

## AUSTRALOPYRUM, BRACHYPODIUM, AND ELYMUS (GRAMINEAE) IN MALESIA

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### SUMMARY

*Brachypodium sylvaticum* (Huds.) Beauv. has 1 species and 2 varieties in Malesia. *Brachypodium longisetum* Hitchc. is transferred to *Elymus*. The Australian genus *Australopyrum* (Tsvet.) Löve (Gramineae-Triticeae) is represented by a new species in New Guinea. The species is curious among grasses not only for having a thin seta at the end of the inflorescence rachis, which is unique among the Pooideae, but especially because of the uncinat awn on the glumes and lemmas. Lateral genetic transfer between families may be present. The latter two taxa represent a tribe (Triticeae) and genera thus far not recorded for the indigenous Gramineae of Malesia.

### INTRODUCTION

#### Taxonomy

*Brachypodium* Beauv. is a small genus of about 17 species. There is no recent revision of it, only some local ones, e.g. the posthumous one for Europe by Saint-Yves (1934), and the one by Honda (1937) for Japan, Taiwan, and Manchuria, who both distinguished a host of taxa in an unwieldy system. Tateoka has published various notes on the genus, the most important of which is his summary in 1968. The genus appears at present to be most variable in the Iberian Peninsula (Schippmann, 1986), but this may well be a secondary centre of diversification: it extends far into Asia with one curious endemic in Taiwan and one species, *B. sylvaticum* (Huds.) Beauv., with two varieties in the mountains of most of Malesia. The New Guinea endemic, *B. longisetum* Hitchc., will be discussed later. In Africa there is one species in Madagascar, which Clayton (1970) implicitly suggested is the same as one of the two species of West, Central and South Africa. He also saw it as being closely related to the single species from Central America; in 1972 he compared it to *B. sylvaticum*. There is also a very curious endemic of the Canary Islands, which is restricted to a subtropical climate, while its congeners on the contrary prefer temperate to Mediterranean conditions. This would seem to indicate a great age. As the genus is absent from Australia, New Zealand, and southern South America, this distribution suggests an origin in Laurasia. See also the map in Tateoka (1968) which suggests a Cretaceous origin in Laurasia. For phytochemical reasons Semikhov et al. (1987) also argued that *Brachypodium* must be a very ancient group. Such an age may ex-

plain the present distribution which clearly shows the fragmented pattern of a formerly more widespread and variable group. As can be expected in such instances, *Brachypodium* is genetically quite diversified causing various taxonomic problems some of which have not been solved yet. For instance, what is its position in the family?

By the rather unspecialized spikelets and the leaf anatomy, *Brachypodium* is obviously a  $C_3$  pooid grass. Within that group it has a number of characters that sets it aside from the others and at present it is usually regarded as a distinct tribe, the Brachypodieae C. O. Harz. This is then usually placed near the Bromeae Dumort. from which it differs by the open (not closed) leaf sheaths, spikes with sessile (not long-pedicelled) spikelets, lemmas with an entire (not bifid), usually awned apex (awn not subapical), more or less hairy (not glabrous) lodicules, a caryopsis tightly enclosed by the palea (not adherent to it), and small chromosomes with a variable base number (not exclusively 7).

Clayton & Renvoize (1986) included the genus in the Triticeae, but regarded it as anomalous with some resemblance to the Bromeae. The cytology and phytochemistry indicate an isolated position of the genus in this tribe, too.

*Brachypodium* and *Bromus* differ from the Triticeae by the starch grains which are more or less uniform in size, while in the latter tribe the grains are variable. They also possess thick-walled cells in the peripheral cell layer of the nucellus which are not present in the Triticeae (Smith, 1969).

*Brachypodium* differs from both the Triticeae and Bromeae in its phytochemistry.

De Cugnac (1931) observing the absence of fructanes placed *Brachypodium* in a group of largely panicoid and cynodontoid (chloridoid) genera. It is now realized that, although it is not an absolute taxonomic criterion, fructanes are mainly produced by  $C_3$  grasses, such as the pooids, while  $C_4$  grasses, such as the panicoids and cynodontoids (but also the  $C_3$  bambusoids!) produce saccharose-starch.

Semikhov et al. (1987) noted the absence of prolamine fractions among the seed proteins, while these are present in the other pooid grasses. They regard the presence as a derived character and the absence as an original one and saw this as an indication that the Brachypodieae are a very ancient group. As prolamines are the typical storage proteins of the Gramineae, their absence in *Brachypodium* seems more like a reversal and hence an apomorphy than an original state and a plesiomorphy. In the latter case it cannot be used in phylogenetic argumentations, in the first case it is impossible to guess when the deletion occurred. The absence of fructanes can also be seen as an apomorphy.

Serologically there is a profound difference between *Brachypodium* and the Bromeae and Triticeae (Smith, 1969), which in view of the absence of prolamines is not surprising as this is basically a protein reaction.

There is also a difference in germination. The mesocotyl is part of the embryo and looks like an internode immediately above the coleoptile node. It elongates in germination pushing up the young tuft. Whatever its homology, it is absent in the Bambusoideae, Bromeae, and Triticeae, and present in all other grasses, e.g. *Brachypodium* (Harberd, 1972).

Phenetically, the similarity with the Triticeae is evident, as was also experienced during the present research. Among the material of *B. sylvaticum* from Papua New Guinea was a specimen remarkable for having reflexed spikelets and lemmas (many glumes, too!) with smooth, slightly bicoloured, crochet-shaped awns. For a while we thought it was an undescribed *Brachypodium* species, but as it did not quite match the facies of *Brachypodium*, we remained suspicious of it. A further search turned up *Australopyrum* Löve, an Australian split-off of *Agropyron* L. of the Triticeae. Especially *Australopyrum pectinatum* (Labill.) Löve so strikingly resembled the New Guinea material that both clearly belong to the same genus and tribe.

While browsing through the material and literature of the Triticeae, the suspicion on the taxonomic status of *B. longisetum* grew as well. And indeed, it turned out to be very similar to the Australian *Elymus scaber* (R. Br.) Löve, and is therefore here renamed as *E. longisetus* (Hitchc.) Veldk. In a way this tribal identity solves at least one problem in the distribution of *Brachypodium*: one outlier is removed, while its occurrence fits with the more general pattern of species common to New Guinea and Australia. It shows the aggressive mimicry between *Brachypodium* and the Triticeae, which in this case has fooled the few, but eminent agrostologists such as Hitchcock, Jansen, and Tateoka who have looked at this species.

The Triticeae are a difficult tribe by all accounts, where generic delimitation according to current practice goes by the various genome types (e.g. Löve, 1984). Not being karyologists we cannot judge the proposed delimitation of *Agropyron* and its off-shoots, but at least *Australopyrum pectinatum* and *A. uncinatum* Veldk. are so curious, that a generic status may well be correct. *Australopyrum retrofractum* (Vickery) Löve var. *retrofractum* is a synonym of *A. pectinatum*, but its var. *velutinum* (Nees) Löve is a very distinct species (Simon, 1986).

Nothing is of course known about the karyology of the New Guinea species, not even the chromosome number. For *Australopyrum pectinatum* and *A. retrofractum* var. *velutinum* Löve (1984) recorded  $2n = 14$ , with a genomic formula W or WW.

Clayton & Renvoize (1986), taking a more conservative position, have retained *Australopyrum* in *Agropyron*.

*Australopyrum uncinatum* and *Elymus longisetus* appear to be the first records of the Triticeae for the native flora of Malesia. As this tribe contains some of the world's most important cereals, e.g. *Hordeum vulgare* L. ('barley'), *Secale cereale* L. ('rye'), and *Triticum aestivum* L. ('wheat'), several races and forms of these have of course been introduced in Malesia at various times, but this did not turn out to be a great success, for although they will grow in the mountains of Malaya, Java, the Philippines, and Papua New Guinea, their cultivation has not been very profitable up to now, and without human care they soon disappear.

The obnoxious weed *Elytrigia repens* (L.) Desv. [*Agropyron repens* (L.) Beauv.] was introduced in E Java by Buysman early this century, but fortunately did not persist. It was not taken up by Monod (1968).

Some Malesian species have been described in *Triticum*: *T. involutum* (Buse) Miq. from Java is a synonym of a widespread SE Asian variety of *Brachypodium sylvaticum*.

Since the description of *Triticum nubigenum* (*Agropyron nubigenum* Koord.), also from Java, no authentic material of it has been seen by later authors, e.g. Miquel (1857), Koorders (1911), Backer (1928), Jansen (1953), Monod (1968), and ourselves. It is therefore curious to note that Löve (& Connor, 1982; 1984), without any comment, placed it in *Elymus* L. sect. *Anthosachne* (Steud.) Tsvet. instead of in *Brevipodium* Löve & Löve. From its description and locality there is hardly any doubt that it is the same SE Asian variety as above of *Brachypodium sylvaticum*.

*Triticum luzoniense* (Presl) Kunth is a misplaced name based on material probably collected in South America and probably belonging to *Bromus catharticus* Vahl. (JFV, M. Eriks & S.S. Smit, msc.).

### Cytology

Avdulov (1931) included *Brachypodium* in the Poatae-Phragmitiformes, which he distinguished from the Festuceae-Bromeae because of the small chromosomes and the basic number which was not 7, but 9. In fact, as was also pointed out by Tateoka (1957), the size of the chromosomes is an insufficient base for distinguishing groups at such a high level, and the basic chromosome numbers  $n = 5, 7, 8,$  and 19 also occur in the genus (Tateoka, 1962; Smith, 1980; Clayton & Renvoize, 1986).

Merely on a difference in this basic number Löve & Löve (1961) distinguished *Brachypodium* ( $x = 7$ ) from *Brevipodium* Löve & Löve ( $x = 9$ ). It will be evident that such a distinction is untenable when both (and other) numbers occur within a single species. '*Brevipodium sylvaticum* (Huds.) Löve & Löve', may have not only  $n = 9$ , but also 7 and 8, for the Asian specimens attributed to *B. sylvaticum* (Huds.) Beauv. certainly are not '*Brachypodium pinnatum* (L.) Beauv.' although the same number ( $2n = 14$ ) has been counted several times for them. This species, contrary to Löve & Löve's idea, also has several basic numbers, e.g. 7 and 8.

Smith (1980) indicated that  $2n = 14$  has not been recorded in Europe for *Brachypodium sylvaticum*, but that the polyploid series has. This suggests two things, a) that *B. sylvaticum* is not of European but of Asian origin, and b) also taking into account the slight morphological differences of the Asian-Malesian material, that we have at least one different variety there.

Another generic split-off of *Brachypodium* encountered in present treatments is *Trachynia* Link, mainly distinct because of encompassing annual species with a very much reduced inflorescence, small anthers, and  $n = 5$ . Longevity does not seem a very useful generic character, while such reduced inflorescences occur in *Brachypodium* species as well. Sizes of anthers may be good at the specific level, at the generic one they are unacceptable. The sole difference then is the basic number and that is insufficient.

Mühlberg (1970) studied the growth forms of European *Brachypodium* and also concluded that a generic split-up was not in order.

Two species with closed leaf sheaths and sessile spikelets formerly placed in *Brachypodium* are presently included in *Festucopsis* (C.E. Hubb.) Melderis of the Triticeae. Clayton & Renvoize (1986) have synonymized this with *Elymus* L. s.l., which again indicates how difficult the delimitation of these genera and supposed tribes are.

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KEY TO THE MALESIAN TAXA OF THE BRACHYPODIEAE AND TRITICEAE

*Note:* measurements should not be taken from the lowermost spikelet of the spike as this is often aberrant. The length of the first lemma relative to the lower glume has been measured in an undissected spikelet, where the length is from the base of the lower glume to the constriction of the apex of the lemma where it passes into the awn.

- 1a. Inflorescence a spike or raceme, spikelets in two rows along an unbranched rachis. . . . . 2
- b. Inflorescence a panicle, all spikelets  $\pm$  long-pedicelled. . . . . **Bromus**
- 2a. Spikelets  $\pm$  erect, appressed against the rachis. Rachis ending in a spikelet. Awn of the lemma scabrous, ending in a straight point . . . . . 3
- b. Spikelets patent to reflexed in fruit. Rachis ending in a filiform, sometimes curled bristle. Awn of the lemma smooth, shiny, ending in a crochet-shaped hook  
**Australopyrum uncinatum**
- 3a. Spikelets up to 3.5 cm long (incl. awns). Awn flexuous, c. 0.5 times as long as the body of the lemma to slightly longer. Lemma with the lateral nerves distally free. Palea glabrous between the 2 shortly to moderately long pilose keels, apex rounded . . . . . 4
- b. Spikelets 3.5–7 cm long (incl. awns). Awn stiff, more than 2 times as long as the body of the lemma, flat at base. Lemma with the lateral nerves distally anastomosing. Palea pubescent between the scabrous keels, apex retuse to bidentate . . . . . **Elymus longisetus**
- 4a. Plants more or less glabrous. Sheaths at most puberulous along the margins and at the contra-ligule; blades below (outside) more or less glabrous. Peduncle glabrous. Inflorescence rachis glabrous to microscopically puberulous. Glumes glabrous; lower glume in situ (0.33–)0.45–0.55(–0.65) times as long as the first lemma. Lemmas glabrous to microscopically spiculose; first lemma 6.9–8.2(–10.5) mm long. – Not in New Guinea  
**Brachypodium sylvaticum var. pseudo-distachyon**
- b. Plants more or less pubescent to sericeous. Sheaths, lower (outside) surface of the blades, peduncle, and inflorescence rachis subglabrous to densely sericeous. Glumes usually more or less setulosely hairy; lower glume in situ (0.43–)0.46–0.75 times as long as the first lemma. Lemmas more or less strigose; first lemma 8–11 mm long. – New Guinea. (For collections of very hairy plants from Pauai, Luzon, see note under the previous variety)

**Brachypodium sylvaticum var. pubifolium**

**AUSTRALOPYRUM**

*Australopyrum* Löve in Feddes Repert. 95 (1984) 442. — *Agropyron* Gaertn. sect. *Australopyrum* Tsvet., Nov. Syst. Pl. Vasc. 10 (1973) 35. — Type: *Australopyrum pectinatum* (Labill.) Löve.

Perennials, tufted, without rhizomes or cataphylls. Leaves involute. Inflorescence a terminal simple raceme. Rachis not breaking up, flattened and slightly excavated opposite the spikelets. Spikelets solitary, briefly pedicelled, laterally appressed against the rachis, several-flowered. Glumes rounded on the back, shorter than the first lemma, briefly connate at base, rather stiff,  $\pm$  equally long, flat to  $\pm$  subulate,  $\pm$  asymmetrically 3–5-nerved, glabrous. Lemmas awned, nerves 5–14, apically not

anastomosing. Anthers 3. Lodicules with 1–few hairs on the outer edge. Styles inserted just below the terminal appendage of the ovary and adnate to it. No ripe caryopses seen. Genomic formula W or WW ( $x = 7$ ).

**Distribution.** 3 species, 2 in Australia, 1 in New Guinea.

***Australopyrum uncinatum* Veldk., spec. nov. – Fig. 1.**

Vaginae superiores pilosae. Inflorescentiae axis apice sub spicula terminali seta laterali (ut videtur) tereti gracili erecta ad patenti stricta ad crispa sine spicula terminali, spiculae 4- vel 5-floribus patentes in fructu, glumis subequalibus 7–9 mm longis  $\pm$  asymmetricis nervatione distincta apice subulato vel uncinato, lemmatibus inferioribus 13–16 mm longis nervis distinctis 10–14 approximatis arista unco abrupte inflexo, paleis carinis dense pectinatis, lodiculis margine exteriore 1-paucis pilis gerentibus. — **T y p e:** LAE 65112 (Croft et al.) (L, holo, no. 233077, iso no. 233076, A, E; BRI, CANB, K, LAE, n.v.), Papua New Guinea, Northern Dist., Mt. Kenive, 3000 m alt., 30 July 1974.

Culms tufted, erect, simple, 30–80 cm tall, intravaginally branched at base; internodes glabrous; nodes yellowish to brownish. *Sheaths* apparently open to base, patent to reflexed pubescent to pilose, the lower ones soon fibrous; ligule collar-shaped, 0.5–1 mm long, margin erose to puberulous; blade  $\pm$  erect, not stiff, usually involute, up to 25 cm by 2 mm, on both sides patently pilose, the upper surface more densely so. Peduncle up to 25 cm long, upwards becoming  $\pm$  appressed pubescent. *Raceme* erect, up to 3 cm long, with 3–5 spikelets; axis flattened, pubescent, terminal node much reduced, appearing as a lateral seta below the uppermost spikelet, terete, thin, erect to patent, straight or curled, without a terminal spikelet, 5–6 mm long. *Pedicel* flattened, c. 1 mm long, callose, pubescent. *Spikelets* appressed in anthesis, reflexed in fruit, cleistogamous, 4- or 5-flowered, lanceolate, 16–18 mm long (incl. awns). *Glumes* subulate to uncinate; lower one 7–9 mm long, distinctly

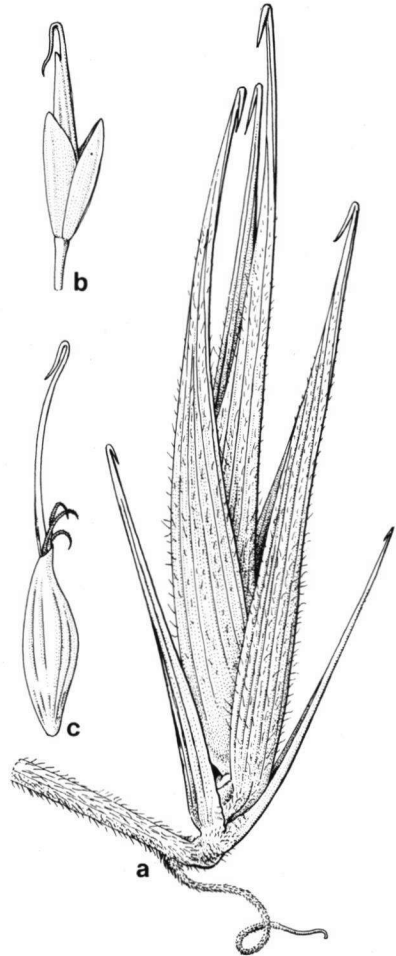


Fig. 1. a. *Australopyrum uncinatum* Veldk. Spikelet,  $\times 7.5$  (LAE 65112 Croft et al.). – b. *Deyeuxia uncinoides* (S.T.Blake) Royen & Veldk. Spikelet,  $\times 7.5$  (Craven 3006). – c. *Uncinia compacta* R.Br. var. *alpina* Noot. Utricle,  $\times 6.8$  (ANU 7289 Wade & McVean).

3-nerved; upper one 7.7–8 mm long, distinctly 4- or 5-nerved. *Rachilla* joints finely puberulous, smooth, 0.5–1 mm long, process ending in a reduced lemma. *Callus* thickened, c. 0.3 mm thick, glabrous, scar oblique,  $\pm$  round. *Lowest lemma* lanceolate, 13–16 mm long, rather stiff, base with a whitish callus on each side of the rachilla, back rounded, gradually narrowed into the terminal, simple awn, acumen abruptly turned on itself, hook-shaped, c. 1.1 mm long; pubescent, nerves 10–14, close-set,  $\pm$  parallel, not anastomosing. *Palea* lanceolate, flat to deeply sulcate, 7.5–10 mm long, apex acute, dorsally pubescent, keels 2, patent to recurved setose, margins inflexed, scarios, pubescent. Lodicules 2, cuneate, c. 1 mm long, scarios, 0-nerved, glabrous. *Anthers* 2–2.5 mm long, yellow (i.s.). *Caryopsis* not seen.

**Distribution.** Only known from the type.

**Ecology.** Subalpine grassland, c. 3000 m altitude.

**Collector's notes.** Erect herb. Height 80 cm. Leaves dull midgreen. Inflorescence green, light brown.

**Notes.** In some aspects *Australopyrum uncinatum* is most remarkable:

The axis of the inflorescence ends in a sterile bristle-like appendage without a terminal spikelet. As all six racemes available had this, it does not seem to be an accidental reduction of the tip of the axis due to damage, drought, etc., but to be the usual condition. There are some other genera with such an indeterminate rachis, e.g. *Dactyloctenium* Willd., *Paspalidium* Stapf, and *Setaria* Beauv. and its allies (all Panicoideae), but we know of no instance in the Pooideae where it is filiform and distinct from the main axis as it is here.

The glumes often, and the lemmas always, have an awn that ends in a hook shaped like that of a crotchet-needle and resembles that of the rachilla of *Uncinia* Pers. (Cyperaceae), representatives of which also occur in the area (see fig. 1c). This is a very rare phenomenon in the Gramineae (*Holcus lanatus* L. has something similar, but not as tightly folded, and the hook turns outside, the other way). It is therefore curious to note that only about 50 km NW on Mt. Victoria we have the endemic *Deyeuxia* (*Ancistragrostis*) *uncinioides* (S.T. Blake) Royen & Veldk. with very similar, smooth, terete, hooked awns. It would seem that this is another example of Went's theory of parallel evolution through natural, horizontal gene transfer (Went, Taxon 20, 1971, 197), which may not be so rare at all.

The present species is apparently close to *Australopyrum pectinatum* (Labill.) Löve because of the spikelets reflexed in fruit, the connecting rim of tissue at the base of the glumes, the smooth awn, etc. *Australopyrum pectinatum* differs significantly by: Upper sheaths  $\pm$  glabrous. Inflorescence rachis ending in a spikelet. Spikelets 5–9-flowered. Glumes 5.5–7 mm long, obscurely nerved, apex subulate. First lemmas 7.5–10 mm long, weakly distantly 5–9-nerved, awn subulate. Paleas with sparsely pectinate keels.

Contrary to Löve's remarks the anthers are only 2–2.5 mm long in these two species. Such dimensions can of course not be regarded to have any value at or above the generic level.



## BRACHYPODIUM

- Brachypodium* Beauv., Agrost. 12 (1812) 100, 155, t. 19, f. 3. — *Brachypodium* sect. *Dryopyron* Dumort., Obs. Gram. Fl. Belg. (1824) 100, *nom. inval.*, autonym required! — *Festuca* L. sect. *Brachypodium* Beauv. ex Steud., Syn. 1 (1854) 316 (correct in *Festuca* because of Dumortier's sections of 1824). — T y p e: *Brachypodium pinnatum* (L.) Beauv.
- Trachynia* Link, Hort. Berol. 1 (1827) 42. — *Brachypodium* sect. *Distachys* Dumort., Obs. Gram. Fl. Belg. (1824) 100. — *Brachypodium* sect. *Trachynia* Nymann, Consp. Fl. Eur. (1882) 843, *nom. superfl.* — *Brachypodium* subg. *Trachynia* Rouy, Fl. Franç. 14 (1913) 294. — L e c t o t y p e: *Trachynia distachya* (L.) Link [= *Brachypodium distachyon* (L.) Beauv.].
- Brachypodium* sect. *Leptorachis* Nevski, Acta Univ. Asiae Med. VIIIc, Bot. 17 (1934) 36. — *Brevipodium* Löve & Löve, Bot. Not. 114 (1961) 36. — T y p e: *Brevipodium sylvaticum* (Huds.) Löve & Löve [= *Brachypodium sylvaticum* (Huds.) Beauv.].
- Brachypodium* Beauv. sect. *Nitakaea* Honda, J. Jap. Bot. 12 (1937) 155. — T y p e: *Brachypodium kawakamii* Hayata.

Perennials (a few non-Malesian annuals). Leaf sheaths open. Inflorescence a spike-like raceme; rachis tenacious. Spikelets solitary, sessile, distichously placed, several-flowered, breaking up above the glumes, subterete to laterally compressed, laterally appressed against the rachis. Glumes 2, unequal, persistent, shorter than the lowest lemma, rounded on the back, 3–9-nerved. Lemmas rounded on the back, apex obtuse to awned, 5–9-nerved. Lodicules 2, obcuneate, truncate or with 2 unequal apices, scarious, apex hairy, 1-nerved. Stamens 3. Ovary with a terminal, hairy appendage; styles 2, inserted below the appendage. Caryopsis tightly enclosed by lemma and palea, but not adnate to it; hilum linear,  $\pm$  as long as the fruit; embryo small; starchgrains simple, uniform in size.

D i s t r i b u t i o n. See map Tateoka (1968).

***Brachypodium sylvaticum* (Huds.) Beauv.**

*Brachypodium sylvaticum* (Huds.) Beauv., Agrost. (1812) (101), 155, 156, 181, t. 3, f. 11; Hook. f., Fl. Br. Ind. 7 (1896) 362; Backer, Handb. Fl. Java 2 (1928) 254; Honda, J. Jap. Bot. 12 (1937) 151; Backer in Heyne, Nutt. Pl. Indon. (1950) 280; Bor, Grasses (1960) 450; Monod de Froideville in Backer & Bakh. f., Fl. Java 3 (1968) 519; Veldk. in Steen., Mt. Fl. Java (1972) t. 22, f. 6; P.M. Smith, Fl. Eur. 5 (1980) 189. — *Festuca sylvatica* Huds., Fl. Angl. (1762) 38. — *Triticum sylvaticum* Moench, Enum. Pl. Hass. (1777) 54; Miq., Fl. Ind. Bat. 3 (1857) 402. — *Brevipodium sylvaticum* Löve & Löve, Bot. Not. 114 (1961) 37; Kerguelen, Lejeunia n.s. 75 (1975) 98. — L e c t o t y p e: *Hudson s.n.* (probably not extant, not in BM, LINN, fide C.E. Jarvis, London, in litt.), Great Britain.

*Bromus sylvaticum* Beauv. var. *leiospicum* auct. non Hara: Hara, Bot. Mag. Tokyo 52 (1938) 227, quoad saltem specim. Mal., Ind.

For further synonymy see Honda (1937), Kerguelen (1975), Hsu, Fl. Taiwan 5 (1978) 428.

Perennial, tufted grass, 40–75 cm high, at base intra- and extra-vaginally branched. *Cataphylls* short, glabrous, shiny, yellowish. *Culms* erect, simple, terete,  $\pm$  glabrous. Nodes blackish, patent to reflexed pilose to puberulous. *Sheaths* usually loose to reflexed,  $\pm$  glabrous to pilose; auricles absent; ligule c. 2 mm long, rounded; blades flat, 8–30 cm by 5–10 mm, sparsely to  $\pm$  patently pilose, above more dense-

ly so. *Inflorescences* nodding, 7–24 cm long. *Pedicels* 0.35–1.5 mm long, glabrous to puberulous. *Spikelets* 3–8, 4–16-flowered, terete or slightly laterally flattened, up to 3.5 cm long (incl. awns), patently pilose. *Glumes* acute; lower glumes  $\pm$  flat, (3.5–)5.5–9 mm long, 5-nerved; upper glumes rounded, longer, (6–)7–12 mm long, 7-nerved, with an up to 2 mm long mucro. Joints of the rachilla 1.5–2.5 mm long, glabrous to setulose; process 2–3.5 mm long. *Lowest lemmas* lanceolate, (8–)10–13 mm long, dorsally rounded, glabrous to shortly pilose, 7-nerved; awn (1–)5–10 mm long (higher ones longer), antrorsely scabrous. Paleas c. 0.8–0.9 times as long as the lemmas (upper ones  $\pm$  as long), apex rounded, keels shortly to moderately long setose. *Lodicules* truncate, c. 1.8 mm long. *Anthers* 3, 3–4.2 mm long, yolk (i.s.). Fruit not seen, ovary apically with a hairy appendage, styles apical, free.

**Distribution.** See under the varieties. It is curious to note that the species occurs on virtually all high mountains of Malesia, but is apparently absent in Borneo, while in Sumatra it only occurs in Aceh (Leuser complex). In this it is again one of these species that somehow has managed to get there, but has not been able to spread further along the B. Barisan (see Schouten & Veldkamp, *Blumea* 30, 1985, 325).

**Notes.** The Malesian representatives and most of the Asian ones differ from the typical European form in the ratio between the length of the awn and the body of the first lemma. In Malesia the awn of the middle lemmas in a spikelet is at most  $\pm$  0.5 times as long as the body, rarely slightly longer, in Europe it is about as long.

Most authors give the basic chromosome number of *B. sylvaticum* as  $x = 9$ . In tropical Asia counts have been made which show that 7 also occurs:  $n = 14$  (Mehra & Sood, 1974),  $14 + 1B$  (Mehra & Sood, 1975) for specimens from the Khasi Hills, India, and  $2n = 14$  (Hsu, *Taiwania* 16, 1971, 236) for Taiwanese material.

All specimens of *B. sylvaticum* that we have seen from the Khasi Hills and Taiwan are identical with most of the Malesian material, which sometimes has been called var. *luzoniense* (Hack.) Hara, a name also adopted by Hsu for his material. Tateoka (1962) also stated to have seen this variety from the Himalayas among material collected by Mr. Nakao.

The chromosome number  $x = 9$ , and the relatively short awns, suggest that these specimens indeed belong to an atypical variety. In fact it also occurs in Kashmir, from where Hooker f. described it as var. *pseudo-distachyon*, which name has been adopted in this study.

As far as the Malesian specimens are concerned we have the impression that they may be separated over two distinct varieties, one widespread in SE Asia, but not found in New Guinea, the other one restricted to New Guinea.

Hooker f. (1896) distinguished four varieties in India, based on the length of the pedicels, awns, pubescence of the callus, etc. Bor (1960) remarked that other abnormal forms could be cited as well, and accepted none. Yet, it seems to us that the var. *pseudo-distachyon* can be distinguished and is identical with a Malesian form. About the others we have no opinion.

There are sometimes 3 styles, rather frequently in the European material studied, less so in Malesia; its occurrence is variable within a single specimen.

var. *pseudo-distachyon* Hook. f.

- Brachypodium sylvaticum* (Huds.) Beauv. var. *pseudo-distachyon* Hook. f., Fl. Br. Ind. 7 (1896) 363. — Lectotype: *Jacquemont 705* (K, holo; P, n.v.), Kashmir.
- Triticum nubigenum* Nees ex Steud., Syn. 1 (1854) 342; Miq., Fl. Ind. Bat. 3 (1857) 401. — *Agropyron nubigenum* Nees ex Steud. ex Koord., Exk. Fl. Java 1 (1911) 164. — *Elymus nubigenus* Löve, Feddes Repert. 95 (1984) 469. — Type: not indicated, probably Junghuhn (not in L, P, fide R. D. Hoogland, in litt.), Java, G. Lawu ('Mons Sawu').
- Brachypodium involutum* Buse in Miq., Pl. Jungh. 3 (1854) 347. — *Triticum involutum* Miq., Fl. Ind. Bat. 3 (1857) 402. — *Brachypodium sylvaticum* (Huds.) Beauv. var. *involutum* Jansen, Reinwardtia 2 (1953) 242; Monod de Froideville in Backer & Bakh. f., Fl. Java 3 (1968) 519. — Type: *Junghuhn s.n.* (L, holo, no 904.84-63, iso), Java, Ceribon, summit of G. Careme ('Tjerimai'), 7-16 Aug. 1837.
- [*Brachypodium sylvaticum* (Huds.) Beauv. var. *glabrum* O. Ktze & forma *glaberrima* O. Ktze, Rev. Gen. Pl. 2 (1891) 763, both *nom. nud.* — Vouchers: *O. Kuntze s.n.* (NY, n.v.) Java, Dieng, 2300 m alt.]
- Brachypodium sylvaticum* (Huds.) Beauv. var. *asperum* Hack., Philip. J. Sc. 1, Suppl. (1906) 269. — Type: *Merrill 4698* (W, holo; K), Philippines, Benguet, Pauai to Baguio, 1770 m, 9 Nov. 1905.
- Brachypodium sylvaticum* (Huds.) Beauv. subsp. *luzoniense* Hack., Philip. J. Sc. 1, Suppl. (1906) 269; Merr., Philip. J. Sc. 1, Suppl. (1906) 387. — *Brachypodium sylvaticum* Beauv. var. *luzoniense* Hara, Bot. Mag. Tokyo 52 (1938) 228; Jansen, Reinwardtia 2 (1953) 241; Mehra & Sood, Taxon 23 (1974) 807; Mehra & Sood, Taxon 24 (1975) 512; Hsu, Taiwania 16 (1971) 126, 130; Fl. Taiwan 5 (1978) 428. — Lectotype: *Merrill 4536* (W, holo; K, L), Philippines, Luzon, Benguet, Lepanto, Mt. Data, Nov. 1905 (here appointed).
- Brachypodium formosanum* Hayata [Icon. Pl. Form. 6, Suppl. (1917) 94, *nomen*] Icon. Pl. Form. 7 (1918) 93, t. 57. — Type: 'Taiwan, Hakkutaisan' (= 'Pai-kou-ta Shan') (n.v.).
- Bromus pauciflorus* auct. non (Thunb.) Hack.: Merr., Philip. J. Sc. 1, Suppl. (1906) 386; Enum. Philip. Fl. Pl. 1 (1923) 92.
- Brachypodium pinnatum* auct. non (L.) Beauv.: De Castro, Garcia de Orta 12 (1964) 60.

Plants more or less glabrous. Sheaths at most puberulous along the margins and at the contra-ligule; blades below (outside) more or less glabrous. Peduncle glabrous. Inflorescence rachis glabrous to microscopically puberulous. Glumes glabrous. Lemmas glabrous to microscopically spiculate. Lower glume (3-)3.4-5.7 (-6.5) mm long, in situ (0.33-)0.45-0.55(-0.65) times as long as the first lemma; upper glume (4.5-)5-7(-9) mm long. First lemma 6.9-8.2(-10.5) mm long.

**Distribution.** Kashmir, Sikkim, India (e.g. Khasi Hills, Assam; Nilgiri Hills, Tamil Nadu), Sri Lanka to Taiwan; Malesia: Sumatra (G. Leuser complex), Java (from the G. Papandayan eastward), Lesser Sunda Islands (Bali, Lombok, Timor), Celebes (G. Bonthain), Philippines (Luzon, Benguet Prov.), Moluccas (Ceram).

**Ecology.** Open places in grassfields, in *Casuarina*-, *Eucalyptus*-, oak-forest, (1500-)2000-3400 m.

**Chromosome numbers.**  $n = 14$  (Mehra & Sood, Taxon 23, 1974, 807),  $14 + 1B$  (Mehra & Sood, Taxon 24, 1975, 512),  $2n = 14$  (Hsu, Taiwania 16, 1971, 126).

Collector's notes. Very scanty: slender herb, bright green; spikelets green; anthers pale sulphurous.

Uses. Readily eaten by cattle with a satisfying nutritional value (Backer, 1950).

Vernacular names. Perketekan (Jav.).

Notes. *Triticum nubigenum* Steud. has been included here because of its description, which does not seem to fit any other Javanese grass. It was described from 'Mons Sawu', a misprint for 'Mons Lawu', where Junghuhn collected, and where var. *pseudo-distachyon* is common (fide *Afriastini 281, Buwalda 8136, Coert 288*). No authentic material has been mentioned by later authors, e.g. Miquel (1857), Koorders (1911), Backer (1928), Jansen (1953), Monod de Froideville (1968), and ourselves. It is therefore curious to note that Löve, without any comment, placed it in *Elymus* L. instead of in *Brevipodium*.

Hackel distinguished a var. *asperum* by the presence of rough culms. An isotype in K indeed was slightly rough but showed no other significant differences.

Hackel described var. *luzoniense* as 'Differt a typo omnibus partibus glaberrimum'. Duplicates of his syntypes have at least the nodes puberulous.

Jansen (1953) distinguished between var. *luzoniense* and var. *involutum* by the blades which in the first would be flat to loosely involute, and in the latter strongly setaceous involute. In fact the material shows a continuous range between flat and involute leaves, both conditions being present even on the same plant. Only in the Philippines the leaves were always flat. Other differences could not be found, however.

Merrill's references to *Bromus pauciflorus* seem to belong here. Swallen (US; in litt. to Van Steenis, 25 April 1952) reported that "Clemens 9204 is *Brachypodium sylvaticum*. We have Merrill 4714 and 4830 which ... are however out on loan." Jansen (1953) identified Merrill 4714 (UC) and Merrill 11729 (L) also as this species. The latter was labeled '? *Bromus pauciflorus*' by Merrill. This and Merrill 4830 (W) are the var. *pseudodistachyon*.

The record of *B. pinnatum* for Timor by De Castro (1964) is erroneous as far as the cited specimen *van Steenis 18448* is concerned. As Cinatti collected in the same area (Van Steenis, oral comm.), his collection (*no. 6*) is most likely the present taxon.

In Pauai, Benguet Subprov., Luzon, a curious form, introduced as *Bromus inermis* Leyss., has been cultivated. This differs from the other Philippine material by having a densely sericeous foliage and puberulous peduncles and inflorescence axes. The ratio of lower glume in situ against the first lemma is slightly larger than in var. *pseudo-distachyon* (0.56–0.6) because the first lemma is longer than usual in that variety (8–8.6 mm). It was distributed as *Bromus commutatus* Schrad (cf. Merr., Enum. Philip. Fl. Pl. 1, 1921, 93). Henrard labeled the Leiden specimen of BS 31966 (*Santos*) as '*Brachypodium holosericeum*', an unpublished name. The other specimen, Merrill 6627, has not been seen. Jansen (1953) included BS 31966 under var. *pubifolium*, but to us it seems to represent the var. *sylvaticum*, which is hairy.

var. **pubifolium** (Hitc.) Jansen

*Brachypodium sylvaticum* (Huds.) Beauv. var. *pubifolium* (Hitc.) Jansen, *Reinwardtia* 2 (1953) 242, excl. *BS 31966*; Henty, *Bot. Bull.*, Lae 1 (1969) 42; Veldk. & Royen in Royen, *Alp. Fl. New Guinea* 2 (1979) 1112, f. 361. — *Brachypodium pubifolium* Hitc., *Brittonia* 2 (1936) 108. — T y p e: *Brass 4650* (NY, holo, BM, K, L; US, n.v.), Papua New Guinea, Central Prov., Wharton Range, Murray Pass, 2840 m alt., 29 July 1933.

*Brachypodium sylvaticum* var. *luzoniense* auct. non Hack.: Jansen, *Reinwardtia* 2 (1953) 241, quoad specim. New Guinea; Henty, *Bot. Bull.*, Lae 1 (1969) 42.

Plants more or less pubescent. Sheaths, lower (outside) surface of the blades, peduncle, and inflorescence rachis subglabrous to densely sericeous. Glumes usually more or less setulosely hairy; lower glume (4–)4.3–7.5 mm long, in situ (0.43–) 0.46–0.75 times as long as the first lemma; upper glume 6–9.3(–10.5) mm long. First lemma 8–11 mm long, more or less setulosely hairy.

**D i s t r i b u t i o n.** New Guinea, from Mt. Carstensz in Irian Jaya to the Milne Bay Prov. (Mt. Aniata).

**E c o l o g y.** Subalpine grasslands, grassy scrubs, bogs to well-drained peaty soils, locally common, at lower altitudes along rivers on wet, mossy rocks, (1750–) 2700–3830 m alt.

**C o l l e c t o r ' s n o t e s.** Culms solitary to tufted, erect to scrambling, up to 1 m long, leaves dull to silvery, pale green, inflorescences nodding, (pale) green, anthers white to yellowish, stigmas white.

**V e r n a c u l a r n a m e.** Eso (Mendi), probably meaning 'grass'.

**N o t e s.** It is possible that in New Guinea two forms may be distinguished: a less and a more hairy one. They usually, but not always, grow together and next to a difference in breadth of their vertical ranges a difference in ecology was noted by JFV in the Star Mts. of Papua New Guinea where the ranges overlapped: the more glabrous form grew in the edge of a calcarous *Ectropothecium* bog (*Veldkamp 6261-a*), while the more hairy one was found in low *Eurya* scrub in the *Deschampsia* tussock grassland (*Veldkamp 6262*). Coode & Stevens also noted on the label (*NGF 46314*) of the 'hairy form': 'found in tussock of ... *Brachypodium*', indicating that they, too, thought that there were two forms in the field. In the herbarium, however, the difference lies mainly in the density of the pubescence and in intermediate specimens a decision as to which of the two forms a specimen belonged was found to be rather arbitrary and unsatisfactory.

The hairy plants from Luzon (*BS 31966*) cited by Jansen (1953) represent var. *sylvaticum* from Europe, introduced and cultivated in Pauai.

## ELYMUS

*Elymus* L., *Sp. Pl.* 1 (1753) 83; Clayton & Renvoize, *Gen. Gram.* (1986) 150. — L e c t o - t y p e: *Elymus sibiricus* L.

Tufted perennials without rhizomes. Leaves usually flat. Ligule short. Racemes with a usually tough rachis. Spikelets homomorphous, sessile (in *E. longisetus* sometimes with a pedicel up to 5.5 mm!), solitary or, at least in the middle of the

spike, 2 or 3 together, up to 20-flowered, laterally compressed. Glumes not subulate, flat, margins usually scarios, back not keeled, veins (1–)3–10, usually scabrous. Lemmas awned, callus subglabrous to pilose, 5–7-nerved, lateral nerves distally anastomosing. Anthers 3. Lodicules glabrous to ciliate. Styles inserted just below the terminal appendage of the ovary and adnate to it. Caryopsis tightly enclosed by the palea, adnate to it or not; hilum linear,  $\pm$  as long as the fruit, embryo small; starch grains simple, of various sizes. Genomic formula HS, HHS, HSS, HHSS.

**Distribution.** About 140 species in temperate areas and tropical mountains. One section in Malesia:

### Section *Anthosachne*

*Elymus* sect. *Anthosachne* Tsvet., Nov. Syst. Pl. Vasc. 10 (1973) 25. — *Anthosachne* Steud., Syn. 1 (1854) 237. — *Agropyron* Gaertn. sect. *Anthosachne* Melderis in Bor, Fl. Iran 70 (1970) 168. — **Lectotype:** *Anthosachne australasica* Steud. [= *Elymus australasica* (Steud.) Tsvet. = *E. rectisetus* (Nees) Löve & Connor].

Spikelets solitary, in 2 rows, laterally facing the rachis, sessile to shortly pedicelled, breaking up below the 6–12 lemmas. Glumes  $\pm$  unequal, distinctly 3–7-nerved. Lemma with a canaliculate to flat awn.

**Distribution.** About 23 species in temperate E Europe and Asia (Iraq to Japan), tropical mountains of Africa (Ethiopia), Asia (Himalaya), Malesia (1 in New Guinea), Australia, New Zealand, Norfolk Island.

### *Elymus longisetus* (Hitchc.) Veldk., *comb. nov.*

*Brachypodium longisetum* Hitchc., Brittonia 2 (1936) 107; Henty, Bot. Bull., Lae 1 (1969) 42; Veldk. & Royen in Royen, Alp. Fl. New Guinea 2 (1979) 1115, f. 362. — **Lectotype:** *Brass* 4446 (NY, holo, K, L; US, n.v.), Papua New Guinea, Central Prov., Mt. Albert Edward, upper Chirima River, 3600 m alt., 10 July 1933 (designated by Veldk. & Royen, 1979).

Perennial, loosely tufted grass, 50–80 cm high, at base intra- and extra-vaginally branched. *Cataphylls* up to 5 cm long, usually hairy, yellowish brown. *Culms* erect, simple, terete,  $\pm$  glabrous. Nodes blackish,  $\pm$  glabrous. *Sheaths*  $\pm$  glabrous to pilose; auricles present or not; ligule 0.6–1 mm long, rounded; blades flat to loosely involute, 9–33 cm by 1–5 mm,  $\pm$  glabrous to  $\pm$  patently pilose, above more densely so. *Inflorescences* nodding, 7–20 cm long. Pedicels up to 1(–5.5) mm long, puberulous. *Spikelets* 4–10, cleistogamous, 4–10-flowered, laterally flattened, 3.5–7 cm long (incl. awns), glabrous. *Glumes* acute; lower glumes 5–15 mm long, 3–5-nerved; upper glumes longer, 6–18 mm long, 5–7-nerved. Joints of the rachilla 2–3 mm long, appressed puberulous to setulose, especially below the callus; process with a vestigial lemma. *Lowest lemmas* lanceolate, 12–16 mm long, dorsally rounded, sparsely puberulous, margins not scarios, setulose; 5–7-nerved, lateral veins confluent below the awn; callus c. 1 mm long, pilose, scar oblique, ovate to ellipsoid; awn 3.2–4.2 cm long (the higher ones shorter), antrorsely scabrous. *Paleas* slightly shorter than the lemmas, apex bidentate to retuse, puberulous between the 2

setulose keels. *Lodicules* obcuneate with 2 unequal apices (see note), c. 2 mm long, apices with a few hairs. *Anthers* 3, 1.5–2 mm long. *Caryopsis* flat, c. 7.5 by 1 mm (unripe), castaneous.

**Distribution.** Papua New Guinea, Western Highlands (Sugarloaf), Chimbu (Mt. Wilhelm), Morobe (Mt. Saruwaket), Central (Mt. Albert Edward, Isuani Basin, Wharton Range), and Milne Bay Prov. (Mt. Suckling).

**Ecology.** Open subalpine treefern grassland, grassy hills, banks of streams, bogs, along paths, dry stony flats with short grass and shrubbery, often growing in other grass tussocks, (1750–)2750–3600 m alt.

**Collector's notes.** In smallish clumps or solitary, glaucous. Leaves light green. Spikelets green, greyish green.

**Vernacular name.** Tangugip (Engga, Poio).

**Notes.** This species is very much like the bewilderingly variable *E. scaber* (R. Br.) Löve, which is very much in need of a thorough revision. Pending that, it seems best not to add to the confusion, and to keep *E. longisetus* separate. At present it seems distinct by a combination of characters: ligules slightly longer, rounded, clasping auricles always absent, glumes and lemmas usually broader, lemmas usually more distinctly nerved.

*Hoogland & Schodde 7049* is slightly aberrant by the presence of a purplish, not green inflorescence, and relatively short awns, only 1.1 cm long. Similar forms are also present in *E. scaber*.

The lodicules seem different from the ones depicted by Tateoka (J. Jap. Bot. 37, 1962, f. 1–7) by having a lateral lobe.

#### ACKNOWLEDGEMENTS

This study was made as part of a course in advanced Angiosperm taxonomy by HJS under the guidance of JFV based on the material available in L, and that seen during brief visits by JFV in B, BM, K. The latter author finished the manuscript. The loan of Hackel's specimens from W is gratefully acknowledged. Dr. C.E. Jarvis is thanked for checking the presence of type material of *Brachypodium* in BM and LINN, and Dr. R.D. Hoogland for that in P. Mr. B.K. Simon (CANB) advised on the generic identity of *Australopyrum uncinatum*. The Keeper of K kindly informed us that the isotype supposedly present there could not be found, while the Keeper from E allowed us to loan the one present there. Both are thanked for their assistance.

#### INDEX TO COLLECTIONS

Only numbered collections have been included. Specimens not seen, but of which the identity seemed certain, have been included with the identity number between brackets.

- 1 = *Australopyrum uncinatum* Veldk.
- 2 = *Elymus longisetus* (Hitchc.) Veldk.
- 3a = *Brachypodium sylvaticum* (Huds.) Beauv. var. *pseudo-distachyon* Hook. f.
- 3b = *Brachypodium sylvaticum* (Huds.) Beauv. var. *pubifolium* (Hitchc.) Jansen

Afriastini 281: 3a – ANU 7630 (Wade): 3b; 10954 (Hope): (3b); 10975 (id.), 15140 (J.M.B. Smith): 3b; 15508 (J.M.B. Smith): 2.

Backer 30311: 3a – van Balgooy 727: 3a/b – Brass 4446: 2; 4650: 3b; 4732: (2); 9310, 11426, 29999, 30081-A: 3b – Brass & Collins 31003: 3b – Brass & Meijer Drees 9714: (3b); 9827: 3b – Brinkman 756: 3a – BS 31966 (Santos): see notes under 3a & 3b; 40180 (Ramos & Edaño), 40237 (id.), 40739 (id.), 44924 (id.): 3a – Bünnemeyer 12083: 3a – Buwalda 8136: 3a.

Cinatti 6: (3a) – Clemens 6116: 2; 6117, 6118, 6118-a: 3b; 6141: 2; 7433: (3b); 9091: 3a; 9204: (3a); 9442c, 10017-A: 3b; 10017-A1: (2); 10055-D: 3b; 10078-bis3: 2; 10078-bis4, 10078-A2: 3b; 10078-A4: 2; 10078-B: 3b; 10078-C: (2); 10097-A: 3b; 11346: 2 – Co 1370: 3a – Coert 288: 3a – Coode & Stevens, see NGF-series – Craven 2863: 3b; 2864: 2 – Croft et al., see LAE-series – Cruttwell 1077, 1289: 3a.

Demoulin 5580: 3b – Docters van Leeuwen 13151: 3a.

Elbert 1349: 3a – Engler 5120: (3a) – Eyma 2074: (3a).

Gillison, see NGF-series.

Hartley 11158: (3b) – Henty & Carlquist, see NGF-series – Hernaez 3516, 3533: 3a – Hoogland 9941: 3b – Hoogland & Pullen 5752: 3b – Hoogland & Schodde 7049: 2 – Hope, see ANU-series.

Koorders 43566, 43631, 43815: 3a.

LAE 54470 (Stevens & Veldkamp): 3a; 54612 (Stevens & Grubb): 3b; 65112 (Croft et al.): 1; 68205 (Croft & Akakavara): 3b.

Mangen 1213: 3b – Merrill 4536: 3a; 4698: (3a); 4710, 4714: 3a; 4830: (3a); 6627: see note under 3a; 11729: 3a.

NGF 16576 (Henty & Carlquist), 25099 (Gillison): 3b; 30106 (van Royen): 2; 39609 (Vandenberg): 3b; 46314 (Coode & Stevens): 3b.

Paijmans 1264: 2 – Pullen 5119, 6078: 3b.

Ramos & Edaño, see BS-series – Raynal 17344: 3b – van Royen, see NGF-series.

Santos 5907, 5933, 5933a, 5994, 5996, 7349, 7994, 7996, 7998, 8022: 3a – Schodde 1967: 3b – J.M.B. Smith, see ANU-series – van Steenis 4106, 4256, 4552, 4822, 7069, 7833, 8603, 10957, 18448: 3a – Stevens & Grubb, see LAE-series.

Tengwall 40: 3a.

Ueda et al. C-4372: 3a.

Vandenberg, see NGF-series – Vanoverberg 3938: (2) – Veldkamp & Stevens 5593: 2; 5669, 5767: 3b; 5914: 2; 5993, 6261-a, 6262, 6576: 3b.

Wade, see ANU-series – Wiakabu & Demoulin 5580: 3a – de Wilde & de Wilde-Duyfjes 16191, 16369: 3a.

Zollinger 2840: 3a.