and develops normally; the uppermost floret never develops. Its apical meristem becomes highly vacuolated and soon becomes a mass of lignified tissue compressed between the palea and the subtending sterile floret. Thus it can be seen that the spikelet in *Phalaris* is indeterminate rather than determinate in development. Unfortunately the dearth of detailed ontogenetic studies in many genera of grasses, especially those with apparently determinate spikelets, prevents the broad use of anatomical development patterns in establishing intergeneric relationships.

Prat (1932, 1936), in a radical departure from the traditional system of classification based primarily upon inflorescence type and spikelet structure, emphasized various anatomical features in the formation of a classification of the
Plate 1. Meiotic figures in *Phalaris*

a. *P. paradoxa*, 2n=14
b. *P. coerulescens*, 2n=14
c. *P. minor*, 2n=28
d. *P. erundinacea*, 2n=28
e. *P. aquatics*, 2n=28
f. *P. trunca*, 2n=12
g. *P. brachystachys*, 2n=12
h. *P. canariensis*, 2n=12
i. *P. angusta*, 2n=14
j. *P. lemnosii*, 2n=14

All figures approximately 800X
grass family. Three sub-families were recognized: Bambusoideae, Panicoideae, and Festucoideae. The Bambusoideae were characterized as having a complex leaf epidermis with papillae, warts and bicellular hairs. Members of the sub-family Panicoideae were reported to possess a complex leaf epidermis with bicellular or cushion-based hairs, silicified cells of complicated forms (hour-glass or dumb-bell shaped), rhomboid stomata, and basic chromosome numbers of 5, 6, or 9. The Festucoideae have a simple epidermis with silicified cells of a rounded or square shape, unicellular hairs, ovoid stomata, and a basic chromosome number of 7. On the basis of these characters, Phalaris is definitely a member of the Festucoideae in having all of the characters attributed to this sub-family. Some of the species of Phalaris have a basic chromosome number of 6, but it is probable that this is derived from an x=7 ancestor. Plate 2 shows the leaf epidermis of three species of Phalaris.

Reeder (1957) studied four embryo characters that seem to possess phylogenetic significance in the grass family. These characters and the corresponding observations made upon Phalaris by Reeder are presented in Table 2.

Stebbins (1956), in a review of previous work on grass phylogeny by various authors, suggests other criteria for estimating phyletic relationships in the Gramineae. Included in these are: relative size of embryo, nature of starch
Plate 2. Glume epidermis, leaf epidermis, lodicules, and starch grains of *Phalaris*

a. Glume epidermis of *P. cenariensis*, 400X
b. Abaxial leaf surface of *P. arundinacea*, 600X
c. Abaxial leaf surface of *P. purpurea*, 600X
d. Flower showing lodicules, *P. arundinacea*
e. Starch grain, *P. cenariensis*
Table 2. Synopsis of Reeder’s observations on grass embryos

<table>
<thead>
<tr>
<th>Character</th>
<th>Festucoid</th>
<th>Panicoid</th>
<th>Phalaris</th>
</tr>
</thead>
<tbody>
<tr>
<td>course of vascular system</td>
<td>coleoptile inserted at about the point where scutellum bundle diverges</td>
<td>coleoptile inserted some distance above the point of divergence of scutellum bundle</td>
<td>festucoid</td>
</tr>
<tr>
<td>epiblast</td>
<td>usually present in the Festucoideae</td>
<td>always absent in the Panicoidae</td>
<td>present</td>
</tr>
<tr>
<td>embryonic leaf</td>
<td>first embryonic leaf with few vascular bundles and margins which meet but do not overlap</td>
<td>first embryonic leaf with many vascular bundles and overlapping margins</td>
<td>festucoid</td>
</tr>
<tr>
<td>lower portion of scutellum</td>
<td>lower portion of scutellum absent or fused with the coleorhiza</td>
<td>distinct cleft between coleorhiza and lower portion of scutellum</td>
<td>festucoid</td>
</tr>
</tbody>
</table>

Starch grains (simple or compound), chromosome size, and number and type of lodicules. Phalaris has relatively small embryos (for example, see Plate 6, d, P. canariensis), compound starch grains (Plate 2, e), relatively large chromosomes (Plate 1), and two, pointed lodicules (Plate 2, d). All of these are festucoid features.

For many years the tribe Phalarideae has been a repository for grass genera whose main distinguishing feature is the possession of one or more sterile or staminate florets.
subtending a single fertile floret. Hackel (1890), Bews (1929) and Hubbard (1944) included six genera in the Phalarideae: Ehrharta, Microlaena, Tetrarrhena, Anthoxanthum, Hierochloë, and Phalaris. Reeder (1957) reported that Ehrharta was panicoid with respect to three of the four embryo features studied. Tateoka (1957) placed Ehrharta, Microlaena, and Tetrarrhena in a new tribe, the Ehrharteae and included it in the sub-family Arundoideae near the tribes Melicoæ, Glyceriæ, Stipeæ, and Aristiæ. Darlington and Wylie (1955) give the basic chromosome number of Ehrharta and Microlaena as x=12. On the basis of floral morphology, embryo structure, and chromosome number it seems probable that Ehrharta, Microlaena, and Tetrarrhena are not closely related to Phalaris, Hierochloë, and Anthoxanthum and should be segregated from them. Riecken (1929) studied spikelet morphology of selected species in Anthoxanthum, Hierochloë (referred to Torreia by Riecken), and Phalaris. Riecken reported that Anthoxanthum differs from the other two genera in having two stamens and no lodicules; Phalaris and Hierochloë both have three stamens and two lodicules. In addition Anthoxanthum has a basic chromosome number of x=5, while Hierochloë has x=7 and Phalaris has x=6 or 7. On the basis of this information, it seems that Anthoxanthum has its affinities elsewhere than with Phalaris and Hierochloë.

Phalaris and Hierochloë possibly represent steps in a
reduction series with *Hierochloë* having staminate rudimentary florets and *Phalaris* having much reduced, sterile rudimentary florets.

In summary, it is evident that *Phalaris* has its strongest evolutionary ties with the festucoid trend of specialization within the Gramineae. The highly modified spikelet structure of *Phalaris* permits no more than speculation as to its relationship with other genera. It would seem probable that the hypothetical "pro-Phalaris" was a festucoid grass with rather large, wingless, or very narrowly winged, sub-equal glumes, four florets, the upper floret being somewhat reduced, and a fairly dense, lobed panicle. These characters are all represented in other festucoid genera. Characters common to many festucoid genera are presumed to be primitive with respect to *Phalaris*. Those characters that are highly modified and restricted to *Phalaris* are presumed to be advanced. Reduction and specialization of several of these features has resulted in species with broadly winged glumes, highly reduced sterile florets, and ovoid or cylindrical inflorescences. A given species of *Phalaris* may possess some advanced features and, at the same time, retain some relatively primitive characters, e.g. *Phalaris arundinacea* has primitive features such as wingless glumes and a lobed inflorescence; advanced features include several levels of polyploidy and reduced, subulate, sterile florets.
PHYLOGENETIC CONSIDERATIONS: INFRA-GENERIC LEVEL

Since the hypothetical primitive Phalaris does not exist today, we can only speculate as to the relationships between the present day species. A phylogenetic chart (Figure 1) is provided as the basis of the following discussion.

The center of diversity of Phalaris is in the Mediterranean region. Seven of the fifteen species in the genus, including P. brachystachys, P. truncata, P. canariensis, P. coerulescens, P. paradoxo, P. minor, and P. aquatica, were probably restricted to this area prior to being distributed to other parts of the world by man (Figure 2). P. minor has extended its range somewhat eastward from the Mediterranean, apparently along some of the old caravan routes.

The following four variations in the structure of the sterile florets have taken place in the Mediterranean species:

1. Reduced, swollen, sterile florets. Two species, P. brachystachys and P. truncata have sterile florets that are reduced to this form. The former is an annual, the latter a perennial. Thellung (1915) states that P. brachystachys is a weed that has evolved the annual habit in response to annual tilling of the soil. Thellung's explanation of the annual habit in this, as well as in other groups, may have some merit but it would seem necessary to obtain more precise data concerned with selective values and evolutionary rates before positive statements can be made with respect to this idea.
Figure 1. Possible phyletic relationships within the genus Phalaris.
CAROLINIANA
annual
2n=14

AMETHYSTINA
annual
2n=？

CALIFORNICA
perennial
2n=28

ARUNDINACEA
perennial
2n=14, 27, 28, 29, 30, 31, 35, 42

AQUATICA
perennial
2n=28

MINOR
annual
2n=28, 29

ANGUSTA
annual
2n=14

ATHERMONII
annual
2n=14

PLATENSIS
annual
2n=14

COERULESCENS
perennial
2n=14, 28

PARADOXA
annual
2n=14

MADERENSIS
annual
2n=？

CANARIENSIS
annual
2n=12

TRUNCATA
perennial
2n=12

BRACHYSTACHYS
annual
2n=12

x=7
Figure 2. Geographic distribution of the genus Phaleria
2. Bract-like, chaffy, sterile florets. The only species in this category is *P. canariensis*. This species approaches the presumed primitive form most closely in its sterile floret type (Plate 6, d). It must be pointed out that, while *P. canariensis* is perhaps primitive with respect to sterile florets, it is advanced as far as glume-wing development and reduced chromosome number are concerned.

3. Obsolete sterile florets. *P. coerulescens*, a perennial, and *P. paradoxe*, an annual, are the only two species represented in this trend. In these two species, the sterile florets are very reduced and consist of only a small amount of tissue at the base of the fertile floret. In addition to the extreme modification of the sterile florets, the spikelets tend to fall in groups, with one fertile spikelet surrounded by several staminate or sterile spikelets. *P. paradoxe* is highly variable in this respect and shows a number of subspecific groups.

4. Subulate sterile florets. On the basis of geographic distribution, this complex can be further divided into the following three lines of development: (1) Old World species, (2) circumboreal species, and (3) New World species.

Three Old World species, *P. minor*, *P. aquatica*, and *P. maderensis*, are included in the first line of development. All of these species have only one well-developed sterile floret. *P. minor* and *P. aquatica* are native to the Mediter-
P. maderensis is apparently restricted to the Madeira Islands, 450 miles northwest of Morocco. A possible explanation for this disjunct distribution is offered by Ridley (1930). Ridley suggests that the flora of the Canary, Cape Verde, and Madeira Islands is derived from the west coast of Africa by an ancient land connection. Another possible explanation for the distribution of P. maderensis is that the ancestral disseminules may have been carried over the oceanic gap by birds. Speciation in response to this new environment may have subsequently taken place.

The second line of development includes a single circumboreal species, P. arundinacea. This is the only species of Phalaris that has a natural range including both the Old and New Worlds. It seems possible that some taxon at least very similar to P. arundinacea may have given rise to the next developmental line treated, the New World species.

The New World species include P. californica, P. caroliniana, P. emethystina, P. lemmonii, P. plethensis, and P. angusta. These six species appear to have evolved along four evolutionary trends as based upon their cytology and inflorescence and spikelet morphology.

The first of these trends includes only P. californica, a tetraploid perennial restricted to California and southern Oregon. Morphologically this species remained relatively unspecialized in retaining wingless glumes and the perennial
habit.

The second evolutionary trend includes *P. caroliniana* and *P. amethystina*. These species are diploid annuals that have winged glumes, somewhat flattened fertile florets, and compact, ovoid inflorescences. *P. caroliniana* has a broad range that includes southern United States and northern Mexico. *P. amethystina* is restricted to central Chile, almost 4000 miles from the nearest station of *P. caroliniana*.

A third evolutionary trend contains two diploid annuals, *P. lemmonii* and *P. platensis*. These taxa have wingless glumes, inflated fertile florets, and somewhat cylindrical inflorescences. *P. lemmonii* is restricted to coastal valleys in California; *P. platensis* is found in northern Argentina and Uruguay.

The fourth trend includes the diploid annual species, *P. angusta*. This species has winged glumes, somewhat flattened fertile florets, and a very compact, cylindrical inflorescence. *P. angusta* is found in southern and western United States and in central South America.

Three of the four evolutionary trends discussed above contain taxa with disjunct distributions including North and South America. Stebbins (1950, p. 544) suggests five ways in which a disjunct distribution can arise: (1) direct dispersal over a long distance (the so-called "sweepstakes dispersal" of Simpson), (2) dispersal over a shorter distance
through wider distribution and greater proximity of the two areas in the past, (3) wider distribution with complete continuity between the two areas in the past, (4) dispersal over a series of short distances by means of "stepping-stones", and (5) migration from a former area outside of the two present areas.

The first proposal, that of sweepstakes dispersal, seems quite possible. Grant (1959) suggests this as a solution to parallel distribution problems in certain taxa of the Polemoniaceae. In this group, as well as in *Phalaris*, a number of bird migratory routes coincide fairly well with the distributional patterns. Shorebirds such as the Wilson phalarope, spotted sandpiper, killdeer, and snowy plover pass from western North America to coastal Peru, Chile, and Patagonia (Grant, 1959). In the Polemoniaceae the distribution of seeds is facilitated by a mucilaginous outer layer which may cause them to stick to the feathers of birds. The mode of dispersal in *Phalaris* would be quite different but fundamentally of the same level of importance. The species involved are commonly found in wet areas of grasslands, near pools, etc. These are the very same areas visited by shore birds in their migratory activities. It is entirely conceivable that *Phalaris* florets have been transported in the digestive tracts of shorebirds from North America, particularly California, to South America. A relative of these species, *P. canariensis*, has been used in
commercial bird seed preparations for many years so there is little reason to doubt the value of these seeds in bird feeding activities. The indurate lemma, which almost completely encloses the caryopsis and palea, could perhaps protect the fruit from digestive breakdown within the bird's system.

The second proposal of Stebbins, that of dispersal over a shorter distance through wider distribution and greater proximity of the two areas in the past, is certainly not without merit. This suggestion would seem to involve either a migration of similar nature to sweepstakes dispersal or a trans-tropical land migration. The latter alternative does not seem acceptable. If we assume that the tropics themselves, regardless of their size or latitudinal position in the past, were of substantially the same climatic character, then a taxon migrating from North to South America must adapt to gradually warmer and more humid climates on the way southward, finally reaching tropical conditions, then gradually reverse this adaptive trend as it emerges on the southern edge of the tropics and moves out onto the coastal areas and pampas. The ranges of the species involved are separated by at least 3000 miles at the present. However, geologic and climatic changes may well have destroyed the closer proximity possessed by the taxa in the past.

Stebbins' third proposal, a wider distribution with complete continuity between the two areas in the past, seems
unlikely as an explanation of the disjunct distributions of species complexes in Phalaris. Grant (1959) rejected this suggestion for vicarious taxa in the Polemoniaceae. He asserts that, if temperate groups on opposite sides of the tropics diverged independently from a tropical ancestor, their systematic relationships with one another will not be particularly close since the evolutionary changes in passing from the ancestral group to either modern group would probably not progress in the same direction at the same speed. The present author is inclined to agree. Certainly it is difficult to conceive that a common ancestor could give rise to two separate complexes, one in each hemisphere, each of which has its component species more closely related to species in the other hemisphere than to the other members of its complex.

The fourth alternative of Stebbins, that of dispersal over a series of short distances by means of "stepping-stones", cannot be summarily dismissed. In the geologic past the broadening areas of cool climates may have reduced the latitude of the tropics considerably. This could also mean that the higher elevations in the tropics may have been much more temperate in climatic character than at the present time. These temperate "stepping-stones" may have provided a means of migration allowing North American taxa to expand their ranges southward to similar environments. Present day distributions in Phalaris provide little evidence for or against
this proposal. Occasional collections of $P. \text{angusta}$ have been made in the Colombian highlands but there is no assurance that these are relict rather than introduced populations.

The last-mentioned proposal of Stebbins, migration from a former area outside of the two present areas, seems quite improbable. If the so-called "former area" were temperate in climate, the migration pattern would involve movement through sub-tropics to tropics, thence, reversing the climatic change, back through sub-tropics to temperate regions. That a single taxon could be subjected to so many environmental and competitive changes and yet remain relatively unchanged seems rather remote. If the "former area" were tropic in nature, the migration pattern would be simpler, but, once again, it seems improbable that a taxon would evolve in the same direction and at roughly the same speed in two separate hemispheres.

A possibility that cannot be overlooked in explaining the vicarious species in $\text{Phalaris}$ existing in North and South America is that they were derived from $P. \text{angusta}$ or basic stock similar to it. $P. \text{angusta}$ has a disjunct distribution embracing sections of both of these continents. The best argument against this proposal is that $P. \text{angusta}$ itself seems to be a relatively advanced species whose morphologic specializations have taken a different evolutionary direction than either of the other species complexes. It appears quite pos-
sible that *P. angusta* has also been distributed from North to South America by migratory birds, but has not undergone morphologic speciation.

In summary, *Phalaris* has its center of diversity in the Mediterranean region. Initial evolution may have produced a series of complexes that were specialized not only in the unique characters of their sterile florets but also, in some instances, reduced chromosome numbers. Along with this initial specialization, a type arose which carried the generic characters almost entirely around the world in the northern hemisphere. This prototype, in its southward migration in the Americas, became specialized in a number of respects such as the development of winged glumes, ovoid or cylindrical inflorescences, and annual habit. Subsequent long distance dispersal may have carried the genus into South America where further speciation occurred.

**Key to the Species of the Genus Phalaris**

1. Fertile floret glabrous or with only a few hairs at the base of the sterile florets; sterile florets obsolete (0.1–0.2 mm. long) . . . . . . . . . . . . .
2. Spikelets falling in groups of seven, one fertile spikelet surrounded by six sterile spikelets, the group falling as a unit; some sterile spikelets deformed and clavate; fertile lemma 2.7–3.3 mm. long; caryopsis 2.2–2.8 mm. long; annual plants with fibrous roots; culms not bulbous at base . . . . . 1. *P. paradoxa*.

2. Spikelets falling singly, not in groups or seven, or, if occasionally falling in groups, these not uniformly consisting of seven spikelets and with more than one
fertile spikelet per group; sterile not deformed or clavate; fertile lemma 2.9–4.2 mm. long; caryopsis 9.4–3.5 mm. long; perennial plants arising from a dense crown; culms bulbous at base.

1. Fertile floret densely or sparsely pubescent; sterile florets usually at least one-third as long as fertile florets, if shorter, then more or less swollen and fleshy (see illustrations of P. truncata and P. brachystachys, Plate 6).

3. Sterile floret one, well developed or obsolete.

4. Sterile floret obsolete, less than 0.3 mm. long.

5. Glumes truncate; inflorescence narrowly cylindrical; caryopsis 1.6–1.8 mm. long; known only from Madeira Islands (see illustration, Plate 7, i–k).

5. Glumes acute to acuminate; inflorescence ovate-oblung to broadly cylindrical; caryopsis more than 2.2 mm. long.

6. Glume wings usually toothed or erose; annual plants with non-bulbous culm bases.

6. Glume wings usually entire; perennial plants from a dense crown; culm bases sometimes bulbous.

3. Sterile florets two.

7. Sterile florets unequal, the longer 1.0–2.2 mm. long, the shorter less than 0.5 mm. long.

7. Sterile florets equal or nearly so.

8. Sterile florets swollen and somewhat fleshy, less than 1 mm. long (see illustrations of P. brachystachys and P. truncata, Plate 6).

9. Glumes 5.5–6.2 mm. long, truncate; caryopsis 2.8–3.0 mm. long, 1.2–1.3 mm. wide; perennial plants arising from a dense crown.

9. Glumes 5.5–6.2 mm. long, truncate; caryopsis 2.8–3.0 mm. long, 1.2–1.3 mm. wide; perennial plants arising from a dense crown.

6. P. truncata.
9. Glumes 6.3–8.5 mm. long, rather abruptly pointed and acute; caryopsis 3.5–3.9 mm. long; 1.5–1.7 mm. wide; annuals 7. P. brechystachys.

8. Sterile florets subulate or chaffy, usually more than 1 mm. long ......... 10

10. Sterile lemmas broad and chaffy, not subulate; more than half as long as fertile lemma .... 8. P. canariensis.

10. Sterile florets subulate, usually less than one-half as long as fertile lemma ........ 11

11. Glumes not winged (very narrowly winged in P. californica) ....... 10

12. Fertile floret turgid, nearly round in cross section, pubescence spreading; annuals; plants of California (adventive, Australia) .... 14. P. lemmonii.

12. Fertile floret not turgid, usually elliptic in cross section, pubescence appressed; perennials with spreading, scaly rhizomes or arising from a dense tussock or annuals. 13

13. Inflorescence broadly ovate with truncate base, usually not more than two times as long as broad; perennial plant without rhizomes, arising from a dense crown; California or Oregon 10. P. californica.

14. Plants perennial from scaly rhizomes; inflorescence usually more than 5 cm. long, lobed or branched at the base; caryopsis 2.0 mm. long or less; mostly northern hemisphere. ......... 15

15. Leaves longitudinally striped with white 4a. P. arundinacea f. picta.

15. Leaves uniformly green ....... 4b. P. arundinacea f. arundinacea.

14. Plants annual from fibrous root system; inflorescence less than 4.5 cm. long, not lobed or branched at the base; caryopsis 2.0 mm. long or more; west coast of Chile ....... 12. P. amethystina.
11. Glumes winged (very narrowly in P. californica) .............. 16

16. Mid-nerve and lateral nerves of glumes sharply scabrous with many (9 or more) short stout hairs ....... 17

17. Fertile lemma turgid, the tip acuminate and glabrous ........ 18

18. Glumes 4.9--6.7 mm. long; California .......... 14. P. lemmonii.

18. Glumes 3.9--4.3 mm. long; southern South America (adventive, Netherlands) ... 13. P. platensis.

17. Fertile lemma more or less flattened; the tip acute and pubescent .... 19

19. Inflorescence broadly ovate, usually not more than two times as long as broad; glume wing very narrow and inconspicuous; perennial plants with scaly rhizomes; caryopsis more than 2.4 mm. long; California ........ 10. P. californica.

19. Inflorescence cylindrical, usually three or more times as long as broad; glume wing broad and well developed; annual plant with fibrous roots; caryopsis less than 2.2 mm. long.... 20

20. Glumes acute to acuminate; caryopsis 2.1--2.2 mm. long; southern South America ... 12. P. amethystine.

20. Glumes naviculate or truncate; caryopsis less than 1.8 mm. long .... 9. P. angusta.

16. Midnerve of glumes scabrous with short, delicate barbs; lateral nerves glabrous or with only a few (less than five) barbs .... 22

21. Fertile lemma turgid, the tip acuminate and glabrous, pubescence spreading;
caryopsis 2.1—2.3 mm. long; California
(adventive, Australia) . . 14. P. lemmonii.

21. Fertile lemma more or less flattened, the
tip acute, somewhat pubescent, pubescence
of lower areas of lemma appressed; caryopsis
1.4—1.6 mm. long; southern United States
west to California . . 15. P. caroliniana.

1. Phalaris paradoxa

Phalaris paradoxa L. Sp. Pl. ed. 2. 2:1665. (1763)
(Holotype in LINN; photograph of holotype in GH)

Phalaris praemorsa Lam. Fl. Frunc. 3:566. (1778)

Phalaris pruinosa Lam. ex Beauv. Agrost. (1819) (Name
given in index as synonym of P. paradoxa L.)

Phalaris appendiculata Roem. and Schult. Mant. 2:216.
(1824)

Phalaris dentata Sieb. ex Roem. and Schult. Mant.
2:216. (1824) (Name given as synonym of P. appendicu-
lata Roem. and Schult.)

5:51. (1840) (Holotype in LE)

ser. 6. 5:51. (1840) (Holotype in LE)

(1843)

Phalaris pseudo-paradoxa Fig. and De Not. Mem. Acc.
Torin. ser. 2. 14:11. (1853)

Alger. 2:24. (1854)

Phalaris paradoxa var. intermedia Coss. and Dur. Expl.
Sci. Alger. 2:24. (1854)

Phalaris paradoxa var. praemorsa (Lam.) Coss. and Dur.
Expl. Sci. Alger. 2:25. (1854) (Based on P. praem-
orsa Lam.)
Phalaris utriculosa L. ex Munro. Jour. Linn. Soc. 6:36. (1862) (Munro cites this name which is from Linnaeus' manuscript notes of Sp. Pl. ed. 1. A marginal note in the manuscript by Linnaeus equates this name to P. paradoxa.)


**DESCRIPTION**

Annual, tufted, culms 20–100 cm. tall; panicle up to 9 cm. long and 2 cm. wide, dense, oblong, tapering to narrow base; spikelets falling from the inflorescence in groups of 6 or 7, slender pedicelled, with 5 or 6 sterile spikelets clustered about a single fertile spikelet; sterile spikelets grading from those with well developed, narrowly-winged glumes up to 9 mm. long to those in which all spikelet parts are reduced to clavate knobs of tissue terminating the pedicel; glumes of fertile spikelet 5.5–8.2 mm. long, about 1 mm. wide, acuminate to subulate, the nerves conspicuous, upper
portion winged, the wing with a tooth-like projection near the middle; fertile florets of fertile spikelets 2.5--3.5 mm. long, 0.8--1.5 mm. wide, indur- te, light-colored, shining, glabrous or with a few short hairs near the apex; sterile florets of fertile spikelets obsolete, represented only by knob-like projections at the base of the fertile floret; grain 2.3--2.6 mm. long, 0.9--1.1 mm. wide, sub-ovoid to ellipsoid; somatic chromosomes 2n=14, the chromosomes ca. 3--5 microns long at diakinesis.

**OBSERVATIONS**

Members of this species are interesting in a number of respects. Some spikelets of the inflorescence are reduced and sterile. Usually the spikelets fall in groups of seven (occasionally six), with six (or five) sterile spikelets and one fertile spikelet.

There are three general types of sterile spikelets. For convenience the author has given these the identifying names clavate, reduced, and normal. The characters of these three kinds of sterile spikelets are presented below:

1. Clavate-sterile spikelets. Sterile spikelets of this group are very much reduced, the entire spikelet represented by a small club-shaped mass of tissue terminating the pedicel. These spikelets are always found at the base of the inflorescence (Plate 3, e).

2. Reduced-sterile spikelets. Spikelets of this group
Plate 3. Phalaris paradoxa and Phalaris coerulescens

a--h. Phalaris paradoxa; a. inflorescences 1/2 X, b. spikelet cluster with "normal" type sterile spikelet glumes 5X, c. fertile spikelet from "b" 5X, d. sterile spikelet from "b" 5X, e. spikelet cluster with "clavate" type sterile spikelet glumes (in foreground) and "reduced" type sterile spikelet glumes in background 5X, f. fertile spikelet of "e" 5X, g. fertile floret 5X, h. caryopsis 5X

i--k. Phalaris coerulescens; i. spikelets 5X, j. fertile floret 5X, k. caryopsis 5X
have glumes that are shorter than those of fertile spikelets in the same inflorescence. The glume tips are truncate in overall outline and are erose (Plate 3, e).

3. Normal sterile spikelets. Sterile spikelets of this class are very similar to the fertile spikelets. The main difference between the two is that the fertile spikelets are quite swollen by the developing floret while the sterile spikelets are flattened and contain aborted florets (Plate 3, b,d).

Preliminary investigations within this species revealed a number of correlations between various features. In order that a more precise concept of this variation pattern might be obtained, the author measured and examined several characters on a total of seventy-one specimens from the same number of collection stations. From these studies it was found that P. paradoxa could be divided into three classes with respect to the various combinations of sterile spikelet types (see previous discussion) making up the inflorescence. These three inflorescence classes are as follows:

1. Clavate-reduced. This inflorescence class has "clavate" type sterile spikelets at the base which gradeate into "reduced" type sterile spikelets at the tip. No "normal" type sterile spikelets are present. Represented by black bars in Figure 3.

2. Clavate-normal. Inflorescences of this class have
Figure 3. Relationship of inflorescence type to inflorescence length classes in *Phalaris paradoxa*.
INFLORESCENCE TYPE

- CLAVATE-REDUCED
- CLAVATE-NORMAL
- CLAVATE-REDUCED-NORMAL

INFLORESCENCE LENGTH (IN CM.) BY SIZE-CLASSES

NUMBER OF INDIVIDUALS

3.0-3.9 4.0-4.9 5.0-5.9 6.0-6.9 7.0-7.9 8.0-8.9 9.0-9.9
"clavate" type sterile spikelets at the base and "normal" sterile spikelets near the tip. There are no "reduced" type sterile spikelets present. This class is represented by cross-hatched bars in Figure 3.

3. Clavate-reduced-normal. In this class of inflorescences there is a complete gradation from "clavate" sterile spikelets at the base to "reduced" sterile spikelets in the middle to "normal" sterile spikelets at the tip. This class is represented by unshaded bars in Figure 3.

The relationships between inflorescence length and inflorescence type are presented in Figure 3. In this figure, the horizontal axis is divided into seven equal size-classes representing inflorescence lengths. The vertical axis is calibrated to represent numbers of individuals.

Occasional intermediate inflorescence types occur; these have been arbitrarily placed in the class that they most nearly resembled.

As can be seen from Figure 3, clavate-reduced inflorescences are relatively short, mostly less than 5 cm. in length. Clavate-normal inflorescence types are, on the average, slightly longer than the clavate reduced type. The third inflorescence type, clavate-reduced-normal, is found throughout the entire range of inflorescence-length values but occurs more commonly in the longer inflorescence size-classes.

None of the inflorescence-sterile spikelet relationships
discussed above could be correlated with other features such as peduncle length, height of the mature plant, or geographic origin.

As can be gathered from the previously presented data, this species presents certain variation patterns. Various workers with the genus have given some of the extreme forms varietal or even specific distinction based upon one or more of the above-mentioned characters. When a large number of specimens are examined, it soon becomes apparent that, while the over-all variation patterns are such that vague sub-specific groups can be discerned, the overlap and merging of these variation patterns precludes any practical sub-division of the species.

CYTOLOGY AND CYTOGENETICS

Chromosome numbers of \(2n=14\) have been reported for this species by Avdulov (1931), Miege (1939), Parthasarathy (1939), Hanson and Hill (1953) and Ambathsa (1956). The chromosome counts obtained by the author are presented in Table 3.

<table>
<thead>
<tr>
<th>Collection</th>
<th>Location</th>
<th>Chromosome number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant Introduction no. 170618</td>
<td>Seed source:</td>
<td>(2n=14)</td>
</tr>
<tr>
<td>Anderson voucher no. 1201</td>
<td>Turkey</td>
<td></td>
</tr>
</tbody>
</table>
Cytological observations by the author showed meiosis to be regular in every respect. This corroborates the findings of Parthasarathy (1939).

Ostergren (1957) has experimentally produced autotetraploids (2n=28) in the self-fertile P. paradoxa by a pressurized nitrous oxide technique. No information concerning the morphology of the tetraploids was included.

**DISTRIBUTION**

Older floras list this species as being native to lands bordering on the Mediterranean Sea. Man’s activities have extended the range throughout the world, primarily to harbor areas and waste places that have served as ballast or refuse dumps.

A map (Figure 4) shows the distribution of the specimens examined by the author.

**SELECTED SPECIMENS EXAMINED**

- **ALGERIA**: Biskra, L. Chevallier 644 (US).
- **AUSTRIA**: Gosting, F. Hopflinger, June 6, 1948 (US).
- **CANARY ISLANDS**: Gomera, C.J. Pitaré 389 (MO); Teneriffe, Parraudiera (F).
- **EGYPT**: Cairo, G. Schweinfurth 1253 (US).
- **ENGLAND**: Colchester, G.C. Brown, June 6, 1920 (US).
- **FRANCE**: Gentilly, rue de l’Hay, Jeampert, June 20, 1919 (F).
- **GERMANY**: Magdeburg, H. Eggert, July 6, 1861 (MO).
- **IRAN**: Baghdad, Y. Lezar 282 (F); Jebel Golat, H. Field and Y. Lezar 442 (F).
- **ISRAEL**: Yokucan, A. Abraham, February 6, 1961 (MO).
- **ITALY**: Corsica, Solenfora, P. Aellen 2908 (MO); Florence, A. Braun 1840 (MO).
- **JORDAN**: Jenin, J. E. Dinsmore 4771b (F).
- **LIBYA**: Tripoli, Post (US).
Figure 4. Geographic distribution of *Phalaris paradoxa*
LEBANON: Beirut, Post, April 21, 1878 (US).
UNITED STATES: California: Butte Co., 7 miles west of Honcut, L.S. Rose 37381 (MO); Contra Costa Co., Byron Hot Springs, R.F. Hoover 2123 (US); Fresno Co., 9 miles southeast of Dos Palos, H.L. Mason 12952 (US); Los Angeles, Sepulveda Blvd., L.C. Wheeler 1874 (F); San Diego, T.S. Brandegee, May, 1889 (F); Hawaiian Islands, Oahu, A.S. Hitchcock 13780 (US); Louisiana, New Orleans, W.T. Penfound, May 13, 1930 (US); Pennsylvania, Philadelphia, ballast, J.C. Martinale, June, 1879 (US); Washington, Klickitat Co., Bingen, W.N. Suksdorf 5337 (US).


2. Phalaris coerulescens

Phalaris coerulescens Desf. Fl. Atl. 1:56. (1799) (Holotype in P)

Phalaris bulbosa Cav. non L. Icon. Desc. Pl. 1:46. (1791)

Phalaris variegata Spreng. Neue Entdeck. 2:101. (1821)

Phalaris aquatica L. var. macrostachys Mutel. Fl. France. 4:15. (1837)

Phalaris villosula De Not. ex Parl. Fl. Ital. 1:73. (1848) pro syn.


Phalaris coerulescens var. concolor Pojero. 3:251. (1908)

Phalaris bulbosa L. f. coerulescens (Desf.) Knoche. Fl. Balearica. 1:289. (1921)


DESCRIPTION

Perennial; culms to 150 cm. tall, bulbous at the base; panicle 3.0—11.6 cm. long, 1.0—2.3 cm. wide, usually cylintric, occasionally ovate-oblong; spikelets falling singly
or in groups of 6 or 7, when falling in groups, 1 or 2 fertile and the rest staminate; glumes 5.3–9.0 mm. long, 1.1–2.0 mm. wide, glabrous or hirsute, winged, the wing up to 1.0 mm. wide and markedly erose-denticulate; fertile floret 2.7–4.4 mm. long; 0.7–1.4 mm. wide, glabrous or with a very few short hairs on the margin of the lemma, shiny; sterile florets obsolete, often with a few short hairs at the base; grain 2.8–3.3 mm. long, 1.2–1.4 mm. wide, somewhat flattened; somatic chromosome number 2n=14, the chromosomes ca. 2.5–4.5 microns long at diakinesis.

OBSERVATIONS

Phalaris coerulescens is a robust perennial with well developed culm bases. The glabrous, lustrous fertile florets of this species serve to separate it from all other members of the genus except the annual species P. paradoxa.

P. coerulescens has somewhat larger spikelets and caryopses than P. paradoxa. A comparison of the two species with regard to these features is presented in Table 4.

Referring to Table 4, it will be noted that there is an overlap in size ranges for all of the given structures except caryopsis size. The mature caryopses of P. coerulescens are somewhat larger than mature caryopses of P. paradoxa. While average size differences are apparent with respect to glume length and fertile floret length, the overlap of size ranges is enough to preclude their use as a practical means of
Table 4. Comparison of *Phalaris coerulescens* Desf. and *P. paradoxa* L.

<table>
<thead>
<tr>
<th>Character</th>
<th>coerulescens</th>
<th>paradoxa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glume length</td>
<td>5.3—9.0 mm.</td>
<td>5.5—8.0 mm.</td>
</tr>
<tr>
<td>Fertile floret length</td>
<td>2.7—4.4 mm.</td>
<td>2.5—3.5 mm.</td>
</tr>
<tr>
<td>Caryopsis length</td>
<td>2.8—3.3 mm.</td>
<td>2.3—2.6 mm.</td>
</tr>
<tr>
<td>Caryopsis width</td>
<td>1.2—1.4 mm.</td>
<td>0.9—1.1 mm.</td>
</tr>
</tbody>
</table>

separating the species.

An unusual characteristic possessed by *P. paradoxa* and some individuals of *P. coerulescens* is that the spikelets often fall in groups when ripe. In *P. paradoxa* the spikelets fall in groups of 7 (occasionally 6) with 6 (or 5) sterile spikelets surrounding the single fertile spikelet. The sterile spikelets are often deformed and reduced in size (Plate 3, b—f) and the florets contain only the aborted remains of the essential flower parts. Spikelets of *P. coerulescens* may fall singly or in groups. The number of spikelets in the groups varies from 5 to 8. Each group may have one or two fertile spikelets; the remaining spikelets are often staminate, although occasionally the flower parts are aborted. The sterile or staminate spikelets of *P. coerulescens* are never deformed and elevated (Plate 3, i,j).
CYTOLOGY AND CYTOGENETICS

Trumble (1935), Parthasarathy (1939), Saura (1943), Hanson and Hill (1953), Hutton (1953), and Ambathsa (1956) report chromosome numbers of 2n=14 for this species. Miege (1939) reports a 2n number of 28. Chromosome numbers obtained by the author are reported in Table 5.

Table 5. Chromosome counts from pollen mother cells of Phalaris coerulescens Desf.

<table>
<thead>
<tr>
<th>Collection</th>
<th>Location</th>
<th>Chromosome number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant Introduction no. 240176 Anderson voucher no. 1224</td>
<td>Seed source: Algeria</td>
<td>2n=14</td>
</tr>
<tr>
<td>Plant Introduction no. 240178 Anderson voucher no. 1226</td>
<td>Seed source: Algeria</td>
<td>2n=14</td>
</tr>
<tr>
<td>Plant Introduction no. 240179 Anderson voucher no. 1225</td>
<td>Seed source: Algeria</td>
<td>2n=14</td>
</tr>
<tr>
<td>Plant Introduction no. 240188 Anderson voucher no. 1179</td>
<td>Seed source: Algeria</td>
<td>2n=14</td>
</tr>
<tr>
<td>Plant Introduction no. 240189 Anderson voucher no. 1220</td>
<td>Seed source: Portugal</td>
<td>2n=14</td>
</tr>
<tr>
<td>Plant Introduction no. 240190 Anderson voucher no. 1175</td>
<td>Seed source: Portugal</td>
<td>2n=14</td>
</tr>
</tbody>
</table>
Hayman (1956) reported \(P. \text{ coerulescens}\) to be self-sterile. This self-sterility is supposedly under the control of two gene loci, each of which has a series of multiple alleles.

**Nomenclature**

A fragment of the holotype of \(P. \text{ coerulescens}\) Desf. from the Muséum National d'Histoire Naturelle, Laboratoire de Phanerogamie, Paris, France was examined by the author. Plate 3, i--k is drawn from the holotype material.

**Distribution**

A map (Figure 5) indicates the geographic origin of the specimens studied.

**Selected Specimens Examined**

**Canary Islands:** Gomera, San Sebastian, J.Bornmuller 292 (MO); Gran Canaria, Santa Brigida, A.C.Cook 632 (F, MO).

**Gibraltar:** Munro 1854 (K)

**Greece:** Crete, Le canée, lieu humides, E.Reverchon, May 29, 1883 (US); Karpatas Isl. Leato 649 (US).

**Italy:** Corsica, seri de Portorecchio, P.Aellen 2906 (MO); Naples (US); Pico, H.Van Heurok 1869 (P); Rome, Berenger, April, 1882 (US); Sicily, Palermo, Todaro 1071 (US).

**Portugal:** Madeira Isl., river near Funchal (US); Herdade do monte das aldeias pr. Estremoz, A.Fernandes 1839 (MO).

**Spain:** Grenada Prov., Barranco del Rio Segura, prairies humides, sur le calcaire, E.Reverchon 1299 (US); Mallorca Isl., Barranco de Soller, E.Bourgeau 2811 (US); Malaga, Estepona, Ellmand and Nelmes 163 (US).

3. \textit{Phalaris minor}


\textit{Phalaris decumbens} Moench. Meth. Pl. 208. (1794)

\textit{Phalaris aquatica} var. \textit{minor} (Retz.) Kutel. Fl. Frang. 4:15. (1837) (Based on \textit{Phalaris minor} Retz.)
Figure 5. Geographic distribution of *Phalaris coerulescens* and *Phalaris truncata*

Phalaris brevis Ehrenb. ex Trin. Serm. Acad. St.-Petersb. Ser. 6. 5:50. (1840) (Holotype in LE)

Phalaris trivialis Ehrenb. ex Trin. Serm. Acad. St.-Petersb. Ser. 6. 5:50. (1840)

Phalaris gracilis Parl. Fl. Nov. 36. (1842)

Phalaris minor var. gracilis (Parl.) Parl. Fl. Ital. 1:70. (1848) (Based on P. gracilis Parl.)

Phalaris ambiguus Fig. and De Not. Serm. Acad. Torin. 14:10. (1853)


DESCRIPTION

Annual; stems 20–100 cm. tall; panicle ovate-oblong, 1–6 cm. long, 1–9 cm. wide; glumes 4.0–6.5 mm. long, more or less equal, keel broadened into a conspicuous wing near the tip, the wing usually erose-denticulate, occasionally entire; fertile lemma 2.7–4.0 mm. long, 1.3–1.8 mm. wide, usually broadly lanceolate-ovate, dull yellow when immature, gray-brown and shiny at maturity, pubescent; sterile floret 1, 1.0–1.8 mm. long or very short, only 0.2–0.3 mm. long; grain 2.3–2.5 mm. long, 1.3–1.5 mm. broad, somewhat flattened; chromosome number 28 or 29, the chromosomes ca. 3–7 microns long.

OBSERVATIONS

Phalaris minor is an annual grass presently of world-wide distribution. Taxonomically the species is quite uniform except for a form with short sterile florets (Plate 4, d,e) which occurs in India and Afghanistan. This form was named Phalaris nepalensis by Trinius in 1828. Twelve years later he named this same form P. brevis. This form differs from P. minor only in that it has a very much reduced sterile floret which is never more than 0.3 mm. long. Neither form differs from the other in features such as glume shape, lemma shape, inflorescence size and shape, stature of plants, etc. Since these two taxa are distinct only as to size of sterile florets and are identical in other morphological features, the author
Plate 4. *Phalaris minor*

a. spikelets, 5X  
b. floret, 5X  
c. caryopsis, 5X  
d. spikelets from holotype of *Phalaris nepalensis*, 5X  
e. florets from holotype of *P. nepalensis*, 5X  
f--h. aberrant meioses, 840X
feels there is not enough difference to warrant nomenclatorial recognition.

Ruiz (1947) reduced *P. minor* to the status of a variety as *P. arundinacea* ssp. *bulbosa* Ruiz var. *minor* (Retz.) Ruiz. *P. arundinacea* differs from *P. minor* in a number of features. These are enumerated below:

1. *P. arundinacea* is a large, robust, rhizomatous perennial while *P. minor* is a rather weak, fibrous-rooted annual.

2. The glumes of *P. arundinacea* are rarely winged; if wings are present, they are very narrow and barely visible under 10X magnification. The glumes of *P. minor* are broadly winged; the wings are easily visible under 10X magnification.

3. *P. arundinacea* has two well-defined sterile florets; *P. minor* has only one sterile floret.

4. The fertile florets of *P. arundinacea* are relatively narrow while those of *P. minor* are much broader by comparison. Fertile florets of *P. arundinacea* are more or less circular in cross-sectional outline; those of *P. minor* are distinctly flattened in this respect.

**CYTOLOGY AND CYTOGENETICS**

Chromosome numbers of 2n=28 have been reported for this species by Avdulov (1931), Perthisarathy (1939), Hanson and Hill (1953), Hutton (1953), and Ambathsa (1956). Counts of 2n=29 have been reported by Hanson and Hill (1953). Chromo-
some counts obtained by the author are reported in Table 6.

Parthasarathy (1939) states that occasional quadriplets are recognizable in side views of metaphase figures in *P. minor*. This would seem to be evidence that homologous segments are present.

Table 6. Chromosome numbers from pollen mother cells of *Phalaris minor* Retz.

<table>
<thead>
<tr>
<th>Collection</th>
<th>Location</th>
<th>Chromosome number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant Introduction no. 208404</td>
<td>Seed source: Transvaal</td>
<td>?n=28,29 (1178)</td>
</tr>
<tr>
<td>Anderson voucher nos. 1178,1190</td>
<td></td>
<td>?n=28 (1190)</td>
</tr>
<tr>
<td>Plant Introduction no. 202678</td>
<td>Seed source: unknown</td>
<td>?n=28</td>
</tr>
<tr>
<td>Anderson voucher no. 1174</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plant Introduction no. 180865</td>
<td>Seed source: Turkey</td>
<td>?n=29</td>
</tr>
<tr>
<td>Anderson voucher no. 1187</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plant Introduction no. 211064</td>
<td>Seed source: Afghanistan</td>
<td>?n=28</td>
</tr>
<tr>
<td>Anderson voucher no. 1200</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Observations of greenhouse-grown material by the author revealed a number of interesting and puzzling meiotic aberrations (Plate 4, f--h). Many metaphase I, anaphase I, and telophase I cells showed lagging univalents (Plate 4, f,h).
Quadrivalent formation was observed with some degree of frequency. Occasional bridges and fragments could be seen (Plate 4, g). Positive counts were difficult to make because of the tendency for the bivalents to stick together in groups, refusing to separate without mutilation of the cell. It is possible that some or all of the observed abnormalities in the author's material may have been due to greenhouse conditions. It is necessary that this species be grown under natural conditions before one can determine whether the abnormalities are determined by innate cytological anomalies or unusual artificial environmental conditions.

Three hybrids have been obtained in crosses involving P. minor as the male parent. Trumble (1935) and Hutton (1953) obtained crosses between the annual, self-compatible P. minor (2n=28) and the perennial, self-sterile P. coerulescens (2n=14). The resulting F₁ hybrid was vigorous but completely sterile. Hutton also used a colchicine technique to produce an allopolyploid (2n=42) between these two species. These were annuals and tended to be less vigorous than either parent. Hutton noted a dominance of P. minor characters in this hybrid and attributes this to the fact that P. minor contributed two-thirds of the chromosomes in the hybrid genome.

Hayman (1955) studied the meiotic behavior of the hybrid reported by Hutton and found that it formed seven bivalents
and seven univalents during meiosis. The seven univalents belonged to the *P. minor* set of chromosomes and showed several kinds of chromosomal aberrations such as short inversions, multiple armed chromosomes, and breakages. Heyman claimed that a considerable degree of homology existed in the pairs of bivalents because of relatively high mean chiasma frequency.

**Hybrids between P. minor and P. aquatica** are reported by Trumble (1935) and Hutton (1953). Hutton reported the resulting F$_1$ to be sterile. Heyman (1955), in studying Hutton's hybrid material, found that linear trivalents occurred in ninety per cent of the cells and that there were between eight and nine univalents, on the average, per cell. Blake (1956) reported that Hutton's allopolyploid showed considerable promise as a forage grass in Australia and named it *X Phalaris daviesii*. According to Blake this taxon is cultivated and has not escaped.

Trumble (1935) obtained hybrids by crossing *P. minor* and *P. erundinacea*. Ambathsa (1956) studied these plants cytologically and reported that they produced a good proportion of normal pollen grains but were highly sterile.

**NOMENCLATURE**

The type specimen of *Phalaris minor* Retz. was not seen. Retzius' original description is quite complete and leaves no doubt as to the typification of the species.
The holotypes of both *P. nepalensis* and *P. brevis* are in the Herbarium of the Department of Systematics and Plant Geography of the Botanical Institute of the Academy of Sciences of the U.S.S.R., Leningrad and were examined by the author. Drawings of spikelets from the holotype of *P. nepalensis* are presented in Plate 4, d,e.

**DISTRIBUTION**

The range of *P. minor* is world-wide at the present time. The original range, as given in older floristic treatments, appeared to be roughly the area bordering upon the Mediterranean Sea. In more recent years specimens have been collected from waste areas (harbor ballast, refuse dumps, etc.) throughout much of the rest of the world.

A map (Figure 6) shows the geographic origin of the specimens studied by the author.

**SELECTED SPECIMENS EXAMINED**

AFGHANISTAN: Shibarghan, A.T.Semple 409 (US); Griffith 6468 (MO).
ANGOLA: Mossemedes, Huilla, Goasweiler 9419 (US).
AUSTRALIA: Tasmania, Campbelltown, R.A.Black 1183007 (US); West Australia, Perth, R.Helms H.140 (US).
AUSTRIA: Tergestem, Noe (MO).
AZORES ISLANDS: Sta. Maria, Correiro 967a (MO).
BRAZIL: Sao Paulo, Seccao, Ville Cerqueira Cesar, F.C.Hoehne 4658 (US).
CANARY ISLANDS: Teneriffe, C.Bolle, 1856 (MO).
EGYPT: Alexandria, J.Bornmuller 11037 (US); Cairo, J. Bornmuller 11038 (US).
ENGLAND: Jersey, Georgetown, L.V.Lester, July 9, 1897 (F).
Figure 6. Geographic distribution of *Phaleria minor*
FRANCE: Cherbourg, L. Corbiere, July 22, 1836 (US); Paris, Villeneuve le ROI, Jeanpert, May 13, 1920 (F).
GERMANY: Magdeburg, H. Eggert, June 1869 (MO).
GREECE: Aegina Isl., T. de Heldreich and T. Holzmann, April 18–26, 1881 (US); Kastriades Isl., W. Barbey 647 (US); Kastriades Isl., C. Beunitz, May 5, 1896 (US).
INDIA: Jhelum Dist., Hirpur, K.L. Kalhotra 15841a (US); Punjab, Bhadwar, Kangere, W. Koelz 4178 (US); United Prov., Dehra Dun, Balpur, U. Singh 314 (F); Kapkot, W. Koelz 20059 (US); Rawalpindi, garden weed, R.R. Stewart 17285a (US).
IRAN: Yesd Prov., J. Bornmuller 4921 (US); pr. Gere inter Abuschir et Schiras, T. Kotschy 88 (MO).
IRAQ: Arbil Prov., M. al Radie 3866 (US); Nasirujah, near Baghdad, Y. Lazar, March 23, 1935 (F).
ITALY: Leghorn, Livorno, Philippl, 1888 (US); Sardinia, Santa Teresa Gallure, E. Reverchon 146 (US); Sicily, Syracuse, G. Rigo 13 (US).
MADEIRA ISLANDS: W. Trelease, June 15, 1896 (MO).
MEXICO: Baja California, Tie Juana, I. L. Wiggins 5105 (US); Puebla, Pueble, Bros. Arsene and Nichols 5785 (MO).
PORTUGAL: Coimbra, M. Ferreira 617 (US); Lisbon, Estremadure, Serra de Monsanto, A. R. da Cunha, 1888 (US); Serra d'Orre, Herdade de Queijearia, A. Fernandes 1737 (MO).
SPAIN: Seville, Estening, M. Gendoger, 1926 (MO).
TURKEY: Smyrna, J. Bornmuller 10108 (US).
SPAIN: Seville, Estening, M. Gendoger, 1926 (MO).
TUNISIA: Sfax, Espina, 1854 (F).
UNITED STATES: Arizona: Pima Co., 15 miles west of Tucson, annual weed, K. F. Parker 8018 (US); Pinal Co., Casa Grande, K. F. Parker 8743 (US); California: Alameda Co., Berkeley, W. C. Blasdale, June 22, 1895 (US); Colusa Co., 4 miles east of Williams, R. S. Ferris 508 (MO); San Bernardino Co., south of Chino, P. A. Munz 15573 (US); San Diego Co., Nestor, H. P. Chandler 5118 (US); San Mateo Co., Crystal Springs, Lake, A. D. E. Elmer 4427 (MO); Santa Barbara Co., Gaviota, A. Chase 5639 (US); Stanislaus Co., 4 miles west of Hoover, R. F. Hoover 1230 (US); Catalina Island, L. W. Nuttall 224 (US); Florida: Lake City, A. W. Eitzing 778 (MO, US); Hawaiian Islands, Oahu, Schofield Barracks, A. S. Hitchcock 13915 (US).
URUGUAY: Soriano, escaped from cultivation, Gallina PE-5379 (US).
4. **Phalaris arundinacea**

*Phalaris arundinacea* L. Sp. Pl. 55. (1753)
(Holotype in LINN; photograph of type specimen in GH)

*Phalaris arundinacea* L. var. *picta*. Sp. Pl. 55. (1753)
(Holotype in LINN; photograph of type specimen in GH)

(Based on *P. arundinacea* L.)

*Typhoides arundinacea* (L.) Xoench. Meth. Pl. 202. (1794)

*Calamagrostis colorata* (Ait.) Sibth. Fl. Oxon. 37. (1794) (Based on *Arundo colorata* Ait.)

*Aurundo riparia* Salisb. Prodr. Stirp. 24. (1796)
(Based on *P. arundinacea* L.)


*Baldingera colorata* Gærtn., Mey., and Scherb. Fl. Wett. 1:96. (1799)

*Digraphis arundinacea* (L.) Trin. Fund. Agrost. 197. (1800)

*Baldingera arundinacea* (L.) Dum. Obs. Gram. Belg. 130. (1803)


*Phalaris arundinacea* var. *colorata* Hartm. Hent. Skand. Fl. ed. 4. 22. (1843)

*Phalaris arundinacea* var. *variegata* Pernell. Grasses Brit. 188. (1845)

(Holotype in L)


*Phalaridenthes arundinacea* (L.) Cariot. Etude des Fl. 900. (1889)

Phalaris arundinacea f. pallida Schwarz. Flor. Nurn.-Erlang. 855. (1892)


Phalaris hispanica de Coiney. Morot. Journ. de Bot. 8:207. (1894)

Phalaris arundinacea f. luteo-picta Voss in Siebert and Voss. Vilmorin's Blumengart. 1198. (1896)


Baldingera arundinacea (L.) Dum. var. rotgesii Husnot. Gram. (1899)


Phalaris arundinacea var. japonica (Steud.) Hack. Bull. Herb. Boiss. 7:646. (1899)


**DESCRIPTION**

Perennial from scaly, creeping rhizomes; culms 50—150 cm. tall; leaves usually green, occasionally striped with white (in f. *picta*); panicle 7—40 cm. long, lobed and branched at the base, the branches up to 5 cm. long, spreading during anthesis; glumes 3.5—7.5 mm. long, more or less equal, acute, usually wingless, when winged, the wing very narrow and inconspicuous, keel scabrous; fertile floret 2.7—4.5 mm. long, lanceolate, dull yellow when immature, gray-brown and shiny at maturity, nerves conspicuous, glabrous or with a few appressed scattered hairs; sterile florets 2, 1.2—2.3 mm. long; subulate, pubescent; grain 1.5—2.0 mm. long, 0.7—1.0 mm. wide, subovoid brown with faintly striate surface; somatic chromosome number 14, 27, 28, 29, 30, 31, 35, or 42; the chromosomes ca. 5.0 microns long at diakinesis.

**OBSERVATIONS**

*Phalaris arundinacea* L., commonly called Reed Canary Grass, is a well-defined though highly variable species. The most distinct variant within the species is *P. arundinacea* f.
pieta (L.) Asch. and Graebn. commonly called "Ribbon Grass" or "Gardener's Garters". This form differs from the typical in having its leaves longitudinally striped with yellow-white aehlorophyllous strips. The spikelets of f. pieta do not differ noticeably from those of f. arundinacea in general shape but they do tend to be somewhat smaller in size. The author did not see any mature caryopses on any living or dried specimen of Ribbon Grass examined. The absence of mature fruits might be attributed to the aberrant meiosis that has been reported for this form (Church, 1929). Church reported that pollen in f. pieta was 30--40% imperfect. Diakinesis and metaphase I revealed 14 bivalents and one or two univalents which consistently lagged on the spindle. The lagging univalents, as well as some of the bivalents, were extruded and disintegrated. More work on the cytology and genetics of this form are needed in order to learn more about the abnormalities in meiotic behavior.

Almost all collections of f. pieta seen by the author were from cultivated stands. Escaped populations are sometimes found near dwellings. The author has never observed any plants of this form in a naturally occurring population of f. arundinacea.

The non-striped populations of Phalaris arundinacea have been divided into no less than ten infraspecific categories, including varieties, sub-species, formae, and races. Many of
the described infraspecific taxa were based upon vegetative characters such as the amount of branching, leaf coloration, and size, shape, and density of the inflorescence.

Baltensperger and Kalton (1958) analyzed several vegetative characters of reed canary grass from an agronomic standpoint. Plant materials used in their study were obtained from 37 seed lots collected in the United States and one each from Turkey and Canada. These seeds were grown in field plots. Their results are useful taxonomically in showing some of the variation patterns within the species. The range in leaf width was from 9 to 25 mm. The total variability in forage value was quite high; much of this variability was attributed to environmental effects.

Field observations by the present author indicated considerable variability in height at anthesis, size and shape of the inflorescence, and overall coloration depending upon the habitat of the plants. Within a single clone, as much as one meter difference in height of flowering culms was observed. The panicle size and shape varies a great deal depending upon the stage of development. None of these variations could be correlated with one another or with geographic distribution to indicate sub-specific populations.

The perennial, prominent scaly rhizomes, lobed or branched panicle, acute, almost wingless glumes, lustrous, narrow, sparsely pubescent lemmas, and two villous sterile florets distinguish this species from others of the genus.
Numerous cytological studies have been made upon members of this species. These studies indicate that at least some members of the taxon are aneuploids. Aneuploid numbers of \(2n=27, 29, 30\) and \(31\), have been reported by Hanson and Hill (1953). Euploid numbers of \(2n=14\) were reported by Church (1929); \(2n=28\) by Church (1929), Avdulov (1931), Jenkin and Sethi (1932), Trumble (1935), Parthasarathy (1939), Hutton (1953), Tateoka (1954), Carnahan and Hill (1956), and Ambathsa (1956); \(2n=35\) by Hanson and Hill (1953); \(2n=42\) by Brock (unpublished, listed in Darlington and Wylie, 1955). Carnahan and Hill (1956) experimentally produced plants with \(2n=56\).

The author's observations and those of the above workers indicate that meiosis seems quite regular in the euploid collections. The aneuploid sections show, as would be expected, various meiotic irregularities (Hanson and Hill, 1953).

To the author's knowledge, no one has attempted a comparison of chromosome number and various other characters such as panicle size, degree of lobing, spikelet size, etc. Until such studies are made, one can only speculate that perhaps some of the rather broad range of variability can be attributed to differences in ploidy.

The meiotic chromosome number obtained by the author is presented in Table 7.
Table 7. Chromosome number from pollen mother cells of *Phalaris arundinacea* L. f. *arundinacea*

<table>
<thead>
<tr>
<th>Collection</th>
<th>Location</th>
<th>Chromosome number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anderson voucher no. 1235</td>
<td>Iowa, Story Co.</td>
<td>2n=28</td>
</tr>
</tbody>
</table>

**NOMENCLATURE**

Photographs (in GH) of the holotypes of both *Phalaris arundinacea* var. *arundinacea* and var. *picta* (in LINN) were examined. These represent the taxa as commonly understood today.

Britton and Brown (1913) designated *P. arundinacea* as the type species of the genus.

**DISTRIBUTION**

Members of this species have been found almost throughout the northern hemisphere and, as introductions, on all of the continents in the southern hemisphere except Antarctica. Large colonies are often found in the northern United States, most frequently in roadside ditches, along pond margins, dredge ditches, and creek banks.

A map (Figure 7) shows the geographic origin of the specimens studied by the author.
Figure 7. Geographic distribution of *Phalaris arundinacea*
SELECTED SPECIMENS EXAMINED

*Phalaris arundinacea f. arundinacea.* CANADA: Alberta, Calgary, A.S. Hitchcock 4985 (US); Alberta, Slave Lake, E.H. Moss 6082 (GH); British Columbia, Vancouver Isl., W.R. Carter 934 (GH); New Brunswick: Campbelltown, R. Chambers 22953 (F, US); Newfoundland: Exploits River, Grand Falls, M.L. Ferdinand, K.M. Wiegand 4526 (F, US); Humber Dist., Serpentine Lake, E. Rouleau 2386 (US); Northwest Territories, south of Fort Smith, 60° 02' N, 112° 36' W, W.J. Cody and C.C. Loan 4683 (NDA); Nova Scotia, Cape Breton Isl., G.E. Nichols 943 (GH); Ontario: Algoma Dist., Corbeil Pt., 47° 00' N, 84° 45' W, T.M. C. Taylor 1104 (GH, US); Bruce Co., Red Bay, G.L. Stebbins 27 (GH); North Shore, Schreiber, 48° 45' N, 87° 15' W, R.C. Hosie 1321 (GH); Quebec: Anticosti, J. Macoun 29254 (US); Gaspe Peninsula, 4 miles above mouth of Bonaventure River, W.G. Dore 47-923 (US); Saskatchewan, Grand Trunk Pacific RR., 20 miles west of Yorkton, J. Macoun and W. Herriot, July 9, 1906 (F, US).


CHINA: Chihli Prov., Peitaiho, M.S. Clemens 7005 (US); Kiansu Prov., Nanking, A.N. Steward 2528 (US); Shansi Prov., Ning-wu Hsien, 7000' elev., T. Tang 1444 (US); Szechuan, Sung-pan Hsien, W.P. Fang 4401 (US).

COLOMBIA: Sopo, 2640 m. elev., Bros. Apollinaire and Arthur 23 (US).

ENGLAND: Lancashire: Lake Windermere, near High Wray, M.R. F. Taylor 3 (US); Mersey, Speke, A.E. Lomax (US); Middlesex, Chiswick, Stand-on-the-Green, F. Ballard 138 (US).

FRANCE: Allier-Yeure, Robe, S.E. Lassimonne, June, 1894 (US).

GERMANY: Nurnberg, F. Eberleu and L. Gross 192 (US); Rheinpfalz, Durkheim, H. Gluck, July, 1932 (US).

HUNGARY: Haidu-Pusnok-Ladany, A. de Degen 54 (US).

IRAN: Azna, M. Koie, June 8, 1937 (GH); Urmia, 13 miles north, Cowan and Darlington 1500 (US).

ISRAEL: Tel-Aviv, Eig, June 26, 1928 (US).

ITALY: Helvajujana, Padule d'Castagnolo (F).

JAPAN: Mino Prov., Hondo, K. Shiota 5219 (GH); Miyazaki Prov., Miyazaki City, Kitakata, N. Eri 100575 (GH).

JAVA: Diegnplatean, Backer 21702 (US).


MANCHURIA: Jalacun, Dorsett and Dorsett 3500 (US).

MEXICO: Valle de Mexico, Santa Anita, Fournier 148 (GH).


PORTUGAL: Coimbra, Choupal, A. Moller, June, 1886 (US).

ROMANIA: Turda Dist., Borsa and Bujorean 724 (US).

SWITZERLAND: Basel, C.Christ (US); Zurich, F.G.Stebler and C.Schroeter, May 8, 1887 (US).


UNION OF SOVIET SOCIALIST REPUBLIC: Kamtchatka, Savoiko-Petropevlovsk, E.Hulten, July 26, 1928 (US); Siberia: Kudia River, J.D.A.Cockerell, July 1923 (US); Tobolsk, Manev 877 (US).


ECUADOR: Tungurahua Prov., Ambato, garden, 2550 m. elevation, M.S. Solis 9399 (US).


GUATEMALA: Jalapa, 1360 m. elev., P.C. Standley 76364 (F).

JAPAN: Shikoku, U. Faurie 4455 (US).

UNITED STATES: Illinois, Cook Co., J.W. Thieret 1398 (F); Indiana, Pine Co., Lake Chicago Basin, C.W. Duesner 1908 (F); Iowa, Calhoun Co., Lohrville, D. McClure 317a (ISC); Maine, Westbrook, P.L. Ricker 659 (US); Massachusetts, Greenfield, E.F. Williams, June 17, 1910 (GH); Michigan, Keeweenaw Co., Copper Falls, F.J. Hermann 7762 (US); Missouri, Garrett Co., Oakland, J.D. Smith, July 1879 (US); New Hampshire, Laco­nia, garden, L.A. Carter 236 (US); New York, N. Hannibal, O.E. Pearson, July 16, 1873 (US); Ohio, Coshocton Co., Coshocton, H. N. Holdenke 12977 (US); Rhode Island, Newport Co., M.L. Fernald, B. Long, and G.S. Torrey 8689 (GH); Vermont, Peacham, A.F. Stevens, 1892 (US); Wisconsin, Sturgeon Bay, J.H. Schuette, July 12, 1885 (F).

5. Phalaris aquatica

Phalaris aquatica L. Amoen. Acad. 4. 264. (1755) (Holotype in LINN. Photograph of holotype in GH)

Phalaris tuberosa L. Mant. Pl. 2:557. (1771) (Holotype in LINN. Photograph of holotype in GH)

Phalaris nodosa Murr. Syst. Veg. ed. 13. 88. (1774) (not P. nodosa L., presumably based on P. tuberosa L.)


Phalaris tuberosa var. alata Batt. and Trab. Fl. Alg. Monocot. 2:140. (1895)

Phalaris tuberosa var. hirtiglumis Batt. (Trab.) Batt. and Trab. Fl. Alg. Monocot. 2:140. (1895) (Based on P. bulbosa var. hirtiglumis Trab.)

Phalaris nodosa var. minor Pojero. Fl. Sic. 3:251. (1908) (Not based on P. minor Retz.)
Plate 5. *Phalaris arundinacea*, *Phalaris aquatica*, and *P. arundinacea* x *P. aquatica*

a--d. *Phalaris arundinacea*: a. inflorescence 1/2X, b. spikelets 5X, c. florets 5X, d. caryopsis 5X

e--i. *Phalaris aquatica*: e. bulbous culm bases of var. *aquatica* 1/2X, f. culm bases of Harding grass 1/2X, g. spikelets 5X, h. florets 5X, i. caryopsis 5X

j--l. *Phalaris arundinacea* x *Phalaris aquatica*: Produced at Aberystwyth, Wales by T.J. Jenkins, drawings made from specimen in US collected by Jenkins (31 bs -1-2, July 13, 1928); j. spikelet 5X, k. floret 5X, l. culm bases 1/2X
**Phalaris stenoptera** Hackel. Repert. Sp. Nov. 5:333. (1908)


**Phalaris tuberosa** var. **stenoptera** (Hack.) Hitchc. Wash. Acad. Sci. Jour. 24:292. (1934) (Based on **P. stenoptera** Hack.)


**Phalaris bulbosa** var. **genuina** Maire. Fl. Afr. Nord. 2:18. (1953) (Based on **P. bulbosa** as misapplied by Maire to **P. aquatica** L.)

**Phalaris bulbosa** var. **alata** Batt. and (Trabut) Maire and Weiller in Maire. Fl. Afr. Nord. 2:18. (1953) (Based on **P. tuberosa** var. **alata** Batt. and Trab. **P. bulbosa** is misapplied by Maire to **P. aquatica** L.)

**Phalaris bulbosa** var. **clausonis** (Maire and Trabut) Maire and Weiller in Maire. Fl. Afr. Nord. 2:18. (1953) (Based on **P. tuberosa** var. **clausonis** Maire and Trabut. **P. bulbosa** is misapplied by Maire to **P. aquatica** L.)

**DESCRIPTION**

Perennial; culms from a dense crown or loose base with short rhizomes, culms often bulbous at the base, up to 1.5 m. tall; panicle 1.5--11.0 cm. long, 1.0--2.5 cm. wide, usually cylindric, sometimes ovate-cylindric, occasionally lobed at the base; glumes 4.4--7.5 mm. long, 1.0--2.0 mm. wide, glabrous, rarely hirsute, broadly winged, the wing margin almost always entire, rarely somewhat erose; fertile floret 3.1--4.6 mm. long, 1.2--1.5 mm. wide, lanceolate, densely pubescent;
sterile florets 1 or sometimes 2, 0.2—2.2 mm. long, when 2 are present the lowermost is often less than 0.5 mm. long; caryopsis 2.2—2.5 mm. long, 1.2—1.3 mm. wide, light brown, surface faintly striate; chromosome number \(2n=28\), the chromosomes ca. 6—7 microns long at diakinesis.

**OBSERVATIONS**

One of the more interesting taxonomic problems within this species is that concerned with *Phalaris tuberosa* var. *stenoptera* (Hack.) Hitchc. (P. tuberosa=P. aquatica. See section on nomenclature), commonly called "Harding Grass" or "Toowoomba Canary Grass". Harding grass first appeared in Australia in the early 1880's. There are two accounts of its introduction into Australia: R. Harding (1884) published a short note in an obscure journal stating that seeds of this grass were received by him from the "Department of Agriculture, America". These seeds were subsequently planted in the nursery at Toowoomba, Australia under the name of *P. commutata*. The grown plants were later dug up and dumped in a corner where they continued to flourish. Harding later (about 1893) began to propagate and distribute the grass. Ewart (1908) claims that a Mr. Charles Ross, manager of the state farm at Westbrook, Queensland, informed him that a Mr. Way, then curator of the Botanic Garden at Toowoomba (about 1888), received seed of *P. aquatica* from the Agricultural Department of New York, U.S.A. This seed was planted in the garden but
much was lost due to extreme climatic conditions of that year. The only surviving material existed in out-of-the-way places such as hedge-rows and rubbish heaps. Ross later began to propagate and distribute this material. Apparently there was a gap of several years between its relegation to waste areas and the systematic distribution for agronomic purposes.

Accepting either solution for its introduction into Australia, the facts are that it (1) was introduced into Australia and (2) that it grew at the Botanical Garden at Toowoomba for a period of years.

For some years the name *P. commutata* R. and S. was applied to this taxon. Ewart quotes Bertolini (place and date of Bertolini's publication not given) as saying that this name was based upon a composite specimen containing vegetative parts of *P. aquatica* and an inflorescence of *P. minor*. The original description would seem to refer to such a composite specimen as Bertolini discussed.

In 1908 Hackel described *P. stenoptera* based on plants and seeds sent to him by Ewart. This species, according to Hackel, was somewhat intermediate between *P. arundinacea* and *P. aquatica*.

In 1932 interest in Harding Grass was revived by Jenkin and Sethi of the Welsh Plant Breeding Station at Aberystwyth, Wales. These two investigators attempted crosses using *P. arundinacea* and *P. aquatica* as the female and male parents,
respectively. The mostly sterile F₁ hybrids were intermediate between the two parents. Reciprocal crosses were not as successful. Back-crosses to either parent gave poor results although it was possible to obtain seedlings by using *P. aquatica* as the male parent. Further backcrossing to the *P. aquatica* parent yielded populations that were relatively fertile. Jenkin and Sethi, due partially to adverse experimental conditions, had little success in obtaining back-crosses using *P. arundinacea* as the male parent; however there was evidence that the pollen of this species did stimulate ovary development. Taxonomically one of the most interesting aspects of this cross was that the F₁ hybrids bore a strong similarity to Harding Grass which had so mysteriously appeared in Australia some thirty years previously. On the basis of this information, Jenkin and Sethi elaborated a hypothesis for the hybrid origin of Harding Grass. They reasoned that since there was a period of time during which *P. aquatica* was growing more or less unobserved in the waste areas of the Toowoomba Botanic Garden, it could have crossed with *P. arundinacea*. Later, a series of back-crosses with *P. aquatica* developed the new hybrid which was called *P. stenoptera* by Hackel. The suggestion of hybrid origin was not new with Jenkin and Sethi. Ewart (1908) had mentioned the possibility but argued against it because Harding Grass had a high seed producing capacity. Jenkin and Sethi showed, however, that
back-crosses to the *P. aquatica* parent and second, third, and even fourth generation plants from the F1 hybrid had good seed producing capacity. Ewart did suggest that Harding Grass might be a hybrid between *P. aquatica* and the very different *P. canariensis*. The present author feels that the latter species is so different from Harding Grass that there must be virtually no possibility that a *P. canariensis* genome could have been involved in its origin. Kennedy (1917) also suggests a possible hybrid origin for Harding Grass.

Daveau (1926) described what he claimed to be a hybrid between *P. nodosa* (misapplied to *P. aquatica* by Daveau) and *P. arundinacea*. This supposed hybrid was named *Phalaris monspelliensis* by Daveau. The plant was found growing in the botanical garden at Montpellier, France and was collected by Loret.

Allan and Zotov (1930) considered the possibility of hybrid origin of Harding Grass but could find no information to support it.

Trumble (1935) obtained F1 hybrids between *P. aquatica* and *P. arundinacea* but did not feel that the Australian plant represented the same taxon as *P. tuberosa* var. *stenop-tera*.

In an effort to gather more information concerning the possible hybrid origin of this variety, the author examined herbarium specimens of all three taxa supposedly involved.
Measurements were made of the inflorescence and spikelet parts. Special attention was paid to glume-wing size and shape, sterile floret number and size, and to the nature of the culm bases and underground plant parts. Of the features examined, the following seemed to possess considerable taxonomic importance: fertile floret length, glume length, sterile floret number and relative size, and the nature of the culm base and underground system. These characters are presented in graphic form in Figure 8. In this figure, each specimen is introduced by plotting its glume length against its fertile floret length. Shaded circles represent specimens of *P. arundinacea* having vigorous, long rhizomes and non-bulbous culm bases; half-shaded circles represent plants with rhizomes absent or very short, tufted growth habit, and non-bulbous culm bases; unshaded circles represent typical *P. aquatica* specimens with markedly bulbous culm bases. The number and relative length of the sterile florets is indicated by diagonal, upwardly-projecting lines. Two equal upward lines represent plants with two equal sterile florets; two unequal upward diagonal lines indicate specimens with one normal-length sterile floret (ca. 1.5 mm.) and one very short sterile floret. The relative length of the lines indicates, roughly, the relative length of the sterile florets. A single diagonal line represents specimens having a single sterile floret; absence of projections indicates that both
Figure 8. Relationship of growth habit and sterile floret type to fertile floret length and glume length in *Phalaris aquatica*
\[ y = \text{STERILE FLORETS 2, EQUAL} \]
\[ \neq \text{STERILE FLORETS 2, UNEQUAL} \]
\[ \neq \text{STERILE FLORET I} \]
\[ = \text{STERILE FLORET OBSOLETE} \]

- = RHIZOMES PRESENT; CULM BASES NOT BULBOUS
- = RHIZOMES ABSENT OR VERY SHORT; CULM BASES NOT BULBOUS
- = RHIZOMES ABSENT; CULM BASES BULBOUS

**FERTILE LEMMA LENGTH IN MM.**

**GLUME LENGTH IN MM.**
sterile florets were obsolete. Specimens used in the construction of this diagram were collected from all parts of the world.

From this diagram several population trends can be recognized. One trend, represented by shaded circles with equal projecting lines, has relatively short glumes and fertile florets, two equal sterile florets, well developed rhizomes, and lacks bulbous culm bases. These are specimens of *P. arundinacea* and are typical of the species. Another trend, represented by unshaded circles and one projecting line, is composed of specimens having relatively long glumes and fertile florets, one sterile floret, bulbous culm bases, and lacks rhizomes. These are specimens of *P. aquatica* var. *aquatica* and are typical of the species from its native Mediterranean region. The specimens intermediate between these two trends are heterogeneous. Many different combinations of characters are represented in this group. Some of these plants have a tufted growth habit, one sterile floret or two unequal sterile florets, occasionally have very short rhizomes, and lack bulbous culm bases (these plants are represented by half-shaded circles with one projecting line or two, unequal, projecting lines). Others had bulbous culm bases and two unequal sterile florets (represented by unshaded circles with two, unequal, projecting lines). It is interesting to note that all of the specimens of the inter-
mediate group were collected at botanical gardens or experimental farms. Only the specimens of *P. arundinacea* and those specimens of *P. aquatica* var. *aquatica* with a single sterile floret or no sterile florets were collected from native stands.

One of the more difficult aspects of the Jenkin and Sethi hypothesis is that there is, as they point out, no proof that *P. arundinacea*, one of the parents of this supposed Australian hybrid, was present at the critical time necessary for the cross to have taken place. The author has not seen any specimens from this area although Allen and Zotov (1930) report *P. arundinacea* from New Zealand. The absence of *P. arundinacea* from the herbaria does not necessarily negate the Jenkin and Sethi proposal. The plants supposedly involved in the production of this hybrid were cultivated in an experimental nursery; it is not uncommon to find that many of our most commonly cultivated plants are not represented in herbarium collections. Another aspect to consider is that perhaps the seed originally brought into Australia was of hybrid derivation. This latter idea seems quite attractive. The fact remains, however, that the artificial hybrids produced by Jenkin and Sethi do bear a very strong similarity to Harding Grass. By its very nature, the evidence presented for the hybrid origin of Harding Grass must remain somewhat circumstantial but the author feels that the
hypothesis elaborated by Jenkin and Sethi provides the most suitable explanation for the origin of this entity.

Ruiz (1947) reduced *P. aquatica* (mistakenly called *P. bulbosa* by Ruiz) to a sub-species of *P. arundinacea*. The differences between *P. aquatica* and *P. arundinacea* are presented below:

1. *P. aquatica* has bulbous culm bases and a fibrous root system or is tufted, rarely with very short, poorly developed rhizomes; *P. arundinacea* has non-bulbous culm bases arising from strong rhizomes.

2. *P. aquatica* has glumes with well-developed, prominent wings; the glumes of *P. arundinacea* are commonly wingless. If winged, the wing is very narrow and inconspicuous.

3. The inflorescence of *P. aquatica* is usually not branched or lobed; the inflorescence of *P. arundinacea* is almost always branched or lobed.

4. The fertile floret of *P. aquatica* is broadly lanceolate, quite strongly flattened, and narrowly elliptic in cross-section; fertile florets of *P. arundinacea* are narrowly lanceolate and more or less circular in cross-section.

5. *P. aquatica* usually has one, occasionally two sterile florets. If two sterile florets are present they are markedly unequal. *P. arundinacea* always has two equal florets.

6. The caryopsis of *P. aquatica* is usually over 2 mm.
in length; the caryopsis of *P. arundinacea* is usually shorter than 2 mm.

In view of the numerous well-defined differences between the two species, the present author has maintained them as distinct.

**CYTOLOGY AND CYTOGENETICS**

Somatic chromosome numbers of $2n=28$ have been reported for this species by Trumble (1930), Jenkin and Sethi (1932), Parthasarathy (1939), Hanson and Hill (1953), Hutton (1953), and Ambathsa (1956). The chromosome count obtained by the present author is presented in Table 8.

Table 8. Chromosome numbers from pollen mother cells of *Phalaris aquatica* L.

<table>
<thead>
<tr>
<th>Collection</th>
<th>Location</th>
<th>Chromosome number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant Introduction no. 202762</td>
<td>Seed source: Transvaal</td>
<td>$2n=28$</td>
</tr>
<tr>
<td>Anderson voucher no. 1209</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Jenkin and Sethi (1932) studied cytologically the hybrid produced between *P. arundinacea* and *P. aquatica*. The *P. arundinacea* plant used in the production of the hybrid had a chromosome number of $2n=28$; *P. aquatica* of the strain used in the experiment also had a chromosome number of $2n=28$. The
chromosomes of *P. aquatica* were slightly larger than those of *P. arundinacea*. Both of the two parental species showed slight lagging of one or two bivalents. A chromosome number of 2n=28 was also reported for the hybrid. The parental chromosomes could not be identified. At metaphase I in the F$_1$ hybrids twelve bivalents and four univalents were consistently formed. The univalents behaved erratically and were often lost. It is possible, but not proved, that the univalents in the F$_1$ correspond to the lagging bivalents occasionally occurring in both of the putative parents.

Ambathsa (1956) studied the hybrid between *P. aquatica* and *P. minor* that was reported by Trumble (1935). These hybrids were short-lived perennials. Laggards were observed at anaphase I and telophase I. Trivalents and quadrivalents were seen at metaphase I. The plants were highly sterile but produced good pollen. Partial synapsis showed that the two species may have some chromosomes in common.

**NOMENCLATURE**

Three incorrect names, *P. bulbosa* L., *P. tuberosa* L., and *P. nodosa* Murr., have been used for this species.

The first, *P. bulbosa* L., is a species of *Phleum*. A photograph (in *GH*) of the holotype in the Linnaean Herbarium, London, England, leaves no doubt that the holotype specimen is not in the genus *Phalaris*.

*Phalaris tuberosa* L. has been widely used as the name of
this species. This name, which was published in 1771, was antedated by *Phalaris aquatica*, published in 1755. Dr. C. E. Hubbard (personal communication) of the Royal Botanic Gardens, Kew, England, kindly supplied detailed descriptions of the holotypes of *P. aquatica* and *P. tuberosa* in the Linnæan Herbarium. These descriptions, in conjunction with the original descriptions by Linnaeus and photographs (in GH) of the specimens in the Linnæan Herbarium, serve to establish the identity of the names. The holotypes of these two names are both the same species. Thus Linnaeus gave different names to the same taxon. This is perhaps explained by the fact that one of the holotypes, that of *P. tuberosa*, is immature and in rather poor condition. Since *P. aquatica* was described sixteen years prior to *P. tuberosa*, the former name is the oldest available, legitimate name.

*P. nodosa*, as first described by Murray (1774), is presumably based upon *P. tuberosa* L. The description of *P. nodosa* provided by Murray is the same as that given by Linnaeus for *P. tuberosa*. In addition the phrase "Mant. 557", the place and page of publication of *P. tuberosa*, was cited. *P. tuberosa* is the only *Phalaris* described on page 557 of the Mantissa.

**DISTRIBUTION**

According to the older literature, *Phalaris aquatica* appears to have been native to the areas bordering the
Mediterranean Sea. In recent years the forage possibilities of this species have been the subject of much agronomic investigation. This has resulted in wide distribution in grassland regions.

A map (Figure 9) gives the geographic origin of the specimens studied by the author.

SELECTED SPECIMENS EXAMINED

ARGENTINA: Buenos Aires, cultivated, L.R.Parodi 5415 (US).

AUSTRALIA: New South Wales, R.A.Black 1183.007 (US); Queensland, Bunya Mts., M.S.Clemens 24-44 (US); Victoria, Canterbury (US); Western Australia, Warren River, W.M.Carne H.143 (US).


CANADA: Quebec, Ottawa, Botanic Garden, D.C.McIntosh 1927 (US).

CHILE: Concepcion Prov., Reamuncho, E.Barros 7045 (US).


ENGLAND: Wales, Aberystwyth, cultivated, T.J.Jenkins (US).

FRANCE: Ajaccio, A.de Forestier (US).

GREECE: Corinth, Heldreich (US); Isle of Rhodes, Bastida, E.Bourgeau 155 (US).

ITALY: Girgenti, M.Gandoger (MO).

JORDAN: Amman, H.F.Mooney (MO).


PORTUGAL: Coimbra, M.Ferreira 615 (US); Madeira Islands, M.Vahl, July 26, 1902 (US).

SYRIA: Aleppum, T.Kotschy, May 20, 1841 (MO).

TURKEY: Constantinople, W.Noewi 732 (MO).


UNITED STATES: California, Humboldt Co., Loleta, J.T. Howell 13721 (US); District of Columbia, Washington, Grass garden, June 9, 1937 (US); Georgia, Experiment, P.I. no. 206710, seed source: Turkey (US); Hawaiian Islands, Maui, floor of Haleakala crater, O.Degener 10828 (US); Mississippi, Starkville, S.M.Tracy, May 25, 1891 (MO); Oregon, Corvallis, cultivated, H.A.Schoth, Jan. 4, 1934 (US); Texas, Renner Co., cultivated, D.S.Correll, June, 1958 (US); Virginia, Arlington Farms, cultivated, P.L.Ricker, July 6, 1923 (US).
Figure 9. Geographic distribution of *Phalaris aquatica*
6. *Phalaris truncata*


*Phalaris truncata* var. *angustata* Trab. in Batt. and Trab. *Fl. Alg. Mon.* 140. (1895)


**DESCRIPTION**

Perennial; culms to 200 cm. tall; panicle 2.0—6.0 cm. long, 0.9—1.6 mm. wide, cylindric, occasionally ovoid-cylindric; glumes 5.5—6.3 mm. long, 1.5—1.9 mm. wide, glabrous or hirsute, truncate, winged, wing up to 1.0 mm. wide; fertile floret 3.7—5.0 mm. long, 1.2—1.4 mm. wide, densely hairy, dark brown and shiny at maturity; sterile florets 2, 0.6—1.2 mm. long, swollen and appearing somewhat fleshy, glabrous except for a tuft of hairs at the base; grain 2.8—3.0 mm. long, 1.2—1.3 mm. wide, sub-ellipsoid, light brown; chromosome number 2n=12, the chromosomes ca. 4—8
microns long at diskinesis.

OBSERVATIONS

The two swollen, somewhat fleshy sterile florets separate this species from all others of the genus except *P. brachystachys*. The differences between these species are enumerated and discussed under *P. brachystachys*.

CYTOLOGY AND CYTOGENETICS

Chromosome numbers of $2n=12$ have been previously reported for this species by Ambathsa (1956). The chromosome counts obtained by the author are reported in Table 9.

Table 9. Chromosome numbers from pollen mother cells of *Phalaris truncata* Guss.

<table>
<thead>
<tr>
<th>Collection</th>
<th>Location</th>
<th>Chromosome number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant Introduction no. 206712 Anderson voucher no. 1164</td>
<td>Seed source: unknown</td>
<td>$2n=12$</td>
</tr>
<tr>
<td>Plant Introduction no. 240197 Anderson voucher no. 1173</td>
<td>Seed source: Algeria</td>
<td>$2n=12$</td>
</tr>
<tr>
<td>Plant Introduction no. 240199 Anderson voucher no. 1163</td>
<td>Seed source: Algeria</td>
<td>$2n=12$</td>
</tr>
<tr>
<td>Plant Introduction no. 240204 Anderson voucher no. 1189</td>
<td>Seed source: Algeria</td>
<td>$2n=12$</td>
</tr>
<tr>
<td>Collection</td>
<td>Location</td>
<td>Chromosome number</td>
</tr>
<tr>
<td>-------------------------------</td>
<td>-------------------</td>
<td>-------------------</td>
</tr>
<tr>
<td>Plant Introduction no. 240205</td>
<td>Seed source: Algeria</td>
<td>2n=12</td>
</tr>
<tr>
<td>Anderson voucher no. 1188</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plant Introduction no. 240206</td>
<td>Seed source: Algeria</td>
<td>2n=12</td>
</tr>
<tr>
<td>Anderson voucher no. 1176</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plant Introduction No. 240207</td>
<td>Seed source: Algeria</td>
<td>2n=12</td>
</tr>
<tr>
<td>Anderson voucher no. 1172</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plant Introduction no. 240208</td>
<td>Seed source: Algeria</td>
<td>2n=12</td>
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<tr>
<td>Anderson voucher no. 1183</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plant Introduction no. 240209</td>
<td>Seed source: Algeria</td>
<td>2n=12</td>
</tr>
<tr>
<td>Anderson voucher no. 1177</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plant Introduction no. 240211</td>
<td>Seed source: Algeria</td>
<td>2n=12</td>
</tr>
<tr>
<td>Anderson voucher no. 1195</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plant Introduction no. 240212</td>
<td>Seed source: Algeria</td>
<td>2n=12</td>
</tr>
<tr>
<td>Anderson voucher no. 1181</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plant Introduction no. 240215</td>
<td>Seed source: Algeria</td>
<td>2n=12</td>
</tr>
<tr>
<td>Anderson voucher no. 1182</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
NOMENCLATURE

The type of *Phalaris truncata* Guss. (in NAP) was examined by the author. The drawings in Plate 6 were made from the type specimen.

Ruiz (1947) has reduced *Phalaris truncata* to varietal status under *P. brachystachya* Link. Reasons for maintaining these two as species are presented in the discussion of *P. brachystachya*.

DISTRIBUTION

*Phalaris truncata* is restricted to the lands bordering the Mediterranean Sea. A map indicating the geographic origin of the specimens examined is presented in Figure 5.

SELECTED SPECIMENS EXAMINED

**ALGERIA:** Chir, vallee de l'Oued-Abdi, B.Balansa 717 (US); Constantine: C.Bolle, 1853 (MO); S.Choulette 289 (MO US); Sidi Mecid, E.G.Paris 385 (MO); Kerrata, E.Reverchon 158 (F).

**FRANCE:** Hérault, Perols, E.Mandon, June 18, 1893 (US).

**ITALY:** Sicily, Panormi, Todaro (US); Sicily, Sclafani, Todaro 1261 (US).

**TUNISIA:** Djerber, A.Letourneaux (US); Guisgyni, Colobia, 1824 (NAP) (Holotype).

7. *Phalaris brachystachya*


*Phalaris quadrivalvis* Lag. Gen. et Sp. Nov. 3. (1816)


Plate 6. *Phalaris canariensis*, *Phalaris brachystachys*, and *Phalaris truncata*

a--d. *Phalaris canariensis*; a. inflorescences 1/2X, b. spikelet 5X, c. floret 5X, d. caryopsis 5X

e--g. *Phalaris brachystachys*; e. spikelet 5X, f. floret 5X, g. caryopsis 5X

h--k. *Phalaris truncata*; h. inflorescence 1/2X, i. spikelets 5X, j. floret 5X, k. caryopsis 5X


**DESCRIPTION**

Annual; culms to 90 cm. tall; panicle ovoid, 1.5--4.0 cm. long, 0.8--1.8 cm. wide; glumes 6.3--8.5 mm. long, 1.4--2.5 mm. wide, with broad wing up to 1.0 mm. wide, glabrous or hirsute; fertile floret 4.4--5.5 mm. long, 1.3--1.8 mm. wide, densely hairy, dark brown and shiny at maturity; sterile florets 2, 0.6--1.2 mm. long, swollen and appearing somewhat fleshy, glabrous except for a tuft of hairs at the base; grain 3.5--3.9 mm. long, 1.5--1.7 mm. wide, sub-ellipsoid, light brown; chromosome number 2n=12, the chromosome ca. 5--10 microns long at diakinesis.

**OBSERVATIONS**

**Phalaris brachystachys** and *P. truncata* form a closely-knit pair involving an annual and a perennial. The two are very close in overall morphology. There are, however, a number of relatively stable differences between the two populations, some of which are presented in tabular form in Table 10.

Ruiz (1947) reduced *P. truncata* to varietal status under *P. brachystachys* Lint. In view of the data presented in Table
<table>
<thead>
<tr>
<th>Character</th>
<th>brachystachys</th>
<th>truncata</th>
</tr>
</thead>
<tbody>
<tr>
<td>duration</td>
<td>annual</td>
<td>perennial</td>
</tr>
<tr>
<td>shape of glume apex</td>
<td>abruptly pointed</td>
<td>truncate</td>
</tr>
<tr>
<td>inflorescence shape</td>
<td>ovoid to ellipsoid, occasionally cylindric</td>
<td>cylindric, occasionally ovoid to ellipsoid</td>
</tr>
<tr>
<td>glume length</td>
<td>6.3—8.5 mm.</td>
<td>5.5—6.2 mm.</td>
</tr>
<tr>
<td>fertile floret length</td>
<td>4.4—5.5 mm.</td>
<td>3.7—5.0 mm.</td>
</tr>
<tr>
<td>caryopsis length</td>
<td>3.5—3.9 mm.</td>
<td>2.8—3.0 mm.</td>
</tr>
<tr>
<td>caryopsis width</td>
<td>1.5—1.7 mm.</td>
<td>1.2—1.3 mm.</td>
</tr>
</tbody>
</table>

The author feels that these two species, though quite close morphologically, are nevertheless distinct enough to deserve nomenclatorial recognition.

Fedtschenko (1915) has reduced *P. brachystachys* to infraspecific status under *P. canariensis*. These two species differ radically in the nature of the sterile florets. *P. canariensis* has thin, somewhat papery, sterile florets that are more than half as long as the fertile floret (Plate 6, c); *P. brachystachys* has short rather fleshy, swollen sterile florets that are less than one-fourth as long as the fertile floret (Plate 6, f). In addition to this, the fertile florets...
of *P. canariensis* tend to be somewhat larger than those of *P. brachystachys*. The author feels that the differences between the two are too well marked and constant to be considered infraspecific rather than interspecific.

**CYTOLOGY AND CYTOGENETICS**

Chromosome numbers of $2n=12$ have been reported for this species by Mlege (1939), Parthasarathy (1939), and Ambathsa (1956). The chromosome number obtained by the author is presented in Table 11.

<table>
<thead>
<tr>
<th>Collection</th>
<th>Location</th>
<th>Chromosome number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant Introduction no. 202677</td>
<td>Seed source: unknown</td>
<td>$2n=12$</td>
</tr>
<tr>
<td>Anderson voucher no. 1186</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

There are three species in *Phalaris* having a basic chromosome number of $x=6$. They are: *P. brachystachys*, *P. truncata*, and *P. canariensis*. Parthasarathy (1939) suggests that the 12-chromosome species are derived from the 14-chromosome type by the fusion of two pairs of chromosomes with sub-terminal constrictions to give one pair with median constrictions. Further discussion of this will be found in
the discussion of the cytology of the genus.

Parthasarathy (1939) reported several types of cytological abnormalities including inversion loops and lack of pairing. Miosis in the author's material showed occasional irregular pairing.

**NOMENCLATURE**

*Phalaris brachystachys* Link was described on the basis of a description of *P. canariensis* made by Brotero (1804). Brotero's original description leaves no doubt that he was referring to some species of *Phalaris* other than *P. canariensis* L. Brotero's description is of an annual plant with "valvulae accessoriae" (sterile florets) in the shape of small nectaries. *P. brachystachys* is the only member of the genus that is an annual and has sterile florets that are swollen and shaped like nectaries. Link (1806), in a review of Brotero's *Flora lusitanica*, declared that *P. canariensis*, as described by Brotero, "1st neu" and provided the new specific epithet for the species. A later publication by Link (1826) included a more detailed discussion of the species and a complete description.

**DISTRIBUTION**

*P. brachystachys* occurs primarily in the lands bordering the Mediterranean Sea and on the Canary Islands. It is an adventive at widely scattered locations in the United States. A map showing the geographic origin of the specimens studied
is presented in Figure 10.

**SELECTED SPECIMENS EXAMINED**

**CANARY ISLANDS:** Gomera, San Sebastian, C.J. Pitard 388 (MO); Gran Canaria, Tafira, A.C. Cook 541 (F, MO, US); Teneriffe, La Questa, C.J. Pitard 700 (MO).

**CYPRUS:** Kanli, A.T. Semple 294 (US); Paphos, M. Haradjian 728 (MO, US).

**FRANCE:** Beziers, Theveneau, June 1, 1869 (MO); Montpellier, J.E. Planchon (US); Paris, Jeannert, May 30, 1911 (F); Port Juvenal, naturalized, Touchy 1039 (F); Toulon, St. Marguerite, A. Theveneau, May, 1865 (US).

**IRAQ:** Daltawah, barley fields, E.R. Guest 1409 (US); Jebel Golat between Ain Tellawi and Balad Sinjar, H. Field and Y. Lazar 441 (F, US).

**ITALY:** Bologna, F. Cavara (US); Bologna, A. Fiori (US); Firenze, M.F. Spencer, May 21, 1893 (F); Sicily, Palermo, Todaro (US); Tuscany, Pisa, Savl 2161 (F).

**JORDAN:** Hebron, T. Kotschy 437 (US); Jerusalem, F. J. Meyers 686 (F).

**LEBANON:** Beirut, Jeannert (F); Beirut, Post (US).

**MADEIRA ISLANDS:** Kuy 2682 (US).

**MOROCCO:** Dj Habibi, M. Gandoger, 1910-11 (MO); R'bat, M. Gandoger 1910-11 (MO).

**PORTUGAL:** Coimbra, A. Kneucker 616 (US); Estremadura, Campolide, A. R. da Cunha, May, 1890 (US).

**SWEDEN:** Malmö, Lundgren, 1864 (F).

**SWITZERLAND:** Champs Honneur, C. Thiebaut, April 30, 1877 (F).

**UNITED STATES:** California, Butte Co., Nelson, A. A. Heller 5446 (F, MO, US); Missouri, Laclede Co., Horseshoe Pond, G. Moore, June 30, 1938 (F); Oregon, Linnton, near Portland, W. N. Suksdorf 1904 (US).

8. **Phalaris canariensis**

**Phalaris canariensis** L. Sp. Pl. ed. 1. 54. (1753)

(Holotype in LINN; photograph of holotype in GH)

**Phalaris ovata** Moench. Meth. Pl. 208. (1794)

**Phalaris avicularia** Salisb. Prodr. Stirp. 17. (1796)

**Phalaris canariensis** var. **nigra** Stokes. Bot. Mat. Med. 1:135. (1812)

Figure 10. Geographic distribution of *Phaleria brachystachya*


**DESCRIPTION**

Annual; culms erect, 30--100 cm. tall; panicle ovate to oblong-ovate, 1.5--4.0 cm. long, 1.5--2.0 cm. wide; spikelets broad, imbricate; glumes 7.0--10.0 mm. long, pale green with darker green longitudinal stripes, keel winged, broadened upward, strigose or glabrous on wingless portion; fertile floret acute, 4.8--6.8 mm. long, densely appressed-pubescent; sterile florets 2, 2.5--4.5 mm. long, broad and somewhat chaffy, sparsely pubescent; grain 3.9--4.2 mm. long, 1.4--1.7 mm. wide, light brown, surface faintly striate; somatic chromosome number 2n=12, the chromosomes ca. 5--9 microns long at diakinesis.

**OBSERVATIONS**

*P. canariensis*, commonly called Canary Grass, is readily separable from all other species in the genus by its relatively large, foliaceous sterile florets which are always more than 2.5 mm. in length and at least 1.5 mm. wide (Plate
Phalaris braehystachys is grossly similar but always has smaller, swollen, sterile florets which are never longer than 1.2 mm. (Plate 6, f). No intermediates are found between these species.

*P. canariensis* is used widely in seed mixtures for pet birds. Selschop and Wolfaardt (1952) discussed the commercial production of bird seed in South Africa. According to these authors, the best yields are obtained when seed is grown under irrigation or with about twelve inches of rainfall in the five month period required for it to mature. Warm, low-altitude areas seem to provide the best environmental conditions. From 30 to 60 pounds of Canary Grass seed per morgen (about 2.1 acres) are sown in May. In frost-free areas planting may be as late as September. Yields are reported to run from 1200 to a maximum of 2000 pounds per morgen.

**CYTOLOGY AND CYTOGENETICS**

Chromosome numbers of $2n=12$ have been reported by Church (1929), Avdulov (1931), Katterman (1931), Parthasarathy (1939), Saura (1943), Hanson and Hill (1953), and Ambathsa (1956). Nakajima (1933) reports a chromosome count of $2n=28$. The count obtained by the present author is presented in Table 12.

Church (1929) and Parthasarathy (1939) both report meiosis to be normal in this species. Meiosis in the author's material likewise appears to be normal.
Table 12. Chromosome count from pollen mother cells of *Phalaris canariensis* L.

<table>
<thead>
<tr>
<th>Collection</th>
<th>Location</th>
<th>Chromosome number</th>
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</thead>
<tbody>
<tr>
<td>Plant Introduction no. 174299</td>
<td>Seed source: Turkey</td>
<td>2n=12</td>
</tr>
<tr>
<td>Anderson voucher no. 1233</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The chromosome count of 2n=28 reported by Nakajima (1933) is certainly quite different from the other counts reported. A voucher specimen was not cited and there can be no sure way to identify the specimen from which the count was made. On the basis of all of the counts made by other workers it would seem possible that Nakajima had some species other than *P. canariensis*. The illustration included with Nakajima's report shows 14 pairs of relatively small chromosomes. Meiotic chromosomes in the author's material were quite large; certainly they appeared much larger than those illustrated by Nakajima. Until positive identification of the original material used by Nakajima is presented this report must remain open to some question.

Ostergren (1957) has experimentally produced autotetraploids (2n=24) and aneuploids (2n=21, 23), in *P. canariensis* by a pressurized nitrous oxide technique. No information concerning the morphology of these plants was included.
NOMENCLATURE

*Phalaris canariensis* is one of two species of *Phalaris* described by Linnaeus in 1753 that can be correctly placed in this genus. Since Linnaeus did not specifically refer to any particular specimen in his herbarium as a basis for his description, it is necessary to choose a lectotype for the species. Accordingly sheet number 78.1 of the Linnean herbarium (LINN) is hereby designated as the lectotype of *P. canariensis*. Dr. C. E. Hubbard of the Royal Botanic Gardens, Kew, England (personal communication) kindly furnished a detailed description of the specimens on this sheet. This description leaves no doubt as to the species involved.

DISTRIBUTION

Raius (1694) gave Sicily, Italy, and southern France as the range of Canary Grass. Unfortunately it is not possible to be sure that Raius was referring to *P. canariensis* alone or whether he was including several of the species in *Phalaris* that were probably native to the area mentioned by Raius. Linnaeus (1753) listed the habitat of this species as southern Europe and the Canary Islands. Early floras agree substantially with this distribution. The widespread interest in this species as a source of bird seed, coupled with its overall viability, doubtless aided it in becoming adventive in many areas not included in its original range. Adventive individuals are frequently found growing in refuse dumps and
ballast deposits.

A map (Figure 11) presents the geographic origin of the specimens examined by the author.

SELECTED SPECIMENS EXAMINED

ARGENTINA: Buenos Aires, between Buenos Aires and La Plata on railroad, W.J. Eyerdam, A.A. Beetle #3154 (MO); Tucuman Prov., Rio Salí, S. Venturi 4550 (US).

AUSTRIA: Salzburg, Dreifuss, August 29, 1872 (MO).

BELGIUM: Brussels, Tilvorde, J.D. Vits, June 30, 1930 (US).


BOLIVIA: La Paz, O. Buchothien 239 (US).

BRITAIN: Minas Gerais, Pocas de Caldas, A. Chase 10680 (US).


DENMARK: Copenhagen, H. Mortensen, Aug. 24, 1889 (MO).


FRANCE: Antibes, Thuret, June 4, 1861 (F); Paris, Gentilly, Jeanpert, July 15, 1918 (F); Montpellier, Cintrect, May 27, 1888 (US).

GERMANY: Karlsruhe, A. Kneucker, July, 1900 (MO);

Schmiedeberg, G. Hieronymus, Aug. 18, 1884 (US).

HONG KONG: Aberdeen, Y.W. Taam 1403 (US).

HUNGARY: Mestalajan, A. De Degen 259 (US).

ITALY: Firenze, M. F. Spencer, May 21, 1893 (F); Corsica, Ile-rousse, P. Aellen 342 (MO).


NORWAY: Vestre Aker, O. Andersen, July 8, 1907 (US).

PERU: Lima, R. J. Seibert 2323 (MO, US); Puno, Salcedo, Saukup, Feb., 1938 (F).
Figure 11. Geographic distribution of *Phalaris canariensis*
SPAIN: Lisiere des champs a Fiscal, Aragon, terrain-calcaire, G. Gautier, June 14, 1879 (F); Porto Santa Maria, E. Bourgeois 505 (US).

SWEDEN: Malmo, B. Lundgren, 1864 (F).

SWITZERLAND: Winterthur, Hirzel (MO); Zurich, Molasse, F. G. Stebler and C. Schroeter 9 (US).

UNION OF SOUTH AFRICA: Pietermaritzburg, A. P. Gooseus 154 (US).

UNITED STATES: Alaska, Fairbanks, A. S. Hitchcock 4577 (US); Arkansas, Little Rock, G. Letterman (MO); California, Yreka, G. D. Butler 498 (US); Colorado, Denver, E. L. Hughes 22 (GH); Connecticut, Bridgeport, E. H. Elmes, July 31, 1895 (GH, US); Delaware, Wilmington, A. Commons, July 8, 1897 (US); District of Columbia, Washington, T. H. Kearney, June 4, 1899 (US); Illinois, Wheaton, W. S. Moffatt 814 (MO); Indiana, Noble Co., east of Ligonier, C. C. Deam 14317 (US); Iowa, Des Moines, C. R. Ball 29 (US); Kansas, Topeka, E. A. Popenoe, June 15, 1879 (US); Maine, Camden, G. G. Kennedy, July 21, 1902 (GH); Maryland, Berlin, F. L. J. Boettcher, June 13, 1898 (F); Massachusetts, Dorchester, "dump", Churchill Estate, J. R. Churchill, Sept. 19, 1911 (GH, MO); Michigan, Cheboygan Co., Cheboygan city dump, L. H. Harvey 671 (US); Minnesota, Springfield, E. P. Sheldon, July, 1891 (GH); Missouri, East St. Louis, H. Eggert, July 4, 1887 (MO); Montana, Bozeman, J. W. Blankenship, Sept. 26, 1888 (NDA); Nebraska, Kearney, C. L. Shear 269 (MO, US); New Jersey, Weehawken, W. M. van Sickle, July 10, 1895 (US); New York, New York City, 86th street, W. H. Reggett, June 15, 1895 (GH); North Dakota, Devil's Lake, T. T. Anderson, August 10, 1905 (NDA); Ohio, Portage Co., Garretsville, R. J. Webb 1411 (GH); Oregon, Portland, W. N. Suksdorf 2758 (US); Pennsylvania, Lancaster Co., Columbia, A. P. Garber, 1869 (US); Rhode Island, Providence, common on waste ground, J. F. Collins, July 9, 1892 (GH); South Carolina, Columbia, K. A. Taylor, May, 1890 (F); South Dakota, Brookings, J. J. Thornber, Aug. 25, 1893 (MO); Texas, Gillespie Co., G. Jermy 36 (MO); Virginia, Smyth Co., Marion, J. K. Small, July 8, 1892 (F, GH, US); Washington, Point Haddock, N. L. Gerdner 33 (US); West Virginia, Wheeling, H. N. Mertz, July 1877 (US); Wisconsin, Sturgeon Bay, J. K. Schuette, July 4, 1900 (F); Wyoming, Mammoth Hot Springs, E. A. Mears 3376 (US).


9. Phalaris angusta


Phalaris chilensis Presl. Rel. Haenk. 1:245. (1830) (Holotype in PR)

Phalaris laxa Spreng. ex Steud. Nom. Bot. ed. 2. 2:315. (1841) **pro syn.**


Phalaris intermedia var. angustata Beal. non Schlech. Grasses N.A. 2:182. (1896) (Photograph of type in US)


**DESCRIPTION**

Annual; culms to 150 cm. tall; panicle narrow and cylindric, 2.5--17.0 cm. long, 0.6--1.5 cm. wide; spikelets usually densely imbricate, lying almost parallel with the inflorescence axis; glumes 2.9--5.5 mm. long, 0.6--1.1 mm. wide, apex usually naviculate, occasionally acute, nerves scabrous along most of length, internerve areas scabrous near the base of the glume; fertile floret 2.2--3.8 mm. long, 0.9--1.5 mm. wide, densely pubescent and shiny; sterile florets 2, 0.7--1.5 mm. long, a tuft of hairs at the base; grain 1.4--1.6 mm. long, 0.7--0.9 mm. wide, somewhat flattened; chromosome number
2n=14, the chromosomes are 4--7 microns long at diakinesis.

**Observations**

*Phalaris angusta*, *P. amethystina*, *P. caroliniana*, *P. platensis*, and *P. lemmonii* are members of a species complex indigenous to several areas in the Americas. *P. platensis* and *P. lemmonii* differ from the remaining three in that they have plump, turgid fertile florets which are almost round in cross section. The fertile florets in these two species are densely pubescent with spreading hairs except for the naked, sharply acuminate apex. *P. angusta*, *P. amethystina*, and *P. caroliniana* have somewhat flattened fertile florets that are more or less evenly pubescent, including the acute, tapering apex. A comparison of *P. angusta*, *P. caroliniana*, and *P. amethystina* for several characters is presented in Table 13.

As can be seen from Table 13, the average lengths of the glumes, fertile florets, sterile florets and inflorescences are somewhat different from those of *P. caroliniana* and *P. amethystina*. The most pronounced quantitative difference seems to be that of the sterile floret length. Sterile florets of *P. angusta* are shorter than 1.5 mm. long; those of the other two species are 1.5 mm. long or longer. The inflorescence of *P. angusta* is rather long and narrow as compared to *P. caroliniana* and *P. amethystina*. Qualitatively, the shape of the glume apex seems to be a good differentiating feature. Glume apices of *P. angusta* are usually naviculate (Plate 7,b),
Table 13. Comparison of *Phalaris angusta*, *P. ceroliniana*, and *P. amethystina*

<table>
<thead>
<tr>
<th>Character</th>
<th><em>P. angusta</em></th>
<th><em>P. ceroliniana</em></th>
<th><em>P. amethystina</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>glume length</td>
<td>extreme 2.9 mm.</td>
<td>4.2 mm.</td>
<td>4.7 mm.</td>
</tr>
<tr>
<td></td>
<td>mean 3.7</td>
<td>5.4</td>
<td>5.3</td>
</tr>
<tr>
<td></td>
<td>extreme 5.5</td>
<td>6.7</td>
<td>6.2</td>
</tr>
<tr>
<td>shape of glume apex</td>
<td>usually naviculate,</td>
<td>acute</td>
<td>acute</td>
</tr>
<tr>
<td></td>
<td>occasionally acute</td>
<td></td>
<td></td>
</tr>
<tr>
<td>glume lateral nerve pubescence</td>
<td>scabrous</td>
<td>glabrous, very</td>
<td>scabrous</td>
</tr>
<tr>
<td></td>
<td></td>
<td>rarely slightly</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>scabrous</td>
<td></td>
</tr>
<tr>
<td>fertile floret length</td>
<td>extreme 2.1 mm.</td>
<td>3.0 mm.</td>
<td>3.3 mm.</td>
</tr>
<tr>
<td></td>
<td>mean 2.8</td>
<td>3.4</td>
<td>3.6</td>
</tr>
<tr>
<td></td>
<td>extreme 3.8</td>
<td>4.2</td>
<td></td>
</tr>
<tr>
<td>sterile floret length</td>
<td>extreme 0.7 mm.</td>
<td>1.5 mm.</td>
<td>1.5 mm.</td>
</tr>
<tr>
<td></td>
<td>mean 1.2</td>
<td>1.9</td>
<td>1.7</td>
</tr>
<tr>
<td></td>
<td>extreme 1.5</td>
<td>2.6</td>
<td>1.9</td>
</tr>
<tr>
<td>caryopsis length</td>
<td>1.4--1.6 mm.</td>
<td>2.0--2.3 mm.</td>
<td>2.1--2.2 mm.</td>
</tr>
<tr>
<td>inflorescence length</td>
<td>extreme 2.5 cm.</td>
<td>1.0 cm.</td>
<td>2.7 cm.</td>
</tr>
<tr>
<td></td>
<td>mean 7.7</td>
<td>3.8</td>
<td>3.7</td>
</tr>
<tr>
<td></td>
<td>extreme 17.0</td>
<td>7.0</td>
<td>4.5</td>
</tr>
</tbody>
</table>
Plate 7. Phalaris angusta, Phalaris californica and Phalaris maderensis

a–d. Phalaris angusta; a. inflorescence 1/2X, b. spikelets 5X, c. florets 5X, d. caryopsis 5X

e–h. Phalaris californica; e. inflorescence 1/2X, f. spikelet 5X, g. floret 5X, h. caryopsis 5X

i–k. Phalaris maderensis; i. inflorescence 1/2X, j. spikelets 5X, k. floret 5X
occasionally acute; glume apices of *P. amethystina* (Plate 8, f) and *P. caroliniana* (Plate 9, f) are almost always acute.

Some specimens of *P. angusta* collected in California differ from the typical form in several features. The inflorescences and spikelets are larger. The glume apices are quite acute, certainly not as naviculate as those of collections of *P. angusta* made in the southeastern United States; the lateral nerves are not as densely scabrous as those of specimens from the remainder of the range; the inflorescences are not as densely imbricate, the spikelets tend to diverge from the inflorescence axis at about a forty-five degree angle. Morphologically, these specimens resemble collections of *P. caroliniana*; the most prominent differences are the scabrous lateral glume nerves, a feature not found in typical *P. caroliniana* collections, and the much larger, somewhat lobed inflorescences, likewise not characteristic of *P. caroliniana*. Overlap of the ranges of *P. angusta* and *P. caroliniana* occurs both in the southeastern United States and in California. On the basis of the very limited number of specimens of this large *P. angusta* seen by the author, it does not seem wise to more than suggest that possible introgression has occurred or is occurring between these two taxa. Further work, especially attempts at crosses and extensive field studies, is needed to determine the nature of the relationships within this species complex.
P. angusta f. macra Hack. ex Stuck. is based upon a depauperate specimen collected in Argentina. A fragment of the type is in US. This form differs from typical P. angusta only in being very short (less than 20 cm.) and having very small inflorescences. Morphologically, the spikelets do not differ noticeably from those of the typical form.

The numerous named varieties of Jansen and Wachter (1916) are apparently extremes of the total variation pattern with respect to inflorescence shape and size.

CYTOLOGY AND CYTOGENETICS

Saura (1943) and Ambathsa (1956) report a chromosome number of 2n=14 for P. angusta. The present author's chromosome count for this species is presented in Table 14.

Meiosis in the material studied by the author appeared normal.

Table 14. Chromosome number from pollen mother cells of Phalaris angusta Nees ex Trin.

<table>
<thead>
<tr>
<th>Collection</th>
<th>Location</th>
<th>Chromosome number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant Introduction no. 202391</td>
<td>Seed source:</td>
<td>2n=14</td>
</tr>
<tr>
<td>Anderson voucher no. 1184</td>
<td>Argentina</td>
<td></td>
</tr>
</tbody>
</table>
NOMENCLATURE

The first description of this species is that of Trinius in 1828. This description was credited to Nees ab Egenbeck but no place of publication by Nees was given by Trinius. The well-drawn plate accompanying Trinius' description leaves no doubt as to the typification of the species. Nees himself provided a full description in 1829.

DISTRIBUTION

Most of the specimens examined by the author were collected in prairie and grassland areas in the southern United States and South America. Occasional adventives have been collected in the Union of South Africa. A map (Figure 12) gives the geographic origin of the specimens seen by the author.

SELECTED SPECIMENS EXAMINED

ARGENTINA: Buenos Aires Prov.: Boradero, Rio Pintas, A.Burkart 8506 (F,US); Delta of Rio Parana, W.J.Eyerdem and A.A.Beetle 23050 (MO); Chaco Prov., Las Palmas, P.Jorgensen (MO,US); Entre Rios Prov., Parana, Isla Puentes, I.Morel 10089 (US); Isla de Frances, fiente a Rosario, A.Burkart 8807 (F); Rio Negro Prov., General Roca, W.Fischer 268 (F,MO,US); Tucuman Prov., Tafi, El Siambon, Schreiter 6876 (F,US).


BRAZIL: Montenegro, Fazeuda Paguate, P.N.Capparelli 552 (US); Rio Grande do Sul: Barro do Ribeiro, p. Guaiba, B.Rambo 37987 (US); Porto Alegre, C.A.M. Lindman A693 (US); Porto Alegre, Vila Manresa, B.Rambo 544533 (US); Pareci, Municipio Montenegro, B.Rambo 26647 (US).


UNION OF SOUTH AFRICA: Cape Peninsula, Bishopscourt, T.M.Salter 9054 (MO); Middleburg, cauliflower field, W.Long 8223 (MO,US).
Figure 12. Geographic distribution of *Phalaris angusta*
UNITED STATES: California: Alameda Co., Alameda, Bolander, July 4, 1866 (MO); Los Angeles Co., Los Angeles, G.B.Grant 970 (F); Mendocino Co., Ukiah, Bolander 38 (US); San Bernardino Co., hills west of Colton, S.B.Parish 2165 (US); San Diego Co., Brooks, G.G.Pringle, May 1, 1882 (F, US) (Isotype, P. intermedia var. angustata Beal); San Luis Obispo Co., Los Osos valley, R.F.Hoover 7128 (US); Santa Cruz Co., Santa Cruz, C.L.Anderson, 1888 (US); Solano Co., 15 miles northwest of Rio Vista, I.Wiggins 5863 (F); Tulare Co., near Visalia, F.V.Coville and F.Funston 1282 (US); Georgia, Savannah, D.E.Eyles 6943 (GH); Louisiana: New Orleans, City Park, W.M.Canby, April 2, 1900 (US); Pointe a la Hache, A.B. Langlois, May 6, 1885 (US); Mississippi, Stoneville, P.R. Henson, May, 1932 (US); Oregon, Curry Co., 5 miles north of mouth of Euchre Creek, M.E.Peck 14553 (US); Texas: Galveston, F.Lindheimer, April, 1843 (MO); Sabine Pass, J.Reverchon, April 24, 1903 (MO).

URUGUAY: Canelones Dept., Aguas Corrientes, W.G.Herter 98074 (F); Canelones Dept., Montevideo, J.Arechesvaleta 52 (US); Florida Dept.: Arroyo Mansavillagra, Gallinal 5824 (US); La Palma, W.G.Herter 10370 (MO,US); Rio Negro Dept., Gerro Largo, Pallero, Rosengurtt B-213 (US); San Jose Dept., Santa Lucia, C.Osten 21698 (US).

10. Phalaris californica


DESCRIPTION

Perennial; culms erect, up to 150 cm. tall; panicle ovoid to oblong, 1.5--5.0 cm. long, 1.0--3.0 cm. wide, more or less truncate at the base; spikelets loosely imbricate; glumes 5.0--8.0 mm. long, 0.9--1.6 mm. wide, acute to somewhat acuminate, without wing or very narrowly winged at the apex, mid-nerve slightly scabrous, glume tips often tinged with purple at maturity; fertile floret 3.5--5.0 mm. long, 1.0--1.5 mm. wide, sparsely pubescent; sterile florets 2, 1.8--3.3 mm. long, densely pubescent; grain 2.4--2.6 mm. long, 0.9--1.1 mm. wide, cylindric, red-brown at maturity;
OBSERVATIONS

_P. californica_ is a tufted perennial with the culms arising from a dense underground crown. The best distinguishing features are the short, relatively broad inflorescence (Plate 7, e), wingless (or very narrowly winged), often purple-tinged glumes (Plate 7, f), and the perennial habit. _P. arundinacea_ is the only other perennial with wingless glumes. _P. arundinacea_ spreads by means of extensive underground rhizomes; _P. californica_ has no rhizomes. In addition, the caryopsis of _P. arundinacea_ is relatively small, being 1.5–2.0 mm. long (Plate 5, d); the caryopsis of _P. californica_ is 2.4–2.6 mm. long (Plate 7, h). The inflorescence of _P. arundinacea_ is usually long and more or less narrowly cylindrical with a tapering or lobed base (Plate 5, a); that of _P. californica_ is broadly cylindrical with a truncate base (Plate 7, e). All of the other perennial species in this genus have broadly winged glumes.

CYTOLOGY AND CYTOGENETICS

Stebbins and Love (1941) and Ambathsa (1956) report a chromosome count of 2n=28 for this species. No material was available to the present author for study.

NOMENCLATURE

A portion of the holotype of _P. californica_ is in the
United States National Museum and was examined by the author. This type represents the species as commonly understood today.

**DISTRIBUTION**

*Phalaris calliformal* is restricted to California and Oregon. Hitchcock (1950) reports that this species grows in ravines and open moist ground. A map (Figure 13) gives the geographic origin of the specimens examined during the course of this study.

**SELECTED SPECIMENS EXAMINED**

UNITED STATES: California: Contra Costa Co., Pt. Isabel, J.Burtt Davy, April 1897 (US); Del Norte Co., Douglas Park, J.W.Thompson 4509 (MO); Marin Co., San Rafael, J.W. Blankinship 58 (GH,US); Mendocino Co., Mendocino, J.McMurphy 456 (US); Monterey Co.: King City, J.Swallen 617 (US); Lime-kiln Creek, J.B.Davy 7706 (US); Moss Beach, Pacific Grove, A.Chase 5660 (US); Sta. Lucia Mts., A.Eastwood, May 1--12, 1897 (US); San Luis Obispo Co., Nipoma, W.H.Brewer 418 (US); San Mateo Co.: Crystal Springs Lake, A.D.E.Elmer 4699 (MO,US); Lake Pelaracitos, J.B.Davy 725 (US); Santa Clara Co.: Congress Springs, A.S.Hitchcock, June 22, 1908 (US); foot hills west of Los Gatos, A.A.Heller 8568 (GH, ISC,MO,US); Sonoma Co., Sherwood, A.S.Hitchcock, June 26, 1908 (US); Angel Island, H.N.Bolander 1529 (F,GH,US); Mendocino coast, H.N.Bolander 6123 (F,MO,US); Oregon, Curry Co., Chetco River, by the sea, T.Howell, June 11, 1884 (F,GH,US).

**11. Phalaris maderensis**

*Phalaris maderensis* (Menezes) Menezes. *As Gramineas do archipelago da Madeira*. 23. (1906)


**DESCRIPTION**

Annual; roots fibrous; culms 10--50 cm. tall, caespitose; panicle 2.5--5.0 cm. long, ovate-oblong to cylindric; glumes 4.5--4.8 mm. long, 1.4--1.5 mm. wide, truncate, winged at the
Figure 13. Geographic distribution of *Phalaris californica*
tip, glabrous, pale or sometimes tinged with purple; fertile floret 3.2–3.4 mm. long, 1.2–1.3 mm. wide, densely pubescent; sterile floret 1, 1.3–1.4 mm. long, slightly pubescent along outer edge; grain about 1.8 mm. long, 0.7 mm. wide, pale brown with surface somewhat striate; chromosome number unknown.

OBSERVATIONS

Only one specimen referable to *P. maderensis* was available for study. On the basis of this limited material it seems to be a well-defined species. Only two other species in the genus have only one sterile floret. These are *P. aquatica* and *P. minor*. The former is a perennial, often with bulbous culm bases and has much larger spikelets. In addition, the glumes of *P. aquatica* are not truncate but are quite acute (Plate 5, g). *P. maderensis* is an annual and has small, more or less truncate spikelets in comparison to *P. aquatica*. The differences between *P. minor* and *P. maderensis* are a little more elusive. *P. minor* has pointed glumes that usually have the margin of the glume wings erose-denticulate (Plate 4, a). The glumes of *P. maderensis* are more or less truncate and have the margins almost entire (Plate 7, j). The single specimen available for study had a narrowly cylindrical inflorescence (Plate 7, i) about 4 cm. long; inflorescences of *P. minor* are often ovate-oblong; when cylindric they are much wider than that of the specimen of *P. maderensis*. 
The description of *P. maderensis* presented in this paper is drawn partly from Menezes' original description and partly from the specimen seen by the author.

**CYTOLOGY AND CYTOGENETICS**

No material of *P. maderensis* was available for cytological study. Chromosome numbers in this species are unknown.

**NOMENCLATURE**

Menezes first named this taxon as a variety of *P. coerulescens* (1894). Twelve years later he elevated it to specific rank (1906). The type specimen of this species was not seen, however Menezes' very complete description leaves no doubt as to the taxon referred to.

**DISTRIBUTION**

The only location from which the author has seen collected material is on the island of Porto Santo off the northwest coast of Africa. Menezes gives Porto Santo as the place of collection of the type specimen.

**SPECIMEN EXAMINED**

PORTO SANTO ISLAND: Kuy, Ilheu dos Embarcaderos. (US 1715395).

12. *Phalaris amethystina*


**Phalaris colchaguensis** Phil. Linnaea. 33:276. (1864)

**DESCRIPTION**

Annual; culms to 60 cm. tall, glabrous; panicle 1.5--4.5 cm. long, 1.0--1.4 cm. wide, ovate-cylindric; spikelets rather loosely imbricate, diverging from the panicle axis; glumes 4.7--6.2 mm. long, 0.8--1.1 mm. wide, somewhat winged, the wings sometimes obscure, acute to acuminate, glume lateral nerves scabrous on lower one-half; fertile floret 3.2--4.2 mm. long, 1.0--1.6 mm. wide, densely pubescent, somewhat flattened; sterile florets 2, 1.5--1.9 mm. long, subulate, a tuft of hairs at the base; grain 2.1--2.2 mm. long, 1.2--1.3 mm. wide, somewhat flattened; chromosome numbers unknown.

**OBSERVATIONS**

*Phalaris amethystina* and *Phalaris caroliniana* are morphologically very similar. The best differentiating character appears to be the presence of scabrous glume nerves in *P. amethystina* (Plate 8, f), a feature ordinarily lacking in *P. caroliniana* (Plate 9, f). In addition to this feature, the inflorescence of *P. amethystina* tends to be less dense than that of *P. caroliniana*; *P. amethystina* is a somewhat shorter plant than *P. caroliniana*. The wide separation in geographic ranges provides additional indication in favor of recognizing these as two separate species.
Plate 8. Phalaris platensis and Phalaris amethystina

a--d. Phalaris platensis; a. habit 1/2X, b. spikelets 5X, c. florets 5X, d. caryopsis 5X

e--h. Phalaris amethystina; a. inflorescence 1/2X, f. spikelets 5X, g. florets 5X, h. caryopsis 5X
CYTOLOGY AND CYTOGENETICS

No living material of *P. amethystina* was available to the author for cytological studies. Chromosome numbers have not been reported for this species.

NOMENCLATURE

A portion of the holotype of this species was examined in the United States National Museum.

The name *Phalaris chilensis* Presl has occasionally been used for this species. Examination of the type specimen, which is in the National Museum, Praha, Czechoslovakia, showed it to be *Phalaris angusta* Nees ex Trin.

DISTRIBUTION

The geographic origin of the specimens of the species studied by the author is indicated by the unshaded circles on the map in Figure 14.

SPECIMENS EXAMINED

CHILE: Aconcagua Prov., R.A.Philippi, 1888 (US); Coquimbo Prov., Claude-Joseph 4623 (US); O'Higgins Prov., Rancagua, Bertero 534 (holotype; clastotype is in US); Santiago Prov.: Santiago, Claude-Joseph A121 (US); Santiago, Claude-Joseph 2346 (US); Valparaiso Prov.: Valparaiso: Claude-Joseph 3616 (US); E.Gunther 13 (US); Cuming 468 (US); Autuco, Poppig 23 (MO); El Pangal, Limache, A. Garraventa 2837 (US).

13. *Phalaris platensis*


DESCRIPTION

Annual; culms to 40 cm. tall; panicle cylindrical, 3--8 cm. long, longer panicles somewhat lobed at the base; glumes 3.9--5.1 mm. long, more or less equal, acute, very narrowly winged near the apex or wingless, the keel and two lateral nerves scabrous; fertile floret 2.7--3.6 mm. long, turgid, covered with spreading or appressed hairs except for the usually naked, sharply acuminate apex; sterile florets 2, 0.8--1.3 mm. long, subulate, with a tuft of hairs at the base; grain 1.7--1.9 mm. long, 1.0--1.2 mm. wide, pale brown; chromosome number 2n=14, the chromosomes ca. 3.4--5.6 microns long (Ambathsa, 1956).

OBSERVATIONS

This species is very closely allied morphologically with P. lemmonii from which it differs by its smaller spikelets and inflorescences. These differences are presented in Table 15.

As can be seen from this table, P. platensis averages somewhat smaller than P. lemmonii for the characters given. There are overlaps in extreme size values but the means are quite well set apart. In addition to these characters, the geographic ranges are quite distinct. P. platensis is limited
Table 15. Quantitative differences between Phalaris lemmonii Vasey and Phalaris platensis Henr.

<table>
<thead>
<tr>
<th>Character</th>
<th>lemmonii</th>
<th>platensis</th>
</tr>
</thead>
<tbody>
<tr>
<td>glume length</td>
<td>extreme</td>
<td>4.9 mm.</td>
</tr>
<tr>
<td></td>
<td>mean</td>
<td>5.6</td>
</tr>
<tr>
<td></td>
<td>extreme</td>
<td>6.7</td>
</tr>
<tr>
<td>fertile floret</td>
<td>extreme</td>
<td>3.5 mm.</td>
</tr>
<tr>
<td>length</td>
<td>mean</td>
<td>4.2</td>
</tr>
<tr>
<td></td>
<td>extreme</td>
<td>5.1</td>
</tr>
<tr>
<td>sterile floret</td>
<td>extreme</td>
<td>1.0 mm.</td>
</tr>
<tr>
<td>length</td>
<td>mean</td>
<td>1.3</td>
</tr>
<tr>
<td></td>
<td>extreme</td>
<td>1.6</td>
</tr>
<tr>
<td>inflorescence</td>
<td>extreme</td>
<td>4.0 mm.</td>
</tr>
<tr>
<td></td>
<td>mean</td>
<td>7.6</td>
</tr>
<tr>
<td></td>
<td>extreme</td>
<td>12.0</td>
</tr>
<tr>
<td>caryopsis length</td>
<td>extreme</td>
<td>2.1 mm.</td>
</tr>
<tr>
<td></td>
<td>mean</td>
<td>2.2</td>
</tr>
<tr>
<td></td>
<td>extreme</td>
<td>2.3</td>
</tr>
</tbody>
</table>

Henrard (1938) has noted Phalaris as one of many genera that possess species occurring in the southern United States and southern South America. The P. lemmonii-P. platensis complex, though P. lemmonii has a range in western rather than southern United States, seems to bear out this relationship. The spikelets and inflorescences of the two species are very similar, yet the rather stable quantitative differences, combined with the very distinct geographic di-
tribution, lead one to believe that these constitute populations at the specific rather than infraspecific levels.

CYTOLOGY AND CYTOGENETICS

Ambathsa (1956) reported a chromosome number of $2n=14$ for this species. No material for cytological study was available to the author.

NOMENCLATURE

The first legitimate specific name for this plant is that of Henrard as used by Heukels (1934). Even though it was published in a key, it satisfied the requirements of valid and effective publication.

In 1938, Henrard published a complete description and a discussion of *P. platensis*. The holotype, as cited in this latter publication is in the Rijksherbarium, Leiden, Netherlands. The drawings of habit and spikelets (Plate 8, a,b) were made from the holotype.

DISTRIBUTION

*P. platensis* is limited to the Parana and Uruguay River valleys in South America. The shaded circles in the map (Figure 14) show the geographic origin of the specimens examined by the author.

Little precise data are available concerning the habitat of the species. The label of the holotype (in L) reads "dans les prairies naturelles".
Figure 14. Geographic distribution of *Phalaris amethystina* and *Phalaris platensis*.
SPECIMENS EXAMINED

ARGENTINA: Buenos Aires Prov.: Manantiales, L.R.Parodi 6625 (US); San Vicente, A.Burkart 13439 (US); Station de San-Vicente, pres de Buenos Aires, B.Balansa, Dec. 5, 1875 (Holotype, in L. Herb. Lugd. Bat. 909.74...456); Villa Ortuger, L.R.Parodi 8968 (paratype in L, duplicate of paratype in US).


URUGUAY: Flores Dept., Sta. Adelaide, Gallinal 1122 (US); Florida Dept.: Estancia Rinconde, Santa Elena, Gallinal 5781 (US); Timota, Sta. Clara, Gallinal 2696 (US); Montevideo Dept., C.Arechavaleta (US); Soriano Dept., Gallinal, P.E. 802 (US).

14. Phalaris lemmonii

Phalaris lemmonii Vasey. Contrib. U.S. Nat. Herb. 3:42. (1892) (Holotype in US)

DESCRIPTION

Annual; culms to 135 cm. tall; panicle cylindrical, 4--12 cm. long, 0.7--1.5 cm. wide, usually lobed near the base, the 3 or 4 lobes up to 2 cm. long; glumes sub-equal, 4.9--6.7 mm. long, 0.9--1.1 mm. wide, acuminate, sharp-pointed, not winged or only very slightly so, the 3 nerves scabrous; fertile floret 4.0--5.1 mm. long, 1.2--1.6 mm. wide, lanceolate, spreading pubescent (occasionally with the hairs appressed, especially in immature specimens) except for the acuminate tip; sterile florets 2, 1.0--1.6 mm. long, narrow, appressed pubescent; grain 2.1--2.3 mm. long, 1.1--1.3 mm. wide, ovoid; chromosome number 2n=14, the chromosomes ca. 3--5 microns long at diakinesis.
OBSERVATIONS

The most distinctive character of this species is the very plump, somewhat inflated fertile floret (Plate 9, c). Usually the floret is covered with spreading hairs although immature specimens occasionally have appressed pubescence. *P. lemmonii* seems most closely related to *P. platensis*. The differences between these two species have been discussed under *P. platensis*.

CYTOLOGY AND CYTOGENETICS

A chromosome number of 2n=14 has been reported for *Phalaris lemmonii* Vasey by Parthasarathy (1939). The chromosome count obtained by the present author is presented in Table 16.

Table 16. Chromosome number obtained from pollen mother cells for *Phalaris lemmonii* Vasey

<table>
<thead>
<tr>
<th>Collection</th>
<th>Location</th>
<th>Chromosome number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Beecher Crampton 4826</td>
<td>Calif., Yolo Co.</td>
<td>2n=14</td>
</tr>
<tr>
<td>Anderson voucher no. 1093</td>
<td>Dunnigan</td>
<td></td>
</tr>
</tbody>
</table>

Meiosis in the author's material appeared quite normal. Parthasarathy considers this species to be intermediate cytologically between the 12 and 14 chromosome types. Further consideration of this and other proposals are presented
Plate 9. *Phalaris lemmonii* and *Phalaris caroliniana*

a--d. *Phalaris lemmonii*; a. inflorescences 1/2X, b. spikelet 5X, c. florets 5X, d. caryopsis 5X

e--h. *Phalaris caroliniana*; e. inflorescence 1/2X, f. spikelet 5X, g. floret 5X, h. caryopsis 5X
in the discussions of cytology of the genus.

**NOMENCLATURE**

The holotype of this species is in the United States National Museum, Smithsonian Institution, Washington, D.C. and was examined by the author. This type represents the species as understood today. There are no other published names for this species.

**DISTRIBUTION**

*P. lemmonii* is restricted to California in the western United States. Hitchcock (1950) gives the habitat as moist areas in the coastal valleys. Two collections from Victoria, Australia, apparently adventives, are in US. A map (Figure 15) shows the geographic origin of the specimens studied.

**SELECTED SPECIMENS EXAMINED**

AUSTRALIA: Victoria: Baddaginnie, R.A.Black 1183.002 (US); Everton, R.A.Black 151 (US).

UNITED STATES: Arizona, J.G.Lemmon 403 (US 1011289); California: Alameda Co., Newark, J.B.Davy 1093 (US); Butte Co.: near Oroville in *Quercus lobata* belt, A.A.Heller 14360 (US); near Nelson, A.S.Hitchcock 5447 (US); Colusa Co., 4 miles east of Williams, R.S.Ferris 547 (MO); Kern Co., near Buena Vista Lake, A.A.Beetle 3992 (GH,MO); Los Angeles Co.: Inglewood, L.Abrams 3234 (GH,MO); Los Angeles, F.W.Gould 2281 (MO,US); Catalina Isl., Avalon, E.Tresk, May, 1897 (MO); Madera Co., 4 miles east of Madera, R.F.Hoover 5282 (US); Marin Co., Black Point, J.T.Howell 21657 (F,ISC,US); Mendocino Co., Ukiah, P.B.Dickey D-881 (NDA); Merced Co., 7 miles north of Merced, R.F.Hoover 2099 (US); Placer Co., B.Crampton (ISC); Sacramento Co., B.Crampton 3352 (ISC); San Benito Co., R.W.Pohl 7263 (ISC); San Diego Co. T.S.Brandegee 3425 (F, GH, MO,US); San Joaquin Co., Kettleman-Terminal road, E.E.Stanford 1466 (MO); San Luis Obispo Co., 1 mile from Creston, R.F. Hoover 6788 (US); Santa Clara Co., Saratoga, R.L.Pendleton 1336 (US); Solano Co.: near Elmira, A.A.Heller 14551 (MO); near Vacaville, A.A.Beetle 1982 (GH); Sonoma Co., Santa Rosa,
Figure 15. Geographic distribution of *Phalaris lemmonii*
R. Hoffmann 737 (US); Stanislaus Co.: Adel, E. E. Stanford 857 (GH); 10 miles west of Modesto, R. F. Hoover 392 (US); 4 miles south of Oakdale, R. F. Hoover 77 (US); Woodward Reservoir, north of Oakdale, R. F. Hoover 1938 (US); Sutter Co., A. A. Beetle 3862 (GH, MO).

15. Phalaris caroliniana

*Phalaris caroliniana* Walt. Fl. Carol. 74. (1788) (lectotype in US)

*Phalaris microstachya* DC. Cat. Hort. Monsp. 131. (1813)


*Phalaris occidentalis* Nutt. Trans. Am. Philos. Soc. n.s. 5:144. (1837) (Holotype in PH)


*Phalaris intermedia* var. *microstachya* (DC.) Vesey Contr. U.S. Nat. Herb. 3:42. (1892)

**DESCRIPTION**

Annual; culms to 100 cm. tall; panicle 1.0--7.0 cm. long, 0.8--2.0 cm. wide, ovoid to sub-ovoid; spikelets somewhat spreading, the glumes not tightly imbricate; glumes 4.2--6.7 mm. long, 0.8--1.5 mm. wide, apex usually acute or acuminate, narrowly winged toward summit, the margin of the wing very finely scabrous, lateral nerves almost always glabrous, very rarely slightly scabrous; sterile floret 3.0--4.7 mm. long, 0.9--1.8 mm. wide, lanceolate, densely pubescent; sterile florets 2, 1.5--2.5 mm. long, subulate, pubescent; caryopsis 2.0--2.3 mm. long, 0.9--1.2 mm. wide; somatic chromosome number 2n=14, the chromosomes 3.0--5.5
164 microns long (Ambathsa, 1956).

**OBSERVATIONS**

The distinctions between *P. carolliniana* and *P. angusta* have been elaborated in the discussion of the latter species. *P. carolliniana* and *P. amethystina* are morphologically quite similar. Some of the differences between these two species are presented in Table 13. The best means of separating the two is the presence or absence of scabrous pubescence on the glume lateral nerves. *P. carolliniana* almost always has glabrous glume lateral nerves; *P. amethystina* has rather heavily scabrous glume lateral nerves. In addition to these, there are some other less well-defined differences. The glumes of *P. carolliniana* are narrowly winged near the apex; glumes of *P. amethystina* are also winged, but the wing is extremely narrow and visible only after close scrutiny under 10X magnification. Glumes of *P. carolliniana* are rather broadly lanceolate (Figure 9, f); glumes of *P. amethystina* are narrowly lanceolate (Figure 8, f). The inflorescence of *P. carolliniana* is somewhat more compact, with the spikelets more densely imbricated than those of the inflorescence of *P. amethystina*. The geographic ranges of the two species are very distinct; *P. carolliniana* is found only in the southern one-third of the United States and the northern two-thirds of Mexico while *P. amethystina* is limited to a small area on the west coast of Chile. The morphologic
differences, as well as the disjunct ranges seem to emphasize that these are two distinct species rather than varieties of a single species.

Vasey (1892) reduced De Candolle's *P. microstachya* (1813) to varietal status under *P. caroliniana*. Vasey's main differentiating features were the height of flowering culms and size of the inflorescence. Measurements were made on a large number of specimens to determine whether distinct populations could be delimited on the basis of these or other characters. Results showed that there were complete gradations in values for the characters that Vasey used in varietal distinction. None of the characters measured, which included glume length and width, fertile floret length and width, sterile floret length, inflorescence length and width, and total height could be correlated with one another or with geographic origin of the collection to show any sub-specific populations.

**CYTOLOGY AND CYTOGENETICS**

Brown (1950) and Ambathsa (1956) report a chromosome number of 2n=14 for *P. caroliniana*. The author was unable to obtain any material suitable for cytological study.

**NOMENCLATURE**

Hitchcock (1905) studied many of the grasses of the Walter herbarium which is in the Natural History section of the British Museum, South Kensington, London, England and was
unable to find any species of Phalaris represented in Walter's collections. He also noted that many of the types were missing from this collection. The author was able to examine photographs of the Walter herbarium which are deposited in the Gray Herbarium Library of Harvard University. None of the few grasses pictured were in Phalaris. From these lines of evidence it must be concluded that the holotype of this species is not available and probably lost.

Walter's description of Phalaris (1788, p. 74) is as follows:


caroliniana panicula spicata ovata, petalis aristatis, calycibus striatis

Walter's generic description leaves some doubt as to which genus he was referring to. The characters provided by Walter are those of several different genera of grasses. When the specific description is also taken into account, the situation is somewhat clarified. Phalaris was the only genus available to Walter from the Carolinas that had an ovate, spike-like panicle, spikelets with equal, prominently-nerved carinate glumes which included the floret. The explanation of "petalis aristatis" is difficult. There seem to be three possible explanations of this phrase:

1. Walter was describing some species that was not even in Phalaris. Without the holotype this possibility can never
be completely ignored, however, as pointed out in the above paragraph, there is no other species of the Carolina grass flora that would fit the description provided by Walter.

2. Walter was describing the two subulate sterile florets found in this taxon as either the "petals" themselves or as short awns of the "petals".

3. Walter was interpreting the acuminate fertile floret as being provided with a very short awn. Walter's use of the term "aristate" varies somewhat throughout Flora Caroliniana. In Vaccinium he uses it to describe the very short, mucronate appendages of the anthers, which, in V. stamineum, are one mm. or less in length; in Alopecurus pratensis it is used to describe the awn, which may be three to five mm. long. Some of the florets of P. caroliniana have quite prominent acuminate tips (see Figure 9, g) which Walter might conceivably have thought of as being aristate.

Even though the holotype is missing and the original description not conclusive, the circumstantial evidence seems to indicate that Phalaris caroliniana should be preserved as the name of this taxon. Muhlenberg (1817) used Walter's name, although, admittedly, it cannot be shown that Muhlenberg saw any of Walter's material.

In accordance with Article 7 of the International Code of Botanical Nomenclature, it becomes necessary to designate a neotype which will serve until such time as the holotype may
be found. The following specimen is here designated as the neotype of *Phalaris caroliniana* Walter:

**UNITED STATES:** South Carolina, McCormick Co., in open field of moist bottomland about 1 1/3 miles due north of Clark Hill Dam. Elevation about 200 feet. Wilbur H. Duncan 9468, May 4, 1949. United States National Museum specimen, accession number 2075588. Deposited in US.

*Phalaris intermedia* Bosc ex Poiret has often been used as the name of this taxon. The original description (Poiret, 1810) calls for bulbous culm bases and a single sterile floret. Neither of these features are ever found in *Phalaris caroliniana*. If the original description is accurate, it would seem to refer to *Phalaris aquatica*. Until this name can be clarified by examination of the holotype it should be excluded from the synonymy of *P. caroliniana*.

**DISTRIBUTION**

*Phalaris caroliniana* is found in the southern one-third of the United States and the northern two-thirds of Mexico. A map showing the geographic origin of the specimens studied is presented in Figure 16.

Hitchcock (1950) gives the habitat as old fields, sandy soil, and moist places. Collections made by the author were from gravelly hilltops in dry, well-drained soil.

**SELECTED SPECIMENS EXAMINED**

**MEXICO:** Sonora, Magdalena, J.N. Rose et al., 15078 (US); Sonora, ca. 31° x 109°, J.V. Santos 2027 (US).

**UNITED STATES:** Alabama, Montgomery, L.H. Pammel, May 26, 1921 (ISC); Arizona, Cochise Co., 8 mi. s.w. Apache, F.W.
Figure 16. Geographic distribution of *Phalaris caroliniana*
Gould and L.M. Fultz 3139 (US); Arkansas: Sebastian Co., Massard Prairie, D.M. Moore 480113 (US); Thos. Nuttall (Holo-
type of Phalaris occidentalis Nutt.) (FH); California: Butte 
Co., 8 miles north of Oroville, A.A. Heller 11307 (F, ISC, MO, 
US); Catalina Isl., Avalon, B. Trask, Mar., 1901 (MO, US); 
Georgia, Clarke Co., A. Cronquist 4364 (GH, MO, US); Kansas, 
Neosho Co., R.W. Pohl 7289 (ISC); Louisiana, Jefferson Par., 
Gretna, C.R. Ball 327 (F, GH, MO, US); Mississippi, Jackson Co., 
Biloxi, A.S. Hitchcock 1074 (ISC, US); Missouri, Jasper Co., 
Webb City, E.J. Palmer 221 (MO); Nevada, Lincoln Co., Virgin 
R. valley, F.V. Coville and F. Funston 1924 (US); New Mexico, 
Grant Co., H.H. Rusby 457 (US); North Carolina, New Hanover 
Co., Wilmington, W.M. Canby, Octo., 1869 (US); Oklahoma, 
Kingfisher Co., Huntsville, L.A. Blankinship, May 20, 1896 
(GH, MO, US); Oregon, Grant's Pass, T. Howell 221 (F US); South 
Carolina: Georgetown Co. Georgetown Landing, C.A. Weatherby 
and L. Griscom 16413 (GH, US); McCormick Co., 1 1/3 miles north 
of Clark Hill Dam, W.H. Duncan 9468, May 4, 1949 (neotype of 
Phalaris caroliniana Walt.) (US); Tennessee, near West Tenn. 
Normal Teachers Coll., C.E. Moore 117 (US); Texas, Mitchell 
Co., R.W. Pohl 4479 (ISC); Virginia, Princess Anne Co., M.L. 
Fernald, L. Griscom, and Bayard Long 4547 (GH).
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1826. De graminibus paniceis. Petropoli, [Russia] Imperialis scientiarum.


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During the terminal year of graduate study, the author was the recipient of a National Science Foundation Cooperative Fellowship. Many of the studies undertaken would not have been possible without the aid provided by the Foundation which is sincerely appreciated.
APPENDIX

Contained in this appendix is a list of unidentified or excluded names. Unidentified names are followed by a question mark and, if necessary, a short explanatory phrase. Excluded names are followed by the name of the species to which they are referred. Evidence for the exclusion of the names is given by a brief statement or by reference to a page in the text of this paper on which that particular name is discussed. If a description is used as evidence, the author and date of publication are cited. Any pertinent information concerned with a particular name is also included.

_Degraphis americana_ Ell. ex Loud. = ? _nomen nudum_. Loudon (1830). _Degraphis_ is apparently a misspelling of _Digraphis_ as proposed by Trinius.

_Digraphis arundinacea_ var. _picta_ (L.) Pacher. Original description not seen. Hitchcock (1950) says this is presumably based on _Phalaris arundinacea_ L. var. _picta_.

_Phalaris alpina_ Jacq. = _Phleum_ sp. Description, Jacquin (1786).

_Phalaris altissima_ Desf. = ? _nomen nudum_. Listed as a synonym of _Phalaris bulbosa_ by Desfontaines (1796).

_Phalaris altissima_ Menezes non Desfontaines. = ? Description (Menezes, 1894) might refer to _Phalaris aquatica_ L.

_Phalaris emmophila_ (Host) Link. = _Ammophila arundinacea_. Description of _Ammophila arundinacea_ Host (1809).

_Phalaris angustata_ Schlecht. = ? Description (Schlechtendahl, 1851) might refer to _Phalaris minor_ Retz.
Phalaris arenaria Huds. = Phleum sp. Description, Hudson (1762).


Phalaris aristata Schousboe ex Willd. = Phleum sp. Description, Willdenow (1801).

Phalaris aristata Gouan ex Beauv. non Schousboe ex Willd. = Polypogon monspeliensis. Published as synonym in index (Beauvoir, 1812).

Phalaris arunculata Dicks. = ? nomen nudum, presumably a mistake for Phalaris utriculata L. Discussion, Dickson (1790).


Phalaris aspera Lam. = ? Description, Lamarck (1783) seems to refer to Phleum.

Phalaris barrelieri Tenore. = ? Original description not seen. Index Kewensis says this = Koeleria villosa.

Phalaris bellardi Willd. = Phleum sp. Description, Willdenow (1801).

Phalaris bulbosa L. = Phleum sp. Examination of photograph (in GH) of type specimen.

Phalaris bulbosa var. aquatica (Willkomm) Perez-Lara (non L.) = ? Description, which is based on P. aquatica as applied by Willkomm, might refer to Phalaris coerulescens.

Phalaris bulbosa var. hirtiglumis Trabut. = ? nomen nudum. Trabut (1885)


Phalaris ciliaris Spreng. ex Jacks. nomen nudum. Jackson (1895).

Phalaris ciliata Lag. = Phleum sp. Description, Legasca (1816).

Phalaris commutata Roem and Schult. (1817) See discussion under Phalaris aquatica in text.

Phalaris cristata Forsk. = Polypogon sp. ? Description, Forskal (1775).


Phalaris cuspidata Beauv. = ? pro syn. Listed as synonym of Chiloachloa cuspidata in index (Beauvoir, 1812).

Phalaris cuspidata Hort ex Steud. (non Beauv.) = ? nomen nudum. Listed as synonym of Phleum cuspidatum in Steudel (1841).

Phalaris cylindrica Lam. and DC. = Phleum sp. Description, Lamarck and De Candolle (1805).

Phalaris daviesii Blake. = P. aquatica x P. minor. Not found in nature. See Blake (1956).


Phalaris dioica Forsk. = Sporobolus sp. ? Description, Forskal (1775).

Phalaris eruciformis L. = Beckmannia eruciformis. Examination of photograph (in GH) of type specimen.

Phalaris erucoides L. ex Beauv. pro syn. Listed as a synonym of Beckmannia eruciformis L. (Beauvoir, 1812). Probably an error for eruciformis.

Phalaris explicata Link. = Heleochloa alopecurooides ? Description, Link (1799).

Phalaris geniculata Sibth. = Heleochloa geniculata. Description, Sibthorpe (1806).
Phalaris glomerata Gueldenst. = ? Original description not seen. Index Kewensis lists the location of the description as "Reisen 2. 214."

Phalaris hispida Thunb. =Arthraxon hispidus. Description, Thunberg (1784).

Phalaris humulis Desv. =Phleum sp. Description, Desveaux (1831).


Phalaris maritima Nutt. =Ammophila arundinacea. Description, Nuttall (1818).

Phalaris mauritii Sennen in Sennen and Mauricio. nomen nudum. Sennen and Mauricio (1933).


Phalaris x monspeliensis Daveau = ? Daveau (1926) claims this to be a hybrid between P. arundinacea and P. nodosa (misapplied by Daveau to P. aquatica).

Phalaris mucronata Desf. nomen nudum. Desfontaines (1815).

Phalaris muricata Forsk. =Tragus racemosus. Description, Forskal (1775).

Phalaris oryzoides L. =Leersia oryzoides L. Photograph (in GH) of type specimen.


Phalaris pectinata Roth. =Phleum sp. ? Description, Roth (1821).

Phalaris phleoides L. =Phleum sp. Photograph (in GH) of type specimen.

Phalaris phleoides var. pratensis Lapey. =Phleum sp. Description, Lapeyrouse (1813).

Phalaris picta Hort. ex Steud. nomen nudum. Steudel (1841).

Phalaris pubescens Lam. =Koeleria villosa ? Description, Lamarck (1783).
Phalaris sativa Pers. = Phleum sp. Description, Persoon (1805).

Phalaris semineutra Roem. and Schult. = Poa semineutra.
Description, Roemer and Schultes (1817).

Phalaris semiverticillata Forsk. = Agrostis semiverticillata.
Description, Forskal (1775).

Phalaris setacea Forsk. = Pennisetum. Description, Forskal (1775).

Phalaris subulata Savi. = Phleum sp. Description, Savi (1798).

Phalaris tenuifolia Hort. ex Steud. = ? nomen nudum.
Steudel (1841).

Phalaris tenuis Host. = Phleum sp. Description and illustration, Host (1802).

Phalaris trigyna Host. = Phleum sp. Description and illustration, Host (1809).

Phalaris utriculata L. = Alopecurus rendlei. See Eig (1937).

Phalaris vaginiflora Forsk. = Helechloa schoenoides.
Description, Forskal (1775).

Phalaris velutina Forsk. = Digitaria sp. Description, Forskal (1775).

Phalaris villosa Michx. = Anthaenantia villosa. Description, Michaux (1803); see also Hitchcock (1908).

Phalaris zizanioides L. = Vetiveria zizanioides. Photograph (in GH) of type specimen.