

SPOROBOLUS (GRAMINEAE) IN MALESIA

G.J. BAAIJENS & J.F. VELDKAMP

Rijksherbarium/Hortus Botanicus, Leiden, The Netherlands

SUMMARY

In Malesia the genus *Sporobolus* R. Br. (Gramineae) is represented by 4 sections, 3 here newly distinguished, with 10 species, 2 new. *Sporobolus indicus* (L.) R. Br. has 5 varieties, 1 new, and 3 with a new rank: var. *creber* (De Nardi) Veldk., var. *flaccidus* (R. & S.) Veldk., and var. *major* Baaijens [*S. creber* De Nardi, *S. diandrus* (Retz.) Beauv., and *S. fertilis* (Steud.) Clayton, respectively]. Some other non-Malesian taxa have also been reduced to varieties, e.g. *S. laxus* Simon from Queensland (var. *queenslandicus* Veldk.), and *S. pyramidalis* Beauv. [var. *pyramidalis* (Beauv.) Veldk., incl. *S. jacquemontii* Kunth] from Africa and America. The Indian species generally known as *S. tremulus* – a superfluous name for *S. virginicus* (L.) Kunth – is reduced to a subspecies of *S. humilis* Presl. *Sporobolus poiretii* (R. & S.) Hitchc., long misapplied for *S. indicus*, is a synonym of *S. junceus* (Beauv.) Kunth. Five new sections are distinguished.

The correct name for *Thysanolaena maxima* (Roxb.) O. Ktze is *T. latifolia* (Roxb. ex Hornem.) Honda.

INTRODUCTION

The genus *Sporobolus* was described by R. Brown (1810) for three taxa represented in his Australian collections which had previously been included in *Agrostis* L. He regarded *A. virginica* L. as very close (which was quite correct because that is a species of *Sporobolus* as well), but he retained it in *Agrostis*, possibly because he had not seen any fruiting material (which is rare) and also because this species has exceptional long glumes. He also included *Agrostis diandra* Retz. in *Sporobolus* but as he had not seen it from Australia he did not make the necessary combination, either.

From the diagnoses he gave of *Agrostis* and *Sporobolus* it may be deduced that he thought that *Sporobolus* differed by the hairy throat, the reduced ligules, perhaps also because of the unequal glumes shorter than the spikelet (usually subequal and as long as the lemma in *Agrostis* proper), and its fruits (hence the name *Sporobolus*, 'seed thrower'; he first had used 'Lysispora', i.e. 'loose seed', on his labels). It is not quite clear whether he distinguished between the pericarp and the seed itself. From the family diagnosis on the page preceding the description of *Sporobolus* it would seem that he used the terms 'pericarpium', 'semen' and 'cariopsis' more or less as synonyms. Later authors also regarded the fruits with their more or less mucilaginous pericarp as the main difference between *Agrostis* and *Sporobolus* and considered this often too insufficient to distinguish between the two.

The fruit of grasses usually is a caryopsis in which the pericarp and testa are completely fused. In *Sporobolus*, however, the two separate at maturity and one could regard it as a kind of utricle. It is most unlikely that this is a retention of the capsules (or drupes?) supposedly present in the ancestors of the grasses. In the descriptions given here the dimensions and shapes are given of the seed after removal of the pericarp as only then their features can be inspected.

The first who directly mentioned the easily separable pericarp of the fruit seems to have been Kunth (1829), who stated "caryopsis libera, decidua; pericarpio membranaceo, hyalino, laxo, solubili."

Ms. Colbry (1957) described the fruits of 20 of the 29 North American species and provided a key.

Satyamurty (1983) has studied the ontogeny of the fruit in *S. coromandelianus* (Retz.) Kunth and Ms. Astegiano (1989) has made a very detailed study of the development of the androecium, gynoecium, and fruit in *S. indicus*. The interested reader is referred to these papers, as they are too extensive to summarize properly here.

Siddiqui & Qaiser (1988) reported non-operculate pollen for *S. arabicus* auct., non Boiss. (= *S. stocksii* Bor, nom. inval. = *S. nervosus* Hochst.), *S. coromandelianus* (Retz.) Kunth, and *S. helvolus* (Trin.) Dur. & Schinz. They pointed out that both operculate and non-operculate pollen occur in many genera, but it must be noted that with acetolysis opercula may get lost. Astegiano (1989) studying fresh or FAA material observed operculate pollen in *S. indicus*. If Siddiqui & Qaiser's observations can be confirmed, it would be interesting to see whether this pollen type is of any value at an infrageneric level.

Duval-Jouve (1866) gave a thorough description of the mode of seed dispersal in *Crypsis schoenoides* (L.) Lamk. and *S. pungens* (Schreb.) Kunth [the Mediterranean sibling of *S. virginicus* (L.) Kunth] and observed that it was identical in both species (whereby it is again obvious that the fruit type alone is not a generic character!).

For a long time *Sporobolus* was closely associated or even equated with *Agrostis* L. For a period the name *Vilfa* Adans. was used for it, but as Adanson cited a species now considered to be *Agrostis stolonifera*, *Vilfa* is either a later synonym of that, or a superfluous name, if *A. stolonifera* is regarded as the type of *Agrostis*, as has been advocated by some (see Veldkamp, 1982, for a discussion on the typification of *Agrostis*).

Beauvois (1812) accepted *Sporobolus* next to *Agrostis* and *Vilfa*. In this extended version of *Vilfa* he included all non-awned species of the old genus *Agrostis*, and so enumerated several taxa now considered to belong to *Sporobolus*.

Roemer & Schultes (1817) regarded *Sporobolus* and *Vilfa* as sections of *Agrostis*.

Kunth's account of 1833 where 44 species and 5 dubious ones of *Sporobolus* are diagnosed needs special mention.

The last monograph was made by Trinius (1840) using the name *Vilfa*, with 77 species. Today we estimate that there may be about 160 (Clayton & Renvoize, 1986).

Triachyrum Hochst. ex A. Braun (1841) and *Diachyrium* Griseb. (1874) were established on account of the bipartite palea. In several species this splits into two under pressure of the expanding ovary. In all species the palea is entire at least in a young stage and later authors have rejected it as a character for the separation of a distinct taxon.

Llanos (1851) was probably unaware of the existence of *Sporobolus* when he described *Spermachiton*. His description, especially that of the seed, applies in all details to that of *Sporobolus*. Although Merrill (1918) doubted its exact identity, it is no doubt *S. indicus* var. *flaccidus* (R. & S.) Veldk.

By tradition *S. indicus* (L.) R. Br. has been regarded as the lectotype species. This was described as *Agrostis indica* by Linné (1753). For a more extensive discussion on its involved nomenclature see under the species.

TRIBAL POSITION

By the initial inclusion of the species in *Agrostis* and its subsequent close association with it, *Sporobolus* has long remained in the Agrostideae.

Trinius (1824) created the rankless, hence invalidly named, *Vilfacea* for *Vilfa* sensu Beauv. He, and many others after him, included and then excluded a hodgepodge of genera of various alliances. Here he confused the split palea in ripe fruits with the lodicules! Later (1840), using the name *Vilfea*, he placed the group in his Agrostideae. By then he had noted that the fruit was "liber in pericarpio solubili hyalino, hinc fisso."

Stuedel (1854) made the Vilfinae (as 'Vilfea') in the Agrostideae.

Bentham (1878) briefly included *Sporobolus* in the Milieae, together with *Eriachne* R. Br. In 1881 he realized that this was a very heterogeneous set and erected the subtribe Sporobolinae (as 'Sporoboleae') in the Agrostideae, still heterogeneous, as it included *Coleanthus* Seidl., *Mibora* Adans., and *Phippsia* R. Br.

Hackel (1887) included *Sporobolus* in the Euagrosteeae.

Stapf (1898) apparently was the first to point out the relationship with the Eragrosteeae. Unfortunately, he gave no reasons for doing so. Hooker f. agreed, but did not adopt it in his treatment of the Sri Lanka grasses (1900).

As today the tribal classification of the Gramineae is especially based on the anatomy of the leaf blades and embryos the similarity between *Agrostis* and *Sporobolus* has turned out to be superficial. *Agrostis* is a pooid genus, and *Sporobolus* clearly a chloridoid/eragrostoid one, close to *Eragrostis* Wolf.

Hubbard (1934, and later) placed the Sporoboleae next to the Eragrosteeae giving *Sporobolus* and *Blepharoneuron* Nash as the only members, but *Blepharoneuron* has little in common with *Sporobolus*, and seems closer to *Erioneuron* Nash (Clayton & Renvoize, 1986).

Roshevits (1937) emendated Bentham's Sporoboleae, adding a host of genera of equally disparate origin.

Ohwi (1941, 1942) regarded the Sporoboleae as a subtribe of the Chlorideae based on part of Roshevits' concept adding *Coelachne*.

Herter (1952) without further explanation divided the grasses into 19 (!) families, among which the Sporobolaceae.

Pilger (1954, 1956) placed the subtribe in the Eragrosteeae with among others *Epicampes* J. & C. Presl (= *Muhlenbergia* Schreb.), next to the monotypic Muhlenbergiinae.

Tateoka (1957) agreed with Ohwi that the Sporobolinae were a subtribe of the Chlorideae (incl. Eragrostinae) and included *Muhlenbergia* as the only other genus.

It is curious to note that in a cluster analysis by Hilu & Wright (1982) *Coelachne* did not associate with *Sporobolus*, but with *Muhlenbergia*. The various genera of the Sporoboleae segregated in different portions of the dendrogram, anyway, and so to the authors the tribe seemed unnatural.

Clayton & Renvoize (1986) recognized in the Chloridoideae the Eragrostideae with the Sporobolinae containing also *Muhlenbergia*, but they pointed out the intergradations to *Eragrostis* ("boundary ... blurred by ... intermediates ... arbitrarily assigned to *Eragrostis*", p. 225).

Watson & Dallwitz (1989) gave as 'nearest neighbour' *Heterachne* Benth. of the Eragrostideae, but this genus is widely different. Near, also, are *Eragrostis*, *Ectrosiopsis* (Ohwi) Jansen, and the Australian *Thellungia* Stapf ex Probst. The latter is indeed very much like *Sporobolus* because of the 1-nerved lemmas and the tumidescient pericarp. It has 2(–several) florets and a rachilla process. Clayton & Renvoize included it in *Eragrostis*, but Watson & Dallwitz (1980) and Simon (in msc.) have kept it separate.

Watson & Dallwitz also gave a proximal place to *Acamptocladus* Nash, which they say has a free pericarp, but we failed to see that. It was included in *Eragrostis* by Clayton & Renvoize.

Especially the species of the section *Triachyrum* (A. Braun.) Veldk. show a close relationship with genera of the Eragrosteae. *Sporobolus* may be thought to be a derivation of *Eragrostis* by the reduction to a uniflorous spikelet. This, as Stebbins & Crampton (1961) and Ms. Phillips (1982) also pointed out, is a rather artificial character. The distinction between Aveneae and Agrostideae mainly based on the same 'difference' has also been abandoned, and likewise a tribe (or subtribe) next to Eragrostideae is hard to defend (Hilu & Wright, 1982).

The free pericarp generally said to be so characteristic for *Sporobolus* is not so unique. In the Eragrostidae it is widely spread and found in several genera attributed to the Uniolineae, Eleusininae (incl. Eragrostinae), and the Sporoboleae, even in some species attributed to *Eragrostis* itself, e.g. *E. advena* (Stapf ex Probst) Phillips (also distinguished as *Thellungia*, see above), *E. australasica* (Steud.) C.E. Hubb., *E. megalosperma* Benth. (but not always!), *E. stapfii* Winter, etc. (See Phillips, 1982). It sometimes also occurs in genera placed in the Leptureae and Cynodonteae in the sense of Clayton & Renvoize (1986), so it does not seem to be reliable as an argument to separate between tribes or subtribes.

In view of the above the Sporoboleae appear to be untenable, and ought to be included in the Eragrosteae, including *Muhlenbergia*.

Jacobs (1987) found it quite likely that *Sporobolus* and *Thellungia* should be included in *Eragrostis* s.l., but this seems a bit too far. The whole mixture then must be reclassified again, so this is not a very helpful suggestion.

A few aberrant taxa have been attributed to *Sporobolus*:

The South African and Madagascan *S. subtilis* Kunth has a well-developed rachilla process. It seems a true *Sporobolus* to us. Stapf (1898) distinguished the monotypic section *Chaetorhachia* Stapf for it (see below).

Sporobolus ramosissimus Kunth was described as having 2 or 3 flowers per spikelet with the upper floret reduced to a hairy rachilla process ('pedicel'). The spikelets,

when uniflorous, with their faintly 1-nerved lemmas are indeed suggestive of *Sporobolus*, but the usually more-flowered spikelets, the S-shaped palea, and the reticulate, adherent pericarp are of the type found in *Eragrostis*, as was also remarked by Boechat & Valls (1986). Peterson (US, in litt.), who saw a fragment of the type in US confirmed Doell's suggestion (1878) that this combination is a synonym of *E. airoides* Nees. It may be noted that this species was rather recently still regarded as an 'abnormal' *Sporobolus* by Harvey (1981).

Bentham (1881) has reported 2-flowered spikelets without a rachilla process in *S. compressus* (Torr.) Kunth and *S. serotinus* (Torr.) A. Gray. These species are now regarded to belong to *Muhlenbergia*, as *M. torreyana* (Schult.) Hitchc. and *M. uniflora* (!) (Muhl.) Fern., respectively.

Muhlenbergia is in general distinct by the membranous ligule, 1-flowered spikelets, a 3-nerved and usually awned lemma, a fusiform fruit with an adherent pericarp, and the basic chromosome number of generally 10, rarely 12. Not all characters are always present, or readily visible, however. (See Clayton & Renvoize, 1986, 227; Soderstrom, 1967.) *Chaboissaea* Fourn. is distinguished from *Muhlenbergia* mainly by the presence of 2 or even 3 florets and a basic chromosome number of 8, not 10 (Reeder & Reeder, 1988).

A curious form of *S. virginicus* (q.v.) from New Caledonia, described as *Aira sabulonum* Labill., has up to 3 florets, while Clayton & Renvoize have reported the occasional occurrence of 2-flowered spikelets in *S. mitchellii* (Trin.) C.E. Hubb. ex S.T. Blake ('mitchellia').

INFRAGENERIC DELIMITATION

Few attempts have been made to subdivide *Sporobolus*. Stapf (1898) distinguished two sections: the monotypic *Chaetorhachia* for *S. subtilis*, and *Eusporobolus* for all the other species. This major division was followed by Pilger (1956), who elevated the sections to subgenera. In subgenus *Sporobolus* he distinguished 6 informal groups ('Gruppe'), based on life form and features of the panicle and glumes. As far as we can judge this is a fairly acceptable attempt.

Bor (1960) enumerated a number of groups based on the shape of the seed for the species of the Indian subcontinent. This classification, although tempting, is not tenable, as species that are obviously close, are separated, and dissimilar ones joined. This system is perhaps practical, but not natural.

Clayton in Clayton et al. (1974) remarked that *Sporobolus* would not be divisible into well-defined sections, although clusters of closely allied species are apparent. We think that in Malesia the following 'clusters' occur, which are recognizable in other areas as well and merit recognition as sections. No doubt there are more.

Sporobolus section *Sporobolus*

Long-living annuals without stolons or cataphylls, branching intra-vaginally at base. Leaf blades usually rather conspicuously keeled, margins usually scabrid, but never pectinate. Panicle large, usually densely to moderately contracted, occasionally

rather effuse, branches solitary or fascicled, not whorled, eglandular. Lower glume very short, upper one but slightly to distinctly longer, but usually at most half as long as the spikelet. Palea not splitting easily. Seed more or less ellipsoid to oblong, in transverse section angular. Anatomical/metabolic type PCK (Hattersley, 1987; Macharia & Imbamba, 1987).

This section ('Gruppe 1' of Pilger, and part of the 'Truncatae' of Bor) consists of the pan(sub)tropical *S. indicus*-complex only. In view of its wide distribution, recent introductions aside, this must be a very ancient group.

Sporobolus section Triachyrum (A. Braun) Veldk., *comb. & stat. nov.*, based on *Triachyrum* Hochst. ex A. Braun, Flora 24 (1841) 712. — Type: *Sporobolus discosporus* Nees.

Distinct annuals (some perennials outside Malesia). Blades often heteromorphous, (i. e. basal ones more or less flat, margins pectinate by usually distinctly bulbous based bristles, cauline ones involute, margins much less pectinate to smooth), underneath usually with a rounded midrib, not conspicuously keeled (keeled in *S. amaliae* Veldk. and *S. coromandelianus*). Panicle branches whorled and more or less spreading, often with glands varying from inconspicuous lines to small warts. Lower glume up to 0.75 times as long as the spikelet, upper glume about as long as the spikelet. Palea easily splitting into two. Seed ellipsoid to obovoid, in transverse section elliptic to lenticular, occasionally tetragonous (in *S. amaliae*, *S. coromandelianus*, and *S. tetragonus* Bor). Anatomical/metabolic types PCK and NAD-ME (Hattersley, 1987; Macharia & Imbamba, 1987), which may be a clue to a future division of the section.

This section (Pilger's Gruppe 3 and 6, partly, and all or part of Bor's Discoideae, Obovatae, Ellipticae, Tetragonae) is widely spread with many species all over the (sub)tropics of the world, which like the previous group suggests an ancient origin. Malesian species are *S. amaliae*, *S. coromandelianus* (leaves flat and more or less homomorphous), *S. harmandii* Henr., *S. novoguineensis* Baaijens, *S. piliferus* (Trin.) Kunth, and *S. sciadocladus* Ohwi.

Sporobolus section Virginicae Veldk., *sect. nov.*

Perennes stoloniferae basi extravaginaliter ramosae. Paniculae contractae dense spiculatae, ramis fasciculatis ad solitariis eglandulosis. Glumae longae superiore ad spiculae longitudinem. — Type: *Sporobolus virginicus* (L.) Kunth.

Stoloniferous perennials branching extra-vaginally at base. Panicles contracted, densely spikeled, the branches fascicled to solitary, eglandular. Glumes long, the upper one up to as long as the spikelet. At least *S. virginicus* and *S. consimilis* Fresen. are NAD-ME (Hattersley, 1987).

This section also includes *S. pungens*. *Sporobolus humilis* Presl and *S. virginicus* fit Pilger's diagnosis of 'Gruppe 2', they are part of Bor's Obovatae. The palea easily splits in the first species, but hardly in the second. Their leaf anatomy differs considerably, too. As the section occurs pan(sub)tropically, it is probably of ancient origin.

Sporobolus section Agrosticula (Raddi) Veldk., *comb. & stat. nov.*

based on *Agrosticula* Raddi, *Agrost. Bras.* (1823) 33. — Type: *Sporobolus tenuissimus* (Schrank) O. Ktze.

Annuals. Leaf blades homomorphous. Panicle branches fascicled, eglandular. Spikelets small. Glumes relatively short. Palea not easily splitting. Anatomical/metabolic type unknown.

Sporobolus tenuissimus belongs to Pilger's 'Gruppe 6' and Bor's *Truncatae*. This is an Afro-American group, and therefore apparently not as ancient as the previous ones.

Another section (non-Malesian) we had to deal with seems arranged around the *S. fimbriatus* aggregate (incl. *S. agrostoides* Chiov., *S. brockmannii* Stapf, *S. macranthelus* Chiov., etc.), and is formed by part of Pilger's apparently heterogeneous 'Gruppe 4', and half of Bor's *Discoideae*.

Sporobolus section Fimbriatae Veldk., *sect. nov.*

Perennes saepe intra-vaginales ramosae, paniculis variabilibus, ramis fasciculatis ad solitariis eglandulosis, glumis inferioribus plerumque brevibus, glumis superioribus spiculis parum brevioribus ad equilongis. — T y p u s: *Sporobolus fimbriatus* Nees.

Perennials, usually branching intra-vaginally, panicle various, but branches fascicled to solitary, eglandular, lower glume usually small, upper glume slightly shorter to as long as the spikelet. Anatomical/metabolic type PCK (Hattersley, 1987; Macharia & Imbamba, 1987). This is also an Afro-American group.

ANATOMY
(G.J. Baaijens)

Thanks to the kindness of Prof. Dr. R. Hegnauer, Leiden, I (GJB) had the opportunity to do some anatomical research on most of the taxa under revision here.

Emphasis was given to both the upper and lower epidermis of the blades. Of course transverse sections were made as well, while spodograms were made to investigate the extent of silification. Whenever possible five specimens were studied; of two taxa there was such ample material of the type specimens that these could be included. Unfortunately the views on grass anatomy have changed so much in the past two decades, that this research ought to be done again to update it. Therefore some notes will have to suffice.

For the method of making the samples and the terminology to describe them Metcalfe (1960) was followed.

Duval-Jouve (1866) gave excellent figures of *S. pungens* (Schreb.) Kunth showing the nature of the papillae, the bulbous based hairs and the bulbiform cells.

A few descriptions have also been given by Metcalfe (1960), Stewart (1965), R.P. Ellis (1977), and Conert & Lobin (1984).

Four studies were devoted to *Sporobolus* entirely, one by Goossens (1938) on African species, the second by Schwabe (1948) on Argentine ones, a third one by Leras & Vignal (1969), who compared it to *Crypsis* Ait., and the fourth by Böcher (1972) on the very aberrant *S. rigens* (Trin.) Desv.

Most of the characters used by the first two were based on transverse sections. The second one paid some attention to the epidermis as well and gave a key to the species exclusively based on anatomical characters. In some cases she appears to have been too optimistic about the constancy of certain features: she thought to be able to differentiate *S. indicus* and *S. poiretii* (R. & S.) Hitchc. (sensu Hitchcock!) by the number of cells between the parenchyma sheath and the adaxial epidermis, but this number has turned out to be rather variable (see also Metcalfe, 1960). Schwabe and Leras & Vignal made an extensive survey of epidermal characters using the dermograms introduced by Prat.

Goossens appears to have been more critical than Schwabe. He also gave a key, but combined both anatomical and morphological characters. He discovered, as might be expected, that some species cannot really be distinguished by their anatomy alone. On the other hand some taxa, or groups of taxa, appear to be distinct by constant character states.

Epidermal cells

Two categories of cells can be distinguished: the 'long-cells', which are distinctly longer than wide, and the 'short-cells', where the dimensions are more or less equal. The latter may be distinguished into silica-cells and cork-cells. All epidermal cells accumulate silica, as spodograms revealed (see below), but only in the silica-cells is the silica deposited into the characteristically shaped silica-bodies. Inside these granula are often visible as small red dots. While silica-cells are usually translucent, the cork-cells are usually dark due to the presence of organic deposits (cf. Grob, 1896). No suberine (cork) was observed.

In the species studied the long-cells were rather similar. In *S. virginicus* the walls were much thicker.

The silica-bodies are variously shaped, but the various types are not so strictly distinct as to be applicable to taxonomy without caution: Grob (p. 42, t. iv, f. 11, 16, 17) already observed transitions between the various types. Cross-shaped bodies are X-shaped and about as long as wide. Dumbbell-shaped bodies are less deeply incised and longer than wide (eragrostoid or chloridoid: Prat, 1932, 1936). Saddle-shaped bodies have convex sides and concave distal and proximal sides. Crescent-shaped bodies are concave at the distal side only (festucoid: Prat, 1932; 1936). Ellipsoid bodies are positioned transversally.

Various types may occur in a single leaf, although not always on the same surface. In some species the silica-bodies on the abaxial epidermis are very uniformly crescent-shaped. Adaxially, however, dumbbell-shaped bodies are found. It is therefore necessary to study both surfaces.

Epidermal appendages

1. The macro-hairs in *Sporobolus* are generally unicellular, some faint septa were once seen in a single hair of *S. humilis*. At the base they are often surrounded by raised epidermal cells, wherefore they have been called cushion-hairs, 'Polsterhaare' or, as here, bulbous based hairs. The basal part of the hair itself is not inflated in contrast with the next type.

2. The prickle hairs, which are also unicellular, have enlarged bases, while the upper part is a rigid, pointed barb. In *S. coromandelianus* angular prickles occur on the leaf margins and are surrounded at base by some epidermal cells, but because of the enlarged base I have considered them to be prickle hairs and not bulbous based ones.

Over the adaxial ribs in *S. indicus* var. *flaccidus* there are shortly pointed prickles or hooks, which show all transitions to short-cells. Metcalfe also reported the presence of such 'unbarbed prickles' in several species.

3. Micro-hairs or 'Winkelhaare' (Grob) were present in all species studied. Jacques-Félix (1962) has stated that all species would have bicellular micro-hairs and, if they appear to be unicellular, the basal cell then would be immersed below the surface of the epidermis. I have seen no trace of such hidden basal cells and there are often truly unicellular micro-hairs, as was also remarked by Metcalfe (1960: 463). Two main types may be distinguished:

- a) Hairs unicellular, ovoid: *Sporobolus*-type.
- b) Hairs bicellular: here there are two main subtypes (cf. Amarasinghe & Watson, 1988, 1990):
 - i) Topcell long and narrow, 1–2(–3) times as long as the basal cell, hair slender: panicoid type, not yet reported for *Sporobolus*.
 - ii) Topcell hemispherical, up to 0.7 times as long as the basal cell: chloridoid type, which can be divided again:

Chloris type: topcell 0.5–0.7 times as long as the basal cell. In *S. virginicus* more or less spherical with a sometimes indistinct septum at about the middle of the hair or lower. In other species the hairs are like an egg in an egg-cup, with the distal cell dome-shaped or spherical. *Sporobolus harmandii*, *S. humilis*, and, less typically, in *S. piliferus*.

Eragrostis type: topcell up to 0.5 times as long as basal cell: *Sporobolus amaliae*, *S. novoguineensis*, and *S. sciadocladus*. (Note: this term is misleading, as Amarasinghe & Watson, 1990, have shown that *Eragrostis* has hairs with a ratio varying between 0.2–3.0!)

As can be seen from the observations in sect. *Triachyrum* the various types may occur in related species, sometimes even on the different sides of the same leafblade as in *S. piliferus*.

In some species where unicellular hairs are the rule some bicellular ones were found on the adaxial surface and on the floral parts, especially at the base of the palea.

The ultrastructure of the micro-hairs of *S. indicus* var. *elongatus* (R. Br.) F.M. Bailey was described by Amarasinghe & Watson (1988) (as *S. elongatus* R. Br.).

4. Papillae are only found on the adaxial surface. Two types of protrusions from the cell wall are present:

- a) Small, globose (the 'Cuticularwärzen' or '-zäpfchen' of Grob).
- b) Large, inflated, more or less dome-shaped protrusions (Grob's 'blasige Aufreibungen').

These structures vary considerably in number and size, sometimes they are completely absent. Perhaps the environment has an influence here.

Spodograms

The spodograms showed that almost all epidermal cells and their appendages may accumulate silica. Large masses of silica were sometimes found in the long-cells, in the subsidiary cells of the stomata, in the walls of the cork-cells, in the small, globose papillae (of e.g. *S. indicus* and *S. virginicus*, quite in contrast with the large, inflated papillae of e.g. *S. harmandii*, where silica was almost completely absent), and in the prickle-hairs, especially in their tips, making them acute. However, only in the silica-cells is silica deposited in the distinct bodies discussed above.

Transverse section

In transverse section the most distinct features are the general shape of the leaf, the presence or absence of a midrib, the vascular bundles, and the bulliform and the colourless cells associated with these.

In some species parenchymatous tissue is found at the adaxial side of the midrib between the vascular bundle and the overlying sclerenchyma.

In some species the basal bulliform cell is much larger than the adjacent ones, in others this difference is less pronounced.

All species of *Sporobolus* so far studied are C₄- or Kranz grasses with double bundle sheaths (XYMS+) around the larger vascular bundles and with an aspartate metabolism. R.P. Ellis (1977) reported the presence of two anatomical and metabolic subtypes, the NAD-ME type and the PCK-type.

In the NAD-ME type the chloroplasts of the double bundle sheath are said to be centripetal (i.e. in transverse section under magnification they are concentrated towards the vascular bundle in the cells of the parenchyma sheath) and have numerous grana; the dominant decarboxylating enzyme is NAD-malic enzyme.

The chloroplasts of the PCK-type are centrifugal (i.e. concentrated away from the bundle), and have only a few grana; the principal decarboxylating enzyme here is PEP-carboxykinase.

Jacobs (1987), however, warned that in the NAD-ME type the position of the chloroplasts is dependent on whether active growth was taking place when the samples were taken: at first the chloroplasts are rather evenly spread, then they become centripetally aligned, and when they have lost all their starch, they become centrifugal! Fortunately (for herbarium taxonomists) gradually dried specimens show the behaviour best.

In the Australian species of *Eragrostis* there is a strong correlation between the type of micro-hair and the type of aspartate metabolism. Amarasinghe & Watson (1990) reported that nearly all species with a NAD-ME-like anatomy had hairs of the chloroid type, while those with a PCK-like anatomy had hairs of the panicoid type. In *Sporobolus* the latter type of hairs has not been reported so far and both types of metabolism occur.

Hattersley (1987) summarized the present knowledge:

NAD-ME: *Sporobolus airoides* (Torr.) Torr., *S. caroli* Mez, *S. cryptandrus* (Torr.) A. Gray, *S. consimilis* Fresen., *S. coromandelianus* (Retz.) Kunth, *S. discosporus* Nees, *S. ludwigii* Hochst., *S. nitens* Stent, *S. pulchellus* R. Br., *S. smutsii* Stent, *S. virginicus* (L.) Kunth [Echevarría et al. (1988) have added *S. pungens* (Schreb.) Kunth].

If we understand Macharia & Imbamba's (1987) table correctly, *S. rangei* Pilger and *S. spicatus* (Vahl) Kunth may be added.

PCK: *Sporobolus africanus* (Poir.) Robyns & Tournay, *S. creber* De Nardi, *S. elongatus*, *S. jacquemontii* Kunth, '*S. poiretii*' (= *S. indicus*), *S. pyramidalis* Beauv., all members of sect. *Sporobolus*, *S. centrifugus* Nees, *S. conrathii* Chiov., *S. festivus* A. Rich., *S. fimbriatus* Nees, *S. lampranthus* Pilger, *S. panicoides* A. Rich., *S. pectinatus* Hack., *S. stapfianus* Gandoger.

Macharia & Imbamba (1987) in a scrambled table seem to mention, moreover, *S. filipes* Stapf, *S. geminatus* Clayton, *S. marginatus* A. Rich., and *S. quadratus* Clayton.

Results

Using the various anatomical and morphological characters of the epidermis and transverse sections of the blades, the Malesian species may be arranged in several groups which usually correspond with the groups based on the macro-morphological characters. So, with the evidence coming from two sides, there seems to be a 'natural' background for a subdivision. The inclusion of *S. humilis* and *S. virginicus* in the same section is not corroborated by their anatomy, however (see below).

Section *Sporobolus*

Short-cells on the abaxial epidermis often paired, cork-cells usually small. Silica-bodies usually more or less crescent-shaped or ellipsoid, never dumbbell-shaped, fitting into the concavity of an adjacent cork-cell. The silica-bodies on the adaxial surface tend to be more elongated, variable in outline, sometimes even dumbbell-shaped. Prickle-hairs on the margins and adaxially over the ribs.

Micro-hairs usually unicellular. In *S. indicus* var. *creber* (De Nardi) Veldk. some bicellular micro-hairs of the *Chloris*-type were also seen.

Papillae small, globose, a few per cell (usually one).

Palmer et al. (1985) gave a description of the epidermis of *S. indicus* var. *capensis* (as *S. africanus*).

Blades in transverse section distinctly keeled, adaxially sometimes with a colourless parenchymatous tissue between the vascular bundle(s) and the overlying sclerenchyma. Bulliform cells in fan-shaped groups of the *Sporobolus*-type.

In the Malesian varieties the epidermis offers little if anything at all in their delimitation. Perhaps some statistical differences are present in the length of the stomata and the micro-hairs. The length of the latter is 9–12 μm in var. *flaccidus*, 10–15 μm in var. *creber*, 12–18 μm long in var. *capensis*, 15–17.5 μm in var. *major*, and 15–22.5 μm in var. *cinereo-viridis* Baaijens.

There may also be some differences in the shape and number of the bulliform cells, but the data were insufficient.

Section Triachyrum (*S. amaliae*, *S. harmandii*, *S. novoguineensis*, *S. piliferus*, *S. sciadocladus*)

Cork-cells often large, with sinuous walls. Abaxially silica-bodies of various types but at least some dumbbell-shaped. Adaxially the silica-bodies tend to be cross-shaped. Bulbous based hairs rather than prickle-hairs on the margins; prickle-hairs over the ribs. Micro-hairs always bicellular, shaped like an egg in an egg-cup, of various types (see below). Papillae often rather abundant over the ribs, inflated [Conert & Lobin (1984) said papillae were absent in their material of *S. piliferus* from Cape Verde]. Blades in transverse section without a distinct midrib; adaxially never with parenchymatous tissue between the vascular bundle(s) and the overlying sclerenchyma, abaxially rounded, distinct ribs absent. Bulliform cells in fan-shaped groups with the basal cell not much larger than the adjacent ones.

The micro-hairs turned out to be of some specific diagnostic value:

Sporobolus amaliae: 30–42.5 μm long; basal cell rather wide; apical cell very short, 7.5–10 μm long; *Eragrostis*-type.

Sporobolus harmandii: 35–40 μm long; basal cell rather wide; apical cell spherical, only slightly shorter than the basal one, 12.5–17.5 μm long; *Chloris*-type.

Sporobolus novoguineensis: 27.5–40 μm long; basal cell fairly large, slender; apical cell very short, low dome-shaped, 5–12.5 μm long; *Eragrostis*-type.

Sporobolus piliferus: 35–50 μm long; basal cell rather wide; apical cell rather large, dome-shaped, 12.5–18 μm long; *Chloris*-type. The abaxial ones often longer, up to 70 μm long, the apical cell 12.5–17.5(–22.5) μm long; *Eragrostis*-type.

Sporobolus sciadocladus: 40–52.5 μm long; apical cell spherical, very short, 10–15 μm ; *Eragrostis*-type.

Sporobolus coromandelianus

This species slightly differs from the above. Silica-bodies on both sides usually more or less crescent-shaped, fitting into the concavity of an adjacent cork-cell, the abaxial ones sometimes dumbbell-shaped. Prickle-hairs on the margins, sometimes resembling macro-hairs. Adaxially micro-hairs rarely bicellular (and then resembling those of *S. virginicus*). Papillae small, globose, one per cell. Blades in transverse section adaxially with a conspicuous midrib due to large amounts of colourless parenchymatous tissue between the vascular bundle and the overlying sclerenchyma; abaxially very conspicuous, flattened. Bulliform cells in fan-shaped groups penetrating deeply into the mesophyll, the basal cell rather large.

Section Virginicae (*S. humilis*, *S. virginicus*)

Sporobolus humilis: Adaxial epidermis with very regular saddle-shaped silica-bodies. Abaxially more elongated and tending to be dumbbell- or cross-shaped.

Prickle-hairs on the margins and over the ribs. Micro-hairs bicellular, 22.5–30 µm long, basal cell about as long as the rather large, rounded, 10–12.5 µm long apical cell. Papillae numerous, several per cell. Cell walls with small globose protrusions. Blades in transverse section with weakly developed ribs due to the thinness of the lamina between the vascular bundles; midrib in dried specimens often quite distinct, after boiling less defined. Bundle-sheaths round, not triangular as in the other species (except for *S. virginicus*). Bulliform cells in fan-shaped groups often without a distinctly larger basal cell.

Sporobolus virginicus: Silica-bodies on both sides usually crescent-shaped or ellipsoid, fitting into the concavity of an adjacent cork-cell. Prickle-hairs on the margins and the ribs. Micro-hairs very rare, spherical, bicellular, 12.5–17.5 µm long, the basal cell about as long as the apical one, sept between the cells often very thin. Papillae numerous. Cell walls with small globose protrusions, often several per cell. Blades in transverse section adaxially with well-developed ribs, abaxially rounded. Midrib absent. Bundle-sheaths round, not triangular as in the other species (except for *S. humilis*). Bulliform and colourless cells in fan-shaped groups, often rather ill-defined, penetrating deeply into the mesophyll, often reaching the abaxial surface; basal cell often not much larger than the adjacent cells.

Because the micro-hairs are so rare it is not surprising that Grob (1896) overlooked them. On the floral parts they are more common but very variable and then sometimes very similar to those occasionally found in *S. indicus* var. *creber*.

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SPOROBOLUS

Sporobolus R. Br., Prod. 1 (1810) 169; Beauv., Agrost. (1812) 26, 178; Kunth, Enum. Pl. 1 (1833) 209; Benth., Fl. Austr. 7 (1878) 620; Hook. f., Fl. Br. India 7 (1896) 247; Stapf, Fl. Cap. 7 (1900) 578 (incl. sect. *Eusporobolus*, nom. inval.); Camus, Fl. Gén. I.-C. 7 (1923) 505; Ridley, Fl. Mal. Pen. 5 (1925) 243; Pilger in E. & P., Nat. Pfl. Fam., ed. 2, 14d (1956) 54; Schmid, l'Agro. Trop. 13 (1958) 484; Bor, Grasses (1960) 623; Clayton, Kew Bull. 19 (1965) 287; Monod de Froideville in Backer & Bakh. f., Fl. Java 3 (1968) 537; Cufodontis, Bull. Jard. Bot. Brux. 38 (1968) 1271; Clayton, Fl. Trop. E. Afr., Gram. 1 (1970) 353; Gill., Rev. Fl. Mal. 3 (1971) 104; Simon, Austr. Syst. Bot. Soc. Newsl. 31 (1982) 16; Siddiqui & Qaiser, Pak. J. Bot. 20 (1988) 161, t. 3a; Astegiano, Kurtziana 20 (1989) 65. — *Agrostis* L. sect.

- Sporobolus* R. & S., Syst. Veg. 2 (1817) 367 ('*Sporoboli*'). — Lectotype: *Sporobolus indicus* (L.) R. Br. [cf. Nash in Britton & Brown, Ill. Fl. N. U.S. ed. 2, 1 (1913) 194].
- Agrosticula* Raddi, Agrost. Bras. (1823) 33, t. 1, f. 2. — Type: *Agrosticula muralis* Raddi [= *Sporobolus tenuissimus* (Schrank) O. Ktze].
- Bennettia* Raf., Bull. Bot. Seringe 1 (1830) 220, not a homonym of *Bennettia* S.F. Gray (1821). — Type: *Agrostis juncea* Michx., nom. illeg. [= *Sporobolus junceus* (Beauv.) Kunth].
- Triachyrum* Hochst. ex A. Braun, Flora 24 (1841) 712; Steudel, Syn. 1 (1854) 176. — Lectotype: *Triachyrum adoense* Hochst. ex A. Braun (= *Sporobolus discosporus* Nees).
- Spermachiton* Llanos, Fragm. Pl. Filip. (1851) 25; in Blanco, Fl. Filip. ed. 3, 4, 1 (1880) 17. — Type: *Spermachiton involutum* Llanos [= *Sporobolus indicus* (L.) R. Br. var. *flaccidus* (R. & S.) Veldk.].
- Cryptostachys* Steudel [Flora 33 (1850) 229, nomen], Syn. 1 (1854) 181. — Type: *Cryptostachys vaginata* Steudel [= *Sporobolus vaginiflorus* (Torr.) Wood].
- Diachyrium* Griseb., Abh. Ges. Wiss. Göt. 19 (1874) 18, 257, t. 2, f. 8. — Type: *Diachyrium arundinaceum* Griseb. [= *Sporobolus rigens* (Trin.) Desv.].
- Bauchea* Fourn., Mex. Pl. 2 (1886) 87. — Type: *Bauchea karwinskyi* Fourn. (= *Sporobolus wrightii* Scribn.).
- Vilfa* auct. non Adans.: Beauv., Agrost. (1812) 16, 181, p.p.; Trin., Gram. Unifl. Sesquifl. (1824) 152; Mém. Ac. Sc. St. Pétersb. VI, 5, 1 (1840) 50, p.p.; Steudel, Syn. 1 (1854) 153. — *Agrostis* L. sect. *Vilfa* auct. non R. & S.: R. & S., Syst. Veg. 2 (1817) 343, p.p. ('*Vilfae*').

Annuals or perennials, often caespitose, sometimes with creeping rhizomes or stolons. Ligule a row of hairs. Inflorescence a panicle. Spikelets 1-flowered, muticous, articulating above the glumes. Glumes usually unequal, thin, the lower one 0- (or 1-)nerved, the upper one 1-nerved. Rachilla rarely produced. Lemmas similar to the glumes, 1- (or 3-)nerved; callus little developed, glabrous. Paleas as the lemmas, 2-nerved. Lodicules 2, asymmetric, obrhomboid, 1-nerved, glabrous. Stamens 2 or 3. Styles free at base. Fruit a utricle, free between the palea and lemma, often deciduous before them, seeds usually ejected by the mucilaginous pericarp, especially when soaked; testa sometimes also mucilaginous; hilum punctiform; embryo usually about half as long as the seed.

Distribution. Pan(sub)tropical with 160+ species, 10 in Malesia, of which one with at least 5 varieties.

Anatomy. The leaves have a panicoid anatomy (XYMS+) with an aspartate (C₄) metabolism (both NAD-ME and PEP-CK), the embryo is chloridoid (P+PF).

Palynology. Siddiqui & Qaiser (1988) reported non-operculate pollen for *S. arabicus* Boiss., *S. coromandelianus* (Retz.) Kunth, and *S. helvolus* (Trin.) Dur. & Schinz, but Astegiano (1989) observed operculate pollen in *S. indicus*.

Chromosomes. $x = 5, 6, 9, 10, 19$, usually 9 or 10, chromosomes small.

Uses. Most species are weedy, some are useful as sandbinders, and as forage. Roig (Parodiana 5, 1989, 355) reports the use in Argentina of *S. airoides* (Torr.) Torr., *S. contractus* Hitchc., *S. cryptandrus* (Torr.) A. Gray, *S. flexuosus* (Thunb.) Rydb., and *S. rigens* (Trin.) Desv. as cereals. *Sporobolus indicus* var. *major* (Buse) Baaijens is mentioned likewise for India by Chaudhuri & Pal [Bull. Bot. Soc. Bengal 32 (1979) 52, as *S. fertilis* (Steudel) Clayton].

Notes. Persoon (Syn. 1, 1805, 73) made the combination *Matrella juncea*, his only species in the new genus *Matrella* Pers., citing "*Agrostis matrella* Lin. Willd. sp. pl. 1. p. 367 ? *A. juncea* Lam. ill. gen. t. 41. f. 2. ... Flor. subnitentes 10-12 in rachi alternatim sessiles." As it turns out two taxa are confused here: *Agrostis ma-*

- 6a. Spikelets longer than 1.25 mm 7
 b. Spikelets 0.9–1.25 mm long. — Anthers 3 **9. S. tenuissimus**
- 7a. Upper glume more or less acute (entire to dentate or erose), 0.4–0.67 times as long as the spikelet, distinctly longer than the lower glume. 8
 b. Upper glume (erose) truncate, less than half as long as the spikelet, slightly longer than the lower glume. — Spikelets 1.7–2.2 mm long. Anthers 3. Not yet found in Malesia **5f. S. indicus var. pyramidalis**
- 8a. Spikelets 1.8–2.6 mm long. — Anthers 3, rarely 2 9
 b. Spikelets 1.25–1.75 mm long. — Anthers 2, rarely 3 11
- 9a. Spikelets 2–2.6 mm long, dark green to greyish or blackish (not the black smut!). Lodicules 0.3–0.45 mm long. Seed usually more than 1.1 mm long. — Anthers always 3 10
 b. Spikelets up to 2 mm long, yellowish to pale or grass green. Lodicules 0.25–0.3 mm long. Seed 0.9–1.1 mm long. — Anthers 2 or 3 12
- 10a. Panicle densely contracted, lobed at base, spiciform in the upper part, branches appressed, the lowermost up to 3.5 cm long . **5a. S. indicus var. capensis**
 b. Panicle laxly contracted, branches slightly patent to curved, the lowermost up to 6 cm long **5b. S. indicus var. cinereo-viridis**
- 11a. Lowermost panicle branches 1.5–9 cm long. Spikelets yellowish to pale or grass green. Lower glume 0.35–0.55(–0.6) mm long. — Panicle with erecto-patent to appressed branches, lax to dense. Widely spread 12
 b. Lowermost panicle branches c. 1.5 cm long. Spikelets dark green. Lower glume 0.7–0.8 mm long. — Panicle densely contracted, lobed at base, upper part spiciform. New Guinea **5c. S. indicus var. creber**
- 12a. Panicle usually somewhat lax and branches loosely spikeled. Spikelets usually 1.4–1.6 mm long. Anthers usually 2, 0.5–0.8 mm long. Seed 0.6–0.9 mm long **5d. S. indicus var. flaccidus**
 b. Panicle usually contracted and branches densely spikeled. Spikelets usually 1.8–1.9 mm long. Anthers usually 3, 0.7–1 mm long. Seed 0.9–1.1 mm long
5e. S. indicus var. major
- 13a. (1). Branches of the inflorescence eglandular or with minute pusticular to linear glands. Spikelets brownish to purple with green. Lower glume 0.5–0.95 times as long as the spikelet. — Seed usually laterally flattened and 0.9–1.4 mm long (quadrangular, 0.75–0.9 mm long in *S. amaliae*) 14
 b. Branches of inflorescence at base with elongated glands. Spikelets usually pale to blackish green. Lower glume 0.25–0.4 times as long as the spikelet. — Ligule 0.35–1 mm long. Blades homomorphous, flat, up to 8 mm wide. Seed quadrangular in transverse section, 0.75–0.95 mm long . **2. S. coromandelianus**
- 14a. Panicle usually more or less lax (more or less compact in *S. novoguineensis*), branches erecto-patent, most or all in whorls, the lowermost 4–20 together, the longest one (0.6–)1.2–2.7 cm long, usually eglandular. — Blades usually heteromorphous 15
 b. Inflorescence contracted, branches more or less appressed against the axis, the lowermost solitary, or fascicled, or up to 4 in a whorl, the longest one up to 0.8 cm long, with small, pusticular glands. — Blades homomorphous. Philippines **7. S. piliferus**

- 15a. Ligule a more or less ciliolate to ciliate rim or collar. The lowest inflorescence branches 4–12 together. Lower glumes 0.5–0.67 times as long as the spikelet. Seed laterally flattened, elliptic in transverse section, 0.9–1.8 mm long . . . 16
- b. Ligule a glabrous to microscopically ciliolate rim. The lowest inflorescence branches 13–20 together. Lower glumes 0.67–0.95 times as long as the spikelet. Seed knucklebone-shaped, quadrangular in transverse section, 0.75–0.9 mm long. — Timor **1. *S. amaliae***
- 16a. Spikelets 1.35–2.1 mm long. Lower glumes 0.6–1.25 mm long. Seed 0.9–1.2 mm long 17
- b. Spikelets 2.2–2.5 mm long. Lower glumes 1.4–1.7 mm long. Seed 1.5–1.8 mm long. — Aru Islands **8. *S. sciadocladus***
- 17a. Inflorescence ellipsoid, lowest whorl with 4–10 branches. Spikelets 1.35–1.9 mm long. Seed 0.9–1.1 mm long. — Sumatra **3. *S. harmandii***
- b. Inflorescence linear, lobed, lowest whorl with 10–12 branches. Spikelets 1.8–2.1 mm long. Seed 1.1–1.2 mm long. — New Guinea, Aru Islands
6. *S. novoguineensis*

1. *Sporobolus amaliae* Veldk., *spec. nov.* — Fig. 1

Annuae rhizomata stolones cataphylla desunt, ligula porciformi glabra ad microscopice ciliolata, foliis plus minusve heteromorphis basalibus planis, marginibus pectinatis, paniculae effusae, ramis erecto-patentibus eglandulosis (basi callosis), in verticillis 10–13, inferioribus 13–20-verticillatis, longissimis 1,5–2,2 cm longis, spiculis 1,5–1,75 mm longis virido-purpurascensibus, glumis inferioribus 0,67–0,95-plo longioribus, superioribus spiculis aequantibus, seminidibus condyliformibus quadrangularibus in sectione transversali ca. 0,75 mm longis. — T y p u s: *Cinatti IV-140* (L, holo; LISC), Timor, Dili, Areia Branca, 30 March 1962.

Annual, tufted and branching intra-vaginally mainly at base. Rhizomes, stolons, cataphylls absent. Culms erect, glabrous, smooth, shiny, up to 52 cm high. *Sheaths* smooth, outer margin finely hairy, otherwise glabrous, throat glabrous or with a few hairs; ligule a minute glabrous to microscopically ciliolate rim, 0.05–0.15 mm high; blades more or less heteromorphous, keeled; the basal flat, margins pectinate, the cauline folded, margins less pectinate, the cauline linear, up to 9.5 cm by 4.5 mm, apex acuminate, above scabrid, sparsely hairy, below smooth, glabrous. *Panicles* effuse, c. 12 by 4 cm, branches in 10–13 whorls, capillary, erecto-patent, simple, eglandular (callose at base), the lowermost 13–20 together, with up to 6 spikelets in the upper 0.5–0.67th, the longest 1.5–2.2 cm long. Pedicels 0.5–0.75 mm long, smooth. *Spikelets* 1.5–1.75 mm long, purplish and greenish. Lower glume narrowly ovate-oblong to -lanceolate, 1–1.45 mm long, 0.67–0.95 times as long as the spikelet, apex acuminate, more or less smooth, nerves 0 or 1; upper glume ovate-oblong, as long as the spikelet, margin scarious, acute, more or less smooth. *Lemma* ovate-oblong to oblong, as long as the spikelet, margins scarious, involute, obtuse, 1-nerved, more or less smooth. Palea oblong, c. 1.4 mm long, obtuse to truncate, easily split by the ovary and/or fruit. Lodicules 0.25–0.3 mm long, acute. Anthers 3, 0.3–0.5 mm long, purple. *Seed* obovate-ellipsoid to oblong, knucklebone-shaped, more or less quadrangular in transverse section, 0.75–0.9 by 0.4–0.5 mm in diam.; pericarp loosely adherent; embryo c. 0.4 mm long.

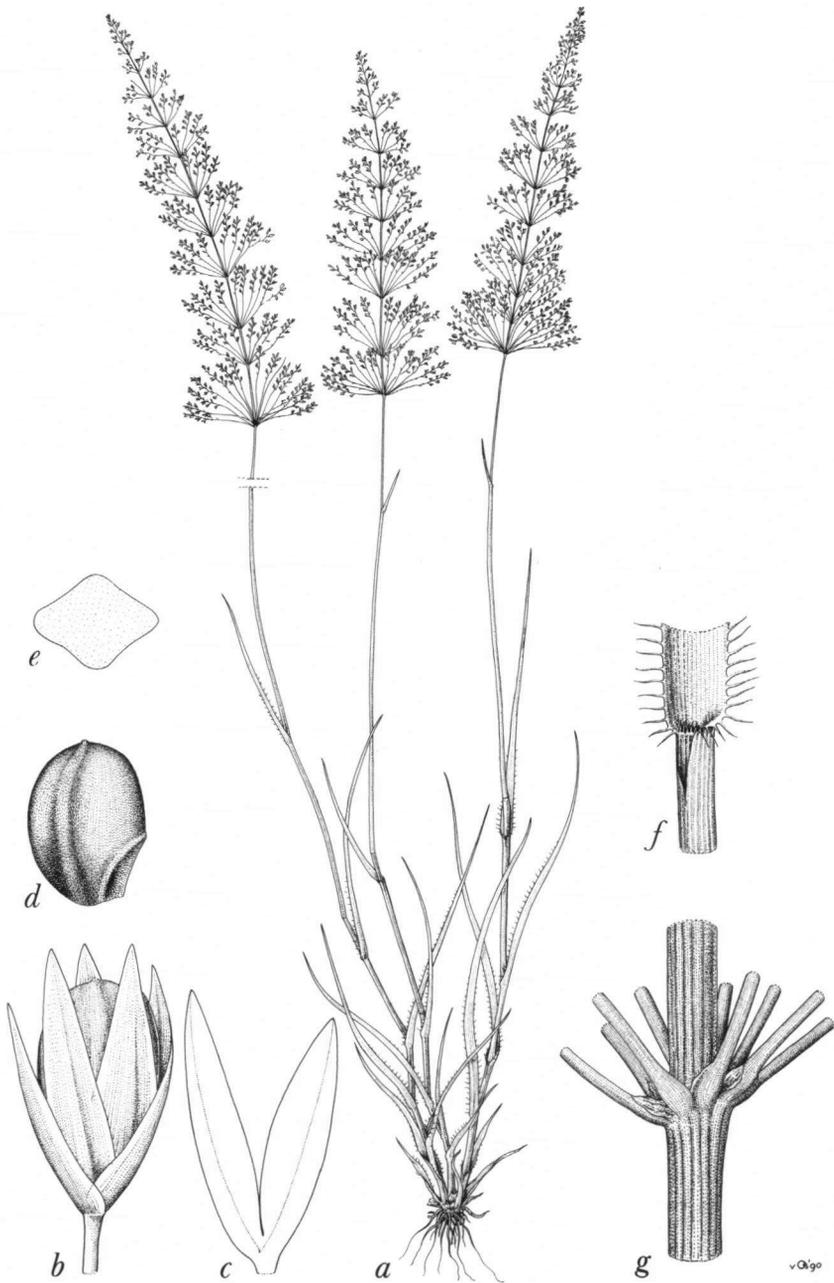


Fig. 1. *Sporobolus amaliae* Veldk. a. Habit, $\times 0.5$; b. spikelet, $\times 25$; c. glumes, $\times 25$; d. caryopsis, $\times 25$; e. transverse section of seed, $\times 25$; f. throat of leaf, $\times 30$; g. lowest whorl of inflorescence branches, $\times 25$ (Cinatti IV-140).

Distribution. Malesia: Lesser Sunda Islands (Timor).

Habitat. Not given.

Anatomy. See Introduction.

Notes. This species is different from all others studied by the lodicules with an acute, not rounded apex. Because of the very reduced ligule, the absence of glands in the inflorescence, and provenance it seems closest related to the Australian *S. lenticularis* S.T. Blake and *S. pulchellus* R. Br. It differs from both by the glabrous to microscopically ciliolate ligule and the longer lower glume, here 1–1.45 mm long, 0.67–0.95 times as long as the spikelet, there 0.5–1 mm long, 0.25–0.5 times as long as the spikelet. *Sporobolus lenticularis* differs moreover by the larger, discoid seed while *S. pulchellus* has 6–11 branches in the lowest whorl of the panicle and spikelets only 0.9–1.25 mm long.

Knucklebone-shaped seeds are not very common in Asia and Australia. They are also found in the Asian *S. tetragonus* Bor. This is different by the more or less homomorphous blades, the ciliate ligule, the scabrous and glandular branches, the lowermost 6–12 together, the 1–1.45 mm long lower glume, 0.5–0.62 times as long as the spikelet, and the c. 0.75 mm long anthers.

Named after JFV's wife, Amalia Visser.

2. *Sporobolus coromandelianus* (Retz.) Kunth

Sporobolus coromandelianus (Retz.) Kunth, Rév. Gram. 1 (1829) 68; Kunth, Enum. Pl. 1 (1833) 213; Hook. f., Fl. Br. India 7 (1896) 252; in Trimen, Handb. Fl. Ceylon 5 (1900) 264; Achariyar & Mudaliyar, Handb. S. Ind. Gr. (1921) 235, t. 181, 182; Bor, Fl. Assam 5 (1940) 120; Grasses (1960) 626; Clayton, Kew Bull. 19 (1965) 295; Bosser, Mém. ORSTOM 35 (1969) 120, t. 37 f–h; Leras & Vignal, Bull. Soc. Bot., France 116 (1969) 425, t. 4; Narayan & Muniyamma, Taxon 21 (1972) 683; Clayton, Fl. Trop. E. Afr. 1 (1974) 363; Christopher & Abraham, Cytologia 39 (1974) 565, t. 14; Ellis, Agroplanteae 9 (1977) 90, t. 33; Srivastava, J. Ind. Bot. Soc. 57 (1978) Suppl., 79; Cope, Fl. Pakistan 143 (1982) 142; Satyamurty, Curr. Sc. 52 (1983) 549; Reddi et al., Rev. Palaeobot. & Palynol. 54 (1988) 34, tab. 50; Siddiqui & Qaiser, Pak. J. Bot. 20 (1988) 161. — *Agrostis coromandeliana* Retz., Obs. 4 (1786) 19; Roxb., Fl. Ind. 1 (1820) 318. — *Vilfa* ? *coromandeliana* Beauv., Agrost. (1812) 16 ('*coromandelina*'), 147 (?), 181 ('*coromandelina*'); Trin., Sp. Gram. Ic. (1823) t. 11; Steudel, Syn. 1 (1854) 153. — Type: *Koenig s.n.* (LD, holo, n.v.; BM, K, L, US, fragm.), India, Malabar, Naguhr, prope Sammelliota (?), 1782.

Vilfa commutata Trin., Gram. Icon. 1 (1823) t. 10; Diss. Bot. (1824) 156; Steudel, Syn. 1 (1854) 154. — *Sporobolus commutatus* Kunth, Enum. Pl. 1 (1833) 214; Nees, Fl. Afr. Austr. 1 (1841) 157 (quoad var. *trinianus* Kunth, nom. inval.: autonym!); Miq., Fl. Ind. Bat. 3 (1857) 376, p.p.; Achariyar & Mudaliyar, Handb. S. Ind. Gr. (1921) 238, t. 183, 184. — Type: *Klein ex Stephan Sr. ex Willdenow* in Hb. Trinius (LE, holo, L neg. 36.3, B in Hb. Willdenow 1713, n.v., microfiche IDC 7440!; *Wallich 3764-A*, K, microfiche IDC 7394!), India, Madras, Red Hills, 15 Nov. 1799.

Vilfa roxburghiana Nees ex Wight, Cat. (1834) 102; Steudel, Nomencl. ed. 2, 1 (1840) 40; 2 (1841) 768 (not in the synonymy, 1854!) (see note). — Lectotype: *Roxburgh s.n.* (K, holo), India (here appointed).

Sporobolus parvulus Stent, Bothalia 2 (1927) 273, nom. inval., not accepted by author, Art. 34.1 (a). — Voucher: *Burtt-Davy 10127* (PRE, holo; BOL, n.v.; K, neg. 10313!), South Africa, Orange Free State, Smitskraal, 9 April 1911.

Sporobolus javensis Ohwi, Bull. Tokyo Sc. Mus. 18 (1947) 12; Jansen, Acta Bot. Neerl. 1 (1952) 475, t. 3; Monod de Froideville in Backer & Bakh. f., Fl. Java 3 (1968) 538. — Type: *van*

Slooten 2394 (BO, holo; K, L, U, US), Java, Malang, G. Semongkrong near Pasuruan, 10 m alt., 9 April 1931.

Agrostis pulchella auct. non R. & S.: R. & S., Syst. Veg. 2 (1817) 367; Roth, Nov. Pl. (1821) 41, quoad specim. Roth (BM).

Sporobolus lindleyi auct. non Benth.: Backer, Handb. Fl. Java 2 (1928) 205.

Sporobolus pyramidatus auct., non Hitchc.: Chippindall, Gr. S. Afr. (1955) 220 [fide Gibbs Russell et al., Mem. Bot. Surv. S. Afr. 51 (1985) 62, 63 (in syn., see note)].

Annual, tufted, branching intra-vaginally at base and often from the uppermost nodes. Rhizomes, stolons and cataphylls absent. Culms geniculately ascending, often widely decumbent, sometimes rooting in the decumbent nodes, hollow at base, becoming solid upwards, glabrous, smooth, up to 45 cm high. *Sheaths* smooth, outer margin often rather densely hairy, inner margin apically with a few scattered hairs, otherwise glabrous, margin of throat densely hairy; ligule 0.35–1 mm long, densely long-ciliate; blades more or less homomorphous, flat, linear, up to 9 cm by 8 mm, margins pectinate, apex acute, above scaberulous often with long, bulbous based hairs in the lower part, below smooth, glabrous, distinctly keeled. *Panicles* effuse, ovoid-oblong, up to 9 by 4 cm diam., branches patent, usually simple, at least the basal ones whorled, the upper ones fascicled, sometimes all in 8–12 ± distinct whorls, flexuous, spikeled in the upper half, glabrous, at least the lower at base with an elongated, sometimes dark coloured or swollen gland, smooth, the lowermost (5–)6–9(–17) together, up to 4 cm long. *Spikelets* 1.25–1.8 mm long, pale to blackish green, sometimes brownish. Lower glume broadly ovate to elliptic, 0.35–0.7 mm long, 0.25–0.4(–0.6) times as long as the spikelet, margins broadly scarios, coloured part smooth to microscopically scaberulous, apex obtuse to rounded, nerves 0; upper glume ovate to ovate-oblong, about as long as the spikelet, apex acute to acuminate, smooth to microscopically scaberulous at the top. *Lemma* ovate, 1.2–1.5 mm long, acute, 1(–3)-nerved, smooth to microscopically scaberulous near the top. *Palea* elliptic, 1.1–1.5 mm long, obtuse to truncate, easily split by the ovary and/or fruit. *Lodicules* 0.1–0.2 mm long. *Anthers* 3, 0.25–0.8 mm long. *Seed* obovoid, quadrangular in transverse section and side view, 0.75–0.95 by c. 0.5 mm in diam.; pericarp loosely adherent; embryo 0.45–0.65 mm long.

Distribution. Africa: Sudan to South Africa, Namibia, Angola, Botswana, Kenya, Mauritania, no doubt elsewhere; Madagascar; Mauritius. Asia: Afghanistan, Pakistan, India (e.g. Punjab, Uttar Pradesh, Gujarat, Madhya Pradesh, Maharashtra, Karnataka, Tamil Nadu, Assam), Sri Lanka, Burma (Mandalay, Shan), SW Thailand (Prachuap Khiri Khan). Malesia: Java (Malang, G. Semongkrong), New Guinea (Central Prov., Tatana Quarry, but not found there by JFV in October 1989). Australia: Northern Territory, W Australia, Queensland. A curious collection is *Clemens 1603* (GENT, L) from China, Prov. Tianjin ("Prov. Chihli, Tientsin, 19 August 1912"), at c. 39° N, 117° E, the only record for China so far, and also the northernmost.

Habitat. Alkaline and saline soils. Open, sunny places, soggy during the west monsoon, in the advanced east monsoon very dry and locally covered by a thin layer of salt, on heavy black clay, more or less at sea-level. Growing between February and June (Backer, 1928). In Pakistan up to 520 m altitude.

In Saurashtra Bhal (India) near the coast on not or not too extreme salty soil, where it germinates about one week after the first heavy rains (c. 6–10 cm/day),

flowers about six weeks later, and grows on until the end of September, when it dies off. Able to withstand flooding for at least 14 days, and then the seeds will not germinate, plants dying immediately after total submersion or gradually after a drought of more than five weeks (coll. *Grontmij NV 30*). Srivastava (1978) briefly described germination behaviour.

Flowering behaviour and pollen. Pollen was observed by Reddi et al. (1988) to be normally shed between 0 and 4 o'clock a.m. It has been described by Siddiqui & Qaiser (1988).

Chromosomes. $2n = 24$ (Christopher & Abraham, 1974), 36 (Narayan & Muniyamma, 1972).

Anatomy. For the leaf and caryopsis anatomy, see the Introduction.

Collector's notes. Glumes dull green. Anthers purple.

Uses. Regarded as a good fodder for cattle by the agronomists of the Grontmij Company (see sub Habitat).

Notes. The type sheet of *Vilfa commutata* Trin. in LE bears 6 plants. The specimen mounted in the middle of the top row was the subject of Trinius' plate and therefore is to be regarded as the type. It is labeled "Vilfa commutata m. ddt specimen Indicum am. Stephan ex coll. patris, cui ddt Willdenow sub nom. Agrost. coromandelinae." The specimen in Willdenow's own herbarium is thus an isotype. It is there annotated as collected by Klein in Madras. *Wallich 3764-A* (K) from the Madras herbarium is similarly labeled and must be regarded as another isotype.

The other specimens on the LE sheet belong to other species of *Sporobolus*, e.g. three isotypes of *S. discosporus* Nees and one possible duplicate of what Wight thought was *Vilfa roxburghiana* Nees ('*Mis. Wight 29*') (Trinius already mentioned that he had received *V. commutata* mixed up, '*commutata*', with *V. coromandeliana*). At first sight *Vilfa roxburghiana* Wight appears to be a nomen nudum, but it was diagnostically described by Wight under *Vilfa commutata*, the species (nr. 1743) following it. Because the whole of *Wallich 3764* is cited, which includes an isotype of *Vilfa commutata*, Wight's name must be regarded as a nomenclatural synonym of the latter. By the implicit reference to Roxburgh we suspect Nees (to which Wight attributed the combination) intended to rename Roxburgh's *Agrostis coromandeliana*.

Wight said that *V. commutata* would have branches spikeled from the base, while *V. roxburghiana* would have them spikeled towards the apex only, but his specimens, at least in K, of *Wight 1742* and *1743* represent the same species and the stated differences are negligible, those of *1742* appearing to be merely smaller younger plants. Later authors have also suggested that *S. coromandelianus* and *S. commutatus* would be distinct species, e.g. Steudel (1840, 1841), Achariyar & Mudaliyar (1921), and Pilger (1956). Achariyar & Mudaliyar (1921) noted that in the herbarium the two would be difficult to separate, but were clearly distinct in the field. However, their remark that the two grow side by side seemed to confirm our suspicion that the differences are due to age and maturity, because, similar to Bor, we failed to see any constant differences.

Although Miquel (1857) already mentioned it as possibly occurring in the Dutch East Indies, it was first found in Java in 1923 by Jeswiet (no. 221, L, WAG). Yet the species may well be native there, for the single locality from which it is known is peculiar for its extreme drought, being in the rain shade of the Tengger (Van Steenis,

oral communication). The presence of the species in Australia and a single locality in Papua New Guinea would also point at it being native in Malasia.

The Java specimens have been variously identified: with the Australian *S. lindleyi* auct. non Benth. (= *S. caroli* Mez); with the American perennials *S. argutus* (Nees) Kunth (see below) or *S. pyramidatus* (Lamk.) Hitchc., or as a distinct species, *S. javensis*.

In fact in Australia it is more similar to *S. pulchellus* R. Br. and *S. lenticularis* S. T. Blake, different from both by the longer, ciliate ligule, the short broad leaves, and the glandular inflorescence with the higher branches often fascicled and not all in distinct whorls. The three can be distinguished as follows:

- 1a. Ligule a minute, c. 0.1 mm long, minutely ciliolate rim. Inflorescence branches all but the uppermost in whorls, filiform, without glands 2
- b. Ligule 0.35–1 mm long, densely long-ciliate. Inflorescence branches patent, the lower ones in whorls, but upwards usually fascicled and solitary, at base with an elongated gland **Sporobolus coromandelianus**
- 2a. Spikelets 0.9–1.25 mm long, lower glume 0.35–0.65 mm long, 0.35–0.57 times as long as the spikelet. Seed more or less terete, hardly angled to knuckle-bone-shaped, 0.5–0.75 by 0.3–0.4 mm, filling the spikelet to c. 0.75th
Sporobolus pulchellus
- b. Spikelets 1.5–1.8 mm long, lower glume 0.6–1 mm long, 0.3–0.5 times as long as the spikelet. Seed ellipsoid in transverse section, 1.25–1.65 by 0.7–1 mm, filling the spikelet to protruding beyond it **Sporobolus lenticularis**

Sporobolus argutus has been united with *S. pyramidatus* by Hitchcock (Manual Grasses W. Ind., 1936, 84). A brief survey of the material in L under these two names has suggested that at least part of it is rather similar to *S. coromandelianus* and that at least two taxa appear to be involved, e. g. differing by the seeds, which are small and oblong in one form, and relatively large and ellipsoid to more or less obovoid in the other. It was beyond the scope of this study to solve this puzzle. Clayton (1974) has remarked that at least in the spikelets his African specimens of *S. coromandelianus* were indistinguishable from *S. pyramidatus*.

His description differs slightly from the one given here: spikelets 1–1.4 mm long, lower glume 0.1–0.5 mm long, anthers 0.2–0.3 mm long, seeds 0.7–0.8 mm long. Chippindall (1955) also stated that the spikelets would be 1–1.3 mm long in what she called *S. pyramidatus*. Unfortunately we could only briefly glance at some African material while in K, and it seemed to belong to the present species. Steudel (1854) already mentioned the occurrence of *V. commutatus* in South Africa. *Sporobolus pyramidatus* sensu Chippindall according to Gibbs, Russell, et al. (1985) is a synonym of *S. coromandelianus*.

Ohwi (1947) followed by Jansen (1952) considered *S. javensis* as distinct from *S. coromandelianus* because the spikelets would be longer than the dimensions given by Hooker f. (1896). A study of Asian material showed that their spikelets are rather often longer than 1.2 mm (up to 1.6 mm). The seeds of Indian and Javanese specimens are identical and the other features shown by the Javanese plants are found in Indian ones as well.

In West Africa the species has been confused with *S. microprotus* Stapf, which differs by having 1–1.2 mm long spikelets, lower glume inconspicuous, up to 0.1 (–0.2) mm long, stamens 2, seed 0.7–0.8 mm long (Clayton, 1974, 363; 1965).

3. *Sporobolus harmandii* Henr.

Sporobolus harmandii Henr. in Fedde, Repert. 21 (1925) 235; Bor, Grasses (1960) 629; Gilliland, Rev. Fl. Mal. 3 (1971) 105. — T y p e: *Godefroy* 823 (L, holo, K; P, n.v.), South Vietnam, Phu Quoc Island, beach of Ham Ninh ('Huen-ninh'), 28 Sept. 1875.

Sporobolus sumatranus Ohwi, Bull. Tokyo Sc. Mus. 18 (1947) 12. — T y p e: *Sohns* 7 (BO, holo), Sumatra, Aceh, Kabanjahe, 1919.

Sporobolus lenticularis auct. non S.T. Blake: Jansen, Acta Bot. Neerl. 1 (1952) 477, t. 4 (seed upside down).

Sporobolus pulchellus auct. non R.Br.: Hook. f., Fl. Br. India 7 (1896) 252 (quoad *Wallich* 8883); Camus, Fl. Gén. I.-C. 7 (1923) 509; Ridley, Fl. Mal. Pen. 5 (1925) 244; Backer, Handb. Fl. Java 2 (1928) 205; Burk., Dict. 2 (1935) 2069; Backer in Heyne, Nutt. Pl. Indon. (1950) 259; Schmid, l'Agron. Trop. 13 (1958) 486, t. 93, f. 3.

? *Sporobolus pulvinatus* auct. non Swallen: Anon., Icon. Corm. Sin. 5 (1976) 858 (see note).

Annual, tufted, branching intra-vaginally at base and from the cauline nodes. Rhizomes, stolons, cataphylls absent. Culms erect or geniculately ascending, glabrous, smooth, up to 60 cm high. Leaves mostly basal. *Sheaths* smooth, outer margin finely hairy, otherwise glabrous, margin of throat more or less glabrous or with up to 2 mm long hairs; ligule c. 0.25 mm long, densely ciliate; blades more or less heteromorphic, up to 7 cm by 6 mm, the basal ones erecto-patent to patent, linear-lanceolate, flattened to involute, rather stiff, margins at least in the lower part pectinate, otherwise glabrous; the cauline ones erect, softer, involute, margins less hairy to nearly glabrous, apex acuminate, above scaberulous on the nerves, below smooth, rounded. *Panicles* ellipsoid, usually effuse, up to 15 by 4 cm, branches erecto-patent, usually simple, in 6–10 whorls, sometimes also some in fascicles, spikelet in the upper 0.5–0.67th part, usually eglandular, sometimes with microscopic pustular glands, the lowermost 4–10 together, the longest 1–2.3 cm long. *Spikelets* 1.35–1.9 mm long, shiny brown to brownish red. Lower glume ovate-oblong to more or less narrowly triangular, 0.6–1.2 mm long, 0.5–0.67 times as long as the spikelet, apex acute to acuminate, smooth, nerves 0; upper glume ovate-oblong to -lanceolate, as long as the spikelet, gradually tapering into an acuminate to cuspidate apex, smooth. *Lemma* ovate-oblong to oblong, 1.3–1.5 mm long, subobtusate, 1-nerved, smooth. *Palea* broadly elliptic, 1.2–1.4 mm long, obtuse to truncate, easily split by the ovary and/or fruit. *Lodicules* c. 0.25 mm long. *Anthers* 3, 0.4–0.5 mm long. *Seed* ovate-ellipsoid, laterally flattened, elliptic in transverse section, with rounded edges, 0.9–1.1 by 0.5–0.7 mm in diam., pericarp rather loosely adherent; embryo c. 0.5 mm long.

D i s t r i b u t i o n. Burma, Thailand (Chieng Mai; Ranong; Satun), Laos, South Vietnam (Phu Quoc I.), China (?; see note below sub *S. pulvinatus*); Malesia: Sumatra (Aceh, Tapanuli, East Coast).

H a b i t a t. *Pinus merkusii* forest, sunny, rather bare grasslands, on dry waste and arable land, volcanic rock, 900–1200 m alt. Locally abundant.

V e r n a c u l a r n a m e s. Jecarum (Gayo); uban-uban (Samosir).

Collector's notes. Resembling *Chrysopogon acicularis*. Spikelets reddish. Anthers dark violet with pale connective area.

Notes. This species has formerly been confused with the Australian species *S. lenticularis* S. T. Blake and *S. pulchellus* R. Br. These differ by having rim-like, c. 0.1 mm long, ciliolate ligules, always glabrous leaf-throats, and blades up to 3 mm wide. *Sporobolus lenticularis*, moreover, differs by the lower glume, 0.3–0.5 times as long as the spikelet, and lenticular, a 1.25–1.65 mm long seed at least as long as the spikelet, while *S. pulchellus* has 0.9–1.25 mm long spikelets, lower glumes 0.35–0.65 mm long, and terete to quadrangular, 0.5–0.75 mm long seeds.

Of the continental Asian species *S. capillaris* Miq. differs by the glandular inflorescences, lowest branches 12–14 together, the longest ones 2–3.5 cm long, spikelets 1.1–1.25 mm long.

Perhaps the *S. pulvinatus* mentioned by Anon. (Icon. Corm. Sin. 5, 1976, 858) is the present species, although the spikelets are described as deep greyish green.

Sporobolus tetragonus Bor is also similar, but is different by the homomorphous, flat, 6–15 cm long leaves, the inflorescence branches with linear glands, the longest lowest inflorescence branches 3–4.5 cm long, pedicels scabrous, the lemma ± as long as the upper glume, the c. 0.75 mm long anthers, and the knucklebone-shaped seeds. In K formerly identified as *S. pulchellus*, e.g. *Wallich* 8883.

4. *Sporobolus humilis* Presl

Sporobolus humilis Presl, Rel. Haenk. 1 (1830) 241; Miq., Fl. Ind. Bat. 3 (1857) 376; Scribn., Rept. Missouri Bot. Gard. 10 (1899) 53, t. 30, f. 2; Merr., Philip. J. Sc. 1, Suppl. (1906) 374, sp. dub.; Monod de Froideville in Backer & Bakh. f., Fl. Java 3 (1968) 538. — *Vilfa humilis* Steudel, Nomencl. ed. 2, 2 (1841) 626, 767; Syn. 1 (1854) 153. — T y p e: *Haenke s.n.* (PR, holo, MO, n.v., fig. by Scribner!; US, fragm.), Philippines, Luzon.

Sporobolus albens Balansa in Morot, J. Bot. 4 (1890) 164; Camus, Fl. Gén. I.-C. 7 (1923) 510; ? Schmid, l'Agron. Trop. 13 (1958) 486, 488 (see note); P.-H. Hô, Niên San 1 (1968) 130, fig. — T y p e: *Godefroy* 98 (L, holo, K; P, n.v.), Cambodia, Pnom Penh, North of the Pyramid, 30 May 1875.

Sporobolus diandrus auct. non Beauv.: Merr., Philip. J. Sc. 1, Suppl. (1906) 372, p.p.

Sporobolus tremulus auct. non Kunth: Backer, Trop. Nat. 9 (1920) 176; McKerral, Bull. Dept. Agric. Burma 20 (1924) 14; Backer, Handb. Fl. Java 2 (1928) 204; Onkr. Suiker. (1928) 107, t. 100; in Heyne, Nutt. Pl. Indon. (1950) 260, 1593.

Sporobolus virginicus auct., non Kunth: Merr. ex Koord., Exk. Fl. Java 1 (1911) 145, pro specim. e 'Djatiwald' (= teak forest); Merr., Enum. Philip. Fl. Pl. 1 (1923) 81, quoad syn. Presl, Steudel, *BS* 7881 (*Ramos*).

a. subsp. *humilis*

Perennial, tufted and mat-forming, branching extra-vaginally at base. Rhizomes short, stolons slender, widely creeping. Cataphylls often broad, large, glabrous, shiny, straw-coloured. Culms geniculately ascending to erect, up to 30 cm high, hollow, glabrous, smooth. *Sheaths* smooth, outer margin glabrous, throat with more or less densely bulbous-based hairs up to 2 mm long; ligule up to 0.2 mm long, sometimes with a few scattered long hairs; blades more or less distichous, erecto-patent to patent, usually rather stiff, flat, folded, or involute, ovate-linear-lanceolate to linear,

0.7–6.5 cm by 1–2 mm, apex acute, above or on both sides glabrous or moderately with bulbous-based hairs, above scaberulous on nerves and margins, below sometimes with a distinct midrib (i. s.). *Panicles* contracted, spiciform, 2–7.5 cm long, branches densely spikeled from the base, finely scaberulous, the lowermost 1–3 together, appressed, up to 2 cm long. *Spikelets* 1.2–1.5 mm long, yellowish. Lower glume ovate-oblong, 0.6–1.1 mm long, (0.5–)0.67 times as long as the spikelet, often erose along the margins and acute to obtuse apex, smooth or microscopically scaberulous upwards, nerves 0 (or 1); upper glume ovate-oblong to -lanceolate, 0.9–1.3 mm long, 0.75–1 times as long as the spikelet, apex acute to obtuse, smooth or microscopically scaberulous upwards. *Lemma* as the upper glume, 1.1–1.4 mm long. *Palea* ovate to oblong, 1.1–1.3 mm long, truncate, easily split by the seed. *Lodicules* 0.1–0.15 mm long. *Anthers* 3, 0.3–0.5 mm long. *Seed* ovoid to ovate-ellipsoid, elliptic in transverse section, 0.7–0.8 by 0.35–0.4(–0.5) mm in diam.; pericarp closely adherent; embryo 0.4–0.5 mm long.

Distribution. Burma (*McKerral B2*, US, sine loc.), Thailand (Chieng-mai, *Kerr 1695*, BM, K), Cambodia (Pnom Penh, Batambang), South Vietnam (Hong Ngu, Can Tho, Gia Dinh); Malesia: Java (Jakarta, Banyumas, Semarang, Yogyakarta, Madiun, Surabaya, Malang, Besuki), Philippines (Luzon).

Habitat. On heavy, periodically marshy or flooded clay, especially in puddles and sawahs, with *Coldenia procumbens* L. and *Ludwigia adscendens* (L.) Hara, salt-resistant, roadsides, coconut plantation, teak forest, very local, then apparently abundant, up to 100 m alt. In Java in areas with a pronounced east monsoon.

Collector's notes. Turf-forming, bright green [cf. *Cynodon dactylon* (L.) Pers.]. *Panicles* bright green or white.

Vernacular name. Dedakan (Jav.; not dedekan, cf. Backer, 1950).

Uses. Disliked by cattle in Central Java (Backer, 1950, where an analysis of the fodder value is given on p. 1593), some slight value (McKerral, 1924).

Notes. Merrill (1906), not having seen any specimens, regarded *S. humilis* as perhaps not indigenous in the Philippines, or a much dwarfed form of *S. diandrus* (Retz.) Beauv. Later (1923) he included it in *S. virginicus*. He then cited two collections, of which *Merrill Philip. Pl. 574* (U) is the true *S. virginicus*, while *BS 7881* (Ramos) (US) is the present species.

Sporobolus virginicus is indeed rather similar and the occasional dwarf form of it is difficult to recognize. Such a specimen differs, as usual, by the larger spikelets, relatively longer glumes (especially the lower one) and longer anthers.

The combination *S. tremulus* (Willd.) Kunth (cf. Backer, 1920, 1928a, b, 1950) has been misapplied to the present species; it is a superfluous one for *Agrostis juncea* Lamk., a synonym of *S. virginicus* (q.v.).

Both subspecies occur in Thailand, Luzon, and perhaps also in Indochina but from there no material attributed to *S. tremulus* by previous authors was available for study. Instead, everything seen from that area belonged to *S. humilis* s. s. The taxon described by Schmid (1958) seems to be something entirely different because of the hairy leaves, and the colour and length of the inflorescence.

Nevertheless, the two agree so much in habitat, habit and all other characters, that we agree with Backer that a single species is involved. As there are some differences between the two, two subspecies have been distinguished here.

The Australian *S. mitchellii* (Trin.) C.E. Hubb. ex S. T. Blake is somewhat similar; it differs by its tufted habit with long stolons with long internodes, glabrous throat of the longer smooth blades, much longer spikelets, relatively longer lower glume, 0-nerved upper glume, the apparently not easily split palea, longer anthers, and caryopses that may be infected by the smut *Bipolaris*.

b. subsp. minor Veldk., subsp. nov.

Vilfa geniculata Nees ex Steudel, Syn. 1 (1853) 156. — [? *Sporobolus geniculatus* Nees ex Aitch., Cat. Punj. Pl. (1869) 165; nom. nud. for T. Thomson s.n., India, Punjab, Moradabad; see note.] — T y p e: not indicated (P, holo, not found), India, Madras.

Agrostis tenacissima auct. non Linné f.: Roxb., Fl. Ind. 1 (1820) 318. — V o u c h e r s: Hb. Roxburgh (BM, K).

Agrostis tremula auct. non Willd.: Willd., Sp. Pl., ed. 4, 1, 1 (1797) 372, pro *Klein s.n.* (anno 1796) in Hb. Willdenow 1725, n.v., microfiche IDC 1538. — *Vilfa tremula* auct. non Trin.: Trin., Diss. Bot. (1824) 155; Mém. Ac. Sc. St. Pétersb. VI, 5, 2 (1840) 98. — *Sporobolus tremulus* auct. non Kunth: Kunth, Rév. Gram. 1 (1829) 67; Enum. Pl. 1 (1833) 210; Hook. f., Fl. Br. India 7 (1896) 250; Achariyar & Mudalyar, Handb. S. Ind. Gr. (1921) 233, t. 179, 180; Camus, Fl. Gén. I.-C. 7 (1923) 509; C.E.C. Fischer in Gamble, Fl. Pres. Madras 3 (1928) 1817; Senaratna, Gr. Ceylon (1956) 96; Schmid, l'Agron. Trop. 13 (1958) 486; Bor, Grasses (1960) 633; Chadha, Wealth of India 10 (1976) 24; Bhandari, Fl. Ind. Desert (1978) 434; Cope, Fl. Pakistan 143 (1982) 138; Britto & Mathew in Mathew, Fl. Tamilnadu Carn. (1983) 1906; Reddi et al., Rev. Palaeobot. & Palynol. 54 (1988) 36, tab. 51.

A subsp. *humili* in foliis plerumque 3 cm brevioribus, glumis inferioribus 1,15–1,25 mm longis spiculis 1,5–2,1 mm longis (0,62–)0,7–0,8-plo longioribus, glumis superioribus 1,5–1,75 mm longis, antheribus 0,6–1 mm longis differt. — T y p u s: *Lazarides 7331* (L, holo; CANB, K, US), Sri Lanka, S Province, Hambantota Dist., SW of Ruhuna National Park Headquarters, c. 3 m alt., 20 Sept. 1970.

Habit apparently more compact. Blades 1–3(–6.5) cm long, usually glabrous. Inflorescences 1–3 cm by 2–4 mm diam. (see note), lowest branches solitary or paired, 0.45–0.7 cm long. Spikelets (1.4–)1.5–2.1 mm long (see note). Glumes usually smooth, sometimes microscopically scaberulous; the lower one (0.9–)1.15–1.25 mm long, 0.7–0.8 times as long as the spikelet; upper glume (1.25–)1.5–1.75 mm long, 0.8–0.9 times as long as the spikelet. Anthers 0.6–1 mm long.

Distribution. Réunion (see note), Pakistan (Punjab), India (from Punjab to Assam, Tamil Nadu), Sri Lanka, ? Burma (Pegu), ? Thailand: N Province (Krungtep, Bangkok, Bangkok), ? Cambodia, ? North Vietnam (Lang Vuc); Malesia: Philippines (Luzon, *Loher 7189*, K).

Habitat. Near the sea and also inland, margins of sawahs, open scrub on hard soil with other small herbs, sometimes co-dominant with *Eragrostis viscosa* in Sri Lanka. Up to 750 m alt. in India.

Flowering behaviour. Pollen was observed to be normally shed between 1 and 3 o'clock p.m. by Reddi et al. (1988).

Chromosomes. $2n = 20$ (Senaratna, 1956).

Collector's notes. Very stoloniferous, 30–60 cm diam., flowering culms erect. Foliage markedly glaucous, blades stiffly imbricate. Spikelets very pale.

U s e s. Said to be an excellent grass for binding the soil and may also prove to be of value as fodder (Bor, 1960). The citation of Walandouw by Chadha (1976) refers to var. *humilis* (see Backer, 1950).

N o t e s. This taxon, as a species, is known in the Asian literature as *Sporobolus tremulus* (Willd.) Kunth, based on *Agrostis tremula* Willd. This, however, is a superfluous name for *Agrostis juncea* Lamk., a synonym of *S. virginicus* (L.) Kunth (q.v.). If subsp. *minor* is to be accepted as a distinct species, the correct name would be *S. geniculatus* (Steudel) ..., a combination not yet made. Bor (1960) attributed it to Aitchinson (1869), but this author merely used the combination in an identification list without any further reference.

A distinction sometimes mentioned (e.g. by Camus, 1923; Fischer, 1928; Senaratna, 1956; Britto & Matthew, 1983) is that in subsp. *minor* the spikelets would be between 1.75 and 2.5 mm long. Bor (1960), Bhandari (1978), and we measured them as 1.5–2.1 mm long, similar to Cope's (1982) report.

Subsp. *minor* generally has smaller panicles than the typical subspecies. Hooker f. (1896) gave as maximum 10 cm long and presumably wider than the 4 mm measured by us, but this may be due to the inclusion of material that belongs to *S. humilis* s.s. However, the sheet *Wallich 3771 A* (K-W, n.v.) according to the microfiche IDC 1157 bears a spike of an estimated 7.5 cm long. Fischer (1928) also said that they were up to 4.5 inch (c. 11.5 cm) long.

Kunth (1833) cited *S. tremulus* auct. for Mauritius, a record probably based on *Sieber 38*. This is the type of *Vilfa intermedia* Trin., a synonym of *S. virginicus*. In L there is a sheet collected by Commerson labeled 'Île de France', i.e. Réunion, which does belong to subsp. *minor*. Cordemoy (Fl. Réunion, 1895) only mentioned *S. indicus*. As Commerson also collected in S India, it may have been mislabeled.

The subspecies was collected only once in Malesia (*Loher 7189*, Manila; K). It indubitably belongs here and not to subsp. *humilis* because of the size of the spikelets (1.8–2 mm), lower glume (c. 1.25 mm), and anthers (c. 0.75 mm). This collection again indicates that the distinction of two species is untenable.

5. *Sporobolus indicus* (L.) R. Br.

Sporobolus indicus (L.) R. Br., Prod. 1 (1810) 170 (pro comb.); Beauv., Agrost. (1812) 26, 147, t. 6, f. 11; Benth., Fl. Austr. 7 (1878) 622; Hook. f., Fl. Br. India 7 (1896) 247; Nauta & Boerlage, Teysmannia 11 (1901) 490; Hitchc., Contr. U.S. Nat. Hb. 12 (1908) 120; Camus, Fl. Gén. 1.-C. 7 (1923) 507; C.E. Hubb. in Allen, New Zeal. J. Sc. Techn. 15 (1934) 256; Bor, Grasses (1960) 630, (t. 76 pert.? see Simon, A.S.B.S. Newsl. 31, 1982, 16); T. Koyama, J. Jap. Bot. 37 (1962) 235, t. 3; Tateoka, Bull. Torrey Bot. Cl. 89 (1962) 78; Clayton, Kew Bull. 19 (1965) 291; C.E. Hubb., Agron. Lus. 28 (1966) 67; Jovet & Guéd., Bull. Centre Ét. Rech. Sc., Biarritz 7 (1968) 47; Davidse & Pohl, Can. J. Bot. 50 (1972) 1443; Pancho, Kalikasan 2 (1973) 180; Mehra & Kalia, Taxon 23 (1974) 807; Christopher & Abraham, Cytologia 39 (1974) 565, fig. 15, 16; Tanaka, J. Jap. Bot. 49 (1974) 313, t. 1-i; J.W. Parham in A.C. Smith, Fl. Vit. Nov. 1 (1979) 308; Pohl, Fl. Costaric. 15 (1980) 544, t. 204; Astegiano, Kurtziana 18 (1986) 69; 20 (1989) 65. — *Agrostis indica* L., Sp. Pl. 1 (1753) 63. — *Agrostis elongata* Lamk., Tabl. Encycl. 1 (1791) 162, nom. superfl. — *Vilfa elongata* Beauv., Agrost. (1812) 16, 147, 181, nom. superfl. — *Sporobolus lamarckii* Hamilt., Prod. Pl. Ind. Occ. (1825) 4, nom. superfl. — *Vilfa indica* Trin. ex Steudel, Nomencl. ed. 2, 1 (1840) 41; 2 (1841) 767; Syn. 1 (1854) 162. — *Sporobolus indicus* forma *indicus*: Peter in Fedde, Repert., Beih. 40 (1931) 291

- (by implication: Art. 26.2). — *Sporobolus indicus* var. *indicus*: T. Koyama, J. Jap. Bot. 37 (1962) 235; Jovet & Guéd., Bull. Centre Ét. Rech. Sc., Biarritz 7 (1968) 63, fig. 4; T. Koyama in Walker, Fl. Okinawa (1976) 190; L.B. Smith et al., Fl. Il. Catar., Gram. 1 (1981) 380, t. 87 d–g, 88; Simon, A.S.B.S. Newsl. 31 (1982) 18. — *Sporobolus indicus* subsp. *indicus*: T. Koyama, Grasses of Japan (1987) 275 (by implication: Art. 26.2). — **L e c t o t y p e**: Clayton 460 B in Hb. Linn. 84.36 (LINN, holo, n.v., microfiche IDC 5075), U.S.A., Virginia.
- Agrostis tenuissima* Spreng., Syst. Veg. 1 (1825) 258. — **T y p e**: not indicated: 'Ind. Occ. Amer. Austr.'
- Vilfa berteroaana* Trin., Mém. Ac. Sc. St. Pétersb. VI, 5, 2 (1840) 100. — *Sporobolus berteroaanus* Hitchc. & Chase, Contr. U.S. Nat. Hb. (= Gr. W. Ind.) 18 (1917) 370. — **T y p e**: *Bertero s.n.* in Hb. Bernhardt (LE, holo; B, MO, n.v.), St. Domingo.
- Vilfa exilis* Trin., Mém. Ac. Sc. St. Pétersb. VI, 5, 1 (1840) 89. — *Vilfa tenacissima* Kunth var. *exilis* Fourm., Mex. Pl. 2 (1886) 99. — *Sporobolus exilis* Trin. ex Balansa in Morot, J. Bot. 4 (1890) 164, pro comb. — *Sporobolus indicus* R. Br. var. *exilis* T. Koyama, J. Jap. Bot. 37 (1962) 235, 240, t. 3a. — **T y p e**: *Schiede s.n.* (LE, holo, n.v.), Mexico, Jalapa.
- Sporobolus angustus* Buckl. or *Vilfa angusta* Buckl. (nom. altern.), Proc. Ac. Sc. Philadelphia 1862 (1863) 88. — **T y p e**: *Buckley s.n.* (PH, holo, n.v.; photocopy in US), U.S.A., Texas, Buchanan County, June (identified with *S. poiretii* by Hitchcock on photocopy in US).
- Sporobolus jacquemontii* auct., non Kunth: Hitchc., Misc. Publ. U.S. Dept. Agric. 243 (Man. Gr. W. Ind.) (1936) 82, t. 47 B, and later American authors (see also Clayton, 1965; Jovet & Guédès, 1968).
- Sporobolus poiretii* auct., non Hitchc.: Hitchc., Bartonica 14 (1932) 32, and subsequent publications, influencing many treatments [see Veldk., Taxon 39 (1990) 327].
- Sporobolus tenacissimus* auct., non Kunth: various authors, e.g. Pilger in E. & P., Nat. Pfl. Fam., ed. 2, 14d (1956) 55; see Bor, Kew Bull. 12 (1957) 233, for the case history.
- For more synonymy see under the varieties.
- The following general description is based on Malesian (i.e. non-typical!) material only.

Long-living annuals, usually densely tufted, branching intra-vaginally at base. Rhizomes short, stolons and cataphylls absent. Culms erect, up to 90 cm high, solid, glabrous, smooth. *Sheaths* smooth, often shiny, margin ciliolate, otherwise glabrous; ligule up to 0.5 mm long; blades folded to more or less flat, linear, filiform in the upper part, gradually tapering to a very fine point, 6–15 cm by 2–7 mm, margins smooth to scaberulous, above scaberulous on the nerves, with a few scattered hairs in the lower part, below smooth, glabrous, slightly keeled. *Panicles* contracted and spiciform, then often interrupted at base, to effuse, 7–60 cm long, branches densely to loosely spikelet, the lowermost 1–3 together, appressed to obliquely spreading, 1.5–12 cm long. *Spikelets* 1.3–2.6 mm long, yellowish, pale to nearly blackish green. Lower glume ovate to elliptic, 0.35–1 mm long, 0.2–0.5 times as long as the spikelet, apex usually erose and denticulate, rounded to truncate, nerves 0; upper glume ovate to oblong, 0.7–1.65 mm long, 0.4–0.67 times as long as the spikelet, margin and the acute to obtuse, often erose apex often denticulate, scaberulous in the upper part. *Lemma* ovate to oblong, 1.3–2.6 mm long, acute to obtuse, 1–3-nerved, often scaberulous near the denticulate apex. Palea elliptic to oblong, 1.2–2.5 mm long, obtuse to truncate, not easily split by the seed. Lodicules 0.25–0.45 mm long. Anthers 2 or 3, 0.5–1.1 mm long. *Seed* ellipsoid to oblong, compressed and angular in transverse section, 0.6–1.25 by 0.35–0.75(–0.8) mm in diam.; pericarp rather closely adherent; embryo 0.3–0.65 mm long.

D i s t r i b u t i o n. Pantropical; a very polymorphous species.

P o l l i n a t i o n. Tanaka (1974) observed in Japan that selfing occurred only rarely [probably in *S. indicus* var. *major* (Buse) Baaijens], but fertilization of neighbouring spikelets (geitonogamy) took place in 35% of the cases.

Ms. Astegiano (1986) in Argentine found (probably in var. *indicus* proper) that cleistogamy occurred for 80–90% in the upper 2 cm of the inflorescence, while lower down all florets were chasmogamous. She thought that cleistogamy is caused here by the lack of water supply to the lodicules. She observed no morphological differences between cleistogamous and chasmogamous spikelets, but deduced cleistogamy from the fact that the anthers remained entangled in the style branches on top of the ripe fruit.

In 1989 she has made an extremely detailed study of the ontogeny of the pollen and ovule, its fertilization and subsequent development of the seed, to which we have to refer the interested reader, as it is too extensive to summarize properly here.

N o t e s. In the Linnean Herbarium (LINN) there are three sheets (84.35, -36, -37) pertaining to *Agrostis indica* L.

The first has been regarded by Hitchcock (1908, and later) as the type of the combination. The specimen, however, was collected by Patrick Browne and not seen before 1758 by Linné. It therefore cannot be the type. A tracing of it is depicted by Jovet & Guédès (1968, t. 1).

Hitchcock caused an enormous confusion in American literature when from 1932 on he used the combination *S. indicus* for *S. jacquemontii* Kunth [here included in the variety *pyramidalis* (Beauv.) Veldk.], and *S. poiretii* (R. & S.) Hitchc. for the true *S. indicus* (see Jovet & Guédès, 1968). For the actual identity of *S. poiretii* see *Species dubiae & excludendae!*

The second Linnaean collection was annotated with '460 B', probably by Gronovius (Jarvis, in litt.) and would then have been collected by Clayton in Virginia. We have not found this number in Gronovius' *Flora Virginica* (1762) under the grasses.

The third sheet represents an entirely different species, *Polypogon viridis* (Gouan) Breistr., as was already remarked by Munro (J. Proc. Linn. Soc., London, Bot. 6, 1862, 40) and confirmed by Hubbard (in sched.). Although stated to have come from India, it occurs only in its northwestern provinces, an area unexplored in Linné's time. As it is widely spread in South Europe it probably came from there.

Linné also referred to Sloane, "Gramen pratense panicula & foliis angustissimis, spicis brevibus muticis locustis minimis, Cat. Pl. Jam. 1 (1696); Voy. Jam. 1 (1707) 115, t. 73, f. 1." The specimen on which this is based is in Hb. Sloane Vol. 2, fol. 41 (BM) and indeed represents the species. However, Linné himself effectively removed these references to his *Poa ciliaris* L. [now *Eragrostis ciliaris* (L.) R. Br.] in the *Species plantarum* ed. 2 (1762, p. 102) and the choice of this element, as proposed e.g. by Parham (1979) therefore is incorrect.

As it is clear from Linné's protologue that he had a specimen available, it seems most likely that it was 84.36, which was therefore taken as the type (see Hubbard, 1966, but also Jovet & Guédès, 1968).

R. Brown (1810) made the combination *Sporobolus indicus*, but his actual specimens do not belong to the American forms of *S. indicus* – as is of course not very surprising – but also not to the forms regarded as originally native in Australia. Instead they belong to var. *capensis* Engl., a taxon most likely introduced from Africa

into Australia, but then at a surprisingly early date when one considers that Brown was one of the first botanists to land and collect there. Brown himself wrote 'probably introduced' on the label of a collection from Port Jackson.

Under the present Code (1988) a specimen may be the type of a generic name. R. Brown's misidentification is therefore nomenclaturally of no consequence, as type and name are indissolubly united with each other: the type of the new combination is the type of the basionym (*Clayton 460-B* in Hb. Linné 84.36), and hence of the generic name.

Sporobolus indicus as accepted here is a very widely spread species containing perhaps as many as 16 forms, most of which Clayton (1965) has tentatively and traditionally recognized as distinct species: e.g. in the Americas *S. indicus* proper at rather high elevations and *S. jacquemontii* at lower ones (Pohl, 1980), in Africa *S. africanus* (Poir.) Robyns & Tournay and *S. pyramidalis* Beauv., in Asia *S. diandrus* (Retz.) Beauv. and *S. fertilis* (Steudel) Clayton, and in Australia *S. creber* De Nardi, *S. elongatus* R. Br., and *S. laxus* Simon. Several of these are native to Malesia or have been introduced there, or the names have been misapplied to Malesian taxa. Some of the species distinguished by Clayton may be 'good' ones, e.g. *S. olivaceus* Napper, *S. pellucidus* Hochst., and *S. quadratus* Clayton, but we have at most glanced at them, as it was not the aim of the present research to disentangle the structure of the *S. indicus* complex completely.

Jovet & Guédès (1968) also have tried to disentangle the complicated taxonomy and nomenclature and concluded that several of the species distinguished by Clayton should be regarded as varieties of *S. indicus*, an opinion with which we concur, especially where they include *S. diandrus*. As far as their delimitation of taxa is concerned, we cannot always follow them. We have seen no material of var. *major* ('var. *fertilis*') from Africa or America. The form in Europe, which at least in the Gironde, France, is a very common wayside weed, is var. *indicus* (see Veldk., Bull. Soc. Sc. Nat. Ouest France, n. s. 11 (1990) in print]. Their var. *laxus* is at least partly var. *flaccidus* (R. & S.) Veldk. (e.g. *Merrill Sp. Bl. 845, Ramos 1867*), partly var. *major* (*Ramos 1401*).

Other authors perplexed by the variability and apparent intermediate forms have united a few or several of them into a single species without a further subdivision (e.g. Bentham, 1878; Hooker f., 1896; Bor, 1960; Monod de Froideville, 1968, as *S. berterianus*), or as named varieties (T. Koyama, 1962; Simon, 1982), or subspecies (T. Koyama, 1987).

The present study showed that the differences among the Malesian specimens are but slight and often statistical, whereby occasionally the identity of the material remained uncertain. From the identifications even by specialists it is clear that the taxa are easily confused. We therefore agree that no more than a varietal rank should be attributed to them.

A hyphomycetous fungus usually called *Bipolaris ravenelii* (Curt.) Shoemaker may infect the ovaries. Hyphae mass within the host cells which are soon completely absorbed. The ovary is replaced by a sclerotoid, pseudo-parenchymatous fungus stroma. Hyphae arising from this emerge between the lemma and palea to form black sticky mats of long, branched conidiophores, which may glue parts of the inflorescence together. The American name 'smutgrass' is derived from this. An extensive

discussion on the life cycle of the smut is given by Luttrell (Cytology & Histology 66, 1976, 260).

According to Alcorn (Mycotaxon 15, 1982, 20) four species of *Bipolaris* are involved [*B. australis* Alcorn, *B. crustacea* (Hennings) Alcorn, *B. cylindrica* Alcorn, and *B. ravenelii* s.s.], and also taxa not belonging to the *S. indicus* complex can become infected. Next to species of *Sporobolus*, *Thellungia advena* and *Eragrostis cilianensis* (Allioni) F.T. Hubb. may become smutted as well (both by *B. australis*), which is of interest when speculating on tribal and generic delimitations. At least in New Guinea *Eragrostis tenuifolia* Steudel may become infected as well. A collection from Irian Jaya (Widjaja & Hamzah 3075, L) seems to be infected with *B. miyakei*, but spore length was at the lower end of the range for the species (Alcorn, in litt.).

There are some reports that the smut might be toxic to stock, but pig-growers in Papua New Guinea assured JFV that this was erroneous, and that the grass was 'very good for them'.

With the present revision of *Sporobolus* another study on the presence of a host specificity in the fungi might be undertaken.

Var. *elongatus*, if correctly identified, is apparently infected by all four species of *Bipolaris* (Alcorn, l.c., table 5; Sivanesan, Mycol. Pap. 158, 1987, 62).

Monod, and Backer before him, thought that *S. diandrus* would never be attacked. This is not quite true, as was also observed by Alcorn (if his identifications are correct), but as the smut might be a possibly useful indicator of affinities in the group, a rough survey of herbarium specimens was made.

There are some biases against a count of infected specimens in the herbarium: the plants are not infected in all stages of development; infected plants do not look 'nice' and may be undercollected; most sheets have several inflorescences, but to simplify matters one sheet was regarded as one 'collection', and duplicates on different sheets as different 'collections'. If infection was found in one panicle, the whole 'collection' was scored as infected.

Except for these distorting factors it was noted by JFV in Papua New Guinea that in areas that were regularly mowed apparently no infection occurred at all, as was also observed by Alcorn in Australia (pers. comm.). Although hundreds of specimens of var. *capensis* were checked in Goroka (very common along the well-tended roads in town, and especially on the airfield), and of var. *flaccidus* in Lae, Port Moresby, and Singapore, none were infected. Outside Goroka, on an untended roadside, however, infection in var. *capensis* was rampant. Apparently mowing reduces the chances of infection.

| | | | |
|-----------------------------|----------|----------------|---------|
| var. <i>elongatus</i> | 0 out of | 10 sheets seen | (0.0%) |
| var. <i>pyramidalis</i> | 2 | 51 | (3.9%) |
| var. <i>cinereo-viridis</i> | 4 | 63 | (6.3%) |
| var. <i>flaccidus</i> | 23 | 326 | (7.0%) |
| var. <i>capensis</i> | 2 | 24 | (8.3%) |
| var. <i>indicus</i> | 6 | 61 | (9.8%) |
| var. <i>creber</i> | 3 | 15 | (20.0%) |
| var. <i>major</i> | 35 | 135 | (25.9%) |
| var. <i>queenlandicus</i> | 4 | 10 | (40.0%) |

As can be seen nearly all taxa of which there was sufficient material were infected, although apparently in a different degree. Some taxa supposedly related and difficult to distinguish appear to have a different susceptibility (e. g. var. *capensis* vs. var. *major*; var. *creber* vs. var. *elongatus*; var. *flaccidus* vs. var. *queenlandicus* Veldk.). The taxa with the high scores usually also have heavily infected inflorescences, while the low ones have only a few diseased spikelets, and one has to look closely to spot them. We may well have missed some instances.

Relatively few infected specimens of var. *capensis* were observed, although Hubbard & Vaughan said it was 'very susceptible' [Grass. Maur. & Rodr. (1940) 55].

The variety *pyramidalis* (incl. *S. jacquemontii*) also has the occasional infected spikelet, another argument for including it in *S. indicus*. This variety has been reported as a pest in Australia and the Pacific, and might occur in Malesia as well.

T. Koyama (1962), who studied the forms of *S. indicus* s.s. in America and Asia, thought he could distinguish between *S. diandrus*, *S. elongatus*, '*S. indicus*', and '*S. poiiretii*' (sensu Hitchcock). In the latter two he recognized two pairs of vicariant varieties in America and Asia, both Asian ones having relatively larger spikelets, and upper glumes 2–3 times as long as the lower one, slightly more than half as long as the palea.

All his dimensions are curiously enough about 3 times too large, but the true sizes can be deduced from his figures and later publications (1976, 1987).

His varieties *indicus* (America) and *pallidior* (Asia) have conspicuously branched inflorescences with patent branches naked at the base, loosely spikeled near the apex only, spikelets yellowish or pale grayish. The typical variety is diploid ($2n = 18$) and has 1.6–1.7 mm long spikelets, while var. *pallidior* is hexaploid ($2n = 54$) with 1.8–2 mm long ones.

His tetraploid ($2n = 36$) varieties *exilis* (America) and *purpureo-suffusus* (Asia) have linear or cylindrical inflorescences with upright short branches, spikeled from the base, spikelets dark grey. Variety *exilis* has 1.9–2 mm long spikelets, and var. *purpureo-suffusus* 2–2.5 mm long ones. The latter would not occur in Malesia.

As far as the American varieties are concerned we have the impression that T. Koyama made a mix-up of names, for the lectotype of *S. indicus* has a contracted, linear panicle with rather short, densely spikeled branches. We do not know the length of the spikelets, but Hubbard (1966) said that in the type they were as long as those of a specimen from Portugal. All European specimens we have seen had contracted inflorescences with spikelets of about 2 mm, and so the Linnean specimen seems best placed in T. Koyama's var. *exilis*. From Trinius' description of *V. exilis* ("radii 3–4-linealibus, a basi floriferis; spiculis ... linea paullo brevioribus") it also is suggested that this is the typical form.

Having seen hundreds of Asian representatives of *S. indicus* s.s. we have been unable to distinguish between the varieties *pallidior* and *purpureo-suffusus* on phenetic characters, which agrees with Clayton's (1965) opinion on the *S. indicus* complex. Basing himself on shape of the panicle, length of the spikelet, apex of the upper glume, and shape of the fruit Clayton thought that he could distinguish 13 taxa which he regarded as species. He concluded that there is only a single, albeit polymorphic form in SE Asia, which he called *S. fertilis* (*S. indicus* var. *major*). He regarded the American pair of varieties also as a single taxon, *S. indicus* s.s.

Clayton did not rule out the possibility that further taxa might be segregated from *S. fertilis* after a closer scrutiny, e.g. on the basis of acute or obtuse lower glumes. This agrees with part of the distinction between the varieties *major* and *cinereo-viridis* Baaijens, but the latter has a much more restricted distribution than suggested by Clayton, so we are not sure whether we are talking about the same subject.

He excluded *S. diandrus* and *S. elongatus* from the complex because of the presence of 2 anthers, as in *S. indicus* s.l. there would always be 3. That this is not an absolute difference has been observed in many instances, viz. the remarks by Jovet & Guédès (1968, p. 55, 58, 68).

Monod (1968) also kept *S. diandrus* separate from *S. indicus* because of the length of the upper glume, which would be 0.75–0.8 mm long in the first, and c. 1.25 mm long in the latter.

In order to see whether the absolute or relative lengths of the glumes would indeed have a decisive function in the distinction of var. *cinereo-viridis*, var. *flaccidus*, var. *indicus*, and var. *major* GJB has measured about 250 specimens, mainly from Malesia, but also from elsewhere. As the glumes are already variable within a single inflorescence he used the mean of c. 15 spikelets/panicle.

The clusters resulting from the ratio of the length of the glumes show a considerable overlap, so a distinction on these is of little use.

The clusters formed when the length of the upper glume and the length of the spikelet are plotted are much more discrete with little overlap.

The mean of the length of the spikelets turned out to be most reliable in a statistical way: three nearly discrete peaks resulted. The last two results therefore support the suggestion that in Malesia three distinct taxa are present.

The first group, var. *flaccidus* (*S. diandrus*), consists of plants with spikelets of usually 1.4–1.6 mm long. Their panicles are often spreading, or at least more or less lax in appearance. Usually 2 anthers are present, but some florets may have 3. These plants are found at relatively low altitudes, 0–525 (–870) m with an average of 110 m. The plants have been considered by all authorities to represent *S. diandrus*.

The second group, var. *major*, has spikelets usually 1.8–1.9 mm long in a panicle of a very variable shape. It is usually contracted and the branches are usually densely spikeled. It was surprising to note that many specimens had both diandrous and triandrous spikelets in the inflorescence, but were otherwise not particularly distinct. The number of anthers seems therefore an arbitrary argument to distinguish *S. diandrus* from the *S. indicus* complex. Representatives are found at higher altitudes, 0–2075 m, with an average of 875 m.

We agree with T. Koyama, Jovet & Guédès, and Simon (1982) that that taxon is but a variety of *S. indicus*. The main difference with *S. indicus* s.s., as said by Clayton, lays in the species' relatively longer seeds, but otherwise there is not much to recognize it. For the distinction of species there should obviously be more than that. T. Koyama apparently regarded var. *pallidior* to represent this form, while Jovet & Guédès, unaware of his work, called it var. *fertilis*. Regrettably, the epithet '*major*' Buse (1854) has to be adopted. The French form is not var. *fertilis*, but var. *indicus*, as JFV could observe in the Gironde, France, where in the summer of 1989 it was one of the most common roadside grasses. It was never infected there by the smut.

The third group has spikelets more than 2 mm long. Two subgroups can be distinguished. One is formed by plants with dense, contracted, more or less spike-like panicles with yellowish to pale green spikelets, occurring at low altitudes in Northern Sumatra, Malaya, West Java, and Cocos Keeling. As we also saw specimens intermediary with var. *major*, they seem to represent robust forms of that.

The other subgroup is composed of plants with more patent and loosely spikeled branches with blackish green to greyish spikelets, growing at (900–)1000–2750 m altitude (average 1880 m) in East Java, the Lesser Sunda Islands, and Central Celebes. This form appears quite distinct, and is here distinguished as var. *cinereo-viridis*.

Some specimens from Papua New Guinea (Central Highlands and eastward) were difficult to place. See the notes under var. *flaccidus*.

A name that turns up time and again in accounts of *Sporobolus* is *S. elongatus* R. Br. The epithet '*elongatus*' has been applied to at least four different taxa of *Sporobolus* from different areas.

The first was *Agrostis elongata* Lamk., Tabl. Encycl. 1 (1791) 162, a superfluous combination based on *Agrostis indica* L. Beauvois (1812) based *Vilfa elongata* on this. These combinations are synonyms of *S. indicus* var. *indicus*.

The second taxon was the diandrous *Sporobolus elongatus* R. Br. from Australia. Trinius' (1824, 1840) use of *Vilfa elongata* clearly pertained to this. Bentham (1878) and Hooker f. (1896) have regarded it as identical with *S. indicus*, but later authors, such as Clayton and De Nardi (1973) have kept it distinct, mainly because of the presence of two anthers. See the remarks under var. *creber* (De Nardi) Veldk.

The confusion in Asia started through a manuscript by Roth, which Roemer & Schultes used for their *Systema vegetabilium* (1817). Here the Australian *Agrostis elongata* (R. Br.) Roth ex R. & S. was united with a variety '*flaccida*' from India. The epithet '*elongata*' was then employed for a while for an Indian species. Hooker mistakenly called it *S. orientalis*, and Bor renamed it to *S. maderaspatanus* Bor (Kew Bull., 1957, 233). All Roth's specimens are in fact what everyone has called *S. diandrus*, and when this taxon is regarded as a variety of *S. indicus*, the epithet '*flaccidus*' has priority. Finally, the combination *S. elongatus* has also been used for *S. harmandii* Henr., q.v.

The combination *Sporobolus tenacissimus* [Jacq.] Kunth, based on *Agrostis tenacissima* Jacq. (1787, non Linné f., 1781, nec Roxburgh, 1820, see below), has been used for this species. This epithet has a very involved history, more fully explained by Bor (1957), so we will not have to go into that here, except that contrary to Bor, Beauvois did mention the basionym of *S. tenacissimus* in his index on p. 148 sub '*Agrostis tenacissimus* Lin. supp.'

The combination *Sporobolus orientalis* (Nees) Kunth, based on *Agrostis orientalis* Nees, is a superfluous combination for *A. tenacissima* Linné f. Smith et al. (1981) wrongly stated this as a synonym of *S. indicus* var. *exilis* (Trin.) T. Koyama. Nees was quite correct to regard Linné f.'s and Jacquin's species as two distinct ones. He should, however, have renamed the latter and not the first species, so *A. orientalis* and *S. orientalis* are both synonyms of *Muhlenbergia mexicana* (L.) Trin.

Smith et al. said that var. *exilis* would be pantropical, but we agree with T. Koyama that it does not occur in Asia.

Agrostis tenacissima sensu Roxb. (1820) from India is *S. tremulus* auct. non Kunth (e.g. Bor, 1960), which is *S. humilis* Presl. subsp. *minor* Veldk., q.v.

5a. var. *capensis* Engl.

Sporobolus indicus (L.) R. Br. var. *capensis* Engl., Hochgeb. Fl. Trop. Afr. (1892) 127; Peter in Fedde, Repert., Beih. 40 (1931) 283, 292. — *Agrostis spicata* Thunb., Prodr. Pl. Cap. (1794) 19, non Vahl (1790). — *Agrostis capensis* Willd., Sp. Pl., ed. 4, 1 (1797) 372, non Lamk. (1783). — *Agrostis africana* Poir. in Lamk, Encycl., Suppl. 1 (1810) 254. — *Vilfa africana* Beauv., Agrost. (1812) 16, 146 ('?'), 181 ('?'). — *Vilfa capensis* Beauv., Agrost. (1812) 16, 147 (see note), 181; Trin., Gram. Unifl. (1824) 153; nom. superfl. — *Sporobolus capensis* Kunth., Enum. Pl. 1 (1833) 212; Hubb. & Vaughan, Grass. Maur. & Rodr. (1940) 55; S.T. Blake, Univ. Ql. Pap. 1, 18/19 (1941) 11; Moomaw et al., Pac. Sc. 13 (1959) 338; Spies & Du Plessis, Bothalia 16 (1986) 270; nom. superfl. — *Sporobolus africanus* Robyns & Tournay, Bull. Jard. Bot. Brux. 25 (1955) 242; Bor, Grasses (1960) 627; Clayton, Kew Bull. 19 (1965) 291, fig. 7; Rotar, Gr. Hawaii (1968) 179, 331, t. 71; Fl. Trop. E. Afr., Gram. (1970) 375; Ellis, Agroplantae 9 (1977) 90, t. 30, 31; Palmer et al., Smithson. Contr. Bot. 55 (1985) 28, pl. 83, 84; Jacobs, Parramatta grass and its control (1985) 11, f. 4a, 6, 7, map 7. — *Sporobolus indicus* var. *africanus* Jov. & Guéd. [Bull. Centr. Et. Sc. Biarritz 7 (1968) 60, nom. inval.], Taxon 22 (1973) 163; nom. superfl. — T y p e: *Thunberg s.n.* (UPS, holo, n.v., microfiche 7646), South Africa, Capetown.

Panicum caudatum Thunb., Prod. Pl. Cap. (1794) 19, non Lamk. (1791). — T y p e: *Thunberg s.n.* (UPS, holo, microfiche 7646, K, n.v.), South Africa, Cape.

Sporobolus batesii Chev., Bull. Mus. Nat. Hist. Nat. II, 20 (1948) 469. — T y p e: *Bates 567* (P, holo, n.v.), Cameroon, Rio Benito, Sanje, Sept. 1897.

? *Agrostis diandra* auct., non Retz.: Hornem., Hort. Bot. Hafn. (1813) 73. — *Agrostis dianthera* Schult. & Schult. f., Mant. 3 (1827) 571. — *Vilfa dianthera* Steudel, Syn. 1 (1854) 162. — T y p e: *Anonymus s.n.* (C, holo), "cult. in hort. hafn., semina e Nepalia."

Sporobolus indicus auct. non R. Br.: R. Br., Prod. 1 (1810) 170 [pro *R. Brown 6208*, BM, see also Hubb. in Allan, New Zeal. J. Sc. Techn. 15 (1934) 256]; Benth., Fl. Austr. 7 (1878) 622, p.p.; Stapf, Fl. Cap. 7 (1900) 586, p.p.

Description based on Malesian material.

Panicle contracted, densely spiciform, often interrupted in the lower part, up to 45 cm long, branches appressed, densely spikeled, the lowermost 1.5–3.5 cm long. *Spikelets* 2–2.6 mm long, dark- to olive green, but often blackish. Lower glume 0.65–1 mm long, up to 0.4 times as long as the spikelet, apex obtuse to rounded; upper glume ovate to ovate-oblong, 1.35–1.65 mm long, c. 0.67 times as long as the spikelet, apex denticulate. *Lemma* ovate to ovate-oblong, 2–2.6 mm long, apex obtuse, 1- (or 3-)nerved. *Palea* oblong, 2–2.4 mm long. *Lodicules* 0.4–0.45 mm long. *Anthers* 3, 0.9–1.1 mm long. *Seed* ellipsoid to oblong, 1.1–1.25 by 0.45–0.65 mm diam.; pericarp rather closely adherent.

D i s t r i b u t i o n. Africa (Cameroon to Ethiopia, to South Africa), introduced elsewhere: Asia (see Jovet & Guédès, 1968, p. 62–65, note 20, 23, but also see note below); Malesia: Philippines (Luzon: locality unknown, *Cuming 2451*, A° 1841; Mt St. Tomas, *Santos 8014*, A° 1976), Papua New Guinea (Chimbu Valley, *ANU 15465*, *J.M.B. Smith*; Eastern Highlands, Goroka, *Veldkamp & Obedi 8568*, *8569*; Morobe Prov., Edie Creek, *NGF 20959*, *Henty & Galore*) (see also under Diseases); Australia (before 1803!, now in all states); Hawaii (from 1906, fide Rotar, 1968).

H a b i t a t. Rough lawn, 1800 m altitude in New Guinea.

Chromosomes. $n = 18$ (Spies & Du Plessis, 1986).

Anatomy. Ellis (1977) reported PCK-type anatomy of the leaves with large inflated bundle sheath cells with centrifugal chloroplasts. It is clearly not NAD-ME, as stated by Jacobs (1985). See Palmer et al. (1985) (SEM epidermis) and the Introduction.

Phytochemistry. Moomaw et al. (1959) reported that the species is a strong aluminium accumulator in Maui, Hawai'i.

Uses. Not very palatable to stock. The young, green leaves have a high protein content. In Australia it has been considered as a possibly dangerous weed (Jacobs, 1985).

Vernacular name. Parramatta grass (E).

Diseases. The spikelets are said to be very susceptible to attacks by various species of *Bipolaris* (cf. Alcorn, Mycotaxon 15, 1982, e.g. tab. 5, p. 34), but we noticed only two infections (one only very slightly) among the 24 specimens (8.3%) available in L.

The variety was also found to occur in Papua New Guinea, where in the town and airfield of Goroka none of hundreds of specimens was infected. Outside the town, however, along an untended roadside infection was nearly 100% (*Veldkamp 8569*), while a specimen of *Eragrostis tenuifolia* Steudel intermingled with a tussock of *Sporobolus*, also had been smutted. It would seem that the variety is much undercollected, and from its abundance in Goroka it may be presumed to be widespread in the Highlands along roads.

Notes. As was pointed out by Robyns & Tournay (1955) Poiret (1810) correctly renamed *Agrostis spicata* Thunb. and *Agrostis capensis* Willd., as both names are later homonyms. If one insists on regarding this taxon as a species, the correct name is *Sporobolus africanus* (Poir.) Robyns & Tournay.

Beauvois (1812) mentioned both *Agrostis spicata* Vahl and *A. spicata* Thunb. The first he referred to '*Vilfa virginica* var.', the second to *V. capensis* (p. 147). Yet, on p. 16, he included a *Vilfa spicata*, which most likely was based on Vahl's combination, as was also the opinion of Bor (1960).

Beauvois' basionym for *Vilfa capensis* is an '*Agrostis capensis* Thunb.', a non-existent combination, most likely an error in an intended reference to Willdenow. It was apparently also regarded as such by Trinius (1824) and subsequent authors.

The correct combination for this variety is var. *capensis* and not var. *africanus*. The varietal epithet was not generated automatically as an autonym when Nees (1841) described *Sporobolus capensis* var. *laxa*, even when he did not formally create the varietal combination (Art. 6.8). Because *Sporobolus capensis* is an illegitimate name, the autonym generated is also invalid (Art. 26.1), but the epithet '*laxus*' ('*laxa*') is legitimate (Art. 68.2) and therefore has priority dating from 1841. Jovet & Guédès' (1973) var. *africanus* being based on the same type is therefore superfluous. What they called var. *laxus* seems to consist of several forms: the Malesian specimens cited belong to var. *flaccidus* (R. & S.) Veldk. and var. *major* (Buse) Baaijens.

The correct author of the combination *S. indicus* var. *capensis* is Engler, because he based this combination on *S. capensis* (Willd.) Kunth, which is an indirect reference to *Agrostis capensis* Willd. This may be regarded as a bibliographic error (cf.

Art. 33.2. Ex. 5, 6, see note). As this basionym was a later homonym, Willdenow as the bracketed author must be deleted (Art. 49.1, but see Art. 46.1) or may be put between square brackets. At the varietal level Engler was free to choose any epithet, so '*capensis*' is valid here. Peter (1931), who was cited by Clayton (1970) as the author of the varietal combination, actually did refer to Engler in his key (l.c., p. 283).

Panicum caudatum Thunb. is also a later homonym. Steudel (Nomencl. ed. 2, 1841, 254) regarded it as a synonym of *Panicum interruptum* Willd. [= *Hymenachne interrupta* (Willd.) Buse]. He may have seen a specimen, as the diagnosis is most uninformative. The isotype in K represents the present taxon.

Agrostis dianthera is doubtfully included here. A specimen presumably with Hornemann's handwriting was seen from C. It is very young, the densely contracted inflorescence hidden for the largest part in the sheath. The long leaves are indeed filiform and curled at the tip as described, and the anthers 2, as the name indicates. However, the spikelets are 2.25–2.35 mm long, which brings var. *capensis* to the mind. This form is even now still unknown to occur in India, which suggests that the provenance is wrong.

5b. var. *cinereo-viridis* Baaijens, var. nov.

Sporobolus berterioanus auct. non Hitchc. & Chase: Backer, Handb. Fl. Java 2 (1928) 202, p.p.; Monod de Froideville in Backer & Bakh. f., Fl. Java 3 (1968) 537, p.p.

Sporobolus diandrus auct. non Beauv.: Buse in Miq., Pl. Jungh. 3 (1854) 343, p.p.; Miq., Fl. Ind. Bat. 3 (1857) 375, p.p.; Koord., Exk. Fl. Java 1 (1911) 145, p.p.; Backer, Handb. Fl. Java 2 (1928) 202, p.p.; Monod de Froideville in Backer & Bakh. f., Fl. Java 3 (1968) 537, p.p.

A varietatibus malesianis ceteris paniculis plus minusve laxe contractis basi lobatis, ramis plus minusve ascendentibus, spiculis 2–2.6 mm longis, lodiculis 0.3–0.4 mm longis, antheris 3, 0.85–1.1 mm longis, seminibus (0.95–)1.05–1.25 mm longis differt. Inter (900–)1000–2750 m alt. (medio 1880 m) crescens, spiculis raro a *Bipolare* sp. infectis. — T y p u s: *Koorders 43810* (L, holo, BO, US), Java, Malang, Lalijiwo, c. 2500 m alt., 24 Aug. 1916.

Panicle laxly contracted, lobed at base, branches slightly patent to curved, rather densely spikeled, 20–40 by 0.8–2.5 cm diam., lowermost ones 1–6 cm long. *Spikelets* 2–2.6 mm long, blackish green to greyish. Lower glume 0.6–1 mm long, c. 0.33 times as long as the spikelet, apex usually rounded; upper glume ovate to elliptic, 1.2–1.6 mm long, 0.5–0.67 times as long as the spikelet, apex usually not erose. *Lemma* ovate to ovate-oblong, as long as the spikelet, apex acute to subobtuse, 1- (or 3-)nerved. *Palea* oblong, 1.9–2.5 mm long. *Lodicules* 0.3–0.4 mm long. *Anthers* 3, 0.85–1.1 mm long. *Seed* (0.95–)1.05–1.25 by 0.55–0.7(–0.75) mm diam.; pericarp rather loosely adherent; embryo 0.45–0.65 mm long.

Distribution. Malesia: Java (Kedu, Semarang, Kediri, Malang, Besuki), Celebes (Central), Lesser Sunda Islands: Bali, Lombok, Flores, Timor; Keeling Is.

Habitat. Sunny to lightly shaded, more or less disturbed, not too wet localities, along roads, in grass fields, etc., locally abundant, (900–)1000–2750 m alt. (average 1880 m).

Diseases. Spikelets rarely infected by *Bipolaris* cf. *ravenelii* (Curt.) Shoemaker (4 out of 63 collections seen).

U s e s. Praised as a good fodder (*Backer 21896*).

V e r n a c u l a r n a m e s. Kacing (Jav.), see also under var. *major*.

N o t e s. By the size of the spikelets this variety resembles var. *capensis*, but while the panicle is densely contracted in the latter, it is lax with ascending and longer branches in the present one.

This variety differs from var. *major*, with which it is at least partly sympatric, especially in E Java, by its more lax panicle with longer lower branches, larger and darker spikelets with a longer upper glume, and longer lodicules. There also seems to be an ecological difference: var. *major* is generally found from sea-level to 2075 (–2700) m with an average of 875 m, while the present variety is more restricted to higher altitudes, occurring at (900–)1000–2750 m with an average of 1880 m. The spikelets of var. *major* are much more often infected by *Bipolaris crustacea* (Henning) Alcorn and *B. ravenelii* (cf. also Alcorn, *Mycotaxon* 15, 1982, 34, tab. 5).

5c. var. creber (De Nardi) Veldk., *comb. nov.*

Sporobolus creber De Nardi, *Contr. N.S.W. Nat. Hb.* 4 (1973) 406, t. 1, 1A; Cunningham et al., *Pl. W. N.S.W.* (1981) 141, col. pl.; Simon, *Austr. Syst. Bot. Soc. Newsl.* 31 (1982) 18. —
T y p e: NSW 121997 (*McDonald*) (NSW, holo, n.v.; K, L, US), Australia, New South Wales, Warrumbungle Range, c. 30 miles E of Gulargambone, 20 May 1971.

Description based on *Kleckham s.n.* (20-10-1960; LAE):

Panicle densely contracted, c. 11 by 0.5 cm, distinctly interrupted in the lower part, upper part spiciform, branches appressed, the lowermost one solitary, c. 1.5 cm long, densely spikeled, the second lowest 0.23–1.11 (mean c. 0.5) times as long as the node above it. *Spikelets* c. 1.5 mm long, more or less dark green. Lower glume 0.7–0.8 mm long, c. 0.5 times as long as the spikelet, apex rounded to obtuse, entire to erose, 0-nerved; upper glume 0.9–1 mm long, 0.6–0.67 times as long as the spikelet, acute. *Lemma* ovate-oblong, c. 1.4 mm long, apex acute, 1-nerved. *Palea* elliptic, c. 1.4 mm long. *Lodicules* c. 0.25 mm long. *Anthers* 2, c. 0.5 mm long. *Seed* c. 0.75 by 0.5 mm diam.; pericarp rather closely adherent; embryo c. 0.3 mm long.

D i s t r i b u t i o n. Malesia: Papua New Guinea (Central Dist., Kerau); Australia (Queensland, New South Wales, Victoria); New Caledonia; Fiji.

H a b i t a t. Not indicated for New Guinea: once found at 2255 m alt.; in Australia widely distributed in open grassland or *Eucalyptus* woodland, on sandy or loamy soils, often near creeks.

D i s e a s e s. In L 3 out of 15 specimens were infected by *Bipolaris* sp. Alcorn (*Mycotaxon* 15, 1982, 34, tab. 5) recorded only *B. cylindrica* Alcorn as an infectant.

N o t e s. *Kleckham s.n.* (20-10-1960; LAE) is the only record for Malesia so far. This variety is closely related to the Australian var. *elongatus* (R. Br.) F.M. Bailey from which Ms. De Nardi distinguished it. As can be seen from the following key, the differences between the two are mainly statistical and some specimens remain difficult to place. This is, unfortunately, also the case with the *Kleckham* specimen. The inflorescence with densely spikeled branches shorter than the following internode so distinctive for typical var. *creber* is here rather lax with less densely spikeled branches, as long as to longer than the internodes, and more like depauperate speci-

mens of *S. elongatus*. Except for the length of the spikelet and relative size of the seed, the dimensions of the spikelets fall in the range of both taxa, but it seems closest to var. *creber*.

— Panicle much more interrupted for more of its length, branches short, stiff, appressed, second lowest branch 0.23–1.11 (mean c. 0.5) times as long as the internode above it. — Spikelets 1.25–1.75 mm (mean 1.55 mm) long, densely crowded. Lower glume 0.4–1 mm long. Upper glume 0.6–1.2 mm long. Lemma 1.2–1.75 mm (mean 1.5 mm) long. Palea 1.1–1.6 mm long. Anthers 0.4–0.5 mm long. Seed 0.5–0.85 mm long, 0.53–0.73 times as long as the spikelet

S. indicus* var. *creber

— Panicle interrupted in the lower 2 or 3 internodes only, branches somewhat spreading, second lowest branch 0.77–2.8 (mean c. 1.6) times as long as the internode above it. — Spikelets 1.65–2.3 mm (mean 1.88 mm) long, rather loosely arranged. Lower glume 0.3–1.1 mm long. Upper glume 0.7–1.4 mm long. Lemma 1.55–2.25 mm (mean 1.8 mm) long. Palea 1.35–1.9 mm long. Anthers 0.5–0.9 mm long. Seed 0.5–1 mm long, 0.48–0.67 times as long as the spikelet. — Australia ***S. indicus* var. *elongatus***

Var. *capensis* Engl. may also be confused with these, but differs by the less interrupted (dense) inflorescence, spikelets 2–2.6 mm long, an upper glume 1.35–1.65 mm long, anthers 0.9–1.1 mm long, and a seed 1.1–1.25 mm long.

5d. var. *flaccidus* (R. & S.) Veldk., *comb. nov.*

Agrostis elongata (R. Br.) Roth ex R. & S. (non Lamk., 1791) var. *flaccida* Roth ex R. & S., Syst. Veg. 2 (1817) 368; Roth, Nov. Pl. (1821) 41; *comb. legit.* (Art. 68.2). — Type: *Roth 80 β* (BM, holo; LE), India.

Agrostis diandra Retz., Obs. 5 (1788) 19; Roxb., Fl. Ind. 1 (1820) 319. — *Sporobolus diandrus* Beauv., Agrost. (1812) 26, 147, 178; Jacq. f., Eclog. Gram. Rar. (1820) t. 28; Brongn. in Duperr., Bot. Voy. Coquille 2 (1829) 17, pro *comb. nov.*; Buse in Miq., Pl. Jungh. 3 (1854) 343 (p.p. & excl. var. *major*); Miq., Fl. Ind. Bat. 3 (1857) 375, p.p.; Benth., Fl. Austr. 7 (1878) 622; Hook. f., Fl. Br. India 7 (1896) 247; Nauta & Boerl., Teysmannia 11 (1901) 490; Merr., Philip. J. Sc. 1, Suppl. (1906) 373, p.p.; Koord., Exk. Fl. Java 1 (1911) 145, p.p.; Achariyar & Mudaliyar, Handb. S. Ind. Gr. (1921) 231, t. 178; Merr., Enum. Born. Pl. (1921) 49; Camus, Fl. Gén. I.-C. 7 (1923) 507; Merr., Enum. Philip. Fl. Pl. 1 (1923) 80; Ridley, Fl. Mal. Pen. 5 (1925) 244, p.p.; Backer, Handb. Fl. Java 2 (1928) 203; Onkr. Suiker. (1928) 106, t. 99; Burk., Dict. 2 (1935) 2069; Backer in Heyne, Nutt. Pl. Indon. (1950) 259; Schmid, l'Agron. Trop. 13 (1958) 486; Bor, Grasses (1960) 629; Larsen, Dansk Bot. Ark. 20 (1963) 243; Clayton, Kew Bull. 19 (1965) 293; Hsu in Hara, Fl. E. Himalaya (1966) 377; Monod de Froideville in Backer & Bakh. f., Fl. Java 3 (1968) 539; Henty, Bot. Bull., Lae 1 (1969) 180; Leras & Vignal, Bull. Soc. Bot., France 116 (1969) 425, t. 2, 7-1; B.C. Stone, Fl. Guam (1970) 193; Gilliland, Rev. Fl. Mal. 3 (1971) 106, t. 18, pl. 14c; P.K. Gupta, Genet. Iber. 23 (1971) 185; Gould & Soderstrom, Can. J. Bot. 52 (1974) 1081; Christopher & Abraham, Cytologia 39 (1974) 563, t. 12, 13; Madulid, Acta Manil. A, 14 (1975) 89; Sarkar et al., Taxon 25 (1976) 636; Hsu, Fl. Taiwan 5 (1978) 501, t. 1410; Chaudhuri & Pal, Bull. Bot. Soc. Bengal 32 (1979) 52. — *Vilfa diandra* Trin., Diss. Bot. (1824) 154; Mém. Ac. Sc. St. Pétersb. VI, 5, 2 (1840) 60 (pro *comb.*). — *Vilfa retzii* Steudel, Nomencl., ed. 2, 1 (1840) 40; 2 (1841) 626, 768; Syn. 1 (1854) 162; nom. superfl. — *Sporobolus diandrus* var. *diandrus*: Buse in Miq., Pl. Jungh. 3 (1854) 343 (by implication). — *Sporobolus indicus* var. *diandrus* (Retz.) Jovet &

Guéd. [Bull. Centre Ét. Rech. Sc., Biarritz 7 (1968) 65, t. 5b; nom. inval.] Taxon 22 (1973) 163. — **T y p e:** *Koenig s.n.* ('*Cinna diandra*') (LD, holo, C, n.v.; BM, K, L), India (the L sheet is annotated in a later hand 'Ceylon').

Vilfa erosa Trin., Mém. Ac. Imp. Sc. St. Pétersb. VI, 5, 2 (1840) 86. — **L e c t o t y p e:** *Koenig s.n.* ex Schwägrichen in Hb. Trin. '*Agrostis diandra* Roxb.' (LE, holo), Sri Lanka.

Spermachiton involutum Llanos, Fragm. Pl. Filip. (1851) 25; in Blanco, Fl. Filip. ed. 3, 4, 1 (1880) 17; [Pilger & Potztl in E. & P., Nat. Pfl. Fam. ed. 2, 14d (1956) 54, in syn., '*Spermatochiton*'].

— **T y p e:** Not extant. "Philippines, Calumpit, Boguion road, February."

Sporobolus diandrus (Retz.) Beauv. var. *nanus* Hook. f. in Trimen, Fl. Ceylon 5 (1900) 261 ('*nana*'). — *Sporobolus trimenii* Seneratna, Gr. Ceylon (1956) 96, nom. inval. (not in Bor, 1960!). — **T y p e:** *Trimen s.n.* (PDA, holo, n.v.), Sri Lanka, Jaffna, Feb. 1890.

Sporobolus exilis auct., non Balansa: Balansa in Morot, J. Bot. 4 (1890) 164, pro specim.

Sporobolus indicus var. *laxus* auct., non Stapf: Jovet & Guéd., Bull. Centre Ét. Rech. Sc., Biarritz 7 (1968) 65, p.p.

Panicles contracted to nearly lax, 7–35 cm long, branches usually loosely spikeled to the base to naked in the lower third, the lowermost often obliquely spreading to patent, 1.5–9 cm long. *Spikelets* (1.3–)1.4–1.6(–1.8) mm long, yellowish to grass green (sometimes with a black smut). Lower glume 0.35–0.5(–0.6) mm long, 0.25–0.33 times as long as the spikelet, apex truncate, rarely obtuse or rounded; upper glume ovate, 0.7–1 mm long, 0.4–0.6 times as long as the spikelet, apex often denticulate, (0- or) 1-nerved. *Lemma* ovate-oblong, as long as the spikelet, acute to obtuse, 1(–3)-nerved. *Palea* elliptic to oblong, 1.2–1.6 mm long. *Lodicules* 0.25–0.3 mm long. *Anthers* 2 (or 3), 0.5–0.8 mm long, 0.4–0.55 mm long in some New Guinea specimens (see note). *Seed* 0.6–0.9(–0.95) by 0.35–0.55 mm; pericarp usually rather closely adherent; embryo 0.4–0.5 mm long.

D i s t r i b u t i o n. Mauritius, Pakistan, India, Sri Lanka, to Polynesia and Australia (Queensland, New South Wales); widespread in Malesia; also reported for Cameroon [Peter in Fedde, Repert., Beih. 40 (1931) 285], but not mentioned in the editions of the Flora of West Tropical Africa.

H a b i t a t. Sunny to lightly shaded, more or less disturbed, dry to slightly moist but not soggy, preferably hard to stony ground localities, on beaches, along roads, in grass fields, etc., locally abundant, up to 525(–870) m alt. (average 110 m), but in New Guinea as high as 2625 m.

C o l l e c t o r ' s n o t e s. Anthers white or violet. Stigmas white.

A n a t o m y. See Introduction.

C h r o m o s o m e s. $2n = 24$ (Larsen, 1963; Gupta, 1971; Gould & Soderstrom, 1974; Christopher & Abraham, 1974; Sarkar et al., 1976).

V e r n a c u l a r n a m e s. Fuka-fuka (Mekeo, Maipa), gorumakwi (Masul, Chimbu), jukut njenjerehan (Sund.), kohsagafi (Dunantina, PNG), kongas (Wahgi, Minj; Hagen, Togoba), kundai (Menado), kwit (Agaun, Papua New Guinea), lancuran (Jav.), lasay (Zamb.), mok (Manggarai), namidzandu (Miruma, E. H. Prov.), namidzata (Asaro, Kefamo), padi-padian, pajarata (Medan), pepunia (Ceram), pim-bik (Jali, Irian Jaya), rehba jakjak (Mad.), rumput jahil (Sumatra, Minggala), rumput podang togae (Sibolga, Sumatra), rumput tuloh belalang (Malaya, Timor), samben (Medan), sinoanoana (Talaud).

U s e s. Some value as a fodder grass when young, when full grown it is said to be too tough and fibrous (Maiden, 1898); also used for brooms in Java. The fodder

value is very satisfactory (Backer, 1950) for horses (Nauta & Boerlage, 1901). An effective sand binder (Madulid, 1975). Stone (1970) regarded it as a minor to sometimes troublesome weed, difficult to eradicate when once established (Achariyar & Mudaliyar, 1921).

D i s e a s e s. The spikelets are only rarely infected by smuts of *Bipolaris*, e.g. *B. crustacea* (Hennings) Alcorn, *B. cylindrica* Alcorn and *B. ravenelii* (Curt.) Shoemaker (cf. Alcorn, Mycotaxon 15, 1982, 34, tab. 5); 23 out of 326 collections seen, c. 7%. Information is obscured by probable misidentifications (cf. Sivanesan, Mycol. Pap. 158, 1987, 62). During a visit to Singapore and Papua New Guinea JFV saw no infected inflorescences. It is suspected that the cutting regime is of influence (see sub *S. indicus*, above).

N o t e s. Retzius (1788) used the epithet '*diandra*', which may be derived from either '*diander*' or '*diandrus*'. For traditional reasons all modern authors have used the more obscure first version '*diander*', which is not found in most Latin text books. Beauvois (1812), however, for once consistent, used '*diandrus*', which orthography must therefore be retained.

The combination *Vilfa diandra* Trin. (1824) was based on *Agrostis diandra* Retz. The specimens studied by Trinius do not belong to the present taxon, however, as can be seen from his description, where he speaks of branches without spikelets in the lower third, and upper glumes as long as the spikelets. Steudel (Nomencl., ed. 2, 1, 1840, 40; 2, 1841, 626, 768; Syn. 1, 1854, 162) against the rules of priority distinguished Retzius' species as *Vilfa retzii* Steudel and Trinius' species as the 'true' *V. diandra*.

The 'true' *Agrostis diandra* was also in the possession of Trinius, but he described it as *Vilfa erosa*.

Hooker f. placed *Vilfa diandra* sensu Trin. in the synonymy of *Sporobolus orientalis*. That combination has had a complicated history, fully discussed by Bor (Kew Bull. 12, 1957, 233), who concluded that this species had no name and described it as new, *S. maderaspatanus* Bor.

In BM a Roth sheet was discovered mounted with sprigs of both his *Agrostis elongata* and his var. *flaccida*, and labeled by J.J. Roemer as "misit amic. Roth". From Roemer this sheet passed to R.J. Shuttleworth and hence to the BM. Trinius (1840) discussed a specimen in Mertens' herbarium, of which there is a piece and a water colour also in his own herbarium in LE. These are clearly part of the base of the combinations published by Roemer and Schultes.

Roth's 'typical' form in the BM is represented by a peduncle with a contracted panicle, the specimen of his 'var. *flaccida*' on the same sheet has indeed a more flaccid inflorescence. Both have small, diandrous spikelets, typical for specimens from the Western part of the distribution of this variety. Unfortunately '*flaccidus*' is the oldest epithet at the varietal level and the well-known epithet '*diandrus*' of this common SE Asian weed had to be changed.

The type of *Vilfa erosa* Trin. bears three labels in König's handwriting: '*Agrost diandr Kön Rottl*', and two with '*diandra* Roxb.' One of the latter Trinius changed to "*Vilfa diandra* (Roxb.) ex Ind. Or. dt Lipsiae cl. Schwägrichen 1836." The specimen represents the current variety. There is another one in the Roxburgh herbarium in K. A Koenig sheet (not the isotype!) labeled '*Agrost. diandra*' in L, however, is var.

major, while a Rottler specimen in K, doubtfully attributed to *Agrostis diandra* by Rottler has 3 anthers, as Rottler noted, and also belongs there.

As already observed by Merrill (Sp. Blanc., 1918, 71) F.-Villar (Nov. App., 1880, 310) erroneously equated *Spermachiton involutum* Llanos with *Eriochloa punctata* (L.) Hamilt. Llanos, mentioning the presence of two anthers, most likely described *S. indicus* var. *flaccidus*. Merrill's illustrative specimen (Merrill Sp. Blanc. 845) is the present variety.

Traditionally the main reason for maintaining var. *flaccidus* as a species distinct from *S. indicus* has been the presence of two anthers (cf. Clayton, 1965, 293). As has occasionally been mentioned here and elsewhere (e.g., by Jovet & Guédès, 1968, 58), three anthers also occur, so this difference is less absolute than we would wish. This and the overall similarity with the *S. indicus* complex has convinced Jovet & Guédès and us that no more than a varietal status is warranted.

It is interesting to note that the spikelets of various varieties are often infected by a black smut. In var. *flaccidus* this is but seldom the case, indicating a physiological difference. The morphologically very similar var. *queenslandicus* Veldk. had an occasional smutted spikelet in 4 out of 10 cases seen.

The shape of the panicle is rather variable, but may locally be constant, as was remarked by Monod de Froideville: "Spreading of the branches of the inflorescence seems to be a hereditary factor, and has nothing to do with ecological factors. In a remote place on the island (Timor) I found only the form with strictly horizontally spreading branches." (Note on *van Maarseveen* 8, BO). In India and Sri Lanka forms are found with a rather few-spikeled, lax panicle, as in the type of var. *flaccidus*, next to more densely contracted ones, as in Roth's 'typical' form of *Agrostis elongata*. We suspect that such lax forms were distinguished as var. *laxus* by Jovet & Guédès. In Queensland there is a form, distinguished by Simon as *S. laxus* Simon (non var. *laxus* Stapf!), with a rather large, few-spikeled inflorescence, hence the branches more distinctly naked at base than is usual, and 3-anthered florets. According to the description the spikelets would be c. 2 mm long. Several isoparatypes were available. The spikelets turned out to be 1.5–2 mm long, and in several specimens 2-anthered florets were encountered, again showing that the number of anthers is not a reliable character. This represents a distinct taxon, but in view of the line here taken, it is another variety of the polymorphous *S. indicus* (q.v.): var. *queenslandicus* (see under Species dubiae et excludendae for the validation).

We have seen nothing like it in Malesia, where in the usual form the panicle is much more contracted and more densely spikeled, whereby specimens mainly differ from var. *major* by the size of the spikelet and the presence of two anthers, both unreliable characters. No wonder some specimens have been difficult to place. Some of these occur in Papua New Guinea (Central Highlands and further East). Their panicles are often rather broad and open, with relatively large, (1.5–)1.6–1.9(–2) mm long and often lead-coloured spikelets. Out of 25 specimens only 2 had occasionally some triandrous spikelets, diandry being the rule. The anthers were very small, 0.4–0.55 mm long. Because of the floral dimensions and number of anthers we have tentatively included them here, but in 'normal' representatives of var. *flaccidus* the anthers are 0.5–0.8 mm long, and 0.7–1 mm in var. *major*. The plants occur between 0 and 2625 m. This form is not the same as var. *queenslandicus*.

Balansa (in Morot, J. Bot. 4, 1890, 164) enumerated specimens (*Balansa s.n.*, 25-10-1886, 10-12-1886, 12-12-1886, L) belonging to this variety as '*Sporobolus exilis* Trin.' This is a new combination indirectly based on *Vilfa exilis* Trin., not recorded in the Index Kewensis.

Hornemann described an *Agrostis diandra* [Hort. Bot. Hafn. 1 (1813) 571, non Retz. — *Agrostis dianthera* Schult. & Schult. f., Mantissa 3 (1827) 571. — *Vilfa dianthera* Steudel, Syn. 1 (1854) 162. — Type: *Hornemann s.n.* (not in C, M), India, cultivated in Copenhagen in 1805], of which we have seen no material.

5e. var. major (Buse) Baaijens, *comb. nov.*

Sporobolus diandrus (Retz.) Beauv. var. *major* Buse in Miq., Pl. Jungh. 3 (1854) 343; Miq., Fl. Ind. Bat. 3 (1857) 375. — Type: *Junghuhn s.n.* (L, holo, no. 903.342-96), Java, Cibogo, June.

Agrostis fertilis Steudel, Syn. 1 (1854) 170. — *Sporobolus fertilis* Clayton, Kew Bull. 19 (25 Feb. 1965) 291, p.p.; Clayton ex Bor, Dansk Bot. Ark. 23 (26 May 1965) 149, pro comb. nov.; Gilliland, Rev. Fl. Mal. 3 (1971) 106, pl. 16a; Mehra & Sharma, Taxon 21 (1972) 341; Bor, Grasses, ed. 2 (1973) iii; Gould & Soderstrom, Can. J. Bot. 52 (1974) 1081, 1082; Mehra & Sharma, Cytologia 40 (1975) 455; ? Tsvet., Grasses Sov. Un. 2 (1976) 645; Hsu, Fl. Taiwan 5 (1978) 501, t. 1411; Chaudhuri & Pal, Bull. Bot. Soc. Bengal 32 (1979) 52; B.C. Stone, Fed. Mus. J. n.s. 26 (1982) 53. — *Sporobolus fertilis* var. *fertilis*: Hatusima, Fl. Ryukyus (1971) 675. — *Sporobolus indicus* var. *fertilis* Jovet & Guéd., [Bull. Centr. Et. Rech. Sc., Biarritz 7 (1968) 50, nom. inval.] Taxon 22 (1973) 163. — Lectotype: *Burger s.n.* (L, holo, no. 908.97-171, K neg. 5613, P, fide Jovet & Guédès, 1968, 55b), Japan (here appointed).

Cinna japonica Steudel, Syn. 1 (1854) 182, non *Sporobolus japonicus* (Steudel) Rendle (1904). — Lectotype: *Ilb. Von Siebold s.n.* (L, holo, no. 908.97-183), Japan (here appointed).

Sporobolus elongatus R. Br. var. *purpureo-suffusus* Ohwi, Bot. Mag., Tokyo 55 (1941) 394; Fl. Japan (1965) 176. — *Sporobolus indicus* var. *purpureo-suffusus* T. Koyama, J. Jap. Bot. 37 (1962) 235; in Walker, Fl. Okinawa (1976) 190; Anon., Icon. Corm. Sin. 5 (1976) 146, t. 7122; Fujita, J. Jap. Bot. 54 (1979) 248, t. 1, 2. — *Sporobolus fertilis* var. *purpureo-suffusus* Keng & Shen, Acta Bot. Bor. Occ. Sin. 5 (1985) 161. — *Sporobolus indicus* subsp. *purpureo-suffusus* T. Koyama, Grasses of Japan (1987) 275, 531. — Type: *Takeuchi s.n.* (KYO, holo, n.v.), Japan, Hondo, Mukoshima, Kyoto, 1929.

Sporobolus indicus (L.) R. Br. var. *pallidior* T. Koyama, J. Jap. Bot. 37 (1962) 236, 240, t. 3e; in Walker, Fl. Okinawa (1976) 190. — *Sporobolus fertilis* var. *pallidior* Hatusima, Fl. Ryukyus (1971) 675 ('*pallidiorus*'), nom. inval., no full and direct reference to basionym. — *Sporobolus indicus* subsp. *pallidior* T. Koyama, Grasses of Japan (1987) 277, 531, fig. 105. — Type: *T. Koyama 7328* (DAO, holo, n.v.), Ryukyu Islands, Okinawa, near Ishikawa City (some material at least in US labeled 'var. *longiglumis*' by Koyama, incd.).

Sporobolus berterioanus auct. non Hitchc. & Chase: Backer & Sloot., Theconkr. (1923) 72, f. 72; Backer, Handb. Fl. Java 2 (1928) 202, p.p.; Onkr. Suiker. (1928) 106, t. 98; Burk., Dict. 2 (1935) 2069; Backer in Heyne, Nutt. Pl. Indon. (1950) 259, p.p.; Monod de Froideville in Backer & Bakh. f., Fl. Java 3 (1968) 538, p.p.

Sporobolus diandrus auct. non Beauv.: Buse in Miq., Pl. Jungh. 3 (1854) 343, p.p.; Miq., Fl. Ind. Bat. 3 (1857) 375, p.p.; Merr., Philip. J. Sc. 1, Suppl. (1906) 373, p.p.; Koord., Exk. Fl. Java 1 (1911) 145, p.p.; Ridley, Fl. Mal. Pen. 5 (1925) 244, p.p.

Sporobolus elongatus auct. non R. Br.: Miq., Fl. Ind. Bat. 3 (1857) 376; Brown, Minor Prod. Philip. For. 1 (1920) 344; Hitchc., Brittonia 2 (1936) 118; Ono & Tadcoka, Bot. Mag., Tokyo 66 (1953) 22, t. 10; Chung, Korean Gr. (1965) 122; Ohwi, Fl. Japan (1965) 176; Henty, Bot. Bull., Lae 1 (1969) 180; Huang, Taiwania 15 (1970) 157; B.C. Stone, Fl. Guam (1970) 193.

Sporobolus indicus auct. non R. Br.: Hook. f., Fl. Br. India 7 (1896) 247, p.p.; Merr., Philip. J. Sc. 1, Suppl. (1906) 373; Koord., Exk. Fl. Java 1 (1911) 146, p.p.; Merr., Sp. Blanc. (1918)

71; Brown, Min. Prod. Philip. For. 1 (1920) 346; Camus, Fl. Gén. I.-C. 7 (1923) 507, t. 42, f. 10, 11; Merr., Enum. Philip. Fl. Pl. 1 (1923) 80, p.p.; Ridley, Fl. Mal. Pen. 5 (1925) 244; Henderson, Mal. Wild Fl. (1954) 318, t. 182 c-f; Schmid, l'Agron. Trop. 13 (1958) 486, t. 93, f. 1; Bor, Grasses (1960) 630; Larsen, Dansk Bot. Ark. 20 (1963) 243.

Sporobolus indicus var. *africanus* auct., non Jovet & Guéd.: Jovet & Guéd., Bull. Centre Ét. Rech. Sc., Biarritz 7 (1968) 65, p.p.

Sporobolus indicus var. *laxus* auct., non Stapf: Jovet & Guéd., Bull. Centre Ét. Rech. Sc., Biarritz 7 (1968) 65, p.p.

Panicle usually contracted, more or less spiciform, lobed at base, 11–60 cm long, branches more or less appressed, usually densely spikeled, lowermost branches up to 5 cm long. *Spikelets* (1.7–)1.8–1.9(–2.1) mm long, yellowish to pale green (often black because of a smut). Lower glume 0.5–0.8 mm long, 0.2–0.4 times as long as the spikelet, obtuse to truncate; upper glume ovate to oblong, 0.8–1.3 mm long, 0.5–0.67 times as long as the spikelet, 1-nerved, apex usually acutish, but also erose and denticulate (and then becoming similar to var. *pyramidalis*). *Lemma* ovate to oblong, 1.6–2 mm long, acute to obtuse, 1–3-nerved. *Palea* elliptic, 1.5–1.8 mm long. *Lodicules* 0.25–0.3 mm long. *Anthers* (2 or) 3, 0.7–1 mm long. *Seed* 0.9–1.1(–1.15) by 0.5–0.75 mm diam., pericarp rather closely adherent; embryo 0.4–0.6 mm long.

Distribution. Sri Lanka, India to Japan and Korea, and the Pacific (rare: Bora-Bora, Fiji, Yap), widespread in Malesia, apparently rare in the Lesser Sunda Islands (Flores, Timor) and New Guinea, Australia (Queensland).

The plants from France regarded as *S. indicus* var. *fertilis* by Jovet & Guédès (1968), followed by Kerguelen (Lejeunia n.s. 75, 1975, 265) belong to *S. indicus* var. *indicus*. Those from the U.S.S.R., unavailable to us, should therefore be looked at again (cf. Tsvelev, 1976).

Habitat. Sunny to lightly shaded, not too dry or soggy, preferably hard or stony areas, especially along roads and paths, withstanding trampling, locally abundant and forming a narrow fringe along paths, 0–2075(–2700) m alt. (average 875 m).

Chromosomes. $2n = 36$ (Ono & Tateoka, 1963; Koyama, 1962), 40–45, 48 (Mehra & Sharma, 1975), c. 48, c. 54 (Larsen, 1963), 54 (Koyama, 1962).

Anatomy. Stem (Fujita, 1979): chloroplasts abaxial; for leaves, see Introduction.

Pollination. Huang (1970) described the grain as 41 μm wide, pore 4 μm wide, annulus 3 μm thick.

Diseases. 35 out of the 135 specimens inspected (c. 26%) had their caryopses infected by the black smut *Bipolaris* sp. The type of *B. crustacea* (Hennings) Alcorn was present on a specimen from Bogor most likely belonging to var. *major*, as well as that of *Helminthosporium tonkinense* Karst. & Roum., which infected a plant misidentified as *S. tenacissimus* (cf. Alcorn, Mycotaxon 15, 1982, 21–22, 24, 34, tab. 5). The latter is considered a synonym of *B. ravenelii* (Curt.) Shoemaker.

Collector's notes. Culms tough. Leaves dark green. Panicles often more or less nodding. Anthers pale lilac to purple. Stigmas white to pale lilac.

Uses. Old culms are used for brooms ('njreh') in Java. A fairly fine straw of

medium length is obtained from the peduncles and utilized in Iloilo as a hat material (Brown, 1920). A moderate fodder when not too old. In some literature its reputation has been much exaggerated and it is not fit for cultivation as the quality of its produce, even when considerable, is far below that of other cultivated grasses (Backer, 1950). Chaudhuri & Pal (1979) reported that the grain is eaten in Bengal in times of scarcity. Stone (1970) said that it is a minor to moderately harmful weed, unpalatable to stock, to be eliminated from pastures. May become a troublesome weed in cultures by the strong development of the root system (Backer & Van Slooten, 1923).

Vernacular names. Bakuit, bangkuit (Iloilo), cusampe (Gajo, Sumatra), bangsom, kecicing, lancuran, gorobada (Papua New Guinea, Fiyugi lang.), rumput ikua kudo padang (Minangkabau), iwang (Simalur), kongi tangele (Mt Hagen), jukut njenjerehan (Sund.), panjuran (Jav.), rumput ayam (Lingga), rumput prenjutan (Kedu, Java), rumput rantai (Padang, Sumatra), sinosoana (Talaud), suket sadan (Jav.), sangsangitan (Bontoc), torojan (Palu, Celebes).

Note. This taxon has been confused with many other ones, e.g. *S. diandrus* in which Buse (1854) included it. For comparative discussions see under the species, var. *cinereo-viridis* Baaijens, and var. *flaccidus* (R. & S.) Veldk.

5f. var. *pyramidalis* (Beauv.) Veldk., comb. & stat. nov.

Sporobolus pyramidalis Beauv., Fl. Oware 2 (1816) 36, t. 80; Clayton, Fl. W. Trop. Afr., ed. 2, 3 (1972) 408; Fl. E. Trop. Afr., Gram. 2 (1974) 373; Simon, Austr. Syst. Bot. Soc. Newsl. 31 (1982) 18. — *Sporobolus indicus* forma *pyramidalis* Peter in Fedde, Repert., Beih. 40 (1931) 280 ('Formen'), 291. — *Sporobolus pyramidalis* var. *pyramidalis*: Jovet & Guéd., [Bull. Centre. Et. Rech. Sc., Biarritz 7 (1968) 60, nom. inval.] Taxon 22 (1973) 163 (by implication: Art. 26.2). — **T y p e:** *Beauvois* s.n. (G, holo, P?, n.v.), Nigeria.

Sporobolus jacquemontii Kunth, Rév. Gram. (1831) 427, t. 127; Clayton, Kew Bull. 19 (1965) 288; Gould & Soderstrom, Can. J. Bot. 48 (1970) 1635; J.W. Parham in A.C. Smith, Fl. Vit. Nov. 1 (1979) 307; Pohl in Burger, Fl. Costaric. 15 (1980) 544; Simon, Austr. Syst. Bot. Soc. Newsl. 31 (1982) 18. — *Vilfa jacquemontii* Trin., Mém. Ac. Sc. St. Pétersb. VI, 5, 2 (1840) 92. — *Sporobolus pyramidalis* Beauv. var. *jacquemontii* Jovet & Guéd., [Bull. Centre. Et. Rech. Sc., Biarritz 7 (1968) 60, nom. inval.] Taxon 22 (1973) 163. — **T y p e:** *Jacquemont* s.n., A° 1827 (P, holo, n.v.; LE), Santo Domingo.

This variety is distinct from all others by the erosely truncate upper glumes, slightly longer than the lower glume, and less than half as long as the spikelet.

Both its facies, usually distinguished as two taxa, have been reported for Australia and the Pacific, and it may turn up in Malesia as well. Jovet & Guédès (1968) reported and depicted a find in China. By the shape of the glumes it would seem this taxon, and then, most likely, was introduced.

Diseases. Alcorn (Mycotaxon 15, 1982, 34, tab. 5) noted infections of the spikelets by the smuts *Bipolaris crustacea* (Hennings) Alcorn in *S. pyramidalis* s.s., and of *B. ravenelii* (Curt.) Shoemaker in both forms of the present variety.

Note. There are two main forms, usually regarded as two taxa, *S. pyramidalis* from Africa and *S. jacquemontii* from South America, but the difference between the two is slight and mainly based on sizes. In W Africa intergrading forms would occur. Clayton, Jovet & Guédès, and Simon gave the following distinctions:

| | |
|---|--|
| <i>jacquemontii</i> | <i>pyramidalis</i> |
| Culms 50–75 cm tall, (1–)2–2.5(–3) mm diam. at base | 90–170 cm, (2–)3.5–4(–5) mm |
| Leaf blades up to 40 cm long, (1–)2.5–3.5 mm wide | up to 70 cm, (3–)6–7(–10) mm |
| Panicle up to 25 cm long, branches loosely appressed, lowermost 3–5 cm long, middle branches 3–3.5 cm long | 20–45 cm, horizontal at anthesis, 5–10 cm, 3–6 cm |
| Spikelets 1.5–2 mm long | 1.6–2.2 mm |
| Seed obovoid-elliptic, 1–1.1 mm long, slightly truncate | obovoid, 0.8–1 mm, conspicuously truncate |

Inspection of the material available in L showed that these characters do not work. Small African plants of course had narrow culms and blades, and short panicles with short branches. Even large plants with large inflorescences may have no branch longer than 4 cm, and usually less than 3 cm. Very few panicles had erecto-patent branches, none horizontally patent ones. The length of the spikelet is useless. As Jovet & Guédès (1968) remarked (p. 60, t. 4) no discrete differences could be observed in the seeds. The only guide to identification remained provenance, and to rely on this seems more like faith than fact.

By necessity the two taxa therefore have to be united. Clayton (1974) has suggested that Peter would have made the varietal combination under *S. indicus*. This is incorrect, and it is debatable whether Peter even made one at the forma level. The combination is cited as '*Sporobolus indicus pyramidalis*' without author or rank, as is done in other instances, e.g. for var. *capensis*, and for the formae under *Microchloa setacea* (p. 254) and *Cynodon dactylon* (p. 256). In the key (p. 280) reference is made to 'Formen' of *S. indicus*, and from this it can be deduced that formae were intended. At the varietal level the combination still had to be made. The oldest epithet available seems to be have been generated by Jovet & Guédès (1973): var. *pyramidalis*.

6. *Sporobolus novoguineensis* Baaijens, *spec. nov.*

Sporobolus lenticularis auct. non S. T. Blake: Henty, Bot. Bull., Lae 1 (1969) 180.

Annuae rhizomata stolones cataphylla desunt, foliis parum heteromorphis, marginibus saltem basi pectinatis, paniculis linearibus parum contractis lobatis, ramis erecto-patentibus, inferioribus 10–12-verticillatis, longissimis 0,6–2 cm longis, cum vel sine glandulis minutis pusticulatis linearibusve, spiculis 1,8–2,1 mm longis brunnescentibus, glumis inferioribus spiculis 0,5–0,63-plo longioribus, glumis superioribus spiculis aequantibus, seminidibus lateraliter compressis ellipsoideis marginibus 2-angulatis in sectione transversali 1,1–1,2 mm longis. — T y p u s: *Barrie 29* (LAE, holo, L, fragm.), Papua New Guinea, Morobe Prov., Finschhafen, Dedua, 26 March 1954.

Annuals, tufted, branching intra-vaginally at base and from the cauline nodes. Rhizomes, stolons, cataphylls absent. Culms erect, glabrous, smooth, shiny, up to 55 cm high. *Sheaths* smooth, outer margin densely finely hairy, otherwise glabrous, throat with some bulbous based hairs; ligule an obscure ciliate rim, c. 0.15 mm long; blades rather stiff, slightly heteromorphic, the basal ones more or less crowded, more or less patent, flat, linear-lanceolate, up to 7 cm by 1–4 mm, margins at least at base pectinate, the cauline ones more or less erect and appressed, involute above the more or less flattened base, linear, the margins nearly glabrous, apex obtuse, above scaberulous on the nerves, below smooth, glabrous, rounded. *Panicles* linear, loosely contracted, lobed, c. 14 by 1.5 cm, branches in 6–21 whorls, erecto-patent, capillary, with or without inconspicuous pusticular to linear glands, spikeled in the upper 0.5–0.67th part, the lowermost 10–12 together, the longest one 0.6–2 cm long. *Spikelets* 1.8–2.1 mm long, brownish. Lower glume ovate to ovate-oblong, 0.85–1.25 mm long, 0.5–0.63 times as long as the spikelet, apex acute to obtuse, smooth to microscopically scaberulous upwards, nerves 0; upper glume ovate to ovate-oblong, subequal to the spikelet, apex acute to acuminate, smooth to microscopically scaberulous upwards. *Lemma* ovate, otherwise as the upper glume. *Palea* ovate to ovate-oblong, slightly shorter than the lemma, obtuse, easily split by the ovary and/or fruit. *Lodicules* c. 0.25 mm long. *Anthers* 3, 0.35–0.5 mm long. *Seed* ellipsoid, laterally compressed, hardly 2-edged in transverse section, 1.1–1.2 by 0.6–0.65 mm in diam.; pericarp loosely adherent; embryo 0.5–0.6 mm long.

Distribution. Malesia: New Guinea: Aru Islands (P. Trangan); Papua New Guinea (Morobe Prov.: Finschhafen).

Habitat. In savannahs at low altitude in P. Trangan.

Anatomy. See Introduction.

Notes. Very similar in aspect, especially of the inflorescence, to *S. balansae* Henr. from Con Son (Poulo Condor), Vietnam, which differs by the longer ligule, hairy blades, more lobed panicles with more spaced whorls, smaller spikelets, and smaller seeds.

It is completely different from *S. lenticularis* S. T. Blake in the shape of the inflorescence, seeds, and other details.

7. *Sporobolus piliferus* (Trin.) Kunth

Sporobolus piliferus (Trin.) Kunth, Enum. Pl. 1 (1833) 211 (pro var. *a minutus* Kunth, nom. inval.); Hook. f., Fl. Br. India 7 (1896) 251; Hack., Philip. J. Sc. 1, Suppl. (1906) 269; Merr., Philip. J. Sc. 1, Suppl. (1906) 373, excl. *S. ciliatus* Presl; Enum. Philip. Fl. Pl. 1 (1923) 80 (id.); Ridley, Fl. Mal. Pen. 5 (1925) 244; Bor, Grasses (1960) 632; Clayton, Fl. E. Trop. Afr., Gram. 1 (1970) 361; Gilliland, Rev. Fl. Mal. 3 (1971) 105; Mehra & Sharma, Taxon 24 (1975) 501; Conert & Lobin, Garcia de Orta, Bot. 6 (1984) 68, t. 4e–j, t. 6f, g; Christopher & Samraj, Taxon 34 (1985) 160; Davidse et al., S. Afr. J. Bot. 52 (1986) 523. — *Vilfa pilifera* Trin., Diss. Bot. (1824) 157; Sp. Gram. Icon. 1 (1828) t. 58A; Mém. Ac. Sc. St. Pétersb. VI, 5, 2 (1840) 68. — *LECTOTYPE*: Wallich 3774 (LE, holo, BM, K, microfiche IDC 7394, US, fragm.), Nepal.

Sporobolus stachydanthus A. Rich., Tent. Fl. Abyss. 2 (1851) 394. — *Vilfa stachydantha* Steudel, Syn. 1 (1854) 156. — *Triachyrum stachydanthum* Aschers. in Schweinf., Beitr. Fl. Aethiop. (1867) 302, 311 ('*stachyanthum*'), nom. inval. (Art. 34.1a). — *TYPE*: *Quartin-Dillon s.n.* (P, holo, n.v.; B, K), Ethiopia, Prov. Chiré, October.

Triachyrum nilagiricum Hochst. ex Steudel, Syn. 1 (1854) 176. — T y p e: *Hohenacker 931* (P, holo, W, n.v.; B, BM, K, L, US, fragm.), India, Nilgiris, 1851.

Sporobolus praecox Chev., Rev. Bot. Appl. 14 (1934) 113; Bull. Mus. Nat. Hist. Nat., Paris 20 (1948) 468. — T y p e: *Chevalier 34907* (P, holo, n.v., K neg. 6194), Guinea, Labé, 17 November 1930.

Sporobolus ciliatus auct. non Presl: Hack., Philip. J. Sc. 1, Suppl. (1906) 269.

Sporobolus lenticularis auct. non S. T. Blake: Henty, Bot. Bull., Lae 1 (1969) 180.

Annuals, rather densely tufted, branching intra-vaginally at base and from the cauline nodes. Rhizomes, stolons and cataphylls absent. Culms erect to geniculate ascending, glabrous, smooth, up to 28 cm high. *Sheaths* sometimes with a few bulbous-based hairs, outer margin finely hairy, otherwise glabrous, margin of throat hairy; ligule 0.15–0.35 mm long, densely ciliate; blades more or less homomorphic, the basal sometimes flat and at least the upper involute, linear, 1–4.5(–11) cm by 0.8–3 mm, margins pectinate to smooth, apex finely pointed, above sometimes with a few scattered, fine, bulbous-based hairs, below smooth, glabrous, more or less keeled. *Panicles* rather dense, 1–7 cm by 4–10 mm diam., axes and branches usually with inconspicuous punctiform pusticular glands, nodes up to 14, usually much less, branches more or less erecto-patently appressed, rather densely spikeled from above the base, the lowermost solitary, paired, or in a whorl of up to 4(–6), up to 0.8(–1.2) cm long, with up to 4(–6) more or less evenly spaced spikelets in the upper 0.33–0.67 part. *Spikelets* 1.9–2.2 mm long, brown. Lower glume more or less narrowly triangular to ovate-oblong, 0.85–1.7 mm long, 0.55–0.75 times as long as the spikelet, margins often erose, apex obtuse to acuminate, smooth, nerves 0; upper glume ovate, 1.6–2.1 mm long, slightly shorter than the spikelet, acute to acuminate, smooth. *Lemma* elliptic to ovate-oblong, as long as the spikelet, obtuse to acute, 1-nerved, smooth. *Palea* ovate to elliptic, 1.7–2 mm long, truncate, easily split by the ovary/fruit. *Lodicules* c. 0.25 mm long. *Anthers* (2 or) 3, 0.35–0.6 mm long. *Seed* ellipsoid to obovoid, roundly elliptic in transverse section, 1–1.25 by c. 0.75 mm in diam.; pericarp rather tight; embryo 0.5–0.7 mm long.

D i s t r i b u t i o n. Tropical Africa (S Ethiopia to Mozambique, Burundi, Zaire to Chad and Niger, Guinea, Cape Verde Islands), Sri Lanka, India (Kashmir to Uttar Pradesh, Karnataka, Tamil Nadu, Assam), Nepal; Malesia: Malaya (Malacca), Philippines (Luzon: Benguet, Baguio). Records for China (Anon., Icon. Corm. Sin. 5, 1976, 858) refer to *S. japonicus* (Steudel) Rendle and those for tropical America probably to *S. ciliatus* Presl (see note).

H a b i t a t. Dry banks, open grasslands, savannahs, disturbed areas, roadsides, 900–2100 m alt. in Luzon.

A n a t o m y. See Introduction and Conert & Lobin (1984).

C h r o m o s o m e s. $n = 10$ (Christopher & Samraj, 1985), $2n = 36$ (Mehra & Sharma, 1975; Davidse et al., 1986).

N o t e s. Closely related to *S. ciliatus* Presl and *S. japonicus* (Steudel) Rendle and sometimes considered to be conspecific with either of them. See Hackel (Bull. Hb. Boiss. 7, 1899, 648; 1906) who was followed by Merrill (1906, 1923) and Honda (J. Fac. Sc. Imp. Univ., Tokyo, III, 3, 1930, 201). We think, however, with Ohwi (Bot. Mag., Tokyo 55, 1941, 393; Fl. Japan, 1965, 176) that three different species are involved.

Sporobolus ciliatus from America differs especially by the flat basal leaves, its pubescence, the longer ligule, and the lenticular, 2-edged seed. The spikelets are 1.65–1.9 mm long, about as long as those seen from Indian specimens (1.5–1.8 mm long, Bor's dimensions, 1.25–1.5 mm, being clearly erroneous). The Philippine material of *S. piliferus* only has slightly longer spikelets, 1.9–2.2 mm long. Clayton (1970) described the spikelets as 1.8–2.5 mm long. We suspect that Trinius' and Kunth's larger variety of *S. piliferus* from Brazil is *S. ciliatus*, although Doell kept *S. piliferus* and *S. ciliatus* separate in the Flora Brasiliensis. Hitchcock, however, in his account of the Central American grasses (Contr. U.S. Nat. Hb. 24, 9, 1930, 597) does not mention *S. piliferus* at all, only *S. ciliatus*.

Pohl (Fl. Costaric. 15, 1980, 542, t. 203, f. A, B) reported $n = 27$ for *S. ciliatus*. He described the spikelets as 1.7–2 mm long.

Sporobolus japonicus from E Asia differs by the leafy stem, more coarsely hairy blades, spikelets 2.25–3 mm long, chaffs usually distinctly acuminate. Ohwi (1965) gave the spikelets as only 2–2.2 mm long, and Lee (Man. Korean Gr., 1966, 260) has them only 2 mm long, but this seems erroneous, as Chung (Kor. Gr., 1965, 122) saw the same range in size as we did. This species has $2n = 40$ (Chung, 1965).

The Australian *Sporobolus lenticularis* S.T. Blake is quite distinct by the shape of its loosely spikeled inflorescence, the absence of glands, spikelets 1.5–1.8 mm long, lower glume less than 0.5 times as long as the spikelet, smaller anthers (0.25–0.3 mm long), and the larger seeds (c. 1.5 by 0.8–0.9 mm diam.), flattened with more or less acute edges, and usually longer than the spikelet.

8. *Sporobolus sciadocladus* Ohwi

Sporobolus sciadocladus Ohwi, Bull. Tokyo Mus. Sc. 18 (1947) 12. — Type: *Buwalda 5459* (BO, holo, K, L, US), Moluccas, Aru Isles, April 1938.

Annual, loosely tufted, branching intra-vaginally at base and from the cauline nodes. Rhizomes, stolons, cataphylls absent. Culms erect or geniculately ascending, branching at base and from the higher internodes, glabrous, smooth, up to 50 cm high. *Sheaths* smooth, outer margin loosely set with up to 1.5 mm long, minutely bulbous based hairs, otherwise glabrous, throat with or without a few hairs; ligule up to 0.3 mm long, ciliolate; blades nearly all homomorphous, more or less flat, linear, up to 20 cm by 6 mm, only the basal ones with pectinate margins, nearly glabrous, apex acute, above scaberulous on the nerves, below smooth, slightly keeled. *Panicles* contracted, up to 10 by 0.5–1.5 cm in diam., branches in 7–9 whorls, spikeled only in the upper part, flexuous, glabrous, smooth, the lowermost 6–10 in a whorl, more or less appressed, the longest ones 1–2.7 cm long, with some inconspicuous punctate to linear glands. *Spikelets* 2.2–2.5 mm long, brownish. Lower glume ovate-lanceolate, 1.4–1.7 mm long, 0.5–0.67 times as long as the spikelet, apex acuminate or tapering into some fine teeth, smooth, nerves 0; upper glume lanceolate, 2.1–2.4 mm long, about as long as the spikelet, apex acute to acuminate, smooth. *Lemma* as the upper glume, 2–2.3 mm long, 1-nerved. *Palea* elliptic, 2–2.1 mm long, emarginate, easily split by the fruit. *Lodicules* c. 0.25 mm long. *Anthers* 3, 0.4–0.5 mm long. *Seed* laterally flattened, ellipsoid in longitudinal and

transverse section, 1.5–1.8 by 0.8–0.9 mm in diam.; pericarp loosely adherent; embryo c. 0.7 mm long.

Distribution. Malesia: New Guinea: Aru Islands (P. Trangan). Only known from the type.

Habitat. Not indicated.

Notes. Contrary to Ohwi's remark we think that this is an annual species: the branching is all intra-vaginal; there are no cataphylls and no other organs indicating survival mechanisms. Most of the species of sect. *Triachyrum* Veldk. are annual as well.

The species is distinct from the other Malesian ones by the nearly homomorphous flat leaves, but for the very basal ones without pectinate margins, the long panicle, with short whorled branches with distal spikelets, and the large flat seed.

9. *Sporobolus tenuissimus* (Schrank) O. Ktze

Sporobolus tenuissimus (Schrank) O. Ktze, Rev. Gen. Pl. 3, 3 (1898) 369; Hack. in Chodat & Hassler, Bull. Hb. Boiss. II, 4 (1904) 278, pro comb. nov.; Hitchc., Contr. U.S. Nat. Hb. 24, 8 (Grasses Ecuador, Peru, and Bolivia) (1927) 391; Bor, Grasses (1960) 633; Bosser, Bull. ORSTOM 35 (1969) 125, t. 36 e–j; Clayton, Fl. Trop. E. Afr., Gram. 1 (1970) 386; Davidse & Pohl, Can. J. Bot. 50 (1972) 1443; Dujardin, Can. J. Bot. 56 (1978) 2140; Renvoize, Gr. Bahia (1984) 61, fig. 21, t. 10. — *Panicum tenuissimum* Schrank, Denkschr. Bayer. Bot. Ges. Regensb. 2 (1822) 26. — **Type:** *Martius s.n.* (M, holo, n.v.), cultivated in Munich from seeds collected in Brazil.

Agrosticula muralis Raddi, Agrost. Bras. (1823) 33, t. 1, f. 2. — *Sporobolus muralis* Hitchc. & Chase, Contr. U.S. Nat. Hb. 18 (Grasses W. Ind.) (1917) 368. — **Type:** *Raddi s.n.* (FI or PI, holo, n.v.), Brazil, Rio de Janeiro.

Panicum tenuiflorum Schrank in Hornschuch, Syll. Pl. Nov. 1 (1823/24) 197, non R. Br. (1810). — **Type:** *Martius s.n.* (M, n.v.), cultivated in Regensburg from seeds collected in Brazil (merotypic with *S. tenuissimus* and *V. minutiflora*).

Vilfa minutiflora Trin., Diss. Bot. (1824) 158; Nees, Agrost. Bras. (1829) 394; Doell in Mart., Fl. Bras. 2, 3 (1878) 31. — *Sporobolus minutiflorus* Link, Hort. Berol. 1 (1827) 88; Hook. f., Fl. Br. India 7 (1896) 248; Schmid, l'Agro. Trop. 13 (1958) 486, t. 93, f. 2. — **Type:** *Martius s.n.* 'Panicum tenuiflorum Hort. Monac.' (LE, holo, L neg. 36.5; M, iso, n.v.), cultivated in Leningrad from seeds collected in Brazil (merotypic with *S. tenuissimus* and *P. tenuiflorum*).

Sporobolus mangaloricus Hochst. ex Miq., Anal. Bot. Ind. 2 (= Verh. Kon. Ned. Inst. Wet. III, 4) (1851) 36. — *Vilfa mangalorica* Hochst. ex Steudel, Syn. 1 (1854) 159. — **Type:** *Hochstetter 137* [U, holo, BM, K, L, TUB (K neg. 10316)], India, Tamil Nadu, Canara, near Mangalore, 'post tempus pluvium' 1847.

Description based on Java specimens.

Annual, tufted, branching intra-vaginally at base. Rhizomes, stolons, cataphylls absent. Culms erect, glabrous, smooth, up to 50 cm high. *Sheaths* smooth, margin glabrous, throat glabrous; ligule 0.1–0.2 mm long; blades folded, linear, 8–15 cm by 2–3 mm, margins smooth, glabrous, apex filiform, glabrous, slightly keeled. *Panicles* effuse, base long-enclosed in the sheath, up to 23 by 6 cm diam., main axis glabrous, branches solitary or fascicled, loosely spikeled, the lowermost few together, erecto-patent, 3–4 cm long. *Spikelets* 0.9–1.25 mm long, greenish. Lower glume ovate, 0.25–0.3 mm long, 0.2–0.37 times as long as the spikelet, apex truncate, erose, nerves 0; upper glume ovate-oblong, 0.4–0.75 mm long, 0.5–0.62 times as long as the spikelet, apex acutish to obtuse. *Lemma* ovate to oblong, as long as

the spikelet, acute, 1-nerved. Palea oblong, slightly shorter than the lemma, obtuse to truncate, not easily split by the fruit. Lodicules c. 0.25 mm long. Anthers 3, c. 0.25 mm long. *Seed* turbinate, compressed and angular in transverse section, 0.5–0.7 by 0.3–0.5 mm in diam.; pericarp rather closely adherent; embryo c. 0.25 mm long.

Distribution. Tropical South America (Caribbean to Paraguay), Africa (Senegal to Kenya, Tanzania), Madagascar, India (Rajasthan, Maharashtra, Tamil Nadu), introduced elsewhere, e.g. in Vietnam (Schmid, 1958); Malesia: Java (Surakarta City, Malang City).

Habitat. Roadsides, greenhouse, presumably at low altitude (not indicated).

Collector's notes. Spikelets pale yellow (i.e. in fruit. JFV). Short living and profusely seeding (Bossler, 1969).

Chromosomes. $2n = 12$ (Davidse & Pohl, 1972; Tateoka ex Bossler, 1969; Dujardin, 1978).

Uses. Bossler (1969) said that cattle seem to disdain it.

Notes. This species was cultivated in München by Sprengel from seeds collected by Martius. From there it was distributed under the names *Panicum tenuiflorum* and *P. tenuissimum*. Within a short time the species was described under 3 different names. Schrank's description is rather vague, so for the application of the epithet we have to go by the opinion of contemporary authors, e.g. Trinius who annotated his specimen "*Vilfa minutiflora* m. *Panicum tenuiflorum* Hort. Monac. s.h.n. ex sem. a Sprengelio missis culta in Hort. Pavlowskiano" (L photo 36.5); see also Renvoize (1984). Contrary to the latter's remark Trinius referred to *Panicum tenuiflorum* 'Ht. Monac.' and not to Schrank. He said he had seen cultivated specimens himself ('V. spp. cc.').

These later synonyms are not homotypic with the accepted combination as long as progeny and parents are not homotypic. Specimens in such a relationship are so-called merotypes which have no standing under the Code (1988). As such the later combinations have been independently published and are not superfluous.

It is curious to note that there is apparently no reference to this species in Sprengel's own *Systema Vegetabilium* 1 (late 1824).

10. *Sporobolus virginicus* (L.) Kunth

Sporobolus virginicus (L.) Kunth, Rév. Gram. 1 (June/July 1829) 67; Brongn. in Duperrey, Voy. Monde 2 (July 1829) 17, pro comb. nov.; Kunth, Enum. Pl. 1 (1833) 210; Benth., Fl. Austr. 7 (1878) 621; Hook. f., Fl. Br. India 7 (1896) 249; Koord., Exk. Fl. Java 1 (1911) 145, p.p.; Backer, Trop. Nat. 9 (1920) 176, t. 3; Camus, Fl. Gén. I.-C. 7 (1923) 510; Merr., Enum. Philip. Fl. Pl. 1 (1923) 81 (excl. syn. *S. humilis* Presl); Backer, Handb. Fl. Java 2 (1928) 204; Onkr. Suiker. (1928) 107, t. 101; S.T. Blake, Univ. Ql. Pap. 1, 18 (1941) 11; Backer in Heyne, Nut. Pl. Indon. (1950) 260; Jansen, Acta Bot. Neerl. 1 (1952) 479; Schmid, l'Agron. Trop. 13 (1958) 488, t. 93, f. 4; Bor, Grasses (1960) 634; Clayton, Kew Bull. 19 (1965) 295; Monod de Froideville in Backer & Bakh. f., Fl. Java 3 (1968) 538; Henty, Bot. Bull., Lae 1 (1969) 181; Bossler, Bull. ORSTOM 35 (1969) 123, t. 37 a–e; Gould & Soderstrom, Can. J. Bot. 48 (1970) 1635; B.C. Stone, Micronesica 6 (1970) 192; Gilliland, Rev. Fl. Mal. 3 (1971) 108, pl. 14d; Davidse & Pohl, Can. J. Bot. 50 (1972) 1443; Clayton, Fl. E. Trop. Afr., Gram. 1 (1974) 370; Madulid, Acta Manil. A, 14 (1975) 90, t. 10; Anon., Icon. Corm. Sin. 5 (1976) 147, t. 7123; Paijmans, New Guinea Vegetation (1976) 35; Ellis, Agroplantae 9 (1977) 91, t. 34; Davidse & Pohl, Ann. Missouri Bot. Gard. 65 (1978) 640; Dujardin, Can. J. Bot. 56 (1978) 2140; Hsu, Fl. Taiwan 5

- (1978) 504, t. 1412; Smith-White, Austr. J. Bot. 27 (1979) 429; Conert & Lobin, Garcia de Orta, Bot. 6 (1984) 60, t. 6a, b, t. 7a; Gallagher & Decker, Am. J. Bot. 72 (1985) 852; Smith-White, Austr. J. Bot. 36 (1988) 23; Smith-White & Adam, W. Austr. Nat. 17 (1988) 118, 1 fig. — *Agrostis virginica* L., Sp. Pl. 1 (1753) 63. — *Vilfa virginica* Beauv., Agrost. (1812) 16, 149, 182; Trin., Sp. Gram. Icon. 1 (1823) t. 48. — *Crypsis virginica* Nutt., Gen. N. Am. Pl. 1 (1818) 49, pro comb. — *Podosemum virginicum* Link, Hort. Berol. 1 (1827) 85. — *Sporobolus virginicus* var. *virginicus*: Smith-White, Austr. J. Bot. 27 (1979) 429; Simon, ASBS Newsl. 31 (1982) 17. — T y p e: Clayton 507 in Hb. Linné 84.30 (LINN, holo, microfiche IDC, BM; US, fragm.), U. S. A., Virginia.
- Agrostis juncea* Lamk., Encycl. 1 (1783) 60; Tabl. Encycl. 1 (1791) 161, t. 41, *Agrostis* f. 2; Bor, Grasses (1960) 634, in syn. — *Agrostis tremula* Willd., Sp. Pl. ed. 4, 1, 1 (1797) 372, nom. superfl. — *Zoysia* sp.: Beauv., Agrost. (1812) 147, combination not made. — *Vilfa tremula* Trin., Diss. Bot. (1824) 155; Mém. Ac. Sc. St. Pétersb. VI, 5, 2 (1840) 98. — *Sporobolus tremulus* Kunth, Rév. Gram. 1 (1829) 67; Enum. Pl. 1 (1833) 210; Bor, Grasses (1960) 633, nom. superfl. — T y p e: Sonnerat s.n. (P, holo, n.v.; US, fragm.), India.
- Agrostis littoralis* Lamk., Tabl. Encycl. 1 (1791) 161. — *Agrostis barbata* Pers., Syn. Pl. 1 (1805) 75, nom. superfl. — *Vilfa littoralis* Beauv., Agrost. (1812) 16, 147 (?), 181. — *Vilfa barbata* Beauv., Agrost. (1812) 16, 147, 181. — *Sporobolus littoralis* Kunth, Rév. Gram. 1 (1829) 68; Enum. Pl. 1 (1833) 213. — *Sporobolus virginicus* var. *littoralis* Hitchc., N. Am. Fl. 17, 7 (1937) 486; Borhidi & Muniz, Bot. Közlem. 58 (1971) 175, pro comb. nov. — L e c t o t y p e: L. C. M. Richard (P, holo, iso in Hb. Lamk., n.v., IDC microfiche 6207, fol. 701, 2nd row from top, 6th from left; US, fragm.), Antilles, Virgin Islands (St. Croix, St. John, St. Thomas: "bayis Trium insularum Danarum"), May (1787?) (here appointed).
- Agrostis littoralis* Lamk. var.: Lamk., Tabl. Encycl. 1 (1791) 161. — *Agrostis barbata* var. *senegalensis* Pers., Syn. Pl. 1 (1805) 76. — *Sporobolus littoralis* var. *elongatus* Dur. & Schinz, Consp. Fl. Afr. 5 (1894) 821, nom. superfl. — T y p e: Roussillon s.n. (P, holo, Hb. Lamk., n.v., IDC microfiche 6207, fol. 701, 2nd row from top, 5th from left), Senegal.
- Vilfa intermedia* Trin., Diss. Bot. (1824) 156; Mém. Ac. Sc. St. Pétersb. VI, 5, 2 (1840) 67. — *Vilfa matrella* Nees, Agrost. Bras. (1829) 400, nom. superfl. — *Sporobolus matrella* Nees, Fl. Afr. Austr. (1841) 152, nom. superfl. — T y p e: Sieber II-38 [LE, holo, K neg. 5638, L neg. 36.4), K, L], Mauritius ('Ind. Occ.' of Trin., 1824, erroneous).
- Aira sabulorum* Labill., Sert. Austr. Caled. (1824) 16, t. 21. — T y p e: Labillardière s.n. (FI, holo, n.v.), New Caledonia, Balade.
- Agrostis congener* Schumach., Beskr. Guin. Pl. (1827) 66. — T y p e: Thonning s.n. (C, holo, n.v., K neg 4212, microfiche 2203), Ghana.
- Calotheca sabulosa* Steudel, Flora 12 (1829) 488. — T y p e: Ecklon 944 (P, holo, n.v.), South Africa, Cape.
- Aira sabulorum* Labill. var. *uniflora* Balansa, Bull. Soc. Bot., France 19 (1872) 318. — T y p e: Hb. Labillardière s.n. sub '*Agrostis virginicus*' (FI, holo, n.v.), New Caledonia.
- Sporobolus virginicus* (L.) Kunth var. *pallidus* Benth., Fl. Austr. 7 (1878) 621, p.p. ('*pallida*'); Ewart & Davies, Fl. N. Terr. (1917) 42; S.T. Blake, Univ. Ql. Papers 1 (1941) 11. — L e c t o t y p e: Bailey s.n. (K, holo), Australia, Queensland, Brisbane River (here appointed).
- Sporobolus virginicus* (L.) Kunth var. *minor* F.M. Bailey, Bot. Bull. Dept. Agric., Brisbane 13 (1896) 15; Simon, ASBS Newsl. 31 (1982) 17. — T y p e: F.M. Bailey s.n. (K, iso, 'rec. Aug. 1896'), Australia, Queensland (Simon's neotype is inadmissible, see below).
- Sporobolus benthami* F.M. Bailey var. *robustus* Dom., Bibl. Bot. 85 (1915) 348. — L e c t o t y p e: Schultz 212 (K, holo), Australia, Northern Territory, Port Darwin (here appointed).
- Sporobolus sundaicus* Ohwi, Bull. Tokyo Sc. Mus. 18 (1947) 13; Jansen, Acta Bot. Neerl. 1 (1952) 479. — T y p e: Van Slooten 2044 (BO, holo; K), Java, Surabaya, near Grisee, 29 Sept. 1928.
- Sporobolus virginicus* (L.) Kunth var. *minor* F.M. Bailey ex Simon, Austrobaileya 2 (1984) 22, non Bailey (1896). — T y p e: E.F. Constable s.n. (BRI, holo, sub no. 55195, NSW), Australia, New South Wales, Cape Solander, Botany Bay, March 1961.

Description based on Malaysian material only.

Perennial, sometimes densely tufted; branching intra- and extra-vaginally at base; stolons long, horizontal, widely creeping and branching virgately, glabrous, smooth, shiny, often yellowish, internodes alternatingly 2 very short ones (up to 2 mm long) and 1 long one (up to 3 cm long); cataphylls therefore sometimes subternate, glabrous, smooth, often shiny, yellow or grey. Culms erect or ascending, up to 50 cm high, glabrous, smooth. Internodes alternatingly long and short, leaves often distinctly distichous, sometimes subopposite. *Sheaths* smooth, glabrous, furrowed, outer margin glabrous, or scaberulous, occasionally with sometimes bulbous-based hairs, throat with a few bulbous-based hairs up to 2.5 mm long; ligule up to 0.25 mm long with some scattered bulbous-based hairs between the cilia; blades usually more or less erect, involute, filiform to acicular, up to 16 cm by 3 mm diam., rarely patent and flat at least at base, up to 5 mm wide, then usually involute upwards, stiff and pungent; glaucous, margins smooth, above scaberulous on the nerves, sometimes with a few scattered hairs in the lower part, below smooth, glabrous, rounded, usually without a distinct midrib. *Panicles* more or less contracted to spiciform, sometimes lobed at base, 3.5–15 cm by 3–13 mm diam., branches moderately densely spikeled from base, about straight, eglandular, the lowermost 1–3 together, up to 4 cm long. *Spikelets* (2–)2.2–2.7(–3) mm long, yellowish, brownish, or greyish. Glumes ovate-oblong, smooth or scaberulous upwards, apex acute to obtuse; the lower one 1.5–2.3(–2.75) mm long, (0.67–)0.75–0.9(–0.95) times as long as the spikelet, nerves 0 or 1; upper glume 2.3–3 mm long, 0.8–1 times as long as the spikelet. *Lemma* broadly ovate, 2.1–2.9 mm long, acute, 1-nerved, rarely scaberulous upwards. *Palea* elliptic to oblong, 1.9–2.3 mm long, truncate, not easily split by the fruit. *Lodicules* c. 0.3 mm long. *Anthers* 2 or 3, 1–1.65 mm long. *Seed* usually absent, broadly ellipsoid, also in transverse section, c. 0.9 by 0.5 mm in diam.; pericarp closely adherent; embryo c. 0.5 mm long.

Distribution. Pan(sub)tropical, Malesia: Malaya: Langkawi, Singapore; Java: mainly N coast: Jakarta, Bogor (S coast: Cikepu), Semarang, Surabaya, Malang, Besuki, Madura, Kangean I., Karimunjawa Arch.; Borneo: Sarawak; Philippines: Luzon (Bulacan, Ilicos Norte, Cagayan, Ilicos Sur, La Union, Rizal); Lesser Sunda Islands: Bali, Sumba, Timor; New Guinea (Irian Jaya: Merauke; Papua New Guinea: E Sepik, Central); Christmas Island (Indian Ocean); no doubt elsewhere on sandy beaches and coastal dunes.

Habitat. Sandy sea beaches above the high water mark, coral outcrops, salt marshes, in river deltas near the coast, along fish ponds, etc. Pioneering on saline, open, sandy, sometimes slightly clayey soil. Locally vegetation forming, growing together with *Lepturus*, *Paspalum vaginatum*, *Spinifex*, *Thuarea*, *Zoysia*, etc. Able to withstand submersion by the sea.

Paijmans (1976) reported for New Guinea the presence of “a sward ... (occupying) the transitional zone between *Avicennia* scrub and dryland grassland or eucalypt savanna inland ... The habitat is probably seasonally flooded by fresh water but is only rarely reached by the tidal salt water.”

Chromosomes. $2n = 18$ (Bossert, 1969), 20 (Davidse & Pohl, 1972; Davidse & Pohl, 1978; Dujardin, 1978; Smith-White, 1979), 30 (Smith-White, 1979), c. 30 (Gould & Soderstrom, 1970), 31 (Smith-White, 1988), 40, 50, 60 (Smith-White, 1988).

Vernacular names. Beach dropseed, jatopa, saltgrass (E.)

Uses. Effective in reclamation for its sand binding properties on beaches and sand dunes in Guam (Stone, 1970), Luzon (Madulid, 1975), and Australia (Smith-White, 1979). Highly esteemed as a fodder grass (S.T. Blake, 1941). In Jamaica used for fattening horses and in Australia considered as a nutritive grass, although not first class (Backer, 1950).

Anatomy. Ellis (1977) has shown that the leaf anatomy is of the NAD-type and eragrostoid, but without a prominent osmophilic layer in the cell walls. The related species *S. pungens* (Schreb.) Kunth has NAD-ME (Echevarría et al., Lagas-calia 15, Extra, 1988, 527).

Collector's notes. In the advanced eastern monsoon conspicuous because of the ashen to pale leaves and panicles. Matforming. Rhizomes deeply buried. Leaves glaucous, sometimes soft. Rarely flowering. [Van Steenis 7601 (BO): Bali, Gilimanuk: Always sterile, with curious galls.] Inflorescence greenish to straw-coloured.

Notes. When Lamarck (Encycl. 1, 1783, 60) described *Agrostis juncea* he remarked "An *Agrostis matrella*? An *Agrostis virginica* Linn. & Forssk. Ægypt. p. 20, n. 69?" In the Tableau (vol. 1, 1791, 161, t. 41, *Agrostis* f. 2) he included *Agrostis matrella* L. as a synonym without any indication of doubt, but this later 'correction' does not make the original combination *A. juncea* superfluous and homotypic with *A. matrella*. The type is *Sonnerat s.n.* as cited by Lamarck in 1783 and on Bor's (Grasses, 1960, 634) authority we have included it here in the synonymy of *S. virginicus*.

Agrostis tremula Willd. (1797) and all the combinations based on it are superfluous, as *Agrostis juncea* Lamk. (1783) was cited in the synonymy (see note under *S. humilis*).

This is a rather polymorphic species. In many accounts from various parts of its pantropical range mention is made of several forms, usually a fine- and a coarse-leaved one with often different ecologies (e.g. Gallagher & Decker, 1985; Hitchcock, 1937, but see 1951; Schmid, 1958; Simon, 1980; Smith-White, 1979). Thus in Malesia Ohwi (1947) distinguished between *S. virginicus* and *S. sundaicus* in which he was followed by Jansen (1952). The first would have relatively wide leaves, spikelets 2.5–3 mm long, anthers 1.5–2 mm long, the latter narrow, c. 1 mm diam. leaves, spikelets 2–2.3 mm long, anthers 1–1.4 mm long (Ohwi msc.). As far as these dimensions are concerned we have found no significant differences between the two, but at first there seemed to be 2 main vegetative types: the '*sundaicus*' form with the leaves fine, erect, involute and usually glabrous above, and a coarser form with the leaves somewhat broader, coarser, patent, less involute and often with some hairs at least at base, more like the 'typical' *S. virginicus*, yet somewhat different in appearance from American representatives. The description given above is therefore based on Malesian material, only.

In Vietnam Schmid (1958) also mentioned the presence of a fine- as well as a coarse-leaved form, the latter with spikelets 3–4 mm long, a size we have never observed.

In Australia generally two such forms have been distinguished as well: the 'typical' form and a var. *minor* Bailey.

Smith-White (1988), looking only at the coastal populations, has reported that at least there the situation is extremely complicated. He distinguishes four morphotypes with six different chromosome numbers ranging from diploid to hexaploid ($x = 10$). There is no correlation between form and ploidy level as each form has at least two cytological races, but there is one between ploidy and latitude, and sometimes in ecology.

The diploid races are limited to the southern parts of Australia while tetraploids occur further North. In the transition zone he found the triploids, while the hexaploids occur even further North. The few pentaploids seem of local origin and their distribution is insufficiently known. At least the tetra- and hexaploids may therefore be expected in Malesia as well.

Flowering specimens are rare in Malesia (Backer, 1928), and seeds have turned out to be extremely scarce in the herbarium, too. The same situation seems to be present elsewhere. Reproduction therefore must be mainly vegetative causing morphologically constant populations which may persist or even obtain a wider distribution by the action of the sea. A most remarkable case of such a local form is that of *Aira sabulonum* Labill. from New Caledonia (see below).

We think we may have seen at least two of Smith-White's morphotypes (1 and 4) among Malesian material, but whether they are actually the same is another matter. The '*sundaicus*' form, although initially reminiscent of his form 3, seems different from it. In this perplexing situation it seems wisest to refrain from naming any of them formally. The more so as precise ecological data are lacking in Malesia, where the species is badly collected anyway, probably due to human nature: people on tropical sandy beaches prefer a tan above a collection. Thus JFV found it to be locally quite common in Wewak, but this was the third record for the whole of New Guinea, where there should be plenty of suitable sites.

A brief survey of the forms present in Malesia with their representatives must suffice at present.

Type 1: Blades erecto-patent to patent, short (up to 7 cm long), narrow (up to 2 mm wide at ligule) (cf. Smith-White's '*var. minor* s.s.'): 4n in NW Australia, 6n in NE Queensland):

Java, Kangean (*Backer 29875*); Luzon, Manila (*Loher 1785*; *Merrill, Philip. Pl. 574*), Malaban (*Loher 1787*), Ilocos Sur (*Clemens 17767*), Bulacan (*Loher 1784*).

Type 2: Blades wider (more than 2 mm wide at ligule) (but not recorded for N Australia by Smith-White and hence most likely different; 2n or 5n):

Java, no locality (*Horsfield s.n.*), Jakarta (*De Wit 4045*), Bogor (S Coast) (*Franck 77*), Semarang (*Kooper 750*), Pasuruan (*Backer 24386*, *Van Slooten 2433*), Madura (*Backer 19986*), Kangean (*Backer 28370*, *29253*); Sumba (*Monod 1310*, *1311*), Timor (*Monod 1014*, *Van Steenis 18346*); New Guinea, E Sepik (*Veldkamp 6908*), Central Prov. (*Carr 11412*).

Type 3: Blades \pm erect and \pm appressed to the culm or with connivent apices above the shoots, long (up to 20 cm), narrow (up to 2 mm wide at ligule) ('*var. pallida* Benth. p.p.', '*var. minor* sensu Bailey' fide original specimen in K; 4n in the

Northern Territory and North Queensland; 6n in Darwin). This seems different from the '*sundaicus*' form which generally is strongly tufted with fine, more or less erect culm leaves:

Java, Jakarta (*Backer 26408, 35106, 37253, Van der Meer & Den Hoed 2112*), Semarang (*Karta 353*), Surabaya (*Backer 37211, 37573, Dorgelo 3272, Van Slooten 2044*, type, *Zippelius s.n.*), Pasuruan (*Backer 24351, Bijhouwer 185, Van Steenis 2636*), Probolinggo (*Backer A9*), Besuki (*Backer 24501*), Madura (*Backer 19465, 20306*), Luzon, Bulacan (*Clemens 17289*) Rizal (*Loher 12030*), New Guinea, Merauke (*McKee 1700*), Central Prov., 50 km NW of Port Moresby (*Paijmans 103, 1857*).

Type 4: Blades erecto-patent to patent, long (up to 25 cm long), wider (up to 7 mm wide at ligule) [*? 'Sporobolus benthami* var. *robustus*', 'var. *virginicus*' sensu Smith-White (1979); 4n, widely spread from N Australia to New South Wales]: Bali (*Van Steenis 7601*, said to be always sterile and with curious galls).

These are all coastal plants, the only inland collections mentioned in the literature are a specimen reported for a jati forest near Kedungjati by Koorders (1911) and some mentioned by Merrill (1923: 81) for the Philippines. These represent *S. humilis* Presl subsp. *humilis* (q.v.).

A curious aberrant form is *Aira sabulorum* Labill. which according to Ph. Morat (P, in litt.) occurred or may still occur in Balade, New Caledonia. It was collected there by Labillardière and many years later by Vieillard (1484, p.p., P). Morat has searched recently for this form in Balade but could not find it, which does not mean that it would not be there still. The plants are slightly more robust than the normal New Caledonian representatives of *S. virginicus*, and have within the same inflorescence spikelets with a single floret (not very frequent), with two florets (the great majority), with two florets with an extended rachilla, and even with three florets. In the latter the upper floret often is exerted from the spikelet on a rachilla of variable length, up to 5 mm long.

Balansa (1972) correctly realized that this *Aira sabulorum* and the normal forms of *S. virginicus* which he, Vieillard (1484, p.p., K, L, P; Vieillard 1485, P), and Labillardière had collected belonged to the same species. It is incomprehensible, however, that he, who cited *Agrostis virginicus* sensu Labillardière, did not include these taxa in *Sporobolus*, but retained them in *Aira*. The combination *A. sabulorum* var. *uniflora* is valid, as it is based on Labillardière's description of *Agrostis virginicus*. Whether this is identical with Linné's species or not is a taxonomic, not a nomenclatural point.

Another curious form was reported by Smith-White and Adam (1988) from W Australia, where the spikelets are proliferous. The plantlets appear to be potentially useful in the reproduction, survival, and spread of this clone.

Sporobolus confertus J.A. Schmidt from the Cape Verde Islands has been cited as a synonym. As is shown by the isotype in B it is distinct and not even remotely related. It differs by being an annual with glandular inflorescence branches, the lower ones whorled, etc. whereby it is clearly a member of sect. *Triachyrum*. See also Lobin (Courier Forsch.-Inst. Senckenberg 53, 1982, 37, t. 11e) and Conert & Lobin (Garcia de Orta, Sér. Bot. 6, 1985, 62, t. 3f).

SPECIES DUBIAE ET EXCLUDENDAE

1. *Sporobolus australasicus* Domin

Sporobolus australasicus Domin in Fedde, Repert. 9 (1911) 553; Bibl. Bot. 85, 1 (1915) 350, t. 77; S.T. Blake, Pap. Dept. Biol., Queensland Univ. 18 (1941) 9; Lazarides, Gr. C. Austr. (1970) 232, t. 68b; Simon, Austr. Syst. Bot. Soc. Newsl. 31 (1982) 17. — **L e c t o t y p e**: *Domin s.n.* (PR, holo, n.v.; K), Australia, Queensland, Hyghenden, Rolling Downs, March 1910.

Sporobolus pulchellus auct. Austr., non R.Br.: e.g. Benth., Fl. Austr. 7 (1878) 623, p.p.; Maiden, Agric. Gaz. New S. Wales Misc. Publ. 1197 (1908) fig.

Domin mentioned this Australian endemic for Southeast Asia. It is distinct among SE Asian and Australian *Sporoboli* by the glandular, mostly whorled, \pm evenly spikeled inflorescence branches, dark, in fruit subglobose, 1.1–1.25 mm long spikelets, and the globose, c. 0.6 mm diam. seed. *Sporobolus coromandelianus* (Retz.) Kunth is similar, but differs by having the spikelets less evenly distributed, and on the upper half of the branches, 1.25–1.8 mm long, lower glume 0.25–0.4 times as long as the spikelet, possibly larger anthers (0.25–0.8 mm long), and the obovoid seed, quadrangular in transverse section, 0.75–0.95 by c. 0.5 mm in diameter.

2. *Sporobolus gigas* (Steudel) Miq.

Sporobolus gigas (Steudel) Miq., Fl. Ind. Bat. 3 (1857) 376; Koord., Exk. Fl. Java 1 (1911) 146, sp. excl. — *Vilfa gigas* Steudel, Syn. 1 (March 1854) 160. — *Myriachaeta glauca* Mor. ex Steudel, Syn. 1 (Nov. 1854) 404 ('Zollinger 1769'), nom. superfl. — *Myriachaeta arundinacea* Zoll. & Mor. in Mor., Syst. Verz. (1846) 101 ('Zollinger 1169'), nom. superfl. — **T y p e**: *Zollinger 1769* ('1359') (P, holo), Java, Ciapus, 15–19 November 1843.

= *Thysanolaena latifolia* (Roxb. ex Hornem.) Honda

Apparently there has been a mix-up in the citation of the type. The only specimen JFV could find in P was *Zollinger 1769*. The species to which it belongs is generally known as *Thysanolaena maxima* (Roxb.) O. Ktze, based on *Agrostis maxima* Roxb. (1820). However, *Melica latifolia* Roxb. was validated earlier by Hornemann [Hort. Vindob., Suppl. (1819) 117], and the epithet provided by it has priority. Honda [J. Fac. Sc. Imp. Univ. Tokyo III, Bot. (1930) 312] did not refer to Hornemann, but under Art. 33.2, Ex. 5 this may be regarded as a bibliographic error to be corrected, and the correct combination is as above. — J.F. Veldkamp & M. Winia.

3. *Sporobolus indicus* (L.) R. Br. var. *elongatus* (R. Br.) F.M. Bailey

Sporobolus indicus (L.) R. Br. var. *elongatus* (R. Br.) F.M. Bailey, Syn. Queensl. Fl. (1883) 651. — *Sporobolus elongatus* R. Br., Prod. 1 (1810) 170. — *Agrostis elongata* Roth ex R. & S., Syst. Veg. 2 (1817) 368, pro specim. Nov. Holl., excl. var. *flaccida*; Roth, Nov. Pl. (1821) 41 (id.); non Lamk. (1791). — *Vilfa elongata* auct. non Beauv.: Trin., Diss. Bot. (1824) 154, 305 (id.). — **L e c t o t y p e**: *R. Brown 6207* (BM, holo, K, US, fragm.), Australia, New South Wales, Port Jackson, 8 January 1803.

Sporobolus indicus auct. non R. Br.: Benth., Fl. Austr. 7 (1878) 622, p.p.

As can be seen from the synonymy and notes under *Sporobolus indicus* var. *major* (Buse) Baaijens this variety has been confused with that taxon.

4. *Sporobolus indicus* (L.) R. Br. var. *laxus* (Nees) Stapf

Sporobolus indicus (L.) R. Br. var. *laxus* (Nees) Stapf, Fl. Cap. (1900) 586; Jovet & Guéd., Bull. Centre Ét. Rech. Sc., Biarritz 7 (1968) 53, 65. [— *Vilfa capensis* var β , Linnaea 7 (1832) 293.] — *Sporobolus capensis* (Willd.) Kunth var. *laxus* Nees, Fl. Afr. Austr. 1 (1841) 155 ('*laxa*'). — *Sporobolus indicus* forma *laxus* Peter in Fedde, Repert., Beih. 40 (1931) 280 ('Formen'), 291. — L e c t o t y p e: *Ecklon s.n.* (B, holo, n.v.; K), South Africa, Cape Div., Devils Mt, December (here appointed).

Jovet & Guédès (p. 53) regarded this taxon as part of the *S. indicus* complex with a pantropical distribution: e.g. Malesia (Java, Borneo, Timor), Tahiti, and Australia. The specimens from Malesia cited by them and seen by us belonged to var. *flaccidus* (R. & S.) Veldk. and var. *major* (Buse) Baaijens (q.v.). Var. *laxus* is not the same as *Sporobolus laxus* Simon [Austrobaileya 1 (1982) 459, fig. 34/1–6] from Queensland, Australia, which is another variety of the complex and therefore had to be re-named *Sporobolus indicus* (L.) R. Br. var. *queenslandicus* Veldk., *nom. nov.*

5. *Sporobolus poiretii* (R. & S.) Hitchc.

Sporobolus poiretii Hitchc., Bartonica 14 (1932) 32. — *Agrostis compressa* Poir., Encycl. Méth. Suppl. 1 (1810) 258, no. 78, non Willd. (1790), nec Poir. l.c., p. 259, no. 82. — *Axonopus poiretii* R. & S., Syst. Veg. 2 (1817) 318. — T y p e: *Bosc s.n.* (P, holo, n.v.; P, iso), U.S.A., Carolina.

= *Sporobolus junceus* (Beauv.) Kunth

This combination traditionally has been associated with and even used for *S. indicus* s.s., but the type turned out to be something quite different. For an explanation of this synonymy see Veldkamp [Taxon 39 (1990) 327].

6. *Sporobolus pulchellus* R. Br.

Sporobolus pulchellus R. Br., Prodr. 1 (1810) 170. — *Agrostis pulchella* Roth ex R. & S., Syst. Veg. 2 (1817) 367, as to the basion. — *Vilfa pulchella* Trin., Mém. Ac. Sc. St. Pétersb. VI, 5, 2 (1840) 59, non Presl (1830). — L e c t o t y p e: *R. Brown 6206* (BM, holo, '*Lysispora pulchella b. minor*'), Australia, 'N Coast', 1803 (here appointed).

This is an Australian species which has occasionally been mixed up with *S. harmandii* Henr. (q.v.).

The use of *S. pulchellus* by Hasskarl (Cat. Hort. Bog., 1844, 17) copied by Miquel (Fl. Ind. Bat. 3, 1857, 377) refers to *Hymenachne aurita* (Nees) Backer [Backer, Handb. Fl. Java, 2 (1928) 168].

7. *Sporobolus scoparius* Presl

Sporobolus scoparius Presl, Rel. Haenck. 1 (1830) 243; Miq., Fl. Ind. Bat. 3 (1857) 376 ('*scoparia*'); F.-Vill., Nov. App. (1883) 321; Merr., Philip. J. Sc. 1, Suppl. (1906) 374, sp. dub.; Enum. Philip. Fl. Pl. 1 (1923) 81; Philip. J. Sc. 35 (1928) 3. — *Vilfa scoparia* Presl ex Steud., Nomencl., ed. 2, 2 (1841) 626, 768; Syn. 1 (1854) 156. — T y p e: *Haenke s.n.* (PR, holo, n.v.; US, fragm.), Philippines, Luzon, Sorzogon.

= *Thysanolaena latifolia* (Roxb. ex Hornem.) Honda.

8. *Sporobolus verticillatus* Nees

Sporobolus verticillatus Nees in Hook., J. Bot. Kew Misc. 2 (1850) 101; Miq., Fl. Ind. Bat. 3 (1857) 375. — *Vilfa verticillata* Steudel, Syn. 1 (1854) 158, as to the basionym, non Beauv. (1812). — *Eragrostis aurea* Steud., Syn. 1 (1854) 267. — T y p e: *Cuming 545* in Hb. Lindley (CGE, holo, BM, BO, K, L; P, n.v.), Philippines, Laguna.

= *Eragrostis japonica* (Thunb.) Trin.

According to Steudel the isotype collection in P was a mixture of a *Sporobolus* and his new species *Eragrostis aurea*, but the holotype in CGE is the *Eragrostis*, and so *E. aurea* is a superfluous combination. Ohwi (in msc) identified the duplicate in BO, which we did not see, as *E. diarrhena* (Schult.) Steudel. As the differences between that species and *E. japonica* are not clear to us, we have here preferred the latter, older combination, with which Clayton also identified the CGE specimen, and Henrard and Jansen the ones in L. [see also Vidal, Phan. Cum. Philip. (1885) 8, sub *E. tenuissima* Schrad., and Jedwabnik in Mez, Bot. Arch. 5 (1924) 180].

We have not seen the part of *Cuming 545* in P that would represent a *Sporobolus*, so we do not know to what species that belongs.

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 lampranthus Pilger: int
 laxus Simon: 5, 5d, exc 4
 lenticularis S. T. Blake: 1, 2, 7
 lenticularis auct. non S. T. Blake: 3, 6
 lindleyi auct. non Benth.: 2
 littoralis (Lamk.) Kunth: 10
 var. elongatus Dur. & Schinz: 10
 ludwigii Hochst.: int
 macranthelus Chiov.: int
 maderaspatanus Bor: 5, 5d
 mangalaricus Hochst. ex Miq.: 9
 marginatus A. Rich.: int
 matrella (Nees) Nees: 10
 microprotus Stapf: 2
 minutiflorus (Trin.) Link: 9
 mitchellii (Trin.) C.E. Hubb. ex S. T. Blake:
 int, 4a

(Sporobolus)

- muralis* (Raddi) Hitchc. & Chase: 9
nervosus Hochst.: int
nitens Stent: int
novoguineensis Baaijens: int, 6
olivaceus Napper: 5
orientalis (Nees) Kunth: 5
orientalis auct. non Kunth: 5, 5d
panicoides A. Rich.: int
parvulus Stent: 2
pectinatus Hack.: int
pellucidus Hochst.: 5
piliferus (Trin.) Kunth: int, 7
 var. *minutus* Kunth: 7
poiretii (R. & S.) Hitchc.: int,
 exc 5
poiretii auct. non Hitchc.: 5
praecox Chev.: 7
pulchellus R. Br.: int, 1, 2, 3, exc 6
pulvinatus auct. non Swallen: 3
pungens (Schreb.) Kunth: int
pyramidalis Beauv.: int, 5, 5f
 var. *jacquemontii* (Kunth) Jovet & Guéd.:
 5f
 var. *pyramidalis*: 5f
pyramidatus (Lamk.) Hitchc.: 2
quadratus Clayton: int, 5
ramosissimus Kunth: int
rangei Pilger: int
rigens (Trin.) Desv.: int, gen
sciadocladus Ohwi: int, 8
scoparius Presl: exc 7
serotinus (Torr.) A. Gray: int
smutsii Stent: int
spicatus (Vahl) Kunth: int
stachydanthus A. Rich.: 7
stapfianus Gandoger: int
stocksii Bor: int
subtilis Kunth: int
sumatranus Ohwi: 3
sundaicus Ohwi: 10
tenacissimus [Jacq.] Kunth: 5
tenacissimus auct. non Kunth: 5
tenuissimus (Schränk) O. Ktze: int,
 gen, 9
tetragonus Bor: int, 1, 3
tremulus (Willd.) Kunth: 10
tremulus auct. non Kunth: 4a, 4b, 5
trimenii Seneratna: 5d
vaginiflorus (Torr.) Wood: gen
verticillatus Nees: exc 8

(Sporobolus)

- virginicus* (L.) Kunth: int, 4b, 10
 var. *littoralis* Hitchc.: 10
 var. *minor* F.M. Bailey: 10
 var. *pallidus* Benth.: 10
 var. *virginicus*: 10
virginicus auct., non Kunth: 4a
wrightii Scribn.: gen
Thysanolaena latifolia (Roxb. ex Hornem.)
 Honda: exc 2, exc 7
 maxima (Roxb.) O. Ktze: exc 2
Triachyrum Hochst. ex A. Braun: int, gen
adoense Hochst. ex A. Braun: gen
nilagiricum Hochst. ex Steudel: 7
stachydanthum (A. Rich.) Aschers.: 7
Vilfa Adans.: int
 africana (Poir.) Beauv.: 5a
 angusta Buckl.: 5
 barbata (Pers.) Beauv.: 10
 berteroana Trin.: 5
 capensis (Willd.) Beauv.: 5a
 commutata Trin.: 2
 coromandeliana (Retz.) Beauv.: 2
 diandra (Retz.) Trin.: 5d
 dianthera (Schult. & Schult. f.) Steudel: 5a
 elongata (Lamk.) Beauv.: 5, exc 3
 erosa Trin.: 5d
 exilis Trin.: 5, 5d
 geniculata Nees ex Steudel: 4b
 gigas Steudel: exc 2
 humilis (Presl) Steudel: 4a
 indica (L.) Trin. ex Steudel: 5
 intermedia Trin.: 10
 jacquemontii (Kunth) Trin.: 5f
 littoralis (Lamk.) Beauv.: 10
 mangalorica (Miq.) Hochst. ex Steudel: 9
 matrella Nees: 10
 minutiflora Trin.: 9
 pilifera Trin.: 7
 pulchella (R. Br.) Trin.: exc 6
 retzii Steudel: 5d
 roxburghiana Nees ex Wight: 2
 scoparia (Presl) Presl ex Steudel: exc 7
 stachydantha (A. Rich.) Steudel: 7
 tenacissima Kunth: 5
 var. *exilis* (Trin.) Fourn.: 5
 tremula (Willd.) Trin.: 10
 tremula auct. non Trin.: 4b
 verticillata (Nees) Steudel: exc 8
 virginica (L.) Beauv.: 10
Zoysia matrella (L.) Merr.: gen