TAXONOMIC STUDIES IN THE GENUS
PANICUM L.

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Dedicated to
the memory of my mother
and to
my father
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ABSTRACT

This thesis contains sixteen chapters, grouped into five parts. Part I introduces the work, introduces the genus *Panicum*, reviews the taxonomic history of *Panicum* and its general ecology and geography. Part II discusses the taxonomic characters available for *Panicum* classification. Macromorphological, micromorphological and anatomical characters, the main data gathered in the work, are defined and evaluated for the *Panicum* species of the Indian subcontinent & S.E. Asia. Part III is an infrageneric classification of Indian subcontinental & S.E. Asiatic *Panicum* including a discussion of taxonomic concepts employed, with keys to subgenera and sections. Three new sections have been recognised. A comparative account of a taximetric classification made in parallel is included. Part IV contains a formal taxonomic revision of the *Panicum* species of the Indian subcontinent & S.E. Asia, incorporating descriptions of species recognised, with some illustrations, a key, notes on putative interspecific relationships, distribution and endemism. Two new species are described and two new combinations made. Seven species, one subspecies, and three varieties have been reduced to synonymy. For two species, lectotypes have been selected. Part V reviews *Panicum* in Australia. Species distribution is discussed in relation to physiography and climate. A conspectus of species, with a key, notes on types and diagnostic features, is provided. The phytogeographical connection of the *Panicum* flora of Australia and that of the Indian subcontinent and S.E. Asia is briefly discussed.

Appendix 1 and 2 contain two manuscript papers accepted for publication. Appendix 3 contains the taximetric data matrix. The table of similarity coefficients forms Appendix 4.
ACKNOWLEDGEMENT

This work was done under the supervision of Dr. P.M. Smith. It is with great pleasure I offer him my sincerest appreciation, thanks and gratitude for his cheerful assistance, advice and encouragement throughout the progress of the study. I remain deeply indebted to him in numerous other ways including his negotiating with the British Council to produce the finance, which made this study possible. For this financial assistance, I am indebted to the British Council, particularly to Mr. George Morrison and Miss Susan Sandeman in Britain, and Mr. P.A. Howson in Bangladesh. Thanks are also due to my second supervisor, Dr. D. G. Mann who has been very supportive.

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PART I

INTRODUCTION AND GENERAL ACCOUNT OF PANICUM
CHAPTER 1: INTRODUCTION

1.1 Objectives of the thesis

This thesis is presented primarily as an investigation intended to provide a taxonomic revision of the genus *Panicum*, as represented in the Indian subcontinent and Southeast Asia. The problem had been suggested by a need for a critical understanding of the *Panicum* species of the Indian subcontinent and Southeast Asia viewed from different aspects of macromorphology, anatomy and micromorphology, with subsequent comparison of results by taximetric analysis. It has been found that the more recent keys, descriptions and other information are too limited in scope to take into account the variation of the species in the region. In addition to the main thrust of this work, there is a part on Australian *Panicum* aimed to provide some understanding of the *Panicum* flora of the continent in relation to those of the Indian subcontinent and Southeast Asia.

It is hoped that the insight gained in the overall work may ultimately contribute to a better understanding of the entire genus. At the same time, it is hoped that it will aid plant geographers by augmenting existing data on plant distribution.

1.2 Background of work

There is no comprehensive taxonomic treatment of the genus from the Indian subcontinent and Southeast Asia, areas which constitute the main Asiatic distribution of *Panicum*. For the purposes of this thesis, the Indian subcontinent is defined as Pakistan, India, Sri Lanka, Nepal, Bhutan, Bangladesh;
Southeast Asia comprises Burma, Thailand, the Peninsula of Indochina, Malaysia, the Archipelago of Indonesia, and Papua New Guinea. The Southeast Asiatic region differs from the region defined as Malesia for the *Flora Malesiana* project by the addition of Burma, Thailand and Indochina. The work was carried out chiefly upon the collections at the herbaria of Edinburgh (E), Kew (K), and British Museum (BM). The extensive Southeast Asiatic collections at Rijksherbarium, Leiden (L) have served as an invaluable aid during this study.

The first general account of *Panicum* (sensu latu) in British India was that of J.D. Hooker in 1896. The next treatment appeared in 1960 in Bor's *Grasses of Burma, Ceylon, India and Pakistan*. He recognised 32 species of *Panicum*. Bor's publication was a major advance in the study of Gramineae in the Indian subcontinent. A partial revision of the genus was made by Majumdar in 1973. It was a semi-technical treatment prepared largely to facilitate the identification of the Indian species of *Panicum*. Much of the remaining literature comprises lists or reports compiled on collections made on pioneering explorations. The Southeast Asiatic component of the genus has been treated fragmentarily in different floras/manuals of different regions. Noteworthy among such contributions are those of Ridley (1907, 1925), Camus and Camus (1922), Merrill (1923), Backer and Brink (1968), Henty (1969), Gilliland (1971) and Jansen's manuscript on Gramineae prepared for the *Flora Malesiana* in 1954. These treatments are of but limited application for the understanding of a widespread genus like *Panicum* and now quite inadequate.

Herbarium holdings of grasses from the area have enormously increased in recent years. There has been increased attention to new characters such as Kranz anatomy, and SEM features in *Panicum* species from other parts of the world. The increased knowledge of the variation within the genus has been accompanied by increased difficulties in the classification of the genus. It has
therefore been found essential to undertake a critical study of the species of the Indian subcontinental and Southeast Asiatic Panicum. Besides the morphological characteristics, techniques of anatomical analysis (including Kranz syndrome investigation) and SEM have provided the main database of the present work.

1.3 The genus Panicum

Panicum is the largest of grass genera. It belongs to the tribe Paniceae of the subfamily Panicoideae. The genus consists of an estimated 500 species, and is distributed throughout the tropics, subtropics and warm temperate regions of both hemispheres. Many species are adapted to warm, humid tropical climates. Others are established in warm temperate climates. Some are important elements of marsh and swamp vegetation, some of coastal dunes, and some inhabit desert regions where the annual precipitation is 5 inches or less.

Panicum is a large, variable genus. Divergent viewpoints have been put forward by different taxonomists towards the interpretation of its generic limitation. The degree of heterogeneity is of particular interest in the taxonomic study of Panicum. Since the time of Linnaeus, the genus has been segregated into many separate genera and subdivided into subgenera and sections of supposedly related species. Some of these subgenera have been raised to generic rank. Even so, Panicum is still a large genus, and further division may well be appropriate in the light of new characters.

The genus is of significant economic potential because it contains the millets, notably common millet, P. miliaceum, and little millet, P. sumatrense subsp. sumatrense. These millets are extensively cultivated in parts of Asia and Europe. Panicum includes a good number of important fodder plants, such as
Guinea Grass, *P. maximum* a native of Africa but introduced into many countries of the world. Senaratna (1956) reports that *P. antidotale* is cultivated in the village gardens in Sri Lanka for use in Ayurvedic medicine. *P. turgidum* is a fodder for camels, and is a good soil binder. The genus also includes some pernicious cosmopolitan weeds such as *P. repens*. Due to the extensive rhizome system developed, this grass is very important as a sand binder on the tropical and subtropical shores of Old and New worlds.
CHAPTER 2 : TAXONOMIC HISTORY OF PANNICUM

2.1 Pre-Linnaean history

The name *Panicum* originates from the Latin *panicula*, a panicle or *panis*, meaning bread. The use of the name can be traced back as early as 44 B.C. in Julius Caesar’s *Bellum Civile* and later in Pliny’s *Historia Naturalis* in 77 A.D. (Lewis & Short 1907). The name was applied to the Italian millet, *Panicum italicum* (*Setaria italicca*), a grass of economic importance to the ancient Romans. It persisted in this sense through medieval times and in herbals to A. Cesalpino’s *De Plantis* (1583), J. Bauhin’s *Historia Plantarum* Vol. 2 (1651). The earliest attempt to give the genus a formal standing was made by Tournefort (1700) in his well known *Institutiones Rei Herbariae*. Tournefort laid particular stress on characters provided by the flowers being aggregated in a spike, and included *Setaria italicca* (L) Beauv. which he figured. There were several heterogeneous elements in his *Panicum* such as *Pennisetum americanum* (L) Scribn., *Echinochloa crus-galli* (L) Beauv., *Polypogon monspeliensis* (L) Desf., and *Gastridum landigerum* (L) Gaud. Hitchcock and Chase (1910) pointed out that the type of present day *Panicum, P. miliaceum*, was considered as the type of a different genus *Milium*, while a different plant, *Setaria italicca* was considered to be the type of *Panicum* as conceived by Tournefort.

2.2 Linnaeus’s treatment of Panicum

Linnaeus’s original concept of *Panicum* was different from its current usage in modern botany. Subsequently there were gradual changes in his concept of
the genus. When Linnaeus recognised *Panicum* and *Milium* in the first edition of *Genera Plantarum* (1737), he cited "Panicea Scheuchzer 2:2" for *Panicum* and "Tournef. 298" for *Milium*. "Tournefort 298" is *P. miliaceum*. The figures and descriptions of *Scheuchzer* were correctly interpreted by Hitchcock and Chase (1910). It would indicate that Linnaeus considered a form of *Setaria viridis* as the type of *Panicum*.

In the first edition of *Species Plantarum* (1753), Linnaeus described *P. miliaceum* (the species represented by plate *Tournef. 298* for *Milium*) under *Panicum* (Table 1), and there is mention of *Milium* as a pooid genus including *M. effusum* and *M. confertum*. (He included the historic type of *Panicum*, *Panicum italicum* under *Panicum*). But Linnaeus still cites "Tournef. 298" crediting *Milium* in the fifth edition of *Genera Plantarum* published after the first edition of *Species Plantarum*. A solution is sought in the description. Comparison of the descriptions of the two genera in the first and the fifth editions of *Genera Plantarum* shows disagreement concerning Linnaeus's concept of the two genera. In the first edition the diagnosis of *Milium* is: the calyx trivalved (presence of lower glume, upper glume and lower lemma). In the fifth edition it is said to be bivalved (presence of only lower glume and upper glume). By this change of 'trivalvis' to 'bivalvis', as Hitchcock and Chase (1910) pointed out, Linnaeus transferred the generic idea of *Milium* from *Panicum miliaceum* to *Milium effusum*. Note again that he included, as has been said, *P. miliaceum* (trivalved) under *Panicum* earlier in *Species Plantarum*. This change is made clearer still by a note of Linnaeus on *Milium* in the second, third and fourth editions of *Genera Plantarum* to the effect that *Milium* with a 2-valved calyx differs from *Panicum* with a 3-valved calyx.
<table>
<thead>
<tr>
<th>SPICATA</th>
<th>PANICULATA</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. <em>P. alopecuroides</em> = <em>Pennisetum caffrum</em> (Borey) Leeke</td>
<td>11. <em>P. dichotomum</em></td>
</tr>
<tr>
<td>2. <em>P. glaucum</em> = <em>Setaria glauca</em> (L.)</td>
<td>12. <em>P. clandestinum</em></td>
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<tr>
<td><em>P. glaucum B</em> = <em>Setaria viridis</em> (L.) Beauv.</td>
<td>13. <em>P. capillare</em> Beauv.</td>
</tr>
<tr>
<td><em>P. glaucum γ</em> = <em>Setaria viridis</em> (L.) Beauv.</td>
<td>14. <em>P. patens</em> = <em>Cyrtococcum patens</em> (L.) A. Camus</td>
</tr>
<tr>
<td>3. <em>P. americanum</em> = <em>Pennisetum americanum</em> (L.) Scribn.</td>
<td>15. <em>P. dactylon</em> = <em>Cynodon dactylon</em></td>
</tr>
<tr>
<td>4. <em>P. italicum</em> = <em>Setaria italica</em> (L.) Beauv.</td>
<td>16. <em>P. miliaceum</em></td>
</tr>
<tr>
<td>5. <em>P. crusgalli</em> = <em>Echinochloa crusgalli</em> (L.) Beauv.</td>
<td>17. <em>P. latifolium</em></td>
</tr>
<tr>
<td>6. <em>P. dissectum</em> = <em>Paspalum dissectum</em> L.</td>
<td>18. <em>P. brevifolium</em></td>
</tr>
<tr>
<td>7. <em>P. dimidiatum</em> = <em>Stenotaphrum dimidiatum</em> (L.) Brongn.</td>
<td>19. <em>P. arborescens</em> = <em>P. brevifolium</em></td>
</tr>
<tr>
<td>8. <em>P. sanguinale</em> = <em>Digitaria sanguinalis</em> (L.) Scop.</td>
<td>20. <em>P. virgatum</em></td>
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<tr>
<td>9. <em>P. filiforme</em> = <em>Digitaria filiformes</em> (L.) Nash</td>
<td></td>
</tr>
<tr>
<td>10. <em>P. compositus</em> = <em>Oplismenus compositus</em> (L.) Beauv.</td>
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</table>
2.3 The Type of Panicum

Selection of a type of *Panicum* has not been found easy because there is no indication which species Linnaeus considered as the type. There is a significant change in Linnaeus’s concept of *Panicum* between 1737, the date of first edition of *Genera Plantarum* and 1754, the date of its fifth edition which is arbitrarily associated with the first edition of *Species Plantarum* in 1753 (Stearn 1957). Study of the twenty species included in the *Species Plantarum* (Table 1) in consultation with the description of the genus in the fifth edition of the *Genera Plantarum* provides evidence towards solving the type species problem.

The twenty species include three categories of species: awnless, awned and involucrate. From the descriptions and notes in the fifth edition of *Genera Plantarum*, it is apparent that Linnaeus did not consider awned and involucrate species as typical. In a note following the description he says: “Obs : Aristae terminant inquibusdum corollae valvulum planiorem. Species datur involucro polyphylo capillari instructa.” It means that he is saying that in certain species (of the genus), awns terminate the flatter valve of the corolla [fertile palea], and certain species are provided with a polyphyllous capillary involucre. This implies that he states that the presence of awns and involucres is unusual.

From the remaining awnless or non-involucrate species, Hitchcock and Chase (1910) selected the most economically important species, *Panicum miliaceum*, as typical according to the American Code of Botanical Nomenclature (Part II. Section IV. Canon 15.d.) (1907). This seems to be a reasonable choice. In conclusion, in the absence of any clear indication by Linnaeus himself, *P. miliaceum* may be regarded as type or standard species of *Panicum*.

I found Linnaean specimens of *P. miliaceum* at the Linnaean Herbarium as well
as in the British Museum despite Hitchcock's and Chase's (1910) remarks that:

"We have not seen the type, which may not be in existence." So far I am aware a type specimen of *P. miliaceum* has not yet been selected.

### 2.4 Post-Linnaean history up to the end of the nineteenth century

Linnaeus classified the twenty species in the *Species Plantarum* into two groups: Spicata and Paniculata. It would indicate that the character states he considered most fundamentally were those of spicate and paniculate inflorescence. This can be considered as the first infrageneric classification of the genus. This *Panicum* concept is very heterogeneous relative to how the genus is classified today. The species of the Paniculata group fall under *Panicum* in the narrower, modern sense, while all the species of the Spicata group have been separated from *Panicum* as other genera such as *Pennisetum*, *Setaria*, *Echinochloa*, *Paspalum*, *Stenotaphrum*, *Digitaria*, and *Oplismenus* (see Table 1). Linnaeus himself established the genus *Paspalum* in 1759 based on *Panicum dissectum*, and transferred *Panicum americanum* to his genus *Holcus* as *H. spicatus*. This latter species was, however, later transferred by Scribner to *Pennisetum*. Except for two, the other species of the Paniculata group come under modern-day *Panicum*. Of these two, *P. dactylon* is a very discordant species which, though spicate, was included, by Linnaeus, in Paniculata. It was first transferred to *Capriola* by Adanson in 1763 and later to *Cynodon*, where it remains, by Richard in 1805. *P. patens* having a paniculate inflorescence, was retained under *Panicum* until early this century when A. Camus transferred it to Stapf's genus *Cyrtococcum* (Bull. Mus. Hist. Nat. 27:118 (1921)). Of the other species, all still retained in *Panicum*, *P. dichotomum* formed the basis of the heteromorphous subgenus *Dichanthelium* by Hitchcock and Chase (1910). *P. clandestinum* and *P. latifolium* also belong to this North American subgenus.
*P. arborescens* is synonymous with *P. brevifolium* (Hitchcock & Chase 1910). I can confirm this from my Linnaean Herbarium investigation. *P. brevifolium* belongs to subgenus *Phanopyrum* while *P. miliaceum*, *P. capillare* and *P. virgatum* belong to section *Panicum* of subgenus *Panicum*.

Linnaeus expanded the genus in the second edition of *Species Plantarum* (1762) which includes 28 species. Eighteen of the original twenty (excluding *P. americanum* and *P. dissectum*) are included in this edition. Of the new species, the only species still retained in *Panicum* is *P. repens*. Another Linnaean species still retained in *Panicum* is *P. coloratum*, which was described by Linnaeus in 1767 in his *Mantissa Prima*.

Until the end of the nineteenth century, subsequent authors mostly added species now placed in other groups to the concept of *Panicum*. Table 2 is intended to show examples of the very broad concepts of the genus adopted by some post-Linnaean authors. Groups containing the 'true *Panicum*' — those having paniculate inflorescences are put within bars. All or most of the other infrageneric taxa shown in Table 2 are now placed, by general consent, in genera other than *Panicum*. The 'true *Panicums'* are variously named. For example, of the nine sections of Hooker (1896), section *Effusae* represents the true *Panicum*. The species of other sections belong to genera such as *Paspalidium*, *Echinochloa*, *Brachiaria*, *Sacciolepis* and others.

### 2.5 History of Infrageneric Classification

The twentieth century history of classification of the genus (*sensu stricto*) begins with the partial infrageneric classification proposed by Hitchcock and Chase (1910). Their work marks a significant change in the classification of the genus. The last revised classification is presented in their *Manual of the*
TABLE 2. Post-Linnaean classification of *Panicum* until the end of the Nineteenth century (Taxa put in bars are 'true Panicums').

<table>
<thead>
<tr>
<th>Subdivisions</th>
<th>Series</th>
<th>Section</th>
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Grasses of the United States (1951). They subdivided the genus into subgenera and 'groups' (see Table 3). Their 'groups' (equivalent to present day sections) were not given any formal nomenclatural standing.

Of the three subgenera, Eupanicum represents the true *Panicum* (i.e. the species group including *P. miliaceum*, which in turn is divided into 19 groups. It is a heterogeneous subgenus. Group Geminata, with secund spikelets in spikelike racemes is now transferred to the genus *Paspalidium*. Groups Purpurescentia and Fasciculata with transversely rugose fruit are now referred to *Brachiaria*. The whole of subgenus Paurochaetium (four species) were included in *Setaria* by Rominger (1962).

Subgenus Dichanthelium constitutes a group of species showing foliar and panicle dimorphism. All are C3 species and occur in the coastal plains of North America. The subgenus includes 17 groups. Its status as a subgenus or genus is controversial. Gould (1974) considered Dichanthelium as a genus separate from *Panicum* - later supported by Clark and Gould (1975), Gould and Clark (1978), Gould (1980) and Brown (1977). Zuloaga (in press) regarded it as a subgenus of *Panicum*. Hitchcock and Chase based their classification upon characters such as panicle type, dimorphism of plants, relative length of lower glume to the spikelet, shape, size and nervation, pilosity and length of spikelets, upper anthecium to separate different groups within the genus.

Stapf (1920) and Pilger (1940) were greatly influenced by Hitchcock and Chase in use of characters for their classification. Stapf divided the genus into 14 sections based on Old World species, mainly African. His section Eriochloideae, containing a single species, is transitional to the genus *Eriochloa*. Pilger treated the genus on a world scale. Of his eight subgenera, *Acroceras* is now regarded as a distinct genus with *Neohusnotia* and *Commelinidium*.
synonymous with it (see Clayton and Renvoize 1986). Subgenus Urochloides has been separated from *Panicum* and is referred to *Brachiaria* by Gardner and Hubbard (1938) and later supported by Blake (1958).

Modern studies have introduced new characters in the treatment of *Panicum*. On the basis of selected characters of lodicules, fertile lemma surface, leaf epidermal pattern, styles and ligules, Hsu (1965) sampled a few species from most of the previous sections of Hitchcock and Chase, Stapf, and Pilger. There is an anatomically and physiologically heterogeneous assemblage of taxa in Hsu's subgenera Phanopyrum and Sarmentosa. For example, Phanopyrum includes sections Dura which is NAD-me, Obtusa which is NADP-me while sections Gymnocalpin and Megista are non-Kranz (for definitions of terms see Chapter 5.2). In the subgenus Sarmentosa, Hsu includes NADP-me sections Agrostioidea and Tenera along with other non-Kranz sections. Brown (1977), in his selectively worldwide treatment, classified previously proposed groups and sections into subgenera, taking into consideration the different photosynthetic physiological types present, including C3 or C4 species, with three kinds of C4 subtypes: NADP-me, NAD-me and PEP-ck. He considers that the genus *Panicum* is artificial and that the only 'true' species are those which are included in the subgenus Panicum with the NAD-me C4 subtype. The classification of Zuloaga (in press) covers the American sections of *Panicum* on the basis of macromorphological, anatomical, and SEM observations. He has recognised six subgenera and 25 sections (Personal communication). Further reference of Hsu’s, Brown's and Zuloaga’s classifications will be found in Chapter 8.4 in connection with my own infrageneric classification for the species of the Indian subcontinent and Southeast Asia.
CHAPTER 3: ECOGEOGRAPHY AND ENDEMISM OF PANICUM

3.1 Geographical distribution and Endemism

*Panicum* is one of the most widely distributed of grass genera. The species of the genus, numbering more than 500, are distributed in the tropics and warm temperate regions of both hemispheres. The distribution pattern (see Table 4) of the genus shows that the zone of maximum concentration is more in the western hemisphere than in the eastern hemisphere. It is abundantly represented in all tropical countries, a few species extending beyond the tropics in the Old World, and a somewhat larger number in North America. Considering its enormous size, the genus is very poorly represented in the drier subtropical areas.

In North America, the genus extends throughout the West Indies, Central America, Mexico, the United States and Canada. The subgenus *Dichanthelium* contains over 50% of the North American species of the genus, and is predominantly found in North America along the Atlantic coastal plain. Subgenus *Eupanicum* includes about 50 annual and perennial species and extends from Maine to British Columbia and southward to South America. The genus as a whole is poorly represented in the mountainous regions of North America. Of about 200 species of South Tropical America, the indigenous species, numbering about 63% of the total, are concentrated mostly in the south-eastern half of the region. They are found in swampy areas, forest shade or open places over a range of altitudes. The introduced species, majority of which are from North America, are found in Western Tropical America, some of them extending to temperate South America. In general, the temperate South American species are found in moist habitats and on the
edges of woodlands.

Of more than 100 species in Africa, almost all are native to Tropical Africa, with a concentration in East Tropical Africa. They occur usually in damp areas, on forest margins, forest shade or in Savanna. A few of the species have been introduced to tropical regions of Asia and Australia. Like the species of South America, the African species collectively cover a wide altitudinal range.

A majority of the Asiatic species are spread over the plains and low hills of the Indian subcontinent and Southeast Asia. Table 4 shows that the indigenous section of the Asiatic species are confined to these two regions. The species introduced to Asia are mostly from Tropical Africa, with few from Australia and North America. *Panicum* is poorly represented in the drier subtropical areas, and the temperate region of Eurasia. Japan and Korea, for example, have only four species—all introduced. In comparison, subtropical parts of southern China and Taiwan have a large number of species chiefly introduced from India and Southeast Asia. There are only six introduced species in Europe, most of which have become naturalised. The drier parts of North Africa and the Orient have few *Panicum* species. The perennial species, *P. turgidum* possibly a native of North Africa, has successfully colonised desert areas. In Australia, *Panicum* occurs in all the states, the numbers of native and introduced species being almost equal. They are found near lakes and rivers, forest floors and margins, and also in some drier parts of central Australia. Of the Polynesian species, more than half are native to the Hawaiian Islands (Rotar 1968). Most of the remaining species are introduced from the United States and some are common forage and weed plants of both hemispheres.
3.2 Ecology

\[Panicum\] species occupy diverse habitats and collectively show a considerable ecological range. Many species occur in plains, in forest shade or margins on low hills in tropical and subtropical regions, or in open woods – as in the Eastern United States. Many occur in damp, moist areas or in waste places. The genus shows a marked preference also for sandy habitats, particularly for moist ones, and is very common around sand dune bush of tropical shores. \[P. repens\] is a good example. Many species occur in marshy habitats in different parts of the world and even in open water, e.g. \[P. paludosum\] in lakes, streams and rivers of Asia and Australia and \[P. elephantipes\] in the rivers of South America and Uruguay. If these species are compared with the desert species, \[P. turgidum\], the extraordinary ecological range of the genus becomes clear (Bews 1929).

The genus is not so common in closed grasslands, though several of the species occur there, e.g. \[P. virgatum\] in the United States. Some species, e.g. \[P. lukwангulense\] \[P. eckii\], grow up to altitudes of 2000 – 4000 m in upland grassland of Tropical Africa, but in North America only one genuinely upland species, \[P. thermale\], is found up to altitudes of about 2000 m.

Apart from the economically important species mentioned in the introduction, some more minor crops can be cited, such as \[P. hippothrix\] which is a native of Africa introduced into India, where it is used as a fast day food, cooked like rice (Bor 1960). \[P. atrosanguineum\] and \[P. coloratum\] are used as fodder grasses. Certain North American species, e.g. \[P. virgatum\] and \[P. bulbosum\] furnish forage in U.S.A. Most species of the genus, as shown in Table 4, are perennials – a greater number being in the Western hemisphere. Among the most
vegetatively aggressive perennials are *P. repens*, *P. virgatum*. Several of the annual species, mostly the weeds such as *P. dichotomiflorum*, *P. capillare*, and *P. trichoides*, have become widespread in several parts of the world. Certain species of the genus are very good soil binders, for example, *P. repens*, *P. turgidum* and *P. antidotale*, of which the former is most noteworthy.
PART II

ASSESSMENT OF TAXONOMIC CHARACTERS

AND THEIR VARIATION
CHAPTER 4: MACROMORPHOLOGICAL INVESTIGATION

4.1 Materials and Methods

Herbarium materials were used for the purpose of morphological investigations. Living plants were also studied in a few species where seed materials were available and could be grown in the greenhouse. Grass plants with typically tough, narrow leaves and large number of spikelets, provide good sample of herbarium specimens, if properly mounted. Most annuals and even many perennials can be conveniently mounted intact on the herbarium sheet. This allows ample scope for investigating the whole plant. Data on the herbarium labels provided sources of information on ecological, distributional, altitudinal and other aspects of the plant collected. For the majority of the species a large number of herbarium specimens were consulted which provided the opportunity for studying degrees of variation of characters in different individuals of the species.

In the course of studying herbarium materials, all available specimens were examined to investigate the range of variation in different features. The vegetative parts of the plant were studied by means of a simple hand lens as well as using a 10x to 20x dissecting microscope. For further details of organs like ligules, pubescence higher magnifications were used. For studying spikelets, mature spikelets usually from the top of panicle branches were used. First they were studied by the use of 10x to 20x dissecting microscope. For detailed investigation of spikelet structures, spikelets were soaked in a petri-dish of water added with a drop of detergent. This method proved to be most easy and effective in dissecting Panicum spikelets rather than boiling them in water or just examining them in pure water. Using a pair of fine
forceps and a needle, spikelet parts were dissected from below upwards and examined under a dissecting microscope using different magnifications ranging from 10x to 50x. They were systematically arranged on a slide moistened with water or finely smeared with an adhesive. For measurements, a measuring lens with a 1cm scale (finest divisions 0.1mm) was used. Comparative studies were made by dissecting and examining a number of spikelets from the same inflorescence as well as from different inflorescence of other individuals. No variation clearly attributable to position and the panicle was found within mature spikelets. Further, it was observed that certain characters like pubescence, nervation, presence or absence of palea and stamens in the lower floret showed variation within limits. For these reasons, and because herbarium specimens sometimes were incomplete, I measured several apparently comparable, mature, branch-terminating spikelets, rather than try to identify a single 'standard' spikelet to compare in each panicle I investigated.

4.2 Characters observed, enumerated and evaluated

4.2.1 Roots

The root system is fairly simple in the genus. It is fibrous, and develops adventitiously from the underground nodes. Roots of *P. turgidum*, a desert species, spread widely in search of moisture. They are very thick and look like small ropes as fine sand particles adhere to the root hairs. Thick fibrous root characterise the robust, stiffly erect annual, *P. trachyrhachis*. They give the plant strong anchorage in mud. Many species of *Panicum*, particularly the shade-loving, decumbent rambling species with slender, weak, branching culms usually root at the nodes, especially below - often forming adventitious prop roots above the soil surface. The entire plant is aerially supported by this
means. This type of adventitious root is characteristic of the C$_3$ species of the subgenus Phanopyrum. Examples from species in this study include: *P. brevifolium*, *P. gardneri*, *P. hayatae*, *P. inornatum*, *P. khasianum*, *P. notatum*, *P. sarmentosum*, *P. trichoides*. There are many others. Fibrous adventitious roots are often provided in certain species of the genus growing in aquatic habitats, as in *P. paludosum*, *P. longiroleum* (see Fig. 44).

4.2.2 Rhizomes

Many *Panicum* species produce horizontal rhizomes below the surface of the ground. They function as only the anchorage function of roots but with the structure of stems. They are distinguished from roots by being jointed and by having reduced bladeless leaves or scales. In some species, rhizomes spread widely and grow for considerable distances through the soil, ending in coriaceous, pointed terminal blades. Eventually they appear above ground so forming a new shoot which in turn produces further rhizomes. *P. repens*, of section Repentia, is a typical example, from this study, exhibiting this type of rhizome. By virtue of these rhizomes, it is able to reproduce very efficiently in the vegetative stage, spreads rapidly and widely and thus functions as an excellent soil binder. However, *P. repens* is often a pernicious weed of cultivated fields due to its very considerable colonising. Rhizomes, when present, aid in the identification of species but they have little taxonomic significance at supraspecific level. For example, Hitchcock & Chase (1910) characterized species of the group "Virgata" on the basis of possessing rhizomes, along with some other characters. But in recent works and in this study, it has been found that some species of this group belong to different sections - for example, *P. repens* to section Repentia and *P. virgatum* to section Panicum. Certainly I regard "Virgata" as an unnatural group. Short
underground stems or rhizomes, often termed rootstocks, are found in *P.antidotale*, *P.plenum*, *P.turgidum*, *P.maximum* and a few others. They are usually stout, short and swollen at the basal part of the aerial stem, serving as a means of perennation and vegetative propagation. Though presence or absence of rootstocks are useful in identifying species of *Panicum*, they cannot be correlated with other characters for use in classification.

4.2.3 Culms

The main aerial stems, the culms, are made up of a number of solid nodes separated by hollow internodes. Internodes at the base of the plant are shortest. Culms in *Panicum* may be 1) erect, growing upright and straight, 2) geniculately ascending, when they are bent at the nodes, obliquely spreading and then erect, 3) decumbent, spreading along the ground before becoming erect or 4) procumbent or prostrate, when they lie flat on the ground for the greater part of their length. Decumbent and procumbent culms frequently root at the nodes in contact with the ground and give support to the plants. All C₃ species in this revision are of this type. It is to be noted that they are not stoloniferous because they do not produce new plants from the nodes. Culms may be glabrous or hairy. C₃ species have glabrous culms. Culms of a majority of the C₄ species also are glabrous, but hairs occur in several species of them as in *P.viale*, *P.camboiense*, *P.atrosanguineum*, *P.paianum*. When a culm is hairy, both internodes and nodes may be hairy, or only the internodes hairy. In a hairless culm, both internodes and nodes may be glabrous but the nodes alone may be hairy. Nodal features are often very useful in keying out very similar species. For instance, *P.atrosanguineum* has hairy nodes while *P.walense* has glabrous ones. When an internode is hairy, it is so only in the exposed parts, not in the parts covered by leaf sheaths (Fig. 6.a,b). Culms of
most species in *Panicum* are terete. Terete culms may be tough and woody as in certain bushy perennials (*P.turgidum, P.antidotale*). Woody culms are also found in some forest species (e.g. *P.sarmentosum, Pincomtum, P.notatum*). In some species, culms may be compressed, soft, even spongy as in *P.paludosum* and *P.longiloreum* (see Fig. 44). These species grow in hygrophilous situations.

4.2.4 Duration and Growth Habit

Duration means the life span of the plant and the habit of the plant is the form of growth. The range of growth form is remarkable in *Panicum*. In the Indian subcontinental and Southeast Asiatic species, it ranges from woody shrubs like *P.turgidum, P.antidotale* to dwarf herbs like *P.atrosanguineum, P.paianum*. Plants may form very low cushions as in the south American species *P.koalensa*. The growth form may be highly variable in individuals of the same species as in *P.walense* where the plant may be 5cm to 70cm in height.

Species may be either annual or perennial in duration. There are more than twice as many perennials as annuals in *Panicum* generally. The proportion is more or less the same in the Asiatic species if the curious C₃ perennial, rambling species are included, but excluding them annuals and perennials are equally common. Annuals are tufted plants with a simple fibrous rooting system, lacking even short rhizomes or stolons. All or most of their shoots bear flower heads. They lack old leaf-blades, naturally, which is a further aid in establishing annual status. They are regarded as more advanced because of the reproductive specialisation required to overwinter as seed. Perennial species are coarse, (large, hard and rough) often woody rhizomatous. Some of the perennial weeds, e.g. *P.repens* have successful spread in both the hemispheres. On the other hand, certain annuals e.g. *P.capillare, P.dichotomiflorum* have become widespread in various parts of the world. In
the infrageneric classification of the species revised in this study, the annual and perennial character of the species is important. With the exception of *P. brevifolium* and *P. trichoides*, all species of the C$_3$ subgenus Phanopyrum are perennial. Species of the subgenera Agrostoides and Megathyrsus are also perennial. In the subgenus Panicum, sections Dichotomiflora (except the annual *P. schinzii*) Dura, and Repentia contain only perennial species while the section Panicum contains many annuals and only a few perennials.

4.2.5 Leaf Sheaths

Grass leaves are differentiated into three distinct parts: a sheath, a blade, and a ligule. The sheath enfolds the culm for most or all of its length forming a hollow cylinder round the culm. It is attached to the whole circumference of the node. The edges of the sheaths are usually free to the base, but in a few grasses the margins are united at least below. This is characteristic of the genera *Bromus*, *Glyceria* and *Melica*. Leaf sheaths in *Panicum* have free margins and are usually light and terete like the culms, but in certain species they may be loose and compressed or keeled. Loose, compressed and glabrous leaf sheaths are characteristics of the species of section Dichotomiflora. Indumentum of leaf sheaths often provides diagnostic characters in distinguishing species. *P. seminudum*, with papillose-hirsute sheath can be differentiated from the closely allied *P. mindanaense* which has glabrous sheaths. Leaf sheaths of *P. paludosum*, *P. longilorum*, *P. schinzii* of section Dichotomiflora are completely glabrous. *P. maximum* has leaf sheaths which are strongly keeled. In *P. plenum*, the leaf sheath is keeled towards the upper end. It differs in this respect from *P. antidotale* in which the leaf sheath is rounded, not keeled. These two species belong to the same subgenus but different sections. The surface of the leaf sheaths are lightly to deeply striated
in the *Panicum* species included in this study. However, although this character appeared to be consistent for a particular species, there was every gradation in the amplitude of the striations among the species. This feature thus varies continuously and is of little taxonomic value beyond its occasional use only as a confirmatory feature for the identification of species.

4.2.6 Leaf blade

The blade of the leaf is attached at the top of the leaf sheath. The blade usually is flat and elongated but is highly modified in some grasses. It is nearly always relatively narrow, many times as long as broad, but in some grasses including certain species of *Panicum*, it may be relatively broad (e.g. *P.brevifolium, P.trichoides*). In the revised species as a whole, leaf blade size and shape vary considerably. In general terms, the blades are linear to linear-lanceolate in species of dry open areas, and ovate-lanceolate to lanceolate in species inhabiting shady places. Longitudinal veins are almost always present on the blade continuous from base to apex. The midnerves are usually larger than others but sometimes there is no distinction between main and smaller veins, as in *P.paiianum, P.turgidum, P.smithii*. The surface of the blade often bears short or long hairs. The hairs may be soft or stiff, scattered or dense. Frequently they have swollen bases. These hair characters are quite useful in the identification of species. For instance, leaf blades of the species *P.sarmentosum* and *P.incomtum* are thickly covered with short soft hairs giving a velvety appearance. In some other species like *P.atrosanguineum, P.paiianum, P.capillare*, the blades are hirsute, pubescent or with tubercle-based hairs. In *P.notatum* the base of the leaf blade is pectinately hairy. However, while taking this hairy character of leaf blade into account, it has to be remembered that the degree of hairiness is variable to a certain limit in individuals of a species.
or even in different leaves of the same individual. There are certain species in which the leaf blade is glabrous, as in *P. paludosum*, *P. longilorum*, *P. smithii*, *P. schinzi*, *P. turgidum*. In *P. trachyrhachis* the adaxial surface of the blade is softly papillate all over. The presence of hairs on the blade is taxonomically important in recognising varieties, for example, *P. notatum* var. *pubescens*.

4.2.7 Ligule

The ligule is a small normally membranous flap of tissue where the blade joins the sheath. It is short, may bear hairs at its margins, or it may be reduced to a fringe of hairs. Very rarely it is lacking (e.g. *Echinochloa crus-galli*). Ligules are very important in the identification of grasses because they have been found to show constant features at species level. According to Gould & Shaw (1983) the type of ligule is usually consistent for all species of a genus. But in *Panicum* there are different types of ligules (Hsu 1965, Gould & Shaw 1983, this study). In some species of *Panicum* the ligule is absent (Hsu 1965, Gould & Shaw 1983). I have detected the following types of ligules in the Indian subcontinental and Southeast Asiatic species of the genus. It is either membranous or reduced to a ring of hairs. Examples of the latter state (Fig. 1.h,i) are *P. atrosanguineum*, *P. vialae*, *P. trachyrhachis*, *P. turgidum*. There is no species in this study in which the ligule is absent. The membranous ligules have different characters. It can be 1) thick with lacerate apex (Fig. 1.f) e.g. in *P. amoenum*, *P. smithii*, *P. hayatae*, *P. humidorum*, 2) thin, papery and fringed with hairs (Fig. 1.d,e) as in *P. antidotale*, *P. bisulcatum*, *P. coloratum*, *P. elegantissimum*, *P. gardneri*, *P. khasianum*, *P. sumatrense* subsp. *psilopodium*, *P. mindanaense*, *P. notatum*, *P. plenum*, *P. seminudum*; 3) leathery and fringed with hairs (Fig. 1.a,g) in e.g. *P. maximum*, *P. sumatrense*, *P. repens*; 4) membranous in the lower part but bearing long cilia at the distal end (Fig. 1.b,c) as in *P. paludosum*, *P. longilorum*. 

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Fig. 1 Types of ligules identified in this study

**Leathery and fringed with hairs:**

a. P. maximum (x 3)

b. P. antidotale (x 3)

g. P. repens (x 3)

c. P. schinzii (x 4)

d. P. bisulcatum (x 3)

e. P. schinzii (x 4)

**Membranous with long silky cilia:**

b. P. longiloreum (x 4)

c. P. schinzii (x 4)

d. P. bisulcatum (x 3)

e. P. antidotale (x 3)

**Papery and fringed with hairs:**

f. P. smithii (x 4)

**Thick with lacerate apex:**

f. P. smithii (x 4)

**Reduced to a ring of hairs:**

h. P. turgidum (x 3)

i. P. atrosanguineum (x 3)
The nature of the ligule sometimes can be helpful in distinguishing between closely allied species. For example, *P.paludosum* with membranous, long silkily ciliate ligules can be separated from *P.repens* with which it is often confused, because the latter has a membranous ligule with a short fringe of hairs. However, this character cannot be used at the supraspecific level. Though in the section Dichotomiflora, distinctly membranous, long ciliate ligules are typically observable, more or less similar ligules are found also in species belonging to other sections and subgenera. According to this study, a classification of sections (Hsu 1965) in *Panicum* on the basis of ligule characters would appear to produce unnatural taxa. For example Hsu (1965) characterized section Sarmentosa in having ligules papery in the lower part and fringed on the distal part. He has included *P.antidotale* in this section. But, *P.antidotale* is a Kranz M. S. NADP-me species, while the other species included by him in this section are all non-Kranz C₃.

4.2.8 Inflorescence

The inflorescence is a compound panicle in the Indian subcontinental and Southeast Asiatic species of *Panicum*. A compound panicle has two or more series of branches and is characterised by the branched laterals from the rachis that terminate in spikelets. Panicle shape in *Panicum* is variable depending on the nature and degree of branching before attachment of the spikelet. In the species here revised, the panicle is usually effuse (Fig. 2.a,b,c,e), branches of the third and fourth order being common. However in *P.auritum*, the branches of the panicle are condensed (Fig. 2.f). In certain species, the branches of the first, second and third order lie parallel to the rachis and the panicle thus
Fig. 2. Examples of types of panicles found in *Panicum* species in this study

a. *P. effusum* (x 1/2): Effuse with lower branches whorled

b. *P. turgidum* (x 1): Effuse with only a few spreading branches

c. *P. bisulcatum* (x 1/3): Effuse without main axis

d. *P. longiloreum* (x 1/3): Branches and branchlets somewhat appressed; main axis soon becoming obscure

e. *P. smithii* (x 1/2): Branches spreading at right angles to the rachis

f. *P. auritum* (x 1/3): Branches and branchlets contracted
appears to be appressed (Fig. 2.d). This contrasts with the branching in *P. smithii*, for instance, in which the panicle spreads widely, the primary branches being angled at 90° to the rachis (Fig. 2.e). The rachis is usually persistent up to the end of the panicle, but in certain species viz. *P. paludosum*, *P. longiloreum*, *P. miliaceum*, *P. repens*, it soon disappears and the lateral branches continue beyond (Fig. 2.c,d). Panicle branching and spikelet attachment offers useful characters for the identification of species in *Panicum*, at least in the species concerned in this study. Though the size of the panicle is variable within individuals of a species, the pattern of branching and the shape are constant features and are therefore often used in distinguishing species. However it has little taxonomic importance above the species level.

4.2.9 Spikelet

The spikelet in *Panicum* consists of two glumes subtending a lower staminate or barren floret and a fertile upper floret. The fertile floret consists of a pair of lodicules, three stamens and a pistil enclosed by the upper lemma and its palea. The different parts of a spikelet of *Panicum* are shown in Fig. 3.a–o. The glumes, the lower lemma and the upper lemma are distichously arranged on a tough rachilla, the point of attachment of the spikelet being a variable distance below the glumes. In *Panicum*, the lemma and palea of the fertile upper floret are indurated and alike in texture, tightly enclosing the caryopsis inside. The caryopsis does not physically adhere to the anthecium. The margins of the upper lemma are inrolled, clasping the edges of the palea and the two together (the ‘anthecium’) provide an extra ‘fruit’ layer to the caryopsis. This is why many authors use the term ‘fruit’ to indicate the upper floret enclosing the caryopsis. The fruit is the propagule which, in most cases, is shed singly or enclosed by the lower lemma and the glumes. The nature of
Fig. 3 Different parts of spikelets of *Panicum (P. miliaceum)*

- a. Dorsal view (x 8)
- b. Ventral view (x 8)
- c. Spikelet partially dissected (x 8)
- d. Lower glume (x 7)
- e. Upper glume (x 8)
- f. Lower lemma (x 8)
- g. Lower palea (x 10)
- h. Upper lemma (x 8)
- i. Upper palea (x 8)
- j. Dorsal view of upper floret (x 8)
- k. Ventral view of upper floret (x 8)
- l. Flower showing androecium and gynoecium (x 8)
- m. Lodicules (x 15)
- n. View of caryopsis showing hilum (x 8)
- o. View of caryopsis showing embryo (x 8)
the fruit is taxonomically highly significant and is one of the chief
distinguishing features of the tribe Paniceae, but with the arrangement
variously modified in different genera.

Shape

Spikelets are dorsally compressed (i.e. in the lemma–palea axis) and
symmetrical in Panicum but a few species have somewhat laterally
compressed and asymmetrical spikelets having a gibbous appearance (e.g.
P.brevifolium, P.trichoides). In the species revised, the shape of the spikelet is
usually ovoid, ovoid–lanceolate, ellipsoid or oblong, but intermediate, variable
shapes, such as ellipsoid-oblong or ovoid-oblong occur and may even be
found in the same species. Figures 4 and 5 illustrate two views of spikelets
together with one view of the upper floret of some representative species of
Panicum in this study. The different shapes of spikelets have been found to be
very useful in identification and separation of closely similar species. As
examples, P.paludosum with narrowly lanceolate spikelets differs from P.schinzii
with ellipsoid spikelets; P.elegantissimum with ovoid spikelets differs from
P.trypheron with ellipsoid-oblong spikelets. At the supraspecific level, this
character cannot be used effectively but, in general, it is ovoid or
ovoid–lanceolate in species of the section Panicum (e.g. ovoid: P.fischeri,
P.miliaceum, P.viale, P.sumatrense, P.cambogiense; ovoid–lanceolate:
P.caudiglume, P.hippothrix, P.mindanaense, P.seminudum). Ellipsoid or
ellipsoid-oblong spikelets are commonly found in species of the C3 subgenus
Phanopyrum (e.g. P.hayatae, P.humidorum, P.incomtum, P.khasianum,
P.sarmentosum).

Apex

The shape of the spikelet apex is important from the taxonomic point of view.
Fig. 4 Two views of spikelets and upper floret in representative species of *Panicum* (All x 15)

a. *P.*maximum  
b. *P.*plenum  
c. *P.*longiloreum  
d. *P.*smithii  
e. *P.*cambogiense  
f. *P.*humidorum
Fig. 5 Two views of spikelets and upper floret in representative species of *Panicum* (All x 15)

a. *P*.trachyrhachis
b. *P*.caudiglume
c. *P*.antidotale
d. *P*.bisulcatum
e. *P*.trichoides
f. *P*.brevifolium
FIG. 5
It may be acute, obtuse or acuminate. However, as the apex may change considerably with age of the spikelet, this character has always to be used with care. For instance, the spikelet of *P.turgidum* is ovoid or ovoid-lanceolate with an acuminate apex when young, but it turns sub-globose, turgid, with an acute to obtuse apex as the spikelet attains maturity. In *P.miliaceum* the shape of the spikelet is ovate but the apex may be *acuminate* or *obtuse*. I have noted some taxonomic significance in the character of spikelet-apex shape at the subgeneric level in the species revised. It is acute to obtuse in the C₃ species - there being no spikelets with acuminate tips. On the other hand, a majority of the species of the subgenus Panicum have acuminate tips, fewer have acute tips, but there are only two species (*P.cambogiense*, *P.luzonense*) which have spikelets with obtuse tips.

**Length**

There is a wide variation in spikelet length in Indian subcontinental and Southeast Asiatic *Panicum* species. The spikelets may be very small, (1-1.5mm in *P.trichoides*) to as big as 5-5.2mm long (in *P.fischeri*). In between these two extremes, a large number of overlapping ranges occur, but the variation cannot be divided up into any satisfactory states. Scoring any length-range assembles species which are, in other features, very distantly related. For example, using length-range of 2.5 - 3mm groups a heterogeneous assemblage of species from three different subgenera. However, any higher length-range was more indicative. The spikelets are usually less than 4mm long in the non-Kranz C₃ species, with the exception of the two species of section Incisa, in which they are 4-5mm in length. But a large number of C₄ species also have spikelets below 4mm long. Though the spikelet length character is not taxonomically very helpful or reliable in making subgeneric arrangements it is a very useful character in identification, and in
distinguishing between species which are closely related or otherwise confused. Examples include: *P. mindanaense* (2–3 mm long)/ *P. seminudum* (3.2 – 3.5 mm long)/ *P. paludosum* (3.4 mm long)/ *P. longilorum* (2.2 – 2.5 mm long)/ *P. humidorum* (1.4 – 1.5 mm long)/ *P. amoenum* (1.7 – 2 mm long)/ *P. atrusanguineum* (1.8 – 2.2 mm long)/ *P. panianum* (2.5 – 3 mm long)/ *P. fischeri* (5 – 5.2 mm long)/ *P. sumatrense* (2 – 3.5 mm long).

4.2.10 Gaping of the spikelets at anthesis

Some spikelets gape at anthesis. This is an interesting character which I have recorded and found useful in this study. It is characteristic of the species belonging to the sections Panicum and Dura in the subgenus Panicum, and section Incisa in the subgenus Phanopyrum, though the degree of gaping varies considerably between the species. In every instance, this character is well correlated with the lower glume being separated by a detectable internode and thus placed distinctly below the rest of the spikelet. This insertion of the lower glume at a lower level lessens its grip on the spikelet and thus, I think, promotes gaping of the spikelet at anthesis. This is in contrast with the species of the section Dichotomiflora and Repentia in which the lower glume is cuff-like, inserted at more or less the same point as the upper glume and firmly clasping the spikelet. A situation differing from the above is found in some New World species e.g. *P. cupreum, P. hians, P. pilosum*. In these species, the spikelets gape because the palea of the sterile floret, which are subequal, becomes subrigid at maturity, forcing open and expanding the spikelet.

4.2.11 Pedicel

The pedicel is the stalk of the individual spikelet. It is longer or shorter than the spikelet as far as the revised species are concerned, but the length varies
continuously, so that it is not desirable to use this character for taxonomic purposes. Variation in pedicel length is found within the same species, e.g. in *P.brevifolium*, *P.khasianum*, in which the pedicel may be either shorter or longer than the spikelet. Examples of spikelets with shorter pedicels are *P.antidotale*, (subgenus Agrostoides), *P.repens*, *P.virgatum* (subgenus Panicum), *P.amoenum*, *P.auritum*, *P.smithii* (subgenus Phanopyrum). Examples of spikelets with longer pedicels: *P.hippothrix*, *P.capillare*, *P.incisum* (subgenus Panicum), *P.bisulcatum*, *P.hayatae*, *P.trichoides*, *P.notatum* (subgenus Phanophyrum). From these examples, it will be seen that this character is shared by species which are otherwise distantly related. However, pedicel length can be usefully employed as a diagnostic character for certain species, e.g. *P.antidotale*, *P.auritum* in which pedicels are always shorter, while in *P.hippothrix*, *P.capillare*, *P.bisulcatum* the pedicels are at least three times as long as spikelets.

On the basis of the shape and surface of the pedicel, I have recognised two taxonomically predictive types of pedicel in this study. In the first type the pedicel is angular with ridges and sinuses, the ridges being always scabrid (Fig. 6.e,f). In the second type, the pedicel is terete and glabrous (Fig. 6.c,d). These two types are very useful in distinguishing the C₄ and C₃ subgenera with only few exceptions. For example, the first type of pedicel is characteristically found in the species of the C₄ subgenera Panicum, Agrostoides and Megathyrsus, while the second type is found in all the species of the C₃ subgenus Phanopyrum except *P.auritum*, *P.gardneri*, *P.khasianum*, *P.incisum*.

4.2.12 Glumes

Each spikelet has two glumes at its base, attached to the rachilla on opposite sides – one inserted below the other. The glumes never subtend a flower or palea. Both the lower glume and upper glume are present in *Panicum* but in
Fig. 6 Scanning electron micrographs of culm and pedicel of *Panicum*

a. b. *P. vialae* : Unexposed and exposed part of culm

c. *P. brevitolium* : Terete and glabrous pedicel
d. *P. sarmentosum* : Terete and glabrous pedicel
e. *P. paludosum* : Angular and scabrid pedicel
f. *P. miliaceum* : Angular and scabrid pedicel
some genera of Paniceae the lower glume may be wanting as in *Paspalam*, *Axonopus*. The glumes vary in size, shape, texture, nervation, and in their size relative to the spikelet. In *Panicum*, the characters of lower glumes differ from those of upper glumes and are much more important taxonomically.

4.2.13 Lower Glume

The characters of the lower glume have been found extremely valuable in the study of the revised species. The relative length (to the spikelet), shape, apex and nervation have served to identify and distinguish many species, and characterize certain sections. For instance, spikelets with lower glumes 1/4 the length characterize the species recognisable in the sections Dichotomiflora and Repentia. This relative length in these species is also typically associated with certain other characters of the lower glume viz. broadly ovate to suborbicular cuff-like shape, obtuse to truncate tips, membranous texture and obscure nerves. Other Old and New World species belonging to these two sections also exhibit these characters of the lower glume. The relative length of the lower glume is fairly consistent in a species. Hence it can be very reliably used in distinguishing closely similar spikelet. For example, *P. bisulcatum* (1/3) is distinguished from *P. smithii* (2/3); *P. brevifolium* (almost as long as) is distinguished from *P. trichoides* (1/3 - 1/2); *P. miliaceum* (2/3 - 3/4) is distinguished from *P. sumatrense* (1/3); *P. maximum* (1/3 - 1/4) is distinguished from *P. plenum* (1/2); *P. atrosanguineum* (2/3) is distinguished from *P. paianum* (1/2). Rarely, the lower glume is longer than the spikelet, as in *P. caudigluma*, which character can be used to separate two other very similar species viz. *P. seminudum* and *P. mindanaense* in which the lower glumes are just as long as the spikelet.

The shape of the lower glume is ovate to broadly ovate. The lower glume
either does or does not partially to entirely surround the base depending on how largely ovate it is. When the lower glume does not surround the base at all, it has rather the shape of an isosceles triangle. The apex of the lower glume is variable (Fig. 7.a-1). It is a very useful character in the identification of species. The apex of the lower glume is truncate (P. repens, P. longiloreum, P. paludosum) or acute (P. antidotale, P. coloratum, P. fischeri, P. paianum, P. viale, P. plenum, P. hayatae, P. notatum, P. trichoides) or acuminate (P. strosanguineum, P. hippothrix, P. mindanaense, P. walense) to long acuminate (P. miliaceum, P. trypheron) or obtuse (P. cambogiense, P. amoenum, P. gardneri, P. sarmentosum) or cuspidate (P. trachyrrhachis, P. virgatum). However in certain species, the apex of the lower glume varies from acute to acuminate (P. capitulare), acute to obtuse P. auritum, P. bisulcatum, P. brevifolium, acuminate to cuspidate (P. trachyrrhachis, P. virgatum).

Nervation of the lower glume is taxonomically a very important character. I have used the number and prominence of nerves in the subgeneric and sectional classification of Indian subcontinental and Southeast Asiatic Panicum. In the C3 subgenus Phanopyrum, the lower glume is uniformly 3-nerved throughout, with the exception of the single species, P. hayatae belonging to the section Hayata. Species included in the subgenus Agrostoides have 3–5-nerved lower glumes, while in P. maximum the only representative of the subgenus Megathyrsus, the lower glume is 3-nerved. In the subgenus Panicum, nerveless or obscurely 1–3-nerved lower glume with one midnerve and two lateral weak nerves are found characteristically in sections Dichotomiflora and Repentia. P. turgidum of section Dura has a prominently 5–9-nerved lower glume. In the rest of the species of the section Panicum, the lower glume nerves come in three ranges: 3–5-nerved (e.g. P. strosanguineum, P. capitulare, P. sumatrense), always 5-nerved (P. caudiglume, P. hippothrix,
Fig. 7 Types of lower glume apex identified in this study

**Truncate**

a. *P. paludosum* (x 20)
b. *P. longiloreum* (x 20)
c. *P. repens* (x 20)

**Acute**

d. *P. bisulcatum* (x 20)
e. *P. antidotale* (x 20)
f. *P. auritum* (x 20)

**Obtuse**

g. *P. luzonense* (x 20)
h. *P. humidorum* (x 20)
i. *P. khasianum* (x 20)

**Acuminate**

j. *P. hippothrix* (x 10)

**Long acuminate**

k. *P. trypheron* (x 10)

**Cuspidate**

l. *P. caudiglume* (x 10)
FIG. 7
P.incisum, P.mindanaense, P.paianum, P.seminudum, P.tryphon, P.viale, P.virgatum), and 5-7-nerved (P.cambogiense, P.elegantissimum, P.fischeri, P.luzonense, P.miliaceum). The midnerve of the lower glume is usually scabrid, particularly above the middle half, as in (P.miliaceum, P.trachyrhachis, P.seminudum, P.elegantissimum, P.tryphon) and many others. However, the lower glume may be completely glabrous, e.g. in P.paludosum, P.longiloreum, P.schinzii and P.repens.

4.2.14 Upper glume

With only a few exceptions, the upper glume is typically as long as the spikelet in the genus Panicum. The upper glume and the lower lemma, which are subequal, enclose the upper fertile floret. As the length of the upper glume is uniform throughout, this character is not useful for taxonomic purposes. The shape of the upper glume does not show much variation, either. It is uniformly more or less ovate, but with some modifications in a few cases e.g. ovate-lanceolate in P.khasianum, P.plenum, P.sumatrense, ovate-oblong in P.gardneri, P.stapfianum, ovate-elliptic in P.cambogiense, broad on the back giving a boat-shaped or hemispheric appearance in P.brevifolium, P.trichoides, P.hayatae. The apex of the upper glume is acute, obtuse or acuminate (Fig. 8.a,b,c). This character is useful taxonomically. In the species revised, the non-Kranz C₃ species mostly have an acute upper glume. Among the C₄ subgenera, species of both Agrostoides (P.plenum, P.antidotata) and Megathyrsus (P.maximum) have an acute upper glume. In the subgenus Panicum, the apex is acuminate to cuspidate in nearly all species of the sections Dura and Panicum (acute in P.viale, P.luzonense, P.cambogiense), while in the species of the sections Dichotomiflora and Repentia, it is always acute.

The number of nerves in the upper glume has taxonomic significance at the
Fig. 8

Types of upper glume apex identified in this study

a. $P.\text{hippothrix}$ (x 15): Acuminate
b. $P.\text{paianum}$ (x 20): Acute
c. $P.\text{gardneri}$ (x 10): Obtuse

Scanning electron micrographs of upper floret surface of Panicum

Smooth

d. $P.\text{atrosanguineum}$: Lemma side
e. $P.\text{atrosanguineum}$: Palea side
f. $P.\text{miliaceum}$: Lemma side
g. $P.\text{miliaceum}$: Palea side
specific and supraspecific levels. The non-Kranz C₃ species uniformly have 5 nerves in the upper glume except *P. hayatae* in which it is 11-nerved. *P. maximum* of the subgenus Megathyrsus has a 5-nerved upper glume. The two sections of the subgenus Agrostoides vary in nervation of the upper glume - section Antidotalia, 5-9-nerved (*P. antidotale*), and section Bulbosa, 5-7-nerved (*P. plenum*). The majority of the species of the subgenus Panicum have either 7 nerves (*P. capillare, P. elegantissimum, P. incisum, P. stapfianum, P. viale*), or 7-9-nerves (*P. cambogiense, P. coloratum, P. longiloreum, P. hippothrix, P. paludosum, P. repens, P. schinzii, P. typheron, P. turgidum*). However, in a few species in this subgenus, I have observed also lower and higher numbers of nerves. In *P. walense*, the upper glume is 3-5-nerved, in *P. paianum*, it is 9-11-nerved while in *P. miliaceum* it is 11-13-nerved. Transverse nerves are sometimes present in the upper glumes. This very much aids the identification of certain species e.g. *P. cambogiense, P. luzonense* in which the glumes are thereby distinctive. In *P. longiloreum* transverse nerves of less prominence are present on the upper glume, particularly near the apex. Margins of the upper glume are uniform in texture throughout the species revised, but in *P. antidotale* and *P. gardneri* the two glumes as well as the lower lemma possess broadly membranous margins. However, though these two species have this character in common, they differ greatly from one another in all other respects.

As regards indumentum, the upper glume is usually glabrous, finely scabrid or, in a few species, sparsely shortly hairy near the tips. I have found the indumentum of the lower glume to be a useful character. Most species of the subgenus Panicum have glabrous upper glumes, but some have lower glumes finely scabrid particularly on the midnerve, as in *P. caudiglume, P. seminudum, P. trachyrhachis, P. virgatum, P. hippothrix*. In the species of the non-Kranz subgenus, the upper glume is usually shortly pilose or sparsely puberulous near
the tip, as in *P.amoenum, P.smithii, P.bisulcatum, P.trichoides*, or glabrous as in *P.hayatae, P.humidorum, P.khasianum*. Sometimes closely related species can be distinguished by the presence or absence of hairs on the upper glume. As for example, *P.humidorum* with glabrous upper glumes differs from *P.smithii* in which the lower glume is pilose at the tip.

4.2.15 Lower lemma

In *Panicum*, the lower lemma is typically similar to the upper glume with very few exceptions, e.g. it is glandular in *P.chapadense*, sulcate in *P.infestum*. In fact, the lower lemma is so similar in its length, shape, apex, nervation, texture and indumentum to the upper glume that it simulates a third glume. The character states and their taxonomic significance just described here for the upper glume can, in general, equally be attributed to the same features of the lower lemma.

The lower lemma often bears in its axil a well developed palea (Fig. 3.g), but this is sometimes reduced or absent. The lower lemma also often subtends a staminate flower, but this may be absent. The palea is hyaline to opaquely membranous and is usually oblong with an acute or obtuse tip. The presence or absence, and, when present, the size of the palea are valuable diagnostic characters in the materials studied. The palea varies from about as long as the lower lemma to reduced to a small size (0.8 – 1mm long). In some New World species, the lower palea becomes enlarged and indurated, expanding the spikelet at maturity, as in *P.pilosum, P.hians*. I have recognised three categories of palea character in the species of the Indian subcontinent and Southeast Asia. These are: 1) absent (e.g. *P.amoenum, P.smithii, P.bisulcatum, P.capillare, P.humidorum, P.khasianum, P.notatum*), 2) small, when it is less than half the length of the lower lemma (e.g. *P.miliaceum, P.atrosanguineum*,
P. coloratum, P. caudiglume, P. mindanaense, P. hippothrix, P. elegantissimum, P. incisum, P. auritum, P. sarmentosum, P. inconstum, P. trichoides, 3) large, when the palea is more than half the length of the lower lemma (e.g. P. paianum, P. schinzii, P. longiloreum, P. stapfianum, P. trachyrhachis, P. turgidum, P. vialae, P. virgatum, P. seminudum, P. walense, P. plenum, P. antidotale, P. cambogiense, P. luzonense, P. fischeri). In P. paludosum and P. repens, the palea is either very reduced or absent. Sometimes closely related species differ in palea size, e.g. P. longiloreum (large) from P. paludosum and P. subalbidum – an African species (reduced); P. atrosanguineum (small) from P. paianum (large). In general, species of the C₄ subgenera have well developed to large paleas and species of the C₃ subgenus have very small palea (but large, nearly as long as the lower lemma, in P. gardneri).

The lower floret is characteristically sterile in Panicum which is a special feature of the subfamily Panicoideae. The lower floret is either staminate or barren (entirely lacking sexual parts). In the species here revised, majority of the C₄ species are barren in the lower floret, but there are species in which the lower floret is staminate, as in P. antidotale, P. schinzii, P. stapfianum, P. turgidum. Further, in the C₃ plants, most of the species have a barren lower floret, except P. brevifolium and P. hayatae in which the lower floret may be either male or barren. There are some instances in the C₄ species where the sexual character of the lower floret is not consistent within individuals of the same species e.g. (P. paludosum, P. repens, P. fischeri, P. coloratum, P. virgatum). This inconsistency can be found even in spikelets of the same panicle, as in P. maximum. This character can therefore not always be used reliably in taxonomy.
4.2.16 Upper floret

The upper floret consists of the upper lemma and its palea, enclosing the flower within (see Fig. 3.c). The upper lemma and the palea are both indurated, similar in texture, and the former encloses the latter by all its margins except the tip. The whole acts as a unit, the external shape, size and other features of which are largely determined by the upper lemma. That is to say, the palea conforms with the upper lemma in size, shape and texture. Taxonomically, the character of the upper lemma is very significant in Panicum. Its different characters are evaluated below with reference to the species found in the Indian subcontinent and Southeast Asia.

Length

The upper lemma is shorter than the spikelet and is always enclosed by the lower lemma and upper glume. The shortness of the upper lemma relative to the spikelet varies in different species. The difference in the relative shortness varies continuously from slightly to much shorter than the spikelet. This character therefore cannot always be satisfactorily brought into account. However, many species are easily recognised on the basis of whether the upper lemma is much shorter than the spikelet, as in P.caudiglume, P.mindanaense, P.seminudum, P.trachyrhachis, P.virgatum, or just shorter than the spikelet as in P.repens, P.longifolium, P.smithii, P.bisulcatum, P.amoenum, P.sarmentosum.

Shape

In general, the shapes of the upper lemma in the revised species are ovoid, ellipsoidal or obtuse (narrowly lanceolate in P.auritum). Shape is a useful character that sometimes can be used in distinguishing species. Examples are,
*P. virgatum* with narrowly ovoid upper lemma differing from *P. trachyrhachis* with ellipsoid upper lemma, *P. paludosum* with oblong upper lemma can be distinguished from *P. longiloreum* with an ellipsoid to broadly ellipsoid upper lemma. However, this character must be used with caution because there are instances in which two similar shapes of upper lemma occur in the same species. For example, lemmas are ovoid or oblong in *P. humidorum*, *P. antidotale*, ellipsoid or oblong in *P. coloratum*; ellipsoid or ellipsoid-oblong in *P. caudigluma*. Sometimes the shape of the upper lemma may vary with age caused due to the maturation of the grain inside. An example is *P. longiloreum* in which the upper lemma is ellipsoid when relatively young but markedly broadly ellipsoid at full maturity. The back of the upper lemma is usually convex, but in some exceptional cases, it is slightly asymmetrically gibbous (Fig. 5.f) as in *P. brevifolium* and *P. trichoides*.

**Apex**

The apex of the upper lemma is acute or obtuse in the species revised except in *P. auritum* in which it is acuminate. It is taxonomically a significant character at the specific and supraspecific levels. All the species of the *C₃* subgenus have upper lemmas with an acute apex. Acute upper lemmas also occur in the species of the subgenus Megathyrsus and Agrostoides, and part of the subgenus Panicum. In the subgenus Panicum, species of the section Dichotomiflora and Dura, and the majority of the species of section Panicum have acute upper lemmas. Obtuse upper lemma are found only in certain species of the section Panicum (e.g. *P. trachyrhachis*, *P. virgatum*, *P. walense*, *P. trypheron*, *P. luzonense*, *P. hippothrix*, *P. fischeri*, *P. elegantissimum*, *P. cambogiense*). The apex of the upper lemma is sometimes useful in distinguishing species with very similar spikelets, as for example, *P. viale* (obtuse upper lemmas) differs from *P. cambogiense* (acute upper lemmas);
*P.trachyrhachis* (obtuse upper lemma) differs from *P.mindanaense* and *P.seminudum* (acute upper lemma).

**Base**

The base of the upper lemma is usually rounded, but there are certain species in which the base is truncate, a feature which can be used as a diagnostic character for identification as, for example, in *P.trachyrhachis, P.caudiglume, P.mindanaense, P.seminudum, P.virgatum.*

**Surface**

The surface of the upper lemma in the species revised is usually smooth (Figs. 8.d-g, 9.a), but in some species it is transversely rugose or rugulose (Figs. 4.a,b; 9.e,f). Where the upper lemma is smooth, it may be polished and shiny, or smooth but not shining. The upper lemma may develop some colours during maturation, including light yellow, light brown, and greenish black which often are of help in differentiating closely related species. For example, *P.atrosanguineum* with dark, chestnut-coloured upper lemmas differs from *P.paianum* with pale yellow upper lemmas.

The texture of the upper lemma surface is taxonomically highly significant at the subgeneric and sectional level of classification. *P.maximum* with distinctly transversely rugose upper lemmas (Fig. 9.e,f), is hence classified in the subgenus Megathyrsus. Another African species, *P.infestum* with transversely rugose upper lemma also belongs to this subgenus. Partly on the basis of the contrasting characters of rugulose and smooth surface of the upper lemma, I have recognised the section Antidotalia in the subgenus Agrostoides (see Chapter 8). In this subgenus there are two sections. They are section Bulbosa, including *P.plenum* and *P.bulbosum* (the latter not in this study) with a
Fig. 9  Scanning electron micrographs of upper floret surface of *Panicum*

a.  *P. antidotale*: Smooth

b,c,d.  *P. plenum*: Papillate

e,f.  *P. maximum*: Transversely rugose
Fig. 10 Scanning electron micrographs of upper floret surface of *Panicum*

a. *P. oblongispiculum:* Apex with tangled hairs

b. *P. khasianum:* Apex with tangled hairs

c.d. *P. auritum:* Papillate and prickly towards apex

e.f. *P. trichoides:* Covered with bottle-like appendage
transversely rugulose upper lemma (Figs. 4.b, 9.b,c,d), and section Antidotalia, including the single Asiatic species, *P.antidotale* with a smooth upper lemma (Fig. 9.a). In subgenus Panicum, all species are characterised by smooth upper lemmas. In the C_3_ subgenus Phanopyrum, some sections are characterised by rugulose upper lemma feature, as in section Monticola (*P.trichoides* Fig. 10.e,f), while in some other sections, plants have smooth upper lemmas, for instance in sections Sarmentosa, Incisa, Hayata and Laxa in this study.

Where the upper lemma is smooth, the differential characters of polished and shiny, or smooth and not shiny surface are useful in the separation of species of certain sections. For example, species of the sections Dichotomiflora and Repentia mostly have a pale upper lemma while those of sections Panicum, Dura, Incisa and Hayata have a polished and shiny upper lemma.

**Nerves**

Nerves are not visible on the upper lemma due to its indurated structure and the smooth/rugose nature of the surface. However, in this study I have observed surface stripes marking obscure nerves on the upper lemma of *P.longilorum* and *P.viale*.

**4.2.17 Flower**

The flower in *Panicum* consists of a pair of lodicules, three stamens, and a pistil (Fig. 3.I,m).

**4.2.18 Lodicules**

Lodicules are delicate structures lying at the base of the ovary in between the lemma and the palea on the lemma side. They are usually minute and
incospicuous, greenish or colourless. Two is the most common number of lodicules in all grasses including *Panicum*, while three or more are characteristic of bamboos. At anthesis, the lodicules rapidly become turgid and force the lemma and palea apart aiding exsertion of the stamens and pistil emergence. The structure and function of lodicules in grasses have long been investigated by various authors. Arber (1934) interpreted lodicules as representing the inner whorl of the perianth, the outer whorl being absent. Stebbins (1956) recognised and illustrated four lodicule types. They are 1) Festucoid, 2) Chloridoid, 3) Panicoid, and 4) Bambusoid. The Panicoid type of lodicules tend to be short, truncate, thick, and extensively vascularised (Gould & Shaw 1983). Hsu (1965) recognised two types of lodicules in Paniceae. The first type is non-plicate as found in genera such as *Digitaria*, *Pennisetum*, *Stenotaphrum* and some others. The second type is plicate as found in *Panicum* and other genera including *Setaria*, *Oplismenus*, and *Pseudoecrinolaena*.

Lodicules provide useful characters for taxonomic purposes in the revised species, but some difficulty results from the fact that they are minute and inconspicuous, and tightly enclosed by the upper lemma and palea. It is hard to manipulate the spikelets for the assessment of lodicule characters. Detailed examination of lodicules usually needs 50 times magnification. I have detected two types of lodicules in the materials studied. The first type is papery and multiple-nerved, and the second type is very thin and obscurely nerved. In general, papery, multiple-nerved lodicules (Fig. 11,a,b) are found in the species of the subgenus Panicum, and thin, obscurely 3-nerved lodicules (Fig. 11,e,f) are found in the species of the subgenus Phanopyrum. Species of the subgenera Agrostoides and Megathyrsus are found to have thin and 5-nerved lodicules (Fig. 11,c,d). However, in some species, the distinction between papery or thin
Fig. 11 Types of lodicules identified in this study (All x 45)

Papery and multiple-nerved

a. P. trachyrhachis
b. P. paludosum

Thin and 5-nerved

c. P. maximum
d. P. plenum

Obscurely 3-nerved

e. P. sarmentosum
f. P. brevifolium
nature of the two types could not be clearly determined, as in, *P.incisum*, *P.palanum*, *P.fischerti*. In *P.schinzi* and *P.repens*, though the lodicules are papery, no veins could be seen.

4.2.19 Stamens

The stamen consists of a long filament supporting a versatile anther. Although the stamens may number more or fewer than three in grasses, it is always three in *Panicum* (Fig. 3.c,l). The uniformity in structure and number of stamens in the materials studied provided little of diagnostic importance in this study.

4.2.20 Gynoecium

The gynoecium consists of a single pistil bearing at the top of the ovary two styles - each one terminating in a feathery stigma (Fig. 3.c,l). These feathery stigmas are well adapted for catching wind-borne pollen-grains. Hsu (1965) observed that the style base may be free or united. He noted a united style base in some genera of Paniceae viz. *Hymenachne*, *Trichachne*, *Trachys*, *Zygochloa*. In *Panicum* and genera like *Echinochloa*, *Eriochloa*, *Melinis*, *Paspalum* and some others, the style base is free. Styles and stigmas were found to exhibit little variation as far as the species examined and provided no characters of useful taxonomic significance in this study.

4.2.21 Caryopsis

In *Panicum*, the caryopsis (Fig. 3.n,o) is dorsiventrally compressed and free within the firmly closed lemma and palea. The embryo can be seen at the base as an oval depression on the side of the caryopsis next to the lemma. The depression is usually one-third to half of the length of the caryopsis in
the species revised. On the other side of the embryo, there is the hilum which is a scar or dot that marks the point of attachment of the seed to the ovary wall. The hilum is distinctive in the different kinds of grasses. In the materials studied the hilum is punctiform with the dot rounded to oval. This is the commonest kind of hilum found in the genus *Panicum*. 
CHAPTER 5: ANATOMICAL INVESTIGATION OF THE LEAF BLADE

5.1 Materials and Methods

Leaf blades from herbarium specimens were used for anatomical investigations. To check for any differences from living material, leaves of fresh specimens were examined in species for which seeds were available and could hence be grown in the greenhouse. Herbarium materials gave good results technically adequate for anatomical studies but better quality sections were more easily obtained from fresh green leaves. With permission to remove samples, materials used were from the herbarium of the Royal Botanic Garden, Edinburgh (E) or were procured on loan from the herbaria of Kew (K) and the British Museum (BM), London, and Rijksherbarium, Leiden (L).

The selection of blades has always been made following a standard procedure. The second or third leaf from the flag leaf was selected and segments of blades were taken at approximately the middle of its length. However, for comparative purposes, the flag leaf was also examined, and segments from areas below and above the central part of the blade were also investigated in many species. In the samples studied with flag leaves, anatomical structures were found to be similar with the second or third leaf. But sections taken at levels below, at, and above the central part of the blade showed variation in the shape, structure and projection of the keel. In selecting specimens, care has always been given to check the condition of the material. As far as materials allowed, green leaves from recent collections, free from cracks, folds, abrasions, or any obvious fungal damage, were used after scrutinising a great number of specimens.

Transverse sections were taken according to Johansen's wax method (1940).
However, I employed modified versions of procedures at many steps including developing my own device for cutting sections with the microtome. In the treatment of material for desilicification, basically Metcalfe's method (1960) was utilised, but I had to adopt different treatments especially for thin-leaved plants grown in shaded places.

5.1.1 Preparation

Two to three segments, each 5mm long, from individual leaf blades were cut by one incision with a sharp razor blade. The dried material was gently boiled in water until it reverted to something like its natural shape and turgidity. The duration of boiling varied from 15 minutes to nearly an hour depending on the material. By gentle use of a soft camel hair brush, the boiled segments were cleaned to remove any remaining dirt. They were placed in F.A.A. solution in 20ml vials for at least 24 hours (Metcalfe 1960). Each leaf segment vial was identified by an attached species-name label. The vials were capped and stored in aluminium racks, until the rinsing stage began.

F.A.A. SOLUTION

<table>
<thead>
<tr>
<th></th>
<th>Quantity</th>
</tr>
</thead>
<tbody>
<tr>
<td>70% Alcohol</td>
<td>90ml</td>
</tr>
<tr>
<td>Glacial Acetic acid</td>
<td>5ml</td>
</tr>
<tr>
<td>40% Formaldehyde</td>
<td>5ml</td>
</tr>
</tbody>
</table>

5.1.2 Rinsing

The pieces were taken out from the vial and washed in cold water in small conical flasks for 15 minutes, with occasional shaking by hand. Several changes of water were made to remove the F.A.A.
5.1.3 Desilification

Silica bodies present on epidermal cells of grasses are very hard. They offer great resistance to the knife edge when sectioning and cause superficial damage or tearing of the epidermis and other tissues. Therefore it is essential to remove the silica before sectioning if really good results are to be obtained. To remove the silica bodies, hydrofluoric acid, in which the substance is soluble, was used.

Hydrofluoric acid (HF) is a highly corrosive substance which can cause serious damage to the skin and eyes, causing severe and painful burns. Vapours from gaseous HF can damage respiratory systems. Due to the experimental hazards involved, every precautionary measure was taken while working with hydrofluoric acid. All treatments with HF were carried out in a fume cupboard using goggles and rubber gloves. As a first treatment, hydrofluoric acid burn jelly (Calcium gluconate antidote gel) was kept available all the time. Any acid that was spilled was neutralised with slaked lime and the area was immediately hosed with water.

Segments of blades were placed in 50ml plastic vials in a fume cupboard. The identification number of the segments was written on outside of the vial. The leaf pieces were covered with 15–20% solution of Hydrofluoric acid (approx. 20ml) and left for 24–36 hours. Thin leaves, of species from shady places, were treated with a lower HF concentration (10%) and left to soak for a shorter time (approx. 16–20 hours). The hydrofluoric acid used could be reused several times if the containers were kept tightly shut.
5.1.4 Rinsing

Segments were taken out carefully with the aid of a camel hair brush avoiding immersing the metal ring of it in the hydrofluoric acid and placed in a plastic petri dish perforated with numerous holes small enough not to allow the pieces to come out. Both parts of the dish were perforated. The petri dish was enclosed in a small package made up of porous nylon stocking. The mouth of this nylon sack was clipped tight and a small identification card was attached. Nylon sacks containing petri dishes were placed in a large plastic bowl and washed in running tap water, in a sink, for 5 hours. This was to remove hydrofluoric acid completely from the plant tissues.

5.1.5 Dehydration

Dehydration was effected by putting the desilicified material through the following alcohol series to remove water from the tissues.

<table>
<thead>
<tr>
<th>Alcohol Type</th>
<th>Duration</th>
</tr>
</thead>
<tbody>
<tr>
<td>10% alcohol</td>
<td>1 1/2 hours</td>
</tr>
<tr>
<td>20% alcohol</td>
<td>1 1/2 hours</td>
</tr>
<tr>
<td>30% alcohol</td>
<td>1 1/2 hours</td>
</tr>
<tr>
<td>50% alcohol</td>
<td>1 1/2 hours</td>
</tr>
<tr>
<td>70% alcohol</td>
<td>2 hours</td>
</tr>
<tr>
<td>Johansen solution 1</td>
<td>2 hours</td>
</tr>
<tr>
<td>Johansen solution 2</td>
<td>2 hours</td>
</tr>
<tr>
<td>Johansen solution 3</td>
<td>2 hours</td>
</tr>
<tr>
<td>Johansen solution 4</td>
<td>2 hours</td>
</tr>
<tr>
<td>Johansen solution 5</td>
<td>2 hours</td>
</tr>
</tbody>
</table>
| Tertiarybutylalcohol (TBA) (2-methyl-propan 2-ol) | 2 hours: followed by 2
changes – one overnight. Stages in the Johansen solutions, and in TBA took place in a vacuum embedder.

It should be pointed out here that specimens were left overnight, as and when required, in any of the above and the following infiltration stages, and started the next series in the following morning. There was found to be no harm in leaving specimens in one of the dehydration and/or infiltration series for a much longer duration than that indicated above as the norm.

**JOHANSEN SOLUTION**

<table>
<thead>
<tr>
<th>Soln.</th>
<th>Distilled water</th>
<th>95% ethyl alcohol</th>
<th>Tertiary butyl alcohol</th>
<th>100% ethyl alcohol</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>50 ml</td>
<td>40 ml</td>
<td>10 ml</td>
<td>-</td>
</tr>
<tr>
<td>2</td>
<td>30 ml</td>
<td>50 ml</td>
<td>20 ml</td>
<td>-</td>
</tr>
<tr>
<td>3</td>
<td>15 ml</td>
<td>50 ml</td>
<td>35 ml</td>
<td>-</td>
</tr>
<tr>
<td>4</td>
<td>-</td>
<td>45 ml</td>
<td>55 ml</td>
<td>-</td>
</tr>
<tr>
<td>5</td>
<td>-</td>
<td>-</td>
<td>75 ml</td>
<td>25 ml</td>
</tr>
</tbody>
</table>

**5.1.6 Infiltration**

Water having been removed from the tissue, the next step was that of infiltration. Methods of infiltration and the following step of embedding the material more or less followed Johansen’s procedure (1940). But I have found that keeping the material in the mixture of paraffin oil and TBA, following the previous step in TBA, for a period of 6 hours instead of 1 hour gives much better results. The folder paper tray of Johansen for embedding the material was found to be much more useful and convenient than brass embedding frames. It displays a clearer view of the embedding surface and allows several or many items for embedding to be manipulated more accurately, quickly and efficiently.
5.1.7 Sectioning

Blocks ready, the next step is cutting sections. It was experienced that sections cut at once after blocking gave better results. Rotary microtomes (Automatic Rotary Microtome: R. & J. Beck Ltd., England) were used for cutting sections. I devised a holder to use safety razor blades instead of depending upon knives in common use. The holder had to be inclined at 16° on the microtome scale which allowed best vertical angle of the blade to give ample clearance. Agar Aids T5016 heavy duty, single-edge, carbon steel razor blades were used for cutting sections. More than half of the blade-edge could be used, and usually one blade was enough for cutting one block if the cut surface of the specimen was not more than 5mm long. Sections were cut at thicknesses of 10-15um but best sections were obtained at 15um. Ribbons were cut more or less 10cm long and were examined under a dissecting microscope. The best sections were cut away with a blade, and the remainder were discarded.

5.1.8 Mounting Ribbons

Mounting ribbons on the slide was done in the simple, standard way. Two drops of water were placed on a slide thinly smeared with egg albumen adhesive. A small piece of ribbon, consisting of a few sections only was gently placed on the water-drops by means of a scalpel and a needle. The slide was put on a warming plate heated at 40-45°C. A few more drops of water were added so that the sections floated freely. As the water warmed up, the ribbons flattened out, and the wrinkles in the paraffin disappeared. At this stage, the slide was slowly taken off the warming plate, then hand-held for about 30 seconds to allow the water to cool down. The excess water was drained off.
the slide and the sections were positioned with the help of a needle. The slide was put back on the warming plate for a few minutes to dry out any trace of water, and then left in a safe, dust-free place to dry overnight. It was then ready for dewaxing. At this final stage, after returning the slide to the warming plate, usually a quick modified technique was adopted. The slide was allowed to stay on the warming plate in the same heat for a longer time until the wax melted, - the last melting state being indicated by the disappearance of the last bubble of wax. Slowly and horizontally, the slide was lifted from the warming plate and left to cool. It was then ready in quarter of an hour for dewaxing.

5.1.9 De-Waxing

Slides were removed from the stored place and taken through the following series of solutions prepared in staining jars containing racks to hold slides. The time limits are only indications in this as well as in the following staining series.

1. Xylene 15 min
2. Xylene 15 min
3. Xylene + absolute alcohol (1:1) 10 min
4. Absolute alcohol 10 min
5. Absolute alcohol 10 min

After the last de-waxing step, slides were transferred to safranin and left overnight.
5.1.10 Staining

The steps in staining follow on from the de-waxing series.

<table>
<thead>
<tr>
<th>Step</th>
<th>Time</th>
</tr>
</thead>
<tbody>
<tr>
<td>6. Safranin</td>
<td>12 hrs</td>
</tr>
<tr>
<td>7. Methylated Spirit</td>
<td>5 min</td>
</tr>
<tr>
<td>8. Absolute alcohol</td>
<td>10 min</td>
</tr>
<tr>
<td>9. Absolute alcohol</td>
<td>10 min</td>
</tr>
<tr>
<td>10. Fast green</td>
<td>5–20 secs (variable)*</td>
</tr>
<tr>
<td>11. Absolute alcohol</td>
<td>10 secs</td>
</tr>
<tr>
<td>12. Absolute alcohol</td>
<td>10 secs</td>
</tr>
<tr>
<td>13. Absolute alcohol</td>
<td>5 secs</td>
</tr>
</tbody>
</table>

* Variable with the thickness of the sections. Thinner sections usually stained in a shorter time than the thicker ones. Often trials with shorter or longer duration were required to determine the best staining. Preparation of fast green with exact proportions of the ingredients followed by a long stirring time was essential. Use of the solution after several days of 'ageing' was very important.

**SAFRANIN**

To make 100ml: Dissolve 1g of Safranin 0 in 48ml Aniline H₂O plus 52ml Methylated Spirit.

Aniline Water - Add 8.5ml Aniline (fresh) to 500ml distilled water at -70°C in a fume cupboard. Mix well to effect solution. Allow to cool to room temperature, then filter.

**FAST GREEN**
Dissolve 0.5% Fast Green F.C.F in a mixture of equal parts of Cellosolve (2-methoxyethanol), absolute ethanol, and oil of cloves. Stir for ten hours.

5.1.11 Mounting

The slides were removed from the absolute alcohol, the excess alcohol was allowed to drip off. The sections were mounted in Euparal and covered with Chance cover slips. The slides were kept on the warming plate for at least 2 days at 45°C.

5.1.12 Cleaning Slides

After the mounting medium was completely dry, the excess medium that had oozed out from the cover slips was scraped away with a scalpel. The powdery substance left around the coverslip was cleaned with a tissue soaked in absolute alcohol.

5.2 Enumeration and Evaluation of Characters Observed

5.2.1 Introduction

Various authors have long recognised that anatomical structures of the grass leaf blade can provide taxonomic information of much value to the classification of Gramineae. Today, it is generally accepted that anatomical details of grass leaf blade, when used in conjunction with other characters, can contribute much data towards a more natural arrangement of grass taxa.

Duval-Jouve (1875) was the first to use leaf anatomical characters in grass systematics. He reported that there are two basic, contrasting types of leaf
anatomy in grasses. Avdulov (1931) successfully utilized these two types in the systematics of the family. According to Brown (1958), these two types are characterized as: 1) in type one the vascular bundle has a thick-walled mestome sheath, a reduced parenchyma sheath, and irregularly arranged chlorenchyma cells as found in e.g. Festuceae, Aveneae, 2) in type two the vascular bundle has parenchyma cells enlarged and the chlorenchyma cells more or less radially arranged as found in e.g. Paniceae, Andropogoneae. Prat (1936) called the first type Festucoid and the second type as Panicoid. To these basic types, Stebbins (1956) added "Bambusiod" and "Chloridoid". Brown (1958) added two further types viz. "Aristidoid" and "Arundinoid". In the first state of the basic two types there are no specialised cells containing chloroplasts around the vascular bundles and is now referred to as non-Kranz, an anatomical type now associated with C₃ photosynthesis. The second state of the basic two types has specialised cells containing chloroplasts surrounding the vascular bundles and is now referred to as Kranz—an anatomical type now associated with C₄ photosynthesis. In German "Kranz" means a ring or wreath, the term was obviously applied to denote the marked parenchyma sheath around the vascular bundle (see Brown 1977, Haberlandt 1884). Kranz species exhibit different anatomical, physiological and biochemical characteristics from non Kranz species. The totality of the different character states as exhibited by the Kranz species is known as the Kranz Syndrome (Brown 1977). Further discussion of this will be found under "vascular bundle sheath", later in this chapter.

Kranz species are said to exhibit C₄-photosynthesis because the first-formed product is a 4-carbon molecule dicarboxylic acid (oxaloacetic acid). In these species, the mesophyll cells form the outer compartment in which the photosynthetic CO₂ is incorporated by phosphoenolpyruvate carboxylase into
Oxaloacetate. The oxaloacetate is converted to either malate or aspartate and the product is then translocated to the Kranz sheath cells, which form the inner compartment, where it is decarboxylated (Ellis 1977). Subsequently, the released CO\(_2\) is assimilated by ribulose biphosphate carboxylase in the chloroplasts of the bundle sheath - the inner compartment. C\(_4\)-photosynthesis occurs in twelve Kranz families (Brown 1977) including some dicotyledons. In the non-Kranz or C\(_3\)-species, the photosynthetic CO\(_2\) is fixed and assimilated in the mesophyll cells through the Calvin cycle. The first-formed product is a 3-carbon molecule, 3-phosphoglycerate and hence plants which exhibit this photosynthesis are commonly called C\(_3\) plants. In C\(_3\) plants, there is no division of function between the mesophyll cells and bundle sheath-cells, even if the latter contain chloroplasts because here the sheath chloroplasts are unspecialised or non-Kranz unlike the Kranz C\(_4\) plants.

The publication of 'Anatomy of the Monocotyledons I Gramineae' by C. R. Metcalfe (1960) provided an enormous contribution to the understanding of grass anatomy. He introduced wide use of definitions and descriptions in anatomical structures. Ellis (1976, 1979) has made a useful contribution by attempting to standardize and stabilise grass anatomical terminology so far employed by all previous authors. More recently, Stace (1984) has discussed the general importance of application of leaf surface characters in plant taxonomy.

In the present study, I have investigated the leaf anatomy, as revealed in transverse section, for all the Indian subcontinental and Southeast Asiatic species of Panicum. The results, taken together in combination with morphology and micromorphology, made it possible to associate species with recognised subgenera and sections including three new sections proposed in this study (see Chapter 8).
5.2.2 Outline of the lamina in transverse section

The shape in transverse section of the lamina is usually determined by whether the lamina is flat or infolded. The blade is always open and flat in the species revised. Some of them may exhibit some infolding or inrolling under conditions of water stress, but are not permanently infolded to any degree so that the internal structure is altered. The degree of infolding or inrolling in grass leaves varies with the environmental conditions and hence is not of much taxonomic value (Metcalfe 1960).

Two major types of lamina outline in transverse section have been recognised in the revised species. It can be described as expanded or flattened when, ignoring the ribs and furrows, a straight line would connect both margins and the midrib or keel. A flat lamina may be undulating gently (Figs. 12.b; 14.b) e.g. *P.atrosanguineum, P.sarmentosum, P.amoeum, P.smithii, P.brevifolium* or it may be undulating deeply with the waves 1) rounded to obtuse (Figs. 13.d; 14.c; 15.b) e.g. (*P.humidorum, P.trypheron, P.plenum, P.miliaceum, P.cambogiense, P.luzonense, hayatae, P.viale, 2) corrugated or pleated (Fig. 12.c) e.g. *P.repens, P.turgidum, P.virgatum, 3) flat-topped i.e. apex flattened (Fig. 13.c) e.g. P.capillara. Alternatively, the outline of the lamina may be V-shaped, when the two lateral halves of the lamina fold toward each other adaxially forming a definite angle with the midrib or keel. The shape of the V varies according to the angle formed by the two arms of the lamina at the midrib. In the revised species, it is commonly a wide very open V with an almost 180° angle, but the presence of the projecting keel gives appearance of V-shape (Fig. 12.d) as in *P.miliaceum, P.sumatrense subsp. sumatrense, P.cambogiense, P.seminudum, P.longiloreum, P.schinzi* and *P.trachyrachis.*
5.2.3 Adaxial and abaxial ribs and furrows

Ribs and furrows commonly occur on the adaxial but sometimes also on the abaxial surface of the leaf blade in the species revised. Ribs are usually more developed in association with the larger vascular bundles, and where there is a rib there is a corresponding furrow. The depth of furrows is variable from shallow to deep correlating with the height of ribs. When present, ribs and furrows are variable in height or depth, spacing and location between different species, but they have been found to be fairly consistent in individual species. Accordingly, this character can be used diagnostically at the species level.

There are species in which no ribs and furrows are present with the lamina surface straight or very slightly undulating (Figs. 12.a,b; 13.b; 14.b). For example, *P. maximum*, *P. atrosanguineum*, *P. paianum*, *P. sarmentosum*, *P. amoenum*, *P. smithii*. The adaxial ribs may be 1) rounded, obtuse i.e. the apex is rounded (Figs. 12.d; 13.d; 14.c) e.g. *P. longiloreum*, *P. trachyrhachis*, *P. hayatae*, *P. paludosum*, *P. miliaceum*, *P. cambogiae*, *P. humidorum*, *P. coloratum*, *P. trypheron*, *P. hippothrix*, 2) flat-topped, the ribs being more or less square shaped with the apex flattened (Fig. 13.c) e.g. *P. capillare*, 3) triangular, in which the apex is more or less pointed (Fig. 12.c) e.g. *P. repens*, *P. turgidum*. There is no abaxial rib development in majority of the species, but in some definite ribs are present on the abaxial surface. Abaxial ribs may be 1) in the form of slight undulations associated with the vascular bundles (Fig. 13.a,b) e.g. *P. trachyrhachis*, *P. brevifolium*, *P. maximum*, *P. walensia*, *P. repens*, 2) smaller than adaxial ribs (Figs. 12.d; 14.c,d) e.g. *P. miliaceum*, *P. trypheron*, *P. virgatum*, *P. longiloreum*, *P. paludosum*, *P. schinzii*, *P. viala*, *P. fischeri*, *P. antidotala*, 3) same size as adaxial ribs giving a 'moniliform' appearance in section (Figs. 13.c; 15.b) e.g. *P. hippothrix*, *P. capillare*, *P. luzonense*, *P. elegantissimum*. Ribs were found usually to be distributed in association with vascular bundles of all orders. In
P. plenum regular ribs are present over all first-order bundles but there is no regular association of ribs over third order bundles (Fig. 14.a,d). Vascular bundles of second order were not detected in the species revised, and hence no corresponding ribs were recognised over them.

5.2.4 Vascular bundles

There are three orders or ranks of vascular bundles in the Gramineae. They differ in size and structure. The three orders of vascular bundles are not always distinct because of the occurrence of intermediate types sometimes. The first order or basic type of vascular bundles are those in which there are large metaxylem vessels present on either side of protoxylem elements (Figs. 15.c; 16.a), and a lysigenous cavity is commonly present. The sclerenchyma is associated as girders or strands with the first order bundles. Second-order vascular bundles are characterized by easily distinguishable xylem and phloem but without any large metaxylem vessels or lysigenous cavities. These bundles are often of similar size to the first-order bundles, and the sclerenchyma arrangement is also usually the same. Third-order vascular bundles are usually very small with metaxylem vessels always lacking, and the xylem and phloem almost indistinguishable (Figs. 15.c; 18.a,b,c; 19.a) consisting of only a few lignified cells together with a few phloem elements. Sclerenchyma is either absent or there may be strands of a few fibres only.

Number

The number of vascular bundles in the lamina was found to be inconsistent, because the number varied with the width of the leaf. For this reason, there is little taxonomic importance in this character. In a count of the total number of first-order vascular bundles in the lamina of the revised species, the following
observations were made. There may be 7 (e.g. *P.atrosanguineum*, *P.gardneri*, *P.walense*, *P.turgidum*) or 9 (e.g. *P.cambogiense*, *P.coloratum*, *P.miliaceum*, *P.paludosum*, *P.bisulcatum*, *P.brevifolium*, *P.humidorum*) or 11 (e.g. *P.sumatrense*, *P.trypheron*, *P.antidotale*) or 13 (e.g. *P.capillare*, *P.virgatum*, *P.incisum*, *P.hipothrix*, *P.auritum*) or 15 (e.g. *P.incomtum*, *P.notatum*) or 17 (e.g. *P.sarmenosum*). The number was observed to be variable within the species in leaves of different width. This character therefore cannot be reliably used in taxonomy.

Arrangement

The arrangement of the vascular bundles in the lamina of the species in this study is fairly uniform. They are centrally positioned in the vertical dimension of the section (Figs. 12, 13, 14, 15.b). In *P.bisulcatum*, however, the third-order bundles are central but the first-order bundles are displaced abaxially in the ribs (Fig. 15.a). There is considerable variation in the arrangement of vascular bundles in the keel or midrib which can be usefully employed in distinguishing species. The common position of bundles in those keels which consist of more than one bundle is always abaxial (Figs. 12.c,d; 13.b,c; 14.a,d) as in *P.antidotale*, *P.plenum*, *P.maximum*, *P.miliaceum*, *P.hipothrix*, *P.repens*, *P.cambogiense*, *P.capillare*, *P.walense*. But in those species in which a single vascular bundle constitutes the keel, the bundle may occupy a central position (Fig. 13.a) (e.g. *P.brevifolium*, *P.hayatae*, *P.amoenum*, *P.smithii*, *P.elegantissimum*), or may be displaced towards the abaxial epidermis (Figs. 12.b; 13.d) (e.g. *P.auritum*, *P.longiloreum*, *P.schinzi*, *P.sarmenosum*, *P.fischeri*, *P.virgatum*, *P.humidorum*).
5.2.5 Vascular bundle sheaths

From the taxonomic as well as comparative anatomical point of view, vascular bundle sheaths are of utmost importance in the Gramineae. One or two single-layered bundle sheaths surround the vascular bundles either completely or partly. In general, single sheaths are characteristic of the Panicoid and double sheaths of the Festucoid grasses (Metcalfe 1960). The structural variations in the anatomy of bundle sheath are very important in providing a tangible indication of important physiological and biochemical differences in the Gramineae. In general, all these structural variations of the bundle sheaths occur in *Panicum*, including the material revised in this study. Observations on the different anatomical types, based on bundle sheath characters, are described here.

5.2.6 Non-Kranz anatomy

All, or only the first-order vascular bundles, are surrounded by two double bundle sheaths in which a) the cells of the inner or mestome sheath are thick walled and lack chloroplasts, and b) the cells of the outer parenchyma sheath are either completely free of chloroplasts (Fig. 16.a) (or perhaps possess a few chloroplasts in them resembling typical mesophyll cells). The mesophyll cells are usually irregularly arranged (Fig. 19.b). Species with this type of bundle sheath characters are called non-Kranz (n-K) or C₃ species because this anatomical condition is correlated with C₃ photosynthesis, there being no specialised Kranz tissue in the bundle sheath (Brown 1977). Fixation of CO₂ and subsequent decarboxylation occurs in both mesophyll and other bundle sheath cells (if they have any chloroplasts), but there is no compartmentalisation of the reactions between the mesophyll and bundle
Fig. 12 Transverse sections of leaf blade of *Panicum* (Diagrammatic)

(See Fig. 15.c for details of illustration)

a. *P. paianum* (x 30)
b. *P. sarmentosum* (x15)
c. *P. repens* (x30)
d. *P. miliaceum* (x20)

**List of abbreviations**

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
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<tbody>
<tr>
<td>Bull.</td>
<td>Bulliform cells</td>
</tr>
<tr>
<td>K.b.</td>
<td>Keel bundle</td>
</tr>
<tr>
<td>Mac.</td>
<td>Macrohair</td>
</tr>
<tr>
<td>Mes.</td>
<td>Mesophyll</td>
</tr>
<tr>
<td>Pap.</td>
<td>Papillae</td>
</tr>
<tr>
<td>Prick.</td>
<td>Prickle</td>
</tr>
<tr>
<td>Scl.</td>
<td>Sclerenchyma</td>
</tr>
<tr>
<td>1 v.b.</td>
<td>First order vascular bundle</td>
</tr>
<tr>
<td>3 v.b.</td>
<td>Third order vascular bundle</td>
</tr>
</tbody>
</table>
FIG. 12

Fig. 13 Transverse sections of leaf blade of *Panicum* (Diagrammatic)

a. *P. brevifolium* (x9)

b. *P. maximum* (x15)

c. *P. capillare* (x13)

d. *P. humidorum* (x13)
FIG. 13
Fig. 14 Transverse sections of leaf blade of *Panicum* (Diagrammatic)

a. *P. plenum* (x30)
b. *P. amoenum* (x15)
c. *P. trypheron* (x30)
d. *P. antidotale* (x30)
Fig. 15

Transverse sections of leaf blade of Panicum (Diagrammatic)

a. P. bisulcatum (x15)
b. P. luzonense (x20)

c. P. virgatum: Transverse section of leaf blade showing anatomical details

List of abbreviations

Ab.ep. Abaxial epidermis
Ad.ep. Adaxial epidermis
Bull. Bulliform cells
Chl. Chlorenchyma
Cut. Cuticle
l.S. Inner sheath
Met. Metaxylem
O.S. Outer sheath
Ph. Phloem
Prot. Protoxylem
Scl. Sclerenchyma
St. Stomata
1 v.b. First order vascular bundle
3 v.b. Third order vascular bundle
Fig. 16  Transverse section of leaf blade

a. *P. brevifolium*: Double sheath with the outer sheath devoid of chloroplasts (characteristics of non-Kranz anatomy; for definition of terms, see Chapter 5.2)

b. *P. brevifolium*: Uniseriate extension of the bundle sheath

c. *P. hayatae*: Uniseriate extension of the bundle sheath
Fig. 17 Transverse section of leaf blade

a. P. antidotale: Single bundle sheath containing chloroplasts, no intervening cells present between the metaxylem and the sheath cells (characteristics of Kranz M.S. anatomy)

b. P. miliaceum: Double bundle sheath with the outer sheath containing centripetal chloroplasts, chlorenchyma more or less radially arranged (characteristic of Kranz P.S. NAD-me anatomy). (Note sunken base of macrohair, and bulliform cells raised above the surface)

c. P. miliaceum: Centripetal chloroplasts in a third order bundle (Note uniform arrangement of Kranz sheath cells)
Fig. 18  Transverse section of leaf blade

a. **P. maximum:** Double bundle sheath with the outer sheath containing centrifugal chloroplast. (Characteristic of Kranz P.S. PEP-ck anatomy). (Note irregular arrangement of Kranz sheath cells)

b. **P. maximum:** Uneven Kranz sheath of a third order bundle (Note short intervascular distance, radial arrangement of chlorenchyma cells)

c. **P. maximum:** Kranz sheath cells in the form of a 'cross' in a third order bundle

d. **P. mindanaense:** Kranz sheath cells in the form a 'cross' in a third order bundle
FIG. 18
Fig. 19 Transverse section of leaf blade

a. *P. walense*: More or less rounded Kranz sheath cells; Kranz chloroplasts spread mostly towards the outer wall

b. *P. brevifolium*: Chiorenychyma irregularly arranged. (Note long intervascular distance; characteristics of non-Kranz anatomy)

c. *P. trachyrhachis*: Elongated adaxial papillae
sheath cells as in \( C_4 \) species (Ellis 1977). Examples include \textit{Poöideae} (Festucoideae), \textit{Bambusoideae}, \textit{Paniceae} in part, \textit{Panicum} in part, and nearly all \textit{Arundinoideae}.

In \textit{Panicum}, the subgenus Phanopyrum is classified partly on the possession of non-Kranz anatomy. All the non-Kranz species revised in this study belong to this subgenus. Different characteristics of the outer bundle sheath have been found to be of taxonomic usefulness in distinguishing species and sections in the species here revised. For example, bundle sheaths having adaxial and abaxial extensions are characteristics of the sections \textit{Hayata} (\textit{P.hayatae}) (Fig. 16.c) and \textit{Parvifolia} (\textit{P.brevifolium}) (Fig. 16.b). Further, the walls of extension cells of \textit{P.hayatae} are much thicker than those of \textit{P.brevifolium}. The outer sheath may completely or incompletely surround the vascular bundle. It completely surrounds the vascular bundle (Figs. 13.a,d; 16.a) in e.g. \textit{P.hayatae}, \textit{P.brevifolium}, \textit{P.humidorum}. In the commoner case, the bundle sheath is incomplete on the abaxial side, being interrupted by sclerenchyma girders, but complete on the adaxial side (Fig. 15.a) (e.g. \textit{P.auritum}, \textit{P.bisulcatum}, \textit{P.notatum}).

In certain species, the sheath may be interrupted on both sides of the bundle by sclerenchyma girders, as in \textit{P.sarmentosum}.

The inner mesomte sheath remains more or less uniform and hence is not taxonomically very useful, at least in the materials included in this revision.

5.2.7 Kranz anatomy (see Tables 5 & 6)

A single or double bundle sheath surrounds the vascular bundles, in which the cells of the single sheath, or cells of the outer sheath of the double sheath are enlarged and inflated with thicker walls than the mesophyll cells. The cells of the single, or of the outer of the two sheaths, contain Kranz or specialised
chloroplasts distinct from those of mesophyll cells. The mesophyll cells are distinctly or indistinctly radiate. Species having this type of anatomy are Kranz (K) or C₄ species, this anatomical syndrome being correlated with C₄ photosynthesis (Brown 1977). During photosynthesis, C₄ acids are formed in the mesophyll and decarboxylation of these acids occurs in the Kranz sheath cells (Ellis 1977). The Kranz sheath is therefore also known as a PCR (Photosynthetic Carbon Reduction) bundle sheath (Hattersley and Watson 1976). The inner mestome sheath lacks chloroplasts, and its cells have very

**TABLE 5** The following table summarises the leaf anatomical variations associated with different photosynthetic mechanisms.

<table>
<thead>
<tr>
<th>Kranz Syndrome</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-Kranz or C₃</td>
</tr>
<tr>
<td>(Species without any Kranz chloroplasts in the bundle sheath)</td>
</tr>
<tr>
<td>Kranz P.S.</td>
</tr>
<tr>
<td>(with Kranz Parenchyma Sheath)</td>
</tr>
<tr>
<td>Parenchyma Sheath with centrifugal chloroplasts</td>
</tr>
<tr>
<td>PEP-ck species</td>
</tr>
<tr>
<td>Kranz or C₄</td>
</tr>
<tr>
<td>(Species with Kranz chloroplasts in the bundle sheath)</td>
</tr>
<tr>
<td>Kranz M.S.</td>
</tr>
<tr>
<td>(with Kranz Mestome Sheath)</td>
</tr>
<tr>
<td>Parenchyma Sheath with centripetal chloroplasts</td>
</tr>
<tr>
<td>NADP-me species</td>
</tr>
</tbody>
</table>

thick walls. Examples include *Chloridoideae, Andropogoneae, Paniceae* in part, *Panicum* in part.
TABLE 6 Summary of diagnostic features in leaf-blade transverse section used to indicate the different anatomical types for the *Panicum* species revised in this study

<table>
<thead>
<tr>
<th>C₃-type</th>
<th>C₄ MS-type</th>
<th>C₄ PS PEP-ck type</th>
<th>C₄ PS NAD-me type</th>
</tr>
</thead>
<tbody>
<tr>
<td>2. XyMS+</td>
<td>2. XyMS−</td>
<td>2. XyMS+</td>
<td>2. XyMS+</td>
</tr>
<tr>
<td>3. Chloroplasts lacking in the outer parenchyma sheath cells</td>
<td>3. Chloroplasts centrifugal/peripheral i.e. aligned towards the outer periphery in the sheath cells</td>
<td>3. Chloroplasts centrifugal/peripheral in the Kranz sheath cells. Sheath cells much inflated, convex, outline of the cells not uniform in size and shape</td>
<td>3. Chloroplasts centripetal in the Kranz sheath cells. Sheath cells with straight or less inflated outer tangential wall, outline of the cells uniform in size and shape</td>
</tr>
<tr>
<td>5. More than 4 mesophyll cells separate successive vascular bundles</td>
<td>5. 2–3 cells separate successive vascular bundles</td>
<td>5. 3 cells separate successive vascular bundles</td>
<td>5. 2 or 3 cells separate successive vascular bundles</td>
</tr>
</tbody>
</table>
Kranz species may be 1) Kranz M.S., – species with a single 'Kranz Mestome' sheath, and 2) Kranz P.S., – species with an outer Kranz parenchyma sheath, and a well developed inner or mestome sheath. Table 7 provides a grouping of the *Panicum* species of the Indian subcontinent and S.E. Asia, inferred from the anatomy of the leaf blade in transverse section.

5.2.8 Kranz M.S. anatomy (M.S. NADP-me)

C4 or Kranz species with a single sheath containing Kranz chloroplasts around the vascular bundles are referred to as Kranz M.S. The single sheath is considered to have evolved from *mestome sheath* (Brown 1977) and hence the name Kranz M.S. The M.S. species are also known as NADP-me because NADP malic enzyme is the dominant decarboxylase in the Kranz tissue (Brown 1977). An inner mestome sheath or an outer parenchyma sheath is absent in this type of anatomy. Kranz M.S. anatomy is most easily recognised when no cells are present between the metaxylem vessel elements and the laterally adjacent Kranz sheath cells (Fig. 17.a). This condition was termed by Hattersley and Watson (1976) as XyMS−, in contrast with the presence (XyMS+) of cells intervening between metaxylem vessel elements and laterally adjacent chlorenchymatous bundle sheath cells of first order bundles. In Kranz M.S. anatomy, the chloroplasts are located usually in a centrifugal position, and the mesophyll cells are normally indistinctly radially arranged. Examples of M.S. species include *Andropogoneae, Paniceae* in part, *Panicum* in part.

In *Panicum*, Kranz M.S. anatomy characterises the subgenus Agrostoides. Two sections *Antidotalia* (*P.antidotalia*) and *Bulbosa* (*P.plenum*) represent the subgenus from Asia.
TABLE 7  The Panicum species of the Indian subcontinent and S.E. Asia grouped into the categories of the Kranz Syndrome inferred from the anatomy of the leaf blade in transverse section. The number of specimens examined in each species is given.

<table>
<thead>
<tr>
<th>NON-KRANZ</th>
<th>KRAINZ</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kranz sheath absent</td>
<td>Kranz sheath present</td>
</tr>
<tr>
<td>C3 species</td>
<td>C4 species</td>
</tr>
</tbody>
</table>

**Kranz sheath absent**
- **MS** Kranz mestome sheath
- **NADP-me species**

**Kranz sheath present**
- **PS** Kranz parenchyma sheath
- **PCK** Centrifugal chloroplast
- **PEP-ck species**
- **NAD** Centripetal chloroplast
- **NAD-me species**

### Subgenus PHANOPYRUM
- **P. amoenum** 3
- **P. auritum** 3
- **P. bisulcatum** 2
- **P. brevifolium** 3
- **P. gardneri** 2
- **P. hayatae** 2
- **P. humidorum** 3
- **P. incisum** 3
- **P. incomtum** 2
- **P. khasianum** 2
- **P. nutatum** 4
- **P. sarmentosum** 2
- **P. smithii** 3
- **P. trichoides** 2

### Subgenus PANICUM
- **P. antidotale** 4
- **P. plenum** 5
- **P. atrosanguineum** 3
- **P. cambogiiense** 3
- **P. capillare** 3
- **P. caudiglume** 2
- **P. coloratum** 7
- **P. eleganissimum** 2
- **P. fischeri** 2
- **P. hippothrix** 2
- **P. longiloreum** 4
- **P. luzonense** 3
- **P. miliaceum** 4
- **P. mindanaense** 5
- **P. palanum** 3
- **P. paludosum** 2
- **P. repens** 4
- **P. shinzi** 2
- **P. seminudum** 2
- **P. stapfianum** 2
- **P. sumatrense** subsp. sumatrense 3
- **P. sumatrense** subsp. psilopodium 3
- **P. trachyrhachis** 5
- **P. trypheon** 3
- **P. turgidum** 2
- **P. viale** 2
- **P. virgatum** 4
- **P. walense** 5

### Subgenus AGROSTOIDES
- **P. antidotale** 4
- **P. plenum** 5

### Subgenus MEGATHYRSUS
- **P. maximum** 3
5.2.9 Kranz P.S. anatomy

These are Kranz species with double bundle sheaths in which there is an outer parenchymatous Kranz sheath and an inner mestome sheath. The Kranz sheath is considered to have evolved from the normal *parenchyma sheath* (Brown 1977), hence the name Kranz P.S. Anatomically, Kranz P.S. anatomy is recognised when intervening (i.e. a mestome sheath) cells are present between metaxylem vessel elements and the laterally adjacent Kranz parenchyma sheath cells (Fig. 17.b). The chlorenchyma is radially arranged in a single layer surrounding the Kranz sheath.

Kranz P.S. species are of two types: 1) Kranz P.S. with centripetal chloroplasts, 2) Kranz P.S. with centrifugal chloroplasts.

**Kranz P.S. with centripetal chloroplasts (P.S. NAD-me)**

These are Kranz P.S. species with the Kranz chloroplasts centripetally positioned i.e. aligned along inner tangential wall of the parenchyma sheath cells (Ellis 1977, Pendergast and Hattersley 1987, this study). These species are also known as NAD-me, because in this type, NAD-malic enzyme is the dominant decarboxylase in the Kranz tissue, in association with C₄ photosynthesis (Brown 1977). This type can be recognised by 1) the parenchyma sheath cells having a more or less straight or less inflated outer tangential wall, and straight radial walls, 2) all the constituent cells being more or less uniform in size and shape giving the Kranz sheath a compact and regular appearance (Ellis 1977, this study) (Figs. 15.c, 17.b,c; 19.c ). A single layer of radially arranged chlorenchyma cells surround the bundle sheath, the individual cells of this being also more or less uniform in appearance. Examples include, *Chloridoideae* in part, *Paniceae* in part, *Panicum* in part.
Kranz P.S. NAD–me species characterise the subgenus Panicum. All the species in this revision having centripetally positioned Kranz chloroplasts in the parenchyma sheath, and an inner mestome sheath, belong to this subgenus. However, in certain species, there is some deviation from the typical P.S. NAD–me leaf anatomy hitherto recognised in the literature. This is pointed out in the discussion of the subgenus Panicum (see Chapter 8.4) The parenchyma sheath may be 1) complete i.e. completely surrounding the vascular bundle (Figs. 14.c; 15.b) (as in *P.turgidum, P.cambogiense, P.tryphon, P.luzonense, P.stapfianum*) or more commonly 2) abaxially incomplete, being interrupted at the abaxial side by sclerenchyma girders but complete on the adaxial side (Figs. 12.a,c; 13.c) (e.g. *P.repens, P.trachyrhachis, P.maximum, P.longiloreum, P.paludosum, P.schinzi, P.capillare, P.caudiglume, P.coloratum, P.fischieri, P.hippothrix, P.mindanaense, P.palanum, P.saminudum, P.sumatrense, P.viale, P.virgatum, P.walense* or 3) incomplete at both ends, being interrupted by sclerenchyma girders e.g. *P.miliaceum* (Fig. 12.d). The inner mestome sheath was found to be fairly uniform and hence did not afford any taxonomically useful character.

Kranz P.S. with centrifugal chloroplasts (P.S. PEP–ck)

These are Kranz P.S. species in which the Kranz chloroplasts are centrifugally located in the parenchyma sheath (Fig. 18.a,b,c). In this category, PEP-carboxykinase is the dominant decarboxylase in the Kranz tissue (Brown 1977) and hence the constituent members are also known as PEP–ck species. They can be recognised by possessing irregularly shaped chloroplasts near the outer tangential walls of the sheath cells. This is most easily seen in the sheaths of the third-order bundles (Fig. 18.c). The Kranz sheath cells are much inflated, with convex outer walls and curved radial walls which hence appear irregular in appearance in contrast with the regular form of the P.S. NAD–me
Kranz sheath. The sheath is surrounded by a single layer of radially arranged mesophyll cells – the individual cells of which are less uniform in size and shape than those of NAD-me species. Examples include Paniceae genera such as Brachiaria, Urochloa, Erichloa and Panicum in part.

The subgenus Megathyrsus of Panicum is characterized by having Kranz P.S. PEP-ck anatomy. *P. maximum* is the only representative of this from Asia. The Kranz sheath cells of the first-order bundles are much smaller and less inflated in comparison with those of the third-order bundles (Fig. 18.a). Usually 4 but sometimes 5 or 6, cells constitute the sheath of third order bundles. These are very much inflated and arranged in the form of a cross (Fig. 18.c). Very similar third-order bundle sheath – cells with centrifugally positioned Kranz chloroplasts were found in *P. mindanaense* (Fig. 18.d), which species is placed in the subgenus Panicum in this study. *P. walense* is another species of the subgenus Panicum with inflated Kranz sheath cells and peripheral Kranz chloroplasts which are unlike characteristic Kranz sheath cells of the P.S. NAD-me species. Further discussion of these two anomalous species will be found in Chapter 8.4).

The inner mestome sheath in the PEP-ck species is much smaller in size and the walls more heavily thickened than the outer.

### 5.2.10 Keel, midrib or median vascular bundle

The degree of projection of the midrib in an individual leaf varies from base to apex. The shape and size of the keel largely depend on the point at which the section is taken. For comparative purposes, sections were taken at a point halfway between the base and the apex. The keel may represent a keel, or a midrib, or just a median vascular bundle. The definitions and descriptions here
followed are after Ellis (1976). It is a median vascular bundle when one vascular bundle is present in the keel region which is structurally indistinguishable from other first-order vascular bundles and which is not associated with any parenchyma cells. No structurally recognisable midrib is present in this type (Figs. 12.a; 15.b) (e.g. *P.turgidum, P.smithii, P.mindanaense, P.paianum, P.luzonense*). It is a midrib when the median bundle is structurally distinguishable from other first-order bundles in size, shape and in association with sclerenchyma, but is without any associated parenchyma. In such structures, the keel often appears inconspicuous (Fig. 14.c) (e.g. *P.atrosanguineum, P.fischeri, P.paludosum, P.trypheron, P.elegantissimum*), but may be conspicuous with an abaxial projection (Fig. 14.b) (e.g. *P.amoenum, P.virgatum, P.notatum*). A keel is characterized by the presence of parenchyma or bulliform cells associated with the median vascular bundle or bundles. It may consist of one vascular bundle (Figs. 12.b; 13.a,d; 15.a) (e.g. *P.bisulcatum, P.brevifolium, P.gardneri, P.humidorum, P.sarmentosum*) or, more commonly, more than one, often many vascular bundles (Figs. 12.c,d; 13.b,c; 14.a,d) (e.g. *P.antidotale, P.plenum, P.maximum, P.hippothrix, P.cambogiense*). The shape of the keel is taxonomically very useful. It is variously shaped in the species here revised. The keel may be of triangular shape, incorporating more than one large vascular bundle (Fig. 14.a) e.g. *P.plenum*. It is U-shaped (Fig. 15.a) and much thicker than the rest of the lamina (e.g. *P.bisulcatum*). The common type of keel is semi-circular with a round abaxial projection and a flat or slightly invaginated adaxial surface. The semi-circular keel may be very large and prominent comprising at least three large and three small vascular bundles, as in *P.maximum* (Fig. 13.b). Alternatively, one large and two or more adjacent small bundles may comprise a semicircular keel (Figs. 12.d; 13.c), as in *P.miliaceum, P.capillare, P.coloratum, P.longifolium*. In certain species, the keel has a rounded abaxial side and an equally rounded adaxial side (Figs. 12.b; 13.a;
14.b), as in *P.brevifolium, P.amoenum, P.gardneri, P.notatum, P.sarmentosum*. The keel may consist of more than one bundle but not be projected i.e. not really distinct from the leaf outline, as in *P.repens* (Fig. 12.c). I consider the shape of the keel to be taxonomically useful at subgeneric or sectional level. For example, distinctive, semicircular keels consisting of 3–5 large bundles are characteristically found in the subgenus Megathyrsus as in *P.maximum, P.infestum*. In *P.plenum* (section Bulbosa), the keel projects abaxially, and is triangular in section which incorporates three large vascular bundles including the median bundle. Thus section Bulbosa can be distinguished from section *Antidotalia* the keel in the latter species of which is semi-circular with three large bundles.

5.2.11 Sclerenchyma

Sclerenchyma tissue areas are strengthening elements of the leaf blade providing mechanical support. They enable the blade to withstand various strains (wind, frictional stresses, grazing damage) imposed on a grass leaf without undue damage to the thin walled softer cells. Sclerenchyma commonly occurs in the midrib or keel, vascular bundles, and leaf margins. It appears in the transverse section as thick walled fibrous cells which stain red with safranin or blue-green when stained with fast green. Sclerenchyma occurs above and below the vascular bundles in the form of sub-epidermal longitudinal strands or 'girders' following the course of the vascular bundles. It forms a strand when the sclerenchyma is not in contact with but separated by parenchyma or mesophyll from the bundle sheath. It forms a 'girder' when the sclerenchyma is in contact with or interrupts the bundle sheath.

The arrangement and distribution of sclerenchyma as strands or girders, particularly at the midrib or keel regions where it predominantly occurs, can be
used as diagnostic characters at the species level. For example, the sclerenchyma may be associated with the keel abaxially as girders and adaxially as strands below and above either a single vascular bundle (Fig. 12.b) (e.g. \textit{P.incomtum}, \textit{P.sarmentosum}, \textit{P.auritum}, \textit{P.longiloreum}, \textit{P.stapfianum}, \textit{P.virgatum}, \textit{P.viale}) or all the bundles (Figs. 12.d; 13.b,c; 14.a,d) (e.g. \textit{P.antidotale}, \textit{P.millaceum}, \textit{P.maximum}, \textit{P.plenum}, \textit{P.capillare}, \textit{P.coloratum}, \textit{P.hippothrix}, \textit{P.walense}, \textit{P.seminudum}, \textit{P.cambogiense}). In some species, the sclerenchyma is associated as strands on either side of a centrally located solitary bundle (Fig. 13.a), as in the keels of \textit{P.brevifolium}, \textit{P.gardneri} and \textit{P.incisum}. In other species, the sclerenchyma may be present as girders at both abaxial and adaxial sides of the central bundle (Figs. 12.a; 13.d; 14.b,c; 15.b) (e.g. \textit{P.pai/ium}, \textit{P.amoenum}, \textit{P.trypheron}, \textit{P.luzonense}, \textit{P.elegantissimum}, \textit{P.fischeri}, \textit{P.hayatae}, \textit{P.notatum}, \textit{P.humidorum}). The shape of the abaxial girder may be arched following the shape of the abaxial rib. The arch may be as wide as (Fig. 13.d) (e.g. \textit{P.auritum}, \textit{P.humidorum}) or wider than the keel bundle (Figs. 14.b; 15.a) (e.g. \textit{P.amoenum}, \textit{P.bisulcatum}, \textit{P.incomtum}, \textit{P.notatum}). The abaxial girder may be anchor-shaped with abaxial 'flukes', which may be shallow (Figs. 12.d; 13.c) as in (\textit{P.capillare}, \textit{P.incomtum}, \textit{P.atrosanguineum}, \textit{P.fischeri}, \textit{P.millaceum}, \textit{P.hippothrix}, \textit{P.elegantissimum}, \textit{P.stapfianum} or deep (Figs. 12.c; 13.b; 14.a,d) as in \textit{P.maximum}, \textit{P.repens}, \textit{P.coloratum}, \textit{P.caudiglume}, \textit{P.cambogiense}, \textit{P.virgatum}, \textit{P.longiloreum}, \textit{P.plenum}, \textit{P.antidotale}.

5.2.12 Mesophyll

In general, the term mesophyll is applied to the ground tissue that occupies the space between the adaxial and the abaxial epidermis other than the space occupied by the vascular bundles, bundle sheaths and sclerenchyma (Fig. 12.c). The mesophyll consists chiefly of assimilatory chlorenchyma, and is often partly
composed of translucent cells in association with bulliform cells.

The arrangement of chlorenchyma has taxonomic significance. In festucoid grasses, the chlorenchyma is more or less homogeneous - not arranged in any definite pattern in relation to the vascular bundles. In panicoid grasses, it is arranged radially around the vascular bundles. Each bundle thus appears to be situated in the centre of a regular circle or partial circle of chlorenchyma. However, the radiate structure of the chlorenchyma is variable. Some grasses have complete and some incomplete 'rings' of chlorenchyma (Metcalfe 1960).

In the *Panicum* species revised, the majority of the C3 species were found to have irregularly arranged chlorenchyma (Fig.19.b ) with little differentiation between the bundles. In a few species, however, the chlorenchyma cells immediately surrounding the vascular bundles appeared to be partially radially arranged, and in the centre irregularly arranged e.g. in *P.amoenum*, *P.sarmentosum*. I observed more or less radiate chlorenchyma in the C4 *Panicum* species (Figs. 17.b, 18.a), though often the radiate condition appeared less regular.

The number of chlorenchyma cells in between adjacent parenchyma sheaths is an important criterion for determining non-Kranz and Kranz species (Hattersley and Watson 1975, this study). This correlates with the "intervascular interval" of Lommasson (1961) and the "interveinal distance" of Kanai and Kashiwagi (1975). I have employed this criterion to distinguish between non-Kranz C3 and Kranz C4. In the C3 species revised, the number of chlorenchyma cells in between the parenchyma sheaths fall into two groups, 5 or more than 5 (Fig. 19.b), whereas in the C4 species they are mostly 2 - 3 and never more than 4 (Figs. 17.b, 18.a).
5.2.13 Epidermal cells in transverse section

5.2.14 Bulliform Cells

Bulliform cells are large, inflated colourless cells comprising the entire epidermis or more commonly, restricted to a part of it. They may occur on both adaxial and abaxial epidermis but are found most commonly at the bases of adaxial furrows (Fig. 15.d). Bulliform cells are part of the epidermis but differ from the epidermal cells by being markedly larger and inflated. In transverse section they often appear in a fan-like pattern (Figs. 16.c, 18.b), because the median cells of a bulliform 'patch' are usually the largest. They are somewhat wedge-shaped. The function of the bulliform cells has long been understood. The common concept is that the opening and inrolling of the leaves are achieved by changes in turgor pressure of these cells.

Though bulliform cells were found to be of fairly consistent form within a species, they can in some cases vary in size, shape and location. In the present study several types of bulliform cells were identified. They were found to occur on the adaxial surface in a majority of the species. In a few species, e.g. *P.sarmentosum, P.incomtum, P.gardneri*, bulliform cells occur on both adaxial and abaxial epidermis. In the commonest case, bulliform cells are situated in groups at every furrow region on the adaxial surface at the same level with the general epidermal surface. Each cell of the group is inflated, with the outer tangential wall shorter than the inner one and the median cell of the group appreciably larger than the remainder (Figs. 16.c; 18.b,d), as in *P.cambogiense, P.coloratum, P.elegantissimum, P.fischeri, P.repens, P.virgatum, P.amoenum, P.notatum, P.walense* and *P.hayatae*. The bulliform cell group projects above the general level of the epidermis e.g. in *P.auritum* and
Bulliform cells may also occur as small cells but conspicuously larger and more inflated than the normal epidermal cells (Fig. 19.b) as in *P.brevifolium, P.incisum*. In certain species, bulliform cells are less prominent over the entire surfaces of the lamina but prominent at the margin, with very conspicuous inflated cells, as in *P.luzonense* (Fig. 15.b).

Finally, bulliform cells can occur in a very irregular manner with regard to location, size and shape of the cells. An example is *P.capillare*.

5.2.15 Other epidermal cells (see also Chapter 6)

Transverse sections of epidermal cells revealed other characters, such as papillae, macrohairs, prickles, stomata and cuticle. Investigation of transverse sections aids understanding of structures seen in surface views. It indicates attachment and structure of the epidermal appendages, nature of the papillae, position of stomata and the form and thickness of the cuticle.

5.2.16 Macrohairs

Unicellular macrohairs are often found on the adaxial and less often on the abaxial epidermis (Figs. 12.b,c; 13.c; 15.b). The visibility of macrohairs in a transverse section depends upon the region through which the section was taken — whether that particular region contained macrohairs or not. In the materials here revised, adaxial macrohairs were found in *P.atrosanguineum, P.capillare, P.repens, P.gardnert*, and *P.miliaceum*. In *P.sarmentosum* and *P.incomtum* macrohairs were seen on both the adaxial and the abaxial epidermis. The number, length, and wall thickness of macrohairs varied considerably even on a single leaf. According to Metcalfe (1960), and this study, these differences in the macrohair characters can be considered to be
useful only as confirmatory characters for the identification of particular species, and are certainly not of general taxonomic significance.

5.2.17 Prickles and hooks

Prickles and hooks are often seen. Usually they are on the adaxial surface, seldom on the abaxial epidermis. Hooks usually occur in the intercostal zone, with curved or straight, pointed barbs (Fig. 14.a,d) (e.g. *P.antidotale* and *P.plenum*). Hooks are usually shorter than prickles. Prickles are usually located opposite the vascular bundles (Fig. 12.c) as thickened prickles with bulbous base but with or without barbs. These are usually larger than hooks. Prickles are commonly found in *P.paludosum, P.longiloreum, P.repens*.

5.2.18 Papillae

Papillae are epidermal cells showing considerable extension or arching of the outer wall and appear in transverse section as small projections from the epidermis (Figs. 12.c, 19.c). They may occur in a single row (e.g. *P.schinzi, P.sumatrense, P.coloratum*) or more than one row (e.g. *P.paludosum, P.longiloreum, P.repens*). Papillae provide useful taxonomic characters at both specific, supraspecific levels. The species of the section Dichotomiflora and Repentia have characteristic papillae on the adaxial surface, and in some cases on the abaxial surface as well (e.g. *P.paludosum*). In these species, the papillae are narrow – less than half the width of the epidermal cells. Usually two, seldom single papillae are present per cell over the entire adaxial epidermis. Quite remarkable adaxial papillae are present in *P.trachyrhachis* which are longer than the horizontal length of the epidermal cells (Fig. 19.c). In transverse section, collectively the papillae appear as numerous, tiny, fingerlike projections on the epidermal surface, at once providing a striking feature of
diagnostic significance. Most often the stomata are over-arched by papillae of the adjacent epidermal cells in these species (see Chapter 6).
6.1 Introduction

Epidermal features of leaf surfaces of all the species of *Panicum* of the Indian subcontinent and Southeast Asia have been studied by Scanning Electron Microscope (SEM) and described in this chapter. Various authors have recognised that the epidermal features of grass leaves provide valuable information in the classification of the family Gramineae (Prat 1936, Tatioka, Inoue & Kawano 1959, Metcalfe 1960, Jacques-Felix 1962, Ellis 1979). Leaf surface characters have traditionally been studied with light microscopy. The introduction of scanning electron microscope has brought about a remarkable increase in the attention paid to leaf characters (Stace 1984). It gives easily comprehensible representations of objects examined at a wide range of magnification. According to Palmer (1976) and Palmer & Tucker (1981) the diagnostic features of grass leaf surface are remarkably well suited for study with SEM. Apart from investigating leaf epidermal surfaces for all the species, for a large number of selected species, I have also examined the upper anthecium and pedicel.

6.2 Materials and Methods

Leaf blade and spikelet materials used for scanning electron microscopy were from dried herbarium specimens obtained from the herbaria of Edinburgh (E), Kew (K), British Museum (BM), and Leiden (L). Mature, undamaged leaves, usually third from the top, were chosen for this purpose. As far as possible, clean material was chosen, because herbarium sheets often had fungal strands.
or dirt on them. In case obscuring features appeared, a different specimen was inspected. I did not attempt cleaning them with any aid because it could result in hurting the specimen, especially the trichomes. Segments were cut from the middle half of the blade in appropriate sizes in relation to the SEM stubs so as to allow mounting two segments—one for the abaxial and the other for the adaxial side—on the same stub. They were then mounted on the stubs with double-sided sticky tape taking care that one piece exposed abaxial or lower surface and the other adaxial or upper surface. Each stub was given a number on the opposite side. An earthing spot of silver paint was applied at one corner of each segment touching the stub to reduce subsequent charging of the material while using the microscope. Following this, the specimens were sputter-coated with gold palladium and observed using a Cambridge S250 and a Cambridge S90B SEM. Technical Pan film was used for photography. An SEM record book was maintained. Notes were taken of different features while using the SEM.

Upper anthecia were dissected out from the spikelet. They were mounted on SEM stubs in the same way as were the leaf segments except that they were mounted whole. Pedicels were either mounted whole when short or as a piece from the tip when long.

6.3 Enumeration and Evaluation of Characters: Leaf Blade

6.3.1 Long cells

The epidermal surface area of the leaf is generally made up of two distinct sizes of cells: long cells and short cells. Long cells usually constitute the greater part of the intercostal zone. They are elongated horizontally and are relatively longer than wide. These cells are also termed as undifferentiated (Davies 1959) or fundamental (Prat 1948) elements. Short cells are smaller and
are usually nearly equidimensional in shape. They are also known as differentiated elements (Prat 1948, Davies 1959). The horizontal axis of long cells and short cells are oriented parallel to the longitudinal axis of the leaf blade. Metcalfe (1960) is of the opinion that although the types of long cells have proved very useful in the broad survey of the grasses, they are not adequate for all taxonomic purposes since there are many intermediates. In *Panicum* species of the Indian subcontinent and Southeast Asia, I have recognised several types of long cells. They are elongated with long and narrow cells, the length being two to three times as long as broad. Such cells are either sinuous (Fig. 20. a,b) as in e.g. *P. amoenum*, *P. bisulcatum*, *P. cambogianse*, *P. capillare*, *P. hippothrix*, *P. maximum*, *P. notatum*, *P.sarmentosum*, *P. stapfianum*, *P. turgidum* or smooth walled (Fig. 20. c) as in e.g. *P. plenum*, *P. antidotale*, *P. auritum*, *P. atrosanguineum*, *P. elegantissimum*, *P. miliaceum*, *P. vialae*. The smoothness or sinuousness of long cell walls are usually the same on both abaxial and adaxial surfaces of the leaf blade for a particular species. However, there are exceptions. In *P. amoenum* for instance, long cell walls are smooth on the adaxial surface and sinuous on the abaxial surface (Fig. 20. d,e). There is another type of long cell in which length is less than twice the breadth. This is rather uncommon in the revised species being found in only a few species e.g. *P. trichoides* (Fig. 20. f).

6.3.2 Short cells

Short cells occur singly or in pairs in longitudinal rows. They are usually present on the costal zones. But they may also be present in the intercostal zones often alternating with intercostal long cells (Fig. 23. c) or in some species they are entirely absent. Short cells are nearly isodiametric in shape and smaller than long cells. In general, the morphology of short cells over the
Fig. 20 Scanning electron micrographs of leaf blade surface

Long cells

a. *P. cambogiense*: Much longer than broad, walls sinuous

b. *P. havatae*: Much longer than broad, walls sinuous.
(Also note dumb-bell shaped silica bodies; concave interstomatal cells; microhair)

c. *P. auritum*: Longer than broad, walls smooth

d. *P. amoenum* (Adaxial): Walls smooth

e. *P. amoenum* (Abaxial): Sinuous (Also note silica bodies)

f. *P. trichoides*: Slightly longer than broad

SB = Silica body
veins are taxonomically more important than the intercostal short cells (Metcalfe 1960). Short cells are classified as silica cells and cork cells (Fig. 21. c). Silica cells contain silica bodies which have a characteristic shape when the leaf attains maturity. Cork cells have walls which are suberized. In this study, the frequency of costal short cells was noted and was found useful diagnostically. They are infrequent (e.g. P. paludosum, P. cambogiense), 2) common (e.g. P. coloratum), or 3) abundant as in the majority of the species (e.g. P. luzonense, P. trichoides, P. inornatum, P. hippothrix, P. gardneri, P. notatum, P. smithii, P. amoenum). In the intercostal zones the short cells were infrequent or absent, and in some cases not clearly detectable with SEM at all. They occur either as pairs of cork and silica cells or as solitary intercostal cells and the cells from which macro-hairs, hooks and prickles arise.

6.3.3 Silica bodies

Silica bodies occur in silica cells. They may be the same shape as the silica cells, or different. Scanning electron micrographs of herbarium materials did not reveal any clear distinction between silica cells and the silica bodies in this study. The shapes seen are therefore taken to be those of silica bodies. Silica bodies have distinct structures and generally are of constant shape in a species, thus offering useful diagnostic characters. In the Indian subcontinental and Southeast Asiatic species of Panicum, the following types of silica bodies have been recognised: 1) vertically elongated, with the vertical dimension greater than horizontal dimensions, 2) equidimensional, with the vertical and horizontal dimensions approximately equal, and 3) horizontally elongated, with the horizontal dimensions greater than vertical dimensions. Examples of vertically elongated silica bodies include, e.g. P. amoenum, P. mindanaense, and a few others. The silica body is kidney shaped (Fig. 21. a) in these species.
Fig. 21 Scanning electron micrographs of leaf blade surface

Silica bodies

a. P. amoenum: Vertically elongated, dumb-bell shaped

b. P. hayatae: Horizontally elongated, dumb-bell shaped. (Note microhairs, sinuous long cell wall, stomata)

c. P. trichoides: Horizontally elongated, dumb-bell shaped. (Note cork cells)

d. P. cambogiense: Equidimensional silica body

Stomata

e. P. incomtum: Parallel-sided

f. P. sumatrense subsp. sumatrense: Parallel-sided

SB = Silica body
CC = Cork cell
FIG. 21
Equidimensional, dumb-bell shaped silica bodies occur in *P. cambogiense* (Fig. 21. d). The majority of the species have category 3 silica bodies, and in general, they are dumb-bell shaped (Fig. 21. b,c) e.g. *P. hayatae, P. auritum, P. paludosum, P. repens, P. trichoides, P. virgatum, P. incomtum, P. notatum, P. smithii, P. khasianum, P. luzonense, P. atrosanguineum* and many others.

6.3.4 Stomata

A stoma is an aperture in the epidermis bounded by two guard cells. The guard cells are somewhat enlarged at their ends and constricted in the middle. In grasses and certain other plants, a subsidiary cell, which differs in shape or size from other epidermal cells, is present adjacent to each guard cell and is usually included in the stomatal apparatus (Booth 1964). These subsidiary cells are also known as accessory cells (Stace 1965). Variation in stomatal form and frequency in grasses have been described by various authors such as Flint and Moreland (1946), Metcalfe (1960), Ellis (1979).

Stomata are restricted to the intercostal zones where they are arranged in one or more well-defined longitudinal rows. But the distribution of stomata in rows has been found to be variable in a species. The shape of the subsidiary cells is very distinctive. I have recognised several types of stomata which vary in the shape of subsidiary cells. The stoma is termed dome-shaped, when the subsidiary cells are rounded. It is *low-domed* (Fig. 22. a) with the vertical width of the subsidiary cells smaller in relation to the horizontal length as in *P. notatum, P. elegantissimum, P. waleansa, P. trypheron, P. luzonense, P. trichoides, P. sumatrense sbsp. psilopodium*, or *medium-domed* (Fig. 22.b) with the vertical width slightly smaller than the horizontal width as in *P. longiloreum, P. seminudum* or *high-domed* (Fig. 22.c) with the vertical width of the subsidiary cells greater in relation to the horizontal length as in
Fig. 22 Scanning electron micrographs of leaf blade surface

Stomata

a. P. walense : Low-domed
b. P. longiloreum : Medium-domed
c. P. turgidum : High-domed
d. P. hayatae : Angular
   (Note V-shaped interstomatal cell)
e. P. antidotale : Stomata hidden by reticulum of waxy spicules
f. P. dichotomiflorum : Stomata over-arched by papillae
The stoma is recognised as parallel-sided (Fig. 21.e,f) when the subsidiary cells are rectangular in outline and the stomata looks long and narrow, e.g. *P. sumatrense, P. incomtum, P. walense, P. smithii*. The third type of stoma noted in this study is angular (Fig. 22.d) in which case the subsidiary cells are long and angular as in *P. coloratum, P. schinzii, P. hayatae*. However, intermediate types may be present amongst all the common types and sometimes it is not easy to make a clear demarcation. Furthermore, there are some species in which the shape of the subsidiary cells cannot be precisely determined. For example, in *P. antidotale* and *P. plenum*, the stomatal subsidiary cells are partially hidden by a curious reticulum of waxy spicules and plates (Fig. 22.e). The subsidiary cells of species of sections Dichotomiflora and Repentia are over-arched by papillae from adjacent epidermal cells (Fig. 22.f). Examples include *P. paludosum, P. longiloreum, P. schinzii, P. dichotomiflorum* (the latter not in this study).

### 6.3.5 Interstomatal cells

Long cells which lie in the same horizontal files as the stomata and separate individual stomata are termed *interstomatal cells*. They are recognisable if the stomata are fairly frequent, regularly spaced, arranged in definite stomatal rows, and particularly when each succeeding stoma is separated from its neighbour in the row by a single interstomatal cell. The end walls of the interstomatal cells fit to the stomata on either side with a characteristic shape. It is usually concave or U-shaped (Fig. 23.a,b), as for example, *P. miliaceum, P. cambogiense, P. paludosum, P. sumatrense, subsp. sumatrense, P. coloratum, P. schinzii*. I have also noted V-shaped end-walls of interstomatal cells (Fig. 23.c) e.g. in *P. mindanaensa, P. smithii, P. hayatae* as well as straight to convex end walls (Fig. 23.d) e.g. in *P. seminudum, P. incisum*. 

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Fig. 23 Scanning electron micrographs of leaf blade surface

**Interstomatal cells**

a. *P. smithii*: End walls U-shaped

b. *P. schinzii*: End walls concave (Note sinuous long cell walls)

c. *P. mindanaense*: End walls V-shaped (Note intercostal silica bodies)

d. *P. incisum*: End walls straight

**Microhairs**

e. *P. trichoides*: Unicellular microhair

f. *P. coloratum*: Unicellular microhair

SB = Silica body
6.3.6 Epidermal appendages

There are four main types of epidermal appendages in grasses. They are: microhairs, macrohairs, prickles and papillae. All these four types occur in *Panicum* including the species revised.

6.3.7 Microhairs:

Microhairs are bicellular trichomes consisting of a basal cell and a distal, apical cell. Unicellular microhairs, homologous with the bicellular hairs also occur, but were found in only two species (*P. trichoides* and *P. coloratum*) in this study (Fig. 23.e,f). Microhairs occur mostly in the intercostal zones of the leaf blade. The occurrence and form of microhairs are very useful for taxonomic purposes (Booth 1964, Reeder et al. 1965). The apical cell of the microhair is very thin and fragile and hence is subject to damage easily (Fig. 24.a). There are quite a few species in this study in which no microhairs were seen. I have recognised three principal types of microhairs based on the relative lengths of the basal and distal cell. In the first type, the two cells of the microhair are approximately equal in length (Fig. 24.b). The apex of the distal cell in such microhairs (e.g. *P. sumatrense* subsp. *sumatrense*, *P. coloratum*, *P. turgidum*) or rounded (e.g. *P. notatum*, *P. elegantissimum*, *P. humidorum*, *P. fischeri*, *P. staptianum*, *P. khasianum*). In the second and third type of microhairs, the basal cell may be shorter than the apical cell or vice versa. Examples in which the basal cells are shorter than distal cells (Fig. 24.c) include *P. hypothrix*, *P. trichoides*, *P. mindanaense*, *P. khasianum*, *P. longiloreum*. In this type, the apices of the apical cells have always been found to be rounded. Microhairs with basal cells longer than distal cells (Fig. 24.d) include species such as *P. miliaceum*, *P. dichotomiflorum*, *P. seminudum*.
Fig. 24 Scanning electron micrographs of leaf blade surface

Microhair

a. P. trichoides : Broken distal cell
b. P. coloratum : Basal and distal cell equal
c. P. longiloreum : Basal cell shorter, distal cell longer
d. P. dichotomiflorum : Basal cell longer, distal cell shorter
e. P. hayatae (Abaxial) : Basal cell longer, distal cell shorter
f. P. hayatae (Adaxial) : Basal cell shorter, distal cell longer
P. smithii, P. amoenum (with rounded apex of distal cells), and P. maximum, P. schinzii (with pointed apex of distal cells). I have found the same type of microhairs on both the abaxial and adaxial surfaces in all the species mentioned above. However, there are certain species which exhibited variation in the relative lengths of the two cells of the microhairs on the two surfaces and even on the same surface. Examples are: P. viale (abaxial: both cells equal or basal shorter, distal longer; adaxial: both cells equal), P. hayatae (abaxial: basal cell longer, distal cell shorter (Fig. 24.e); adaxial: basal cell shorter, distal cell longer (Fig. 24.f)).

6.3.8 Macrohairs

Macrohairs are much larger and with thicker walls than microhairs. They can be seen by the naked eye or in low (hand lens) magnification. Macrohairs are usually one-celled, but sometimes fine, transverse partitions are visible (Metcalfe 1960). In P. capillara I have observed a curious feature on a macrohair. In this species it bears a hook near the tip (Fig. 25.c). Macrohairs are variable in size, shape and in the raised epidermal cells at their base. The frequency of macrohairs is variable, too. In some species they are entirely lacking e.g. P. paludosum, P. longioreum, P. antidotale, P. smithii, P. auritum, P. dichotomiflorum (the latter not in this study) P. bisulcatum, P. incisum, P. trachyrrhachis. Often it is difficult to distinguish between short macrohairs and large prickles, because the former grades into the latter. An example in this study is P. hayatae in which the macrohairs can be considered as prickles with long barbs (Fig. 25.d).

Macrohairs have been found to be of limited taxonomic use. The length, frequency, and the extent to which the base is raised above the general leaf surface are all very variable. However, in general, these characters can be
Fig. 25  Scanning electron micrographs of leaf blade surface

Macrohair

a. *P. sarmentosum* : Abundant
b. *P. brevifolium* : Abundant
c. *P. capillare* : Hook on macrohair
d. *P. hayatae* : Prickle like macrohair
e. *P. hippothrix* : Flat base of macrohair
f. *P. capillare* : Moderately raised base of macrohair
FIG. 25
diagnostically helpful, i.e. in identification at the species level. The frequency of macrohairs is roughly recognised as 1) infrequent e.g. (P. cambogiense, P. miliaceum, P. gardneri, P. hippothrix), 2) common e.g. P. atrosanguineum, P. trichoides, P. stapfianum, P. luzonense, and 3) abundant (Fig. 25.a,b) e.g. (P. capillare, P. brevifolium, P. sarmentosum, P. incomtum, P. elegantissimum). But there are all grades of variations in these three categories, and the frequency of macrohairs varies in individuals of the same species and even in different leaves of the same plant. As regards the base of the macrohair, I have noted three categories in the species revised. It has been considered flat when the epidermal cells at the base of the macrohair are not raised (Fig. 25.e) e.g. P. elegantissimum, P. hippothrix, P. trypheron. In the commonest form, the base is slightly to moderately raised (Fig. 25.f) as the macrohair is associated with visibly elevated epidermal cells at base (e.g. P. capillare, P. brevifolium, P. atrosanguineum, P. cambogiense, P. repens, P. gardneri, P. incomtum, P. stapfianum, P. luzonense). In some rare instances the base of the macrohair was found to be markedly raised (Fig. 26.a,b) as in P. miliaceum, P. notatum, P. atrosanguineum.

6.3.9 Prickles

Prickles are robust, stout, short and sharply pointed cells with enlarged bases. They are thick-walled and their short points are generally directed towards the apex of the leaf (Fig. 26.c,d). Prickles are unicellular bodies arising from the epidermal cells and are part of the epidermis. They are usually located in the costal zones and along the leaf margins. Some can also be found in the intercostal zone. Taxonomically, prickles are no more important than for species identification (Metcalfe 1960, this study). The frequency of occurrence, shape and size were not found to be consistent. The frequency of prickles was
Fig. 26 Scanning electron micrographs of leaf blade surface

**Macrohair**

a. *P. atrosanguineum*: Markedly raised base of macrohair

b. *P. miliaceum*: Markedly raised base of macrohair

**Prickles**

c. *P. longiloreum*: Directed towards apex

d. *P. coloratum*: Directed towards apex

e. *P. miliaceum*: Large prickles

f. *P. turgidum*: Large prickles
Fig. 27 Scanning electron micrographs of leaf blade surface

**Prickles**

a. *P. amoenum*: Small prickles

**Hooks**

b. *P. notatum*

c. *P. hippothrix*

d. *P. elegantissimum*

**Papillae**

e. *P. sumatrense subsp. sumatrense*: Papillae concealing stomata partly

f. *P. sumatrense subsp. psilopodium*: Papillae on subsidiary cells
noted as absent, rare or infrequent, and common. In size, prickles can be divided into prickles and hooks. Hooks are very small prickles with much more rounded base, and short abruptly curved tips (Fig. 27.b,c,d). They are usually located in the intercostal zones. But, often it is not possible to distinguish between prickles and hooks due to the presence of intermediate types. Based on the degree of inflation at the base and the length of the barb, two types of prickles are recognised here in this study with SEM. Relatively small, non-recurved prickles (Fig. 27.a) were found in species, as for example in, P. coloratum, P. sumatrense subsp. psilopodium, P. incisum, P. plenum, P. amoenum, P. longiloreum, while large prickles (Fig. 26.e,f) were observed in others, as for example in, P. miliaceum, P. bisulcatum, P. repens, P. turgidum, P. virgatum, P. antidotale, P. humidorum. Examples of species in which hooks were found include P. cambogiene, P. hippothrix, P. notatum, P. elegantissimum, P. seminudum, P. hayatae.

Hooks and prickles may be present together in the same species, in the same leaf. Either or both may be lacking.

6.3.10 Papillae

Papillae are variously shaped outgrowths on the outer walls of the epidermis. They are found frequently on the adaxial surface of the leaf but seldom on the abaxial side. There may be one or more papillae on a single cell. The number may vary in specimens of the same species. Papillae are very useful in diagnosing species. They also show some taxonomic importance at sectional level in this study. For example, species of the sections Dichotomiflora and Repentia always possess numerous papillae - one, two or more per cell of the adaxial epidermis (except intercostal bulliform cells). Sometimes they are present even on the abaxial epidermal cells e.g. in P. paludosum.
Fig. 28 Scanning electron micrographs of leaf blade surface

Papillae

a. P. paludosum : Elongated (Note concealing of stomata by papillae)

b,c,d. P. schinzii : Globose

e,f. P. trachyrhachis : Elongated (Note stomata in the intercostal zone)
P. elephantipes (the latter not in this study). But there are quite a few other papillate species that belong to the section Panicum. I have noted three shapes of papillae in this study. They are 1) globoso (Figs. 27.e; 28.b,c,d) e.g. in P. sumatrense subsp. psilopodium, P. repens, P. schinzii, 2) shortly elongated (Figs. 22.f; 28.a) e.g. in P. paludosum, P. dichotomiflorum (the latter not in this study), 3) markedly elongated (Fig. 28.e,f) e.g. in P. trachyrhachis. Another feature is the occasional concealing of the stomata by papillae on the subsidiary cells (Fig. 27.f), e.g. in P. sumatrense subsp. psilopodium, or arching of the stomata by papillae from the adjacent cells. They can overarch the stomata either completely (Figs. 22.f; 28.a) as in P. repens, P. paludosum, P. dichotomiflorum, or partly (Fig. 27.e) as in P. sumatrense subsp. sumatrense. Palmer and Tucker (1983) reports elongated papillate prickles in Colpodium chionogeiton (Pilger) Tzvelev. The same authors (1981) have reported overarching of stomata by papillae in tribes Bambuseae and Oryzeae.

6.4 Enumeration and Evaluation of Characters: Upper anthecium and Pedicel

6.4.1 Upper anthecium

Upper anthecial surface features seen with SEM were found to be useful in the infrageneric classification of the Panicum species of the Indian subcontinent and Southeast Asia. The upper anthecium was found to be remarkably homogeneous in the species of the subgenus Panicum. It is smooth and shining over all its surface (Figs. 8.d,e,f,g; 9.a). In subgenus Phanophyrum, the anthecial surface was observed also to be smooth and glabrous in sections Hayata, Incisa, Parvifolia, and Sarmentosa. However, in one species, P. khasianum, of the last section, the apex of the upper anthecium bears a few
long, tangled unicellular hairs (Fig. 10.b), though the rest of the surface is smooth and shining. The other two monotypic sections of this subgenus differ markedly in their anthecial surface ornamentation. For instance, in *P. auritum* of section Laxa, the upper anthecium bears retrorse prickle hairs towards the apex and simple papillae on the rest of the surface (Fig. 10.c,d). In section Monticola, *P. trichoides* bears numerous more or less bottle-like appendages (modified microhairs) all over the surface of the upper anthecium (Fig. 10.e,f).

In subgenus Megathyrsus, as here represented by *P. maximum*, the upper anthecium is strongly transversely rugose with simple papillae on the wrinkles (Fig. 9.e,f). The ornamentation and surface of the upper anthecium can be used to separate the two sections included in subgenus Agrostoides. For example, in *P. antidotale* of section Antidotalia, the anthecium is glabrous and smooth; in *P. plenum* of section Bulbosa it is more or less transversely rugose, with wavy transverse rows of simple papillae (Fig. 9.c,d). Thus a character (anthecial rugosity) in which *P. plenum* is frequently deemed to resemble *P. maximum* is, in fact more complex than was thought.

### 6.4.2 Pedicel

The shape and surface of the pedicel are taxonomically useful; SEM studies revealed. In the subgenus Phanophyrum, the pedicel is cylindrical and smooth (Fig. 6.c,d), except for a few species. On the other hand, species of the subgenera Panicum, Agrostoides and Megathyrsus were found to be uniform - their pedicels having ridges, sinuses, and prickles (Fig. 6.e,f). Further, in section Dichotomiflora of subgenus Panicum, the pedicel ridges and sinuses were found to be covered with longitudinal rows of numerous papillae (Fig. 6.e).
PART III

INFRAGENERIC TREATMENT OF PANICUM FROM
INDIAN SUBCONTINENT AND SOUTHEAST ASIA
CHAPTER 7 : CONCEPT OF CATEGORIES

7.1 Introduction

It is desirable to present in this chapter a brief analysis of the concepts of the taxonomic categories utilised in this study. Most of the categories from genus down to variety have been used while revising the Indian subcontinental and Southeast Asiatic *Panicum*. To speculate the concept of the genus needs particular consideration because the present study involves a genus whose delimitation has long been disputed. With its establishment by Linnaeus in 1753 to very recent times, many genera have been split from *Panicum*. Naturally, there arises the question, what is a genus? What biological and practical factors should determine the boundary of a genus? With regard to the other categories, some fundamental ideas are put forward here, which I had in mind while attributing rank to taxa in this study.

7.2 Genus

The genus is a category of long standing. It is highly probable that genera were recognised as groups of plants of affinity before science came of age and written languages existed. For example, many colloquial or common names like 'oak' and 'pine' parallel modern generic concepts.

Theophrastus accepted and used aboriginal classifications in "De Historia Plantarum" (3rd century B.C.). Several names used therein survive as modern generic names, e.g. Daukon (*Daucus*), Aspharagos (*Asparagus*). Among the herbalists, O. Brunfels is credited with having had the clearest concept of the genus. His genera such as *Pisum* and *Brassica* apply to the same plants today.
In 1700, Tournefort in his *Institutiones Rei Herbariae* used the concept of genus consistently, with emphasis on floral features. For example, *Castanea* distinctive by echinate calyx; *Aconitum, Rosa* defined on flowers and fruits. Basically, the Linnaean concept of the genus, based on the sexual system, was in accord with that of Tournefort in that flower characters played the most important part.

That phase of the genus concept was followed by thinking on "natural affinities" or "natural systems". Thus the genera of Hooker, Gray, Rafinesque, and Torrey were based on the realisation that a genus groups together species which have more similarities with each other than they do with the species of other genera within the same family.

The philosophy of the generic concept based on theory of evolutionary descent is to treat the genus as a phyletic unit. From this viewpoint, taxonomic studies of genera involve not only morphological similarities but also origins, cytogenetic, physiological and ecological behaviour, geography and geology associated with its species. Lawrence (1951) writes, "the re-evaluation of existing genera by the tenets of this concept must result in some genera being divided into segregates, others being combined with what were thought to have been distinct genera, and still others maintaining their status quo." In other words, when evolutionary relationships are supposedly established, the difficult business of rank attribution begins. In a group containing groups, where should generic boundaries be drawn?

Modern taxonomists have continued to grapple philosophically and operationally with the genus – its nature and boundaries (Bartlett 1940, Camp 1940, Davis & Heywood 1963, Clayton 1983). All of them have stressed that the important characters of the genus is its natural delimitation which depends
on the size and homogeneity of the groups and the number of individuals intermediate between them. Davis & Heywood state: “Two or three species intermediate between genera each of a hundred species hardly justify reduction to a single genus, whereas if these genera contain only a few species their separation may not be justifiable on grounds of convenience”. Clayton (1983) states that: “a concentration of closely related species is the most obvious characteristic of generic clusters.”

I incline to believe that the formation of a theoretical concept of a category is not difficult, but that it is hard to determine generic boundaries in practice. However much time one may spend in trying to define a genus objectively or to standardise generic criteria, personal opinion is bound to come in. A genus ought to be a natural construction embracing comprehensive information on similarities, differences and evolutionary relationships, and offering pragmatic usefulness. These points are clarified below:

**Natural construction:** The most important function of the genus as a category is to bring together species preferably in a natural manner, i.e. using all available evidence. It should be made up of a group of species more closely related to each other than to species in any other group of about the same rank.

**Relationship:** The genus should reflect inferred phylogeny. If it is delimited by as many different but correlated characters as possible, then there is a greater chance for the genus to represent natural, that is to say probable phylogenetic units.

**Pragmatic usefulness:** The genus represents an essentially utilitarian entity. It should be sufficiently inclusive/exclusive to permit easy correlation and utilisation of species data. In the end, the customer is King!
Infrageneric classification should be considered if it is a practical need when
two groups are not recognisably, generically distinct or when in doubt as to
whether to accord generic rank to a group. Every attempt should be made to
find natural sections, if not found, informal groups can be adopted based on a
few technical characters. Rank attribution at and around generic level is
therefore weighted in favour of convenience, appreciating the practical
advantages of simple and unambiguous identification when as many characters
as possible have been displayed.

A subdivided genus should be more natural, useful unit than any of its parts
might be if uprated to generic status.

7.3 Subgenus and Section

Consequent upon what has been discussed above, subdivisions of the genus
into subgenera and sections often becomes significant. It was found to be
useful in the grouping of the Panicum species of the Indian subcontinent and
Southeast Asia in this study. Evidence from technical characters of anatomy as
well as morphology were utilised in order to circumscribe these groupings.

7.4 Species

Davis and Heywood (1963) quote Crombie - "the idea of the species as the
lowest unit of biological classification has a long history: it derives from
Aristotelean logic and philosophy." Early concepts of species, up to the pre-
Darwinian age, followed the belief that each species was created in its present
form. The number of species on earth was the same number that had been
there since the beginning of time - the only task of the taxonomist, a
devotional as well as practical one, was to distinguish between the various entities created. This idea completely changed with the development of the theories of evolution. These theories postulated species are no more fundamental to a phylogenetic schema than is any other category, and all mark only degrees of separation in a process of gradual change from an ancestral stock (Core 1962). From this point of view, a species is a concept that cannot be defined in exact terms, and not absolute and inelastic.

Even so, in taxonomic practice, biologists continued to feel there was something about a species that made it a definite entity. The smallest groups of individual plants which are 'fundamentally alike' are generally treated as a species. Ideally, individuals of this smallest group, i.e. the species, are separated by a distinct discontinuity from other closely related species. Sometimes it is difficult to delimit a species precisely because there remains a question about the degree of 'fundamental alikeness' among individuals of the species-unit. How to judge this? I argue and answer this way. The forms and appearances assumed by plants and their parts are infinite. Hence mathematical accuracy must not be expected. If each minor variation were to be made the basis of species distinction, there would be no end to the number of species. In taxonomic practice, differences in features should not be allowed to obscure greater resemblances. In this work a species is taken to be a group of individuals exhibiting constant resemblances in features considered to be of relatively major importance. To this, other characters of minor importance were added. This secondary consideration was given in the analysis of minor characters because it might supplement the resemblance to the recognised species.

A taxonomically 'ideal' species should pose no taxonomic problems because it is always recognizable as a distinct entity, and does not merge with other
species (Stace 1980). The individuals of such a species are able to exchange genes and are reproductively isolated from other such groups. This is a 'biological' species. A biological species is recognised when it is kept separate from other species by genetic isolating mechanisms which prevent or greatly reduce gene exchange between them.

But one of the disadvantages of a biological species is the lack of existence of a practical criterion of zero gene flow in the field (P. M. Smith, Pers. comm). There is evidence in *Panicum* that closely related species can hybridize. For instance, the North American species *P. amarulum* and *P. virgatum* Palmer (1975) found hybrid swarms of these two species growing in close proximity. She further refers to D.B. Woodward's statement (her pers. comm.) that these two species are known to hybridize freely in transplant gardens.

Many plant species coming into contact may be able to exchange genes producing fertile hybrids (Jones and Luchsinger 1979). "For this and other reasons," they stress, "the ability or lack of ability to produce hybrids and exchange genes cannot be used as a general criterion for the erection of species boundaries in most plants." Experimentation for gene flow information would have been welcome in this revision, but it was not possible in a three-year time period. The information must be sought later, now the taxa are better defined.

7.5 Subspecies

Davis and Heywood (1963) say "the subspecies has been widely accepted in a sense similar to that of Du Rietz and Rothmaler, i.e. as a considerable segment of a species with a distinct area and more or less distinct morphology, often showing intergradation, and clearly fulfils a useful purpose." This idea was the
foundation of the subspecies concept in this study. Subspecies represent
groups of specimens distinguished by relatively few small differences in
morphological characters. But the differential characters are consistently
correlated. They may have overlapping distributions. They may often show
intergrades in some features. Thus two subspecific groups show some
well-marked characters but in most features, they resemble typical specimens
of the species.

7.6 Variety

A variety is regarded as a variant of the species or subspecies. It is used to
provide formal taxonomic recognition of minor variation which nevertheless
produces a notable change in the ordinary appearance of a species. As to the
degree of variation, the term variety has been used and applied in several
senses. Some practising taxonomists employ variety for local facies of species,
morphologically distinct and occupying a restricted geographical area (Du Rietz
1930). It is in this sense that the variety has been accepted in this study. But
a variety may be a morphological variant of a species without regard for
distribution or a variant showing an area in common with one or more other
varieties of the same species or subspecies.
CHAPTER 8: INFRAGENERIC CLASSIFICATION

8.1 Introductory comments

I present in this chapter my own infrageneric treatment of the genus *Panicum* as represented in the Indian subcontinent and S.E. Asia using evidence of macromorphology, anatomy and micromorphology. In Chapters 1 and 2, it was said that the genus has been continually subdivided due to its heterogeneity. Even so, questions about the naturalness of the genus remain. The present study considers mainly the infrageneric classification of *Panicum* as represented in the Indian subcontinent and S.E. Asia. The results of my investigations have been considered in relation to other current information on the genus.

The basis of this classification is: 1) a thorough morphological investigation of a large sample of herbarium specimens, 2) examination of anatomical characteristics of leaf blades and 3) micromorphological studies of leaf epidermal surfaces using scanning electron microscopy. Discrete groups of species sharing similar characters were recognised using Indian subcontinental and S.E. Asiatic samples. Subgenera and sectional divisions were evaluated after comparing these groupings with those proposed for the genus on a world scale by various previous authors.

Emphasis has been given to the detection and utilisation of patterns of leaf anatomy which have been associated with C\textsubscript{3} and C\textsubscript{4} photosynthetic pathways. These patterns are significant in the systematics of *Panicum* (Brown 1977) and indeed, in the systematics of the *Gramineae* as a whole (Avdulov 1931, Prat 1936, Brown 1958, Stebbins & Crampton 1961). Brown assumed that leaf anatomical characters are more fundamental and conservative than the morphological characters traditionally used in the *Paniceae* except the basic spikelet plan. Many recent works, e.g. Brown (1977), Ellis (1977), Waller & Lewis...
(1979) have provided evidence that the taxonomic distribution of C₃ and C₄ photosynthetic pathways in the *Gramineae* represent natural groups. For this reason present day agrostologists attach great taxonomic significance to these characters.

The photosynthetic types C₃ and C₄ as well as the three biochemical variants of C₄ photosynthesis - NADP-me, PEP-ck and NAD-me types that have been recognised (for explanation of terms see Chapter 5.2) can be distinguished anatomically by whether or not they exhibit Kranz anatomy. *Panicum* is unique at least among grasses with representatives in all three groups of C₄ as well as C₃ species (Brown 1977). The Indian subcontinental and Southeast Asiatic species of the genus include species in each of these four groups which correspond to the different photosynthetic types known to occur in the *Gramineae* (apart from a few intermediate C₃/C₄ types which have not been observed any in this study). These types can be distinguished on anatomical criteria and individual species were assigned to them using bundle sheath and mesophyll characteristics. The groupings thus obtained were evaluated combining new evidence of other anatomical characters of the leaf blade with micromorphological (SEM) characteristics of the leaf epidermis, and correlating them with macro-morphology. In this way, an attempt has been made to define the taxa as naturally as possible. These taxa were then compared with the formally recognised subgenera and sections that have been recognised in other areas. It was found necessary to propose three further sections to accommodate the variation which has been detected. It has naturally not been possible to revise the subgeneric and sectional classification for *Panicum* as a whole, because of the necessarily limited geographical area of my study.

The infrageneric classification is explained and argued in discussion at the end of each subgeneric enumeration in this chapter.
the infrageneric taxa is provided. Finally, infrageneric concepts are argued in a
general discussion at the end of the chapter.

8.2 Synopsis of the subgenera and sections recognised in this work

1. **Subgenus** Phanopyrum Raf.
   Type
   1. **Section** Laxa Hitchc. & Chase
      Type *P.jaxum* Swartz
   2. **Section** Incisa M. Rahman
      Type *P.incisum* Munro ex C. B. Clarke
   3. **Section** Hayata M. Rahman
      Type *P.hayatae* A. Camus
   4. **Section** Sarmentosa Pilger.
      Type *P.sarmentosa* Roxb.
   5. **Section** Parvifolia (Hitchc. & Chase) Pilger
      Type *P.parvifolium* Lamk.
   6. **Section** Monticola Stapf
      Type *P.monticolum* Hook. f.

2. **Subgenus** Panicum
   Type *P.miliaceum* L.
   7. **Section** Dura Stapf
      Type *P.turgidum* Forssk.
   8. **Section** Panicum
      Type *P.miliaceum* L.
   9. **Section** Dichotomiflora (Hitchc. & Chase) Honda
      Type *P.dichotomiflorum* Michx.
10. Section Repentia Stapf
Type P. repens L.

Type P.rigidulum Bosc ex Nees

11. Section Antidotalia M. Rahman
Type P.antidotale Retz.

12. Section Bulbosa Zuloaga (in press)
Type P.bulbosum H. B. K.

4. Subgenus Megathyrsus Pilger
Type P.maximum Jacq.

8.3 Generic description and key to subgenera and sections

Generic description


Annuals, or rhizomatous or tufted perennials of various habit and size. Culms erect, ascending or decumbent, sometimes long creeping and climbing, sometimes branching at the nodes, glabrous or hairy. Leaf-sheaths terete or compressed, open, mostly striate when dry, hairy or glabrous; ligule membranous, leathery or papery, lacerate or short to long-ciliate. Leaf blades linear to linear-lanceolate or ovate to ovate-lanceolate or filiform, flat or inrolled. Inflorescence a panicle of varied shape and size, occasionally condensed about primary branches. Spikelets variable in shapes and sizes, articulated below the glumes, more or less dorsally compressed and symmetrical, sometimes weakly laterally compressed and asymmetrical in lateral view; pedicels angular and scabrous or terete and glabrous; glumes 2,
membranous (rather darkly hyaline) or herbaceous, equal or the lower usually shorter than upper, ovate to broadly ovate or orbicular, sometimes deltoid, obovoid, usually acute, sometimes obtuse or truncate, usually with 3- or 5-nerved, or 1-nerved or nerveless when membranous and very small; upper glume typically equalling the lower lemma, rarely shorter, hence usually as long as the spikelet, rounded on the back, 5- 9-nerved, rarely 11-13 (-17)-nerved; lower floret male or barren, its lemma very similar to the upper glume, usually glabrous, sometimes pubescent, rarely scabrid; with or without palea; palea membranous or hyaline, subequal to the lemma, sometimes smaller or vestigeal; upper floret hermaphrodite, upper lemma more or less as long as the spikelet though distinctly shorter in some species, subcoriaceous to crustaceous, rarely thinly coriaceous, obtuse to subacute, rarely acuminate, nerves obsolete, margins firm and inrolled over the edges of palea, its palea subequal to the lemma and of similar texture; lodicules 2, broadly cuneate, nerves obscure or numerous and prominent; stamens 3, filaments slender, anthers versatile; stigmas laterally exserted from top of the floret. Caryopsis more or less ellipsoid or oval, dorsally flattened, tightly enclosed by the hardened lemma and palea; hilum sub-basal, punctiform.


Key to subgenera and sections:

1. Spikelets with upper lemma strongly transversely rugose. Kranz P.S. PEP–ck species Subgen. 4 Megathyrsus

1. Spikelets with upper lemma rugulose or smooth.
Kranz M.S. NADP-me or Kranz P.S. NAD-me or non-Kranz species

2. Plant with stout rootstock. Kranz M.S. NADP-me Subgen. 3 Agrostoides

3. Upper lemma smooth, glabrous; spikelets clustered, margins of glumes and lower lemma broadly membranous Section 11 Antidotalia

3. Upper lemma rugulose, minutely ciliate at apex; margins of glumes and lower lemma not membranous Section 12 Bulbosa

2. Plant not with stout rootstock, if so, then plants suffruticose or with scaly creeping rhizomes. Kranz P.S. NAD-me or non-Kranz species

4. Scrambling perennials; if annual, then decumbent or if erect, then panicle condensed and the upper lemma thinly coriaceous. Non-Kranz species Subgen. 1 Phanopyrum

5. Spikelets asymmetrical from lateral view

6. Upper lemma finely rugulose, lower glume about 1/2 as long as the spikelet Section 6 Monticola

6. Upper lemma smooth, lower glume about as long as the spikelet Section 5 Parvifolia
5. Spikelets symmetrical

7. Panicle condensed, upper lemma thinly coriaceous and flexible, acuminate, minutely ciliate at apex

Section 1 Laxa

7. Panicle effuse, upper lemma coriaceous, hard

8. Spikelet 4–5 mm long, lower glume separated by a distinct internode; spikelets gaping at maturity

Section 2 Incisa

8. Spikelets 2–3 mm long, lower glume not separated by distinct internode; spikelets not gaping at maturity

9. Lower glume strongly 5-nerved, upper glume and lower lemma strongly 11-nerved

Section 3 Hayata

9. Glumes not strongly nerved; lower glume 1–3-nerved, upper glume and lower lemma 5-nerved

Section 4 Sarmentosa

4. Erect annuals with loose panicles or erect stout perennials. Kranz P.S. NAD-me species

Subgen. 2 Panicum

10. Lower glume 1\(\frac{1}{5}\) to 1\(\frac{1}{4}\) as long as the spikelet, nerveless or obscurely nerved, truncate to
obtuse with a short point

11. Ligule membranous to coriaceous, shortly ciliate, (0.5 – 1 mm long); culms tough, with long creeping rhizomes

Section 10 Repentia

11. Ligule membranous with long silky hairs about 2 mm long, culms soft, rhizomes lacking

Section 9 Dichotomiflora

10. Lower glume 1/3 to as long as the spikelet, prominently nerved, acute or acuminate

12. Plants suffruticose; spikelets turgid

Section 7 Dura

12. Plants not suffruticose; spikelets not turgid

Section 8 Panicum
8.4 Systematic account and discussion of the infrageneric groups


Type species: Panicum gymnocarpon Elliot (Raf. I. c.)

Non-Kranz \( \text{C}_3 \) species. Bundle sheaths double around the vascular bundles with the outer sheath cells lacking specialised chloroplasts but cell walls being distinctly thicker than the walls of the chlorenchyma cells; inner mestome sheath thick walled; 5–12 irregularly arranged mesophyll cells separate the successive vascular bundles, therefore the distance between the bundles is considerable.

Panicle open or contracted, or spikelets disposed in racemose unilateral branches, or panicles spikelike (in some American sections). Spikelets with lower glumes 1/3, or 2/3 to about as long as the spikelet, uniformly 1–3-nerved (5-nerved in section Hayata); upper glume and lower lemma 5-nerved (but in section Hayata 11 (~13)-nerved); lower palea may be present or absent; upper lemma smooth or rugulose.

Macrohairs common, often abundant, base only slightly raised; microhairs of various types – basal and distal cell equal or basal shorter and distal longer or basal longer and distal shorter; stomata usually with parallel sided subsidiary cells, sometimes triangular; prickles small to medium i.e. relative length of the base of prickles smaller or bigger than stomata; long cells with sinuous or smooth walls; silica bodies saddle – or dumb-bell shaped.
Species in this subgenus are shade-loving, procumbent plants in forests or forest margins of Old and New Worlds.

Basic chromosome number: n=9 and n=10.


Type species: *P. laxum* Swartz (Zuloaga, in press)

Keel well developed, distinct from the leaf outline in transverse section, constituted by one median bundle or one median plus two first order bundles; more than 4 chlorenchyma cells lie between the successive bundles.

Panicle usually contracted, branches erect with numerous crowded branchlets; spikelets narrowly lanceolate to lanceolate-oblong; lower glume ovate to orbicular, membranous, 3-nerved, upper glume and lower lemma 5-nerved, lower palea small; upper lemma narrowly lanceolate, acuminate, with a few minute teeth, whitish.

Microhair with shorter basal and longer distal cell, the latter lanceolate with a pointed end; stomata parallel-sided to low-domed; prickle base slightly bigger than stomata, barbs erect or flat; long cells with thick, smooth walls.

Found in damp rather shady places, at the edges of forests or in open places.

Only one species, *P. auritum* Presl ex Nees, from Asia.

Section 2. Incisa M. Rahman, Sect. nov.

Type species: *P. incisum* Munro ex C. B. Clarke
Panicle very lax, widely spreading; spikelets large, 4-5mm long, ellipsoid to ellipsoid-oblong, sharply acute or acuminate; glumes distant on a distinct inarticulate rachilla; lower glume inserted much below the rest of the spikelet; upper lemma ellipsoid or ellipsoid-oblong, polished, shiny.

Grows on hills.

Sri Lanka, Southern India, and Northeastern India.

The only other closely related species which belongs to this section is *P. gardneri* Thw.

Intervascular distance long, 4-5 chlorenchyma cells separate successive vascular bundles; bundle sheaths two, outer sheath without any chloroplasts, complete; metaxylem smaller or bigger than sheath cells; keel well developed, a single median bundle constitutes the keel.

Macrohair present or absent, when present base slightly raised; microhair rare, basal and distal cell equal in length, the latter with an acute apex; stomata rounded, silica body dumb-bell shaped; long cells with walls smooth at the abaxial side but sinuous on the adaxial side; prickles present or absent.

**Section 3. Hayata M. Rahman, Sect. nov.**

Type species: *P. hayatae* A.Camus

Panicle loose, ovate in outline, with axillary cushions; spikelets ellipsoid, pedicels glabrous, lower glume 3/4 the length of the spikelet, 5-nerved, not clasping; upper glume and lower lemma boat-shaped, strongly 11 (-13)-nerved, lower floret male, its palea about as long as the lower lemma; upper lemma much shorter than the spikelet, smooth, shiny.
A monotypic section, species growing in wooded paths or in open patches. Southeast Asia.

6-8 outer sheath cells surround the third order bundles, these bundles being linked with the upper and lower epidermes by uniseriate adaxial and abaxial extensions of the outer sheath, walls of the sheath and extension cells quite thick; keel represented only by a median vascular bundle with large abaxial and adaxial sclerenchyma girders; chlorenchyma irregular, 5 cells lie between successive vascular bundles.

Intercostal microhairs very common; basal cell much longer than distal, distal cell broadest at base and gradually tapered to a point, stomata triangular, long cell walls sinuous; costal silica bodies dumb-bell shaped, ends angular; prickles medium; adaxial microhairs with sunken bases.


Type species: P. sarmentosum Roxb. (Pilger l. c.)

Midrib conspicuous, consisting of a single median vascular bundle, the adaxial projection more prominent than abaxial; chlorenchyma of two types, radiate around the bundles and diffuse in the central part of the intercostal zone; 4 or more than 4 chlorenchyma cells lie between adjacent bundle sheaths.

Perennials with decumbent, slender or woody culms; creeping and rooting at nodes, often straggling in bushes; panicles open, lax, few to many branched; spikelets ellipsoid or ellipsoid-oblong, glabrous or pilose above; lower glume 1/2 to a little more than half the length of the spikelet, 1-3-nerved, not clasping; upper glume and lower lemma 5-nerved; lower palea present or absent; upper lemma smooth, often shiny.
Macrohair abundant, base slightly raised; microhair bicellular, narrow, basal and distal cell equal in length, but the ratio variable, often with basal cell up to double the length of the distal cell; stomata usually parallel-sided; prickle-base very much smaller, less than 1/2 the length of the stomata, barb shorter than base, often larger; silica bodies dumb-bell shaped; long cell walls sinuous or smooth.

Plains and hills in forest and on forest margins to open grasslands near streams or margins of pools.

Southern to Eastern India, Southeast Asia. A well developed section in Asia.


Type species: P.parvifolium Lamarck (Zuloaga, in press).

Vascular bundles are separated by 5 chlorenchyma cells, keel developed with adaxial and abaxial sclerenchyma strands, keel not very distinctive; vascular bundles linked to both the adaxial and abaxial epidermis by uni- or bi-seriate bundle sheath extensions.

Decumbent creeping annuals, often with aerial roots from the lower nodes; leaf blades ovate-lanceolate, amplexicaul; panicle open, many flowered in capillary, spreading branches; spikelets ovoid to lanceolate, glabrous or sparsely puberulous; lower glume 1/5 to about as long the spikelet, (1-) 3- nerved; upper glume and lower lemma 5-nerved; upper lemma smooth, shiny.
Macrohairs abundant, base not raised; microhair bicellular, basal and distal cell almost equal, distal cell tapered; stomata low-domed, rare; silica bodies dumb-bell shaped; walls of intercostal long cells sinuous.

Damp places in forest or forest margins, trailing on the ground or on other vegetation.

Represented in Asia by only one species, *P. bravifolium* L. Old and New Worlds.


Type species: *P. monticolum* Hook. f. (Zuloaga, in press).

Vascular bundles are separated by more than 4 chlorenchyma cells and hence widely spaced; bundle sheaths are double with the outer sheath being entire without specialised chloroplasts; midrib conspicuous; a single median bundle constitutes the keel with prominent adaxial and less pronounced abaxial projections.

Very slender annuals with decumbent culms, often rooting at the lower nodes; leaf blades ovate-lanceolate to lanceolate; panicle with numerous fine branches, diffuse; spikelets obovoid-ellipsoid, minute, 1-1.5mm long, glabrous or pilose, lower glume 1/3 to 1/2 the length of the spikelet, obscurely-nerved to clearly 3-nerved; upper glume and lower lemma 5-nerved; upper lemma finely rugulose.

Base of macrohair slightly raised; microhairs bicellular, very thin, distal cell usually longer than the basal, tapering to a point; stomata low-domed to triangular, separated by single interstomatal long cells; silica bodies dumb-bell shaped; intercostal long cells with sinuous cell walls.
Shady areas, e.g. wet, shady or open forest floors or forest margins.

Only one introduced species, *P. trichoides* Sw., in Asia.

**Discussion**

This is a non-Kranz C₃ subgenus. Brown (1977) subdivided the non-Kranz C₃ species into two subgenera on the basis of rough or smooth upper lemma. I do not agree in the delimitation of subgenera for non-Kranz C₃ species based on this character and consider that all non-Kranz C₃ species (except the North American subgenus *Dichanthelium* Hitchc. & Chase) should be grouped in one subgenus. The importance of the texture character of roughness or smoothness of the fertile lemma surface - should be given consideration at the next lower level of category in the classification of non-Kranz C₃ species.

The subgenus *Phanopyrum* Rafinesque was treated by Brown (1977) as a separate genus based on *Panicum gymnocarpon* Ell. which is a non-Kranz C₃ species from North America. In his studies of the New World species of *Panicum* Zuloaga (in press) indicated that there are other non-Kranz C₃ species in some sections of the genus, to which *P.gymnocarpon* conforms morphologically and anatomically. Therefore, *Phanopyrum* has to be treated as a subgenus of *Panicum*, containing all non-Kranz sections which differ from subgenus *Dichanthelium*. His treatment of *Phanopyrum* as a subgenus including all non-Kranz species (except *Dichanthelium*) is accepted here in this study.

I have recognised two new sections in the non-Kranz Asiatic species. Section *Hayata* stands out separate from all other C₃ Asiatic species or from any other C₃ section in *Panicum*. This monotypic section, containing the single species *P.hayatae* A. Camus, is unique in its increased number of strongly-nerved
spikelets, and in its leaf anatomical structure. The lower glume is 5-nerved and the upper glume and lower lemma are 11-13-nerved. This is in contrast with the typically constant nervation of spikelets of the subgenus where the lower glume is uniformly 1-3-nerved and upper glume and lower lemma are uniformly 5-nerved. Anatomically, the adaxial and abaxial uniseriate, one or two thick-walled extension cells of the outer bundle sheath characteristically separate this species from all other non-Kranz species in Asia. Thin-walled uni- or biseriate extension cells have been found in *P. brevifolium* L. in this study but they are of different type, and there is certainly no similarity in other respects between these two species. Section *Incisa* includes two species *P. incisum* Munro ex C. B. Clarke, and *P. gardneri* Thwaites. The two species of this section are non-Kranz C₃, and exhibit typical non-Kranz plant habit like other species of the subgenus, but in certain features of spikelet, they depart from the rest of the non-Kranz Asiatic species. These two species possess large, 4-5mm long spikelets, the lower glumes are separated by a short internode and inserted much below the rest of the spikelet, and the spikelets gape at maturity. These characters show affinity of this section to the section *Panicum* of the subgenus *Panicum*.

I do not accept the association of *P. brevifolium* L. and *P. trichoides* Swartz together in the same group e.g. in Group Trichoidea Hitchc. & Chase (1910) or in section *Ovalifoliae* by Stapf (1920). In *P. brevifolium* the fertile lemma is smooth whereas in *P. trichoides* it is finely rugulose. Though the two species have some morphological features in common, they should be treated in different sections on the basis of the rugosity of the upper lemma. *P. brevifolium* is a native of Africa while *P. trichoides* is a native of America. They do not resemble any other C₃ species from Asia. The addition of *P. trichoides* Sw. to section *Monticola* Stapf and of *P. brevifolium* to section
Parvifolia (Hitchc. & Chase) Pilger by Zuloaga (in press) appears to me to be justified. However, his treatment of whole of the section Ovalifoliae Stapf as synonymous with section Monticola Stapf is not acceptable because the former section contains also P.brevifolium which he has included in section Parvifolia.

Subgenus Panicum

Kraz P.S. C₄NAD-me species. Bundle sheaths double, with usually centripetally concentrated Kranz chloroplasts in the outer Kranz sheath, individual sheath cells being uniform with straight radial walls; 2 or 3 radially arranged tabular cells represent the distance between each vascular bundles.

Panicle open or condensed, branches lax or appressed. Spikelets ovoid-lanceolate to ovoid-oblond or ellipsoid, glabrous or hairy; lower glume 1/4 - 1/3, 1/2, 2/3 or 3/4 to about as long as the spikelets, obscurely - or 1-nerved to 5-7-nerved; upper glume and lower lemma usually 7-9-nerved, sometimes 11-13 (-17)-nerved, upper lemma smooth and shiny.

Macrohairs with markedly raised base; microhair with basal and distal cells equal in length or the basal longer than the distal; stomata dome-shaped with rounded subsidiary cells; prickles in one or two rows in the costal zone, medium to large with the base as long as stomata or longer, its barbs longer or shorter or as long as the base; long cells with sinuous walls; papillae elongated, rounded or globose, present on many or all adaxial epidermal cells (Section Dichotomiflora, Repentia) or none.

Plants of usually dry and open places but species of some sections grow in muddy banks of streams and canals, or wet places.

Throughout the Indian subcontinent and S.E. Asia. Old and New Worlds.
Basic chromosome number n=9.


Type species: *P. turgidum* Forssk. (here designated as lectotype; in the key to species of the genus, Stapf has mentioned two species viz. *P. turgidum* and *P. rigidum* under section Dura. As *P. turgidum* is mentioned first, this is designated as the type species of this section.)

Third order bundles surrounded by 7-10 outer bundle sheath cells, 13-17 sheath cells surround the first order bundles; keel absent — represented by a median bundle only, hardly distinguishable from the adjacent first order bundles; only 2 radial cells represent the distance between each vascular bundles, hence the bundles are closer together.

Suffrutescent perennials, leaf blades much reduced, pungent; ligule reduced to a ridge of hairs; panicle subpyramidal with few spreading branches, often much reduced; spikelets ovoid or subglobose; lower glume as long as or almost as long as the spikelet, acuminate, 5-9-nerved; upper glume and lower glume 7-9-nerved; upper lemma polished, shiny.

Microhair elongated with the distal cell slightly longer than broad, tapering to a definite point, basal cell parallel sided; infrequent intercostal hooks with short barbs; stomata in two rows in the intercostal zone, subsidiary cells medium-domed on the abaxial and high domed on the adaxial epidermis.

Desert species.

Northwest India, Pakistan, Iran through Arabia, North Africa.

Included species: *P. turgidum* Forssk.
Section 8. Panicum

Type species: *P.miliaceum* L.

Kranz sheath conspicuous; 6–9 sheath cells surround the third order bundles; first order bundles are surrounded by 11–15 cells; chloroplasts distinctly centripetally disposed, outer tangential walls of sheath cells straight or slightly inflated, radial and inner tangential walls straight; 2–3 radial chlorophyll cells lie between each vascular bundle; keel well developed, constituted of 1–3 first order bundles; adaxial epidermis sometimes papillate.

Branching annuals or caespitose perennials, culms erect; leaf sheaths mostly hairy, occasionally glabrous; ligule membranous, ciliate; panicle mostly diffuse with loosely scattered spikelets; spikelets ovoid to lanceolate, glabrous or finely scabrid on midnerves of glumes; lower glume 1/2 to 3/4 the length of the spikelet, 3–7-nerved; upper glume and lower lemma 5–7, 9–11 or 11–13 (–17)-nerved; lower palea present, sometimes absent; upper lemma smooth, polished, shiny.

Macrohairs with high-domed bases common; basal and distal cell of microhair equal in length, apex of distal cell broadly rounded or tapered to a point; stomata with low-domed subsidiary cells i.e. vertical dimension smaller in relation to horizontal dimension; prickles large; papillae absent or, when present, not usually overarching the stomata, globose (markedly elongated in *P.trachyrhachis*), plants of usually dry, open ground, sometimes growing in moist open places.

Indian subcontinent to S.E. Asia, Australia. Old and New Worlds.

*P.fischeri* Bor., *P.hippothrix* K. Schum., *P.luzonense* Presl, *P.miliaceum* L.,
*P.mindanaense* Merr., *P.paanum* Naik & Patun., *P.seminudum* Domin,
*P stapfianum* Fourc., *P.sumatrense* Roth ex Roem. et Schult., *P.trachyrhachis*

Sect. 3 (Bot.) 3 (1):246 (1930); Group Dichotomiflora Hitchc. & Chase in Contr.

Type species: *P.dichotomiflorum* Michx. (Zuloaga, in press).

Third order vascular bundles surrounded by 6 regular Kranz cells, 11–17 outer
sheath cells surround the first order bundles, the Kranz chloroplasts usually
lying closer to the outer tangential cell wall and occupying a small proportion
of cell area; distinctive keel always present; papillae developed on the adaxial
or sometimes on both adaxial and abaxial epidermal cells.

Annuals or perennials, culms smooth, somewhat succulent, compressed, ligule
membranous with dense silky cilia, 2–3mm long; panicle branches with short
and appressed secondary branches, spikelets lancelolate to ellipsoid, glabrous,
shortly pedicellate; lower glume 1/4–1/5 the length of the spikelet, broadly
triangular or suborbicular, obscurely — or 1–3–nerved; upper glume and lower
lemma 7–9–nerved; upper lemma smooth and shiny.

Microhair with longer basal and shorter distal cell; adaxial epidermis
conspicuously papillate, sometimes also the abaxial epidermis towards the
margins (*P.paludosum*); papillae shortly elongated and rounded at the apex;
stomata overarched by papillae from adjacent interstomatal cells; walls of
abaxial long cells thick or sinuous; prickles large.
Hydrophytic plants preferring damp or aquatic habitats.

S.E. Asia, India except NW. Old and New Worlds.


Type species: *P. repens* L. (Zuloaga, in press).

Third order vascular bundles surrounded by 6–7 irregular outer sheath cells with the adaxial cell inflated and elongated; 10–12 sheath cells surround the first order bundles; Kranz chloroplasts scattered around in small patches unlike regular centripetal disposition; 2 chlorenchyma cells lie between successive bundles; keel virtually absent; adaxial epidermal cells papillate.

Perennials from stout, creeping stolons or runners; culm hard; ligules membranous, shortly ciliate, leaf blades distichous, firm, often convolute; panicles open or contracted; spikelets ovoid–lancelolate or ellipsoid, glabrous; lower glume 1/4–1/3 the length of the spikelet, truncate or obtuse, membranous, nerveless or obscurely 1–3-nerved; upper glume and lower lemma 7–9-nerved; upper lemma smooth, pale.

Base of macrohair markedly raised; costal prickles overlying vascular bundles in single file, barb much smaller; papillae globose, costal and intercostal, adaxial; stomata overarched by papillae.

Prefers sandy soil, mostly maritime beaches of both hemispheres.

Included species: *P. repens* L.

Discussion:
This subgenus includes all C\textsubscript{4} Kranz P.S. species with two bundle sheaths and smooth and shining upper lemmas. Brown (1977) described this subgenus to be homogeneously NAD-me. This type of leaf anatomy is characterised by having two bundle sheaths around the vascular bundles, the Kranz chloroplasts being centripetally disposed in the outer bundle sheath cells (Ellis 1977). However, this characterisation does not appear to be wholly reliable in sections \textit{Dichotomiflora} and \textit{Repentia} as here investigated for the Indian subcontinental and S.E. Asiatic material.

Species belonging to the section \textit{Dichotomiflora} - \textit{P.paludosum}, \textit{P.longiloreum} and \textit{P.schinzi} exhibit a somewhat centrifugal arrangement of chloroplasts, more or less similar to the PEP-ck type of anatomy. For a comparative study, I examined \textit{P.dichotomiflorum} Michx., the type species of section \textit{Dichotomiflora}, and observed a similar arrangement of Kranz chloroplasts, which indicates a PEP-ck anatomy. However, Ohsugi, et al. (1980, 1982) observed decarboxylating enzymes in \textit{P.dichotomiflorum} and \textit{P.schinzi}, and classified them biochemically as NAD-me species. On the other hand, Hattersley and Browning (1981) and Hattersley (1984) anatomically classified \textit{P.schinzi} as PEP-ck species and consider \textit{P.dichotomiflorum} along with other species of the \textit{Dichotomiflora} group to be NAD-me species. In \textit{P.repens} of section \textit{Repentia}, Kranz chloroplasts were found scattered round the sheath cells or they lie in thin peripheral layer. Cells of the outer sheath are irregular and inflated, with the adaxial cell most inflated and elongated. These indicate the PEP-ck subtype of photosynthesis. Renvoize (1987) also reported \textit{P.repens} anatomically as a PEP-ck species (but his report that \textit{P.paludosum} is a non-Kranz C\textsubscript{3} species appears to be incorrect). \textit{P.repens} has been classified by Brown (1977) as NAD-me and is placed in the section \textit{Repentia} of the subgenus \textit{Panicum} (Brown 1977; Zuloaga, in Press). A further anatomical peculiarity was observed in
In an examination of a sample of 5 specimens of *P. coloratum*, I found centripetal chloroplasts in three cases where the outer sheath cells had flat outer tangential walls and straight radial walls, - characteristic of NAD-me leaf anatomy. But 2 specimens (correctly identified as *P. coloratum*) were found to have distinctly centrifugal chloroplasts with the four outer sheath cells of the third order bundles greatly inflated and unevenly arranged - clearly indicating a PEP-ck anatomy. Ohsugi, et al. (1982) investigated four specimens of *P. coloratum* and observed centrifugal chloroplasts in all of them but, on biochemical grounds, classified them as NAD-me species. Thus *P. coloratum* appears to have both centripetal and centrifugal chloroplasts but is a NAD-me species. Provided these biochemical typifications are correct, the above investigations and reports strongly suggest that the PEP-ck photosynthetic subtype and centrifugal arrangement of chloroplasts are not perfectly correlated.

My infrageneric classification differs in some details from Hsu’s (1965) and Brown’s (1977) work. *P. coloratum* is placed by me in section *Panicum* not in *Dichotomiflora*. I transfer *P. paludosum* from section *Repentia* to *Dichotomiflora*. Section *Dichotomiflora* forms a remarkably homogeneous assemblage of species with similar anatomy, vegetative morphology and ecology. All are hydrophytic, preferring damp or aquatic habitats. They have compressed, soft, even spongy culms, and usually long, silkily ciliate ligules. These characteristics are typically found in *P. paludosum*. On the other hand, members of the section *Repentia* have usually long creeping rhizomes with tough culms, stiff leaf blades and shortly ciliate ligules. *P. coloratum* is a morphologically variable species with tough, erect culms growing in usually open, sunny places unlike species of the section *Dichotomiflora*. My other rearrangements include the placement of *P. stapfianum*, *P. seminudum*, and
*P.silopodium* (now *P.sumatrense* subsp. *silopodium* (Trin.) de Wet.) in section *Panicum*. They have been found to have the NAD–me subtype of leaf anatomical structure and they are all species with smooth, shiny fertile lemmas. *P.virgatum* is included in section *Panicum* as a NAD–me species. This is in agreement with Brown (1977), but Renvoize (1987) has reported it to be a PEP–ck species. In its habit and habitat, the species approaches section *Repentia* but its spikelets are strikingly different and are similar to those of the species of section *Panicum* (e.g. *P.trachyrhachis*).

The leaf anatomy in *P.walense* was found to be interesting. 5–6 rounded outer sheath cells surround the third order bundles with Kranz chloroplasts lying closer to the outer tangential walls of the sheath cells. It appears to have the PEP–ck type of leaf anatomy, though it was classified by Brown (1977) as a NAD–me species. However, the species has a smooth, shiny upper lemma, and other characteristics of the section *Panicum*. Another very interesting anatomical structure was observed in the Australian species *P.mindanaense* Merr. which has smooth and shiny upper lemmas. The species possesses distinctly centrifugal chloroplasts in the Kranz sheath cells. The four inflated Kranz sheath cells surrounding the third order bundles are arranged in the form of a cross, similar to the configuration as found in *P.maximum* Jacq. - a PEP–ck species with strongly transversely rugose upper lemma. If *P.mindanaense* is shown to be a NAD–me species, it can be concluded in this case that the correlation between centrifugal chloroplasts and PEP–ck photosynthetic subtype is never perfect. This species forms a group of closely allied annuals (Blake 1969) with two other species from S.E. Asia, having similar habit, spikelet morphology and ecological requirements. These are *P.caudiglume* Hack. and *P.seminudum* Domin. Both have been found to be NAD–me species in this study. They have smooth and shiny upper lemmas. *P.mindanaense* is placed
with them in section *Panicum*, however, its biochemical typification is still to be established.

**Subgenus Agrostoides** Zuloaga (in press)

Kranz M.S. C₄ NADP-me species. A single bundle sheath surrounds each vascular bundle, cells of this sheath being Kranz with specialised chloroplasts usually centrifugally located; 2–3 generally isodiametric chlorenchyma cells separate each successive vascular bundles.

Panicle lax to contracted. Spikelets lanceolate to oblong-ellipsoid; lower glume nerveless to 3–5-nerved, variable in size from 1/3 to 1/2 to 2/3 the length of the spikelets; upper glume and lower lemma 3–5, 5–7 or 5–9-nerved; lower palea well developed or reduced, or even completely absent, upper lemma smooth and shiny or transeversely rugulose, glabrous or bearing cilia at the apex.

Microhairs with basal cell longer than distal cell, length of basal cell 3 times the breadth, distal cell slightly longer than broad, tapering to a round apex; stomata medium-domed, partially covered with fragmentary elements (almost a farina), interstomatal cells slightly concave; prickles with base longer than stomata, its barbs longer than base.

Basic chromosome number: \( n=9 \) or \( n=10 \).

There are seven sections containing approximately 16 species, all from the New World. Only one native monotypic section from Asia.

**Section 11. Antidotalia** M. Rahman Sec. nov.

Type species: *P.antidotale* Retz.
Stout perennials with creeping, villously sheathed, stoloniferous rootstock; panicle broadly oblong or ovate in outline; spikelets ellipsoid, clustered; lower glume mostly 2/3 the length of the spikelet, 3-5-nerved, margins broadly membranous; upper glume and lower lemma 5-9-nerved, with broad membranous margins; lower palea almost as long; upper lemma glabrous, smooth, shiny.

A monotypic section, – the species occurring from Sri Lanka, Southern India through NW India Westwards up to Arabia. Introduced to Australia, tropical Africa, and the U.S.A. The species grows in thickets in sand dunes, dry sandy places and desert regions.

Third order vascular bundles surrounded by 8-9 sheath cells, similar in size and shape; 14-15 sheath cells surround the first order bundles; Kranz chloroplasts centrifugally disposed in the sheath cells; keel large but not markedly emergent, one median, 2 first order, and 2 third order bundles constitute the keel.

Micromorphological characters: Same as for the subgenus.

**Section 12. Bulbosa** Zuloaga (in press)

Type species: *P. bulbosum* H.B.K. (Zuloaga, in press)

Third order bundles surrounded by 8-10 sheath cells; 12-13 sheath cells surround the first order bundles; keel large and markedly emergent on the abaxial side, 2 first order, 2 third order and 1 median bundle constitute the keel.

Caespitose perennial with or without corm-like at base; panicle pyramidal, laxly flowered; spikelets lanceolate or oblong-ellipsoid, glabrous; lower glume 1/2 the length of the spikelet, 3-5-nerved; upper glume and lower lemma
lanceolate or ovoid-ellipsoid, transversely rugulose, apex minutely ciliate.

Microcharacters same as for the subgenus, but prickles much less in abundance than section *Antidotalia* long cell walls smooth.

Damp places in rocky hills and valleys.

Only one species, *P.plenum* - introduced to Pakistan and India. Two or three New World species.

Discussion:

All the Kranz M.S. NADP-me species are here retained in one subgenus, *Agrostoides*. While establishing this subgenus, Zuloaga (in press) emphasised correlations of anatomical, physiological and morphological characters in the different groups belonging to the "Miscellaneous Assemblage" of Brown (1977) (see Chapter 2. 5). They are all NADP-me species wholly represented in the New World except for one species from India. Brown (1977) considered the M.S. groups of his "Miscellaneous Assemblage" of *Panicum* to be unrelated and out of place in the genus. He suggested that they be considered as distinct genera. However, Zuloaga (in press), in his investigation of the New World species of *Panicum* did not find any significant taxonomic evidence to raise them to independent genera. He mentioned a number of correlated characters which bind together the groups of the subgenus rather well.

Partly for the sake of convenience of treating all the NADP-me species in a single taxon, the subgenus *Agrostoides* is accepted here. In any case, it is necessary to wait until more details are known about the species of this largely New World subgenus largely outwith the scope of this thesis, before reaching an independent evaluation.
I have recognised the new monotypic section *Antidotalia* having segregated it from the group 'Plena' of W. V. Brown (1977), on the basis of the presence or absence of rugosity on the fertile lemma. The sectional concept adopted here is similar to that of Brown (1977) who assumes characters of the fertile lemma surfaces to be useful in the delimitation of categories next lower to the subgenus. *P.antidota/e* was placed along with the other two New World species *P.plenum* Hitchc. & Chase and *P.bulbosum* H.B.K. in the group 'Plena', all of them being NADP-me species. In *P.plenum* and *P.bulbosum* the fertile lemmas are transversely rugulose whereas in *P.antidotale* fertile lemmas are smooth and shiny. *P.antidotale* differs from these two species also in several other characters of panicle and spikelets. The proposed section *Antidotalia* is represented by a single species from Asia.


Type species: *P.maximum* Jacq. (Zuloaga, in press).

Kranz P.S. C₄ PEP–ck species. Bundle sheaths double, with centrifugally arranged specialised chloroplasts in the outer Kranz sheath; third order vascular bundles are surrounded by 4 (rarely 5, 6, or 7) Kranz bundle sheath cells which are arranged as a cross; the inner tangential walls of the sheath cells are straight, whereas the outer tangential and radial walls are inflated and elongated; 13–15 outer sheath cells surround the first order bundles, these being markedly smaller than those of the third order bundles; keel is very large, and is constituted by 2 first order, 2 third order and 1 big median bundles.

Tall, robust perennial. Leaf sheaths firm, compressed, keeled towards the top. Panicle large, pyramidal in outline, many flowered. Spikelets oblong or
narrowly ellipsoid, glabrous or pilose; lower glumes 1/3-1/4 the length of the spikelet, nerveless or obscurely 3-nerved; upper glume and lower lemma 5-nerved; upper lemma transversely strongly rugose.

Microhair with basal cell longer than distal cell, basal cell narrow, more than 3 times longer than broad, distal cell longer than broad, tapering to a more or less fine point; stomata with low-domed subsidiary cells; hooks overlying costal zones, barb recurved.

Represented by a single species, *P. maximum* Jacq., in Asia. It is a native of Africa and has been introduced to many parts of the World. It grows in shaded or open ground.

Basic chromosome number: n=8

Discussion:

*P. maximum* is the only representative of this subgenus in Asia. The subgenus was established by Pilger, the type species of which is *P. maximum* Jacq. Another species, *P. bulbosum* H.B.K. with rugulose upper lemma was mentioned by Pilger which is a M.S. NADP-me species and is now included in the subgenus *Agrostoides*.

*P. maximum* is a PEP-ck species which exhibits a specific configuration of outer bundle sheath cells with Kranz chloroplasts being centrifugally arranged. The upper lemma of the species is transversely rugose. According to Gutierrez et al. (1976), Brown (1977), most of the species of this category are of doubtful taxonomic position and their classification in *Panicum* is questionable. Brown (1977) suggested that those species with PEP-ck anatomy and transversely rugose upper lemmas should be transferred to *Brachiaria* together with *Urochloa* and *Eriochloa*. He removed *P. maximum* from *Megathyrsus* and
retained the latter as a subgenus to include all the non- Kranz C₃ species with rugose upper lemmas. But he overlooked the fact that *P. maximum* is the type species of the subgenus *Megathyrsus*. This was pointed out by Zuloaga (in press) who has reduced subgenus *Megathyrsus* so that it contains only PEP-ck species with transversely rugose upper lemmas. This arrangement is supported in the present study.

The suggestions of Gutierrez et al. (1976), Brown (1977) about the transfer of PEP-ck species (centrifugal chloroplasts in inflated outer sheath cells) with rugose upper lemma to *Brachiaria, Urochloa* and *Eriochloa* do not provide a general solution because the correlation between PEP-ck anatomy and transversely rugose upper lemma is not perfect. We have seen in the discussion of subgenus *Panicum* that there are some *Panicum* species with smooth, shiny lemmas and PEP-ck type anatomy (i.e. centrifugal chloroplasts in inflated outer sheath cells) which quite obviously belong to the above complex of species.

8.5 Relationship

An attempt has been made in the key to arrange the subgenera and sections in an order of their relationship. Subgenus *Panicum* which represents the 'true Panicums', having polished and shining upper lemmas, and Kranz P.S. NAD–me anatomy is placed near the centre (see Fig. 29). Subgenus *Megathyrsus* with transversely rugose upper lemma and Kranz P.S. PEP–ck anatomy, resembles genera like *Brachiaria, Eriochloa* and hence furthest removed from typical *Panicum* stock. In the subgenus *Agrostoides*, section *Antidotalia* with smooth and shining upper lemma suggests its affinity with section *Panicum*, while section *Bulbosa* with rough upper lemma might have remote relationship with
Fig. 29 Putative relationships among the infrageneric taxa recognised for the species of *Panicum* in the Indian subcontinent and S.E. Asia (see text for details).
subgenus Megathyrsus.

The sections of the two main subgenera are arranged to display, in my judgement, their affinity. In subgenus Phanopyrum, section Sarmentosa is near the centre of the series, which typically represents the Asiatic non-Kranz section. Two sections Hayata, with the lower glume more than half the length of the spikelet, boat shaped upper glume and broad leaves, and Incisa, with very lax panicle, 5-7-nerved upper glume and lower lemma appear to be more closely related to Sarmentosa than is section Laxa, which is in my view furthest removed from the Sarmentosa 'centre' of subgenus Phanopyrum, the inflorescence and spikelets resembling Hymenachne. Section Incisa, with the character of spikelets gaping at maturity, and the lower glume separated by an internode, also suggests an affinity with section Panicum. Sections Parvifolia and Monticola are more distant than Hayata/Incisa in my view, the spikelets of which are asymmetrical in both. Section Monticola with finely rugulose upper lemmas is probably most different.

Section Panicum occupies a nearly central position in the subgenus Panicum which is built up around the central idea of the genus as typified biologically, not merely technically by P. miliaceum. In the same way, section Repentia is an outlying group of the subgenus Panicum, showing anatomical characteristics closest to the PEP-ck type.

8.6 General discussion on infrageneric concepts

In Chapter 7 and elsewhere in Chapter 8, I discuss my concepts of taxa, and argue a case for recognising the sections and subgenera which I list. I now defend my view that Panicum is a useful, natural genus, as I see it after my study of the Indian subdontinental and S.E. Asiatic species. I also explain here
my choice of subgeneric and sectional status for the two levels of infrageneric taxa I have detected, i.e. I discuss the attribution of rank.

I consider *Panicum* to be a natural genus because of the large number of shared characters which are found in all the taxa which I can see within it. If *Panicum* were not to be recognised as a genus, it would have to be raised to tribal or subtribal status, i.e. Paniceae or Panicinae. This would obscure, in my view, the very close link between *Panicum* as conceived as a genus with genera such as *Cyrtococcum*, *Sacciolepis* etc. If *Panicum* had to be made a tribe, then *Cyrtococcum* would similarly need tribal status Cyrtococceae. This does not make any pragmatic or biological sense. Nobody would accept Cyrtococceae in my opinion.

I am saying that a subdivided genus should be a more natural, useful unit than any of its parts might be if uprated to generic status. In other words, if they are raised to genera, then it would be less useful, communicate the relationships less clearly and, I think, less accurately. Now the question remains as to why I chose subgenera and sections rather than, sections and subsections for the infrageneric taxa.

There are two hierarchical levels which I have detected. The taximetric work also shows this pattern. These two levels need to be assigned two different ranks. To illustrate my thought process, I cite the example of my new section Incisa. These species, formerly considered in section Sarmentosa, seem to me to share the same number and weight of taxonomic characters as does section Sarmentosa, after they have been removed from it. Therefore it is not possible to regard Incisa as hierarchically inferior to what is left of Sarmentosa. Since there is a level above these sections (i.e. units of this taxonomic weight), if that is truly their rank, this level must be a subgenus. The only change which I
have made to the circumscription of *Panicum* is to export *P. sparsicomum* to the closely related genus *Cyrtococcum*—which I certainly do not believe to be tribally or subtribally distinct from *Panicum*!

It would technically be possible to rank the two infrageneric hierarchical levels detected in this work as sections and subsections. However, the subgenera recognised in the study show discrete demarcation from one another. Although macromorphologically some of their species approach some species of other genera in appearance, they are very distinct from each other from the anatomical point of view. Therefore, I think it right to accord subgeneric, not sectional, rank to these taxa. The outcome is thus attribution of subgeneric and sectional rank throughout my work.

This is a happy outcome, since I have looked at only a sample of *Panicum*, and the typical infrageneric pattern recognised elsewhere in *Panicum* is also one of sections in subgenera.
CHAPTER 9: TAXIMETRIC ANALYSIS OF INFRAGENERIC TAXA

9.1 Introduction

This chapter presents a comparative assessment of my own classificatory treatment of the species of *Panicum* from the Indian subcontinent and Southeast Asia with that produced by the computer estimating the resemblance of species and classifying by cluster analysis. As a fundamental requirement for obtaining estimates of resemblance between the species by such a method, I organised a database of eighty characters chosen from macromorphology, micromorphology and anatomy. The lowest category employed in this study is the species which is the Operational Taxonomic Unit (OTU).

Each of the eighty characters was scored for the possession of one or other character state or attribute. The classification of the character states was done in a binary or two-state system, for example + and −, where + denotes presence and − denotes absence of the character state. In this way a data matrix of two-state attributes for eighty characters was constructed for the computer programme. This is shown in Appendix 3. Similarity measures between the OTUs were estimated by means of a similarity coefficient — the 'Simple Matching Coefficient', (Ssm) (Sneath and Sokal 1973):

$$Ssm = \frac{a+d}{a+b+c+d}$$

where

- a represents a positive match (++),
- d represents a negative match (−−),
- b & c each represents a mismatch (+−) or (−+).

The simple matching coefficient was then applied to obtain clusters of OTUs in a pair-wise cluster analysis using UPGMA clustering strategy (unweighted pair-group method using arithmetic averages). The results were expressed by the
production of a table of similarity coefficients (Appendix 4) which reveals a measure of similarities in all possible combinations of pairs of OTUs, and finally in the production of phenograms of similarities (Figs. 30 & 31). The dendrograms were constructed using the Hierarchical Cluster Analysis methods provided in Genstat A Statistical Programme Manual Release 4.04B (Rothamsted Experimental Station 1983). The Edinburgh Mainframe Computer was used, accessed via the EMAS-A system.

There are 43 OTUs in the first phenogram. It includes 42 species and one subspecies (formerly a species) which represents the species of the Indian subcontinent and Southeast Asia. The second phenogram consisting of 48 OTUs includes five further species. These five species (including *P. sparsicolum* transferred under *Cyrtococcum*), belong to three different genera - *Hymenachne, Sacciolepis* and *Cyrtococcum*. The purpose of this selection was to examine the systematic position of two species, *P. auritum* (in between *Panicum* and *Hymenachne* or *Sacciolepis*) and *P. sparsicolum* (in between *Panicum* and *Cyrtococcum*). The former species is retained by me in *Panicum* while the transfer of the latter to *Cyrtococcum* is accepted in this study (see Chapter 11.3). Identical characters from two species of *Sacciolepis*, and one species each from *Hymenachne* and *Cyrtococcum* were chosen and compared in a similar manner as for the other species of *Panicum*.

**9.2 Results and Discussion**

The different aspects of the phenograms are analysed taking into consideration the infrageneric groups which I have recognised according to my own experience and intuitive judgement (see Chapter 8). In Phenogram 1 (Fig. 30), at phenon 65, three clusters have joined - the largest one at the bottom, the
Fig. 30 Phenogram of 43 OTUs based on UPGMA cluster analysis (see text for details)
Fig. 31 Phenogram of 48 OTUS based on UPGMA cluster analysis (see text for details)
smallest one in the middle and the second largest one at the top. The largest cluster exclusively contains all species of the subgenus Panicum, no member being excluded from this cluster at this level. The smallest cluster represents two small subgenera, - the monotypic Megathyrsus (\textit{P. maximum}), and Agrostoides which in turn clusters two monotypic sections at 85-phenons, -section Antidotalia (\textit{P. antidotale}) and section Bulbosa (\textit{P. plenum}). Most of the subgenus Phanopyrum is clustered in the top assemblage, but for a curious portion which includes two monotypic sections, Parvifolia (\textit{P. brevifolium}) and Monticola (\textit{P. trichoideae}). These two sections nevertheless unite with the subgenus only at 60-phenons. Apart from this, the subgenera are distinctive at a phenon line of 65.

The reason of split of these two sections from the rest of the subgenus Phanopyrum can be explained. They are characterised by certain distinctive features which the computer has probably overvalued. For instance, both sections have asymmetrical spikelets, gibbous upper floret, and ovate-lanceolate leaves. Furthermore, the surface of the upper lemma in \textit{P. trichoideae} is finely rugulose unlike other members of the subgenus in which it is smooth. By virtue of these characters, these two sections are somewhat apart from section Sarmentosa which represents the mass of the subgenus in Asia. In my intuitive classification, I placed these two sections certainly as outlying members of the subgenus. However, though distantly, but certainly they belong to subgenus Phanopyrum, in my view, because they are non-Kranz C3 species having other characters of the genus \textit{Panicum}. The computer fails to record this because of its \textit{a priori} character weighting, i.e. giving all characters equal weighting.

Let us consider the results revealed for the sections. Within subgenus \textit{Panicum}, at 70-phenons, are revealed, - 1) most of the section Panicum, 2) two
species of section Panicum, *P.cambogiense* and *P.luzonense*; 3) the monotypic section Dura (*P.turgidum*) plus two species of section Panicum – *P.coloratum* and *P.stapfianum*; 4) section Repentia (*P.repens*), section Dichotomiflora (*P.paludosum*, *P.longiloreum*, *P.schinzi*), and one species of section Panicum (*P.sumatrense*). These associations need to be discussed.

The two species *P.cambogiense* and *P.luzonense* possess a unique pair of characters. The glumes and lower lemmas are reticulately veined and the upper lemma is obovate-lanceolate, which characters have separated them from the rest of section Panicum. In the second instance, section Dura comes very close to the two very similar species, *P.coloratum* and *P.stapfianum* belonging to section Panicum, by virtue of common characters of perennial habit, spikelets less than 4 mm long, acute lower glume which is less than half as long as the spikelet, and the staminate lower floret. But section Dura, represented by a single species, *P.turgidum*, is a highly xerophytic suffruticose perennial with very turgid spikelets, so differing from these two species. These characters were not coded in the data matrix, and obviously the computer has given other characters equal weighting placing the two species of section Panicum together with section Dura. It shows that the fewer the number of characters coded, the greater the chance of unsatisfactory results.

In a third feature of the fourth cluster, one species of section Dichotomiflora (*P.paludosum*) shows affinity with section Repentia at 80-phenons. The rest of the section Dichotomiflora (*P.longiloreum* and *P.schinzi*) are similar at 85-phenons. The single species, *P.repens* of section Repentia shares some characters with *P.paludosum*. For example, the lower glume is 1/4 the length of the spikelet, membranous, nerveless, truncate and the leaf epidermis is papillate. But *P.paludosum* manifests distinct characteristics of section Dichotomiflora. These include soft culms, long silkily ciliate ligule, glabrous
leaf sheath and blade-sheath junction in contrast with tough culms having long
creeping rhizomes, shortly ciliate ligules and hairy blade-sheath junction in
P. repens of section Repentia. The incapability of the computer in recording this
similarity and dissimilarity is a drawback. P. paludosum joins its two other
fellow members of section Dichotomiflora at 75-phenons. Lastly, in the same
fourth cluster, P. sumatrense (including its two subspecies showing similarities
at 90-phenons), of section Panicum, is curiously near section Dichotomiflora at
80-phenons. This anomalous–seeming position is probably because of the
presence of the character of papillae on the leaf epidermis, and the stomata
being partly concealed by papillae, while species of sections Dichotomiflora and
Repentia are also papillate. The computer has reacted to that apparent
similarity. Otherwise there are great differences between P. sumatrense and
members of sections Dichotomiflora and Repentia. P. sumatrense has an acute,
5-nerved lower glume which is separated by a distinct internode and is about
1/2 the length of the spikelet. These are characteristics of section Panicum
and absent in Repentia or Dichotomiflora. Here again, absence of weighting of
characters is obvious and account for the different classification.

Turning to the subgenus Agrostoides, it is seen that the two sections
Antidotalia (P. antidotala) and Bulbosa (P. plenum) show similarity at 85–
phenons. Subgenus Megathyrsus is monotypic, and unites with Agrostoides at
70–phenons. Their closer link than other subgenera is acceptable. There is
still a discontinuity discernable. In the subgenus Phanopyrum, all the species
of section Sarmentosa cluster at 80-phenons except one species, P. notatum,
which shows affinity with P. gardneri – one of the two species of section Incisa
(P. incisum). These two species along with the monotypic section Hayata (P.
hayatae) join with section Sarmentosa at 75-phenons. P. notatum and
P. gardneri have a common ligule type and a central keel bundle with a
projected keel – which characters have been accounted by the computer. But in my own treatment it will be seen that *P. notatum*, with straggling and climbing woody culms, large, almost subpetiolate leaf blade, 2 – 2.5 mm long spikelets is very similar to *P. sarmentosum* and *P. incomtum* which constitutes the core of section Sarmentosa. On the other hand, *P. gardneri* with sharply acute to acuminate, 4 – 5 mm long spikelets and glumes distant on a distinct, inarticulate rachilla, is very closely related to *P. incisum* of section Incisa. At a phenon line of 70, section Laxa and part of section Incisa link with the joint cluster formed by sections Sarmentosa, Hayata, and the remainder of section Incisa.

In the second phenogram (Fig. 31), *P. auritum* shows similarity with *Hymenachne* at a phenon line of 75. It joins with the cluster of *Panicum* subgenus Phanopyrum at 65–phenons. At the same phenon line, it links with the other genus *Sacciolepis*. *P. sparsicomum*, on the other hand, shows affinity with *Cyrtococcum* at a phenon line of 85. The two species are linked with the section Monticola (*P. trichoides*) of subgenus Phanopyrum at 80–phenons, and with section Parvifolia (*P. brevifolium*) at 70–phenons. The similarity between the *P. sparsicomum/Cyrtococcum* cluster and these two sections of *Panicum* is due to the presence of shared characters of asymmetrical spikelets and gibbous upper floret.

**9.3 Conclusion**

The computer analysis indicates several facets in agreement with my own classification. However, there are areas of disagreement, both at subgeneric and sectional level. All subgenera are distinctive at the same phenon level, with the exceptions of two sections in subgenus Phanopyrum. Closer
relationship of subgenus Agrostoides with subgenus Megathyrsus is supported. All members of subgenus Panicum are contained in one cluster. In subgenus Phanopyrum two sections are split apart. Though it answers my placement of these sections as outlying members in the subgenus, it does not value the chief characteristics of the subgenus as I have done i.e. this difference arises from equal weighting. Clustering major portion of section Panicum agrees with my own treatment of species in that section. But its intriguing separation of \textit{P.cambogiense} and \textit{P.luzonense}, \textit{P.coloratum} and \textit{P.stapfianum}, and particularly \textit{P.sumatrense}, from section Panicum, is questionable. Inclusion of section Repentia and Dichotomiflora in one cluster indicates their close relationship – also been recognised by me. But I do not accept separation of \textit{P.paludosum} from section Dichotomiflora (see above), although its placement with \textit{P.repens} is not wholly illogical. The separation of \textit{P.notatum} from section Sarmentosa, and of \textit{P.gardneri} from section Incisa is rather strange, and the groupings together of these two species is unaccepted. Except in a few instances, specific affinity is more or less satisfactorily manifested – i.e. close to that of my own judgement.

The systematic position of \textit{P.auritum} is really controversial and it seems to occupy an intermediate position between \textit{Panicum} and \textit{Hymenachne}. From the phenogram, it appears to be more closely related to \textit{Hymenachne} than \textit{Panicum} or \textit{Sacciolepis}. However, the computer appears to have underweighted certain diagnostic characters of the genus \textit{Panicum}. For instance the entire gripping of upper palea by upper lemma in \textit{Panicum} in contrast to that free in \textit{Hymenachne}. The spiciform inflorescence in \textit{Hymenachne} is another important aspect. Considering these diagnostic characters I have decided to retain \textit{P.auritum} as an outlying member of subgenus Phanopyrum of \textit{Panicum}.

\textit{P.sparsicomum} is found to have high similarity with \textit{Cyrtococcum} and both are
related at a lower level with sections Monticola and Parvifolia. In my classification these two sections were treated as outlying members of subgenus Phanopyrum. Further, *P.sparsicomum* is shown in the numerical analysis to be further from its closest ally in *Panicum (P.trichoides)*. Therefore the transfer of *P.sparsicomum* to *Cyrtococcum* seems to be supported.
PART IV
TAXONOMIC REVISION OF THE SPECIES OF PANICUM
FROM THE INDIAN SUBCONTINENT AND
SOUTHEAST ASIA
CHAPTER 10: METHOD OF PRESENTATION

10.1 Introduction

The genus *Panicum* has been revised for the regions covered by the Indian subcontinent and S.E. Asia. Herbarium studies were carried out at the herbaria of the Royal Botanic Gardens, Edinburgh (E) and Kew (K). In addition the collections of *Panicum* at the herbaria of British Museum (BM), Linnaean Society (LINN) at London; Rijksherbarium, Leiden (L) were studied. The latter currently incorporates all the *Panicum* collections on loan from Herbarium Bogoriense, Indonesia (BO). Apart from this, specimens at the herbaria of Jardine Botanique de Belgique, Brussels (BR), Museum Nationale d’histoire Naturelle, Paris (P), Botanischer Garten and Botanisches Museum, Berlin (B) provided useful information. Herbarium specimens, including many types, were obtained on loan from most of these institutions.

In this work, the genus is represented by 42 species, one subspecies and three varieties, recognised under twelve sections and four subgenera. In the largest subgenus, *Panicum*, there are four sections covering 25 species, one species being recognised as new. Subgenus *Megathyrsus* is represented by a single species from the area. Subgenus *Agrostoides* includes two monotypic sections, one of which is newly recognised. The second largest subgenus, *Phanopyrum*, comprises six sections and fourteen species – there being two new monotypic sections and one new species. In this study, seven species, one subspecies and two varieties previously recognised have here been reduced to synonymy, and two new combinations have been made. Accounts of the two new species, accepted for publication, are appended (Appendix 1 and Appendix 2).
10.2 Concepts in the usage of categories

The concepts I have adopted in the recognition of infrageneric taxa were outlined in Chapter 7.

10.3 Keys

Two keys are provided — one for subgenera and sections in the chapter on Infrageneric classification (Chapter 8), the other for the species under individual sections in the chapter on Taxonomic descriptions of the species (Chapter 11). In these keys, the attempt is made to combine ease of use with certainty of identification.

10.4 Descriptions

Descriptions of all the species have been drawn up after closely examining specimens of each species. Information about flowering and fruiting time, habitat and altitude has been cited based on materials from regions under study. For all the species, notes have been made on affinity, variation, taxonomy or on other special features at the end of descriptions. References to illustrations of species from literature are given. For those for which there is no record of illustrations, photographs from herbarium sheets are here included. As regards synonyms, I have cited only those which are important ones, which have been in wide use, and of which I feel certain.
10.5 Citation of specimens

As far as available, specimens have been cited from every main region within the distributional area. In few cases where Indian/S.E. Asian specimens have not been available to me, I have checked specimens from other regions, and carefully evaluated the literature. All specimens seen for each species have been cited except for those which are represented by a large number of specimens. In order to limit the size of the thesis, citations have been restricted in the latter cases. All specimens cited have been seen unless otherwise indicated. In the case of type specimens, an exclamation mark after the collector's name or number indicates that they have been seen. Specimens are cited by countries or islands with a general sequence from west to east in the Indian subcontinent, and south to north in Southeast Asia. In addition to the internal distribution, the general range of external distribution of all species has been given as indicated by herbarium specimens, and on the basis of literature records.

10.6 Typification

For all taxa, type details are cited as it appears to have been published. The whereabouts of the type material are indicated by the abbreviation as adopted in Index Herbariorum (Stafleu 1981). From the original citation, the name of the country of origin of the type specimens have usually been provided in square brackets, i.e. when the author has not indicated it. For two species lectotypes have been selected here. Two of the six Linnaean species in this study have been previously typified by A.S. Hitchcock (1908). As for the other four species, specimens have been carefully examined at the Linnaean Herbarium and the British Museum but the task of typification remains for the future.
10.7 Relationship

I have tried to arrange the species under each section on the basis of certain evident affinities. In section Sarmentosa there are two groups of species. An alliance of *P. sarmentosum*, *P.incomtum* and *P.notatum* is suggested by the woody, climbing habit and large lanceolate leaves. Likewise, *P.amoenum*, *P.smithii*, *P.bisulcatum*, *P.humidorum* constitute a fairly natural unit characterised by the ovate to triangular lower glume and epiapate lower floret. *P.khasianum* possibly has relationship with *P.auritum* as suggested by its upper lemma with ciliate apex. In section Dichotomiflora, *P.paludosum*, *P.schinzi* and *P.longiloreum* constitute a group of closely allied species, sharing the feature of membranous, nerveless, truncate, clasping lower glume, long silky ciliate ligules and papillate epidermal surface of leaves. They appear to be related to *P.repens* of section Repentia because of the characters of the lower glume. Section Panicum comprises a few groups of species in which the members appear closely related. An alliance of species like *P.seminudum*, *P.mindanaense*, *P.caudigluma*, *P.hippothrix*, *P.trachyrhachis*, *P.virgatum*, *P.elegantissimum*, *P.trypheron* is suggested by their widely gaping spikelets at maturity, with the lower glume very distinctly separated from the rest of the spikelet. *P.coloratum* and *P.stapfianum* seem closely related - both having a membranous, short lower glume. In this respect they suggest some relationship with members of sections Dichotomiflora and Repentia. Another alliance is shown by *P.cambogiense* and *P.luzonense*. Both have reticulate nerves on glumes and an obovate upper lemma. An ally of *P.miliaceum*, *P.sumatrense* subsp. *sumatrense* and subsp. *psiopodium* is marked by the increased number of nerves on upper glume and lower lemma. *P.atrosanguineum*, *P.paianum* and *P.capillare* constitute a fairly close alliance,
characterised by finely branched panicle branches and branchlets and hairy culms, leaves and sheaths. Due to the increased number of nerves on upper glume and lower lemma as well as the markedly raised bases of macrohairs, P. paianum may also have affinity with P. miliaceum/sumatrense.
11.1 Key to the species

A key to subgenera and sections has been provided in Chapter 8.3. To save space it is not repeated here, and a key only to the species under respective subgenera and sections is given below.

Subgenus Phanopyrum

1. **Section Laxa**: A single species
   1. *P. auritum*

2. **Section Incisa**:
   - Leaves linear-lanceolate, narrowed at base; glumes not silvery hyaline on the margins; ligule membranous, large, glabrous
     2. *P. incisum*
   - Leaves broadly lanceolate; glumes silvery hyaline on the margins; ligule papery, small, ciliate on the back
     3. *P. gardneri*

3. **Section Hayata**: A single species
   4. *P. hayatae*

4. **Section Sarmentosa**:
A. Upper lemma tip minutely ciliate
   - Upper lemma entirely glabrous

B. Spikelets 1 - 1.5 mm long
   - Spikelets 1.7 - 2.5 mm long

C. Lower glume 1/3 or less than the length of the spikelet
   - Lower glume 1/2 to 2/3 as long as the spikelet

D. Panicle branches spreading at right angles to the axis; spikelets few; leaf blade 3-4 mm broad
   - Panicle branches ascending at least at 60° to the axis; spikelets numerous; leaf blade 8 - 30 mm broad

E. Leaf blades 8 mm - 12 mm broad, glabrous; spikelets pilose towards tip
   - Leaf blades 10 - 30 mm broad, pectinate - ciliate at base or thickly hairy on both surfaces, spikelets glabrous

F. Lower palea absent; leaves pectinate - ciliate at base, base cordate
   - Lower palea present, leaves thickly, softly hairy on both surfaces, base not cordate

G. Panicle axis and branches smooth, panicle usually large, ovate in outline, branches and branchlets

12. *P.khasianum*  
B

8. *P.humidorum*  
C

5. *P.bisulcatum*  
D

6. *P.smithii*  
E

7. *P.amoenum*  
F

9. *P.notatum*  
G
free, pedicels usually not recurved; spikelets greenish, shining, nerves obscure

- Panicle axis densely pubescent; panicle usually small, usually oblong in outline, branches and branchlets usually entangled, viscid, pedicels usually recurved; spikelets dull, often yellowish, nerves prominent

10. *P.sarmentosum*

11. *P.incomtum*

5. **Section Parvifolia:** A single species

13. *P.brevifolium*

6. **Section Monticola:** A single species

14. *P.trichoides*

Subgenus Panicum

7. **Section Dura:** A single species

15. *P.turgidum*

8. **Section Panicum**

A. Plants perennial, lower glume acute, spikelets not gaping at maturity B

- Plants annual or if perennial, then lower glume acuminate to cuspidate, and spikelets gaping at maturity E

B. Spikelets 5 mm or more long, rachilla of spikelets
produced beyond the upper floret as a membranous apiculate scale

- Spikelets 2 – 3 mm long, rachilla of spikelets not produced.

C. Culms tuberculate – hispid; spikelets acuminate

- Culms glabrous, spikelets acute

D. Plants densely tufted, ligule a membranous rim with long fine cilia, lower floret male

- Plants not densely tufted, ligule a membranous rim with short cilia, lower floret male or sterile

E. Spikelets 1.5 – 2.2. mm long

- Spikelets 2.5 – 5 mm long

F. Leaf blades and sheaths glabrous; palea of lower floret nearly as long as floret; upper lemma colourless

- Leaf blades hirsute, leaf sheaths thickly clothed with long hairs; palea of lower floret small; upper lemma dark chestnut coloured

G. Upper glume 11 – 13 or more nerved, nerves prominent

- Upper glume 5 – 7-nerved or 7-9-nerved, nerves less prominent

25. P. tischiari

C

24. P. viale

D

20. P. stapfianum

21. P. coloratum

F

16. P. walense

17. P. atrosanguineum

H

I
H. Spikelets 2 - 3.5 mm long, lower glume acute or obtuse, 1/3 - 1/2 as long as the spikelet
- Spikelets 4.5 - 5 mm long, lower glume long acuminate, 2/3 - 3/4 as long as the spikelet

26. *P. sumatrense*

27. *P. miliaceum*

I. Spikelets obtuse, nerves anastomosing in glumes
- Spikelets acute or acuminate, nerves not anastomosing in glumes

J. Panicle 7 - 20 cm long, all branches of about the same length with an iterative branching pattern
- Panicle 25 - 50 cm long, sub-thrysiform, lower branches very long

22. *P. luzonense*

23. *P. cambogiense*

K. Culms hairy
- Culms glabrous

L. Nodes glabrous; spikelets acute; lower glume 1/2 as long as the spikelet; inflorescence not falling at maturity
- Nodes densely bearded; spikelets acuminate; lower glume 1/2 - 2/3 as long as the spikelet; inflorescence deciduous at maturity

18. *P. paianum*

19. *P. capillare*

M. Lower glume up to 1/2 or less than 1/2 as long as the spikelet, leaves subradical
- Lower glume not less than 3/4 as long as the spikelets; leaves not subradical

28. *P. elegantissimum*
N. Stout perennial, culms with creeping rhizome
- Annuals

O. Leaf narrow, 2 – 4 mm broad, midrib much broader than each half of the lamina; plant robust, semi-aquatic
- Leaf blades much broader, midrib much narrower than each half of lamina; plant not robust, terrestrial

P. Spikelets 4 – 4.5 mm long
- Spikelets up to not more than 3.5 mm long

Q. Lower glume 2/3 as long as the spikelet; plant glabrous
- Lower glume at least 3/4 as long as or exceeding the spikelet; plant hairy

R. Lower glume longer than spikelet
- Lower glume shorter than spikelet

S. Spikelets 3 – 3.7 mm long; panicle branches stiff
- Spikelets 2.3 – 3 mm long; panicle branches not stiff

9. Section Dichotomiflora

A. Plant annual
- Plant perennial
B. Spikelets 2 - 2.5 mm long, ellipsoid, acute
   - Spikelets 3 - 4 mm long, narrowly lanecolate, acuminate

10. Section Repentia: A single species
    39. P. repens

Subgenus Agrostoides

11. Section Antidotalia: A single species
    40. P. antidotale

12. Section Bulbosa: A single species
    41. P. plenum

Subgenus Megathyrsus: A single species
    42. P. maximum

11.2 Taxonomic Descriptions

SUBGENUS PHANOPYRUM Rafinesque

Section Laxa (Hitchc. & Chase) Pilger

1. P. auritum Presl ex Nees, Agrost. Bras. 176 (1829); Presl, Rel. Haenk. 1: 305 (1830);
Syn: *Hymenachne aurita* (Presl) Balansa in Morot, Journ. de Bot. 4: 144 (1890).


Stout perennial. Culms upto 2m, erect, soft or hard, nodes glabrous, dark. Leaf sheaths rather loose, striate, glabrous but densely ciliate at the margins, mouth villosly bearded, ligule a narrow membranous rim; blades 20–60cm long, (.6-) 2–4cm broad, smaller and narrower in less robust plants, linear–lanceolate with a broadly cordate base, flat, glabrous or sparsely hairy beneath. Panicle 20–40cm long, usually contracted or more or less effuse, branches erect with numerous crowded branchlets. Spikelets (2-) 2.5 – 2.6 (-3)mm long, narrowly lanceolate to lanceolate-oblong, subacute, glabrous, pedicels shorter than spikelets, scabrous; lower glume 1/3 the length of the spikelet, broadly ovate to orbicular, obtuse or acute, clasping, membranous, 3–nerved; upper glume ovate–lanceolate, acute or acuminate, 5–nerved; lower lemma almost subequal to upper glume, ovate–lanceolate, acute, 5–nerved, sterile, its palea small; upper lemma almost equalling the lower lemma, narrowly lanceolate, acuminate, thinly coriaceous, with a few minute teeth at the tip, whitish, faintly 5–nerved. *Fl. & Fr.: April to November.*
Type: [Philippines], "Hab. ad Sorsogon Luzoniae." Haenke (PR ?).

Representative specimens:

INDIA. Dehra Dun, Hojai Nowzong, 6 VI 1942, 500ft., N. L. Bor 16209 (K); Thadikkarakonam, 26 VIII 1960, 1000ft., J. Christopher G 479 (K). Khasia Hills, Griffith s. n. (E); Khasia, J. D. H. & T. T. s. n. (E); Cachar, 13 V 1868, C. B. Clarke 6999 (E); Assam, Danang, IV 1902, A. C. Chatterjee s. n. (E).

SRI LANKA. Thwaites No. 3242 (K).

BANGLADESH. Bandarban district, Ruma, bank of Sangu river, 28 X 1984, M. Rahman et al 1813 (E).

BURMA. Upper Chuidwein district, 23 VIII 1908, 500ft. J. H. Lace 4225 (K); Insein district, Myaukhaing Reserve, 14 IX 1948, Po Khant 828 (K).

THAILAND. Tepa, 23 III 1928, under 50m, A. F. G. Kerr 14721 (K); Kuring, 23 I 1927, A. F. G. Kerr 11616 (K).

MALAY PENINSULA. Kampong Seronok, Penang, 19 XI 1950, J. Sinclair SF 39115 (E); Pahang, Pekan, H. N. Ridley s. n. (E); Singapore, Tanglin, IX 1892, J. B. Fielding s. n. (E); Jurong, 24 IX 1958, J. Sinclair 9829 (E).

SUMATRA. N. Sumatra, Medan, 31 III 1928, 15 to 20m, J. A. Lorzing 13034 (K); N. Sumatra, Serdang, 3 VI 1928, 1/2 to 10m, J. A. Lorzing 13292 (K).

JAVA. Bantam, 17 V 1937, +125m, P. Buwalda 2737 (K).

BORNEO. West Borneo, Nanga Serawai, V 1954, 67m, H. Winkler 138 (E).

Sri Lanka, India, Bangladesh, SE Asia, China.

Common in damp rather shady places, in forests near water falls, forest
clearings and forest margins. 50–500m.

A good fodder grass.

The densely spiculate condensed nature of the panicle and the thinly coriaceous, lanceolate upper lemma close the species to *Sacciolepis* and *Hymenachne* - two segregated genera from *Panicum*. But the oblique and laterally compressed, gibbous spikelets with saccate upper glume in *Sacciolepis* readily separate the species from *Sacciolepis*; the membranous upper lemma and palea that are free towards the tip in *Hymenachne* separate the species from *Hymenachne*.

Section *Incisa* M. Rahman


Hook. f., Fl. Brit. Ind. 7: 51 (1896); Bor, Grass. Burm. Ceyl. Ind. Pak. 326 (1960);


Slender perennial. Culms 30–60cm, creeping at base and ascending, quite glabrous. Leaf sheaths glabrous, striate, smooth; ligule membranous, elongate-oblong, scarious, blades 10–25cm long, 1–1.6cm broad, linear-lanceolate, finely acuminate, flat, quite rigid, glabrous or scabrid, base narrow. Panicle 20–30cm long, effuse, very lax, main axis short, branches long, very slender, scaberulous. Spikelets 4–5mm long, ellipsoid, acuminate, solitary, remote, pedicels very much longer than spikelets, scabrous, glumes distant on a distinct inarticulate rachilla; lower glume 2/3 the length of the spikelet, ovate,
acute, 5-nerved; upper glume ovate, acuminate, 5-nerved; lower lemma subequal to the upper glume, ovate, acuminate, 7-nerved, male, its palea small; upper lemma ellipsoid, acuminate, with a scar at base, subcoriaceous, brown, polished, shiny.

Type: [India, Assam], "in Griffith Kew, n. 6505" (K, holo!, E, iso!).

Representative specimens:

INDIA. Assam, Sulen, 8 IX 1935, 2500', N. L. Bor 6470.

Upper Assam, India. Endemic.

On hills.

The membranous, elongate-oblong ligule and the presence of a prominent scar or 'incision' at the base of the upper lemma immediately differentiate this species from others.


Syn.: Isachne gardneri Benth. in Benth. et Hook. f., Gen. Pl. 3: 1100 (1883);


Fig. 32.

Slender perennial. Culms 30–100cm, decumbent below and often sending aerial roots from lower and upper nodes, smooth, nodes glabrous. Leaf sheaths sulcate, glabrous except ciliate margins, purplish; ligule papery, ciliate on the back; blades 5–10cm long, 1.2–1.8cm broad, ovate-lanceolate to broadly
Fig. 32 *Panicum gardneri* Thwaites: Lazarides 7208(K)
Inset: spikelets x 2 1/2
lanceolate, acuminate, flat, thin, sparsely hairy, base cordate. Panicle 5-20 cm long, ovate in outline, very lax, branches widely spreading, long, filifrom. Spikelets 4-5 mm long, oblong, few, distinct, margins of the glumes and lower lemma silvery, hyaline; lower, glume 3/4 the length of the spikelet, ovate, obtuse, separated from the upper glume by an internode, not clasping; upper glume ovate-oblong, obtuse, 5-nerved; lower lemma subequal to the upper glume, elliptic-oblong, acute, 5-nerved, sterile, its palea nearly as long; upper lemma ellipsoid-oblong, acute, smooth. *Fl. & Fr.: April to November.*

Type: [Sri Lanka], "Hab. Forests of the Central Province at an elevation of 4000 to 6000 feet". *Thwaites* C. P. 894 (K!, BM!).

Representative specimens:

INDIA. Kulhussy, Bababuden, XI 1908, 6000 ft., *Meinhold* 10473 (E); Munnar, 14 VIII 1960, 4500 ft., *J. Christopher* G. 441 (K).

SRI LANKA. Central Province, Kandy district, Knuckles Range, 3 IX 1970, 1815 m, *M. Lazarides* 7208 (K); 28 IV 1969, *Kostermans* 23354 (L); 17 X 1974, *G. Davidse* 7642 (L).

Sri Lanka and Southern India.

Hills on slopes with dense mixed herbs. Upto 1815 m.

*P. incisum* Munro ex Clarke from Northeastern India — has very similar, large spikelets, occurs in partially shady situations and has the same type of non-Kranz anatomy. *P. gardneri* differs from that species by its ovate-lanceolate leaf blades and its spikelets having glumes and lower lemmas with silvery hyaline margins.

Section *Hayata* M. Rahman
4. **P. hayatae** A. Camus in Lecomte Not. Syst. 4: 46 (1923).


**Syn.:** *Panicum costatispiculum* Ohwi in Bull. Tokyo Sci. Mus. 18: 47 (1947);
Jansen in Reinwardt. 2: 315 (1953).

**Icon.:** Fig 33.

Slender perennial. Culms 70cm to 1m, creeping and rooting at base, then erect, smooth, glabrous, yellowish, nodes glabrous, dark purplish. Leaf sheaths shorter than internodes, rather loose, striate, glabrous or with fine hairs on the margins only, ligule membranous; blades 10–20cm long, 1–1.8cm broad, lanceolate, acuminate, flat, glabrous or sparsely pilose, narrowed towards base, contracted. Panicle 13–20cm long, ovate in outline, open, well exserted, marked with axillary cushions, branches and branchlets spreading, filiform. Spikelets 3.3–3.5 (-4)mm long, ellipsoid or ellipsoid-oblong, acute, glabrous, yellowish, pedicels longer than spikelets, terete, glabrous; lower glume 3/4 the length of the spikelet, narrowly ovate-acute, not clasping, 5-nerved; upper glume boat-shaped, obtuse, strongly 11–(-13)-nerved, lower lemma similar to the upper glume, ovate, 11-nerved, male, its palea well developed, nearly as long; upper lemma much shorter than the spikelet, smooth, brown, shiny. **Fl. & Fr.:** April to January.

Type: [Indochina], “Annam: Dalat [Hayata no. 94.]” (K, holo, photo!).

**Representative specimens:**

**THAILAND.** Kuo Soi Dao Tranj, 28 IV 1930, 1800m, A. F. G. Kerr 19207 (K).

**MALAY PENINSULA.** Malacca, Fraser's Hill, Path below Methodist’s Mission, 21 X 1956, 4000ft, H. B. Gilliland 40968 (K); Malacca, 17 I 1954, van Steenis 18532 (L).
Fig. 33 *Panicum hayatae* A. Camus: *Alston* 15161 (BM)
Inset: spikelets x 3
SUMATRA. Tapanuli, Lae Pondon to Silalahi, 2 IV 1954, A. H. G. Alston 15161 (BM); 10 V 1979, J. Larzing 6605 (L).

Indochina, Thailand, Peninsular Malaysia, Sumatra.

Wooded paths or in open patches in evergreen forest. 1200m to 1800m.

This is an elegant grass with bright green leaves and greenish yellow culms. It bears much resemblance to *P. incisum* Munro, the leaves being narrowed down at base, their spikelets being ellipsoid with brown, very shiny upper lemma and palea. However in *P. hayatae* the spikelets are rather smaller, upper glume and lower lemma strongly 11- or more nerved, and the upper lemma being without any scar at base.

Section *Sarmentosa* Pilger


Hsu, Taiwan Grasses, Pl. 169 (1975).

Hsu in Li et al, Fl. Taiwan 5: 570, Pl. 1435 (1978).

BLACKSEED PANIC

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Slender perennial. Culms 30-120cm, weak, erect, geniculately ascending at base, glabrous, nodes glabrous. Leaf sheaths shorter than internodes, glabrous, ciliate on margins; ligule a fringe of hairs; blades 5-30cm long, 4-10mm broad, linear, acuminate, flat, thin, glabrous, contracted at base. Panicle (7-) 15-40cm long, very effuse, lax flowered, branches sub-solitary, branchlets capillary, few flowered. Spikelets 2-2.3mm long, ovate-oblong, acute, glabrous or sparsely puberulous, brownish or greenish black, sometimes purplish, pedicels much longer than spikelets, terete, glabrous; lower glume 1/3 the length of the spikelet, ovate or triangular, acute or obtuse, not clasping, 1-nerved or faintly 3-nerved; upper glume ovate, acute, membranous, 5-nerved; lower lemma subequal to the upper glume, ovate, acute, membranous, 5-nerved, sterile, epaleate; upper lemma ellipsoid-oblong, acute, thinly coriaceous, pale yellow, smooth, shiny. *Fl. & Fr.: September to October.*

Type: Not indicated, [Japan], UPS, Thunberg Herb. 1817, 1818 microfiche!

Representative specimens:

INDIA. Dehra Dun, 15 XI 1942, N. L. Bor 17061 (L); Assam, 27 IX 1950, W. N. Koelz 26295a (L).

AUSTRALIA. Queensland, Moreton district, 16 IV 1938, S. T. Blake 13758 (K); New South Wales, Manning River bank, 1 VI 1975, R. Coveny et al 6412 (K).

Northern and North-eastern India, China and Japan to Malaysia and Australia.

Along hillsides, margins and clearings of forests in rather swampy situations, 75-1500m.

This species is closely allied to *P. amoenum* Bal., *P. smithii* M. Rahman sp. nov. All these three species are often confused with another species *P. humidorum*.

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Buch.- Ham ex Hook. f. They may be distinguished as follows.

1. Spikelets 1.4–1.5mm long, ellipsoid, obtuse  
   \( P. \text{humidorum} \)
   - Spikelets 1.7–2.3mm long, ovate-oblong, acute  
   2

2. Lower glume 1/3 as long as the spikelet,  
   spikelets glabrous or shortly puberulous  
   \( P. \text{bisulcatum} \)
   - Lower glume 2/3 as long as the spikelet,  
   spikelets pilose towards tips  
   3

3. Panicle 20–30cm long, branches at 45\(^{\circ}\)–60\(^{\circ}\) angle with the axis; leaves 10–15cm x 8–12mm,  
   spikelets olive green  
   \( P. \text{amoenum} \)
   - Panicle 5–15cm long, branches at right angle to the axis;  
   leaves 4–8cm x 3–5mm, spikelets greenish black  
   \( P. \text{smithii} \)

6. \textit{P. smithii} M. Rahman SP. nov.  

Icon.: Fig. 34.

Slender perennial. Culms 15–35cm, 1–2mm in diameter, erect or ascending from nodes of a long creeping stolon, often rooting at the lower nodes, nodes glabrous. Leaf sheaths longer than internodes, striate, ciliate on the margins, otherwise glabrous; ligule a shortly lacerate membrane; blades 4–8cm long, 3–5mm broad, linear, acuminate, glabrous, margins slightly convolute, base rounded, median nerve obscure. Panicle 5–15cm long, broadly ovate in outline, erect, branches few, 7–10, spreading at right angles to the axis, 3–7cm long, very lax, lower branches longer than the upper ones, rachis and branches slightly scabrous, branchlets few, filiform, short, bearing few spikelets, pedicels longer or shorter than spikelets, terete, glabrous. Spikelets 2–2.3mm long, ovate-oblong, acute, pilose above the middle, geminate, greenish black; lower
Fig. 34 *Panicum smithii* M. Rahman (Holotype): *Balansa* 468 (L)
Inset: spikelets x 2
glume 2/3 the length of the spikelet, ovate, subacute or obtuse, 5-nerved, pilose at the margins, margins not membranous; upper glume as long as the spikelet, ovate, acute, pilose below the summit but less than the lower lemmas, 5-nerved; lower lemma subequal to the upper glume, ovate, acute, pilose below the summit, 5-nerved, sterile, epaleate; upper lemma obovoid-ellipsoid, acute, with a scar at base, smooth, glossy. *Fl. & Fr.: January.*

Type: Indochina, Tonkin, *B. Balansa* 468; Holotypus at L; isotypus at L, K).

Tonkin.

Sandy margins of Langson river, and in grassy patches.

The type of this new species was cited as one of the syntypes of B. Balansa's *P. amoenum* Although there is resemblance in the spikelets of the two species, they can be easily distinguished from each other as follows.

Panicle 5-15cm long, branches at right angles to the axis;
leaves small, 4-8cm long x 3-5mm broad; culms 1-2mm in
diameter. Spikelets 2-2.3 mm long, mostly caducous, greenish black

Panicle 20-30cm long, branches ascending at 45°-60° angles
with the axis; leaves large, 10-17cm long x 8-12mm broad;
culms 3-4 mm in diameter. Spikelets 1.7-2mm long, persistent, olive green

7. *P. amoenum* Balansa in Morot, Journ. de Bot. 142 (1890).

Icon: Fig. 35.

Slender perennial. Culms 1-1.8m, 3-4mm in diameter, prostrate and often
Fig. 35  *Panicum amoenum* Balansa: *Balansa* 1632 (L)
Inset: spikelets x 3
sending long aerial roots from the nodes, nodes with a dark band, glabrous. Leaf sheaths shorter than internodes, glabrous or very shortly hairy or hairs only at the margins; ligule membranous, shortly lacerate; blades 10–15cm long, 8–12mm broad, linear, long acuminate, flat, glabrous, base cordate, median nerve prominent. Panicle 20–30cm long, largely pyramidal in outline, erect, loose, spreading, rachis straight, grooved, smooth or slightly scabrous, branches numerous, 20–30, ascending and spreading at 45°–60° angle with the axis, lower branches 10–14cm long, branchlets elongated, filiform, bearing numerous spikelets. Spikelets 1.7–2mm long, ovoid-oblong, acute, pilose towards the tip, greenish, pedicels longer or shorter than spikelets, terete, glabrous; lower glume 2/3 the length of the spikelet, ovate, obtuse, 3–nerved, margins hyaline; upper glume as long as the spikelet, ovate, acute, pilose towards the tip, 5–nerved; lower lemma subequal to the upper glume, ovate, acute, 5–nerved, sterile, epaleate; upper lemma ovoid-oblong, acute, smooth, glossy. Fl. & Fr.: October.

Type: [North Vietnam], "Tu-Phap, Hanoi, Langson, dans les bois, le haies (Balansa 468, 470, 1631, 1632)". Lectotypus, Balansa 1632 (LI), isolecotypus (LI); selected here.

North Vietnam, Lankok (Mount Bavi), Ouonbi.

In grassy places, margins of streams.

Balansa no 468 is a different plant and is the basis of a new species Panicum smithii M. Rahman sp. nov. Both the species have very similar spikelets but they sharply differ in their habit, panicle branching and the shape and size of leaf blade (for a key see under P. smithii).

P. amoenum is often confused with another species, P. humidorum. This is
evident in Balansa's own material *Balansa* 1632, one of the isolectotypes of *P. amoenum* in which he has mounted both *P. amoenum* and *P. humidorum* on the same sheet. Later Dr. Th. Henrard erroneously took them both as *P. amoenum*. The origination of this error has led him (Blumea, 1941) to accept 3 Bornean specimens of J. & M.S. Clemens collected from Mount Kinabalu during the years 1932–33, – *Clemens* 28275, 28755A and 51562 (all at LI) as *P. amoenum* which are in fact *P. humidorum*.


Syn.: *P. humidorum* Buch.-Ham. in Wallich Cat. n. 8721. (1828) nom. nud.

*P. humidorum* Buch.-Ham. ex Hook. f. var. *perakense* Hook. f., Fl. Brit. Ind. 7: 54 (1896); Ridley, Mat. Fl. Malay Pen. 3: 137 (1907).

*P. perakense* (Hook. f.) Merr. in Philip. Journ. Sci. 11: 52 (1916);

Ridley, Fl. Malay Pen. 5: 226 (1925); Jansen in Reinwardt. 2,2: 317 (1953).


Robust perennial with culms up to 3m, base procumbent, creeping and rooting at the lower nodes, then erect, terete, glabrous. Leaf sheaths shorter than internodes, glabrous except the ciliate margins, terete; ligule membranous with lacerate apex; blades 10-25cm long, 6-12mm broad, linear, acuminate, base narrow, cordate. Panicle 15-30cm long, large, loose, branches numerous, capillary, smooth, branchlets bearing numerous spikelets. Spikelets 1.4-1.5mm
long, ellipsoid, obtuse, glabrous, geminate, pedicels shorter or longer than spikelets, terete, glabrous; lower glume 2/3 the length of the spikelet, ovate, 3-nerved; upper glume, ovate, acute, obscurely 5-nerved; lower lemma subequal to the upper glume, ovate, acute, 5-nerved, sterile, epaleate; upper lemma ovoid or oblong, chartaceous, smooth. *Fl. & Fr.: October to December."

Type: [India], "Assam; Goalpara, Hamilton'. Buch.-Hamilton in Wall. Cat. n. 8721 (K, holo!).

Representative specimens:

INDIA. Cachar, VI 1874, R. L. Keenan s. n. (K); Assam, Palasbari, 5 XI 1949, near sea level, T. Rupchand 2455 (K); Dehra Dun, Nuga hills, 28 X 1943, N. L. Bor 18063 (K).

BURMA. Insein district, Thadugan, 9 XI 1950, 25ft, Po Khant 1805 (K); 26 X 1947, U. Thein Lwin 352 (L).

THAILAND. Bangkok, 17 X 1920, A. F. G. Kerr 4520 (K).

MALAY PENINSULA. Johor, Sempang Kui, XI 1890, HNR 11007 (K); Johor, Buloh Kasap near Segamat, 20 XI 1946, M. R. Henderson SF 38230 (K); Perak, XI 1881, Dr. King's Collector 2546 (K).

BORNEO. Upper Kinabalu, Lamot's ridge above Kadamian, 30 XII 1933, 2500ft., J. & M. S. Clemens 51562 (K); I 1932, J. & M. S. Clemens 28275 (L); Koempa ming, F. H. Endert 1484 (L).

North-eastern India to S. E. Asia.

Jheels, rice fields, margins of pools, or in moist shady places in the forests.

Concerning *P. humidorum* var. *perakense* Hook. f. (l. c.), it should be noted that
Merrill (I.c.) raised the variety to specific rank. Having studied a multitude of specimens including the type (Perak, King's collector no. 2546, K!), I do not find any reliable basis to distinguish this form from *P. humidorum*. There are all grades of variation in the robustness of culms, breadth of leaves and the size and nervation of spikelets. Gilliland (1971) rightly merged this under *P. humidorum*.


Hsu, Taiwan Grasses, Pl. 175 (1975).

Perennial. Culms 1 to 2m, firm, smooth, sparingly branched, branches smooth and rigid, nodes glabrous. Leaf sheaths glabrous or pubescent, ciliate at margins; ligule of a fringe of hairs; blades 8–18cm long, 1–3cm broad, lanceolate, flat, thin, base broad, deeply cordate, glabrous or pilose, margins at base often pectinately ciliate. Panicle 10–30cm long, loose widely spreading at maturity, distant, very long, lower as long as the panicle, capillary, smooth. Spikelets (1.5–) 2–2.6mm long, ellipsoid or oblong, obtuse or subacute, distant, glabrous or sparsely hairy, pedicels much longer than spikelets, scabrous.
Lower glume 2/3 to 3/4 the length of the spikelet, ovate, acute, 3–5 nerved;
upper glume ovate, acute or obtuse, 5-nerved, glabrous or sparingly hairy;
lower lemma subequal to the upper glume, ovate, acute or obtuse, 5-nerved,
sterile, epaleate; upper lemma ovoid, subacute, rounded on the back, pale
brown, smooth, polished. *Fl. & Fr.: January to December.*

Type: “In Sumatra lectum dedit nuper nominatus *D. Wennerberg*” (LD, n.v.; K,
Photo!).

**Representative specimens:**

**INDIA.** Munger, 16 IX 1811, *Buch.-Ham.* 294 (E); Kumsi, Mysore, X 1908, 2000ft.,
*Meebold* 10409 (E); Malabar, *Hocks et al* s. n. (E).

**SRI LANKA.** 24 XI 1974, *G. Davidse & B. Sumitrarachchi* 8780 (L); 15 IV 1970,
*F. W. Gould* 13390 (L).

**BURMA.** Tavoy district, Tenasserim, X 1961, 800ft., *J. Keenan et al* 1825 (E);
Tavoy district, Tenasserim, *J. Keenan et al* 1792 (E).

**THAILAND.** Payap, Doi Sutep, 29 IX 1958, 700m, *Th. Sorensen et al* 5320 (E);
Payap, Wang Tao, north of Chiangmai, 13 II 1958, 800m, *Th. Sorensen et al* 1034
(E).

**INDOCHINA.** Tonkin, 4 XI 1887, *B. Balansa* 1633 (L).

**PHILIPPINES.** Luzon, Bataan, XI 1904, *A. D. Elmer* 6735 (E); 27 XII 1934,
*J.V. Santos* 6140 (L).

**SUMATRA.** 24 III 1957, *W. Meijer* 5653 (L); 30 VII 1975, *J. F. Veldkamp* 7148 (L);
4 XII 1927, *J. A. Lorzing* 12659 (L).

**JAVA.** 17 X 1913, *C. A. Bàcker* 9546 (L); 30 IV 1950, *van Ooststroom* 13825 (L).
BORNEO. XI 1915, M. S. Clemens 10028 (L); 4 III 1954, S. Darnton 267 (L).

SEONDA HILL. 29 V 1950, M. Froidville 1856 (L); 3 VIII 1937, Eyma 1521 (L).

Southern and North Eastern India, Bangladesh, S. E. Asia, China.

In lightly shaded slopes of hills, old clearings of forests at low altitudes. Upto 1200m.

Of little value as fodder (Gilliland 1971).

**P. notatum** Retz. var. merrilli (Hack.) M. Rahman Comb. nov.


This differs from the species in having narrower leaves and by the lower glume and lower lemma being equal. *Fl. & Fr.: May to December.*

**Representative specimens:**

PHILIPPINES. 27 XII 1934, J. V. Santos 6140 (L); V 1913, E. D. Merrill 9319 (L).

Philippines.

**P. notatum** Retz. var. pubescens (Boerl.) M. Rahman Comb. nov.


Distinguished from the species by its thickly pubescent, broader leaf blades. *Fl. & Fr.: February to September.*
Representative specimens:


SUMATRA. 19 IV 1917, H. Surbeck 354 (L).

JAVA. 21 II 1951, Nedi & Idjan 440 (L); 9 IV 1912, van Djokjo 2601 (L).


CELEBES. 2 V 1961, Kostermans 18641 (L).

Less common than the species.

Bor, Grass. Burm. Ceyl. Ind. Pak. 330 (1960); Ho, Cay. Mien Nam Viet. 666 (1960);

Syn.: **P. vacillans** Steud. Syn. Pl. Glum. 1: 75 (1854);

**P. sarmentosum** Roxb. var. **parvispiculatum** P.Jansen in Reinwardt.
2:318 (1953); **Synon. nov.** Type: Celebes, Kendari, Beccart.

Herb Firenze 12128 (Fl, holo, photo!).

Icon.: Ho, Cay, Mien Nam Viet. 667, Pl. 258 F (1960).


Scrambling perennial. Culms upto 15m, straggling and stretching over shrubs or small trees, woody, much branched, forming thickets, branches rooting at the nodes from which flowering branches arise, nodes swollen. Leaf sheaths hairy, hairs dense on creeping stems; ligule a short membrane with a brush of hairs; blades 25–40cm long, 1–3cm broad, lanceolate, acuminate, base rounded, hairy on both surfaces. Panicle 15–50cm long, largely pyramidal or ovate in
outline, loosely branched, sub-whorled, branches and branchlets capillary,
glabrous, peduncle glabrous, rarely with short, scattered hairs at base.
Spikelets 2–2.2 (–2.4)mm long, ellipsoid–oblong, obtuse, glabrous or slightly
hairy at the tip, shiny, nerves on glumes and lower lemmas faint, pedicel terete,
glabrous; lower glume mostly 1/2 the length of the spikelet, rarely more, ovate,
obtuse, semi-clasping, 3-nerved, upper glume as long as the spikelet, ovate,
boat-shaped, acute, 5-nerved; lower lemma similar to the upper glume, ovate,
acute, 5-nerved, sterile, its palea hyaline; upper lemma ellipsoid, subacute,
uniformly rounded on the back, yellowish brown, smooth. *Fl. & Fr.: January to
December.*

Type: “A native of Sumatra: and from thence introduced by Dr. Charles
Campbell into the Botanic Garden in 1804.” Type not indicated. The Botanic
Garden referred to is Calcutta, India.

Representative specimens:

INDIA. Assam, Khasia, *J. D. H. & T. T. s. n.* (E).

BANGLADESH. Sylhet, 10 XIII 1885, 250ft., *C. B. Clarke 42421 A* (E); Chittagong,
21 IV 1921, *J. M. Cowan 2448* (E).

BURMA. Rangoon district, Tadagale, 26 XI 1948, 50ft., *D. R. 1029* (K).

THAILAND. Puket, south of Panawng, 30 I 1958, c. 100m, *Th. Sorensen et al 852*
(E).

INDOCHINA. Vietnam, Cay-minh, 4 XI 1919, 800m, Poilane 714 (E).

PHILIPPINES. Luzon, Baatan, Mt. Mariveles, 22 XI 1903, 220ft., *R. S. Williams 217*
(K); Luzon, Baatan, Mt. Mariveles, 8 XII 1908, c. 8m, *Merrill in Kneucker 732* (E).
MALAY PENINSULA. Johor, J. B. Fielding s. n. (E, BM).

SUMATRA. Korinchi expedition 1914, H. C. Robinson & C. B. Kloss s. n. (K)

Throughout S. E. Asia, introduced to India in 1804 and found in the hills of north eastern India, Philippines, S. China.

Widespread in plains and hilly forests upto 1200m.


Differs from the species in having narrow panicles, smaller spikelets and leaf blades being 4–7mm broad.

Type: Thorel s. n. (P, holo, n. v.)

Laos.

P. sarmentosum has long been confused with Trinius’s P. incomtum, described from the Philippines. They are widely distributed straggling species scrambling over other vegetation in forests and forest margins of north–eastern India to S. E. Asia. They are very closely similar to each other and their status is therefore disputed. For example, those who consider them to be different species are: A. Chase (1939), Blake (1948), Bor (1960), Majumdar (1973); those who consider them as members of one wide-ranging, polymorphic species: Reeder (1948), Jansen (1953).

The differences noted from the type descriptions during this investigation are: Panicle ovate, composed of many, single, alternate, patent, compound, smooth branches, glumes slightly marked with green nerves in P. sarmentosum; panicle oblong, dense with pubescent axis, implicate in P. incomtum. The
manifestation of these characters is clear cut in many specimens but less so in some others, and hence puzzling. Having carried out a study and review of a large number of specimens from India and S. E. Asia, I am disposed to recognize them as two different species though in a few instances it is not always easy to recognise the differential characters. The two species may be distinguished as shown in the following table.

<table>
<thead>
<tr>
<th></th>
<th>P. sarmentoseum</th>
<th>P. incomtum</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Panicle axis and branches smooth, rarely scantily pubescent at base of the axis</td>
<td>1. Panicle axis finely densely pubescent, may be less pubescent but never glabrous</td>
<td></td>
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<tr>
<td>2. Panicle usually large, ovate in outline, branches and branchlets open, free; pedicels usually not recurved</td>
<td>2. Panicle usually oblong in outline, branches and branchlets usually entangling, viscid, pedicels usually recurved</td>
<td></td>
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<tr>
<td>3. Spikelets slightly more than 2mm long, rarely 2mm, glumes and lemmas greenish, shining, nerves obscure</td>
<td>3. Spikelets 2mm long, crowded, glumes and lemmas dull, often yellowish, nerves marked</td>
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Syn.: **P. sarmentosum** sensu Hook. f., Fl. Brit. Ind. 7: 54 (1896) non Roxb.
Scandent perennial. Culms woody up to 15m, straggling, nodes bearded, swollen, with whorls of slender, wiry roots. Leaf sheaths shorter than internodes, sparsely hairy; ligule shortly membranous with long hairs; blades 8–40cm long, 1–3cm broad, linear–lanceolate, finely acuminate, thickly, softly hairy, base narrow rounded or subcordate. Panicle 10–20cm long, oblong, globular or ellipsoid, rarely ovate in outline, usually contracted, peduncle thickly villous, less so in less dense panicle, branches capillary, subverticillate, short, often viscid, branchlets and pedicels recurved, entangling. Spikelets 1.6–2mm long, ellipsoid or ovoid, obtuse, commonly very crowded, glabrous or with a few short hairs near the tip, dull or yellowish, becoming dark when dry, nerves well marked on glumes and lower lemmas, pedicels terete, glabrous, lower glume mostly 2/3 to 3/4, sometimes about 1/2 the length of the spikelet, ovate, obtuse, 3–5 nerved; upper glume as long as the spikelet, ovate to suborbicular, obtuse, 5-nerved; lower lemma subequal to the upper glume, ovate, obtuse, sterile, its palea small, narrow; upper lemma ovoid–oblanceolate, subacute, shortly humped on the back, apex bent forward, brown at maturity, smooth. Fl. & Fr.: January to December.

Type: [Philippines], “Spp. Manill. (Chamisso)”. (LE, n. v.).

Representative specimens:

INDIA. Assam, Griffith s. n. (E); Assam, Masters s. n. (E); S. Lushai hills, 8 IV 1899, 3–4000ft, A. T. Gage 166 (E).

BANGLADESH. Chittagong Hill Tracts, Ruma, Rainkhyyong Valley, 24 I 1965, M. S.
Khan 1003 (E); Chittangong district, Cox's Bazaar, Jadi Pahar, 19 IV 1971, Khan & Huq K2469 (K).

BURMA. Myitkymia district, Watugyi, 15 XI 1911, 500ft. J. H. Lace 6310 (E, K); Kachin State, Sumprabum, 28 II 1962, 4000ft., J. Keenan et al 3757 (E).

THAILAND. Udawn, Loey, Phu Luang, 3 XII 1965, M. Tagawa et al T1035 (E); Kanchanaburi, Khao Yai, 28 III 1968, C. 800-1000m, ven Beuskom & C. Phengkhai 159 (K).

INDOCHINA. Cochinchina L. Pierre s. n. (E).

PHILIPPINES. Island of Paragua, 20 II 1903, E. D. Merrill 825 (K); Cumming 2284 (BM).

MALAY PENINSULA. Selangor, Kualalumpur, 26 XII 1963, M. Sidek 9107 (K); Kepong, 16 XI 1953, J. Sinclair SF 40169 (E, K).

BORNEO. Sarawak, Kapit, 25 V 1929, 100ft, J. & M. S. Clemens 21322 (K); Upper Kinabalu, 6000-13500ft., J. & M. S. Clemens 28300 A (K).


AUSTRALIA. Queensland, North Kennedy district, 3 VIII 1976, M. Lazarides 8131 (K); Cook district, Daintree, 21 VII 1943, S. T. Blake 14989 (K).

North eastern India down to eastern Bangladesh, Burma to S. E. Asia.

Plains and hills in forests and forest margins. Grows in a large entangling mass, straggling over other vegetation. Grows upto 2000m.
Closely allied to and often confused with *P. sarmentosum* Roxb., but see note under that species. This species is more common and widely distributed than *P. sarmentosum*


**Syn.:** *P. oblongispiculum* Ohwi in *Bull. Tokyo Sc. Mus.* 18: 15 (1947);

**Synon. nov.** Type: Sumatra, Atjeh, *v. Steenis* 8779 in Herb. Bogor. (K, L, iso!).


Fig. 36.

Slender perennial. Culms 1–2m, ascending from a creeping base, rooting at the nodes, nodes smooth, glabrous. Leaf sheaths striate, rather loose, smooth or hairy, mouth bearded; ligule ciliate, very short; blades 15–30cm long, 1.8–3cm broad, linear-lanceolate, thin, glabrous, subscabrid, base narrowly cordate, abaxical midnerve prominent, yellowish. Panicle 15–30cm long, often as broad, branches long, slender, scabrous. Spikelets 2.3–2.5mm long, ellipsoid or ellipsoid-oblong, subacute, glabrous, pedicels shorter or longer than spikelets; lower glume 1/4 the length of the spikelet, deltoid, not clasping, nerveless or obscurely 3-nerved; upper glume ovate-lanceolate, acute, 5-nerved; lower lemma subequal to the upper glume, ovate, acute, 5-nerved, sterile, epaleate; upper lemma ellipsoid-oblong, subacute, smooth, apex ciliate. *Fl. & Fr.: July to September.*

Type: [India], "Khasia Hills, in marshes, alt. 4–6000ft., Griffith, & C." Lectotypus: *Griffith* HEIC no. 6498 (K!), selected here.
Fig. 36 *Panicum khasianum* Munro ex Hook. f.: *Chand* 3631 (K)
Inset: spikelets x 2 1/2
Representative specimens:

INDIA. Kohima, Naga hills, 10-23 IX 1950, 4000ft., T. Rupchand 3631 (K);
Laitlynkot, Khasi hills, 29 VII 1949, 6000ft., T. Rupchand 1837 (K); Darjeeling, 30
VIII 1875, 6500ft., C. B. Clarke 27301 (BM).

North eastern India, Khasia and Naga hills, Sumatra.

Marshy places on hills. 4-7000ft.

A very similar plant only once collected by C. G. J. van Steenis (No. 8779) from
Sumatra bearing few undeveloped spikelets was described by Ohwi as *P. oblongispiculum*.
It resembles *P. khasianum* in all features, but the oblong shape of the spikelets, which are in an immature state and imperfectly grown.

Since in *P. khasianum* immature oblong spikelets are often found near panicle bases which gradually become ellipsoid as the grain inside grows to maturity, this character is taken as only a matter of development in this case. In fact there are one or two nearly mature spikelets that appear more ellipsoid than oblong at the ends of the panicle branches in one of the isotype specimens of *P. oblongispiculum*. Other characters of the spikelets including the ciliate apex of the upper lemma are same in both the species (Fig. 10.a,b). Transverse sections of leaf blades exhibit similar anatomical structures. Undoubtedly this species is conspecific with *P. khasianum*.

Section *Parvifolia* (Hitchc. & Chase) Pilger


Slender annual. Culms 15–120cm, decumbent, creeping and often with aerial roots from the lower nodes, finally ascending, terete, glabrous, usually leafy upto the base of the panicle. Leaf sheaths shorter than internodes, glabrous or densely ciliate at the margins; ligule very short, ciliate, blades 3–10cm long, 1–3cm broad, ovate-lanceolate, acuminate, flat, thin, amplexicaul, base obliquely cordate, glabrous or pilose, cross veined. Panicle 5–15cm long, ovate in outline, acuminate, many branched, branches capillary, spreading, rachis glabrous or with scattered hairs, sometimes villous. Spikelets 1.5–1.9mm long, asymmetric from the lateral side, ovate or oblong, acute, glabrous or sparsely puberulous to pilose, pedicels equal or longer than spikelets, terete, glabrous; lower glume almost as long as the spikelet, ovate-oblong, acute or obtuse, hyaline, (1–) 3–nerved, not clasping, separated by a short swollen internode at base; upper glume ovate, hemispheric, obtuse, herbaceous, 5–nerved, pubescent or villous; lower lemma subequal to the
upper glume, ovate-oblong, obtuse, 5-nerved, sterile or male, its palea narrow, oblong; upper lemma ellipsoid-oblong, somewhat gibbous, subcoriaceous, smooth, shiny. *Fl. & Fr:* January to December.

Type: "Habitat in India". (Linn., 80/64!). The only traceable specimen is 80/64 in the Linnaean Herbarium which fits the description as given by Linnaeus – though the material is not very well developed. This may be regarded as the holotype, however, further investigation may reveal the existence of better specimens elsewhere.

Representative specimens:

SRI LANKA. 7 I 1951, *F. Ballard* 1415 (L).

INDIA. Mysore, Aglassi, XI 1908, 3500 ft., *Meebold* 10414 (E); Mysore, Gersoppa falls, X 1908, 2000 ft., *Meebold* 10412 (E); Khasia, Walong, 8 XI 1872, 2500 ft., *C. B. Clarke* 19372 A (E).


SUMATRA. 25 VIII 1957, *Maradjo* 328 (L); 4 XII 1927, *J. Lorzing* 12668 (L).
Throughout the tropics of Asia and Africa.

Fairly commonly growing in forests and forest margins, in thickets in shady habitats trailing on the ground or on other vegetation.

*P. hirtifolium* Ridley described upon specimens from Semangkok, Malay Peninsula (*H. N. Ridley 12046*) are smaller plants with hairs on culms and both sides of leaf blades. But there are all grades of variation in the size and hairiness from the smaller to the longer plants whilst the spikelets are indistinguishable. Having checked a large number of specimens, I agree with Gilliland (1971) who includes the form within *P. brevifolium*.

**Section Monticola Stapf**


Loosely tufted annual. Culms mostly 15–40 cm, very slender, often with long creeping, stoloniferous bases, ascending and rooting at lower nodes, freely branched below, hairy at nodes. Leaf sheaths usually shorter, sometimes longer than internodes, pubescent or hispid, often with tubercle-based hairs, margins ciliate; ligule a narrow, shortly ciliolate membrane; blades 2–8 cm long, 5–22 mm broad, ovate-lanceolate to lanceolate, narrowly acute or acuminate, flat, very thin, glabrous or sparsely hispid, base broad, asymmetrically cordate. Panicle 4–25 cm long, ovate-oblong in outline, usually 2/3 or more as broad as long, with symmetrically arranged numerous fine branches and branchlets. Spikelets 1–1.5 mm long, obovoid-ellipsoid, obtuse asymmetric in side view, sparsely pubescent, pedicels longer than spikelets, scaberulous; lower glume 1/3 to 1/2 the length of the spikelet, ovate, acute, 1-nerved or obscurely 3-nerved; upper glume broad on the back, acute to obtuse, 3–5-nerved; lower lemma slightly longer than the upper glume, otherwise similar, 3–5-nerved, sterile, its palea reduced, oblong, hyaline; upper lemma ellipsoid, acute, light brown, finely rugulose at maturity, glossy. Fl. & Fr.: February to November.

Type: “Jamaica, Hispaniola.” Swartz s. n. (S, holo, n. v.).

Representative specimens:

INDIA. Dehra Dun, IX 1888, J. F. Duthie 7734 (E); Peninsular Ind. Orientalis, Wight 3206 (E); W. Bengal, Pukhuria, Manbhum, A. Campbell s. n. (E).

THAILAND. Udawan, Poo Kradeng, 22 III 1958, c. 300 m, Th. Sorensen et al 2426 (E).

INDOCHINA. Tonkin, 31 XII 1886, B. Balansa s. n. (L); 30 XI 1969, N. Van Khien 84 (L).
JAVA. 18 VI 1914, C. A. Backer 13083 (L); 19 III 1927, C. A. Backer 36934 (L).

BORNEO. 28 VIII 1938, Agama 9490 (L).

SEONDA ISLAND. 20 II 1939, J. Blaembergen 3155 (L).


CHRISTMAS ISLANDS. C. W. Andrews s. n. (E, K).

AUSTRALIA. Queensland, Cook district. 11 IV 1984, J. R. Clarkson 5266 (K); Cook district, near Cairns, 16 VI 1935, S. T. Blake 9451 (K).

Tropical America, introduced into Asia and island of the Pacific.

Waste places, shaded areas and open parts of forests. Often found as a weed of cultivated fields. 0–900m.

Very much similar to Panicum brevifolium L. in habit, but differs in its upper lemma being finely rugulose and the lower glume being half or less than half as long as the spikelet.

SUBGENUS PANICUM

Section Dura Stapf

15. P. turgidum Forssk. Fl. Aegypt. – Arab. 18 (1775).

Suffruticose perennial. Culms 40-120cm, woody with very stout rootstock clothed at base with imbricating scarious scales, prostrate or erect, much branched at the nodes, branches alternately or proliferously fascicled forming low dense bushes, nodes glabrous. Leaf sheaths terete, striate, glabrous; ligule a complete ring of hairs; blades 2-15cm long, 1-6mm broad, linear-lanceolate, acuminate, flat or margins convolute, rigid, pungent, glabrous, glaucous, smooth, slightly rounded at base, often much shorter than their sheaths. Panicle 2.5-15cm long, subpyramidal in outline, variable, of few spreading branches each carrying only a few spikelets, branches erect, glabrous or subscabrous. Spikelets (3-) 3.5-5mm long, ovoid or subglobose, ovate-lanceolate when young, turgid when mature, acuminate when young, acute to obtuse towards maturity, solitary, subsecund, broadly gaping at anthesis, pedicles shorter or slightly longer than spikelets, finely scabrous; lower glume 3/4 the length or about as long as the spikelet, broadly ovate, acute to obtuse, 5-9-nerved, separated by a short internode and inserted much below the upper glume; upper glume as long as the spikelet, broadly ovate, acute or acuminate, 7-9-nerved; lower lemma subequal to the upper glume, broadly ovate with ciliate keels, acuminate, 7-11-nerved, male, its palea almost as long; upper lemma ovoid, acute, brownish or yellowish, smooth, polished, shiny. **Fl. & Fr.: March to May.**

Type: [Egypt], “In desertis Kahirinis” Forsskal (C, microfiche!).

**Representative specimens:**
PAKISTAN. Baluchistan, Makran, 13 IV 1965, J. Lamond 440 (E.K).


North Africa through Arabia, Cyprus, Southern Iran, Pakistan to North-West India.

As low dense bushes in desert areas, stony places, coastal dunes. Upto c. 150m.

A good fodder for camels, horses, donkeys and other animals. The grain is said to be collected and used like millet for human consumption in Sahara (Bor 1968). It is a good soil binder in coastal dunes.

*P. turgidum* and another desert species, *P. rigidum* Balf. from Socotra, mark one extremity of the extraordinary ecological range of adaptation of the genus when compared with those occurring in a variety of habitats ranging from Savanna to forests and swamps and even to open water.

**Section Panicum**

16. *P. walense* Mez in Engler, Bot. Jahrb. 34: 146 (1904), as "*P. watense*".


Caespitose, slender annual. Culms 5–70cm, erect or geniculate below, often dwarf, branched, quite glabrous. Leaf sheaths shorter than internodes, loose, glabrous, often ciliate on the margins; ligule a ciliolate rim; blades 4–20cm long, 2–4mm broad, linear, acute or acuminate, flat, glabrous, base rounded, hardly cordate. Panicle 5–20cm long, ovate to oblong in outline, effuse, lax flowered, diffusely branched, branches spreading or ascending, capillary, scaberulous. Spikelets 1.5–2mm long, ellipsoid, acute or shortly acuminate, solitary, glabrous, gaping at anthesis; lower glume 2/3 to 3/4 the length of the spikelet, broadly ovate, acuminate, often obscurely awn pointed, 3-nerved, separated by a very short internode; upper glume as long as the spikelet, ovate to ovate-lanceolate, acuminate, 3–5-nerved; lower lemma slightly shorter than the upper glume, ovate, acute, 3–5-nerved, sterile, its palea nearly as long, ovate; upper lemma much shorter than the spikelet, broadly oblong, obtuse, whitish, glossy. Fl. & Fr.: January to December.

Type: [Africa, Senegal] “Senegambien, auf überschwemmten Flachen bei Wato” Leprieur s. n. (B, n. v.).

Representative specimens:

PAKISTAN. Rawalpindi, 15 IX 1959, R. R. Stewart 5411 (K).

INDIA. Bihar, Chota Nagpur, Ranchee, 22 X 1873, C. B. Clarke 21426 (E); Maharastra, Chanda district, 12 XII 1889, J. F. Duthie 9986 (E); W. Bengal, Pokhuria, Manbhum, A. Campbell, Herb. G. Watt no. 9833 (E).

SRI LANKA. Thwaites 3243 (E).
NEPAL. Near Kusma, 1 x1 1954, 3,000 ft., Stainton et al. 9230.

BANGLADESH. Bandarban district, Ruma, 28 X 1984, M. Rahman et al 1806 (E).

THAILAND. Payap, Doi Sutep, 6 X 1958, 500m, Th. Sorensen et al 5480 (E).

INDOCHINA. Tonkin, 12 IX 1885, B. Balansa 473 (L).

PHILIPPINES. 20 I 1956, J. V. Santos 6419 (L); X 1922, E. D. Merrill 4466 (L); XII 1912, J. Reillo BS no. 19191 (L).

Senegal to Sudan and south to Zambia; Indian sub-continent to S. E. Asia, southern China and Taiwan.

Common as a weed of cultivated fields in damp sandy soil. Upto 1600m.

A good fodder.

Mez was in error when naming the plant as “Watense”. He mistook “l” as a crossed “t” in the name of its type locality, correctly spelled Walo. This has caused confusion over the use of the specific epithet by many subsequent authors. However, Clayton corrected this error in transcription in Kew Bull. 20: 264 (1966).


Dwarf tufted annual. Culms 10–40cm, geniculately ascending, often hairy. Leaf sheaths thickly clothed with long white hairs; ligule long ciliate; blades 4–15cm long, 5–15mm broad, linear–lanceolate, acute, flat, hirsute, base narrow. Panicle 5–20cm long, ovate or oblong in outline, much branched, branches, branchlets and pedicels filiform, scabrous. Spikelets 1.8–2.2mm long, ovoid–ellipsoid, acute or shortly acuminate, glabrous, solitary, pedicels equal to or longer than spikelets, scabrous, lower glume 2/3 the length of spikelet, ovate, acuminate, 3–5-nerved; upper glume ovate, 5–7-nerved, acute; lower lemma subequal to the upper glume, ovate, 5–7-nerved, acute, sterile, its palea smaller, oblong; upper lemma ellipsoid, acute, orange–brown to dark–chestnut coloured, smooth, subcoriaceous, shiny. Fl. & Fr.: August to October.

Type: [Ethiopia], 'Prope Tchelat–Cheranne', Schimper 1709 (K, iso!).

Representative specimens:

PAKISTAN. Rawalpindi, 3 IX 1959, 2000ft, R. R. Stewart 28575 (E); Rawalpindi, IX 1928, R. R. Stewart 10174 (K).

INDIA. Alligargh, 7 IX 1887, J. F. Duthie 6728 (K); 12 VIII 1963, D. M. Verma 429 (L).

Eastern and central to northwest India, Pakistan. Introduced from tropical Africa.

Plains, in disturbed places and as a weed of cultivated fields.

An excellent fodder grass.

Very similar to *P. paianum* Naik & Patun. in its vegetative features and panicle branching but can be distinguished by its smaller spikelets (1.8–2.2mm long), lower glume 2/3 the length of the spikelet, upper glume 5–7-nerved, and the
dark brown fruit.


Icon.: Naik & Patunkar in Reinwardt. 9, 4: 408, fig. 3 (1980).

Slender tufted annual. Culms 6–50cm, erect or geniculately ascending, rooting at lower nodes, hairy with tubercle-based hairs, nodes glabrous. Leaf sheaths shorter than internodes, rather loose, covered with tubercle-based hairs; ligule a ciliate rim; blades 2–10cm long, 5–9mm broad, linear-lanceolate, acute, flat, glabrous or pubescent, rounded at base. Panicle 4–15cm long, ovate in outline, effuse, branches and branchlets capillary, scabrous; lower glume 1/2 the length of the spikelet, ovate, acute, 5-nerved; upper glume as long as the spikelet, ovate-lanceolate, acute, 9–11-nerved; lower lemma subequal to the upper glume, ovate-lanceolate, acute, 7-nerved, sterile, its palea well developed; upper lemma ellipsoid, acute, greenish-black, smooth, shiny. *Fl. & Fr.: October.*

Type: [India], "Holotypus: Patunkar 2430a in Herb. MU Aurangabad." (Herb. Marathwada University, holo, n. v.; K, iso!).

Maharastra, India. Endemic.

Common along water courses as well as in open grasslands.

The culm and leaf sheath covering of white spreading hairs is very characteristic of this species. This character, along with the panicle shape and capillary branches and branchlets, as well as the habit of the plant recall *P. atrosanguineum* Hochst. ex A. Rich., but see note under that species. The spikelets are, however, more closely similar to those of *P. sumatrense* Roth ex Roem. et Schult. subsp. *psilopodium* (Trin.) de Wet, and, in fact, *P. paianum* var. *minor* Naik & Patun. is a synonym of that subspecies.


Syn.: *P. capillare* Linn. var. *occidentale* Rydb. in Contr. U. S. Nat. Herb. 3: 186 (1895); Bor, Grass. Burm. Ceyl. Ind. Pak. 332 (1960);


**WITCHGRASS**

Densely hispid annual. Culms 20–80cm, tufted, erect or somewhat spreading at base, papillose–hispid to nearly glabrous, nodes densely bearded. Leaf sheaths hispid with spreading hair, longer than internodes; ligule long ciliate but lower part membranous; blades 10–25cm long, 5–15mm broad, linear to narrowly lanceolate, sharply pointed, pubescent. Panicle 15–50cm long, large and diffuse, often half or more the entire length of the plant, included at base until maturity, divaricate, the whole panicle breaking off from rest of plant at maturity. Spikelets 2.5–3.5mm long, ellipsoid, acuminate or attenuate, glabrous, pedicels much longer than spikelets, scabrous; lower glume 1/2 to 2/3 the length of the spikelet, ovate, acute or acuminate, 3–5–nerved; upper glume acuminate to attenuate; lower lemma subequal to upper glume, attenuate, 7–nerved, sterile, epaleate but occasionally developed; upper lemma ellipsoid, acute, yellowish to olive brown or pale, smooth and shiny. *Fl. & Fr.: June to November.*

Representative specimens:

PAKISTAN. Baluchistan, Ziarat, 7 VII 1982, 8000ft, Crookshank 426 (K).

INDIA. Peninsular India Orientalis, Prof. Herman s. n. (K).


Native of North America. Introduced to Pakistan and naturalised as a weed of cultivated ground in Baluchistan (Cope 1982).

This grass belongs to the class of "tumble weeds" (Bor 1960) in which the whole inflorescence breaks off at maturity. As the broken inflorescence is blown by the wind, it scatters seeds around as it rolls along.


Syn.: *P. minus* Stapf in Dyer, Fl. cap. 7: 410 (1899), non Nash (1895).

Icon.: Fig. 37.

Densely tufted perennial. Culms upto 45cm, with short, oblique rhizomes, caespitose, base decumbent, at length erect, glabrous. Leaf sheaths tight, enclosing the culm, striate, glabrous or hairy; ligule a membranous rim with long fine cilia; blades 8-15cm long, 2-4mm broad, linear, acuminate, flat or convolute, somewhat rigid, glabrous or ciliate towards base, base rounded. Panicle 7.5-15cm long, oblong in outline, open, lax, branches filiform, erect or spreading. Spikelets 2.5-3mm long, lanceolate or oblong, acute, solitary, green
Fig. 37 *Panicum stapfianum* Fourc. : *Norris* 168 (K)
Inset : spikelets x 2 1/4
suffused with purple, glabrous; lower glume 1/3 the length of the spikelet, broadly ovate, acute or acuminate, membranous, 1-nerved or sometimes with 2 weak lateral nerves, upper glume as long as the spikelet, ovate-oblong, acute or subacute, 7-nerved; lower lemma subequal to the upper glume, ovate-oblong, acute or subacute, 7-nerved, male, its palea oblong, obtuse; upper lemma ellipsoid, subacute, yellowish, smooth, shiny. *Fl. & Fr.: June.*

Type: [Lectotypus selected by Bor (1970)], South Africa, *Drege* (K!). (This is one of the specimens in the type folder named *P. minus* by Stapf).

Representative specimens:


South Africa, introduced to Pakistan but not naturalised (Cope 1982).

Rocky hillsides.

This species bears a resemblance to *P. coloratum* L., but its densely tufted habit and narrower leaf blades distinguish it from the latter species.


COOLAH GRASS

Caespitose perennial often with intravaginal stolons. Culms 15-100cm or more, stout and erect or geniculate ascending from often decumbent and branched base, nodes glabrous or rarely hairy. Leaf sheaths terete, glabrous or more or less pilose or with tubercle-based hairs; ligule a membranous ciliolate or densely ciliate very short ridge; blades 10-30cm or more long, 5-10mm broad, rarely 3cm long and 4mm broad, linear to linear-lanceolate, acute or acuminate, flat, glabrous or sparsely pilose, base slightly rounded and constricted, slightly rigid or flaccid. Panicle 4-30cm long, ovate, oblong or obovate in outline, erect or nodding, contracted or spreading, usually much branched, quite glabrous. Spikelets 2-2.5 (-3)mm long, ovoid-ellipsoid or ovoid-oblong, acute or acuminate, glabrous, green, often tinged with purple, not or moderately gaping at maturity, pedicillate with scabrous pedicels; lower glume 1/4 to 1/3 the length of the spikelet, ovate to broadly ovate, acute, membranous, cuff-like, 1-3-nerved or 3-5-nerved; upper glume as long as the spikelet, broadly ovate, acute, 7-9-nerved; lower lemma similar to the upper glume, male or sterile, its palea well developed; upper lemma oblong or ellipsoid, acute, smooth, glossy, pale or yellowish to yellow. Fl. & Fr: January to December.

Type: [Egypt], "Habitat Cairi. Forskohl" [Forsskal]. Cult. in Hort. UPS. (LINN, 80/46!).

Representative specimens:
Tropical Africa, introduced to Indian subcontinent and Australia. Wet, clayey, grassy areas to dry grassland and bushland. Also thrives in drier regions with the habit much smaller (Bor 1960). Plains to 2000m.

A fodder grass and a soil binder.

There is a wide range of variability in general habit and habitat of this grass. Clayton & Renvoise remark (1982) that the variation ranges from small spreading plants with slender culms to stout erect plants, and from subglabrous to closely hispid plants. The inflorescence increases in size with the increased height of the culms. The variation in stature, panicle size and degree of hairiness is almost continuous.

Similarly variable features are found also in plants from Pakistan and India. Though they may differ in habit but the spikelets are similar with no variation and, interestingly, the leaf anatomy is similar too. A critical study of external morphology and anatomy has revealed that two newly described species, *P. phoinicifolius* Naik & Patn., and *P. Jainii* Karthik & Raghavan from India are
indistinguishable from *P. coloratum*


**Syn.:** *Panicum oryzetorum* Balansa in Morot, Journ. de Bot. 4: 141 (1890).

**Icon.:** Fig. 38.

Caespitose annual. Culms 10-65cm, geniculately ascending, often rooting at the lower nodes, internodes hairy where exposed, nodes bearded. Leaf sheaths slightly shorter than internodes, loose, hirsute with tubercle-based hairs; ligule with a very shortly ciliolate rim; blades 8-20cm long, 4-10mm broad, linear-lanceolate, acuminate, base broad, hairy on both surfaces, rarely subglabrous. Panicle 7-20cm long, rarely shorter or longer, rather lax, axis and main branches with long scattered hairs, all branches of about the same length, with an iterative branching pattern. Spikelets 1.5-2.2mm long, broadly ovoid, somewhat turgid, obtuse, glabrous; lower glume 1/3 the length of the spikelet, ovate, obtuse, 5-7-nerved, clasping, pedicels longer than spikelets; upper glume as long as the spikelet, ovate, rather convex, acute, 7-9-nerved, nerves reticulate; lower lemma subequal to the upper glume, ovate, acute, 7-9-nerved, sterile, its palea well developed; upper lemma obovoid, obtuse, smooth, shiny. *Fl. & Fr.: January to December.*

**Type:** [Philippines], “Hab. in Luzonia.” Type not indicated, possibly *Haenke* (PR ?).

**Representative specimens:**
Fig 38 *Panicum luzonense* Presl : *den Hoed* 464 (K)
Inset : spikelets x 3
THAILAND. Near Wangka, Kwae Woi River Basin, 11 V 1946, 150m, G. den Hoed 464 (K); Kuan Karon, N. W. of Satun, 14 X 1970, Charoenphol et al. 3789 (E).

MALAY PENINSULA. Singapur, Chassevian estate, IX 1892, J. B. Fielding s. n. (E); Johore, Bukit Muar, J. B. Fielding s. n. (BM).

PHILIPPINES. Luzon, Bataan Province, X 1903, E. D. Merrill 3107 (K);Bayninan, Ifugao Mt. Province, 22 VII 1963, H. C. Conklin & Buwaya PNH 80712 (K).

S.E. Asia to India.

Abundant in open places, lowlands. Also occurs as a weed in rubber plantations and other cultivated land.

23. P. cambogiense Balansa in Morot, Journ. de Bot. 4: 142 (1890).


Hsu, Taiwan Grasses, Pl. 171 (1975).

Densely tufted robust annual. Culms upto 1m or more, stout, erect, hairy, nodes bearded. Leaf sheaths clothed with tubercle-based hairs, hairs soft, spreading; ligule a ridge of long hairs; blades 10-25cm long, 6-15mm broad, linear, flat, glabrous or more or less hairy, base narrow, subcordate, long ciliate.
Panicle 25–50cm long, sub-thyrsiform, stout peduncle with tubercle-based hairs, upright with rigid suberect branches, lower branches very long. Spikelets 2–2.5mm long, broadly ovoid, obtuse, turgid, subsessile, glabrous, red brown, pedicel scabrous; lower glume slightly less than 1/2 the length of the spikelet, broadly ovate, obtuse, clasping, 5–7-nerved, nerves anastomosing; upper glume ovate-elliptic, acute, 7–9-nerved, nerves anastomosing towards the tip, lower lemma subequal to the upper glume, ovate-elliptic, acute, 7–9-nerved, nerves anastomosing, sterile, its palea as long, membranous; upper lemma ovoid-ellipsoid, obtuse, yellow or pale brown, smooth, shiny. Fl. & Fr.: March to November.

Type: [Indo-China], “Cambodge. Godefroy 62, 257” (L!; K, No.62 fragment!).

Representative specimens:

SRI LANKA. Thwaites 3890 (K).

THAILAND. S. E. of Fang–Chiengrai trail, 26 VII 1968, 550m, Kai Larsen et al 2752 (E, L); Bhawng, Ke N. Sawan, 28 XI 1928, Peet 2162 (E).

PHILIPPINES. Sulu Province, Tawitawi, VII–VIII 1924, Ramos & Edano BS 43968 (K); Rizal Province, 10 VII 1976, J. V. Santos 7880 (L); Luzon, IX 1905, E. D. Merrill 4229.

NEW GUINEA. Madang district, 20 XII 1969, E. Henty & D. Foreman NGF 42898 (L); Sepik district, 31 X 1959, R. Pullen 1637 (L); North division, 9 VIII 1953, R. D. Hoogland 3557 (L).

AUSTRALIA. Northern Territory, 30 miles S. E. of Darwin, IV 1963, M. Lazarides 6803 (K); Humpty Doo, Darwin area, 10 II 1961, H. S. Mukee 8317 (K).

North-eastern India to S. E. Asia.
Low lands in open waste grounds, old clearings & low altitudes upto 550m. Of little value as fodder.

This species is closely allied to *Panicum luzonense* Presl but its usually larger subthyrsiform panicle and robust habit distinguish it from *P. luzonense* in which panicles are smaller with branches of about the same length and the plants themselves are smaller.


Icon.: Fig. 39.

Caespitose perennial. Culms 45-100cm, erect or ascending, sparingly braching, nodes and exposed parts of the culm tuberculate-hispid. Leaf sheaths much shorter than internodes, tuberculate-hispid like the culms and nodes; ligule a ring of stiff hairs; blades 8-20cm long, 2-4mm broad, linear, flat to partially convolute, rather stiff, papillose-piloseto strongly tuberculate-hispid. Panicle 15-35cm long, diffuse, shortly exerted, branches numerous, flexuous but rather stiff, scabrous, finally spreading. Spikelets 2mm long, ovate, acuminate, solitary, plump, abruptly short-pointed, glabrous, pedicles as long as or somewhat longer than spikelets, scabrous; lower glume 1/2 as long as the spikelet, ovate, acute, clasping, 5-nerved with one strong midnerve and 2 obscure lateral ones on either side; upper glume as long as the spikelet, ovate, acute, 7-nerved; lower lemma subequal to the upper glume or slightly shorter, ovate, acute, sterile, its palea nearly as long, hyaline; upper lemma broadly ellipsoid, acute, olive-brown, shiny. *Fl. & Fr.: February to December.*

Type: [New Guinea], “Brass 3631, collected April 11, 1933, fairly common on
Fig. 39 *Panicum viiale* Chase : *Carr* 11104(BM)
Inset : spikelets x 3
roadsides, Rona, Laloki River, Central Division." (GH, holo, n. v.; US, iso, n.v.; K, holo, photo!).

Representative specimens:

NEW GUINEA. Central Division, Kanosia, 1 II 1935, C. E. Carr 11048 (BM, L); Kanosia, 5 II 1935, C. E. Carr 11104 (BM, L); 10 V 1967, R. Pullen 6939 (L); 14 XII 1964, A. N. Gillison NGF 22054 (L).


Fairly common on roadsides, open savanna lands.

Resembles *P. cambogiense* Bal. chiefly in its tuberculate hispid leaf sheaths but differs by its lower glume being 1/2 as long as the spikelets, upper glume and lower lemma without any reticulate veins and leaf blades being narrow, stiff and pilose.


Fig. 40.

Tufted perennial. Culms 60-80cm, slender, terete, nodes glabrous. Leaf sheaths hairy, striate; ligule long ciliated; blades 15-30cm long, 6-8mm broad, linear, flat, attenuate towards base, hairy. Panicle 25-30cm long, very effuse, spikelets very distant, peduncle glabrous, branchlets capillary. Spikelets 5-5.2 (-9)mm long, ovoid, acuminate, glabrous, rachilla produced beyond the upper floret as a membranous apiculate scale, pedicel scabrous; lower glume 1/2 or
Fig. 40 *Panicum fischeri* Bor: Gamble 21316 (K)
Inset: spikelets x 2 3/4
slightly less than 1/2 the length of the spikelet, ovate, acute, glabrous, 5-7-nerved; upper glume elliptic, acuminate, glabrous, 9-nerved; lower lemma subequal to the upper glume, elliptic, acuminate, glabrous, 9-nerved, male or sterile, its palea hyaline, oblong-elliptic; upper lemma ellipsoid, obtuse, smooth, pale. *Fl. & Fr.: August to October.*

Type: [India], "Ind. or.: Madras State; Nilgiris, Kullar, 450m, Aug. 1886, J. S. Gamble 17814; ibidem, Oct. 1889, 750m, J. S. Gamble 21388 (Typus in Herb. Kew)"!

Representative specimens:

INDIA. Tamil Nadu, Cuddapah district, Mogilipenta, IX 1889, 3000ft., J. S. Gamble 21316 (K).

Endemic to Tamil Nadu, Southern India.

Hills, 450m to 900m.

Easily recognised by its large spikelets having a membranous rachilla appendage below the upper lemma.

C. E. C Fischer erroneously incorporated a note under *P. psilopodium* Trin. (now *P. sumatrense* subsp. *Psilopodium*) in J. S. Gamble's *Flora of Madras* 3: 1782 (1934). He states that the spikelets of that species have a coriaceous linear, ensiform appendage 1/3 to 2/3 as long as the upper lemma found attached to the rachilla between the two lemmas. The error had no doubt originated from his wrongly identifying 3 Southern Indian specimens of J. S. Gamble (*Gamble* 17814 (K), *Gamble* 21388 (K), *Gamble* 21316 (K)) having linear rachilla extensions below the upper lemma of the spikelets and as such annotated on the sheets "abnormal with coriaceous appendage between the
two lemmas”.

Later, these specimens formed the basis of describing the new species *P. fischeri* by Bor - the specific epithet obviously being intended to commemorate C. E. C. Fischer.


Tufted slender annual. Culms 15-100cm, erect or decumbent. Leaf sheaths glabrous or hairy; ligule shortly hairy; blades 8-60cm long, 5-20mm broad, linear to lanceolate, flat, usually glabrous. Panicle 5-40cm long, open or contracted, branches slender; spikelets 2-3.5mm long, ovoid or ellipsoid, acute, solitary or geminate, pedicels scabrous; lower glume less than 1/3 to 1/3 the length of the spikelet, ovate, acute or obtuse, 3-5-nerved, upper glume as long as the spikelet, ovate-lanceolate, acute or acuminate, 11-nerved; lower lemma subequal to the upper glume, acute or acuminate, 9-nerved, sterile, its palea oblong, upper lemma oblong to broadly ovoid, acute or apiculate, smooth, shiny.

The species was divided into two subspecies (de Wet et al. 1983) viz. subsp. *sumatrense* and subsp. *psiopodium* (Trin.) de Wet, the latter being considered to be the wild progenitor of the widely cultivated former. Previously they were treated as two different species by various authors. They have many features in common between the two and often it is hard to separate one from the other. A key is provided to distinguish the two subspecies.

Key to the subspecies:

- Spikelets 2-3.5mm long, subpersistent, pedicels usually shorter than spikelets; panicle contracted; leaf blades usually less than 9mm broad. Cultivated, but escapes *sumatrense*
- Spikelets 2–3mm long, deciduous, pedicels usually longer than spikelets; panicle open; leaf blades usually more than 9mm broad.

Wild, but sometimes in fields

26.a subsp. sumatrense Bor, Grass. Burm. Ceyl. Ind. Pak. 701 (1960);

Syn.: Panicum miliare non Lamk., Tab. Encycl. Meth. Bot. 1: 173 (1791);


LITTLE MILLET OF INDIA

Tufted annual. Culms 20–100cm, slender, erect or decumbent and rooting at lower nodes, simple or branched, glabrous, leafy upto the panicle. Leaf sheaths loose, glabrous, sometimes hirsute with a few short tubercle-based hairs; ligule a fringe of hairs; blades 30–60cm long, 6–20mm broad, linear to narrowly lanceolate, acumiante, flat, glabrous to sparsely hirsute, base rounded. Panicle 5–40cm long, oblong, open or contracted, much branched, branches erect or nodding, slender, alternate, lower branches long. Spikelets 2–3.5mm long, turgidly ovoid or ellipsoid, acute, solitary or geminate, glabrous, pedicels variable in length, usually shorter than spikelets; lower glume 1/3 the length of the spikelet, broadly ovate, acute or obtuse, 3–5–nerved, nerves arching and anastomosing at the apical region; upper glume ovate-lanceolate, acute or acuminate, herbaceous, 11–nerved; lower lemma ovate, acute or acuminate, 9–nerved, herbaceous, sterile, its palea well developed, linear-oblong, upper
lemma broadly ovoid, acute, yellowish or brownish, smooth, shiny. *Fl. & Fr.*: January to December.

Type: "In Sumatra. Heyne. E. Coromandelia quoque specimen possidemus." (K, holo, photo!).

Representative specimens:

INDIA. Bombay, 30 IX 1945, *J. Sinclair* 4476 (E); Saharanpur district, IX 1884, *J. F. Duthie* s. n. (E); W. Bengal, Pukhuria, Manbhum, *A. Campeb* 9484 (E).  


INDOCHINA. Tonkin, V 1886, *B. Balansa* 1621 (L).  

PHILIPPINES. 9 X 1970, *J. V. Santos* 7566 (L); V 1914, *E. D. Merrill* 1764 (L).  


Sri Lanka, India and S. E. Asia. 0–2100m. Considered to have originated in India (Purseglove 1972) from the wild growing subsp. *psilopodium* (Trin.) de Wet.  

Cultivated at all elevations for the grain. The crop is sown in second class garden lands at the beginning of the rains. The grain is inferior in quality to the common millet and is only cultivated and eaten by poorer class. The straw is used as a good fodder.  

Syn.: *Panicum psilopodium* Trin., Gram. Panic. 217 (1826);


*P. paianum* Naik & Patun. var. *minor* Naik & Patun. in Reinwardt. 9, 4: 408 (1980); Synon. nov. Type: India, Nanded, *Patunkar* 2439a (Herb. Mu Aurangabad, holo, n. v.; K, iso!).


Slender tufted annual. Culms 15–80cm, erect or decumbent. Leaf sheaths rather loose, glabrous or often covered with bulbous-based hairs, compressed; ligule membranous, lacerate, shortly hairy; blades 8–15 (–30)cm long, 5–10mm broad, linear or linear-lanceolate, flat, usually glabrous, or with a few short hairs at base, base subcordate. Panicle 10–25 (–30)cm long, effuse, branches long, spreading at length. Spikelets 2–3mm long, ovoid-lanceolate or ovoid-oblong, acute, geminate or solitary, often purplish, readily disarticulating at maturity, some often deformed and larger, pedicels usually longer than spikelets, scabrous; lower glume less than 1/2 to 1/3 the length of the spikelet, ovate, obtuse, membranous, 3–5-nerved, nerves anastomosing towards tip; upper glume ovate-lanceolate, acute or acuminate, herbaceous, 11-nerved; lower lemma subequal to the upper glume, ovate, acute or acuminate, herbaceous, 9-nerved, sterile, its palea narrowly oblong, hyaline; upper lemma oblong, acute, apiculate, pale yellow, smooth, shiny. *Fl. & Fr.: August to January.*
Type: "Spp. Ind. Or. (Lindley s. n. Pan. ramosi Koen. et Pan. virgati Roxb.)."

Type not found.

Representative specimens:

INDIA. Rajputana, Mt. Abu, 14 X 1887, J. F. Duthie 6730 (E); Dehra Dun, 31 X 1888, J. F. Duthie 7729 (E); Mysore, Shimoga, XX 1908, 2000ft., Meebold 10420 (E); Bombay, 11 VIII 1952, R. R. Fernandez R 101 (E); Manipur, 26 X 1950, 3500ft., W. N. Koelz 26727 (K).

SRI LANKA. Anuradhapura district, Sinharaguma, 25 XI 1969, 122m, T. Soderstrom & S. Kulatunge 171i (K); Point Pedro, Jaffna district, N. Province, 13 I 1970, 1m, D. Clayton 5208 (K); Puliyankulum, Vavuniya district, N. Province, 15 I 1970, 70m., D. Clayton 5300 (K).

NEPAL. Katmandu, 21 VIII 1954, 4,200 ft., Stainton et al 5959; Mayangdi Khola, 26 VIII 1954, 5000 ft., ibid 4032.

BANGLADESH. Cox's Bazar, Signal Hill, 18 VII 1943, J. Sinclair 3055 (E).

BURMA. Rangoon, Oakkyin, 3 VIII 1932, C. E. Parkinson 14700 (K); Rangoon University Campus, 16 VII 1951, K. R. Ramachandran 247 (K).

Sri Lanka, India, China, S. E. Asia.

Aggressive colonizer of cultivated fields, often invading fields of cultivated P. sumatrense. Sea level to 1800m.


Syn.: *Milium esculentum* Moench, Meth. Pl. 203 (1794).


Icon.: Bhide in Blatter & McCann, Bomb. Grass., Pl. 100 (1935).


Hsu, Taiwan Grasses, Pl. 174 (1975).

**COMMON MILLET, BROOMCORN MILLET, PROSO MILLET, HOG MILLET.**

Tufted annual. Culms 30–150cm, erect or geniculately ascending, often branching, sparsely to densely hispid below the nodes. Leaf sheaths terete, somewhat loose or upper tight, clothed with long spreading hairs; ligule of long hairs; blades 15–40cm long, 0.8–2.5cm broad, linear to narrowly lanceolate, tapering to a fine tip, glabrous or ciliate; cordate to amplexicaul. Panicle 15–35cm long, thyrsiform, branches fascicled, densely crowded, nodding. Spikelets 4.5–5mm long, ovate-acuminate or ovate-acute, glabrous, strongly nerved on glumes and lower lemmas; lower glume 2/3 to 3/4 the length of the spikelet, broadly ovate, acuminate, 5–7-nerved, separated by a short internode from the upper glume; upper glume as long as the spikelet, ovate, long acuminate, 11–13 (–17)-nerved; lower lemma subequal to the upper glume, ovate, acuminate to long acuminate, 11–13-nerved, sterile, its palea very small; upper lemma shorter than the spikelet, ovoid or ovoid-oblong, acute or obtuse, white to reddish-brown, very smooth and polished, shiny. **Fl. & Fr.: July to September.**

Type: “Habitat in India.” (LINN, 80/49!; BM, Herbarium Clifford 27 Panicum 4!).
Representative specimens:

PAKISTAN. Dera Ismail Khan, V 1888, D. I. K. 721 6(E); East Himalaya, Herb. Griffith 6490 (E).

INDIA. Bashahar State (Himachal Pradesh), 9 VII 1890, J. H. Lace 493 (E); Simla, 5,000ft., Maddens 802 (E); Madras, Cleghorn s. n. (E); Rajmahal, VII 1820, Roxburgh s. n. (E).

BURMA. Mandalay College Farm, IX 1921 A. Sawyer 1577.

AUSTRALIA. Queensland, Canberra, A. C. T., II 1962, H. S. Muku 8947 (K); Brisbane, Toowong, 23 XI 1934, S. L. Everist s. n. (K).


Commonly cultivated for its grain in the Indian subcontinent and Southeast Asia and other warm and temperate countries over the globe. According to Smith (1976) the crop might have been domesticated first in central or eastern Asia but an Indian or eastern Mediterranean origin has also been suggested though not known for certainty.

Used as a green fodder. Uphof (1959) cited in Bor (1960) reports that this is one of the cereal grains used in East Europe and Asia minor to produce the alcoholic beverage Braga or Busa.

Damp or dry situations up to 4000m.

There is an overall resemblance to the cultivated little millet, P. sumatrense Roth ex Roem et Schult., but P. millaceum can be distinguished by its larger spikelets, lower glume 1/2 to 2/3 the length of the spikelet and hairy nodes.
and leaf sheaths.


Tufted perennial. Culms erect upto 1.2m, branched from the base, very slender, stiff, nodes glabrous. Leaf sheaths hairy, mouth villous, ligule a fringe of hairs; blades 2–45cm long, 3–6mm broad, linear, flat, tough, mostly subradical, softly pubescent all over, base narrow. Panicle 30–45cm long, very effuse, laxly flowered, branches long and solitary, branchlets capillary, quite smooth. Spikelets 3–3.3 (~4)mm long, ovoid, acuminate, permanently gaping at maturity, pedicels scabrous; lower glume 1/2 or less than 1/2 the length of the spikelet, ovate, mucronate, 5–7-nerved, separated by an internode from the upper glume, tip purplish; upper glume ovate, long acuminate, stipitate, 7–nerved, tip purplish; lower lemma subequal to the upper glume, ovate, cuspidately acuminate, 7–nerved, sterile, its palea small; upper lemma ellipsoid-oblong, obtuse, white, smooth, shiny. *Fl. & Fr.: May to December.*

Type: "Malay Peninsula; Perak, Ridley." Perak, Lumut, Ridley 3116 (K!).

Representative specimens:


MALAYA PENINSULA. Setul, III 1910, H. N. Ridley 14865 (BM).

Malaya, Burma, Thailand, S. China, introduced to India.

Low lands and hills, rare.

Very similar to *P. trypheron* Schult., but that species may be distinguished by its lower glume being long acuminate and mostly 2/3 or slightly less than the length of the spikelet.


Syn.: *Panicum tenellum* Roxb., Fl. Ind. 1: 309 (1820) non Lamk. (1791).

*P. suis/laense* Hayata, Icon. Pl. Form. 7: 62, f. 33 (1918);

Hsu in Li et al, Fl. Taiwan 5: 578 (1978).

*P. papuanum* Mez, Bot. Jahrb. 56 (Beibl. 125): 6 (1921);


Icon.: Hayata, Icon. Pl. Form. 7: 63, f. 33 (1918).


Tufted slender annual. Culms 10–30 (~90)cm, erect or geniculate, leafy mainly at the base, glabrous. Leaf sheaths glabrous below, with few hairs above; ligule long ciliated; blades 7–30cm long, 3–9mm broad, linear or narrowly
lanceolate, suberect, flat, thin, glabrous or slightly hairy or hirsute especially on the lower surface. Panicle 10–25 cm long, ovate or broadly oblong in outline, effuse, branches long, stiff, flexuous, divaricate, scaberulous. Spikelets 2.5–3.5 (~4) mm long, ellipsoid-oblong, acuminate, glabrous except for the scabrid midnerve of lower glume, solitary or in pairs, widely gaping at maturity, pedicels capillary, scaberulous, often with a few hairs; lower glume 1/2 to 2/3 the length of the spikelet, mostly 2/3, broadly ovate, cuspidate-acuminate, 5-nerved, separated by an internode below the upper glume; upper glume ovate, recurved, sub-cuspidate, 7–9-nerved; lower lemma subequal to the upper glume, ovate, sub cuspidate, 7-nerved, sterile, its palea oblong, obtuse, rounded on the back, white to yellowish, smooth, shiny. *Fl. & Fr.: March to November.*

**Type:** Of *P. tenellum* Roxb., [India], type not indicated/found.

**Representative specimens:**

**PAKISTAN.** Multan, IX 1891, *A. V. Monro* (E).

**INDIA.** Dehra Dun, IX 1888, *J. F. Duthie* 6535 (E); Peninsular India Orient., 1837. *Wight* 3206 (E); Manbhum, Pukhuria, *A. Campbell* s. n. (E).

**SRI LANKA.** Polonnaruwa district, North Central Province, 5 miles north of Habarane, 23 II 1970, 160 m, *D. Clayton* 5867 (K); 20 miles E. of Kandy on Mahiyangana road near Urugala, 12 IV 1970, 600–700 m, *F. W. Gould* 13371 (K).

**THAILAND.** Udawn, Sitthan, 22 III 1958, *Th. Sorensen et al* 2426 (E); Chiangmai, Doi Sutep, 26 VII 1958, 450 m, *Th. Sorensen et al* 4439 (K).

**PHILIPPINES.** Luzon, district of Lepanto, XI 1905, *E. D. Merrill* 4478 (K); Island of Culion, II 1908, *E. D. Merrill* 678 (K).
Plains and low hills of Sri Lanka, India, S. E. Asia, Southern China and Taiwan.
Rare in Pakistan (Cope 1982).

Open grassland, borders of cultivated fields. Upto 1700m.

Of some fodder value.


Icon.: Bhide in Blatter & McCann, Bomb, Grass., Pt. 99 (1935).

Tufted annual. Culms 30–100cm, geniculately ascending, often sparingly branched, glabrous, smooth. Leaf sheaths hirsute with tubercle-based hair, terete, striate, ligule membranous with densely long cilia, blades 15–50cm long, 4–8mm broad, linear, acuminate, flat, straight or slightly attenuated at base, sparsely hairy or glabrous or scabrid. Panicle 25–40cm long, ovate in outline or oblong, incompletely enclosed by the uppermost leaf sheath at base, branches and branchlets spreading or ascending, stiff, wiry. Spikelets 3.5–4.5mm long, narrowly ovoid or ovoid-lanceolate, acuminate, gaping at maturity, glabrous or scabrid on nerves, pedicels longer than spikelets, scabrous; lower glume 3/4 the length of the spikelet, ovate, acuminate, inserted much below the upper glume, 5-nerved; upper glume narrowly ovate, acuminate, rounded on the back, 7–9-nerved, nerves prominent; lower lemma slightly shorter than the upper glume, 7–9-nerved, sterile, its palea well developed; upper lemma ellipsoid,
obtuse, yellowish, smooth, glossy. *Fl. & Fr.: May to December.*

Type: [Tanzania, Usambara], "Muva – Holst n. 3117" (K,isol).

**Representative specimens:**

INDIA. Jeur, Sholapur district, XII 1897, *Woodrow s.n.* (E).

Kenya, Tanzania, introduced to Maharastra, Southern India.

Margins of cultivated fields and bushlands. 0–900m.

Grains are eaten as a fast-day food, and cooked like rice. (Woodrow 1898).

Woodrow (1898) reports that the whole inflorescence breaks off and is rolled by the wind almost like the American tumbleweeds.


**Icon:** Fig. 41.

Loosely tufted annual. Culms 30–100cm, erect or geniculately ascending, terete, glabrous or somewhat hairy, nodes glabrous. Leaf sheaths shorter than internodes, loose, with tubercle-based hairs, ciliate on the margins; ligule very short papery, densely ciliated; blades 5–25cm long, 4–12mm wide, linear-lanceolate, acute, flat, both upper and lower surface with tubercle-based hairs. Panicle 15–45cm long, oblong, open, diffuse, often congestedly nodding, very lax with capillary, scabrous branches, the long pedicelled spikelets arranged toward the ends of the ultimate branchlets. Spikelets 2.5–3 (~3.5)mm long, ovate-lanceolate, or oblong, acuminate when closed, widely gaping at maturity, purplish; lower glume as long as or longer than the spikelet, caudate
Fig 41 *Panicum caudiglume* Hack. : *Ramos* BS NO. 2403 (K)  
Inset : spikelets x 3
acuminate, often cuspidate to shortly awned, 5-nerved, separated by a distinct internode and inserted much below the upper glume; upper glume shorter than the lower glume, acuminate, 5-7-nerved; lower lemma sub-equal to the upper glume, tip variable – acute or acuminate or obtuse, 5-nerved, sterile, its palea minute; upper lemma much shorter than the spikelet, ellipsoid to ellipsoid-oblong, acute, with truncate base, smooth, shiny. Fl. & Fr.: April to January.

Type: "Java: Anjer Point, leg. Ridley" [= Kneucker 731] (KR, n. v.).

Representative specimens:

PHILIPPINES. Luzon, XII 1915, M. Ramos BS no. 24083 (K); I-II 1911, E. D. Merrill 7436 (L).

MALAY PENINSULA. Malacca, 23 III 1938, Anang 270 (L).

JAVA. Besoeki, 15 VI 1918, C. A. Backer 24687 (K); VI 1950, A. Kostermans 4019 (L).

SEONDA ISLAND. Lesser Sunda, Wetar, 17-18 IV 1939, 2m, J. Ohwi 3835 (K); Kisar, east of Wonreli, 22 IV 1939, 5-200m, J. Ohwi 3839 (K); Timor, Loli, 25 I 1963, Loeters 1975 (L).


Malay Peninsula, Malesian Archipelago, New Guinea.

Common in dry, well drained fallow lands, open or shady situations, dry forests.

Occasionally used as a fodder grass.

This species bears great similarity to two other species from New Guinea viz.
*P. mindanaense* Merr. and *P. seminudum* Domin. Apart from their general resemblance in habit, they have lower glumes being 3/4 the length of the spikelet, separated by short internodes and inserted much below the upper glumes, and the spikelets being widely gaping at maturity. For a key to separate them see Blake (1969).


*P. macrocladum* Chase, Journ. Am. Arb. 20: 308 (1939);


Icon.: Biblioth. Bot. 85: 320, fig. 74 (1915), sub *P. seminudum* var. *cairnsianum* Domin.

Slender annual. Culms upto 1–1.2m, erect or ascending, glabrous, nodes often black, glabrous. Leaf sheaths much shorter than internodes, papillose to hirsute, the upper sheaths nearly glabrous below; ligule a densely ciliate ring; blades 18–30cm long, 4–7mm broad, linear, attenuate, sparsely hirsute on both surfaces or scabrous only towards the apex, margins scabrous. Panicle 40–50cm long, diffuse, nodding, shortly exserted from the uppermost sheath, branches and branchlets slender, subcapillary, scabrous, finely spreading with the spikelets mostly crowded towards the ends. Spikelets 3.2–3.5mm long, ovate–lanceolate, acuminate, glabrous, gaping at maturity, pedicels as long as to twice as long as the spikelet, scabrous; lower glume 3/4 to almost as long
as the spikelet, ovate, acuminate, 5-nerved, separated by an internode from the
rest of the spikelet; upper glume ovate, acuminate, 5–7-nerved; lower lemma
slightly shorter than the upper glume, ovate, acuminate, 7-nerved, sterile, its
palea well developed; upper lemma shorter than the spikelet, ellipsoid, smooth,
shiny.  

Fl. & Fr.: April to August

Type: "Nordost-Queensland: Savannenwalder bei Yarraba (Domin, l. 1910)." (PR,
n. v.; K, fragment!).

Representative specimens:

NEW GUINEA. Mabaduan, Western division, Fly River, IV 1936, L. J. Brass 6568
(BM); 13 VI 1973, E. Henty NGF 49700 (L); 4 VIII 1967, C. E. Ridsdale NGF 33608
(L); 15 VII 1962, R. Pullen 3302 (L).

AUSTRALIA. Queensland, Cook district, Cairns, 14 VI 1935, S. T. Blake 9365 (K).

Native of Australia. New Guinea.

Damp or swampy ground in savanna, forest and open grassland.


Merrill, Enum. Philip. Fl. Pl. 1: 65 (1923); Hitchc. Brittonia 2: 121 (1936); Reeder,

Syn.: P. mindanaense Merr. var. pilosum Reeder in J. Arn. Arb. 29:270
(1948); Synon nov. Type: Netherlands New Guinea: Waren, Kanehira &
Hatushima 13093 (A, holo, n.v.).
Densely caespitose annual. Culms 20-80cm, slender, erect or geniculately ascending at base, much branched, glabrous, nodes glabrous. Leaf sheaths shorter than internodes, loose, glabrous, or somewhat papillose near the apex, sometimes ciliated on the margins above; ligule a short ridge-like with long stiff hairs; blades 5-15cm long, 2-4mm broad, linear, acuminate, flat, ascending. Panicle 10-15cm long, diffuse, branches few, slender, filiform, rather distant, scabrous, spreading, angular. Spikelets 2-3mm long, ovate-lanceolate acuminate, glabrous except the scabrous midnerve of the glumes, purplish, gaping at anthesis; lower glume almost as long as the spikelet, ovate-lanceolate, acuminate, clasping, 5-nerved, separated by a distinct internode and inserted much below the upper glume, pedicels scabrous, longer than spikelets; upper glume ovate, acuminate, 5-7-nerved; lower lemma subequal to the upper glume, ovate, acuminate, 5-nerved, sterile, its palea about half the length, hyaline, upper lemma ellipsoid-oblong, smooth, shiny. Fl. & Fr.: August to December.

Type: [Philippines], "Mindanao, Lake Lanao, Camp Keithley, 99 Clemens". (K, holo-photo!).

Representative specimens:

THAILAND. Tung Juan, Petchaburi, 10 XI 1931, 50m, A. F. G. Kerr 20629 (K).

PHILIPPINES. Luzon, Zambales Prov., Anuling, XI - XII 1924, M. Ramos & G Edano BS No. 44622 (K).

NEW GUINEA. Lake Daviumbu, Middle Fly river, VIII 1936, L. J. Brass 7522 (BM).

AUSTRALIA. Queensland, Burke district, 18 V 1976, B. K. Simon & T. Farrell 3082
Fig. 42 *Panicum mindanaense* Merr.: Ramos & Edano 44622 (K)
Inset: spikelets x 2
Philippines, Thailand to New Guinea. Native of Australia.

Low wet ground in the open or on creek flats, common on old grass-grown garden lands, or in savanna on patches of hard ground.

34. *P. trachyrhachis* Benth. Fl. Austr. 7: 490 (1878).


*Ichnanthus harmonii* A. Camus in Lecomte Not. Syst. 3: 84 (1914);

*Synon nov.* Type: Siam, province de Siemreap, Harwand s. n. (K, holo, photo!).


*Ichnanthus harmonii* A. Camus.


*P. Kerrii* C. E. Hubbard in Kew Bull. 1927: 78 (1927); *Synon nov.*

Type: Siam, Chantabum, Makam, A. F. G. Kerr 9581 (K, holo!, BM, iso!).

Icon.: Fig. 43.

Robust semi-aquatic annual. Culms 1.3–2.5m, rigid, erect, terete, internodes long, glabrous. nodes glabrous. Leaf sheaths loose, striate, glabrous or lightly to densely tuberculate-hirsute; ligule a densely ciliated rim; blades 50–90cm long, 2–4mm broad, linear, acuminate, narrow, convolute (seldom expanded towards the distal end and then 5–6mm broad), rigid, glabrous, smooth at the abaxial surface but rough at the adaxial surface due to the presence of papilla all over, margins scaberulous. Panicle 35–100cm long, large, effuse, branches
Fig 43 *Panicum trachyrhachis* Benth. : *Clarkson 4859(K)*
Inset: spikelets x 3
numerous, long, rather rigid, scabrous, lower ones usually verticillate. Spikelets (2.5–) 3–4mm long, oblong or ovate-oblong, acuminate, solitary, shortly scabrid on mid-nerve of lower glume, otherwise glabrous, gaping at maturity, pedicels shorter or as long as spikelets, scabrous; lower glume 3/4 to as long as spikelet, ovate or ovate-lanceolate, acuminate or cuspidate, maybe aristate, 3–7-nerved, separated by an internode from the rest of the spikelet; upper glume ovate, or ovate-lanceolate, acuminate or cuspidate, 5–9-nerved; lower lemma subequal to the upper glume; ovate, acute or obtuse, 5–9-nerved, sterile, its palea well developed, ovate-oblong; upper lemma ellipsoid or obovoid-ellipsoid, obtuse, smooth, shiny. Fl. & Fr.: June to January.

Type: “N. Australia. Victoria River, Elsey; Port Darwin, Schultz, n. 343; Arnherm’s Land, M’Kinaly.” Port Darwin, Schultz n. 343 (K, lectotype!).

Representative specimens:

INDOCHINA. Phuoc Tuy, 8 I 1971, Nguyen Van s. n. (L).

NEW GUINEA. Koerik, Noord sawah, 21 VI 1962, A. Hoogerwerf 275 (L); Western district, mouth of Morehead river, C. 1 mile north of Bula village, 5 VIII 1967, R. Pullen 7015 (L, K).

AUSTRALIA. Queensland, Cook district, Mapoon, 8 VIII 1983, J. R. Clarkson 4977 (K); Northern Territory, near Brock’s creek, 25 VI 1946, S. T. Blake 16134 (K).

S. E. Asia. Native of Australia.

Edges of swampy depressions, forming dense clumps in open grasslands at low altitudes.

This species shows resemblance in spikelet form to *P. caudiglume* Hack., *P. seminudum* Domin and *P. mindanaense* Merr. However, it differs greatly in its
habit, the plants being robust with long internodes and the leaf blades very narrow, and convolute.

35. *P. virgatum* Linn. SP. Pl. ed 1: 59 (1753).


Syn.: *Panicum coloratum* Walt. Fl. Carol 73 (1788) non Linn. (1753).


Gould, Grass. Texas 455, fig. 242 (1975).

**SWITCH GRASS**

Tufted, stout perennial. Culms 1–2m., rarely 3m, with numerous scaly, creeping: rhizomes, erect, tough and hard, robust, glabrous and glaucous, nodes glabrous or pubescent. Leaf sheaths longer than lower internodes, shorter than the upper, rounded, glabrous, rarely hairy; ligule shortly membranous, densely ciliate; blades 10–60cm long, 3–15mm broad, firm, flat, elongate, glabrous but occasionally pilose. Panicle 15–55cm long, open, long exserted, many-flowered, branches slender with most spikelets in clusters. Spikelets 3–5mm long, ellipsoid-ovoid, acuminate, solitary, strongly nerved, gaping at anthesis, rather short pedicellled; lower glume 2/3 to 3/4 the length of the spikelet, broadly ovate, acuminate to cuspidate, separated by a short internode and inserted much below the upper glume, 5-nerved; upper glume longer than the lower lemma, ovate, sub-cuspidate, 5–7-nerved; lower lemma ovate, sub-cuspidate, male or sterile, its palea large, membranous; upper lemma much shorter than the spikelet, narrowly ovate, obtuse, light coloured, smooth and shiny. **Fl. & Fr.: Late August to October.**

Representative specimens:


Many regions of the United States extending to Mexico and Central America. Introduced into India as a fodder grass. Bor (1960) reports of its successful introduction to India.

Moist lowlands, open woods and salt marshes.

Used as hay and forage.

Closely allied to *P. trachyrhachis* Benth., differing in the possession of scaly, stout, creeping rhizomes, rigid culms, flat, broader leaf blades and in the possession of shorter, erect, spreading panicle.

Section *Dichotomiflora* (Hitchc. & Chase) Honda

36. *P. longiloreum* M. Rahman SP. nov.

Icon.: Fig. 44.

Aquatic perennial. Culms 2.25m, spongy, soft, compressed, glabrous, finely rooting at basal nodes, whole plant dull yellowish in appearance. Leaf sheaths usually longer than internodes, loose, glabrous, compressed; ligule membranous with 2–2.5mm long white silky cilia; blades 10–35cm long, 5–7mm broad, linear-lanceolate, acuminate, flat, glabrous, base rounded. Panicle 25–35cm
Fig. 44 *Panicum longiloreum* M. Rahman (Holotype): *Kerr* 19709 (K)
Inset: spikelets x 2
long, 3–5cm broad, oblong, elongated with branches, branchlets and spikelets somewhat appressed, the main axis soon disappearing, primary branches 10–20cm long, virgate, naked at base, scabrid, lying parallel with secondary and tertiary branches. Spikelets 2.2–2.5mm long, 0.8–1mm broad, ellipsoid to ovoid-ellipsoid, acute, glabrous, dull-yellowish, pedicels longer than spikelets, angular, scabrous; lower glume 1/4–1/6 the length of the spikelet, orbicular, membranous, clasping, obscurely nerved at base; upper glume as long as the spikelet, ovate, acute, 7–9 nerved, with a few cross nerves below the summit; lower lemma subequal to the upper glume, ovate, acute, 9-nerved, with few cross nerves below the summit, sterile, its palea about as long, narrow, hyaline; upper lemma 1.7mm long, 0.8–0.9mm broad, ellipsoid to broadly ellipsoid and yellowish to tawny as it grows to maturity, acute, smooth, polished, shiny, the 7 nerves slightly marked as pale stripes, its palea of same texture. Fl. & Fr.: September.


Thailand, South Vietnam.

Flooded rice fields.

*P. longiloreum*, *P. paludosum* Roxb., *P. repens* L. and two other species from Africa, *P. subalbidum* Kunth and *P. schinzii* Hack. have apparently similar spikelets with lower glumes c. 1/4 as long as the spikelets, membranous, broadly ovate to sub-orbicular, cuff-like, and clasping the base of the spikelets. Another species with closely similar spikelets, *P. dichtomiflorm* Michx., a North American annual weed, has become widely naturalized in Japan and Taiwan and is likely to be found in Indochina though Southern China. All are moisture
loving species and can grow even in aquatic habitats. The species may be
distinguished as follows.

1. Ligule membranous to coriaceous, shortly ciliate with 0.5–1mm
   long cilia; culms with rhizomes short and early disintegrating
   or long, creeping and widely spreading  
   - Ligule membranous with long silky hairs about 
   2mm in length, culms not rhizomatous  2

2. Leaves distichous, stiff, hairy at base; rhizomes
   long creeping and widely spreading; lower glume
   suborbicular, truncate or obtuse  
   - Leaves not distichous not stiff, glabrous
   at base; rhizomes short and early
   disintegrating; lower glume broadly
   ovate, acute or obtuse  
   $ P. repens $

3. Plant annual  
   - Plant perennial  

4. Lower floret male  
   - Lower floret sterile  

5. Spikelets 3–4mm long, narrowly
   lanceolate, acuminate  
   - Spikelets 2–2.5mm long, ellipsoid, acute


Stapf in Fl. Trop. Afr. 9: 715 (1920); Merxmuller, Prod. SudwestAfrik. 160: 142

Syn.:  $ Panicum laevifolium $ Hack. in Bull. L'Herb. Boiss. 3: 378 (1895);

SWEET PANIC

Tufted, slender annual. Culms 25-120cm, fascicled, erect or subgeniculate at base, glabrous, branches soft, smooth, nodes glabrous. Leaf sheaths shorter than internodes, loose, terete, glabrous; ligule a long, densely ciliate, narrow, membranous ring; blades 7-30cm long, 4-8mm broad, linear-lanceolate, flat, glabrous, smooth, base broadly rounded. Panicle 15-35cm long, ovate or more or less oblong in outline, effuse, erect, branches and branchlets finely filiform, scaberulous. Spikelets 2-2.3 (-2.5)mm long, ellipsoid or ovoid-oblong, acute or shortly acuminate, glabrous, pale or tinged with purple, or slightly brownish; lower glume 1/4 or less the length of the spikelet, very broadly ovate, obtuse or truncate, clasping, one-nerved or sub-3-nerved, membranous; upper glume ovate-oblong, acute, 7-9-nerved; lower lemma subequal to the upper glume, ovate-oblong, 7-9-nerved, male, its palea almost as long, oblong, obtuse; upper lemma oblong, smooth, subacute, whitish to yellowish, glossy. Fl. & Fr.: September to February.

Type: [South-West Africa], "Standort: Olukonda, Ondonga Stamm (Amboland)." H. Schinz 641 (Z, possibly).

Representative specimens:

AUSTRALIA. Western Australia, Tambellup, 20 II 1920, T. H. Hall K 151 (K); New South Wales, Glen Innes, 8 IV 1931, 3520ft., C. E. Hubbard 8210 (K).

No representative specimens have been seen from India or Southeast Asia.
Fig 45 *Panicum schinzii* Hack. : *Warton* 438 (E)
Inset : spikelets x 2 1/2
Native to South Africa, introduced into India. Cultivated and naturalised in many warm countries including Australia as a fodder grass; found here and there in Malaysia, cultivated in Java (Jansen ms.).

Swampy areas and wet places in open grasslands. Upto 5100 feet.

According to Bor (1960) it is made into an excellent hay which is relished by stock in South Africa.


Syn.: *Panicum proliferum* sensu Hook. f. Fl. Brit. Ind. 7: 50 (1896);

Mezin Perk. Frag. Fl. Philip. 143 (1904) non Lamk.,


Hsu, Taiwan Grasses, Pl. 176 (1975).

SWAMP PANIC

Aquatic perennial. Culms 25–130cm, spongy, floating, base climbing in mud, erect or ascending from the creeping lower portion, rooting at the nodes, nodes glabrous. Leaf sheaths mostly longer than internodes, loose.
compressed, glabrous, smooth; ligule a ridge of long silky hairs; blades 15-36 cm long, 6-16 mm broad, linear to ensiform, blunt or acute, glabrous, margins serrulate, base broad, sometimes cordate. Panicle 10-35 cm long, ovate or oblong in outline, at first contracted, ultimately spreading widely, branches fasciculate below, angular, scabrid, trigonous, rachis scarcely distinct from the branches. Spikelets 3-4 mm long, solitary or in pairs, narrowly lanceolate, acuminate, glabrous, pedicels longer than spikelets, slender, scabrous, nearly parallel to the axis bearing them; lower glume less than 1/4 the length of the spikelet, orbicular, hyaline, clasping, obscurely nerved; upper glume ovate, acuminate, 7-9-nerved; lower lemma subequal to the upper glume, lanceolate, acuminate, 9-nerved, sterile or male, its palea reduced, linear-oblong, upper lemma oblong, acuminate, coriaceous, pale yellow, smooth, shiny. **Fl. & Fr.: January to December.**

Type: [India], "it grows generally in sweet water amongst the Cirpar mountains". Type not found (there is a specimen of this plant in herb. Forsyth (K!) attributed to Dr. Roxburgh, E. India which may be taken as being authentic *P. paludosum* Roxb. although the name is not written on it).

Representative specimens:

**INDIA.** Hissar, Hariana, autumn 1884, *Meebold* s. n. (E); Shaharanpur, Govt. Garden, VIII 1884, *J. F. Duthie* s. n. (E); Mysore, Hassan district, 22 I 1970, *C. J. Sardanha* 16108 (E).

**SRI LANKA.** Anuradhapur district, Kahatagasdigillia, 27 XI 1969, c. 70 m, *T. R. Soderstrom & S. Kulatunge* 1727 (K); Eastern Province, Ampara district, 3 XII 1974, 3 m, *G. Davidse & D. B. Sumitrarachchi* 8962 (K).

**NEPAL.** Pokhara, 7 IX 1954, 3,500 ft. *Stainton et al.* 7127.
BHUTAN. Gaylegphug, 29 V 1979, C. 300m, *Grierson & Long* 1437 (E).


BURMA. Insein district, Tadagale, 14 IX 1950, 50ft., *P. Khant* 1340 (K); Manhkapng, 5 miles N. of Myitkyina, 6 VII 1958, 150m, *H. S. McKee* 6265 (K).

THAILAND. Chiangmai, 26 X 1909, 300m *A. F. G. Ker* 858 (E); Rachasima, c. 100km north of Korat, 24 III 1958, c. 400m, *Th. Sorensen et al* 2506 (E).


PHILIPPINES. Luzon, Manila, 19 VII 1902, *E. D. Merrill* 97 (K); Baguio, Province of Benguet, III 1904, *E. D. Merrill* 5972 (K).

SUMATRA. 27 V 1921, *J. A. Lorzing* 8434 (L); 27 II 1937, *van Steenis* 9381 (L).

JAVA. 25 XII 1940, *P. Buwalda* 8030 (L); 19 III 1950, *van Oostsroom* 13018 (L).

NEW GUINEA. Kajabit Mission, 18 IX 1939, 900ft. *M. S. Clemens* 10696 (E).

AUSTRALIA. Queensland, Moreton district, 28 II 1934, *S. T. Blake* 5229 (K); North Kennedy district, Cromarty, 27 III 1935, *S. T. Blake* 8291 (K); Northern Territory, *F. Mueller* s. n. (K).

Tropical Asia, Southern China, southwards to New Guinea, Australia.

Lowland swamps, marshes.

“A fodder grass but as it is of a coarse nature, cattle are not fond of it” (Roxburgh 1820).
Bor incorrectly quoted the type of this species as: "Bengalen, Boruti, and Kulus-nar; Teling., Soda," Roxburgh, in Bor in Rech. f., Fl. Iran. 70: 471 (1970). These are merely vernacular names of the species as mentioned by Roxburgh in Flora Indica (1820), meaning, in Bengali, Boruti, and Kulusnar; Telegu, Soda, i.e. 'Bengalen and Teling' are latinised names for two languages of the Indian subcontinent.

*P. paludosum* is often confused with *P. repens* especially when the latter grows in aquatic situations with its culms becoming much softer, leaves longer and not so stiff. *P. paludosum* can be distinguished by its narrowly lanceolate, slightly larger spikelets, silky long ciliated ligule and the leaf blade base being completely glabrous.

**Section Repentia** Stapf

**39. P. repens** Linn. SP. Pl. ed. 2: 87 (1762).


*P. miliare* Mez in Perk. Frag. FI. Philip. 142 (1904) non Lamk.

*P. deccanense* Naik & Patunkar in Reinwardt. 9,4:405 (1980) et in Patunkar, Grass. Marath. 154 (1980); **Synon. nov.** Type: [India], Nanded, Degloor, 24 September 1974, Patunkar 2350a (Herb. Marathwada Univ. Aurangabad, holo; K, iso, not found).
TORPEDO GRASS, TORPEDO PANICUM, COUCH GRASS.

Creeping perennial. Culms 30–100cm, with long horizontal, stout, scaly, widely spreading rhizomes, tough and strict, erect or ascending, often from a knotty base clothed with bladeless sheaths, nodes glabrous or the lower ones hispid. Leaf sheaths glabrous or ciliate at the margins, chiefly near the mouth; ligule a ciliated coriaceous ring; blades 5–30cm long, 2–8mm wide, linear, acuminate, flat or the sides folded especially when dry, distichous, commonly stiff and pungent, plants growing in more hygrophilous habitats often have rather soft culms and leaves, often glaucous, smooth, glabrous but pilose at base near ligule on the adaxial side, base rounded. Panicle 5–20cm long, narrowly oblong in outline, often contracted, irregularly branched, the somewhat distant branches stiffly ascending, scaberulous. Spikelets (2.2–) 2.5–3 (~3.2)mm long, ovoid-lanceolate or ellipsoid, acute or acutely acuminate, solitary or geminate, white or pale, sometimes tinged with purple, glabrous, sessile or shortly pedicillate, pedicels scabrous; lower glume 1/4 the length of the spikelet, sub-orbicular, truncate or obtuse, almost cup shaped, hyaline, clasping the base of the spikelet, nerveless or obscurely 3-nerved; upper glume ovate, acute to subacute, membranous, 7–9-nerved; lower lemma subequal to the upper glume, ovate, acute or subacute, 7–9-nerved, male or sterile, its palea well developed or reduced; upper lemma ellipsoid-oblong, acute, smooth, pale. Fl. & Fr.
Type: "Habitat in Hispania? inde missum a claud. Alstroemer" (LINN, 80/47 & 80/48 !).

Linnaeus gives his own diagnosis and refers Alstroemer’s collection. The specimen in the Linnaean Herbarium, 80/47, appears to be a good case for regarding it as the holotype but further investigation of Alstroemer’s collections elsewhere at SBT & UPS may be required. 80/48 pinned to 80/47 is the same.

Representative specimens:

INDIA. Hydrabad, 7 VIII 1979, 600m, *van der Maesen* 3869 (K); Mysore, Hassan district, 7 VIII 1970, *T. Ramamoorthy* HFP 260 (E); W. Bengal, Ranigonj, 11 X 1894, *J. D. Nusker* 1146 (E).

SRI LANKA. East province, Ampara district, 3 XI 1972, *Van cuylenberg* Gt 60 (K); 20 X 1974, *G. Davidse* 7809 (L); 11 I 1970, *Clayton & Albert* 5172 (L).

BANGLADESH. Jessore, 15 VI 1874, *C. B. Clarke* 21776 (E); Chittagong, 15 IV 1920, *J. M. Cowan* 721 (E).

THAILAND. Chiang Mai, Doi Suthep, 8 IX 1967, 350–700m, *K. lwatsuke* et al 9435 (E); Bangkok, 10 VI 1923, *A. F. G. Kerr* 7065 (L).


PHILIPPINES. Luzon, Manilla, 26 VIII 1955, *M. L. Steiner* 655–A (L); 26 XII 1963, *J. V. Santos* 7377 (L).

SUMATRA. 7 V 1957, W. Meijer 5770 (L); 24 III 1926, J. A. Lorzing 184 (L).

JAVA. 2 II 1951, Nedi & Idjan 66 (L); 4 X 1978, A. P. Everaarts 378 (L).

BORNEO. 6 X 1955, W. A. Brooke 10627 (L); 8 X 1940, P. Buwalda 7970 (L).

CELEBES. 12 X 1975, J. F. Veldkamp 6978 (L); 29 XII 1953, van Steenis 18639 (L).

AUSTRALIA. Queensland, Moreton district, Wynnum, 17 XII 1959, S. McDonald s. n. (K).

Throughout the tropics and subtropics of both hemispheres especially in the coastal areas.

Lowlands in marshy situations, rice fields, margins of rivers and lakes, maritime beaches, usually prefers sandy soil but also grows on dry slopes of hills. Sea level to 2000m.

It is a good pasture grass, often cut for fodder. It may become a very pernicious weed but is an excellent soil binder because of the presence of its strong, well developed rhizomes. The rhizomes are reputed to be used as a remedy against inflammation (Jansen, ms.).

In Pakistan, this widely distributed plant has been introduced but apparently has not persisted (Cope 1982).

SUBGENUS AGROSTOIDES Zuloaga (in press)

Section Antidotalia M. Rahman

BLUE PANICUM

Stout perennial with creeping villously sheathed stoloniferous rootstock. Culms 30-185cm, rarely 3m, erect or ascending, firm or hard, often glaucous, much branched and bushy when old, nodes thickened or swollen, pubescent. Leaf sheaths shorter than internodes, quite smooth; ligule papery with a fringe of hairs; blades 5-35cm long, 3-15mm broad, linear, acuminate, flat, glabrous or the lower ones pubescent, base narrow, rounded. Panicle 10-35cm long, narrowly pyramidal to broadly oblong or ovate in outline, open or somewhat dense and contracted, branches slender, glabrous, subverticillate to sparingly divided. Spikelets 2.5-3 (-3.6)mm long, ellipsoid or broadly ovoid, acute, clustered or solitary, shortly pedicellate, pedicels scabrous; lower glume 1/2 to 2/3 the length of the spikelet, broadly ovate with broad membranous margins, acute, 3-5-nerved; upper glume ovate, acute or obtuse, 5-9-nerved, margins broadly membranous; lower lemma resembling the upper glume, male, its palea almost as long and large; upper lemma ovoid or oblong, acute, smooth and shiny. Fl. & Fr.: March to December.
Type: [India], "Colitur in hortis Malabarorum. Honor. Koenig." J. Koenig s. n. (BM, holo; K, holo, fragment!).

Representative specimens:

PAKISTAN. Peshawar, near Akora, 15 IV 1958, Burtt 558 (E); Kohat, SE of Cherat, 12 VIII 1958, Burtt 1073 (E); Attock, Jand to Fatehjang, 14 VIII 1958, Burtt 1092 (E); Jhelum, 11 X 1902, Kabir in J. R. Drummond 14751 (E); Karachi, Bhabra Road, 18 XII 1968, Asad Raza 66 (E).

INDIA. Hariana, Hissar district, 28 III 1904, Kabir in J. R. Drummond 15234 (E); Hissar, 1884, Coldstream s. n. (E); Punjab, Hosiarpur, A. Meebold 8785 (E).

SRI LANKA. R. B. G. Peradeniya, 19 IV 1962, 1,550 ft., J. T. Ekanayake 13 (K); Thwaites 971 (K).


JAVA. Djakarta, 4 III 1953, van Leewen 6 (L).

AUSTRALIA. Queensland, Port Curtis district, near Grantleigh, 16 V 1956, S. T. Blake 19978 (K); Moreton district, Gatton Agr. College, cult. on farm, 1 IV 1931, C. E. Hubbard 8102 (K).

Pakistan, NW India, Sri Lanka, Afghanistan, throughout Iran, Arabia. Introduced to tropical Africa, Australia, U.S.A. Naturalised in New Guinea as a weed on livestock stations (Jansen, ms.).

Sand dunes, dry sandy places and desert regions. 200-1065m.

An excellent soil binder. Its value as a fodder grass is doubtful (Duthie 1886). Reported to have medicinal use (Thwaites 1864).
Anatomically a Kranz M. S. species. The only other representative of M. S. species in this study is *P. plenum* which is an introduced plant from North America. Both species are erect perennials with stout rootstock and possess indistinguishable ligules, but otherwise they sharply differ especially in panicle and spikelet characters.

Section **Bulbosa Zuloaga** (in press)


Syn.: *Pan/cum garadel* Ragh. & Karthik in Bull. Bot. Surv. Ind. 24, 1–4: 146 (1982); **Synon nov.** Type: India, Karnataka, Dharwar, L. D.

*Garadei* s. n. (CAL, holo, n. v.; K, isol).

Icon.: Hitchc. & Chase in Contrb. U. S. Nat. Herb. 15: 80, fig. 69 (1910).

Large clumped perennial. Culms 1 to 2m, erect from a stout rootstock, firm, compressed when dry, mostly glaucous, nodes glabrous. Leaf sheaths striate, somewhat keeled, compressed, margins membranous; ligule shortly membranous with a fringe of cilia; blades 20–35cm long, 4–14mm broad, linear, acuminate, flat, glabrous or sometimes hairy. Panicle 10–50cm long, open, more or less spreading, branches slender. Spikelets 3–3.5mm long, oblong-ellipsoid, acute, solitary or geminate, glabrous, pedicels angular, scabrous; lower glume 1/2 the length of the spikelet, broadly ovate, acute, 3–5-nerved; upper glume as long as the spikelet, ovate-lanceolate, acute, 5–7-nerved; lower lemma subequal to the upper glume, ovate-lanceolate, acute, 5–7-nerved, sterile, its palea about as long, oblong, hyaline; upper lemma ovoid-ellipsoid, acute, obscurely rugose, apex minutely pubescent. *Fl. & Fr.*
May to September

Type: "Type U. S. National Herbarium no. 495701, collected September 18, 1903 at Mangas Springs, 18 miles north-west of Silver City, Grant County, New Mexico, by O. B. Metcalfe (no. 739), altitude 4770ft." (US, holo, n. v.).

Representative specimens:


Native of North America, introduced to Pakistan and India.

Moist places in rocky hills.

*P. garadei* Karth. & Ragh. from India is synonymous with *P. plenum*. It is based on a single collection of L. D. Garade in 1907 from Southern India and said to differ from *P. maximum* Jacq. An investigation of the isotype material shows that the distinguishing characters between this species and *P. maximum* are the same as those between *P. plenum* and *P. maximum*. The faintly rugose upper lemma of *P. garadei* simulates a striolate appearance as also found in *P. plenum*. The morphological similarity of the two species is further evidenced by their common type of leaf blade anatomy, namely, Kranz M. S. together with an unusually prominent abaxial keel. *Panicum antidotale* is the only other Indian species in which this type of anatomy is found.

It is evident from the vain efforts of the authors to discover more sites for this plant that *P. plenum* an introduced species from North America has apparently not become naturalised in Southern India, just as it has not in Pakistan (Cope 1982).

SUBGENUS MEGATHYRSUS Pilger


**Syn.:** *Panicum jumentorum* Pers, Syn. Pl. 1: 83 (1805).


**Icon.:** Jacquin. l.c. Pl. 1, t. 13 (1781-86).


Gilliland, Rev. Fl. Malay 3, Pl. 17a & fig. 24 (1971).

Hsu in Li et al, Fl. Taiwan 5: 575, Pl. 1438 (1978).

**GUINEA GRASS**

Loosely to densely tufted perennial. Culms upto 3m, with a short sometimes stout rhizome, erect or geniculately ascending, branching, branches terete or compressed below, glabrous and smooth or hirsute and rough, nodes glabrous or bearded. Leaf sheaths firm, compressed, often bearded at the mouth; ligule leathery, ciliate and often with dense beard at the abaxial side; blades 30-60cm long, 1.2-3.5cm broad, broadly linear or linear-lanceolate, acuminate, flat, glabrous or sparsely pilose or pubescent, narrowed or straight at base. Panicle 12-45cm long, oblong or pyramidal in outline, erect or nodding, much
branched, lower branches whorled, erect, filiform, smooth or scaberulous. Spikelets (2.5-) 3.2–3.8mm long, oblong or narrowly ellipsoid, rounded on the back, somewhat turgid, acute or obtuse, glabrous or pubescent, light to bright green; lower glume 1/3 to 1/4 the length of the spikelet, broadly ovate, acute or obtuse, nerveless or weakly 3-nerved; upper glume ovate-oblong, acute, 5-nerved, lower lemma subequal or slightly shorter than the upper glume, ovate-oblong, 5-nerved, male or rarely sterile, its palea well developed; upper lemma ellipsoid-oblong, acute, transversely rugose, its palea similar in texture.

Fl. & Fr.: January to December

Type: [Lesser Antilles], "in insula Guadeloupe Sponte crescit". Herb. Jacq. (W, holo, n. v.).

Representative specimens:

INDIA. Madras, below Ootacamund, 4 III 1948, 5000ft., W. Koelz 19875 (E); Eastern Pen. India, J. Campbell s. n. (E).

SRI LANKA. Central Province, Peradeniya, 19 I 1970, 500m, D. Clayton 5345 (L).

PHILIPPINES. 23 XI 1974, J. V. Santos 7701 (L); 10 X 1909, E. D. Merrill in Kneucker 819 (L).

MALAY PENINSULA. Singapur, Junction of Cluny Road and Bukit Road, 30 IX 1948, J. Sinclair 5280 (E); Singapur, Tanglin, IX 1982, J. B. Fielding s. n. (E).

SUMATRA. 4 X 1928, J. Larzing 14022 (L); 23 X 1917, Bunnemeyer 1711 (L).

JAVA. 6 III 1894, V. Schiffner 1529 (L); 26 XII 1925, Wansen 6262 (L).


NEW GUINEA. 23 I 1963, E. Henty NGF 14896 (L); 24 II 1950, D. Fryar NGF 4047
AUSTRALIA. Queensland, South Kennedy district, near Eungella National Park, 7 IV 1978, B. K. Simon 3313 (K); Moreton district, Kalinga Park, 25 IV 1930, C. E. Hubbard 2390 (K).

Native of Africa, widely introduced throughout the tropics of both hemispheres due to its fodder value.

Shady or open situations. Usually on damp sites. 0–2400m.

Considered as one of the best fodder grasses. Cultivated widely in the Indian subcontinent.

*P. maximum* resembles *P. plenum* Hitchc. & Chase in habit and in the spikelets being oblong, but is very distinct in its lower glume being 1/3–1/4 the length of the spikelet and the strongly rugose upper lemma and palea. It is a considerably variable species (Clayton & Renvoize 1982). The distinguishing characters described for subspecies *pubescens* Sharma are not dependable. The correlation between pubescent spikelets and male lower floret in subsp. *pubescens* and between glabrous spikelets and barren lower floret in the typical subspecies cannot be maintained because in the many Indian specimens examined, I have found glabrous spikelets with male lower floret. Sometimes both male and sterile lower floret may even be found in the same panicle. The characters of length and indumentum of spikelets are also variable. Reports of spikelets being glabrous or sparsely hairy may be found widely in the literature including Hooker's *Flora of British India* (vol. 7: 49). Varieties earlier described from specimens with pubescent spikelets cannot be reliably recognised as formal taxa because of the continuity of variation in these characters (Clayton & Renvoize 1982).

This species was originally described by Steudel in 1854 in his *Synopsis Plantarum Glumacearum*. It is a species endemic to Sri Lanka and Southern India. After the erection of the genus *Cyrtococcum* by Stapf, A. Camus (1921) transferred the species from *Panicum* to *Cyrtococcum* (*C. sparsicomum* Nees ex Steud.) A. Camus in Bull. Mus. Hist. Paris 27:118 (1921). Bor (1960), however, was of a different opinion and maintained its original position in *Panicum*. Anatomically, the species is a non-Kranz C3. *Cyrtococcum* is typically a non-Kranz genus, while *Panicum* includes both non-Kranz and Kranz species.

I have critically studied the species to evaluate its systematic position. The diagnostic characters of *Cyrtococcum* suggest that this species should be in *Cyrtococcum* not in *Panicum*. The species is unusual in *Panicum* with its laterally compressed spikelets, gibbous, thin upper lemma, and upper glume longer than lower lemma— which characters are diagnostic to the genus *Cyrtococcum*. *Panicum*, on the other hand, has typically dorsally compressed, symmetrical spikelets, dorsally rounded, coriaceous upper lemma, and upper glume typically subequal to the lower lemma. Furthermore, overall features of plant habit with filiform, diffusely branched, almost capillary culms, panicle with few capillary branches and branchlets borne on a filiform peduncle indicate affinity of the species to *Cyrtococcum* rather than *Panicum*.

In my opinion therefore, the transfer of the species to *Cyrtococcum* by A. Camus (l.c.) is justified. This is further indicated by numerical analysis of characters from macro- and micromorphology, and anatomy, as shown in Phenogram 2 (Fig. 31) in Chapter 9.
2. *Panicum auritum* Presl ex Nees, Agrost. Bras. 176 (1829); Presl. Rel. Haenk. 1:305 (1830)

The systematic position of this species was first changed by Balansa (1890) who placed it in *Hymenachne*. It was again changed by A. Camus (1922) when she transferred the species to *Sacciolepis*. Ohwi (1947) also maintained the species under *Sacciolepis*. The original position of the species was restored by Bor (1960). *P. auritum* is a non-Kranz species. Both *Hymenachne* and *Sacciolepis* are non-Kranz genera while *Panicum* includes both non-Kranz and Kranz species.

I have made a critical study of this species and of the genera *Hymenachne* and *Sacciolepis*. The principal features which characterise the genus *Hymenachne* are: a spiciform panicle, membranous upper lemma clasping the palea below but free towards tip. In *P. auritum* the panicle is never spiciform, though not typically effuse; the upper lemma is not membranous but tough though not typically coriaceous. The upper lemma and its palea is not free at the tip, and the former grips the palea by its entire margin. Hence it appears that though *P. auritum* with its condensed panicle and thinly coriaceous upper lemma does not represent a true *Panicum* it introduces a discordant element in *Hymenachne*. It is a natural genus of five species, particularly by virtue of its membranous upper lemma with free palea tips. I have therefore decided not to transfer the species to *Hymenachne*.

Regarding its position with *Sacciolepis*, a critical study indicates that the genus is characterised by a spiciform panicle with stout rachis, asymmetrical and obliquely obovate, laterally compressed spikelets, prominently ribbed glumes and lower lemma, saccate, upper glume and a thinly coriaceous to cartilaginous upper lemma. *P. auritum* has a contracted panicle without any tough rachis,
spikelets symmetrical and dorsally compressed, glumes never ribbed, and upper glume never saccate. When found with an open or contracted panicle, this with the thinly coriaceous to cartilagenous upper lemma, could confuse *Sacciolepis* spp. with *P. auritum* but the gibbous spikelet with saccate upper glume and ribbed glumes and lower lemma afford distinctive features of *Sacciolepis* which do not allow inclusion of *P. auritum* into that genus. My view is that the species should be retained in its original genus *Panicum*. A further discussion will be found in Chapter 9, on the basis of results obtained by numerical analysis.


There is a specimen in the herbarium of the Royal Botanic Garden, Edinburgh lacking any written detail other than an initial by 'Roxburgh' and the stamp 'INDIA' on the back of the sheet. The specimen was determined as *Panicum fasciculatum* Sw. by Bor in 1950. However, he did not incorporate this in his 'Grasses of Burma, Ceylon, India and Pakistan' published in 1960. The determination is correct, it is *P. fasciculatum* Sw., an American annual weed, but the specimen is too lacking in information to be very helpfully reported from India. I searched for other Indian specimens of this species in different herbaria, but found none.
12.1 Introduction

The object of this chapter is to provide in brief a general idea of the topographic, climatic and phytogeographic aspects of the Indian subcontinent and Southeast Asia - the area of the present study of *Panicum*. Endemism and relative distribution of the species in the different Phytogeographical Regions within this territory are discussed at the end of Part IV, following this chapter.

12.2 Geographical Outline

The area covered comprises the Indian subcontinent including the whole of India with Pakistan, Sri Lanka, Nepal, Bhutan, Bangladesh, and Southeast Asia. The geographical outline of these territories here defined is as follows: to the north, the foothills of Himalaya including Nepal; to the west, Pakistan; to the east, Bhutan, Bangladesh, Assam and northern Burma; and to the south Sri Lanka. Southeast Asia includes southern Burma, Thailand, Indochina (comprising Laos, Cambodia, and North and South Vietnam), the whole of the Malay Peninsula, the Philippines, Sumatra, Java, Borneo, New Guinea, and numerous other smaller islands in the territory. The extremities of southeast Asia in the south meet the Australian continent. In this regard, the study region forms a connecting bridge between Australia at one end and southwest Asia at the other. Phytogeographically, this vast geographical area conforms, with the exception of northwestern India and most of Pakistan, the Indomalesian subkingdom of the Paleotropical Kingdom as classified by Takhtajan (1988).
12.3 Topography

Indian subcontinent

The subcontinent of India lies entirely to the north of the equator, between latitudes 6°N and 36°N, and between 61°E to 97°E. The area within this limit covers c. 1,614,000 square miles. Diversity and complexity are keynotes of the topography of this vast region which includes deserts, hills and high mountains, plateaus, plains and long rivers.

The Indian Peninsula proper extends to the south of 22°N (the Tropic of Cancer) to the southernmost point of India. It is of comparatively low elevation, and has a backbone of hills near the west and east coast. The important physiographic divisions (see Fig. 46) are 1) the Western Ghats hills running parallel and very close to the west coast of the peninsula, together with the Nilgiris and adjoining hills, 2) the Eastern Ghats hills and outlying hills in the east coast, and 3) the vast Deccan Plateau. The general elevation rarely exceeds 1600 ft. in the south, and is 3000 ft. in the north. The area is dominated by many creeks and Deccan rivers with fertile flats near their banks. The coastal plains of the peninsula are washed by the Arabian sea on the west and the Bay of Bengal on the east, the Indian Ocean touching the narrow tip of the triangle. To the north of the Peninsula is the low plateau of Central India, which gradually falls to the extensive Indo-Gangetic Plain. The Gangetic Plain slopes from northwest to southeast, with almost imperceptible undulations—the highest part being about 600 feet above sea level. To the north of the Indo-Gangetic plain is the continuous mountain barrier of the Himalayan mass, the elevation of which averages over 20,000 feet. The northwest portion is also very mountainous—the hills beyond the Indus form a series of ranges.
almost like a continuation of the Himalayas, and connecting with the Sulaiman Range. The plains of this northwestern region are large expanses of alluvial clay and loam intersected by the main rivers of the region, of which the Indus is the chief. The valley of the lower Indus widens in the south to a flat plain. To the southwest lie the deserts of Baluchistan of Pakistan which are the most drought-striken areas in the subcontinent. A range of mountains, the Aravalli Hills, runs through Rajasthan in an approximately NE/SW direction. It overlooks the semi-arid to arid plains of western Rajasthan and Sind and adjoining areas, with the Thar desert as the nucleus. Aravalli is the oldest of all physical features of India, considered to be depressed and degraded relics of a paleozoic mountain system (Holdich 1909, Chatterjee 1973). The Thar desert represents the eastern end of the vast arid belt extending from the Sahara eastward through Arabia and Baluchistan.

In the eastern and northeastern part of the subcontinent, are the eastern Himalayas (see Fig. 46). They occupy Bhutan, north-eastern corner of India (Assam), and its adjoining territories, and the northern part of Burma. Assam contains the two valleys of the rivers, Brahmaputra and Surma, and the coastal hill tracts (Garo hills, the Khasi and Jaintia hills, Naga hills). The chief feature of the remaining area is the low Bengal Basin – the Gangetic-deltaic alluvial plains of West Bengal and Bangladesh lying between the eastern Himalaya and the Bay of Bengal. The Bengal Basin is very flat and low, and a mere 15 – 20 feet rise of the sea level would submerge the whole of coastal areas. Flooding is frequent in these areas.

The island of Sri Lanka is edged by a belt of level land, which forms extensive plains at the northern extremity, and is traversed by a meridional chain of mountains. These mountains rise to about 1,000 feet in the north and nearly 9,000 feet in the south. This range extends eastwards from Adam's Peak to
Maha Ellia and Newera Ellia with a mean elevation of 6,000 – 7,000 feet.

Southeast Asia

Southeast Asia, as here defined, lies mainly to the north of the equator and extends from 28°N to 11°S and from 92°E to 150°E. Within these extreme limits, the sea area exceeds the land in ratio of roughly four to one (Fischer 1964). Over a third of the total land surface is accounted for by the peninsular mainland, and the remaining two thirds are divided among the numerous islands.

The land area of Southeast Asia is a complex of islands and peninsulas (see Fig. 46). They are continental in extent though fragmented in form (Hill 1979). Lying between the Indian and the Pacific Oceans, and between the Asian and Australian continental masses, the region is a cross-roads and meeting place for the flora (also fauna) of the two continents (Fischer 1964). Geographically, the continents and ocean floors have converged in this region, creating the mountain ranges, the island chains and the sea-filled basins that dominate the area (Fischer 1964). The small sub-continental part of Southeast Asia contains prominent north/south physical structures, best developed in west Thailand and Burma. The east/west sweep of the Himalayas abruptly gives way, on the borders of Burma, to the north/south trend of the Arakan ranges. Due to the north/south position of the hill ranges of mainland Southeast Asia, the rivers run in a similar direction (Dobby 1973). These rivers have highly elongated basins. Insular Southeast Asia is distinctive from the mainland because the hill ranges show a more or less latitudinal alignment. In most cases the topography is dominated by rugged mountain chains. Many peaks rise well over 10,000 feet over the sea level.
12.4 Climate

Climate is a very important element in determining the geographical distribution of plants (Hooker 1855). Temperature and humidity are the two main factors which react naturally upon one another and determine the nature of the climate.

Because of its physical features, the Indian subcontinent necessarily presents a variety of climatic conditions. It includes every climate ranging from the burning heat and absolute drought of the Sind and Rajastan deserts, to the humid jungles of Assam and adjoining hills, and to the permanent snows of Himalaya. The mean annual rainfall varies from 450 inches in the hills of Cherapunji in Assam, and from between 300 and 400 inches in Western Ghats and the Arakan hills to less than 5 inches in the Thar desert of Sind and Rajasthan. Simultaneously, parts of the subcontinent are deluged with heavy and frequent rain, while others experience tropical heat and higher humidity. In other places, again at the same time of year, persistent dry weather with clear skies may prevail for weeks or months. Cyclones occasionally sweep over the low coast lands of lower Bangladesh, West Bengal and Orissa destroying crops and other vegetation.

The rainfall of the subcontinent is governed mainly by an alternation of seasons known as the monsoons. The presence of the Asiatic continent, extending from the neighbourhood of the equator northwards, greatly affects the air movement or pressure conditions very largely in the Indian Ocean and seas. This is converted into a periodic, or monsoon, air movement. There is an alternation of monsoon climates (Baness 1881, Basu 1973) known as the southwest and northeast monsoons. The influence of the southwest monsoon
during the months of May to October causes much of the annual rainfall. The northeast monsoon prevails for only a short period during the rest of the year. Another feature of precipitation is the heavy snowfall in the western Himalayas and the higher mountain ranges of Afghanistan and Baluchistan of Pakistan. In Sri Lanka, during the southwest monsoon, the north and east parts of the island receive little rain, but the lowlands in the south are very wet in the same season. During the northeast monsoon, the rainfall on the mountains is less than during summer.

The climate of Southeast Asia is unusually uniform for a region of this extent. With the exception of the northeastern portion of mainland Southeast Asia, the annual mean sea level temperatures over nearly all parts of Southeast Asia are close to 80°F. (In Timor and its immediate neighbourhood the climate is, however, much drier and closely resembles that of north of Australia).

Rainfall is generally high throughout the region except for the drier belts of upper Burma and coastal Thailand. There are two broad patterns of precipitation. Near the equatorial regions between 5° north and south, an equatorial monsoon type climate is found, and there are heavy rains at all times of the year – over 80 inches per annum. In regions beyond the latitudinal limits mentioned above, a tropical monsoon climate prevails in the lowlands. Here there is greater seasonal variation of temperature and rainfall, although the mean precipitation does not fall significantly below that of the equatorial monsoon type.

12.5 Phytogeography

The phytogeographical divisions as adopted by Good (1964), and Takhtajan (1986), include the Indian subcontinent and Southeast Asia in the Indomalesian
floristic subkingdom of the Paleozoic Kingdom. Certain areas of Pakistan and northern India extend beyond this subkingdom. According to Takhtajan (1986), the territory of this floristic subkingdom includes four regions viz. Indian, Indochinese, Malesian and Fijian (see Fig. 47). The first three regions coincide almost entirely with the area of the present study, with the exception of:

1) the Sindian Province which includes province of Sind in Pakistan, the plains of Punjab in Pakistan and India, the Thar Desert and adjoining areas. The Sindian Province belongs to Takhtajan’s Sudano-Zambezian Region. The dominant vegetation types of this province are open woodland, tropical desert, thorn forest and desert dune scrub.

2) the northern Baluchistan Province, which includes some characteristic xerophytic elements of the Irano-Turanian flora, and the western Himalayan Province. These two provinces belong to the Irano-Turanian Region. A considerable part of the latter province is characterised by a monsoon climate.

3) the Khasi-Manipur Province in the northeastern border regions of India, the eastern Himalayan Province and the Northern Burmese Province. All three provinces belong to the Eastern Asiatic Region. The Khasi-Manipur and Northern Burmese Provinces are placed in the Indo-Malesian subkingdom by Good (1964). The flora of these provinces consists of eastern Asiatic elements including large number of endemic genera which are largely monotypic or oligotypic.

Apart from the above provinces which belong to the Sudano-Zambezian, Irano-Turanian, and Eastern Asiatic Regions, the whole of the Indian subcontinent and Southeast Asia come under the Indomalesian subkingdom. Although the extent of this vast region is diverse and fragmentary, there are many common elements of various taxonomic ranks. Endemism is unusually high, there being 16 endemic vascular plant families (Takhtajan 1986). According to him, the
Indomalesian subkingdom is classified as follows:

1. Indian Region
   a. Sri Lanka Province
   b. Malabar Province
   c. Deccan Province
   d. Upper Gangetic Plain Province
   e. Bengal Province

2. Indochinese Region
   a. South Burmese Province
   b. Andamanese Province
   c. South Chinese Province
   d. Thailandian Province
   e. North Indochinese Province
   f. Annamese Province
   g. South Indochinese Province

3. Malesian Region
   3a. Malesian subregion
      a. Malay Province
      b. Kalimantan (Bornean) Province
      c. Philippinean Province
      d. Sumatran Province
      e. South Malesian Province
   3b. Papuan Subregion
      a. Celebesian (Sulawasian) Province
      b. Moluccan Province
      c. Papuan Province
      d. Bismarkian Province

4. Fijian Region
   a. New Hebridean Province
   b. Fijian Province

The Indian Region comprises the Indian Peninsula proper, plains of the Ganges, subtropical flanks of the Himalayas, and Sri Lanka. According to Hooker (1909), the Indian subcontinent is a meeting place of floras from the west, the north and the east. It does not contain any endemic family but there is a number of endemic genera including many in such families as the Gramineae, Acanthaceae, and the Podostemaceae. As to the small size of the endemic element, the region is of much less botanical character in comparison with
The Indochinese Region covers Indochina, Thailand, tropical Burma, eastern and south eastern border parts of Bangladesh, southeastern China and Hainan. According to Takhtajan (1986) there are many endemic genera in the region and one endemic family, Plagiopteraceae. He states that floristically the region is richer than the Indian Region. It is described as transitional or intermediate between the rich floras of Malaysia in the south and of China in the north. A small but conspicuous group of genera links it with the Indian Region (Good 1964).

The flora of the Malesian Region is extremely rich (van Steenis 1950). It includes four endemic families and about 400 endemic genera (Takhtajan 1986). The region comprises the entire Malesian Archipelago (which includes the Philippines, the Molucca islands, the Sunda Islands and other smaller islands), the southern part of the Malay Peninsula, New Guinea, the Aru islands, Christmas island, the Nicobar islands and numerous other small island groups. Good (1964) reports that the Flora Malesiana divides Malaysia into three parts: southern Malaysia which includes the islands from Java to Timor, western Malaysia comprising the Malay Peninsula, Sumatra, Borneo, and the Philippines and eastern Malaysia including Celebes, the Moluccas, Kai Aru and New Guinea. Malaysia has great floral richness but is still not yet adequately explored (Takhtajan 1986).
13.1 Distribution

The distribution of the species of *Panicum* in the Indian subcontinent and Southeast Asia is predominantly over tropical and subtropical plains and low hills. Few species occur at altitudes higher than 6000 ft in the study region. The genus is poorly represented in dry arid or the colder Himalayan regions, and is absent from higher Himalayan altitudes. There are 30 native (three doubtful) and 16 introduced taxa in the study region. Of the introduced species, four are from North America, three from Australia, and the rest from Africa. A species is likely to be introduced in an area when its spread depends on human agency, conscious or unconscious; it is regarded as native when it is present in an area without the aid of man (see Smith 1986, Webb 1985). Several of the introduced species such as *P. atrosanguineum*, *P. brevifolium*, *P. mindanaense*, *P. seminudum*, *P. trachyrhachis*, *P. walense* have become widely naturalised in the Indian subcontinent and Southeast Asia.

The internal distributions of the indigenous *Panicum* species of the Indian subcontinent and Southeast Asia are shown in outline maps (Figs. 48–57). In addition, the overall phytogeographical distribution of the native and introduced species of the Indian subcontinent and Southeast Asia are noted in Table 8. The main concentration is found to be in the Malesian region but the Indian region and the Indochinese regions come close to it, their percentages being 65%, 63% and 54% respectively of the total number of 46 taxa. The Irano-Turanian region contains 15% of the taxa, while both the eastern Asiatic and the Sudano-Zambezian regions have only 13% of the total number. These calculated figures are approximate, and better, future collections of existing...
Fig 48 Map showing species distribution in the Indian subcontinent and S.E. Asia
Fig. 49 Map showing species distribution in the Indian subcontinent and S.E. Asia.
Fig. 50 Map showing species distribution in the Indian subcontinent and S.E. Asia
Fig. 51 Map showing species distribution in the Indian subcontinent and S.E. Asia
Fig. 52 Map showing species distribution in the Indian subcontinent and S.E. Asia
Fig. 53 Map showing species distribution in the Indian subcontinent and S.E. Asia
Fig. 54 Map showing species distribution in the Indian subcontinent and S.E. Asia
Fig. 55 Map showing species distribution in the Indian subcontinent and S.E. Asia
Fig. 56 Map showing species distribution in the Indian subcontinent and S.E. Asia
Fig. 57 Map showing species distribution in the Indian subcontinent and S.E. Asia

- ▲ P. paludosum
- ● P. trypheron
TABLE 8 Phytogeographical distribution of the indigenous and introduced Panicum species (including subspecies and varieties) in the Indian subcontinent and Southeast Asia (Explanation in the text)

* = Endemic species  + = Occurrence  (+) = Penetrants from other regions  +? = Doubtful nativity

<table>
<thead>
<tr>
<th>Name of Taxa</th>
<th>Native</th>
<th>Introduced</th>
<th>Irano-Turanian Region</th>
<th>Sudano-Zambezian Region</th>
<th>Indian Region</th>
<th>Eastern Asiatic Region</th>
<th>Indochinese Region</th>
<th>Malesian Region</th>
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<tr>
<td>P. amoenum*</td>
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<tr>
<td>P. antidotale</td>
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<td>Name of Taxa</td>
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<td>Introduced</td>
<td>Irano-Turanian Region</td>
<td>Sudano-Zambezian Region</td>
<td>Indian Region</td>
<td>Eastern Asiatic Region</td>
<td>Indochinese Region</td>
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species from new areas or discovery of new species may yet change them considerably. Information is sometimes insufficient to distinguish between truly biregional or triregional taxa and those characteristic of one or two regions and occurring only as penetrants in others. In the table the likely penetrants are denoted by (+) signs. In this respect, the Malesian elements predominate: out of nine taxa of the Malesian and seven of the Indochinese region one is a penetrant to the Indian region. In contrast, it appears that only two taxa from the Indian region, and one from each of the other regions penetrate into the Indochinese and Malesian regions. It may be that *P. hayatae* is a truly biregional species, *P. humidorum* a truly triregional and *P. auritum, P. inconstum* and *P. sarmentosum* are three tetraregional species with a wide range of distribution.

A few taxa have dubious native status in the Indian subcontinent and Southeast Asia. They have been indicated by '−?' For instance, *P. bisulcatum* occurs throughout northern and northeastern India, China and Japan to Malaysia. Its native area is not certain. The place of origin of *P. repens* which occurs throughout the tropics and subtropics of the Old and New Worlds, is not known. *P. milaceum* is a cultivated cereal crop which is believed to be a native of Europe and Asia.

### 13.2 Endemism

There are only a few species which are endemic in the various regions of this study. For the present purposes, endemic species have been defined as species actually confined to one floristic region. Most of the species are local and occupy much less than the whole of an average region.

Endemism has been analysed for specific as well as for infraspecific taxa as
has been shown in Table 8. Endemic taxa are marked with asterisks. It would appear that both the Indian and the Indochinese regions contain three endemic species while the Malesian region has two and Eastern Asiatic region only one endemic species. Two varieties show endemic distribution - one in the Malesian region, the other in the Indochinese region. No species is endemic to the Irano-Turanian or Sudano-Zambezian regions. Taking together the species and varieties, it appears that of the 46 taxa recognised, 8% are endemic to the Indochinese region, 6% to each of the Indian and Malesian regions, and 2% to the Eastern Asiatic region.

13.3 Discussion

It is not possible to say, from this analysis or from that of distribution reviewed earlier, that any one part of the area is an obvious centre of frequency, or active evolution. Though 'Indian region' is species-rich and the Sudano-Zambezian region is species-poor, this indicates more than the aridity of the latter - which is hence 'inimical' to subtropical grasses.

The distribution pattern may be analysed in terms of possible centres of frequency or diversity and ecological conditions. The main concentration of the C₃ species are found in the forest floors and margins of Eastern India and Indochina. They occur at higher altitudes along the mountain ranges in summer rainfall areas. Whereas the C₄ species are prevalent on the drier, hotter plateau of India, Indochina and Malesia.
PART V

PANICUM IN AUSTRALIA
CHAPTER 14: PHYTOGEOGRAPHY, TOPOGRAPHY 
AND CLIMATE OF AUSTRALIA

14.1 Introduction

This work has offered an opportunity to compare taxonomic observations on 
the species of *Panicum* occurring in Australia with those of the Indian 
subcontinent and Southeast Asia. Many species of the genus are common to 
both these regions. Phytogeographically, the Australian flora, particularly that 
of northeast Australian, has close links with the flora of Malesian region (Good 
1964, Takhtajan 1986). Broadly speaking, the objective of this work was to gain 
some knowledge of the relationships of *Panicum* 'floras' between Australia and 
Asia.

The work here presented is not intended to include a taxonomic revision of the 
Australian species concerned. This work has been done but there is no space 
to include it within the specified size of the thesis. Taxonomic and anatomical 
information has been obtained but problems in detailed classification are not 
addressed. No attempt has been made formally to define infrageneric taxa but 
some indications are made in the last Chapter. An outline of phytogeography, 
physiographic features and climatic conditions are given to assist 
understanding of the distribution patterns of *Panicum* species in Australia.

14.2 Phytogeography, topography and climate

14.2.1 Phytogeography

The continent of Australia supports one of the richest of the world floras
containing a large number of endemic families, genera and species. There is a high degree of peculiarity in its flora which results from long geographical isolation of the continent (Good 1964). Phytogeographically the Australian continent is recognised to have three regions: northeastern, southwestern, and central. The northeastern region stretches in a wide coastal belt round the continent embracing northern, eastern, and southeastern parts of Australia including Tasmania. The vegetation is of savanna or savanna woodland. There are considerable areas of forest along the north-east and south-east coast. The northern part of this region exhibits a considerable admixture of Malesian elements, particularly of New Guinea type. The southwestern region occupies a small territory in the southwestern corner of the continent and its flora resembles that of the Cape Region of South Africa which occupies also the extreme corner of a continental mass. The central region comprises most of the interior of the continent. Desert or semi-desert conditions prevail over most of the region and the flora of this great area is comparatively limited (Good 1964).

14.2.2 Topography

Australia lies approximately between latitudes 10°S and 44°S and longitudes 112°E and 152°E. The mainland is of low relief with a plateau of 150 - 600m in altitude. It occupies most of the western two-thirds of Australia. The eastern sector of the mainland is almost separated from the western plateau by an extensive north-south trough. On the eastern edge of this trough, the land rises to form the Great Dividing Range whose height averages from 1200m to 1500m. The Dividing Range runs close to the eastern edge of the continent along its whole length from northern Queensland south to Victoria.
Australia presents a wide range of climatic conditions, ranging from the hot and humid northern tropics to the southern temperate regions. The annual rainfall in much of the inland area of the continent averages less than 25 cm per annum. It gradually increases towards the coastal regions of the north, east, south-east and south-west with average annual precipitation of 100 - 150 cm (more in some places). A high humidity prevails throughout the northern tropics and also extends down the subtropical eastern coastal regions.

In general the distribution of native and introduced *Panicum* species shows a correlation with the hot, humid climates and physiography. For example, they are to be found in the northern tropics, extend down to tropical and subtropical portions of eastern Queensland and northeastern New South Wales, and ultimately to the extreme east of Victoria.
15.1 Introduction

A brief enumeration of the species of *Panicum* found in Australia is presented in this chapter. The indigenous species of Australia are discussed in relation to their indiginousness, diagnostic features, and ecological and geographical distribution in Australia. Formal description, citation of synonymy and specimens examined are omitted because of lack of space. However, the type locality and type specimen are indicated. Anatomical studies were made on all the species except *P. latifolii* for which materials were not available. Instead of going into detailed assessment of anatomical characters, I have only mentioned anatomical types for each species. With regard to introduced species, these have only been listed with a note on naturalisation and distribution. This abbreviation is justified because they were earlier described in detail in Chapter 11.2. However, three introduced species not found in the Indian subcontinent and Southeast Asia are fully described. A key to the native species together with these three introduced ones is given.

15.2 Key to the Australian native species, and the few introduced species not found in the Indian subcontinent and Southeast Asia (marked *).

1. Upper lemma finely transversely rugose
   - Upper lemma smooth

2. Lower glume almost as long as the spikelet. Plants annual

   *P. bulbosa*
- Lower glume not more than 2/3 the length of the spikelet. Plants annual or perennial 5

3. Leaf blade narrow, 2–4mm broad, midrib much broader than lamina halves; semi-aquatic, stout, robust, 1.3–2.5mm
   - Leaf blade much more than 4mm broad, midrib many times narrower than lamina halves; terrestrial, slender, small, 20cm–1.2m 4

4. Spikelets 3–3.7mm long; panicle branches stiff
   - Spikelets 2.3–3mm long; panicle branches flexible, fine  P. mindanaense

5. Upper and lower glumes inserted close together
   - Lower glume separated from upper glume by a distinct internode, inserted markedly below the spikelet 11

6. Plants annual
   - Plants perennial 7

7. Upper floret half the length of the spikelet
   - Upper floret only slightly shorter than the spikelet 8

8. Upper glume scabrous especially towards the apex
   - Upper glume smooth 9

9. Spikelets 2.7 to 3.3mm long; leaf blade not narrowed at the blade–sheath junction; semi-aquatic
   - Spikelets 2–2.5mm long, leaf-blade abruptly narrowed into the sheath at the blade–sheath junction; grasses of forest floors and margins 10

10. Panicle contracted; leaf blades tough; upper lemma hairy at the apex  P. lachnophyllum
- Panicle with few but spreading branches; leaf blades soft; upper lemma not hairy at apex
  
  _P. pygmaeum_

11. Palea of lower floret vestigeal
- Palea of lower floret well developed

12. Primary branches of panicle whorled at the lowermost inflorescence node
- Panicle branches not whorled

13. Nodes prominently ciliate; upper lemma finely rugulose
- Nodes glabrous; upper lemma smooth

14. Spikelets 3.5–5mm long; lower glume 2/3 the length of the spikelet
- Spikelets 2.5–3mm long; lower glume 1/2 as long as the spikelet

15. Plant annual; upper glume strongly 9– or 11–nerved; upper floret dark brown
- Plant perennial rhizomatous; upper glume 5– or 7–nerved; upper floret not dark brown

16. Spikelets 3.3–4.1mm long; leaf blade scabrous on the adaxial surface
- Spikelets 2.1 to 3.2mm long; leaf blade smooth on the adaxial surface

17. Plant annual
- Plant perennial

18. Panicle branches appressed, lower primary branches not whorled; leaf blades narrow, filiform
- Panicle spreading, rigid, lower primary branches whorled; leaf blade usually broad

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15.3 Enumeration of the Species

1. **P. antidotale** Retz.

Introduced. Native of India; widely introduced as a forage species or soil binder into Northern Territory, Queensland, New South Wales and Western Australia.

2. **P. bisulcatum** Thunb.

Introduced. Occurs in Japan, China, India, Philippines and in the southeastern coastal region of Australia.


Introduced. A tufted perennial typically with a hard, swollen corm-like crown at ground level. Diagnostic features of this species include the finely but clearly transversely rugose upper lemma with a bluntly pointed pubescent apex. A Kranz M.S. NADP-me species, this is related to **P. plenum**, but that species is distinguished by creeping rootstock and decumbent, not corm-like base of the culm, compressed culm, and by the upper lemma being obscurely rugose. **P. bulbosum** is cultivated as a forage species in semi-arid regions of the southern United States. It is introduced to New South Wales. **Fl. & Fr. : November to April.**

A. Kranz M.S. NADP-me species.


Native. This is a glabrous, rhizomatous erect perennial 30 to 70cm tall. The
species is characterised by the membranous glumes and lower lemma, the broadly ovate lower glume, and the upper floret being only about 1/2 as long as the spikelet. It occurs in forests and clay soil regions of Queensland and New South Wales. *Fl. & Fr.: March to July.*

A Kranz P. S. NAD-me species.

5. *P. cambogiense* Balansa

Introduced. Native to India and Malesia, occurs as a weed in rice fields in the Northern Territory.


Introduced. Native of North America but introduced to India, Malaysia and Australia. An annual weed in disturbed sites in Western Australia, South Australia, New South Wales, Victoria, and Tasmania.

7. *P. coloratum* Linn.

Introduced. Native to tropical Africa, widely introduced as a forage species in India, Australia. New South Wales, Victoria, and Western Australia.


Native. A tufted perennial forming large, usually blue-green tussocks 30-80cm or more in height. The axis of the panicle is deeply grooved or 4-angled with stiffly spreading angular or flattened branches and branchlets. This is a morphologically variable species with intergrading forms occurring over a wide area of arid, semi-arid and mesic Australia. *Fl. & Fr. January to December.*

A Kranz P.S. NAD-me species.

Native. Caespitose erect perennial 20–50 cm tall, rhizomatous. Panicle with usually stiff, long spreading branches, the lower ones mostly clustered. It is a mesophytic species which occurs in all the territories of Australia. **Fl. & Fr. Throughout the year.**

A Kranz P.S. NAD-me species.


Introduced. This is a mesophytic, weedy annual, 15–60 cm tall. Very similar to **P. schinzii**. It is a native of Southern Africa and introduced to Australia. Diagnostic characters which serve to distinguish include the membranous upper glume and lower lemma with smooth but pronounced nerves, and the obscurely nerved upper lemma. The species falls under section Dichotomiflora of subgenus Panicum. Introduced to Queensland, New South Wales, and Victoria. **Fl. & Fr. January to June.**

A Kranz P.S. NAD-me species.

11. **P. incomtum** Trin.

Introduced. Native of Southeast Asia and northeastern India. Climbs over understory vegetation in shady tropical rainforest in Queensland.


Native. A stoloniferous perennial with basally decumbent almost wiry culms
10-30cm tall. The upper floret of spikelets is hairy at apex and obscurely nerved. The inflorescence is similar to that of Cyrtococcum oxyphyllum. This species occurs in the shaded forest regions of southeastern Queensland and northeastern New South Wales. **Fl. & Fr. February to September.**

A non-Kranz C₃ species.


Native. Perennial species with 40-100 cm culms and filiform leaf blades. Primary branches of panicle usually appressed to the main axis. Resembles *P. whitei*, in having panicles with slender primary branches and numerous spikelets. However, *P. whitei* is an annual with spreading primary panicle branches. This species occurs in Queensland. **Fl. & Fr. July to May.**

A Kranz P.S. NAD-me species.


Native. An arhizomatous erect perennial 40-80cm tall. Very similar to *P. decompositum*, but can be distinguished by its filiform, rigid leaf blades, hairy axils of primary branches of panicle and larger spikelets. A mesophytic species occurring across the subtropics of northern Australia. **Fl. & Fr. February to July.**

*Probably a Kranz P.S. NAD-me species.*

**15. P. maximum** Jacq.

Introduced. Native to South Africa, cultivated as a forage grass or growing
spontaneously in parts of Southwestern Australia.

16. **P. miliaceum** Linn.

Introduced. Native to Europe and Asia. In Australia widely introduced and planted as a forage species in Queensland, New South Wales, Victoria, South Australia, and Western Australia.


Native. This is a densely caespitose erect annual 20–80cm tall, with few, filiform, diffusely branched panicles. Spikelets are borne only towards the branch tips on slender pedicels usually as long or longer than spikelets; lower glume about as long as the spikelet, upper lemma narrow. Very similar to *P. seminudum*, this species occurs in Western Australia, Northern Territory, and Queensland. *Fl. & Fr.*: August to December.

A Kranz P.S. NAD-me species (? but see Chapter 8.4, discussion on subgenus Panicum).

Reeder (1948) recognised a variety called *P. mindanaense* var. *pilosum*, having pilose leaf sheaths and blades. But there is a gradual transition between the hairy and glabrous forms and no other variable character could be detected. I have therefore placed this variety in synonymy (Chapter 11.2).


Native. An erect perennial grass 1–2 m tall, decumbent only at base, nodes glabrous. Panicle fully exserted at maturity with spreading primary branches and numerous filiform branchlets; lowest branches of the panicle whorled,
upper ones scattered, axils glabrous; spikelets 2.5–3 mm long, lower glume slightly less than 1/2 the length of the spikelet. This species occurs in tropical and subtropical rain forests, and sub-humid woodlands in Queensland. Fl. & Fr: May to September.

A Kranz P.S. NAD-me species.


Introduced. Rarely found annual, 30 – 120 cm tall. The species is characterised by the strongly 9 – 11-nerved upper glume and dark brown upper floret. Queensland. Fl. & Fr: February to May.

A Kranz P.S. NAD-me species.


Native. This is a basally decumbent perennial 10 – 30 cm tall. It grows in semi-aquatic habitats, rooting freely at the nodes in mud around streams and swamps. The panicle is rather reduced with recemose primary branches. Other diagnostic characters of the species include membranous, truncate and nerveless lower glumes which are 1/4 as long as the spikelet. It resembles species of the section Dichotomiflora. Occurs in Queensland, New South Wales and Victoria. Fl. & Fr: October to May.

A Kranz P.S. NAD-me species.


Native. A stoloniferous perennial with decumbent culms 8–30 cm tall. Its leaf blades are very soft and small, 1 – 4.5 cm long. Panicle 2 – 8 cm long with spreading primary branches and ellipsoid spikelets 1.7 – 2 mm long. This weak-culmed, shade-loving grass occurs on floors and margins of tropical and subtropical forests in Queensland and New South Wales. In habit and habitat, the species resembles species in the non-Kranz section Sarmentosa. *Fl. & Fr.* January to May.

A non-Kranz species.

23a. **P. queenslandicum** Domin var. *queenslandicum* Fedde Repert. spec. nov. 10:58 (1911). Type: Queensland, Condamine River, *Hartmann* (PR, holo, n.v.)

Native. This is a mesophytic perennial, 30 – 80 cm tall. Panicle 15 – 35 cm long, with lowermost primary branches whorled, spikelets with lower glume 2/3 its length and the upper floret with an abrupt swelling at base. The latter suggests an affinity of this species with *Yakirra* and *Ichnanthus*. *Fl. & Fr.* November to June.

A Kranz P.S. NAD-me species.


This variety differs from the species by its distinctly longer (5.1 to 7 mm) spikelets and pronounced nerves on upper lemma.

24. **P. repens** Linn.
Introduced. Probably a native of tropic or subtropic of the Old World. Occurs on sandy coastal areas in Queensland and New South Wales.


Introduced. Native to southwest Africa and introduced in India, Java and Australia. New South Wales, South Australia, Western Australia.


Native. A slender erect or ascending annual with stiff, duffusely branching nodding panicle. Lower glumes of spikelets are almost as long as the spikelet and the lower glume inserted much below the spikelet. Occurs in tropical and subtropical rain forests and subhumid woodlands. Distributed in Western Australia, Northern Territory, Queensland and New Guinea. *Fl. & Fr. April to August.*

A Kranz P.S. NAD-me species.


Native. A small, slender, tufted perennial with culms 8 – 20 cm long. The panicle is about 4 – 20 cm long with racemose primary branching, rarely with secondary branching. Spikelets often blotched with purple. Lower glume 1/2 as long as the spikelet. This rhizomatous grass occurs in tropical and subtropical forests of *Acacia* and *Eucalyptus* shrublands in Queensland, New South Wales and Victoria. *Fl. & Fr. April to September.*

A Kranz P.S. NAD-me species.

Queensland, Great Dividing Range near Jericho, *Domin* III (PR, holo, n.v.).

Native. A mesophytic to xerophytic perennial species with stout wiry culms 40 - 70 cm long. Diagnostic characters include spikelets evenly distributed along the length of primary branches; scabrous upper glume and lower lemma (the roughness pronounced towards the apex). This species occurs in temperate, sub-humid woodlands and also in semi-arid shrub woodlands of Queensland and New South Wales. *Fl. & Fr. November to June.*

A non-Kranz C3 species.


Native. This robust semi-aquatic or aquatic annual is characterised by large panicle over 1 m long with rather rigid, spreading branches - lower ones being usually verticillate. The leaf blade is narrow and is composed mainly of the midrib. The upper floret is shorter than the spikelet and has a poorly formed stipe at base which relates this species to *P. seminudum, P. queenslandicum* and the genus *Yakirra*. The species occurs in tropics and subtropics of northern Australia, New Guinea, Thailand and Indochina. *Fl. & Fr. June to January.*

A Kranz P.S. NAD-me species.

30. *P. trichoides* Sw.

Introduced. Commonly found as a weed. A native of tropical America, introduced into Africa, Asia, Australia. Northern Territory, Queensland and Western Australia.

Australia, Strzelecki Creek, $S.A. White$ 3 (K, iso!)

Native. This is an annual or short-lived perennial with geniculate, branched, erect culms 30 – 40 cm tall. Plants usually entirely hairless. Primary branches of the panicle slender, drooping, bearing spikelets clustered at the ends of branchlets. Spikelets green or becoming suffused with violet; lower glume 1/4 as long as the spikelet, membranous, truncate to obtuse and weakly 1-nerved. The species resembles $P. decompositum$ but that species differs by the primary branches of panicle being rigid, distinctly flattened and swollen at the base. $Fl. & Fr. Throughout the year.$

A Kranz P.S. NAD-me species.
Thirty one species of Panicum have been recorded in Australia; this is about two-thirds of the total species of the Indian subcontinent and Southeast Asia. Most Australian Panicum species occur in all its mainland states. The Australian Panicum species can be conveniently considered in two parts—the native species and the introduced species. There are sixteen native species and fifteen introduced ones (Table 9). All four types of leaf anatomy occur in the species found in Australia. The subgenera Agrostoides and Megathyrsus are represented by only introduced species—the former includes P. bulbosum (Section Bulbosa) from North America and P. antidotale (Section Antidotalia) from India and the latter includes the single African species, P. maximum.

It is clear from the table that nearly half of the introduced species are from Asia. Africa comes next with five species, closely followed by the New World with three species. Noteworthy among the Southeast Asiatic and Indian subcontinental species are P. cambogiense, occurring as an annual weed in rice fields in the Northern Territory; P. incomtum, a widely spreading perennial in the shady tropical rainforest of Queensland; P. bisulcatum, a helophytic annual, frequently associated with muddy stream banks in the southeastern coastal region of Australia. Quite a few species (including P. antidotale, P. miliaceum, P. maximum, P. bulbosum, P. coloratum, P. schinzii) have been introduced as forage species or for soil binding. P. repens occurs in the sandy coastal areas of Queensland and New South Wales. Two remarkable annual weeds from the New World, P. trichoides and P. capillare are widespread in all parts of tropical and subtropical Australia.
TABLE 9 Some data on the species of *Panicum* found in Australia (see text for details).

[\( N = \text{Native}, I = \text{Introduced}, A = \text{Annual}, P = \text{Perennial} \)]

[\( + = \text{Occurrence} \quad (+) = \text{Penetrants to S.E. Asia} \)]

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>I</th>
<th>A</th>
<th>P</th>
<th>Anatomical Types</th>
</tr>
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<tr>
<td><em>P.antidotale</em></td>
<td>+</td>
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<td>Kranz M.S.NADP-me</td>
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<tr>
<td><em>P.bisulcatum</em></td>
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<td>+</td>
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<td><em>P.cambogiense</em></td>
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<td><em>P.coloratum</em></td>
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<tr>
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<td><em>P.maximum</em></td>
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<tr>
<td><em>P.mindanaense</em></td>
<td>(+)</td>
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<td><em>P. paludosum</em></td>
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<td><em>P. pygmaeum</em></td>
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<tr>
<td><em>P. queenslandicum</em></td>
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<tr>
<td>var. queenslandicum</td>
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<td><em>P. repens</em></td>
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<tr>
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<td><em>P. simile</em></td>
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<tr>
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<tr>
<td><em>P. trachyrhachis</em></td>
<td>(+)</td>
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<tr>
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<tr>
<td><em>P. whitei</em></td>
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<td></td>
<td>Kranz P.S.NAD-me</td>
</tr>
</tbody>
</table>
Let us now consider the native species. Out of sixteen species, thirteen (79%) are perennial. They are confined within Australia. Only three (21%) are annual which also occur in Southeast Asia. Of the perennials, two occur in the tropical rainforest floors and margins, one in temperate subhumid/semi-arid shrub woodland, one in semi-aquatic habitats and the remaining eight species are, in general, distributed in mesophytic areas.

The native species of Australia include only three C3 species, these are: *P. iachnophyllum*, *P. pygmaeum*, *P. subxerophilum*. There does not seem to be any particular affinity between the Australian C3 species and the C3 species of Asia, and indeed the Australian C3 species do not themselves seem to form a closely related group. However, *P. iachnophyllum* and *P. pygmaeum* possess very short, thin, weak culms, the former shows resemblance with *Cyrtococcum* in its panicle features. This species also resembles the genus *Entolasia* in its panicle characters and in the surface of upper lemma being hairy, particularly at the tips. *P. pygmaeum*, with narrow, small leaf blades and reduced panicle shows much resemblance with *P. pusillum* from Tropical Africa. *P. subxerophilum* displays unusual, pronounced scabrosites on the upper glume and lower lemma. This feature is never found in the Asiatic non-Kranz species. Additionally, this species is unique among the Australian and Asiatic non-Kranz species in its occurrence in semi-arid shrublands. The other two non-Kranz species are significantly similar in that both are shade-loving species of forest floors and margins.

The native Kranz species are all Kranz P.S. NAD-me. There are thirteen species which are particularly well represented in the mesic plains of Queensland and New South Wales. Altogether they comprise a somewhat variable group differing in habit, duration, indumentum, and certain features of spikelets. A common feature includes the structure of panicle and the distinct separation of
lower glume from the rest of the spikelet (except *P. buncei, P. obseptum*). Usually the panicle is large and open with long slender, much branched branches and branchlets on which small, long pedicilled spikelets rise singly or in pairs.

One of the curious native Australian Kranz NAD-me species is *P. buncei* in which the upper floret is half the length of the spikelet with a membranous, rounded to truncate lower glume. This species cannot be related to any other species from Asia or Australia. Another species, *P. obseptum*, with the lower glume 1/4 the length of the spikelet, clasping, membranous, nerveless and truncate, is clearly attributable to section Dichotomiflora. Like other members of section Dichotomiflora, it has a papillate leaf surface and shows a semi-aquatic growth-habit.

Including the three closely allied annuals, *P. trachyrhachis, P. seminudum* and *P. mindanaense* which occur fairly commonly in Southeast Asia, four native Kranz P.S. NAD-me species can be related to the species of section Panicum. They are *P. queenslandicum, P. effusum, P. mitchellii* and *P. simile*. These species have effuse panicles, ovate, acute or acuminate 3- or 5-nerved lower glumes which are 1/2 to 2/3 the length of the spikelet and are separated by a short distinctive internode. They exhibit similarities with species of section Panicum from the Indian subcontinent and Southeast Asia.

The remaining four Kranz P.S. NAD-me species form a coherent group of allied species centered around *P. decompositum*. They are *P. decompositum, P. larcomianum, P. latzii* and *P. whitei*. Their panicles have rigid or flexible, spreading or appressed primary branches with usually whorled lower primary branches (Fig. 2.a). Their spikelets are obovate, nerveless or obscurely nerved. The lower glume is membranous and 1/4 the length of the spikelet. It is
notable that most of the spikelet characters of these species resemble those of the species of section Dichotomiflora, while other features of inflorescence, the obovate shape of lower glume, plant habit and habitat keep them apart from this section. A further difference from species of section Dichotomiflora is that these species have the lower glume separated from the upper by a distinct internode. In this character in particular, they exhibit a link with those Kranz P.S. NAD-me species which were shown above probably to be related to species of section Panicum. They seem to form a group of species within subgenus Panicum that bridge section Panicum and section Dichotomiflora.
APPENDIX I
A NEW SPECIES OF PANICUM (GRAMINEAE) FROM NORTH VIETNAM

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Department of Botany, University of Edinburgh, The King's Buildings, Edinburgh, EH9 3JH

SUMMARY

Panicum smithii is newly described from North Vietnam.

INTRODUCTION

During a study of the Southeast Asiatic materials of the genus Panicum in the Rijksherbarium, Leiden (L), some Balansa material from North Vietnam was investigated. These specimens had been identified as *P. amoenum* Balansa. After critical study, they were found to be markedly different, and are here recognised as a new species. The type of this new species had been cited by Balansa as one of the syntypes of *P. amoenum*. Though there is an apparent resemblance between the spikelets of *P. amoenum* and those of the new species, the distinctness of the taxa is easily perceived by characters of the culm, blades, panicle and size of the spikelets, as is shown in the key below.

*P. amoenum* sensu Balansa is often confused with another species, *P. humidorum* Buch.-Ham. ex Hook. f. (*P. humidorum* var. *perakense* Hook. f.; *P. perakense* (Hook. f.) Merr.). This is evident in Balansa's own material Balansa 1632, one of the isolectotypes of *P. amoenum*, in which he has mounted both *P. amoenum* and *P. humidorum* on the same sheet. Later Dr. Th. Henrard erroneously took them both as *P. amoenum*. The origin of this error has led him (Blumea 1941) to recognise three Bornean specimens of J. & M.S. Clemens collected from Mount Kinabalu during the years 1932-33, *Clemens* 28275, 28755A and 51562 (all at L!) as *P. amoenum* which are in fact...
P. humidorum

The species of the taxa is named after Dr. P.M. Smith, Department of Botany, University of Edinburgh, who is an eminent specialist of the grasses.

Panicum smithii M.M.Rahman, Spec. nov.

P. amoeno Balansa culmo tenuiore, ramis paniculae valde patentiorabbus, foliis 4-8 cm x 3-5 mm, spiculis paucis, max. caducis, minoribus olivaceis differt.

Gramen perenne tenue. Culmi 15-35 cm alii, 1-2 mm latae e nodis stolone, longo repenti erecti vel ascendentes, ei ad nodos inferiores saepe radicantes, nodi glabri. Vaginae foliorum quam internodi longiores, striatae, margine ciliatae, cetera glabrae; ligula membranacea, breviter lacerata; laminae 4-8 cm longae, 3-5 mm latae, lineares acuminatae, glabrae marginibus paulo convolutis, base rotundato, nerva mediana (costa) obscura. Panicula 5-15 cm longa, ambitu late ovata, erecta, rami panic. 7-10, patentes, 3-7 cm longi, laxissimi, inferiores quam superiores longiores, rachis ramique scabridiusculi, ramuli panic, filiformes, breves, spiculos pocos ferentes; pedicelli quam spiculae longiores brevioresve, teretes, glabri. Spiculae 2-2.3 mm longae, ovato-oblongae, acutae, supra medium pilosae, geminatae, viride-nigrae; gluma inferior longitudine 2/3 spiculae partes aequans, ovata, subacuta vel obtusa, 5-nervosa, ad margines pilosa, marginibus non membranaceis; gluma superior spiculam aequans, ovata, acuta, infra apicem pilosa sed minus quam lemmatibus inferioribus, 5-nervosa; lemma fiosculi inferioris glumam superiorem subaequans, ovatum, acutum, infra apicem pilosum, 5-nervosum, sterile, sine palea; lemma fiosculi superioris obovoides - ellipsoideum, acutum, ad basem cicatrice provisum, laeve, nitidum; palea superior texturae similis; caryopsis dorsaliter-ventraliter compressus, liber intra anthecium firme clausum. - Typus B. Balansa 468, North Vietnam, Tonkin, 25 January 1886 (L,
Slender perennial. Culms 15–35 cm long, 1–2 mm broad, erect or ascending from nodes of a long creeping stolon, often rooting at the lower nodes, nodes glabrous. Leaf sheaths longer than internodes, striate, ciliate on the margins, otherwise glabrous; ligule a shortly lacerate membrane; blades 4–8 cm long, 3–5 mm broad, linear, acuminate, glabrous, margins slightly convolute, base rounded, median nerve obscure. Panicle 5–15 cm long, broadly ovate in outline, erect, branches few, 7–10, spreading at right angles to the axis, 3–7 cm long, very lax, lower branches longer than the upper ones, rachis and branches slightly scabrous, branchlets few, filiform, short, bearing few spikelets, pedicels longer or shorter than spikelets, terete, glabrous. Spikelets 2–2.3 mm long, ovate-oblong, acute, pilose above the middle, geminate, greenish black; lower glume 2/3 the length of the spikelet, ovate, subacute or obtuse, 5-nerved, pilose at the margins, margins not membranous; upper glume as long as the spikelet, ovate, acute, pilose below the summit but less than the lower lemmas, 5-nerved; lower lemma subequal to the upper glume, ovate, acute, pilose below the summit, 5-nerved, sterile, epaleate; upper lemma obovoid-ellipsoid, acute, with a scar at base, smooth, glossy; the upper palea of same texture; grain dorsoventrally compressed, free within the firmly closed lemma and palea.

\textit{Fl. \\ & Fr.: January}

Distribution. Northern parts of North Vietnam, only known from types.

Ecology. Sandy margins of rivers and in grassy patches.

The species has been collected only once, so far as is known (all cited specimens are from the same gathering): efforts to collect more specimens should be made. \textit{P. smithii} is allied to \textit{P. amoenum} Bal. and \textit{P. bisulcatum} Thunb. The three species can be distinguished as follows:
1a Lower glume 1/3 as long as the spikelet,  
spikelets glabrous or shortly puberulous.  

**P. bisulcatum**

b. Lower glume 2/3 as long as the spikelet,  
spikelets pilose towards tips.

b. Lower glume 1/3 as long as the spikelet,  
spikelets glabrous or shortly puberulous.  

**P. bisulcatum**

2a. Panicle branches ascending at 45°–65°  
angles to the axis; leaves large, 10–17 cm  
long x 8–12 mm broad; culms 3–4 mm in  
diameter; spikelets smaller, persistent,  
olive green.  

**P. amoenum**

b. Panicle branches at right angles to the axis;  
leaves small, 4–8 cm long x 3–5 mm broad;  
culms 1–2 mm in diameter; spikelets larger,  
mostly caducous, greenish black.  

**P. smithii**

ACKNOWLEDGEMENT

I am grateful to Dr. J.F. Veldkamp, Rijksherbarium, Leiden for encouraging me to visit Leiden, and for kindly going through the manuscript. I would like to thank Dr. R. R. Mill of the Royal Botanic Garden, Edinburgh for the Latin transcription.

REFERENCES


Fig. 1. *Panicum smithii* M.Rahman. A. plant; B. two views of spikelets; C.  
lower glume; D. upper glume; E. lower lemma; F. two views of upper  
anthecium; G. two views of grain; H. ligule.
Gramen perenne aquaticum. Culmi 2.25m alti, spongiosi, molles, compressi, glabri, ad nodos basales ramulos tenues emittentes; tota planta straminea. Vaginae foliosum plerumque quam internodi longiores, incohaerentes, glabrae, compressae, ligula membranacea cilics 2.5mm longis albis sericeis; lamiae 10 - 35cm longae, 5 - 7 mm latae, lineari-lanceolatae, acuminatae, planae, glabrae, basi rotundato. Panicula 25 - 35 cm longa, 3 - 5 cm lata, oblonga, elongata, ramis ramulis spiculisque aliquantum adpressis, axis principalis mox evanescens, rami primarii 10 - 25cm longi, virgati, ad basem nudati, scabridi, ad ramos secundarios tertiariousque paralleli. Spiculae 2.2 - 2.5mm longae, 0.8 - 1mm latae, ellipsoideae ad ovoideo - ellipsoideae, acutae, glabrae, stramineae; pedicelli quam spiculae longiores, angulares, scabridi; gluma inferior spicula 4 - 6-plo brevier, orbicularis, membranacea, amplexicaulis, ad basem obscure nervosa; gluma superior spiculam aequans, ovata, acuta, 7 - 9-nervata, infra apicem venis transversalis pannis; lemma flosculi inferioris glumam superiorem subaequans, ovatum, acutum, 0-nervatum, infra apicem venis transversalis pannis, sterile; palea subaequalis, angusta, nyalina; lemma flosculi superioris 1.7mm longum, 0.8 - 0.9mm latum, ellipsoideum usque ad late ellipsoideum, primum stramineum devide acutum, laeve, nitidum; veni fulvum 7, velut striae pallideae notati exigue, palea texturae similis; caryopsis in lemma paleaque arcte inclusum, nilum basale.

Aquatic perennial. Culms floating, 2.25m, spongy, soft, compressed, glabrous, finely rooting at basal nodes, whole plant dull yellowish in appearance. Leaf sheaths usually longer than internodes, loose, glabrous, compressed; ligule membranous with 2 - 2.5 mm long white silky cilia; blades 10 - 35 cm long, 5 - 7 mm broad, linear-lanceolate, acuminate, flat, glabrous, base rounded. Panicle 25 - 35 cm long, 3 - 5 cm broad, oblong, elongated with branches, branchlets and spikelets somewhat appressed, the main axis soon becoming
Fig. 1 Panicum smithii M. Rahman Sp. nov.
APPENDIX 2

A new species of Panicum (P. longiloreum) from Thailand

MD. MATIUR RAHMAN

Department of Botany, University of Edinburgh, The King's Buildings, Mayfield Road, Edinburgh EH9 3JH

Summary. A new species of Panicum is described and distinguished from allied species in a key.

In the course of revisionary studies of Panicum from Southeast Asia, a new species was detected. This species is based on material collected by A.F.G. Kerr, which was growing in a rice field in Sena, Thailand. Other material was later collected from Long Xuyen, Southern Vietnam. This is a distinctive species that is recognised by its long, whip-like panicle, its very short, orbicular lower glume, its soft compressed culms, glabrous leaf sheath, and prominent long-ciliate, membranous ligule. The whip-like panicle with its somewhat appressed branches place this new species very close to P. subalbidum Kunth, and the membranous, short, lower glume recall P. repens L., P. paludosum Roxb. and P. schinzii Hack., but P. longiloreum can be separated from all these by the key given below. The species name is derived from its long strap-shaped (Latin, loreus = thong-like) appearance of the panicle.

Panicum longiloreum M.M. Rahman sp. nov. affinis P. subalbidum Kunth sed gluma inferiore truncata, palea flosculi inferioris lemma subaequanti, et ciliis ligulae 2 – 2.5 mm longis differt. Typus: Thailand, Kerr 19709 (holotypus K; isotypus BM,L).
obscure, primary branches 10 – 20 cm long, virgate, naked at base, scabrid, lying parallel with secondary and tertiary branches. Spikelets 2.2 – 2.5 mm long, 0.8 – 1 mm broad, ellipsoid to ovoid-ellipsoid, acute, glabrous, dull-yellowish, pedicels longer than spikelets, angular, scabrous, lower glume 1/4 – 1/6 the length of the spikelets, orbicular, membranous, clasping, obscurely nerved at base; upper glume as long as the spikelet, ovate, acute, 7 – 9 nerved, with a few transverse nerves below the summit; lower lemma about equalling the upper glume, ovate, acute, 9-nerved, with few transverse nerves below the summit, sterile, its palea about as long, narrow, hyaline; upper lemma 1 – 7mm long, 0.8 – 0.9mm broad, ellipsoid to broadly ellipsoid, yellowish, becoming tawny towards maturity, acute, smooth, polished, shiny, the 7 nerves appearing only as pale stripes, the upper palea of same texture; grain tightly enclosed by lemma and palea, hilum basal. Fl. & Fr: September.

Habitat. Aquatic situations.

THAILAND. Sena, Agathia, in rice fields flooded with about 1m of water, 23 September 1930, A.F.G.Kerr 19709 (holotype K; isotype BM,L); Southern Vietnam, Long Xuyen, University de Can-Tho No. 1033 (L).

KEY TO PANICUM LONGILOREUM AND ALLIED SPECIES

1. Ligule chartaceous, shortly ciliate with 
   0.5 – 1 mm long cilia; culms rhizomatous

2. Leaf blade hairy at base, distichous, 
   stiff, rhizomes long creeping; lower 
   glume suborbicular, truncate

   P. repens
2. Leaf blade glabrous at base; neither
distichous or stiff, rhizomes short
and soon disintegrating; lower glume
broadly ovate, acute or obtuse  \textit{P. subalbidum}

1. Ligule membranous with long silky hairs
about 2 mm in length; culms not rhizomatous

3. Plant annual  \textit{P. schinzii}

3. Plant perennial

4. Spikelets 2 - 2.5 mm long, ellipsoid, acute  \textit{P. longiloreum}

4. Spikelets 3 - 4 mm long, narrowly lanceolate,
acuminate  \textit{P. paludosum}

ACKNOWLEDGEMENT

I thank Dr. P.M. Smith for scrutinising the manuscript and Dr. Robert R. Mill for help with the Latin description.

\textbf{FIG.1.} \textit{Panicum longiloreum} M.M. Rahman. A. habit x 1/2; B. two views of spikelets (x20); C. lower glume (x20); D. upper glume (x20); E. lower lemma (x20); F. lower palea (x20); G. two views of upper antherium (x20); H. two views of grain (x20); J. ligule (x3).
Fig. 1 Panicum longiloreum M. Rahman Sp. nov.
<table>
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<th>CHARACTERS</th>
<th>(a)</th>
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<tbody>
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<tr>
<td>PANICLE EFFUSE</td>
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<tr>
<td>PANICLE SPICIFORM</td>
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</tr>
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<td>SP. ELLIP. TO ELLIP.-OBLONG</td>
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<td>SP. SUB-ACUTE TO OBTUSE</td>
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<td>L.G. SEPARATED BY INTERNODE</td>
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<td>L.G. AS LONG AS OR NEARLY SO</td>
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<tr>
<td>UPPER GLUME SACCATE</td>
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<td>UPPER GLUME AS LONG AS SPIKELET</td>
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<td>SCL. CENTRIFUGAL IN SHEATH CELLS</td>
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<td>MICROHAIR PRESENT</td>
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<td>SILICA BODY DUMB-BELL SHAPED</td>
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<td>ST. OVER-ARCHED BY PAPILAE</td>
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\[\text{[Image: schematic diagram of plant structures, including leaf sheaths, vascular bundles, and spikelet components.]}\]
APPENDIX 4 Similarity matrix, showing a measure of the phonetic similarities between all possible pairs of 48 species (including one subspecies) of Panicum, Cyrtococcum, Hymenachne, and Sacciolepis.

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- 748.


161 - 173.


Davies, I. (1959). The use of epidermal characters for the identification of


in the Poaceae : I, The leaf blade as viewed in transverse section.

Eragrostoidae and Panicoideae according to bundle sheath anatomy


Stearn, W.T. (1957). The *Genera Plantarum* and the typification of Linnaean
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<td>Node glabrous or nearly so</td>
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<td>L.B. glabrous or nearly so</td>
<td>Panicule effuse</td>
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<td>Panicule bicneml</td>
<td>Pedicel terete</td>
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<td>Sp. shortly pedicelled</td>
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<td>Sp. in cluster</td>
<td>Sp. symmetric</td>
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<tr>
<td>Sp. dorsally compressed</td>
<td>Sp. gibbous</td>
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<td>Sp. capitating at maturity</td>
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<td>Sp. less than 4mm long</td>
<td>Sp. ellip. to ellip.-oblong</td>
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<td>Sp. sub-acute to obtuse</td>
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<td>L.G. separated by internode</td>
<td>L.G. long as or nearly so</td>
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<td>L.G. suborbicular</td>
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<td>Ribs gently undulating</td>
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<td>Ribs rounded to obtuse</td>
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<td>Keel bundle central</td>
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<td>Ab. keel-scl. as girdler</td>
<td>Ad. keel-scl. as strands</td>
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<td>Bull. cells highly inflated</td>
<td>St. cells absent, EU. v.b.</td>
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<td>Vascular b.s. single</td>
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<td>B.S. with ad. extension</td>
<td>Bundle sheath complete</td>
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<td>Outer, smaller than sheath cells</td>
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<td>Microhair present</td>
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<td>Macronair present</td>
<td>Prickles and hooks present</td>
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<td>Prickles and hooks present</td>
<td>L.C. 1-3 x as long as broad</td>
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<tr>
<td>L.C. 1-3 x as long as broad</td>
<td>Silica body dumb-bell shaped</td>
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<td>Silica body dumb-bell shaped</td>
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APPENDIX 4 Similarity matrix, showing a measure of the phenetic similarities between all possible pairs of 48 species (including one subspecies) of Panicum, Cyrtococcum, Hymenachne, and Sacciolepis.

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## APPENDIX 4

**Similarity matrix**, showing a measure of the phenetic similarities between all possible pairs of 48 species (including one subspecies) of Panicum, Cyrtococcum, Hymenachne, and Sacciolepis.

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Note: The values in the table represent the similarity measure between species, with higher values indicating greater similarity.