A REVISION OF ORYZA (GRAMINEAE) IN MALESIA AND AUSTRALIA

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SUMMARY

In Malesia and Australia there are nine species of Oryza L. (Gramineae). Oryza meyeriana (Zoll. & Mor.) Baillon has two varieties. Oryza schlechteri Pilg. is only known from Irian Jaya (Indonesian New Guinea). Oryza australiensis Dom. and O. meridionalis Ng are endemic to Australia. The numerous forms of O. sativa L. have not been treated. Oryza rufipogon Griff., supposedly the wild progenitor of O. sativa, is considered as a distinct species. The name for the subfamily Oryzoideae is validated.

INTRODUCTION

Oryza L. (Gramineae) is taxonomically a difficult genus because of the polymorphic cultivated O. sativa L., which occurs in numerous forms, partly due to selection, partly possibly also of introgressive hybridization. Oryza is generally considered to belong to the tribe Oryzaeae, which usually has been included in the Pooideae (or Festucoideae, nom. inval.). Recently it has been regarded as an aquatic offshoot of the Bambusoideae (Campbell, 1985, citing Ghorai & Sharma, 1980, who never even mentioned Oryza; Dahlgren et al., 1985). The tribe has also been considered to represent a subfamily of its own, Oryzoideae, because of characters shared with the Bambusoideae on one side (leaf anatomy, see also Renvoize, 1985; stamens 6; small chromosomes with as the basic number x = usually 12, exceptionally 15 or 17), and with the Pooideae (embryo type) on the other. It was first Spanish only, whereby the name is invalid. I have searched in vain for a validating description or reference and none was known to Dr. F. Butzin (B, in litt.). A formal Latin description is therefore given here.

Recently Watson et al. (1985) in a numerical taxonomic analysis of the genera of the Gramineae have distinguished a supertribe, Oryzanae, for Oryza, its allies, and the so-called herbaceous bamboos of the Bambusoideae.
ORYZOIDEAE Duistermaat


Culms and leaves ± aerenchymatous. Leafblades linear, without transverse veins, not articulating at base, silica bodies transversally dumb-bell-shaped, midrib of the vascular system complex, chlorenchyma consisting of arm-cells. Ligule membranous. Spikelets unis- or bisexual, disarticulating above the glumes at maturity, 1- or 3-flowered, then the lower two flowers reduced to scale-like, 1—7-nerved lemmas. Glumes suppressed, at most represented by obscure lips at the apex of the pedicel. Fertile lemma 3—9-nerved, muticus or with an apical awn. Palea similar to the lemma, 3-nerved. Lodicules 2, entire to 2-lobed. Anthers (1—3 or) 6 (or up to 14). Styles 2. Caryopsis with a small, festucoec embryo, without a scutellar tail (Zizania excepta), hilum well-developed, linear. First leaf of the seedling without a blade. Chromosomes small, x = 12, rarely 15, 17.

The delimitation of the genus Oryza against the others of the Oryzoideae is sometimes difficult, while the delimitation of its species sometimes has been rather arbitrary.

The only species recognized by Linné (1753) was O. sativa. He described it as having two glumes ('calyx') and a bivalvate corolla. Stapf (1917) was the first to suggest that the bilobed apex of the pedicel would represent two rudimentary glumes. What until then had been called glumes would in fact be empty, or sterile, lemmas. The third, or fertile, lemma and palea then enclose the floret. Roshevits (1937) referred to the glumes and sterile lemmas as the lower, rudimentary and upper glumes, respectively. Anatomical (Terrell et al., 1983) and comparative (Backer, 1946) studies have suggested that the rudimentary glumes are merely the modified ends of the pedicels. Michaud (1944) studied some anomalous structures in spikelets of greenhouse plants of O. sativa. These supported Stapf's idea that the spikelet consists of two rudimentary glumes, two sterile, epialeate lemmas, and one fertile, paleate lemma. This explanation was also accepted by Jacques-Félix (1962), Tateoka (1963), and most other authors.

A different and also plausible theory on the homology of the spikelet is the one proposed by Peterson (1935), Pilger (1939, 1956), and Parodi (1939), demonstrated for O. barthii by Schweickerdt & Marais (1956) and followed by De Winter (1951) and Campbell (1985). They argue that the spikelet is actually biflorous, with a perfect lower floret and a male or sterile upper one (depending on how one wants to ex-
plain the 6 stamens). Both have lost their paleas, the number of lodicules has also been reduced, and what others regard as the palea, curiously enough with 3 nerves, not 2, as is usual in grasses, is in fact the lemma of the upper floret. De Winter mentioned the no doubt much related Bambusoideae. Some of these may have more-nerved and dorsally keeled paleas as well. Their anthoecia are arranged in 1—several-flowered (pseudo-)spikelets with paleas which obviously are not derived from reduced florets. I do not think that the number of nerves in a structure in the position where one would expect a palea to be, can be used as a strong argument pro or contra its derivation. The usual number of nerves of a palea is two, with a depression in between, but in several instances also outside the Bambusoid-Oryzoid alliance a different number has been encountered without such complicated hypothetical derivations.

For simplicity's sake I will here call the structure in the position of the palea, the palea.

**INTERGENERIC DELIMITATION**

Dumortier (1823), when he proposed the tribe Oryzeae, included only Asprella Schreb., a synonym of Leersia Sw., which generic name for reasons of nomenclature therefore must be the type of the tribal name and not Oryza, although this name is obviously indirectly referred to. Had that genus occurred in Belgium, Dumortier would certainly have included it under this tribe. The name Oryzeae had previously been used by Adanson (1763), but the latter used it for a 'section', which is contrary to Art. 33.4, and the name was then invalidly published.

A number of genera have later been added, many mistakenly so, e.g. Pharus L. and Leptaspis R.Br. (incl. Scrotochloa Judziewicz) as was done by Kunth (1833), Steudel (1853), Baillon (1894), Prodoehl (1922), which are now considered to belong to the Bambusoideae proper as a separate tribe Phareae (Soderstrom, 1981) because of their seedling type, leaf anatomy, 3 lodicules, 6 stamens, 3 stigmas, small embryo and long hilum.

Kunth (1833), Steudel (1853) and Roshevits (1937) also included Ehrharta Thunb., Microlaena R.Br. and Tetrarrhena R.Br. As Willemsen (1982) has shown, these are not generically distinct and are best placed in a distinct tribe, Ehrharteae, which differs from the Oryzoideae especially by the anatomy of the leaf blades, which points to affinity with the Arundinoideae. They were doubtfully included in the Oryzanae by Watson et al. (1985).

Bentham & Hooker f. (1883), Baillon (1894), Stapf (1917) and Roshevits (1937) included Beckera Fresen. (now a synonym of Snowdenia C.E. Hubb.), which Endlicher (1841) and Richard (1851) had placed in the Phalarideae, Hackel (1887) and Bews (1929) in the Melinideae (= Tristegineae), and Pilger (1954) in the Arthropogoneae, the latter two members of the Panicoideae. Hubbard (1967) has placed Snowdenia in the Paniceae next to Beckeropsis Fig. & De Not., to which he thought it to be very much related because of the similarity in habit and structure of the spikelet.
The spikelets of *Snowdenia* consist of two glumes, one awned sterile lemma, a fertile lemma, and a bidentate, not nerved palea. It seems best placed in the Panicoideae. Metcalfe (1960) reported a typical panicoid leaf anatomy.

Hackel (1887) also included *Achlaena* Griseb. and *Reynaudia* Kunth (1833) in the Oryzoideae. I agree with Hitchcock & Chase (1917) and Hitchcock (1936), respectively, that they are better placed in the Melinideae. *Achlaena* has an awnlike, awned sterile lemma, a small, scarious fertile lemma, two lodicules and three anthers. The spikelets of *Reynaudia* consist of two awned sterile lemmas, a bifid, subapically awned fertile lemma with two very deeply incised lodicules, and two anthers.

The genera mentioned above have been excluded from the alliance. Some others that do belong to the alliance will be discussed now.

*Potamophila* R. Br. (1810) has been divided by some (Hubbard, 1967; Clayton, 1970) into three genera: *Potamophila* s.s. (*P. parviflora* R. Br., Australia, an aquatic, tussocky grass with uni- or bisexual spikelets), *Prosphytochloa* Schweickerdt (*P. prehensilis* (Benth.) Schweickerdt, South Africa, a heterophyllous forest rambler with bisexual spikelets), and *Maltebrunia* Kunth (5 species, tropical and South Africa, Madagascar, a forest grass with bisexual spikelets; Clayton, 1970). Although I have not closely studied these genera, I have the impression that they should not be distinguished, as there is no fundamental difference in the structure of the spikelets (see also Clayton, 1970). However, see also the scheme given by Second (1985, fig. 1).

Terrell & Robinson (1974) have confirmed the suggestion of Pohl & Davidse (1971) that *Hydrochloa* Beauv. (1812) cannot be differentiated satisfactorily from *Luziola* Juss., as it appears to differ mainly from the latter by the reduced inflorescence. They have distinguished in the Oryzeae the subtribes *Zizaniinae* (for *Zizania* L.), *Luziolinae* (*Luziola* s.l., *Zizaniopsis* Doell & Aschers.), and the *Oryzinae* (at least *Leersia*, *Oryza*, *Porteresia* Tateoka). This distinction was partly based on the presence of unisexual florets in the non- *Oryzinae*, but they were apparently not aware of the fact that in the spikelets of the Australian species *Potamophila parviflora* R. Br. the florets may be both uni- and bisexual.

Griffith (1851) placed *Oryza coarctata* Roxb. in a new genus, *Sclerophyllum* Griff. This name, however, was a later homonym of a genus of the Compositae, and Tateoka (1965) therefore proposed the name *Porteresia* for it. Cope (1982) has retained the species in *Oryza*, but I think that the species is well-distinct at the generic level by the anatomy and morphology of the leaf and embryo.

The monotypic genus *Rhynchoryza* Baill. (1894), sometimes included in *Oryza*, has rightly been distinguished by Baillon because of the coriaceous leaves and the subulate spikelets.

The genus *Padia* was described by Zollinger & Moritzi (1846) with as the only species *P. meyeriana*. I agree with Baillon (1894) and later authors that it should be regarded as a species of *Oryza*, albeit in a series of its own (see below).

In order to ascertain the specific limits in *Oryza* I of course looked at the African representatives as well. Because the sterile lemmas are completely absent, I fully agree with Launert (1965) that the following species should be placed in *Leersia: O.*
**H. Duistermaat: Oryza in Malesia and Australia**

*Oryza* C.E. Hubb. (= *L. nematostachya* Launert, non *L. angustifolia* Munro ex Prodoehl), *O. perrieri* A.Camus (= *L. perrieri* (A.Camus) Launert), and *O. tisserantii* Chev. (= *L. tisserantii* (Chev.) Launert). Launert also added some anatomical features of the leaf and number of vascular bundles in the awn (when present), whereby *Leersia* and *Oryza* are distinct. Pyrah (1969), in his study of the non-African representatives of *Leersia*, was not entirely convinced of this, as the scantily known *L. stipitata* Bor from Thailand resembles the type found in *Oryza* (i.e.: 239). According to Terrell et al. (1983) the epidermal anatomy of the lemma and palea of *Oryza* and *Leersia* is different, but in *L. nematostachya* the anatomy is different from these two again. The absence or presence of an awn is irrelevant in the distinction of these genera.

In the next paragraph an artificial key is given to those genera here retained in the Oryzoideae.

**KEY TO THE GENERA OF THE ORYZOIDEAE**

<table>
<thead>
<tr>
<th>1 a. Spikelets bisexual</th>
<th>2</th>
</tr>
</thead>
<tbody>
<tr>
<td>b. Spikelets unisexual</td>
<td>9</td>
</tr>
<tr>
<td>2 a. Sterile lemmas absent or very rudimentary</td>
<td>3</td>
</tr>
<tr>
<td>b. Sterile lemmas more or less well-developed, 2</td>
<td>5</td>
</tr>
<tr>
<td>3 a. Leaves narrow, linear</td>
<td>4</td>
</tr>
<tr>
<td>b. Leaves short, broadly lanceolate</td>
<td>Hygroryza Nees</td>
</tr>
<tr>
<td>4 a. Spikelets dorso-ventrally compressed at anthesis</td>
<td>Chikusiochloa Koidz.</td>
</tr>
<tr>
<td>b. Spikelets laterally compressed at anthesis</td>
<td>Leersia Sw.</td>
</tr>
<tr>
<td>5 a. Sterile lemmas acuminate, entire, sometimes small, setiform</td>
<td>6</td>
</tr>
<tr>
<td>b. Sterile lemmas short, very broad, dentate, involucrate at the base of the antheroecium</td>
<td>Rhynchoryza Baill.</td>
</tr>
<tr>
<td>6 a. Fertile lemma and palea herbaceous to crustaceous</td>
<td>7</td>
</tr>
<tr>
<td>b. Fertile lemma and palea membranous (incl. Maltebrunnia Kunth, Prosphytocha cloa Schweickerdt)</td>
<td>Potamophila R. Br. (p.p.)</td>
</tr>
<tr>
<td>7 a. Leaves herbaceous, margins often scabrous</td>
<td>Oryza L.</td>
</tr>
<tr>
<td>b. Leaves coriaceous, margins prickly tuberculate</td>
<td>Porteresia Tateoka</td>
</tr>
<tr>
<td>8 a. Sterile lemmas absent</td>
<td>9</td>
</tr>
<tr>
<td>b. Sterile lemmas 2, very small or setiform</td>
<td>Potamophila R. Br. (p.p.)</td>
</tr>
<tr>
<td>9 a. Pistillate spikelets ovate to elliptic. Embryo many times smaller than the caryopsis</td>
<td>10</td>
</tr>
<tr>
<td>b. All spikelets linear. Embryo as long as the caryopsis</td>
<td>Zizania L.</td>
</tr>
<tr>
<td>10 a. Staminate and pistillate spikelets usually in different panicles, or, when in a single one, the staminate spikelets terminal on the end of the branches (incl. Hydrochloa Beauv.)</td>
<td>Luziola Juss.</td>
</tr>
<tr>
<td>b. Staminate and pistillate spikelets in a single panicle, the staminate ones basal, the pistillate ones apical on each branch</td>
<td>Zizaniopsis Doell &amp; Aschers.</td>
</tr>
</tbody>
</table>
INTRAGENERIC DELIMITATION

Although this revision was intended to be limited to the Malesian area, the Australian Oryza australiensis Dom. and O. meridionalis Ng have been included, as it cannot be ruled out that they may turn up in New Guinea, the Moluccas, or the Lesser Sunda Islands, of which the flora is still so imperfectly known.

Much attention has been paid to the life form, length of the ligule, features of the spikelet (deciduous or not, shape, length), the relative length and the shape of the sterile lemmas, surface structure of the fertile lemma and its palea, and the presence of an awn and its length.

In the everwet tropics which are favoured by the species of Oryza it is difficult to distinguish between annual and perennial plants because of the absence of the distinct seasons of the more temperate zones. Thus it has often been stated that O. sativa is annual, but whether this is really so is open to question. The plants are usually removed after the harvest of the first cut, to make place for the next crop. But when left standing, as in the so-called ratoon method, some races turn out to be definitely long-living, if not perennial. The latter is obviously the case with those cultivated at present in the Leiden Botanical Garden. These plants are cut down to their roots in autumn to sprout again next spring. For a farmer it will be more advantageous to have the plant store as much energy as possibly in its fruits and not elsewhere, as perennials will do, especially when he has no intention to maintain it after the harvest. Thus in selection annual races will be favoured, formerly unconsciously, now on purpose. And therefore, as was also remarked by Second (1985: 24, 27), the life cycle of O. sativa s.l. over the ages has become intermediate between a true annual and a perennial. The latter seems to be the plesiomorphic condition, however.

Oryza sativa has persistent spikelets, whereas the wild species have spikelets that are rapidly deciduous. No doubt it is of a great advantage that the spikelets do not immediately fall during the often rough process of harvesting, and persistence will have been selected for, consciously or unconsciously, at an early stage of the agricultural history of rice, in the same way as it was done for other cereals. In the herbarium, however, this is a rather useless character, for even in cultivated rice the spikelets will fall when the plants are dried.

The presence or absence of an awn on the fertile lemma is fairly constant within a given species of Oryza. Oryza sativa, however, in its multitudinous forms has the whole range between absent to no less than 6 cm long awns.

Chang (1979) has listed all species with their chromosome number and genome group as far as these have been recorded. From his enumeration the Malesian and Australian taxa are given here in table 1. Genome A shows partial homology with genomes B and C, i.e., some chromosomes of set A appear to be identical to those of B and/or C, as is shown by the pairing at meiosis and the occurrence of fertile hybrids. The D genome is poorly understood. Before man disturbed the original situation, the distribution of the genome groups could have been as follows: B in Africa, C in South Asia, D in China, and E in Australia (Second, 1985). Group A would then be a later combination of B and C due to intercrossing when the two met.
Table 1. Chromosome number and genome group of Malesian and Australian taxa (after Chang, 1979).

<table>
<thead>
<tr>
<th>Species</th>
<th>2n</th>
<th>genome group</th>
<th>comment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oryza australiensis</td>
<td>24</td>
<td>EE</td>
<td></td>
</tr>
<tr>
<td>Oryza granulata</td>
<td>24</td>
<td>?</td>
<td>(= O. meyeriana var. granulata)</td>
</tr>
<tr>
<td>Oryza meyeriana</td>
<td>24</td>
<td>?</td>
<td>(= O. meyeriana s.s.)</td>
</tr>
<tr>
<td>Oryza minuta</td>
<td>48</td>
<td>BBCC*</td>
<td></td>
</tr>
<tr>
<td>Oryza officinalis</td>
<td>24</td>
<td>CC</td>
<td>(= O. minuta)*</td>
</tr>
<tr>
<td>Oryza ridleyi</td>
<td>48</td>
<td>?</td>
<td></td>
</tr>
<tr>
<td>Oryza rufipogon</td>
<td>24</td>
<td>AA</td>
<td></td>
</tr>
<tr>
<td>Oryza sativa</td>
<td>24</td>
<td>AA</td>
<td></td>
</tr>
<tr>
<td>Oryza schlechteri</td>
<td>24</td>
<td>?</td>
<td></td>
</tr>
</tbody>
</table>

*Two different genomes also occur in Oryza eichingeri Peter: 2n = 24, 48, also with genome groups CC and BBCC, respectively. Oryza punctata Steud. from Africa has a diploid, annual race with the BB genome and a tetraploid, perennial one also with BBCC. According to Second (1985: 100) some introgression in O. officinalis with the DD-genome (not present in Malesia and Australia) may have occurred as well.

The first attempt to make an infrageneric classification was made by Baillon (1894). Two of his originally four sections are now regarded as distinct genera (Potamophila with or without Maltebrunia). Roshevits (1932) also had four sections, one of which is now also regarded as generically distinct (Rhynchoryza), while the type of his section Coarctata, O. coarctata, is now that of Porteresia. Sharma & Shastry (1965, emended in 1971) have placed the Malesian species O. ridleyi and O. schlechteri in section Padia. After a comparison of the various schemes their last one is the one I can agree best with on the provision that series Sativa ought to be called series Oryza (autonym) and that their series Australienses should be included in the series Latifolia, as was also suggested by Second (1985).

The latter accepted a modification of Tateoka's (1962a, b) system of 4 groups of species with O. brachyantha Chev. & Roehrich from Africa and O. schlechteri Pilg. from New Guinea as isolated species. He has attempted to analyze the relationships between various wild and cultivated forms of the Oryza s.s. ('Sativa') and Latifolia groups on the basis of electrophoretic patterns of a number of isozymes. From his data he concluded that there is a strong structure on a geographical basis in the Old World species of Oryza s.s. The Australian, Asian and African taxa are clearly discriminated. The American forms of O. rufipogon did not present any frequent allele that could not be considered as original, which is not so surprising if it is assumed that these forms were introduced.
The series *Australienses* and *Latifolia* differ only by the scabrous branches and pedicels in the first and smooth ones in the latter, which seems an insufficient criterion. The following division can then be made for Malesia and Australia:

Section *Padia* (Zoll. & Mor.) Baill., emend. Sharma & Shastry  
Series *Meyeriana* Sharma & Shastry: *O. meyeriana*  
*Ridleyana* Sharma & Shastry: *O. longiligumis, O. ridleyi*  
*Schlechteriana* Sharma & Shastry: *O. schlechteri*

Section *Oryza*  
Series *Latifolia* Sharma & Shastry: *O. australiensis, O. minuta*  
*Oryza*: *O. meridionalis, O. rufipogon, O. sativa.*

For descriptions and synonymy see Sharma & Shastry (1965).

**PHYLOGENETIC SPECULATIONS**

Sharma & Shastry (1971) have thoroughly studied the hypothetical phylogeny of the genus. They have given some criteria to decide the polarity of certain character sets. Karyological data seemed to be of prime importance to them. A low ploidy level, long chromosomes, a uniform distribution of heterochromatin, a central position of the centromere are regarded as plesiomorphic ('primitive') states by them. They have made the remarkable statement that dominant character states, as they appear in interspecific hybridization, indicate the *plesiomorphic status of the dominant character state!*

To back up their claim they cited Babcock (1947) and Dobzhanski (1951). It is unfortunate that Sharmy & Shastry have not cited the relevant pages, as I have been unable to find such a statement. Some kind of confusion must be present and it would seem that a misinterpretation of another rule is present, viz. that the *most common* character state (in the higher taxon, e.g. the genus) will *in general* be the plesiomorphic character state. Even this hypothesis is untenable, as has been shown by Estabrook (1977) and De Jong (1980). As far as Sharma & Shastry's 'rule' is concerned, it is not difficult to find reversed situations, i.e., where the dominant factor must be the apomorphic one.

In population genetics it is a well-known fact that recessive character states can dominate populations within not too many generations whenever selection pressure favours these recessive states. This can be understood theoretically by means of the Hardy-Weinberg equation (see e.g. Falconer, 1981: 29–30), while practical cases have been described by Ford (1964: 267–270). The latter demonstrated that the apomorphic character state for industrial melanism is in most cases a dominant, but recessive cases are also known.

It is clear that the pairs dominance/recessiveness and apomorphy/plesiomorphy are completely independent qualities of character states and all four combinations are possible. It should be realized better that selection pressure acts on the phenotype and not directly on the genotype (see Van Valen, 1976).
Finally, Sharma & Shastry have assumed that the Gramineae are monophyletic and that therefore the character states in the outgroup of genera related to *Oryza* are an absolute indication of primitiveness of their status within that genus. This is an elementary fallacy. The number of character states a group shares with an outgroup may give an indication on the measure of relationship between the two. One may, however, not assume that the most common value of any single character state indicates that this is the plesiomorphic one. An example of this are the 6 anthers in the Bambusoideae and Oryzaeoidae. Although the normal condition within the family of the Gramineae is 3 anthers, this is by itself not ipso facto to be regarded as the plesiomorphic state in the family. On the contrary, because of the 'basic' number of 6 anthers in the outgroup it is probable that the presence of 6 anthers is the plesiomorphic state and 3 anthers the apomorphic one. A similar discussion might be held for the number of nerves in the palea: is the even number, usually 2, the plesiomorphic one, and the odd number 1, 3 (as in Oryzoideae), to many the apomorphic one, or is it just the other way round?

Morphological characters which Sharma & Shastry have considered to be plesiomorphic are:

1. a perennial habit (all except *O. meridionalis* and possibly *O. sativa*),
2. lanceolate sterile lemmas (*O. australiensis*, *O. meridionalis*, *O. meyeriana*, *O. minuta* Presl, *O. rufipogon*, *O. sativa*, *O. schlechteri* Pilg.),
3. fertile lemmas with a smooth surface (*O. longiglumis* Jansen, *O. ridleyi* Hook. f., *O. schlechteri*),
4. fertile lemmas without an awn (*O. meyeriana*, *O. sativa* p.p., *O. schlechteri*),
5. a large, cylindrical caryopsis (*O. longiglumis*, *O. meridionalis*, *O. meyeriana*, *O. ridleyi*, *O. rufipogon*, *O. sativa*).

According to Clayton (1975) the ancestor of the Oryzoideae lived in Gondwanaland. Differentiation of the subfamily started after this supercontinent broke up and drifted apart (140 m.y. B.P.; see also Second, 1985). *Leersia* and *Oryza* are the only two genera within the subfamily with a pantropical distribution; they resemble each other closely and therefore most likely shared the same ancestor thought to have lived in Africa. According to Second (1985) the ancestor of *Oryza* migrated in the Paleocene from Africa to Eurasia (60 m.y. B.P.), but Chang (1979) thought that it lived much earlier in a humid zone of Gondwanaland before it broke up. Taking into consideration the 'primitive' characters of the Oryzoideae and the present distribution with the different genera generally being present in different continents, Second's theory seems more plausible.

The differentiation of the series *Latifolia*, *Meyeriana*, *Oryza*, and *Ridleyana* (*O. schlechteri* of series *Schlechteriana* was left out of consideration by Second as he had too little material available) presumably started in the Eocene and was accomplished in the Miocene (10–15 m.y. B.P.). Fossil spikelets found in an excavation of Miocene age in Germany were described as *O. exasperata* (A. Braun) Heer. They closely resemble those of *O. meyeriana*, and might actually belong to that species as we know
it now! Second set up his model on the basis of genetic distances in and between the series *Latifolia* and *Oryza*, and on the basis of paleo-geography. Divergence of the three cultivated taxa, *O. glaberrima* Steud., *O. sativa* subsp. *indica* Kato and subsp. *japonica* Kato started 2–3 m.y. B.P., coinciding with the elevation of the Himalaya which then formed a migration barrier.

Domestication started independently in Africa, South and Southeast Asia, and China, respectively. *Oryza glaberrima* was thought by Chang (1979) to have been derived from the annual *O. barthii* Chev., which in its turn may have originated from the perennial *O. longistaminata* Chev. & Roehr. On the other hand, Second (1985) regarded *O. breviligulata* Chev. & Roehr (= *O. barthii*) and *O. longistaminata* genetically so distant that this theory was rejected by him: *Oryza breviligulata* would have been derived from *O. nivara* Sharma & Shastry to which it appears to be much closer genetically.

The place of origin of *O. glaberrima* is not clear. According to Chang (1979) it was first cultivated in tropical West Africa around 3500 y. B.P. in a swampy area of the Upper Niger. Second (1985) suggested that it had a non-centered origin with a relative important role of the zone near the Lake Chad.

*Oryza sativa* is thought to have originated through the annual *O. nivara* from the perennial *O. rufipogon* (Chang, 1979; Second, 1985). *Oryza nivara* has here been included in *O. sativa*. According to Second subsp. *indica* had had its origin in Southeast Asia and subsp. *japonica* in South China. When the two subspecies were first cultivated is not certain (Gorman, 1977; Ho, 1977; Vishnu-Mitre, 1977). The earliest dates for India go back to c. 3500 y. B.P., for South China to c. 5000 y. B.P., but difficulties arise in the dating of the archaeological sites and in the decision whether the rice found in them was actually cultivated or not.

As *Oryza* is thought to be monophyletic, *O. glaberrima* and *O. sativa* must at one time have had a common ancestor. It is not clear what this must have looked like, nor whether it is still in existence.

The African cultivar, *O. glaberrima*, is presently being replaced by *O. sativa* due to the fact that *O. sativa* is more variable. Forms could therefore be made that are photoperiod indifferent and show tolerances to lower temperatures, whereby it has become possible to cultivate the species in more temperate areas.

Although cultivated rice originated directly from wild, annual progenitors, weed races (escaped cultivars, in Asia called ‘field spontaneas’, and the other wild perennial species, especially *O. minuta*, seem to have contributed much to the great development of the many cultivars by introgressive hybridization.

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When this study had been accepted, the thesis of Second (1985) was received. I have tried to insert here and there some of his results, but to include and discuss them all was impossible without redoing a major part of my study. I hope the reader will understand and will study Second's most interesting paper for himself. He will then discover that in general we agree in our results.

REFERENCES

DUMORTIER, B.C. 1823. Observation sur les graminéées de la flore Beligue 8: 125. Tournay.


ORYZA


Type: Oryza sativa Linne.

Padia Zoll. & Mor. in Mor., Syst. Verz. (1846) 103; Steud., Syn. 1 (1853) 3; Miq., Fl. Ind. Bat. 3 (1857) 373. — Type: Padia meyeriana Zoll. & Mor. (= Oryza meyeriana (Zoll. & Mor.) Baill.).

Plants annual or perennial. Culms erect or (geniculately) ascending. Sheaths ± terete, with ± distinct transverse veinlets, persistent, the lower ones gradually decaying. Blades flat, lanceolate to linear. Inflorescence a panicle. Spikelets laterally compressed, usually articulating above the glumes (persistent in the cultigens), 3-flowered, the lower two florets sterile, the upper one bisexual. Glumes 2, reduced to microscopic auricles in an infraspicular cup at the apex of the pedicel. Sterile lemmas 2, subequal, usually shorter than the spikelet, 1-nerved. Rachilla not prolonged. Fertile lemma boat-shaped, 5-nerved; awn apical, sometimes absent. Palea 3-nerved, usually mucronate. Lodicules 2, free, glabrous. Anthers 6, basifix, (linear-)lanceolate. Ovary 1(—7), glabrous; styles 2, shortly connate at base; stigmas at anthesis protruding from the lower part of the spikelet. Caryopsis laterally compressed, 2-ribbed, or cylindrical, freely enveloped by the lemma and palea; hilum linear, as long as the caryopsis; embryo very small.

Distribution. Pan(sub)tropical, c. 18 species. In Malesia 7 species, of which one cultivated.

Ecology. Moist areas, in stagnant or slowly running fresh, rarely brackish water, up to 1500 m altitude.

Chromosome number. Basic number x = 12.

KEY TO THE MALESIAN AND AUSTRALIAN TAXA

1a. Awn usually present, stout, callose at base, when absent the ligule longer than 6 mm ................................. 2
   b. Awn usually present, slender, not callose at base, when absent the ligule up to 5 mm long ............................................. 4

2a. Anthers 0.8—2.2(—2.5) mm long ....................................... 3
   b. Anthers (3.5—)4—6.2 mm long ................................. 1. O. rufipogon

3a. Spikelets obovate-lanceolate. Caryopsis 1.7—2 mm wide. — Awn of the fertile lemma 6.5—12 cm long. Wild in Australia .......................... 2. O. meridionalis
   b. Spikelets oblong to oblong-lanceolate. Caryopsis 2.2—3.8 mm wide. — Awn of the fertile lemma up to 6(—15) cm long. Cultivated ............... 3. O. sativa
4a. Nodes glabrous. Spikelets more than 3 mm long ............................. 5
b. Nodes hairy. Spikelets up to 2.2 mm long .................................... 9. O. schlechteri
5a. Fertile lemma awned ................................................................. 6
b. Fertile lemma muticous ................................................................. 9
6a. Spikelets 6.5—12.7 mm long ......................................................... 7
b. Spikelets 3.7—6.4 mm long ......................................................... 5. O. minuta
7a. Pedicel glabrous to slightly scabrous ........................................... 8
b. Pedicel with glassy hairs .............................................................. 4. O. australiensis
8a. Sterile lemmas 0.8—1.3 times as long as the spikelet. Awn of the fertile lemma
12—25 mm long ............................................................................. 8. O. longiglumis
b. Sterile lemmas 0.3—0.85 times as long as the spikelet. Awn of the fertile lemma
3—12 mm long ............................................................................ 7. O. ridleyi
9a. Spikelets in fruit oblong, 3.2—5.1 times as long as wide. Caryopsis 4.1—7.3 mm
long ............................................................................................. 6a. O. meyeriana var. meyeriana
b. Spikelets in fruit elliptic, 2.1—2.7 times as long as wide. Caryopsis 3.4—4.1 mm
long ............................................................................................. 6b. O. meyeriana var. granulata

1. Oryza rufipogon Griff. — Fig. 1a.


O. sativa L. var. fatua Prain, Beng. Pl. (1903) 1184, n.v.; reprint (1963) 891!. — O. sativa L. subsp. fatua De Wet, Kulturpfl. 29 (1982) 188. — Type: not indicated, very likely new combinations for O. fatua were intended, but that name was not cited. From India (Orissa, Sundrihuns, W. Bengal, N. Bengal).


O. aquatica Rosh., Grasses (1937) 214, nom. inval., descr. russ. — Synotypes: not indicated, from India, Indochina, and Thailand.

Plants perennial, tufted or stoloniferous. *Culms* decumbent and floating, or ascending to erect, branching intra- and extravaginally at base, 70–90(–300) cm long, usually rooting in the basal and submerged higher nodes, glabrous, smooth. Internodes, at least the lower ones, broadly tubular, strongly ribbed (i.s.). Nodes glabrous. Lower sheaths slightly inflated, the upper ones tight. Auricles sometimes present, linear-lanceolate to linear, falcate, 1–7 by 0.3–0.9 mm, glabrous or hairy, hairs up to 1.5 mm long. Ligules triangular to narrowly triangular, 9–38 by 5–8 mm, acute, herbaceous, tearing (at least i.s.), nerved, with transverse veinlets, glabrous, smooth. *Blades* linear, 27–60 by 0.7–2.5 cm, glabrous, smooth to scabrous on both sides, margins scabrous, midrib below protruding, transverse veinlets absent. *Panicle* loosely contracted, 12–30 by 1–7 cm diameter. Peduncle and axis ± terete, ribbed (i.s.), smooth, becoming scabrous upward. Branches ascendingly patent to ± erect, wavy, glabrous, only the axes sometimes with a tuft of white hairs, the lowermost 1–5 together, the longest 2.5–12 cm long, either simple, 5–9-spikeled, or with 1 secondary branch, 2-spikeled, and terminally 6-spikeled. Pedicel ± clavate, adaxially curved inward, 1–3 mm long, glabrous or minutely pubescent. *Spikelets* obliquely inserted on their pedicels, oblong to obovate-oblong, lanceolate, 7.3–11.4 by 1.95–4.4 mm, 2.72–4.4 times as long as wide, acuminate. Glumes c. 0.3 mm long. *Sterile lemma* triangular, lanceolate to linear-lanceolate, 1.25–7.5 by 0.3–0.7 mm, 0.17–0.42(–0.75) times as long as the spikelet, margin serrate upwards, apex acute to acuminate, glabrous or hairy on the midrib or margins, herbaceous. *Fertile lemma* obovate, obovate-lanceolate to lanceolate, 7–11 by 1.4–2.2 mm, margin curled inward, apex acuminate, slightly sulcate and finely reticulate, covered by glassy hairs, bony, sometimes purplish at the apex; awn very variable, up to 110 mm long, antitrosely scaberulous, stout, callose at base. *Palea* as the lemma, linear-lanceolate, 6.9–10.5 by 0.75–1.2 mm, margin narrowly scariosus, not incurved, apex acuminate, not sulcate; awn 0.3–2.3 mm long, erect. Lodicles obovate to obovate-lanceolate, oblong, 0.5–1.6 by 0.2–1.1 mm, apex truncate, scariosus to ± fleshy, nerves distinct. Anthers (3.5–4–6.2 mm long, yellow or brown. Stigmas blackish purple, sometimes brown. *Caryopsis* oblong, lanceolate to obovate-lanceolate, cylindrical, 5.2–6.7 by 1.4–2 mm diameter, red-brown; embryo 0.17–0.23 times as long.

**Distribution.** Sri Lanka (see Senaratna, 1956); India (Maharashtra, Uttar Pradesh, Assam); Bangladesh (see type of *O. rufipogon*); Burma (Mandalay); Thailand (Chiang Mai, Pretchabun, Chainat, Bangkok, Chantaburi, Ratchaburi); Cambodia (Battambang); South Vietnam (Sông Bé, Long An); China (Kwangsi, Kwantung, fide Second, 1985, 43, 44); Taiwan (Taoyuan); Malesia: Sumatra (Palembang), Malaya (Perlis, Kedah, Malacca), Singapore, Java (Jakarta, Priangan), Kangean I., Borneo (W. Kutai), Philippines (Mindanao), New Guinea (Merauke, E. Sepik, Western Highlands); Australia (Northern Territory; Queensland: Cook, North Kennedy); South America (Amazon, Cuba, fide Second, 1985).

**Ecology.** Moist, black soil or dark, clay loam, swampy places, in or between sawahs, in up to 20(–200) cm deep water in pools, lakes, rivers, up to 1000 m altitude. Locally common.

**Collector's notes.** Perennial, tufts up to 20 cm diameter. *Culms* decumbent...
Fig. 1. Spikelets of a. *Oryza rufipogon* Griff. (Endert 1532) and b. *O. meridionalis* Ng (Craven 4501), both × 12.
or half-floating, 1—3 m long, green. Blades not as long and erect as in *O. sativa*, green, becoming brown as the grain ripens. Panicles erect. Spikelets pale. Lemma green, green to yellowish green when ripe, dark red at the apex, awn pink.

**Uses.** Cut and eaten, but not planted (Kangean, Beguin C2).

**Vernacular names.** Padi hantu (Malaya, Alor Siar), p. burung (Sumatra, Pager Dewa), paparean (Priangan), p. apa, p. toda (Kangean), p. pedara (Borneo, Kutai), waiwi (Sepik, Timbunke), owada (Balimo Gogodala).

**Chromosome number.** $2n = 24$ (Chang, 1979).

**Notes.** *Oryza sativa* forma *spontanea* Rosh. (1931) has been included here although the type was not seen. Roshevits himself reduced it to *O. fatua* in 1937, a name he apparently validated then. We may assume that he knew his own taxa best. The use of 'spontanea' is apparently fortuitous, for there is no reference to Backer's earlier use of that epithet.

Second (1985: 27, f. 5, table 6—9) reported the presence of annual forms.

Some four collections from the E. Sepik (Hoogland & Craven 10164, 10165, 10331, Pullen 1641) had extraordinary large spikelets with long sterile lemmas. Otherwise they were identical with the rest of the current species; they seem to represent a local form.

For the differences with the closely related *O. sativa*, see there.

Second (1985) mentioned the species for South America. I have not seen any American collection and doubt its originality there, the more so as apparently all 16 collections seen by him came from rice fields and may have been contaminations of the seed used.

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2. *Oryza meridionalis* Ng — Fig. 1b.

*O. meridionalis* Ng in Ng et al., Bot. J. Linn. Soc. 82 (1981) 328, f. 1; Ng. et al., Biol. J. Linn. Soc. 16 (1981) 303. **Type:** IRRI 101147 (Langfield) (K, holo; BIRM, IRRI, n.v.), Australia, Northern Territory, Port Darwin, 1974.


Plants annual or perennial, sometimes forming small tufts, stolons absent. **Culms** erect to geniculate, branching intravaginally at base, 100—200 cm long, rooting in the lower nodes, glabrous, smooth. Internodes, at least the lower ones, broadly tubular, strongly ribbed (i.s.). Nodes glabrous. Lower sheaths slightly inflated, the upper ones ± tight. Auricles, when present, linear-lanceolate, falcate, 5.5—6 by 0.5—0.9 mm, serrate at base, glabrous. Ligules ovate- to linear-lanceolate, 13—25 by c. 4 mm, acute, herbaceous, tearing (at least i.s.), nerved, with transverse veinlets, glabrous, smooth. **Blades** linear, 18—30 by 0.9—1.2 cm, glabrous, upper surface scabrous, lower surface smooth, margins scabrous, midrib below protruding, transverse veinlets absent. **Panicle** contracted, 11—24 by 2—4 cm diameter. Peduncle and axis ± terete, ribbed (i.s.), glabrous, smooth. Branches ± erect, wavy, scabrous, only the axis sometimes with a tuft of white hairs, the lowermost 1 or 2 together, the longest 2—6.5 cm long, 5—7-spikeled. Pedicel ± clavate, adaxially curved inward, 1—3 mm long, glabrous. **Spikelets** obliquely inserted on their pedicels, obovate-lanceolate, 6.5—8.9 by 2.1—
2.5 mm, 3.1–3.8 times as long as wide, acute. Glumes 0.3–0.4 mm long. Sterile lemma ovate-lanceolate, 1.8–3 by c. 0.5 mm, 0.25–0.35 times as long as the spikelet, margin sometimes serrate upward, apex acuminate, glabrous, nerves with some hairs, herbaceous. Fertile lemma obovate-lanceolate, 6.9–8 by 1.6–1.7 mm, margin curled inward, apex acuminate, slightly sulcate and finely reticulate, covered by glassy hairs, bony, sometimes purplish at the apex; awn 70–120 mm long, antorsely scaberulous, stout, callose at base. Palea as the lemma, linear-lanceolate, 6.7–7.8 by c. 0.95 mm, margin narrowly scarious, not incurved, apex acuminate, not sulcate; awn 0.3–0.35 mm long, (patento-)erect. Lodicules obovate-lanceolate, 0.5–0.7 by 0.2–0.3 mm, apex obtuse, scarious, nerves more or less distinct. Anthers 1.6–2.2 mm long, yellow. Stigmas blackish purple. Caryopsis lanceolate, cylindrical, 6–6.4 by 1.7–2 mm diameter, red brown; embryo 0.15–0.25 times as long.

Distribution. Australia: Northern Territory, Port Darwin, Adelaide R., Munmarlary, Elcho I., Lagoon; Queensland, Cook Dist.: 30 miles S. of Cooktown, influence of Morgan and McIvor R.

Ecology. Dark clay loam, black soil; on moist ground, in seasonal Melaleuca swamp or shallow water up to 20 cm deep. Locally common. Up to 200 m altitude.

Collector's notes. Plants annual or perennial, forming a fringe. Culms decumbent. Panicles erect.

Notes. Ng (1981) described this species as having a 2.1–2.3 mm wide caryopsis. I have only seen fully mature ones of 1.7–2 mm wide. This makes it distinct from O. sativa, from which it also differs by the shape of the panicle and spikelets.

3. Oryza sativa Linné — Fig. 2a.

It will be obvious that the literature on this most important crop is vast. Only some taxonomically relevant references are therefore given here. The numerous forms described from Southeast Asia are likewise not enumerated. This belongs to more specialized accounts, e.g. Alefeld (1866), Körnicke & Werner (1887), Portères (1956), etc.


Plants usually annual, sometimes perennial (see note and introduction) forming small tufts, stolons absent. Culms erect to ascending, branching intra-, rarely extra-vagnally at base, 50–190 cm long, usually rooting in the basal and submerged higher nodes, glabrous, smooth. Internodes, at least the lower ones, broadly tubular, strongly ribbed (i.s.). Nodes glabrous. Lower sheaths slightly inflated, the upper ones tight. Auricles often present, linear-lanceolate, falcate, 1–5 by 0.5–1 mm, with up to 2 mm long hairs. Ligule ovate- linear-lanceolate, (6–)10–36 by 2.5–8 mm, acute, rarely obtuse, herbaceous, tearing (at least i.s.), nerved, with or without transverse veinlets, glabrous, smooth. Blades linear, 24–60 by 0.6–2.2 cm, glabrous, smooth to scabrous on both sides, margins scabrous, rarely smooth, midrib below protruding, transverse veinlets absent. Panicle loosely contracted, 9–30 by 1–8 cm diameter. Peduncle and axis ± terete, strongly ribbed (i.s.), smooth or becoming scabrous upward. Branches ascendingly patent to ± erect, wavy, glabrous, only the axils sometimes with a tuft of white hairs, the lowermost 1–3 together, the longest 2–13 cm long, either simple, 4–6-spikeled, or with 1–3 secondary branches, each 1–5-spikeled, and terminally 4–7-spikeled. Pedicel ± clavate, adaxially curved inward, 1–7 mm long, glabrous or adaxially slightly pubescent. Spikelets obliquely inserted on their pedicels, oblong to oblong-lanceolate, 7–10.9 by (2.25–)2.65–4.6 mm, 1.8–3.6 times as long as wide, acute to acuminate. Glumes c. 0.2 mm long. Sterile lemma ovate-oblong to lanceolate, 1.45–3.95(–10.4) by 0.5–1.7 mm, 0.2–0.4 (–0.95, see note) times as long as the spikelet, margin serrate upward, apex acuminate to cuspidate, glabrous, herbaceous. Fertile lemma oblong to lanceolate, 6–10.2 by 1.6–3.1 mm, margin curled inward, apex acuminate, slightly sulcate and finely reticulate, covered by glassy hairs, bony, sometimes purplish at base or at the apex; awn very variable, ± straight when developed, up to 60(–150) mm long, antrorse scaberulous, thin to stout, callose at base. Palea as the lemma, lanceolate to linear-lanceolate, 5.8–9.5 by 0.9–1.65 mm, margin narrowly scarious, not incurved, apex acute to acuminate, not sulcate; awn 0.2–0.45 mm long, (patento-)erect. Lodicules obovate to obovate-lanceolate, 0.7–1.3 by 0.25–0.6 mm, apex retuse, scarious to ± fleshy, nerves more or less distinct. Anthers 0.8–2(–2.5) mm long, white or yellow. Stigmas white, yellow, red, or blackish purple. Caryopsis ovoid or elliptic to lanceolate, cylindrical, 5.1–7.5 by 2.2–3.8 mm diameter, whitish yellow, brown to fuscos, embryo 0.2–0.3 times as long.

Distribution. Originally from Southeast Asia, now cultivated all over the world in tropical to Mediterranean areas.
Fig. 2. Spikelets of a. *Oryza sativa* Linné (*Koorders 35675*) and b. *O. australiensis* Dom. (*S.T. Blake 17433*), both × 12.
Ecology. Marshes and wet, inundated fields, in fresh and brackish water, or on dry hill slopes, up to 1500 m altitude in Malesia.

Uses and Vernacular names. The staple food in many parts of the world, grown in innumerable forms. See the various Dictionaries and other publications.

Chromosome number. 2n = 24, rarely aneuploid: 22, 26 (Mukherjee et al., 1975).

Anatomy. Metcalfe (1960) on O. sativa L. var. violacea auct. (hardly Blanco, 1837; cult. in K) with additional citations of literature on O. sativa and related species.

Notes. Smith et al. (1982) mentioned as the type of O. sativa the reference to the Pinax of Bauhiniius (1623) 24. It is Hb. Linnaeus 460-1, however.

According to Chevalier (1932) this is not a true biological species, but a polyphyletic group of forms which originated as hybrids between O. rufipogon Griff. and O. minuta Presl. The most important common character is that the spikelets do not drop off at maturity. Because of the tremendous variability it is difficult to see whether this assumption is correct. A few specimens have been seen which are intermediate between 'typical' O. sativa and O. rufipogon, which most certainly may be regarded as a progenitor. These may be explained by hybridization between these two taxa or by back mutations of O. sativa itself.

Some authors have been able to distinguish between a subsp. indica Kato and subsp. japonica Kato (J. Dept. Agric. Kyushu Imp. Univ. 2, 1930, 275). The forms cultivated in Malesia would mainly belong to the first one, but the 'javanica' form to the second (see Second, 1985: 31). The distinction is especially based on biochemical, genetical, geographical (cf. the map given by Second, 1985: f. 24), pathological, physiological, and serological evidence. In the herbarium they are apparently indistinguishable.

Oryza formosana has been included in the synonymy here although the holotype has not been seen. Suzuki & Masamune described it as having anthers of c. 2 mm long and with a white or red caryopsis, characters which plainly refer to the present species.

Oryza nivara has been included here although its holotype was not seen. Two paratypes (Lowrie 9975, DD, W; Put 1979, BM, DD) were seen, however, and these clearly belong to the present species: anthers short (1.5—2 mm long) and a caryopsis wider than 2 mm. There is also nothing in the description that suggests that another species might be involved. It was described as a wild annual, which brings Watt's remark (1891) to mind, who stated 'aquatic, inferior forms of O. sativa which manifest great facility in becoming naturalized, wherever favourable circumstances are offered.'

Most authors (e.g. Bor, 1960; Tateoka, 1963) have distinguished O. sativa and O. rufipogon on the shedding habit of the last species. This is very difficult to see in the herbarium. Roshevits (1937) used the pigmentation of the glumes, awns, and grains, which, however, is not a trustworthy character either, and the development of the aawn, which seems to be so variable in true O. sativa, to be useless. In the herbarium the most clear difference seems to lay in the length of the anthers. Moreover, the caryopsis of O. sativa is wider (more than 2 mm in O. sativa, less in O. rufipogon). As a consequence mature spikelets of O. sativa are also somewhat thicker (2.25—4.6 mm vs. 1.95—2.7 mm).
It is usually stated that this species would be an annual. This is difficult to ascertain in the herbarium, for roots are often not collected, while in the field the paddi fields are plowed under after the harvest. The races cultivated in the Leiden Botanical Garden, however, are perennial and propagated as small clumps from their small rootstocks.

Very curious was an anonymous collection (24 Nov. 1890, L) from continental Asia, where 5–7 well-developed pistils were present in one floret. This may represent what has been called *O. sativa* var. *plena* Prain by some authors, e.g. Bor (1960), but the descriptions are not too clear. Bor said '2–3 grains in a spikelet', but not whether these are derived from one or more florets. Tsvelev (1976) noted that the lower florets would develop and form 1 to 2 additional grains. Whatever it may be, in neither case such mere monstrosities should be distinguished at any rank.

Tsvelev (1976) also mentioned this name, but described it as having a greatly enlarged lemma of one or both the lower reduced flowers which are sometimes developed and form 1 or 2 additional grains. This is obviously something different. I have not seen such spikelets.

Another curiosity was *Pierre 9* (South Vietnam, L), which had well-developed sterile lemmas, 0.85–0.95 times as long as the fertile one, but without florets.

4. *Oryza australiensis* Dom. — Fig. 2b.


Plants perennial, in tufts, stoloniferous. *Culms* ± erect, branching intra- and extra-vaginally at base, 80–220(–240) cm long, rooting in the basal and submerged higher nodes, glabrous, smooth. Internodes, at least the lower ones, broadly tubular, strongly ribbed (i.s.). Nodes glabrous. Lower sheaths slightly inflated, the upper ones tight. Auricles absent. Ligules ovate-triangular to lanceolate, 4–8 by c. 2.5 mm, acute to obtuse, herbaceous, tearing (at least i.s.), nerved, sometimes with transverse veinlets, glabrous, smooth. *Blades* linear, 25–35 by 0.4–1.4 cm, upper surface hairy at base, lower surface glabrous, smooth to scabrous on both sides, margins scabrous, midrib below protruding, transverse veinlets absent. *Panicle* loosely contracted, 18–50 by 2–15 cm diameter. Peduncle and axis ± terete, strongly ribbed (i.s.), smooth below, becoming very scabrous upward, covered by glassy hairs. Branches ascendingly patent to ± erect, wavy, scaberulous pubescent, the axils with a tuft of white hairs, the lowermost (1–)3–7 together, the longest 11–21.5 cm long, with 1–5 secondary branches, each 2–5-spikeled, and terminally 4–7-spikeled. Pedicel ± clavate, adaxially curved inward, 0.5–8.5 mm long, covered by 0.15–0.4 mm long glassy hairs. *Spikelets* ± obliquely inserted on their pedicels, ovate-oblong to lanceolate, 6.5–8.4 by 2.25–3.1 mm, 2.3–3.1 times as long as wide, acuminate. Glumes 0.45–1.2 mm long.
Sterile lemma ovate to ovate-lanceolate, 1-3.2 by 0.4—0.9 mm, 0.15—0.4 times as long as the spikelet, margin entire, apex acute to acuminate, glabrous, herbaceous. Fertile lemma ovate-lanceolate, 6.5—8 by 2—2.25 mm, margin curled inward, apex acuminate, slightly sulcate and finely reticulate, nerves with glassy hairs, bony; awn 5—55 mm long, antrorsely scaberulous, slender, not callose at base. Palea as the lemma, linear-lanceolate, 6.2—7.1 by 0.7—2.2 mm, margin narrowly scarious, not incurved, apex acuminate, not sulcate; awn 0.6—4.4 mm long, (patento-)erect, antrorsely scaberulous. Lodicules obovate to obovate-oblong, 0.5—0.9 by 0.25—0.5 mm, apex truncate, scarious to fleshy, nerves distinct. Anthers 3.15—4.45 mm long, brown. Stigmas white or yellowish white. Caryopsis oblong, laterally compressed, 2-ribbed, 4.7—6.4 by 2—2.5 mm, brown to redbrown; embryo 0.25—0.35 times as long.

Distribution. Australia: W. Australia: Meda; Northern Territory: Sturt's Creek, 25 miles E. of Stuart Highway at Daly Waters, Katherine; Queensland: Cook Dist.: 50 km NW. of Mungana, 5 km W. of Mt Surprise, Toonpan near Townsville, 8 miles from coast on Settlements Creek; North Kennedy Dist.: Antil Plains near Townsville; Burke Dist.: SSE. of Camooweal.

Ecology. Red, loamy soil, clay, on undulating plains, in (seasonally dry) swamps, low Eucalypt-woodland with grassy ground layer, slight depressions with Eucalyptus microtheca and Leptochloa brownii, 100—225 m altitude. Locally (very) common.

Collector's notes. In tufts or erect, coarse tussocks. Rhizomes short. Culms tall, green, 100—240 cm long. Spikelets green, turning black.

Chromosome number. 2n = 24 (Gopalakrishnan & Shastry, 1966; Chang, 1979).

Notes. Second (1985: 29) reported the presence of annual forms.

Oryza australiensis differs from O. rufipogon by the hairy pedicels and the absence of a callus at the base of the awn. By the latter the spikelets are very much similar to those of O. minuta, but this has much smaller spikelets, shorter anthers, and a smaller caryopsis.

5. Oryza minuta Presl — Fig. 3a.


*O. malabarensis* (auct.?) fide Second, Orstrom Etudes & Thèses (1985) 91, 93 (see note).

Plants perennial, tufted, stoloniferous. *Culms* erect, branching intra- and extra-vaginally at base, 50–200 (–230) cm long, rooting in the basal and submerged higher nodes, glabrous, smooth. Internodestubular, ribbed (i.s.). Nodes glabrous. Lower sheaths slightly inflated, the upper ones tight. Auricles often present, obovate-lanceolate, lanceolate to linear-lanceolate, falcate, 0.5–8 by 0.1–2 mm, with up to 2 mm long hairs. Ligules collar-shaped to triangular, 1–8 by 2–5 mm, truncate to obtuse, herbaceous, tearing (at least i.s.), nerved, without transverse veinlets, glabrous, or with c. 1.5 mm long white hairs, smooth. *Blades* linear, 15.5–80 by 0.7–2.3 cm, glabrous, or both sides with up to 2 mm long white hairs, smooth to scabrous, margins smooth to scabrous, midrib below protruding, transverse veinlets absent. *Panicle* loosely contracted, 7.7–42 by 0.5–24 cm diameter. Peduncle and axis ± terete, ribbed (i.s.), smooth, becoming scabrous upward. Branches ascendingly patent to erect, wavy, glabrous, only the axils sometimes with a tuft of white hairs, the lowermost 1–6 together, the longest 3–28 cm long, either simple, 6- or 7-spikeled, or with 1–8 secondary branches, each 2–9-spikeled, and terminally 5–8-spikeled. Pedicel clavate, not or slightly adaxially curved inward, 0.5–2.5 mm long, glabrous. *Spikelets* horizontal or obliquely inserted on their pedicels, elliptic to oblong, 3.7–6.4 by 1.6–2.85 mm, 1.75–2.95 times as long as wide, acute to acuminate. Glumes 0.2–0.3 mm long. *Sterile lemma* oblong, lanceolate to linear-lanceolate, 0.5–3 (–3.4) by 0.1–0.5 (–0.7) mm, 0.1–0.4 (–0.6) times as long as the spikelet, margin entire, apex acuminate, scaberulous pubescent, herbaceous. *Fertile lemma* oblong to lanceolate, 3.7–6.2 by 1.2–2 mm, margin curled inward, apex acuminate, sulcate, finely reticulate, the midnerves densely covered with glassy hairs, otherwise sparsely pubescent, herbaceous to bony, awn 4.5–23 mm long, antrorsely scaberulous, slender, not callose at base. Palea as the lemma, lanceolate, 3.6–5.15 by 0.5–1.85 mm, margin narrowly scarious, not incurved, apex acuminate, not sulcate; awn 0.2–1 mm long, erect. Lodicules broadly obovate, obovate to elliptic, or obovate-oblong, 0.1–1 by 0.2–0.55
mm, apex acute to retuse, scarious, nerves more or less distinct. Anthers 1.45—2.8 mm long, yellow or brown (i.s.). Stigmas blackish purple, sometimes dark brown. Caryopsis elliptic, oblong to obovate-oblong, laterally compressed, 2-ribbed, 2.3—4.4 by 1.3—2.3 mm, orange-brown; embryo 0.15—0.35 times as long.

Distribution. Sikkim; India (Maharashtra, Madhya Pradesh, Andhra Pradesh, Assam); Sri Lanka (see Senaratna, 1956); Burma; Thailand (Sukothai, Phra Nakhon, Kanchanaburi, Ratchaburi); Cambodia; South Vietnam; Malesia: Sumatra (Aceh, W. and E. Coast, Palembang, Lampung), Malaya (Kedah, Perak, Selangor, Johore), Java (all over), Borneo (Sarawak, Sabah, Samarinda), Philippines (Luzon, Mindoro, Leyte, Bohol, Mindanao), Celebes (Makassar), Lesser Sunda Islands (Flores), Moluccas (Halmahera, Buru), New Guinea (Merauke, Western Dist.).

Ecology. Sandy loam soil, marl or limestone, in (swampy) primary rain forest, (disturbed) mixed deciduous forest, marshy grasslands, alluvial flats, savannahs, plantations (bananas, coconuts, sago, teak), sawahs, etc., up to 750 m altitude; locally very common to rare.


Uses. In Java used as fodder, but the people of Njatoh (Sumatra) consider it to be poisonous (Anonymous).

Vernacular names. Padi burung (Johore), si marpadi-padi, si marene-eme (Sumatra, Asahan), eme morbuk (Bila), padi-padi, padi monyet (E. of Lubuk Pakam), paparean (Java, Priangan), padi pipit (Borneo, Sai Paring), palaypalay (Philippines, Subano), padi hutan (Flores), mawo darat (Manggerai), padi ayer (Halmahera, Kau).

Chromosome number. 2n = 24, 48 (Hu, 1967; Rao, 1975; Chang, 1979).

Notes. Oryza latifolia Desv. has been confused with this species, but as Tateoka (1962) and Second (1985) have shown, O. latifolia is a totally different, New World species.

The fact (see table 1) that two chromosome races, a diploid ('O. officinalis' with the CC genome, perhaps with some influence of the BB or the mysterious, as it is so far unknown in its diploid state, DD genome: China?, see Second, I.c.: 100) and an allopolyploid one ('O. minuta s.s.' with the BB + CC genome), appear to be present in this taxon, apparently is not correlated with clear morphological characters. Oryza punctata Steud. from Africa has a diploid, annual race with the BB genome and a tetraploid, perennial also with BBCC.

Tateoka (1962) has suggested that O. minuta would differ from O. officinalis by the habit and size of the plant, the size of the panicle, the width of the spikelet, etc., but I have been unable to observe this in any way and am therefore forced to consider them as a single species here without being able to suggest a possible, sensible way to recognize infraspecific taxa on a phenetic base.

Second (1985: 24, 93, 95, f. 18) appeared to have been able to distinguish O. officinalis by its isozymatic pattern. It would seem that a priori he distinguished the taxon mainly by its chromosome number. Two distinct groups then appeared to be
Fig. 3. Spikelets of a. *Oryza minuta* Presl (*Lörzing 1690*), b. *O. meyeriana* (Zoll. & Mor.) Baill. var. *meyeriana* (Backer s.n.), and c. *O. meyeriana* var. *granulata* (Watt) Duistermaat (*Beumée s.n.*), all × 12.
represented, one corresponding with the ancestral genome CC, the other showing introgression with the BB group (see also table 1).

Although I have not seen the type of *O. malampuzhaensis*, I find nothing in its original description that makes it different from the present species and thus have had no compunction in reducing it here. If I understand Second correctly, it would be a tetraploid race (i.e.: 93) and as far as the isozymes are concerned it would be indistinguishable from a certain ‘*O. malabarensis*’, a name I have been unable to trace.

6. *Oryza meyeriana* (Zoll. & Mor.) Baill.

*For the synonymy, see under the varieties.*

Plants perennial, loosely tufted or stoloniferous. *Culms* erect to ascending, sometimes branching intra- and extravaginally at base, 23–78 cm long, rooting in the lower nodes, glabrous, smooth. Internodes tubular, ribbed (i.s.). Nodes glabrous. Sheaths tight to slightly inflated. Auricles linear-lanceolate, falcate, 0.5–3 by c. 0.2 mm, glabrous or with up to 1 mm long hairs. Ligules ± collar-shaped, 0.5–5 by 2–4 mm, apex erose, herbaceous, nerved, without transverse veinlets, glabrous, smooth. *Blades* ovate-lanceolate, linear-lanceolate to linear, 8–27 by 0.7–3.2 cm, glabrous, smooth to scabrous on both sides, margins scabrous, midrib below protruding, transverse veinlets absent. *Panicle* narrowly contracted, 4–15 by c. 0.5 cm diameter. Peduncle and axis ± terete, ribbed (i.s.), smooth. Branches erect, wavy, glabrous, the lowermost solitary, 1.3–6.3 cm long, either simple, 2–5-spikeled, or with 1 or 2 secondary branches, each 2-spikeled, and terminally 2–4-spikeled. Pedicel not clavate, not adaxially curved inward, 0.5–10 mm long, glabrous. *Spikelets* ± horizontally inserted on their pedicels, ovate, ovate-oblong, lanceolate to linear-lanceolate, 4.9–10.5 by 1.5–2.65 mm, 2.1–6.4 times as long as wide, acute to acuminate. Glumes 0.2–0.3 mm long. *Sterile lemmas* deltoid, triangular, ovate to lanceolate, 0.05–2.45 by 0.2–0.8 mm, 0.01–0.25 times as long as the spikelet, margin entire, apex acute to acuminate, glabrous, herbaceous. Fertile lemma ovate to ovate-oblong, lanceolate to linear-lanceolate, 4.85–9.3 by 1.4–2.75 mm, margin curled inward, apex acuminate, sometimes hook-shaped, slightly sulcate and finely reticulate, at the base of the midrib often covered by glassy hairs, bony; awn absent. Palea as the lemma, linear-lanceolate to linear, 4.5–9.4 by 0.5–1.35 mm, margin narrowly scarious, not incurved, apex acuminate, not sulcate; awn absent. Lodicules obovate to obovate-oblong, 0.5–2.2 by 0.15–0.7 mm, apex obtuse, scarious, nerves more or less distinct. Anthers 1.5–3.9 mm long, yellow or brown. Stigmas white, yellow, or brown. Caryopsis ovoid, ovoid-oblong, oblong, ovate-lanceolate, cylindrical, 3.4–7.3 by 0.8–1.95 mm diameter, brown; embryo 0.1–0.3 times as long.

**Chromosome number.** 2n = 24 (Chang, 1979).

**Notes.** Prodoehl (1922) did not see *Oryza meyeriana*, but cited Steudel’s (1853) diagnosis in which the length of the spikelets is not given. She distinguished between *O. granulata* Watt and a closely related new species, *O. abromeitana* Prodoehl, by the
length of the spikelet. The type specimen of _O. granulata_ has c. 6.2 mm long spikelets, those of _O. meyeriana_ are c. 8.75 mm long, while those of _O. abromeitana_ (according to Prodoehl, 1922: 234, see note sub var. _meyeriana_) would be c. 9 mm long. I agree with Roshevits (1937) that this difference is insufficient to distinguish between _O. abromeitana_ and _O. meyeriana_ at the specific level in view of the variability shown by the additional specimens. The differences between _O. granulata_ and _O. meyeriana_ are also too slight to maintain them as distinct. There are gradual differences between the extreme forms thus distinguished without any geographical or ecological distinction, and they are therefore at best regarded as varieties.

a. var. _meyeriana_ — Fig. 3b.


Auricles c. 1 by 0.2 mm. Ligules 1—5 mm long. Blades ovate-lanceolate, linear-lanceolate to linear, 0.8—3.2 cm wide. Spikelets lanceolate to linear-lanceolate, (6.1—)6.8—10.5 mm long, 3.1—6.4 times as long as wide. Sterile lemmas 0.15—2.45 mm long. Lodices obvotate to ovobata-lanceolate, 0.5—1.4 mm long. Caryopsis oblong to ovate-lanceolate, 4.1—7.3 mm long; embryo 0.1—0.2 times as long.

**Distribution.** Malesia: Sumatra (Aceh), Java (Bogor, Priangan, Banyumas, Kediri, Besuki), Borneo (Sabah, Kalimantan Timur), Philippines (Palawan, Panay, Negros, Mindanao), Celebes (Menado, Palu, Kendari, Baubau), Moluccas (Halmahera).

**Ecology.** Brown laterite, fine grey sand with lumps of eroded chalk, clay; primary or 6—10 m high secondary forest, in disturbed places, on dry to swampy, sometimes silty places, up to 750 m altitude. Locally common.

**Collector's notes.** Habit stiff, bambusoid, in small, loose tussocks. Culms erect, greenish. Inflorescence green. Spikelets green, pale when dry. Flowers white to pale green, open at 10.00 hrs. Stigmas white, far protruding. Fruit pale green to green.

**Uses.** Food for birds (Celebes, Baubau).
Vernacular names. Papadian (Java), padi-padian (Borneo, Tawau), padi hiang (Batulicin), pará-agwáy (Palawan, Tagba, Tagbanwa), hehawa (Celebes, Baubau).

Phytochemistry. Leaves contain flavone C-glucosides and trian glucosides (J.B. Harborne, University of Reading, on label of SAN 72044 (Saikeh Lantoh).

Note. The type specimen of *O. abromeitana* has not been seen; it was not among the specimens received on loan from the various herbaria where *Merrill 116* could have been.

b. var. granulata (Watt) Duistermaat, *comb. nov.* — Fig. 3c.


Auricles 0.5—3 by c. 0.2 mm. Ligules 0.5—2 mm long. Blades (linear-)lanceolate, 0.7—2 cm wide. Spikelets oblong to lanceolate, 4.9—6.2 (—6.45) mm long, 2.1—3.25 times as long as wide. Sterile lemmas 0.05—1.4 mm long. Lodicules obovate-oblong, 0.8—2.2 mm long. Caryopsis oblong to obovate-oblong, 3.4—4.1 mm long; embryo 0.2—0.3 times as long.

Distribution. Sikkim; India (Uttar Pradesh, Mysore, Kerala, Andhra Pradesh, Bihar, Assam); Sri Lanka (see Senaratna, 1956); Thailand (Sukothai, Chanthaburi, Kanchanaburi, Ratchaburi, Prachuap Khiri Khan, Trang); Laos; Cambodia; China (Guangdong, Yunnan); Malesia: Sumatra (E. Coast), Malaya (Perak), Java (Jakarta, Priangan, Pekalongan, Semarang, Rembang, Madiun, Surabaya), Kangean, Philippines (Luzon, Palawan, Panay, Mindanao).

Ecology. Blackish clay, red volcanic soil, limestone or marl, in evergreen or deciduous primary and secondary forest, teak forest where light penetrates, on the more moist places, up to 780 m altitude, locally common.


Vernacular names. Jungle Oryza (India, Madras), rumput lorodan (Java, N. Krademan), lorodan pari (Gedangan), papadia, padi hutan (Cepu).

Note. Prodoehl (1922) stated that this species would have 3 anthers only, hence *Oryza triandra* Hb. Heyne ex Steud. (1853, nomen). Because this has thus been reported from two sources, it may well be true that this exceptional situation does occur in this variety, but all specimens I have seen, among which some duplicates of the numbers mentioned by Prodoehl (*Wight 2354, Merrill 6697, 7244*), had 6 anthers, as usual.
Fig. 4. Spikelets of a. *Oryza ridleyi* Hook. f. (*Brass 13810*) and b. *O. longiglumis* Jansen (*Brass 8721*), both × 12.
7. Oryza ridleyi Hook. f. — Fig. 4a.


Plants perennial, tufted, stoloniferous. **Culms** erect, branching intra-, rarely extra-vaginally at base, 75—220(−300) cm long, rooting in the basal and submerged higher nodes, glabrous, smooth. Internodes short, sometimes tubular, slightly ribbed (i.s.). Nodes glabrous. Sheaths tight. Auricles often present, linear-lanceolate, falcate, 2—6 by 0.2—1 mm, with up to 2 mm long hairs. Ligules collar-shaped, deltoid, triangular or oblong-triangular, 2—5 by 2—4 mm, truncate or obtuse, herbaceous, tearing (at least i.s.), nerved, without transverse veinlets, glabrous, smooth. **Blades** linear, 21—42 by 1.2—2.4 cm, glabrous, smooth to scabrous on the lower side, margins scabrous, midrib below protruding, transverse veinlets absent. **Panicle** loosely contracted, 15—40 by 1—5 cm diameter. Peduncle and axis ± terete, ribbed (i.s.), smooth or becoming scabrous upward. Branches ascendingly patent to ± erect, wavy, glabrous, only the axils with a tuft of white hairs, the lowermost solitary, 4.1—12 cm long, either simple, c. 6-spikeled, or with 1—5 secondary branches, each 2—4-spikeled, and terminal- ly 4- or 5-spikeled. Pedicel not or slightly adaxially curved inward, 1—3 mm long, glabrous, somewhat scabrous. **Spikelets** horizontally inserted on their pedicels, obovo-te obovate-lanceolate, 7.6—12.7 by 1.65—2.9 mm, 3.45—5.25(−6.35) times as long as wide, acuminate. Glumes c. 0.2 mm long. **Sterile lemmas** linear, setaceous, 2.3—10.5 by 0.15—0.45 mm, 0.3—0.85 times as long as the spikelet, scaberulous pubescent, herbaceous. **Fertile lemma** linear-lanceolate, 6.8—10.5 by 1.35—2.1 mm, margin curled inward, apex acuminate, slightly sulcate, somewhat granulate by small grooves, on the nerves with 1 or 2 rows of glassy hairs, herbaceous; awn 3—12 mm long, antrorsely scaberulous, slender, not callose at base. **Palea** as the lemma, linear-lanceolate, 6.7—10.4 by 0.85—1.2 mm, margin scarious, not incurved, apex acuminate, not sulcate; awn 0.1—1.2 mm long, patento-erect. **Lodicules** obovate, oblong, lanceolate, or obovate-lanceolate, 0.55—1.3 by 0.2—0.5 mm, apex acute to obtuse, scarious, nerves more or less distinct. **Anthers** 1.1—3.5 mm long, brown (i.s.). **Stigmas** brown to blackish purple. **Caryopsis** linear-lanceolate, cylindrical, 5.9—7 by 0.7—1 mm diameter, brown; embryo 0.13—0.18 times as long.

**Distribution.** Burma (Tenasserim); Thailand (Lop Buri, Phra Nakhon, Prachin...
Buri, Chanthaburi, Krabi, Nakhon Si Thammarat, Trang); Cambodia (Stung-streng); Malesia: Sumatra (E. Coast, Riau Arch.), Malaya (Kedah, Perak, Pahang, Selangor, Johore), Java (see note), Borneo (Sabah, W. Kutai), New Guinea (Irian Jaya: Mamberamo R., Idenburg R.).

Ecology. Shaded grassland, along paths, rivers, or streams, at the margin of or in (secondary) evergreen forest in damp places, in old gardens, and open places, up to 100 m altitude, common except in New Guinea.


Uses. Eaten as ordinary rice in Sabah (Maidin 1558).

Vernacular name. Paroi tasur (Sabah).

Chromosome number. 2n = 48 (Nezu, 1958).

Notes. Although the type has not been seen, it is perfectly clear that Hooker’s name belongs to this species. Oryza stenothisus could likewise not be checked, but its description is unambiguous.

Ridley (1891) already remarked that this might be a form of 'common', i.e. cultivated rice, but the chromosome number and karyogram makes that unlikely.

Backer (1925) has suggested that this species might also occur in Java, but it has not been collected as yet.

8. Oryza longiglumis Jansen — Fig. 4b.


Plants perennial, forming tufts, stolons absent. Culms erect, sometimes branching intravaginally at base, 85–120 cm long, rooting in the basal and submerged higher nodes, glabrous, smooth. Internodes tubular, strongly ribbed (i.s.). Nodes glabrous. Sheaths tight. Auricles absent (deciduous?). Ligules collar-shaped, c. 1 mm long, apex erose, herbaceous, not tearing, nerved, without transverse veinlets, glabrous, smooth. Blades linear, 25–40 by c. 1 cm, glabrous, smooth, margins scabrous, midrib below protruding, transverse veinlets present. Panicle loosely contracted, 28–30 by 3–3.5 cm diameter. Peduncle and axis ± terete, smooth, becoming scabrous upward. Branches ascendingly patent to ± erect, wavy, glabrous, only the axils with a tuft of white hairs, the lowermost solitary, 9–11 cm long, with 3–8 secondary branches, each 1–5-spikeled, and terminally 4- or 5-spikeled. Pedicel slightly clavate, adaxially slightly curved inward, 1–9.5 mm long, glabrous. Spikelets obliquely to horizontally inserted on their pedicels, obovate-lanceolate, 7.2–8 by 1.85–2.25 mm, 3.25–4.2 times as long as wide, acuminate. Glumes c. 0.2 mm long. Sterile lemmas linear, setaceous, 6.3–13 by 0.13–0.2 mm, 0.8–1.6 times as long as the spikelet, apex acute, scaberulously pubescent, herbaceous. Fertile lemma obovate-lanceolate, 6.6–13 by 0.13–0.2 mm, margin curled inward, apex acuminate, sulcate, somewhat granulate by small grooves, on the nerves with 1 or 2 rows of glassy hairs, herbaceous; awn 12–
25 mm long, antorsely scaberulous, slender, not callose at base. *Palea* as the lemma, linear-lanceolate, 6.65–7.3 by 0.7–0.85 mm, margin narrowly scarious, not incurved, apex acuminate, not sulcate; awn 0.1–0.5 mm long, erect. Lodices obovate-oblong, 0.8–1 by 0.4–0.5 mm, apex truncate, scarious, nerves distinct. Anthers 1.6–2.2 mm long, brown (i.s.). Stigmas brown or black. *Caryopsis* lanceolate, cylindrical, c. 4.2 by 1.1 mm diameter, brown; embryo c. 0.17 times as long.

**Distribution.** Papua New Guinea: Western Dist., Tarara, Wassi Kussa R., Morehead-Arufi Road. Apparently rare: only 3 collections seen.


**Collector's notes.** Weak-stemmed. Awns green.

**Chromosome number.** 2n = 48 (Second, 1985).

**Note.** This species is most closely related to *O. ridleyi*. Jansen thought that the absolute length of the sterile lemmas was the most important delimitating character, but there is a considerable overlap. Their size in relation to the length of the spikelet gives a much more dependable character. The best differences, however, lay in the length of the ligule, the width of the leaves, and the length of the awns. The spikelets of *O. longiglumis* are somewhat smaller, also.

9. Oryza schlechteri Pilg. — Fig. 5.


Plants perennial, tufted, stoloniferous. *Culms* erect, branching extravaginally at base, 25–85 cm long, rooting in the lower nodes, glabrous, smooth. Internodes narrowly tubular, ribbed? (i.s.). Nodes hairy. Sheaths tight. Auricles often present, linear, falcate, c. 1 by 0.1 mm, with c. 1 mm long hairs. Ligules collar-shaped, c. 1 mm long, apex erose, herbaceous, tearing (at least i.s.), nerved, without transverse veinlets, glabrous, smooth. *Blades* linear, 10–30 by 0.6–1.2 cm, with white hairs on both sides, smooth to scabrous on both sides, margins scabrous, midrib below protruding, transverse veinlets absent. *Panicle* loosely contracted, 4.2–6.5 by 0.6–3.5 cm diam. Peduncle and axis ± terete, ribbed (i.s.), smooth to scabrous. Branches ascendingly patent to ± erect, somewhat wavy, glabrous, only the axes with a tuft of white hairs, the lowermost solitary or paired, the longest 1.5–3.5 cm long, with c. 4 secondary branches, each 2–5-spikeled, and terminally 5–7-spikeled. Pedicel not clavate, not adaxially curved inward, 0.5–2 mm long, glabrous or scaberulously pubescent. *Spikelets* obliquely to horizontally inserted on their pedicels, ovate, 1.75–2.15 by 0.95–1.25 mm, 1.65–1.85 times as long as wide, acuminate. Glumes c. 0.1 mm long. *Sterile lemmas* deltoid, broadly ovate, ovate-oblong to linear, setiform, 0.1–0.55 by 0.01–0.2 mm, 0.05–0.27 times as long as the spikelet, margin entire, apex acute, glabrous, herbaceous. *Fertile lemma* oblong to lanceolate, 1.7–2.1 by 0.6–1 mm, margin curled inward, apex acuminate, not sulcate, longitudinal-
ly finely ribbed, midrib scabrous in the upper half, otherwise glabrous, herbaceous, awn absent. *Palea* as the lemma, oblong, 1.4—1.95 by 0.4—0.65 mm, margin narrowly scarious, not incurved, apex acute, not sulcate; awn absent. *Lodicules* oblong, c. 0.45 by 0.2 mm, apex obtuse, scarious, nerves indistinct. Anthers and stigmas not seen. *Caryopsis* elliptic, laterally compressed, 2-ribbed, 1.15—1.3 by 0.75—0.85 mm diameter, dark brown; embryo 0.5—0.8 times as long.

**Distribution.** New Guinea: Van der Sande R., Beaufort R. bivouac; Madang (Jamu Gorge). Rare, only 3 collections have been seen.

**Ecology.** On rocks, up to 300 m altitude.

**Note.** According to Roshevits (1932) *O. schlechteri* can only be separated from *Leersia* on the presence of the ‘glumes’ (= sterile lemmas), which would be very much reduced or even completely missing (see also Henty, 1969). In the three collections seen I have not found any spikelet lacking the sterile lemmas, although they were sometimes very small (c. 0.1 mm long). This is the only species of *Oryza* I have seen with pubescent nodes. At present further anatomical studies of the leaves, epidermis of the lemma and palea and the awns will have to support or reject the taxonomic position adopted here (see also Launert, 1965; Terrell et al., 1983). I have only seen fruiting material collected in October and November, the anthers and stigmas must therefore remain unknown at present.

**NOMINA DUBIA ET EXCLUDENDA**

*Oryza coarctata* Roxb., Fl. Ind., ed. 2, 2 (1832) 206; Bor, Grasses (1960) 604. — *Type: Buchanan s.n.* (BM, holo, n.v.), Bangladesh, Ganga Delta, 1796.

This species would also occur in Malesia according to Bor (1960), but I have seen no specimens of it. The species belongs to the monotypic genus *Porteresia* Tateoka: *P. coarctata* (Roxb.) Tateoka.

The description of this species is insufficient for clear identification, while the type has apparently been lost. The name has been applied to O. alta Swallen, O. latifolia Desv., and O. sativa in South America, to O. barthii Chev. and O. longistaminata Chev. & Roehr. in African and to O. rufipogon and O. sativa in Asian literature. It was described as perennial, which has suggested that it could not be O. sativa, which is generally regarded as an annual, but as said above, races of O. sativa cultivated in the Leiden Botanical Garden are perennial. I agree with Tateoka (1963) that as a nomen dubium this name should not be used for any taxon.

INDEX OF COLLECTORS

Only numbered collections have been included. Specimens cited in literature but not seen have been included with their identifications between brackets when these seemed reasonable, otherwise they have been deleted.

A 1551 (Tangulon): 6a — Aban, see SAN-series — Alston 14390, 14391, 16446: 3 — Amdjah 814: 5 — Anang, see de Haan — Anta 118: 1.

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