

Origin, taxonomy, and morphology of *Vigna unguiculata* (L.) Walp.

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Abstract

Cowpea (*V. unguiculata*) represents the main food legume in tropical Africa. Germplasm collecting missions launched over the past 10 years have provided genebanks with a wide array of variability within the cultivated and wild taxa of the species. Based on detailed studies on morphological diversity of live materials along with extensive survey of materials in major *Vigna* herbaria and ecogeographical information, a new intraspecific classification recognizing 13 varieties of wild cowpea has been proposed and described. The study points out that the southernmost region of Africa is most probably the center of origin for the species *V. unguiculata*, while its domestication might have taken place in West Africa.

Introduction

Considerable progress has been made during the past 10 years on germplasm collection, characterization, evaluation, ecogeographic studies, and taxonomy of cowpea and its wild relatives. These efforts have greatly contributed towards a better understanding of species diversity, ecogeographical distribution, and evolution of *Vigna unguiculata*. Germplasm collection activities have broadened the genetic materials available in genebanks for use in crop improvement and related research.

Taxonomy

Cowpea is a *Dycotyledonea* belonging to the order *Fabales*, family *Fabaceae*, subfamily *Faboideae*, tribe *Phaseoleae*, subtribe *Phaseolinae*, genus *Vigna*, and section *Catiang* (Verdcourt 1970; Maréchal et al. 1978). *Vigna* is a pantropical genus with several species, whose exact number varies according to authors: 184 (Phillips 1951), 170 (Faris 1965), between 170 and 150 (Summerfield and Roberts 1985), 150 (Verdcourt 1970), 154 (Steele 1976), and about 84 (of which some 50 species are indigenous to Africa) (Maréchal et al. 1978).

In their revision of the genus *Vigna*, Maréchal et al. (1978) subdivided the genus described earlier by Verdcourt (1970) into seven subgenera. In this classification, *V. unguiculata* (L.) Walpers and *V. nervosa* Markotter constitute the section *Catiang*, one of the six sections of the subgenus *Vigna*. Species of the section *Catiang* are characterized by spurred stipules below the attachment point of the leaf stalks and canoe-shaped keel with beak. The

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surface of their pollen grains are reticulate with raised exine (De Leonardis et al. 1993). Interspecific crosses made between the two species have not been successful (Mithen 1987; Ng and Apeji 1988; Ng 1995). On the basis of a study on isoenzyme variation in the genera *Phaseolus* and *Vigna*, Jaaska and Jaaska (1988) proposed to raise the section *Catiang* to the rank of a subgenus.

All cultivated cowpeas are grouped under *V. unguiculata* subspecies *unguiculata*, which is subdivided into four cultigroups, namely Unguiculata, Biflora, Sesquipedalis, and Textilis (Westphal 1974; Maréchal et al. 1978; Ng and Maréchal 1985). There has been no major contention on this classification, since its adoption over 10 years ago.

The classification and nomenclature of the wild taxa within *V. unguiculata*, however, is complicated, and could sometimes be confusing. More than 20 epithet names have been used in the past to designate wild taxa within *V. unguiculata* species complex. An extensive work on characterization of over 400 wild *V. unguiculata* accessions was conducted at IITA (Ng and Padulosi 1991; Padulosi 1993). This work, coupled with surveys of live materials in the field and specimens in major herbaria in Europe and Africa, as well as cytological studies, has led to the description of new taxa, and a change of nomenclature of some species (Padulosi 1993; Ng 1995). Parallel work on taxonomy of wild species within section *Catiang* was also conducted elsewhere (Piennaar and Wyk 1992; Pasquet 1993a).

Table 1. Classification and nomenclature of the wild *Vigna unguiculata* species complex.

Maréchal et al. (1978)	Piennaar (1992)	Pasquet (1993a)	Padulosi (1993)
<i>V. unguiculata</i>	<i>V. unguiculata</i>	<i>V. unguiculata</i> ssp. <i>unguiculata</i> var. <i>spontanea</i>	<i>V. unguiculata</i>
ssp. <i>dekindtiana</i> var. <i>dekindtiana</i>	ssp. <i>dekindtiana</i> var. <i>dekindtiana</i> var. <i>huliensis</i>	ssp. <i>dekindtiana</i> var. <i>dekindtiana</i>	ssp. <i>dekindtiana</i> var. <i>dekindtiana</i> var. <i>huliensis</i> var. <i>congolensis</i> var. <i>grandiflora</i>
var. <i>mensensis</i>	ssp. <i>mensensis</i>	ssp. <i>letouzeyi</i> ssp. <i>burundiensis</i> ssp. <i>baoulensis</i>	var. <i>ciliolata</i>
var. <i>protracta</i>	ssp. <i>protracta</i>	ssp. <i>stenophylla</i>	ssp. <i>protracta</i> var. <i>protracta</i> var. <i>kgalagadiensis</i> var. <i>rhomboidea</i>
var. <i>pubescens</i>	ssp. <i>protracta</i>	ssp. <i>pubescens</i>	ssp. <i>pubescens</i>
ssp. <i>stenophylla</i> ssp. <i>tenuis</i>	ssp. <i>stenophylla</i> ssp. <i>tenuis</i> var. <i>tenuis</i> var. <i>ovata</i>	ssp. <i>stenophylla</i> ssp. <i>tenuis</i>	ssp. <i>stenophylla</i> ssp. <i>tenuis</i> var. <i>tenuis</i> var. <i>oblonga</i> var. <i>parviflora</i>

For clarity, the synonyms of the various wild *V. unguiculata* species and their classification system proposed by different researchers are presented in Table 1. In our present discussion, we use the nomenclature and classification system proposed by Padulosi (1993). In this classification system, the three subspecies *dekindtiana*, *tenuis*, and *stenophylla* as recognized by Maréchal et al. (1978) were retained, but var. *protracta* and var. *pubescens* were raised to the level of two distinct subspecies, because of their very distinctive hairy characteristics in pods and other plant parts, morphology of their flowers, pollen, grains, and leaves, as well as their root systems.

Within subspecies *protracta*, three varieties, namely var. *protracta*, var. *rhomboidea*, and var. *kgalagadiensis*, were distinguished. Similarly, three varieties *tenuis*, *oblonga*, and *parviflora* were recognized within the subspecies *tenuis*, while four new varieties, namely var. *huillensis*, var. *congolensis*, var. *ciliolata*, and var. *grandiflora*, have also been proposed and added to the subspecies *dekindtiana*.

Ng (1995) proposed to reinstate var. *rhomboidea* to a species ranking in its own right, because of its strong incompatibility with other taxa within *V. unguiculata*. Pasquet (1993a) proposed that the name subspecies *unguiculata* var. *spontanea* be used to describe all the weedy forms and the intermediates between truly wild var. *dekindtiana* and cultivated cowpea. The subspecies *burundiensis* (Pasquet 1993a) is a variant of var. *ciliolata*. It is found in mid-altitudes in Zaïre, Burundi, Kenya, and Uganda.

Morphology of wild cowpea

Great variability in plant morphology has been observed in wild cowpea. Considerable variation in protein and molecular marker electrophoretic band patterns has also been detected (Vaillancourt and Weeden 1992; Vaillancourt et al. 1993; Panella et al. 1993; Pasquet 1993b). Tables 2 and 3 show the variation of some vegetative and reproductive organs of wild cowpea, and plant growth habit. These traits are useful to discriminate the various subspecies and varieties of the species. Figures 1 and 2 depict the general morphology of plants of a typical variety of each of the five subspecies described. Figure 3 shows the detailed morphology of the stigmas of the different subspecies. Most subspecies, except var. *dekindtiana* and var. *ciliolata* of the subsp. *dekindtiana*, and var. *kgalagadiensis* of the subsp. *protracta*, have the tendency to live for longer than a year (biennial or perennial).

Subsp. *pubescens* and *protracta* are pubescent, with their stems, leaves, and pods covered with hairs. Vestiture of the former subspecies is sericeous, with its hairs generally longer and denser than those of the latter species. The hairs are silky, straight, soft, and appressed to the surface of the stems and pods. On the other hand, the hair type of the subsp. *protracta* is hispid. The hairs are bristly, erect, straight, and harshly stiff. They are especially pronounced in var. *rhomboidea*, a taxon with typical rhombic leaves ranging from 4 to 15 cm long and 1.7 to 5 cm wide. This taxon has thick root stock and its stigmas are strongly bearded and thus easily recognizable from all other taxa. The varieties *protracta* and *kgalagadiensis* can be distinguished from one another by the shape and size of leaves, as well as by length of rachis and peduncle. Variety *protracta* is an annual or a perennial herb up to 2 m long, with a prostrate growth habit. Its inflorescence rachis is shorter than 0.7 cm and peduncle about 7 (4–15) cm long. Its lateral leaflet is oblique, slightly to deeply lobed on the inside only, up to 7 cm long and 6 cm wide; terminal leaflet

Table 2. Summary of range of variation of some plant parts and growth habit within wild cowpea taxa†.

Taxa	Growth habit	Stem/ branch rooting	Stem width	Stipule size (mm) [§] length	width	Leaf texture	Stem hairiness type and intensity	Raised nerivation on leaf blade
<i>ssp. dekindiana</i> var. <i>dekindiana</i>	an-rarely pe	absent	med-thick	11(5-23)	5(3-10)	mem-thick	glab-sparsely	scarce-med
<i>ssp. dekindiana</i> var. <i>ciliolata</i>	an	absent	med-thick	11.5(7-15)	5(3.5-6)	med	glab	scarce
<i>ssp. dekindiana</i> var. <i>congolensis</i>	an-pe	absent	tiny-med	10(5-16)	4.5(3-16)	med-thick	glab	scarce
<i>ssp. dekindiana</i> var. <i>grandiflora</i>	an-pe	absent	med-thick	11(7-20)	4.5(3.5-7.5)	med	glab	scarce
<i>ssp. dekindiana</i> var. <i>hulliensis</i>	pe	absent	med-thick	10-15	4-6	le	glab	very high
<i>ssp. pubescens</i>	an/biennial	absent	thick	11.5(6-20)	5.5(3.5-8.5)	med-thick	int-pubescent	med-high
<i>ssp. protracta</i> var. <i>protracta</i>	an-pe	absent	med	11(9-16)	4-5	med-thick	med-int bristly hairiness	med-high
<i>ssp. protracta</i> var. <i>kgalagadiensis</i>	an	absent	tiny-med	11(7-16)	5(3-7)	med-thick	scattered bristly hairiness	med-high
<i>ssp. protracta</i> var. <i>rhomboidea</i>	pe	absent	med-thick	12(7.5-16)	5(4-7)	thick-le	int-bristly hairiness	med-high
<i>ssp. tenuis</i> var. <i>tenuis</i>	pe	present	tiny	10(6-13)	4(3-6)	med	glab	scarce
<i>ssp. tenuis</i> var. <i>oblonga</i>	an-pe	present	tiny	9(6-10)	4(3-6)	med	glab	scarce
<i>ssp. tenuis</i> var. <i>parviflora</i>	pe	present	tiny	6(6-10)	4-4.5	med	glab-sparsely hairy	scarce
<i>ssp. stenophylla</i>	an-pe	absent	tiny-med	11(7.2-14)	4(3.2-5)	med-thick	glab	scarce

† an = annual; glab = glabrous; int = intensely; le = leathery; med = medium; mem = membranaceous; pe = perennial.

§ Figures in parentheses are ranges.

Table 3. Summary of range of variation within wild cowpea taxa of some plant parts*.

Taxa	Peduncle length [§] (cm) [¶]	Rachis length (cm)	Standard color	Standard blotch	Standard length (mm) [¶]	Standard width (mm) [¶]	Calyx lobes length (mm) [¶]	Stigma bearding
<i>ssp. dekindtiana</i>	15 (2–40)	7–8 [†]	white–light mauve purple	narrow	19 (17–34)	27 (15–44)	3 (1–8)	low–med
var. <i>dekindtiana</i>								
<i>ssp. dekindtiana</i>	15 (7–25)	6–8 [†]	deep purple	flame-like	30 (25–33)	31 (17–36)	9 (6–13)	low–med
var. <i>ciliolata</i>								
<i>ssp. dekindtiana</i>	15 (5–30)	< 2.5	purple	narrow	29 (22–39)	34 (25–40)	3 (1.7–5.5)	low
var. <i>congolensis</i>								
<i>ssp. dekindtiana</i>	12 (4–23)	6–7 [†]	pale mauve	narrow	40 (24–47)	43 (36–49)	3 (1.2–6)	low
var. <i>grandiflora</i>								
<i>ssp. dekindtiana</i>	20 (8–27)	4–5 [†]	purple	–	30–35	35–40	< 4–6	low
var. <i>huillensis</i>								
<i>ssp. pubescens</i>	20 (4–41)	20–25 [†]	deep mauve	flame-like	25 (22–39)	30 (24–38)	4 (2–6.5)	low
<i>ssp. protracta</i>	7 (4–15)	< 0.7	deep purple	narrow	29 (26–33)	33 (30–36)	7 (4–10)	med–int
var. <i>protracta</i>								
<i>ssp. protracta</i>	9.5 (5–20)	3–4	mauve	narrow	24 (22–27)	26 (21–30)	4 (2.2–7)	low–int
var. <i>kgalagadiensis</i>								
<i>ssp. protracta</i>	16 (7.5–30)	< 1	deep purple	narrow	26 (25–27)	40 (24–41)	4–5.5	int
var. <i>rhomboidea</i>								
<i>ssp. tenuis</i>	8 (3–23)	< 0.7	deep purple	narrow	27 (20–32)	31 (25–43)	4 (2.5–6)	low
var. <i>tenuis</i>								
<i>ssp. tenuis</i>	8 (3–13)	< 1	deep purple	narrow	25 (19–30)	23 (18–29)	3.7 (2.7–5)	low
var. <i>oblong</i>								
<i>ssp. tenuis</i>	6 (4–8)	< 0.8	purple	narrow	20 (17–25)	25 (21–28)	3.5 (2–4.5)	med–int
var. <i>parviflora</i>								
<i>ssp. stenophylla</i>	12 (5–20)	< 1.5	mauve–lilac pale	narrow	23 (20–26)	26 (25–31)	4 (2.5–5)	low

† Int = intense; med = medium. Keel shape (how beaked?) was only markedly beaked in *ssp. dekindtiana* var. *huillensis* and scarcely so in others. Pollen exine reticulation (how raised?) was slightly raised for all except for *ssp. dekindtiana* var. *huillensis*, *ssp. protracta* var. *protracta* var. *kgalagadiensis*, and var. *rhomboidea* with markedly raised reticulation.

§ Measured at flowering stage.

¶ Figures in parentheses are ranges.

† Values up to the range mentioned.

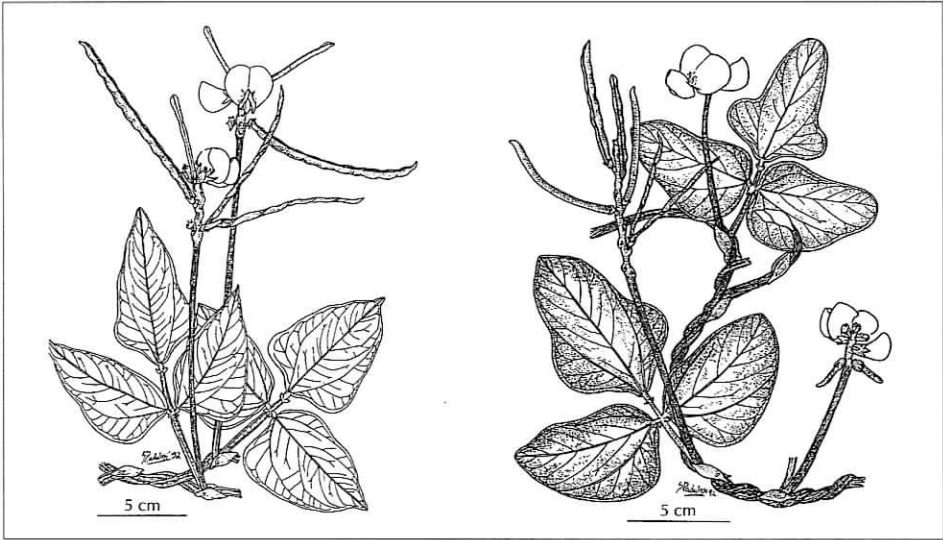


Figure 1. *Vigna unguiculata* ssp. *dekindtiana* var. *dekindtiana* (left), and ssp. *pubescens* (right).

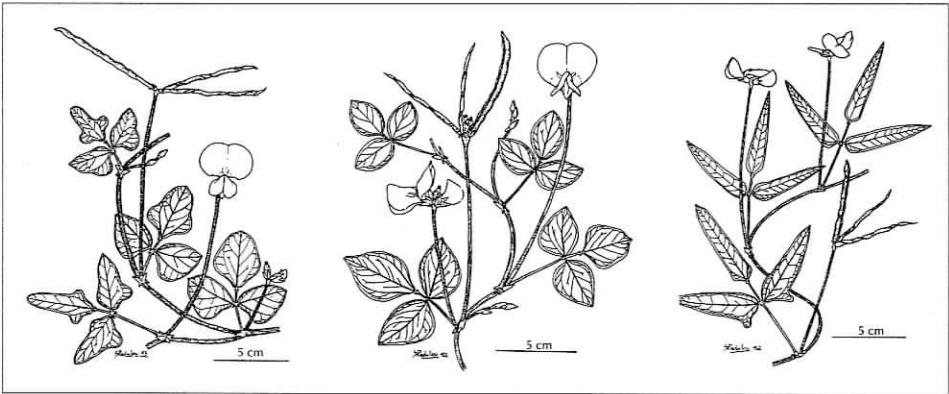


Figure 2. *Vigna unguiculata* ssp. *protracta* var. *protracta* (left), ssp. *tenuis* var. *tenuis* (centre), and ssp. *stenophylla* (right).

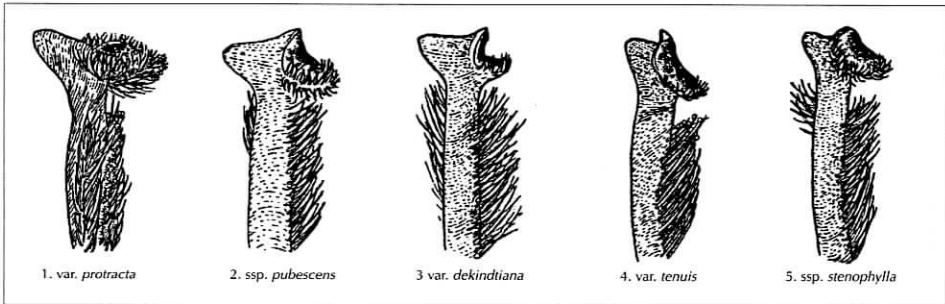


Figure 3. Stigmata of the indicated subspecies of *Vigna unguiculata* (L.) Walp.

ovate to subhastate or hastate, 5 (3–8) cm long and 3 (2–6) cm wide. Leaflets of var. *protracta* are wider than var. *kgalagadiensis*, whose lateral leaflet is up to 3 cm wide and terminal leaflet 2 cm wide. Inflorescence rachis of var. *kgalagadiensis* is 3–4 cm long and peduncle 9.5 (5–20) cm long. This taxon is an annual herb up to 1.5 m long, with a prostrate growth habit. Subsp. *pubescens* has the longest peduncles and rachis, and thickest stems, as compared to other taxa within wild *V. unguiculata*. It has a deep mauve flower.

Plants of the subsp. *tenuis* are small, delicate, and tender. They produce small fleshy tuberous roots. Occasionally, adventitious rooting occurs from nodes of creeping branches. Their peduncles and rachis, similar to those in var. *protracta*, are shortest among the wild *V. unguiculata*. Three varieties are recognized in this subspecies, namely var. *tenuis* (with ovate-shaped leaves), var. *oblonga* (with oblong leaves), and var. *parviflora* (with small flowers).

Subspecies *stenophylla* has very narrow (lanceolate) and sometimes, hastate terminal leaflets, 6 (3–10) cm long and 1 (0.3–2) cm wide. Its lateral leaflets are oblique, slightly lobed on the inside, up to 7 cm long and 3 cm wide. It also produces small tuberous root. Its peduncle is intermediate in length (12 cm). Rachis is shorter than 1.5 cm. Its flower is small, pale, and mauve.

Subspecies *dekindtiana* consists of a very diverse group of varieties, represented by five taxa. Variety *grandiflora* has the largest flower in the species and is easily distinguished from all others by the size of its flowers. The standard color of the flower is pale mauve. Variety *congolensis* has small leaves; terminal leaflet is ovate-lanceolate to subhastate, 5 (3–8) cm long and 2.5 (1.2–7) cm wide; lateral leaflets are oblique, up to 6 cm long and 3 cm wide. This variety from Congo is quite similar to subsp. *tenuis*. Variety *huillensis* has a very long peduncle, with an average of 20 (8–27) cm. It has a large purple flower, with its keel markedly beaked. Its leaves are rather leathery. It is a pyrophytic species. It produces abundant flowers from peduncles originated directly from its woody rootstock, soon after bush fires occur in the savanna. It also produced flowers without bushfires, during growing seasons in Ibadan, Nigeria. Variety *ciliolata*, on the other hand, is an annual plant which is distinguishable from others by its long calyx lobes (over 9 cm long); otherwise it is very similar to var. *dekindtiana*. The calyx lobe length seems to be stable, across the different environments in Ibadan and in East Africa. The general morphology and growth habit of var. *dekindtiana* is very similar to cultivated cowpea landraces, except that its mature pods are usually black, scabrous, and much smaller than the cultivated cowpea. The pods which shatter at maturity contain tiny, dark speckled or solid black seeds, similar to other varieties of the wild species. Variation in the seed size of this variety is greater than others, and the average size (2 g/100 seeds) is also bigger.

Center of origin

The precise location of the center of origin of a species is rather difficult to determine. Previous speculation on the origin and domestication of cowpea had been based on botanical and cytological evidence, information on its geographical distribution and cultural practices, and historical records (Faris 1965; Steel and Mehra 1980; Ng and Maréchal 1985; Ng 1995).

De Candolle (1886) thought that the origin of a cultivated plant could be found where it grows wild. This procedure of locating the place of origin of a crop is correct to a certain

degree, but too often it produces erroneous interpretation. The wild plant may have been common in one area but domestication may have taken place in another, such as in the case of African cottons and the Peruvian tomato (Hawkes 1967).

A detailed study of the variation of a crop, both morphological and genetical, in relation to the geographical distribution of such variation could help in speculating on the origin of cultivated plants. Vavilov (1926) postulated that an area with intensive variation was one where the crop must have been cultivated for a long time, since in that area there would have been time for large numbers of mutations and gene recombinations to take place, as a result of interbreeding among different varieties. It is generally observed that a very large number of varieties or high variation of the species is found towards the center of the distribution area of the crop, and this is accompanied by a corresponding thinning out of the variability towards the periphery.

Based on our present investigation, the range of variation and number of varieties found in wild cowpea, as well as their primitive characteristics, such as perenniality, hairiness, small size of the pods and seeds, pod shattering, with pronounced exine on the surface of pollen, outbreeding, and bearded stigma, the highest genetic diversity and most primitive of the wild *V. unguiculata* occur in southern Africa in the region encompassing Namibia from the west, across Botswana, Zambia, Zimbabwe, and Mozambique to the east, and the Republic of South Africa and Swaziland to the south. Probably, the Transvaal region of the Republic of South Africa was the center of speciation of *V. unguiculata*, due to the presence of most primitive wild varieties, var. *rhomboidea*, var. *protracta*, var. *tenuis*, and var. *stenophylla*. Variety *rhomboidea* has a very narrow geographical distribution in the Transvaal, stretching approximately from 20 to 27 °S and 26 to 32 °E, with an isolated occurrence in Cape Town. It is found growing in the mid-altitude region. It is very commonly found in Swaziland, especially in the northwest region of the Highveld (Padulosi et al. 1990). This taxon shows a relatively high degree of variability among populations found in the region. It overlaps in geographic distribution with var. *protracta*, while the latter taxon has a wider range of geographical distribution stretching from Republic of South Africa and Swaziland to Mozambique and Zimbabwe (Padulosi et al. 1991). The var. *protracta* thrives well in a range of geographical regions and in a wide range of altitudes (from sea level up to 1800 masl). This might suggest that var. *rhomboidea* represents a sort of relic species, which has undergone a speciation process of its own, or it could well be the ancestral form of other varieties of the species *V. unguiculata*. There exists a strong genetic barrier for gene flow between var. *rhomboidea* and other taxa (Ng and Apeji, unpublished), and it was pointed out earlier that this taxon may well be a distinct species.

Continuing on our speculation on the possible evolution of *V. unguiculata*, we further hypothesize that from the Transvaal, the species moved northward to Mozambique and Tanzania where it evolved into subspecies *pubescens*. The two glabrous subspecies, *tenuis* and *stenophylla*, have high morphological similarities, and they share some similar ecogeographical distribution from South Africa to Zimbabwe and Mozambique. The taxa are found in woodland and savanna ecologies, on sandy soils. Genetically, they are probably closer to one another than to other wild taxa. They probably evolved in the Natal-Transvaal region of South Africa, from where they radiated outwards to the coastal regions in South Africa and Mozambique, and to the west in Namibia and Angola.

Variety *congolensis* closely resembles ssp. *tenuis* and it also shows some similar characteristics with ssp. *stenophylla*. It is a perennial plant with a tuberous root. It is found in the Congo Basin. This suggests that a process of natural selection must have taken place in the Zaïrean and Congo region, operating on materials naturally distributed there in the early history of the evolution of *V. unguiculata*.

Variety *huillensis*, var. *dekindtiana*, var. *ciliolata*, and var. *grandiflora* of the subspecies *dekindtiana* represent the latest varieties in the evolutionary line of *V. unguiculata*. Var. *huillensis* is found in the savanna ecology in Angola and Zambia, and in woodland/savanna regions across Namibia and Miombo vegetation in South Africa. It was found at different altitudes, but with a higher frequency in the mid-altitude region. It is quite similar to var. *dekindtiana*, but it has a perennial growth habit, with a thick woody/tuberous root system. This is a pyrophytic species. It may represent the most primitive variety among the subspecies *dekindtiana*.

Variety *ciliolata* is found in the forest ecologies in Burundi, Malawi, Zambia, Zimbabwe, southwestern Cape Flora in South Africa, and in the eastern Kivu region in Zaïre. It is found growing in places of a medium to high altitude (600–1800 masl). Except for its long calyx tubes, it resembles var. *dekindtiana*. Variety *grandiflora* is occasionally found in parts of East and West Africa. Except for its large flower size, var. *grandiflora* resembles var. *dekindtiana* and var. *ciliolata*.

Taxa within the subspecies *dekindtiana* are closely related. Variety *dekindtiana* is a pantropical variety, which is distributed throughout Africa, south of the Sahara, including Madagascar. This taxon has a wide range of morphological variation and ecological tolerance. It has the largest seeds, while the smallest seeds are those of subspecies *pubescens*, subspecies *tenuis* and subspecies *stenophylla*. Variety *dekindtiana* is believed to be the probable progenitor of the cultivated cowpea (Rawal 1975; Lush 1979; Steele and Mehra 1980; Ng and Maréchal 1985). However, it is not certain to what extent the other wild varieties or subspecies of *V. unguiculata* have contributed to the origin and diversity of cowpea.

Domestication and diffusion

Ng (1995) postulated that during the process of evolution of *V. unguiculata*, there was a change of growth habit, from perennial to annual breeding and from predominantly outbreeding to inbreeding, while cultivated cowpea (subsp. *unguiculata*) evolved through domestication and selection of the annual wild cowpea (var. *dekindtiana*). During the process of domestication and after the species was brought under cultivation through selection, there was a loss in seed dormancy and pod dehiscence, corresponding with an increase in seed and pod size. The precise location or region where cowpea was first domesticated is still under speculation. The wide geographical distribution of var. *dekindtiana* throughout sub-Saharan Africa suggests that the species could have been brought under cultivation in any part of the region. However, the center of maximum diversity of cultivated cowpea is found in West Africa, in an area encompassing the savanna region of Nigeria, southern Niger, part of Burkina Faso, northern Benin, Togo, and the northwestern part of Cameroon (Ng and Maréchal 1985; Ng 1995).

In this region, many weedy forms of var. *dekindtiana*, intermediate between truly wild forms and those very small-seeded cultivated cowpeas are found (Rawal 1975). Carbon

dating of cowpea (or wild cowpea) remains from the Kimtampo rock shelter in central Ghana has been carried out (Flight 1976), and this is the oldest archaeological evidence of cowpea found in Africa. This shows the existence of gathering (if not cultivation) of cowpea by African hunters or food gatherers as early as c. 1500 BC.

In most African countries which produce cowpea today, landraces are cultivated as a component of mixed cropping systems, particularly in millet and sorghum-based farming systems in the semiarid and subhumid tropics in Africa. The haulm is gathered to feed cattle, particularly in northern Nigeria, Niger, Mali, Burkina Faso, and northern Cameroon, as well as in Senegal. It is equally important as a pulse in these regions.

Both flowers and mature pods can be found at the same time on wild and weedy var. *dekintiana*. Under natural conditions, very few pods can be found on a plant at a given time; however, the plant continues to produce flowers and pods over a long period. The low seed set per plant and low population density of the wild species suggest, therefore, that in preagricultural times, wild cowpea seeds could not have constituted a major portion of the human diet. At present, African farmers collect cowpea haulm by uprooting the whole plant, while it still carries green leaves and both mature and immature pods. It could be assumed that earlier African farmers similarly gathered wild cowpea plants to feed their cattle. In following this practice of gathering wild cowpea plants to feed cattle, it is probable that some seeds of the earliest mature pods, which could already have dehisced and ejected their seeds before or during the harvest, were missed, and this would have resulted in the selection of types with less shattering, while at the same time leaving behind the dehiscent wild type. Archaeological findings indicate the existence of cattle in West Africa as far back as 3000 BC (Clutton-Brock 1989). Ng (1995) postulated that cowpea cultigroup *Unguiculata* was, in the first place, domesticated in West Africa through this process of selection c. 2000 BC. Later, the selection for types with very long peduncles for fiber resulted in the cultigroup *Textillis* (Ng and Maréchal 1985). The crop was brought to Europe probably through northeastern Africa around 300 BC and to India about 200 BC. The cowpea underwent further diversification in India and Southeast Asia, producing the cultigroup *Sesquipedalis* with its long pods used as a vegetable and the cultigroup *Biflora* for its grain (Steele and Mehra 1980). The crop was introduced from Africa to the tropical Americas in the 17th century by the Spanish in the course of the slave trade. It has been grown in southern USA since the early 18th century.

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