

Genus *Vigna* and Cowpea (*V. unguiculata* [L.] Walp.) taxonomy: current status and prospects

R.S. Pasquet^{1*} and S. Padulosi²

¹ICIPE, PO Box 30772, Nairobi, Kenya

²Biodiversity International, Via dei Tre Denari, Maccaresse (Rome), Italy

*Corresponding author: rpasquet@icipe.org

Abstract

Since the mid-nineties, thanks to DNA sequence studies, phylogeny of Phaseoleae, Phaseolinae, and genus *Vigna* has been greatly improved. Genus *Vigna* is now reduced to a monophyletic group including five reorganized subgenera: American subgenus *Lasiospron*, a subgenus *Vigna* reduced to yellow and blue-flowered species which includes Bambara groundnut, subgenus *Haydonia*, Asian subgenus *Ceratotropis*, and a subgenus *Plectrotropis* enlarged to all pink-flowered species. At the infraspecific level, although a precise phylogeny is not yet established, the different wild and domesticated cowpea groups are now well known. The nine subspecies can be split between a “mensensis” forest group (remote secondary gene pool) and a “dekindtiana” savanna group (close secondary gene pool) which includes subsp. *unguiculata*. Subsp. *unguiculata* represents the primary gene pool and includes the domesticated cowpea, var. *unguiculata*, and its wild progenitor, var. *spontanea* (previously known as subsp. *dekindtiana sensu* Verdcourt non Harms). However, if cowpea domestication occurred before 1500 BC in Harlan’s African non-center, a precise center of domestication is yet to be identified.

Introduction

Over the last 30 years, cowpea and *Vigna* taxonomy has been reviewed by several workers, including Baudoin and Maréchal (1985), Ng and Maréchal 1985, Pasquet 1996a, Pasquet 1996b, and Padulosi and Ng (1997) with substantial improvement. It is however particularly from the mid-nineties onward, that novel molecular technologies applied to taxonomy, such as DNA finger printing, have provided major advancement on the front of the phylogeny of Phaseoleae, Phaseolinae, and genus *Vigna*. With regard specifically to cowpea, studies have revealed at the same time that trnK/matK sequences as well as ITS have not been variable enough to improve the infraspecific phylogeny of this crop, while SSRs and SNPs will likely appear too variable (as in the case for AFLPs or RAPDs) to help infraspecific biosystematics. Within cowpea’s immediate gene pool, great progress is recorded in its classification thanks to genetic diversity made available by well-targeted, collecting expeditions and phytogeographic surveys. In fact, while Maréchal et al. (1978) based their studies on just seven wild cowpea accessions, a lot of material was collected in the eighties (Padulosi 1990c) and taxonomists today can rely on more than a thousand samples.

Phaseoleae and Phaseolinae

Genus *Vigna* Savi belongs to tribe Phaseoleae DC. Within Leguminosae, the Phaseoleae is the largest tribe in term of number of genera and number of economically important species. The concept of a group of papilionaceous legumes with trifoliolate leaves and twining stems developed at an early stage since genera presently placed in the Phaseoleae

were already associated in the first edition of *Species Plantarum* (Linnaeus 1753). De Candolle (1825) proposed the first rational classification of the tribe, and Bentham (1837, 1865), produced the first real synthesis, in which all the present subtribes were outlined. Based on morphological data, Lackey (1981) divided Phaseoleae into eight subtribes, viz. Cajaninae, Clitoriinae, Ophrestiinae, Kennediinae, Erythrinae, Diocleinae, Glycininae, and Phaseolinae.

In the nineties, DNA data (Doyle and Doyle 1993, Bruneau et al. 1994) demonstrated that Phaseoleae was a rather unnatural grouping. Phaseoleae was paraphyletic since Desmodieae was nested within Phaseoleae, and Phaseoleae was polyphyletic since several of its genera (from Ophrestiinae, Clitoriinae, and Diocleinae) appeared to be more closely related to members of Millettieae than to other Phaseoleae. This was subsequently confirmed using chloroplast and nuclear DNA sequences (Doyle et al. 1997, Lavin et al., 1998, Hu et al. 2000, Wojciechowski et al. 2004). Most of the constituent genera of Millettieae and Phaseoleae clade were therefore grouped into two very well-supported subclades, one including the majority of Millettieae, and one dominated by Phaseoleae. While subtribes Ophrestiinae and Diocleinae grouped with most Millettieae, the strongly supported Phaseoleae clade includes currently the following subtribes (Kajita et al. 2001, Wojciechowski et al. 2004):

- Erythrinae
- Glycininae
- Phaseolinae
- Kennediinae
- Cajaninae
- Desmodieae (except subtribe Bryinae)
- Psoraleae.

Within subtribe Phaseolinae, *Vigna* position has stayed always stable. Since Linnaeus (1753), species from genus *Vigna* were associated with genera *Phaseolus* and *Dolichos*. Bentham's (1837) subtribe Phaseolinae was built in fact on these two genera, with the inclusion also of the genera *Vigna*, *Lablab*, *Sphenostylis*, *Psophocarpus*, *Diesingia*, *Taeniocarpum*, *Dunbaria*, and *Pachyrhizus*. More recently, Lackey (1981) moved *Dunbaria* to Cajaninae, and *Pachyrhizus* to Diocleinae. Bruneau et al.'s (1994) cpDNA results confirmed this classification with a monophyletic Phaseolinae which included *Phaseolus*, *Vigna*, *Lablab* (*Dolichos* was not included in their study), *Sphenostylis*, and *Psophocarpus* (which appeared at the basis of the clade). With the exception of *Psophocarpus*, the whole group was characterized by a 78kb DNA inversion of the chloroplast genome (Bruneau et al. 1990), which highlighted its monophyletic trait. With *matK* sequence analyses, the delimitation of the subtribe Phaseolinae is now restricted to a monophyletic group excluding *Psophocarpus* and *Otoptera*, which are now known to be more closely related to Glycininae genera and including the following genera (grouped by clades) (Thulin et al. 2004, Delgado et al. 2011).

- *Wajira* (formerly included in Phaseolastrae),
- *Sphenostylis*, *Nesphostylis*, *Dolichos* and *Macrotyloma*, (excluded from Phaseolastrae)
- *Lablab*, *Dipogon*, *Spathionema* and *Vatovaea* (included in Phaseolastrae),
- *Physostigma*, *Vigna*, *Phaseolus* and closely allied genera (included in Phaseolastrae).

Within Phaseolinae subtribe, Baudet and Maréchal (1976) introduced the concept of Phaseolastrae, a cluster of a various genera characterized by species with a style with the inner face bearded, i.e., *Phaseolus*, *Vigna*, and minor allied genera. Excluded from the Phaseolastrae were the genera characterized by style with inner face glabrous, i.e., *Dolichos*, *Macrotyloma*, *Sphenostylis*, and *Nesphostylis*. The Phaseolastrae was the major focus of Maréchal et al. (1978). It is interesting to notice however, that this grouping was not validated by *matK* analysis as the *Wajira* genus (species with bearded style) showed to be paraphyletic to the clade including *Sphenostylis*, *Dolichos*, and other Phaseolastrae (Thulin et al. 2004). In the end, the Phaseolastrae includes all the genera characterized by a style with the inner face bearded, but with the exception of genus *Wajira*.

Genus *Vigna*

Savi created genus *Vigna* in 1824. Previously, all *Vigna* taxa were described as *Dolichos* or *Phaseolus*. Savi's genus *Vigna* included two species, *Vigna glabra* Savi and *V. villosa* Savi (now both *V. luteola* (Jacq.) Benth. synonyms). He separated *Vigna* from *Dolichos* based just on two morphological characters, i.e., standard callosities convergent versus divergent and pod curved versus straight. These traits appeared subsequently not as solid as discriminating traits as initially thought. Later, Bentham (1837) clearly separated *Vigna* from *Dolichos*, i.e., stigmatate lateral instead of terminal and style bearded instead of glabrous. He included present sections *Catiang* and *Plectrotropis* within genus *Vigna*. Walpers (1843) published the combination *Vigna unguiculata* (L.) Walp. a few years later and after 1845, almost all present *Vigna* taxa were described as *Vigna* (or *Phaseolus*) and no longer *Dolichos*.

While the distinction between *Dolichos* and *Vigna* seemed rather clear by the mid-nineteen Century, this was not the case for *Phaseolus* and *Vigna* which needed more time to be sorted out. For Bentham (1837), *Phaseolus* genus, characterized by a spiralized keel (straight in *Vigna*) included six sections: *Drepanospron*, *Euphaseolus*, *Leptospron*, *Strophostyles*, *Macroptilium*, and *Dysolobium*. This initially huge genus *Phaseolus* was gradually downsized with the removal of *Strophostyles* in 1822, of *Dysolobium* in 1897, and of *Macroptilium* in 1928. But the main change was made by Wilczek in 1954, who characterized *Vigna* species by their produced stipules and style prolonged beyond the stigma by a beak. Such a concept led to the transfer of the whole Asiatic section *Ceratotropis* from *Phaseolus* to *Vigna*.

In 1970, Verdcourt (1970) went one step further. He gave a very restricted concept of *Phaseolus* (species with a tightly coiled style and a pollen exine devoid of wide reticulation). After moving to *Vigna* sections *Sigmoidotropis*, *Cochlianthus*, and *Lasiospron*, *Phaseolus* then became a very homogenous natural group, well characterized by the presence of hooked hairs. On the other hand, *Vigna* became much enlarged and contained three subgenera from the Old World and three neotropical subgenera representing the excluded sections of *Phaseolus*. Even if *Vigna* did then appear as a "rag bag" genus, to use Verdcourt's own words, Verdcourt showed that the different groups inside *Vigna* most probably had closer phyletic affinities between themselves than with members of *Phaseolus*. Maréchal et al. (1978) confirmed Verdcourt's concept and thus moved the section *Leptospron* (i.e., *Phaseolus adenanthus* G.F.W Mey.), to genus *Vigna*. Maréchal's genus *Vigna* became a very wide taxonomic group of 87 species with these further interpretations.

The advent of chloroplastic and nuclear DNA characterization (Delgado et al. 1993, Vaillancourt et al. 1993, Thulin et al. 2004, Delgado et al. 2011, Feleke et al., unpublished data) led to a very different picture of the *Phaseolus*–*Vigna* group, i.e., a complex of no less than 20 genera corresponding to former Baudet and Maréchal's Phaseolastrae 12 genera. With the move of subgenus *Macrorhynchus* to genus *Wajira* (Thulin 2004) and the exclusion of subgenera *Sigmoidotropis* and *Leptospron* from genus *Vigna* (Delgado et al. 2011), the genera (grouped by clades) closely linked to *Phaseolus* and *Vigna* are now:

- *Physostigma*
- *Vigna*
- *Oxyrhynchus*, *Ramirezella*, and *Phaseolus*
- *Cochliosanthus* and *Condylostylis*
- *Ancistrotropis* and *Sigmoidotropis*
- *Helicotropis* and *Leptospron*
- *Macroptilium*, *Mysanthus*, *Dolichopsis*, and *Strophostyles*.

Harms (1915) can be credited with having developed the first *Vigna* infrageneric classification. Although the present subgenus *Ceratotropis* and *V. kirkii* (Baker) Gillett were kept in *Phaseolus*, his four-section-based classification was indeed very accurate: section *Microdontae* included Verdcourt's subgenera *Vigna* and *Haydonia*, the section *Appendiculatae* included present section *Catiang*, the section *Macrodontae* included present sections *Macrodontae* and *Reticulatae* (which was surprisingly pooling all taxa with a purple flower and a $2n = 20$ chromosome number), and the section *Vexillatae* fitted Verdcourt's subgenus *Plectrotropis*. E.G. Baker (1929) modified this classification by adding a section *Liebrechtsia* dedicated to pyrophytic taxa and a section *Procerae* meant to include only *Vigna procera* Hiern (it must be added though that the discriminating characters used by Baker (i.e., pyrophytic vs non pyrophytic and calyx-lobe length) appeared of poor taxonomic value in the end).

Verdcourt's enlarged genus *Vigna* (1970) was accompanied by the creation of several subgenera and sections. His genus *Vigna* included eight subgenera (*Vigna*, *Plectrotropis*, *Ceratotropis*, *Macrorhynchus*, *Haydonia*, *Dolichovigna*, *Sigmoidotropis*, and *Cochliosanthus*), and his subgenus *Vigna* included nine sections (*Vigna*, *Condylostylus*, *Macrodontae*, *Lasiospron*, *Catiang*, *Liebrechtsia*, *Procerae*, *Reticulatae*, and *Glossostylus*). However, while Verdcourt's (1970) work on *Vigna* will always be considered as the major contribution towards the proper taxonomy of this genus, his infrageneric classification may be seen as somewhat weak since it did not solve some major inconsistencies of E.G. Baker's work. For instance, Verdcourt overemphasized the importance of the pocket of the keel (which made him overrank *Plectrotropis*) and the pyrophytic habit (which made him create a superfluous subgenus *Plectrotropis* section *Pseudoliebrechtsia* and retain section *Liebrechtsia*). Maréchal et al. (1978) slightly improved this infrageneric classification, especially with the creation of subgenus *Vigna* section *Comosae* and an enlarged subgenus *Haydonia* with three sections (*Haydonia*, *Microspermae*, and *Glossostylus*). On the other hand, they failed to correctly assess *Plectrotropis* by assigning too much importance to the trait of style and keel spiralization. Maréchal's classification included seven subgenera, i.e., *Vigna*, *Haydonia* (including all species with smooth pollen grains), subgenus *Plectrotropis* (including *V. vexillata* and allied species), Asian subgenus *Ceratotropis*, American subgenus *Lasiospron*, American subgenus *Sigmoidotropis*, and subgenus *Macrorhynchus*.

The genus was also further divided by these authors into 18 sections. With regard to the setting of the taxonomic boundaries of the genus *Vigna*, recent cpDNA data (Vaillancourt et al. 1993, Delgado-Salinas et al. 2011, Feleke et al. unpublished) have contributed to redesign the genus, now pruned of its subgenera *Sigmoidotropis* and *Macrorhynchus* and reduced it to only five subgenera:

1. *Lasiospron* (American subgenus)
2. *Vigna* (now including only yellow and blue flowered species and comprising the cultivated species *Vigna subterranea* (L.) Verdc.)
3. *Haydonia* (now reduced to two sections, viz. *Haydonia* and *Glossostylus*)
4. *Ceratotropis* (Asian subgenus with three sections viz. *Ceratotropis*, *Angulares*, and *Aconitifoliae* (Tomooka et al. 2002),
5. *Plectrotropis* (enlarged from previous classifications and bringing together all the pink-flowered species under four sections viz. *Plectrotropis*, *Macrodonatae*, *Reticulatae*, and *Catiang*). The section *Catiang*, which is characterized by peltate stipule (i.e., stipule prolonged below insertion point by a single appendage), includes two species, the cowpea *V. unguiculata*, and its sister species *V. schlechteri* Harms (formerly *V. nervosa* Markotter).

This reduced genus *Vigna* still includes 80 species. While several of Maréchal's subgenera were removed from genus *Vigna*, several infraspecific *Vigna* taxa needed a species status, i.e., *V. parviflora* Baker, *V. pubigera* Baker, *V. pseudovenulosa* (Maréchal et al.) Pasquet and Maesen, *V. trinervia* (Wight & Arnott) Tateishi & Maxted, *V. caesia* Chiov., and *V. hapalantha* Harms. In addition, a few new species were described, i.e., *V. verdcourtii* Pasquet, *V. nyangensis* Mithen, *Vigna exilis* Tateishi and Maxted, *Vigna nepalensis* Tateishi and Maxted, *Vigna tenuicaulis* Tomooka and Maxted, and *Vigna aridicola* Tomooka and Maxted. With regard to the regional spread of *Vigna* out of 80 species, seven are of American origin (subgenus *Lasiospron*), 21 are Asian (subgenus *Ceratotropis*), and 52 are African species. The African species now represent the bulk of all *Vigna* species. But this has not been always the case. From Linnaeus' Species Plantarum first edition (1753) to 1827, the taxa described were all domesticated (four out of the five present cowpea cultigroups, bambara groundnut, Asian domesticated *Vigna* species) or of pantropical origin (*V. vexillata* (L.) A.Rich., *V. marina* (Burm.) Merr., and *V. luteola*) and surprisingly none from African specimens. The first African taxa were described during the 1830s mainly from coastal areas such as those from Ghana (by Schumacher and Thonning 1827), Senegal (by Guillemin et al. 1832), Sao Tome (Don 1832), and South Africa (Meyer 1836). The 1840s marked a change in this trend with major studies on inland African *Vigna* such as those of Richard (1847) and Hooker and Bentham (1849). The greatest contributors in identifying new taxa on African *Vigna* were Baker (1871) with 12 taxa, Harms (1915) with 11 taxa, Wilczek (1954) with eight taxa, Verdcourt (1970) with five taxa, and Maréchal et al. (1978) with four taxa.

Wild cowpea

Due to its economic importance, cowpea, *Vigna unguiculata*, can be considered as the main African species within *Vigna*. It includes the domesticated cowpea in its different forms (called cultivar groups), its wild progenitor, and few closely allied taxa. It is interesting to note that from 1800 to 1970, 21 supposedly new taxa were described from specimens that were subsequently identified as wild *V. unguiculata*. The first ones were described as

Dolichos species but Walpers started to move these taxa into the genus *Vigna* in 1839. The link between wild and domesticated cowpea started to be mentioned by Richard in 1847. It was much discussed by Kornicke in 1885, and definitely proved by Piper in 1913. In the meantime, Schweinfurth described *V. sinensis* (L.) Hassk. var. *spontanea* Schweinf. in 1896. At the beginning, most wild cowpea were described as independent species and during the 1930s we record the greatest split as far as *Vigna unguiculata* is concerned: seven species in E.G. Baker 's (1929) treatment, and five species in Burt Davy's (1932) work on Transvaal-Swaziland flora. These wild species were progressively merged, especially by Verdcourt (1970). In the end, Maréchal et al. (1978) considered all of them under the same species. We believe that Maréchal's lumping of the wild cowpea variants under a single species is one of his greatest scientific contributions.

However, if Verdcourt can be considered as the *Vigna unguiculata* concept godfather, he also contributed to the confusion surrounding wild cowpea infraspecific taxonomy. While he cleverly pointed out the main split between forest taxa and savanna taxa, he very unfortunately chose type specimens destroyed during the 1943 March bombing of the Berlin herbarium. He chose *Vigna mensensis* Schweinf. as a type specimen of the forest taxon, and *Vigna dekindtiana* Harms as a type specimen of the main savanna taxon, on the basis of poor isotype specimens kept respectively in Lisbon and Brussels. Then, his subsp. *mensensis sensu* Verdc. and subsp. *dekindtiana sensu* Verdc. became widely used, and misused. The discovery of an excellent *V. mensensis* isotype in Geneva confirmed that *V. mensensis* was a *V. membranacea* A. Rich. synonym (Padulosi 1993, Pasquet 1993), therefore not that of a wild cowpea. Later, discovery of a fertile *V. dekindtiana* isotype in Montpellier also confirmed that *V. dekindtiana* was a *V. huillensis* Baker synonym (Pasquet 1993). However, if the name *V. huillensis* is older by 30 years, subsp. *dekindtiana* is older in the subspecies rank thanks to Verdcourt, and the name subsp. *dekindtiana* (Harms) Verdc. must be applied to the perennial wild cowpea subspecies from South Angola. However, subsp. *dekindtiana sensu* Verdc. non Harms was unfortunately widely used to designate the very common and widely distributed wild/weedy annual cowpea, i.e., subsp. *unguiculata* var. *spontanea*. (Schweinf.) Pasquet.

Since Maréchal et al. (1978), wild cowpea infraspecific taxonomy has greatly improved, thanks to the study of living material through morphology (Padulosi 2003) and isozyme polymorphism (Pasquet 1999). Surprisingly cpDNA RFLP, *trnK/matK* and nuclear ribosomal ITS DNA sequences (Vaillancourt and Weeden 1992, Feleke et al. unpublished) failed to provide a reliable phylogeny for this group. The only phylogeny is derived in fact from isozyme work. That means that the hypothesis of a wild cowpea origin in southern Africa (Baudoin and Maréchal 1985) is yet to be corroborated by genetic studies.

Padulosi (1993) studied exhaustively all morphology aspects, and, in the end, few morphological characters appeared useful to discriminate cowpea infraspecific taxa: stem, leaf, and pod pubescence, inflorescence rachis, flower size, calyx-lobe length, keel and style twisting, and number of ovules per pod. In addition, though not a subspecies discriminating character, stigma orientation is an important character controlling breeding system.

Most subspecies have scabrous stems and pods although subsp. *tenuis* (E.Mey) Maréchal et al. have smooth stems and subsp. *baoulensis* smooth black pods. Subsp. Most subspecies have scabrous stems and pods although subsp. *tenuis* (E.Mey) Maréchal

et al. have smooth stems and subsp. *baoulensis* smooth black pods. Subsp. *pubescens* (R.Wilczek) Pasquet shows stems and pods densely pubescent with appressed white hairs almost devoid of basal glands. Var. *protacta* (E.Mey.) Verdc. shows pods and stems bristly pubescent with straight and stiff hairs whose basal glands are very raised above the surface conferring a unique rough appearance to the plant surfaces.

Inflorescence rachis is reduced to one node in subsp. *tenuis* only. All subspecies show short internodes except subsp. *pubescens* which is characterized by long internodes (Fig. 1).

Keel shape seems to be one of the most important characters. Seen from the top, the tip of the keel is twisted toward the left in subsp. *dekindtiana sensu stricto*, subsp. *baoulensis*, subsp. *pawekiae*, and subsp. *stenophylla sensu lato*. The tip of the keel is twisted toward the right (sometime very slightly) in all other subspecies (Fig. 2). Inside the keel, the style is also twisted. Seen from the right side, stigmatic surface and hair brush are in front when the keel is twisted toward left while they are behind when the keel is twisted towards the right (Fig. 2). In addition, the keel can show a rather long beak in subsp. *dekindtiana*, a short beak (usually associated with a twisting toward the right) or no beak at all (usually associated with a twisting towards the left [Fig. 3]).

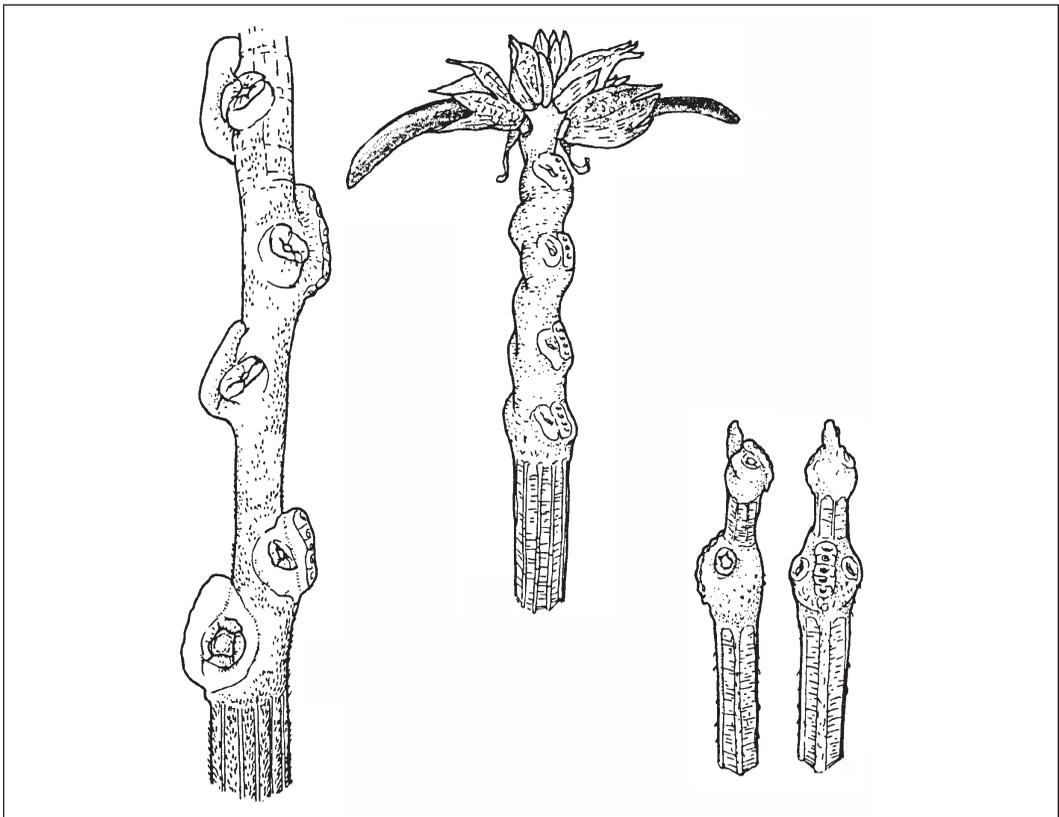


Figure 1. Inflorescence rachis. From left to right, subsp. *pubescens* (multinoded rachis with long internodes), subsp. *unguiculata* var. *spontanea* (multinoded rachis with short internodes) and subsp. *tenuis* (one-two-noded rachis).



Figure 2. Keel (seen from top of the inflorescence) and style twisting. From left to right: subsp. *unguiculata* var. *spontanea* keel (twisted toward right), subsp. *baoulensis* keel (twisted toward left), subsp. *unguiculata* var. *spontanea* style (twisted toward right with an autogamous morphology), subsp. *baoulensis* style (twisted toward left with an allogamous morphology).

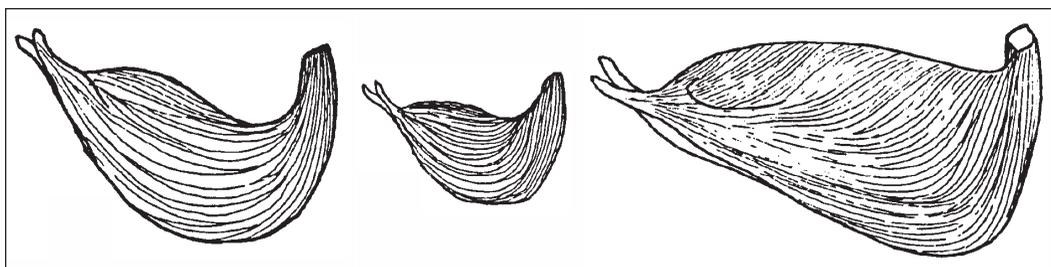


Figure 3. Keel shape. From left to right: subsp. *dekindtiana* (keel with a beak up to 6 mm long), subsp. *unguiculata* var. *spontanea* (keel with a short beak), subsp. *baoulensis* (keel with no beak).

Stigmatic surface orientation and other style and stamen morphological traits directly influence breeding system (Lush 1979). Figure 3 shows subs. *baoulensis* allogamous morphology, with an upward looking stigmatic surface protected by a beard preventing its pollen from reaching it, and a style brush (where pollen accumulates at the anthesis) stopping a few mm below the stigmatic surface. In addition, subs. *baoulensis* anthers are a few mm below the stigmatic surface, and the absence of keel beak makes the stigmatic surface almost outside the keel. On the other hand, Figure 3 shows subs. *unguiculata* var. *spontanea* autogamous morphology with a sideward looking stigmatic surface directly in contact with the style brush. In addition, subs. *unguiculata* var. *spontanea* anthers are just facing and in contact with the stigmatic surface, and the keel beak keeps the stigmatic surface well inside the keel.

Taking into consideration both morphological and molecular data we are inclined to suggest a cowpea genepool split between two main groups of taxa: (1) a forest group including subs. *pawekiae* Pasquet, subs. *baoulensis* (A.Chev.) Pasquet, and subs. *letouzeyi* Pasquet; and (2) a savanna group including subs. *dekindtiana* (Harms) Verdc., subs. *stenophylla* (Harv.) Maréchal et al., subs. *alba* (G.Don) Pasquet, subs. *tenuis*, subs. *Pubescens*, and subs. *unguiculata*.

Since both terms have been widely used since 1970, we could refer instead to the forest group as the “**mensensis group**” and the savanna group as the “**dekindtiana group**”. A few morphological characters make the nine wild cowpea subspecies grouped under these two clusters easy to be identified:

1. Keel twisted towards the left, with a marked beak 6–8 mm long, calyx-lobe 2–5 mm long, flower 24–33mm long, pod 13–15 ovuled **subsp. dekindtiana**.
2. Keel twisted toward left with a short beak or without beak
Calyx-lobe 5–15 mm long, flower 20–32 mm long, pod 15–18 ovuled **subsp. pawekiae**.
3. Calyx-lobe 2–6 mm long, pod 10–14 ovuled **subsp. stenophylla**.
4. Calyx-lobe 0.5–2 mm, pod 16–20 ovuled, pod black and smooth, flower 24–38 mm **subsp. baoulensis**.
5. Keel twisted toward right with a short beak up to 3 mm long
Pubescent stem, leaflet, and pod, long inflorescence internodes, calyx-lobe 1.5–5 mm, flower 17–24 mm, pod 13–17-ovuled **subsp. pubescens**.
6. Scabrous or smooth stem and pod, short inflorescence internodes
Inflorescence 1–2-noded, calyx-lobe 1–4 mm, flower 14–22 mm, pod 12–17-ovuled **subsp. tenuis**.
7. Inflorescence multinoded
Seed 3–6 mm long, calyx-lobe 4–15 mm, flower 23–30 mm, pod 17–21-ovuled **subsp. letouzeyi**.
8. Seed 2–3 mm long, calyx-lobe 0.5–4.5 mm, flower 17–23 mm, pod 16–22-ovuled **subsp. alba**.
9. Seed 3–5 mm long, calyx-lobe 1.5–4 mm, flower 15–23 mm, pod 10–18-ovuled **subsp. unguiculata**.

However, if Pasquet’s (1993) subsp. *letouzeyi* and subsp. *burundiensis* Pasquet need to be merged due to weak morphological differences and high similarity in ITS sequences (Feleke et al. unpublished data), further refinements of the proposed above classification are needed that would also consider the following pending issues:

- subsp. *aduensis* Pasquet (omitted from the key) could be merged with subsp. *pawekiae* or treated as a subsp. *pawekiae* variety.
- as suggested by Padulosi (1993) subsp. *tenuis* could be split between a highland taxon with smaller flowers and lower ovule number and a coastal taxon closer to subsp. *unguiculata*. Whether this subsp. *tenuis* offspring should be treated as a variety or as an additional subspecies is yet to be decided.
- subsp. *stenophylla sensu lato* is definitely made of three taxa, i.e., subsp. *stenophylla sensu stricto*, var. *kgalagadiensis* Mithen, and var. *protracta*. Whether the three taxa should be treated as three subspecies or three subsp. *stenophylla* varieties is yet to be decided.
- subsp. *unguiculata* is currently split between var. *unguiculata* (domesticated plants) and var. *spontanea* (wild plants). Few additional varieties could be considered.

For most of these decisions to be taken, living material is available but not adequately studied yet. The following part of our paper provides a description of the components of the two *mensis* and *dekindtiana* groups.

The *mensis* group

Although no DNA sequence phylogeny exists, the *mensis* group seems to be the primitive one according to the isozyme-derived phylogeny. The subspecies from the *mensis* group show a very high molecular diversity and a rather poor morphological variability: no special leaflet shapes, no pubescence, no inflorescence variability. Subsp. *pawekiae* and subsp. *letouzeyi* are separated only by the twisting of the keel. All the plants show flowers with an outcrossed morphology and the three subspecies share a forest ecology. In addition, it is difficult to hybridize plants from the *mensis* group with subsp. *unguiculata*, while the hybridization is easier within the *dekindtiana* group (Kouadio et al. 2007). The *mensis* group is the remote part of the secondary gene pool.

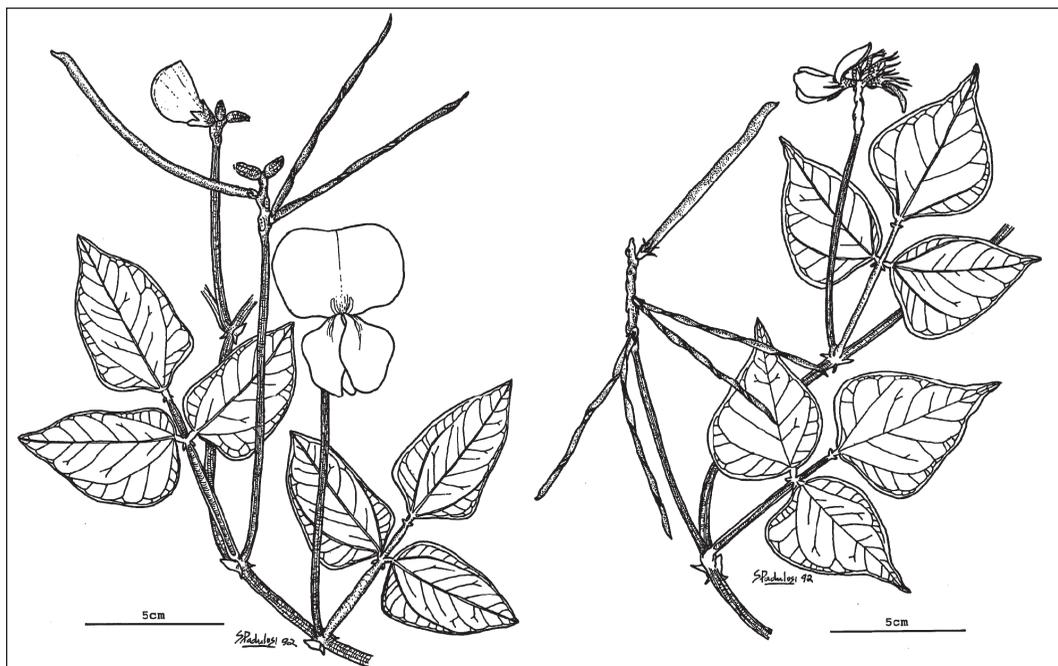


Figure 4. Subsp. *baoulensis* (left) and subsp. *pawekiae* (right) subsp. *baoulensis* (A.Chev.) Pasquet, Bulletin du Jardin Botanique National de Belgique 62: 158 (1993).

Vigna baoulensis A.Chev., Mém. Soc. Bot. Fr. 8: 163 (1912)

subsp. *dekindtiana* sensu Verdc., Kew Bulletin 24–3: 544 (1970) non Harms pro parte

subsp. *dekindtiana* var. *dekindtiana* sensu Maréchal Mascherpa & Stainier non Harms pro parte
subsp. *grandiflora* Padulosi, Genetic diversity, taxonomy and ecogeographic survey of the wild relatives of cowpea: 189 (1993) nom. nud.

Subsp. *baoulensis* is characterized by its very large pale flowers (Fig. 4) and its black smooth pods. It is found in lowland forests from Sierra Leone to Cameroon (Fig. 5).

subsp. *letouzeyi* Pasquet, Bulletin du Jardin Botanique National de Belgique 62: 159 (1993)
[*Vigna unguiculata* subsp. *mensis* sensu Verdc., Kew Bull. 24–3: 545 (1970), non Schweinf.] pro parte

[subsp. *dekindtiana* var. *momensis* sensu Maréchal et al., Taxon 27–2/3: 200 (1978) non Schweinf.] pro parte

subsp. *burundiensis* Pasquet, Bulletin du Jardin Botanique National de Belgique 62–1/4: 162 (1993)

Subsp. *letouzeyi* is characterized by the long calyx lobes and the keel twisted towards the right. It is encountered in lowland forests from Cameroon to western Kenya (Fig. 5). The very high genetic distance found between few accessions from Cameroon and one accession from Burundi justified for a while subsp. *burundiensis* as a separate subspecies (Pasquet 1999). However, additional living material made available since 1999 shows that it is impossible to separate both subspecies on a morphology basis. In addition, the few available ITS sequences available clearly show that the different accessions are part of the same group. Subsp. *letouzeyi* is likely to be a very diverse subspecies like subsp. *pawekiae*, where very high genetic distances can be found.

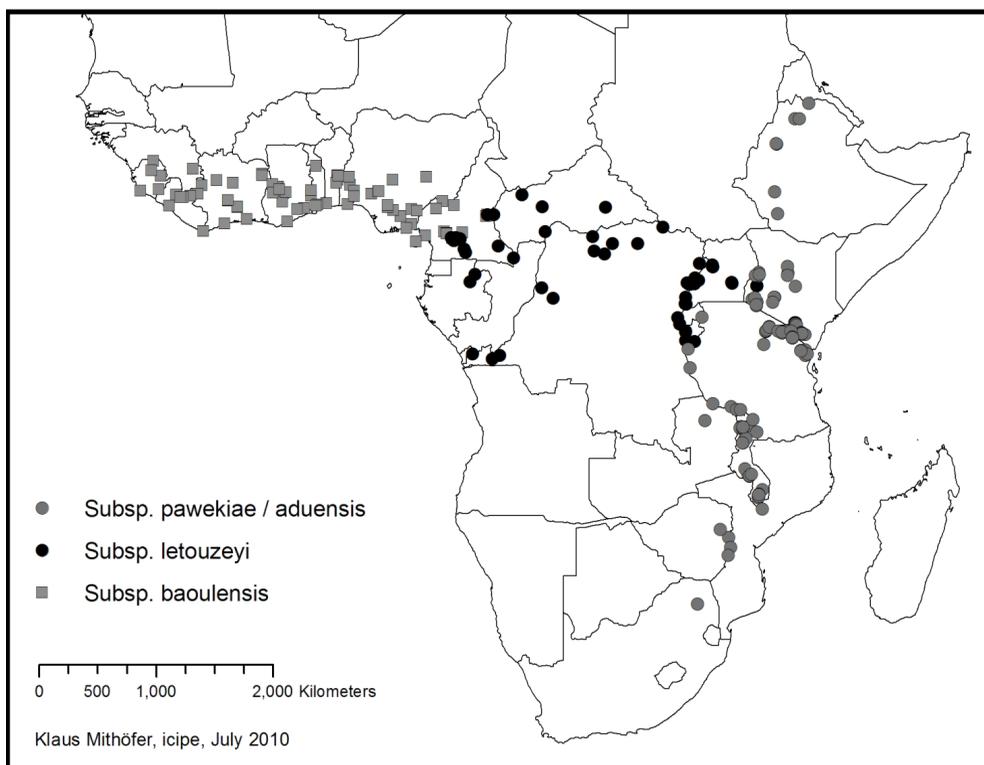


Figure 5. Geographical distribution (herbarium specimens and living accessions) of subspecies from the *mensesis* group.

subsp. *pawekiae* Pasquet, Kew Bulletin 48: 806 (1993)

[*Vigna unguiculata* subsp. *mensesis* sensu Verdc., Kew Bulletin 24–3: 545 (1970), non Schweinf.] pro parte

[subsp. *dekindtiana* var. *mensesis* sensu Maréchal et al., Taxon 27–2/3: 200 (1978) non Schweinf.] pro parte

subsp. *ciliolata* Padulosi, Genetic diversity, taxonomy and ecogeographic survey of the wild relatives of cowpea: 188 (1993) nom. nud.

subsp. *aduensis* Pasquet, Kew Bulletin 52: 840 (1997)

Subsp. *pawekiae* is characterized by the long calyx lobes and the keel twisted towards the left. It is encountered in montane forest from Ethiopia to South Africa (Fig. 5). Subsp. *aduensis* was separated from subsp. *pawekiae* due to its very large stipules, and a clear geographical distribution North of the Blue Nile river. However, a molecular confirmation would definitely be needed. When available material will be studied, the subspecific ranking of subsp. *aduensis* might be revisited and possibly the merging of this taxon with subsp. *pawekiae* be proposed on the basis of more solid data.

The dekindtiana group

The dekindtiana group includes six subspecies with a savanna ecology. Each subspecies includes plants with outcrossed flower morphology and plants with inbred flower morphology, although the presence of flowers with inbred morphology could be due to introgression from domesticated cowpea or inbred weedy var. *spontanea*. Compared to the mensensis group the molecular diversity is lower while the morphological diversity is more important, especially leaf shape and pubescence traits, likely linked to an adaptation to drier ecologies. This adaptation to drier ecologies includes the pyrophitic habit of subsp. *dekindtiana* like *Vigna frutescens* A.Rich., *Vigna antunesii* Harms, and many species from the Zambezi area highlands, subsp. *dekindtiana* plants are often flowering directly from the burnt root at the beginning of the rainy season before the leaves appear. Genetic barriers are weaker between these subspecies as well as between these subspecies and subsp. *unguiculata* (Kouadio et al. 2006, Kouadio et al. 2007), although some crosses remain difficult (Fatokun and Singh 1987, Aliyu 2005). The dekindtiana group is the close part of the secondary gene pool while subsp. *unguiculata* var. *spontanea* is the cowpea primary gene pool. It includes two subspecies with a keel twisted towards the left (subsp. *dekindtiana* and subsp. *stenophylla*) and four subspecies with a keel twisted towards the right (subsp. *alba*, subsp. *tenuis*, subsp. *pubescens*, and subsp. *unguiculata*).

subsp. *alba* (G.Don) Pasquet, Kew Bulletin 48(4): 805 (1993)

Clitoria alba G.Don, Gen. Syst. 2: 215 (1832)

[subsp. *dekindtiana sensu* Verdc., Kew Bulletin 24(3): 544 (1970) non Harms] pro parte

[subsp. *dekindtiana* var. *dekindtiana sensu* Maréchal Mascherpa & Stainier non Harms] pro parte

subsp. *dekindtiana* var. *congolensis* Padulosi, Genetic diversity, taxonomy and ecogeographic survey of the wild relatives of cowpea: 191 (1993) nom. nud.

Subsp. *alba* is encountered in coastal areas from Sao Tomé to Angola (Fig. 6). It is characterized by its high ovule number and its very small seeds. Plants encountered at higher altitudes in the Bateke plateau area are intermediate with var. *spontanea*: larger seed size, lower ovule number, and var. *spontanea* isozyme profile. Plants from the Bateke plateau are also showing leaflets with obtuse apex and long flower peduncles.

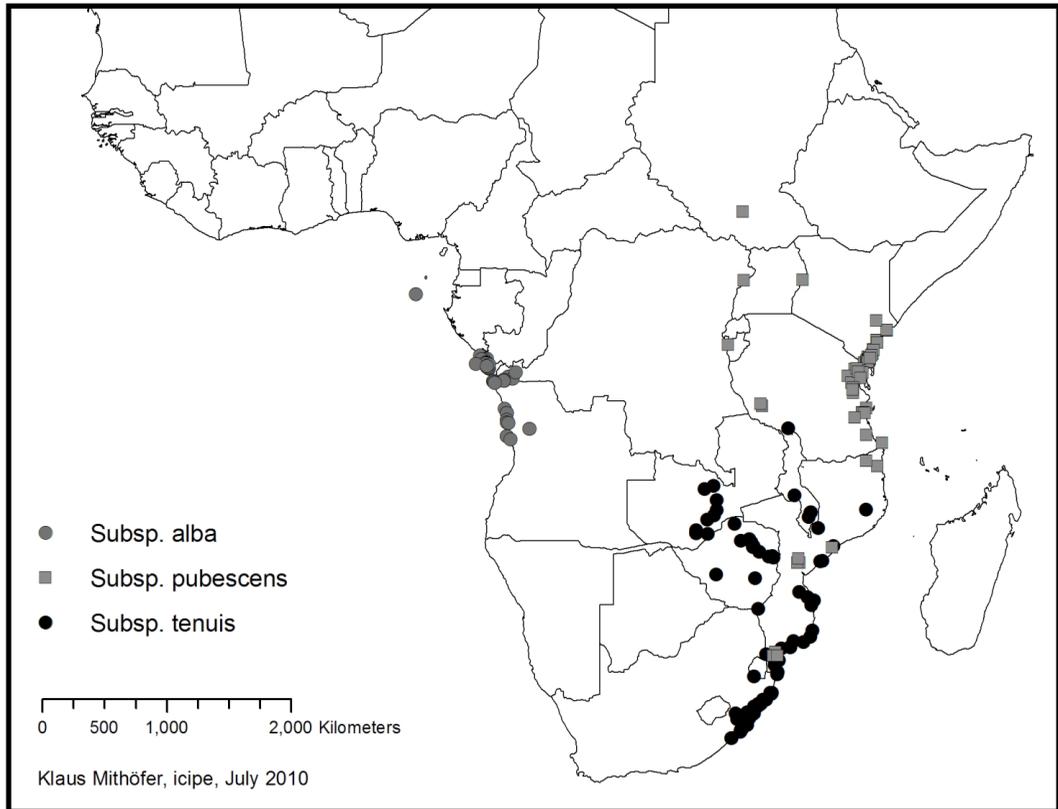


Figure 6. Geographical distribution (herbarium specimens and living accessions) of subspecies from the *dekindtiana* group with a keel twisted towards the right.

- subsp. *dekindtiana* (Harms) Verdc. (Harms) Verdc., Kew Bulletin 24(3): 544 (1970)
[subsp. Verdc., Kew Bull. 24-3: 544 (1970) non Harms] pro parte
- [subsp. *dekindtiana* var. *dekindtiana sensu* Maréchal Mascherpa & Stainier non Harms] pro parte
- subsp. *dekindtiana* var. *huillensis* (Welw. ex Baker) Mithen, Kirkia 14(1): 109 (1993)

Subsp. *dekindtiana*, characterized by its keel beak much longer than in every other cowpea subspecies, is mainly encountered in South Angola. In Zambia, herbarium specimens show a smaller flower size and a shorter keel beak. However, there are also few typical herbarium samples from Zimbabwe (Fig. 7). Unfortunately, there is not a single accession available and the status of the subspecies remains unclear.

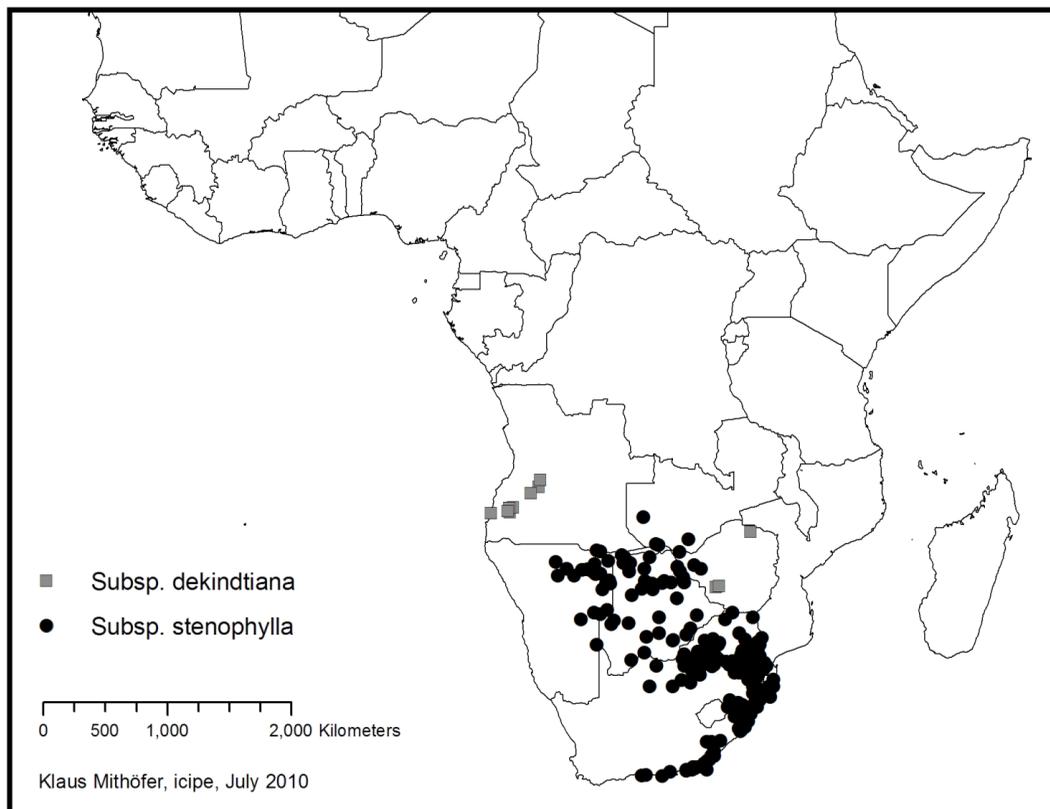


Figure 7. Geographical distribution (herbarium specimens and living accessions) of subspecies from the *dekindtiana* group with a keel twisted towards the left.

subsp. *stenophylla* (Harv.) Maréchal et al., Taxon 27-2/3: 200 (1978)

Vigna triloba Walp. var. *stenophylla*, Harv., F1. Cap. 2: 241 (1862)

Vigna rhomboidea Burt Davy, Man. Flow. Plant & Ferns Transvaal: xxxiv & 421 (1932)

Vigna angustifoliolata Verdc., Kew Bulletin 24(3): 547 (1970)

subsp. *dekindtiana* var. *stenophylla* (Harv.) Mithen, Kirkia 14(1): 103 (1993)

[subsp. *dekindtiana* var. *huillensis sensu* Pienaar, S. Afr. J. Bot. 58(6): 422 (1992) non Welw. ex Baker]

subsp. *dekindtiana* var. *kgalagadiensis* Mithen, Kirkia 14(1) : 105 (1993)

subsp. *protracta* var. *kgalagadiensis* (Mithen) Padulosi, Genetic diversity, taxonomy and ecogeographic survey of the wild relatives of cowpea: 191 (1993) comb. nud.

Scytalis protracta E.Mey., Comm. Pl. Afr. Austr.: 146 (1836)

subsp. *unguiculata* var. *protracta* (E. Mey.) Verdc., Kew Bulletin 24(3): 546 (1970)

subsp. *dekindtiana* var. *protracta* (E. Mey.) Maréchal et al., Boissiera 28: 195 (1978)

subsp. *protracta* (E.Mey.) Pienaar, S. Afr. J. Bot. 58(6): 420 (1992)

subsp. *protracta* var. *rhomboidea* Padulosi, Genetic diversity, taxonomy and ecogeographic survey of the wild relatives of cowpea: 191 (1993) comb. nud.

Subsp. *stenophylla sensu lato* (Pasquet 1993) includes three taxa previously treated as varieties. These three taxa are clearly differentiated by their leaf shape and their pilosity. Var. *protracta* is characterized by its lobed or rhomboid pubescent leaflet and its pubescent pods and is encountered in Cape Province, Natal, Swaziland, and Southeast Transvaal.

The variety is rather variable morphologically, especially in Transvaal and Swaziland where plants with rhomboid leaflets (*Vigna rhomboidea* Burt Davy) and plants with long calyx lobes are encountered (Padulosi 1990a, Padulosi 1990b, Padulosi 1993). Var. *stenophylla* Harv. is a scabrous plant with linear leaflets encountered in the highveld and in the Kruger area lowland. Var. *kgalagadiensis* Mithen is similar to var. *protracta* but with a weak pilosity and scabrous pods and is encountered in the Kalahari area (Fig. 7 and Fig. 8).

There are rather few intermediate herbarium specimens between these varieties, likely because the ecologies are very different. However, the three varieties show the same flower (slightly larger in var. *protracta* and slightly smaller in var. *stenophylla*), the same inflorescence, and very similar low ovule numbers. The molecular data do not confirm perfectly the tree varieties: for example, the lowland var. *stenophylla* accession from the Kruger National Park area is closer to var. *protracta* than to upland var. *stenophylla*. And var. *stenophylla* characteristic linear leaf shape is also encountered in subsp. *tenuis* (Padulosi 1993): all the very narrow leaflet plants do not belong to a single subspecies. Logically, the three taxa should be treated as varieties of subsp. *stenophylla* since it could be a single taxon adapted to very different ecologies. But isozyme data as well as ITS data would suggest three independent subspecies, the link between them being weaker than the link between each of them and other subspecies. However, only a minor part of the available material has been studied and more work is needed in order to clearly choose the rank deserved by the three taxa.



Figure 8. The different taxa currently within subsp. *stenophylla sensu lato*. Var. *kgalagadiensis* (top left), var. *stenophylla* (from specimen Zeyher 529, top right), var. *protracta* with rhomboid leaflets (bottom left), and var. *protracta* with lobed leaflets (bottom right).

subsp. *tenuis* (E. Mey.) Maréchal et al., Taxon 27-2/3: 200 (1978)
Scytalis tenuis E.Mey., Comm. Pl. Afr. Austr.: 145 (1836)
Scytalis tenuis var. *oblonga* E.Mey., Comm. Pl. Afr. Austr.: 145 (1836)
Scytalis tenuis var. *ovata* E.Mey., Comm. Pl. Afr. Austr.: 145 (1836)
 subsp. *dekindtiana* var. *tenuis* (E.Mey.) Mithen, Kirkia 14(1) : 106 (1993)
 subsp. *tenuis* var. *parviflora* Padulosi, Genetic diversity, taxonomy and ecogeographic survey of the wild relatives of cowpea: 192 (1993) nom. nud.

Subsp. *tenuis* is characterized by its glabrous stems and leaves and its one- or two-noded inflorescence. It occupies two different areas: a highland one in Zambia, Malawi, and Zimbabwe, and a coastal one in Mozambique (where it is locally abundant, like for example in Inhaca Island) and South Africa (Fig. 6). The highland form has smaller flowers and should be treated as an independent variety as suggested by Padulosi (1993). However, the var. *ovata* E.Mey. and var. *oblonga* E.Mey., based on leaflet shape and widely used since Meyer (1836), are not confirmed by molecular data nor by biogeography and are not justified.

subsp. *pubescens* (R. Wilczek) Pasquet, Bulletin du Jardin Botanique National de Belgique 62(1/4): 164 (1993)
Vigna pubescens R. Wilczek, Bull. Jard. Bot. Brux. 24: 442 (1954)
 subsp. *dekindtiana* var. *pubescens* (R.Wilczek) Maréchal et al., Taxon 27-2/3: 200 (1978)

Subsp. *pubescens* is characterized by its white and appressed pubescence, different from var. *protracta* bristly one, and its long noded inflorescence rachis. It also shows leaflets with obtuse apex, rather long inflorescence peduncles, and no rootstock (Fig. 9). This a wetland plant and its distribution overlaps those from subsp. *tenuis* and subsp. *unguiculata* (Fig. 6), which may explain the stronger genetic barrier between subsp. *pubescens* and subsp. *unguiculata*. (Fatokun and Singh 1987).

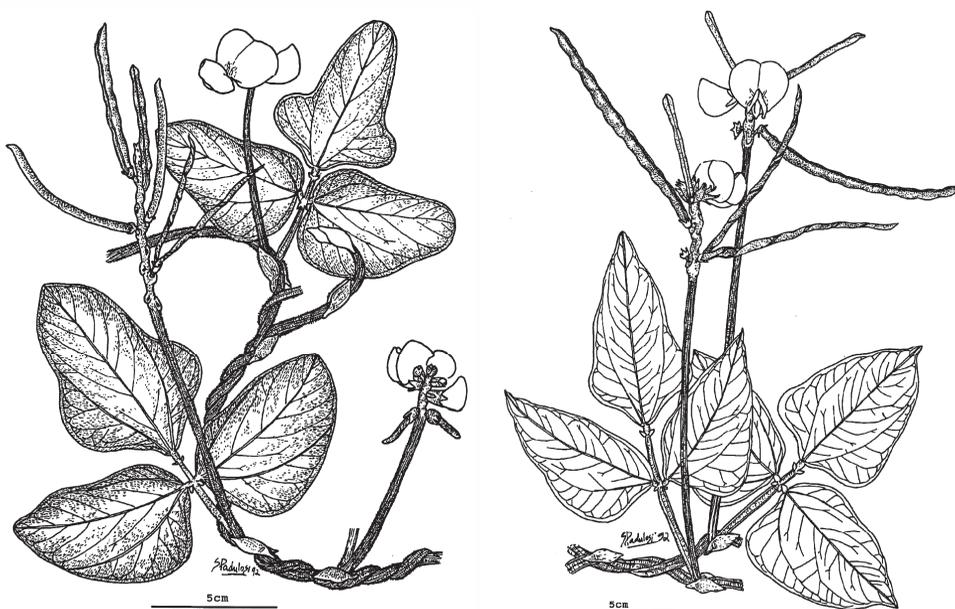


Figure 9. Subsp. *pubescens* (left) and subsp. *unguiculata* var. *spontanea* (right).

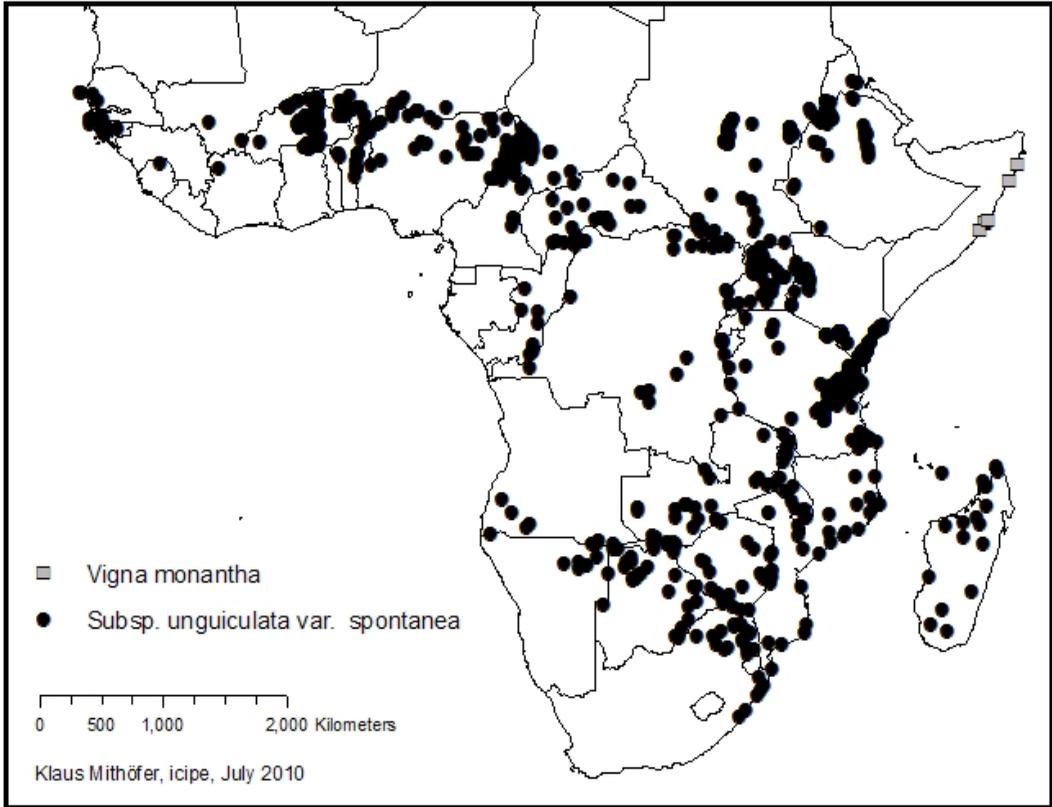


Figure 10. Geographical distribution (herbarium specimens and living accessions) of subsp. *unguiculata* var. *spontanea* and *Vigna monantha*.

Subsp. *unguiculata* var. *spontanea* (Schweinf.) Pasquet

Vigna brachycalyx Baker, Journ. Linn. Soc., Bot. 25: 310 (1890)

Vigna sinensis var. *spontanea* Schweinf., Bull. Herb. Boiss. 4, app. 2: 260 (1896)

subsp. *dekindtiana* sensu Verdc., Kew Bulletin 24(3): 544 (1970) non Harms pro parte

subsp. *dekindtiana* var. *dekindtiana* sensu Maréchal Mascherpa & Stainier non Harms pro parte

This is the common wild/weedy annual cowpea (Fig. 9), widely known as subsp. *dekindtiana* sensu Verdc., encountered all over the continent (Fig. 10), very often on field margins or within fields, therefore usually close to domesticated cowpea. It interbreeds and produces fertile offspring through hybridization with domesticated cowpea (var. *unguiculata*) (Kouadio et al. 2007). Var. *spontanea* is a weed, especially in some areas of West Africa (Rawal 1975), and a crop-weed complex occurs all over Africa between the Sahara and Kalahari deserts (Coulibaly et al. 2002, Feleke et al. 2006). It is the cowpea's primary gene pool.

Soon, a few additional varieties should be added within subsp. *unguiculata*. While most var. *spontanea* plants are annual without a rootstock, several groups of plants currently considered as var. *spontanea* show a rootstock and would deserve to be considered as independent new varieties of subsp. *unguiculata*: the plants from the Bateke plateau in Congo, the plants from the Indian Ocean coastal area, and the plants from Somalia currently

treated as *Vigna monantha* Thulin. However if abundant living material exists for these potentially new varieties, *V. monantha* is known from very few herbarium specimens and no living accession is available, which is very unfortunate.

Domesticated cowpea

Linnaeus described *Dolichos unguiculatus* L (later renamed *Vigna unguiculata* (L.) Walp) in 1753. Between 1753 and 1845, more than twenty binomials were described from domesticated *V. unguiculata* specimens. These binomials were considered as conspecific and ranked at infraspecific levels during the second half of the 19th Century. Now, domesticated forms are pooled in *V. unguiculata* subsp. *unguiculata* var. *unguiculata* and wild annual forms in subsp. *unguiculata* var. *spontanea*. The choice of these ranks was due to the extremely low genetic distances observed between wild annual cowpeas and domesticated cowpeas.

From that point, two opposing approaches have been suggested for the classification of domesticated *V. unguiculata*. One was issued from Piper's (1912) study of US domesticated forms. Three groups, known since as the Linnean works (1763), were separated according to seed and/or pod sizes. Later, these groups were ranked at all the possible taxonomic levels, and Westphal (1974) finally used the cultigroup rank (group of cultivars). Now widely accepted (Maréchal et al, 1978), this classification is not always convenient. Cultivar group (Cv gr) *Biflora* is not easily separated from cv gr *Unguiculata* as pod orientation is closely dependent upon pod and seed weight (Piper 1912). Steele (1972), recognizing that Piper's (1912) system and Verdcourt's (1970) classification were not fitted with African domesticated forms, proposed a fairly complex key, including seed testa texture and photosensitivity. Later, Steele admitted Piper's trilogy, while pointing out some divergences between photosensitive and photoindependent groups (Steele and Mehra 1980).

Another concept, strangely not used, is that of Chevalier (1944). Chevalier's classification considered the number of seeds per pod, which was an important difference with Piper's classification. Chevalier divided West African cowpeas into two subspecies according to seed number per pod. The subspecies with low seed number per pod was divided into four groups : wild, domesticated with smooth testa seeds, domesticated with wrinkled testa seeds (var *melanophthalmus* (DC.) A.Chev.), and domesticated with long inflorescence peduncles. Unfortunately, Chevalier's classification included Asian cowpeas (Piper's classification *in extenso*) and West African cowpeas without discussing the connections between the two.

Therefore, Pasquet (1998), highlighting the difference between late flowering photoperiod-independent cultivars and early flowering photoperiod-independent cultivars (the latter close to photosensitive cultivars), added cv.gr. *Melanophthalmus* to the 4 cultigroups of Westphal (1974), and proposed the following key. The key seems to work well with landraces, but as breeding lines often involves parents from different cultivar groups, the key is less effective with breeding lines:

- **Cultivar group *Textilis*** Long floral peduncle
- **Cultivar group *Biflora*** Short or medium floral peduncle
- Pod 10–17-ovuled, plant able to flower quickly from the first nodes under inductive conditions. Seed testa smooth and thick

- **Cultivar group *Melanophthalmus*** Seed testa thin and often wrinkled
- **Cultivar group *Sesquipedalis*** Pod 17–24-ovuled, plant flowering late, even under inductive conditions. Long (> 30 cm) fleshy pod, kidney shaped seed spaced within the pod
- **Cultivar group *Unguiculata*** Not as above

Unfortunately, this morphology-based organization of the domesticated gene pool is poorly correlated with isozyme data (Pasquet 2000). Hopefully, the study of landraces with SNP and SSR markers should bring more light on the organization of the cowpea domesticated gene pool and its evolution.

Cowpea was domesticated once (Pasquet 1999) from its wild progenitor var. *spontanea* somewhere in Harlan's (1971) African non-center, between Senegal and Eritrea. This domestication took place well before 1500 BC as clearly identifiable cowpea seeds were found in archaeological deposits dated 1500 BC both in central Ghana (D'Andrea et al. 2007) and in India (Fuller 2003). However, a precise center of origin is yet to be established and numerous domestication hypotheses were proposed: mainly Ethiopia (Vavilov 1926, Steele 1972, Pasquet 2000), and West Africa (Murdock 1959, Faris 1963, Rawal 1975, Maréchal et al. 1978, Vaillancourt and Weeden 1992, Ng 1995), while a "diffuse" domestication in the savanna after the dispersal of cereals was also hypothesized (Chevalier 1944, Steele 1976, Garba and Pasquet 1998). Here again, study of var. *spontanea* and landraces with SNP and SSR markers should help solve the problem.

Conclusion

Genus *Vigna* phylogeny and the position of *Vigna* within Phaseolinae is now firmly established. Below species level, the different wild cowpea groups are now well known, even if the rank of some taxa needs to be clarified. However, we do not have a precise cowpea infraspecific phylogeny yet. In addition, a precise cowpea center of origin is yet to be identified, which is an important point considering the forthcoming deployment of genetically engineered cowpea in Africa.

In the meantime, the good knowledge of gene pool organization should help the start of the use of wild cowpea in cowpea breeding. Wild cowpea should be helpful in improving disease and *Striga* resistance in breeding line. More important, wild cowpea should allow the set up of a cytoplasmic male sterility system which, thanks to the huge heterosis potential of cowpea (Adu-Dapaah et al. 1988), should allow the development of and hybrid cowpea seed system, leading to at least a doubling of cowpea yields.

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