Promoting the conservation and use of underutilized and neglected crops. 15.

Black nightshades

Solanum nigrum L. and related species

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Institut für Pflanzengenetik und Kulturpflanzenforschung
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Contents

Foreword

Humanity relies on a diverse range of cultivated species; at least 6000 such species are used for a variety of purposes. It is often stated that only a few staple crops produce the majority of the food supply This might be correct but. the important contribution of many minor species should not be underestimated. Agricultural research has traditionally focused on these staples, while relatively little attention has been given to minor (or underutilized or neglected) crops, particularly by scientists in developed countries. Such crops have, therefore, generally failed to attract significant research funding. Unlike most staples, many of these neglected species are adapted to various marginal growing conditions such as those of the Andean and Himalayan highlands, arid areas, salt-affected soils, etc. Furthermore, many crops considered neglected at a global level are staples at a national or regional level (e.g. tef, fonio, Andean roots and tubers, etc.), contribute considerably to food supply in certain periods (e.g. indigenous fruit trees) or are important for a nutritionally well-balanced. diet (e.g. indigenous vegetables). The limited information available on many important and frequently basic aspects of neglected and underutilized crops hinders their development and their sustainable conservation. One major factor hampering this development is that the information available on germplasm is scattered and not readily accessible, i.e. only found in 'grey literature' or written in little-known languages. Moreover, existing knowledge on the genetic potential of neglected crops is limited. This has resulted, frequently, in uncoordinated research efforts for most neglected crops, as well as in inefficient approaches to the conservation of these genetic resources.

This series of monographs intends to draw attention to a number of species which have been neglected in a varying degree by researchers or have been underutilized economically. It is hoped that the information compiled will contribute to: (1) identifying constraints in and possible solutions to the use of the crops, (2) identifying possible untapped genetic diversity for breeding and crop improvement programmes and (3) detecting existing gaps in available conservation and use approaches. This series intends to contribute to improvement of the potential value of these crops through increased use of the available genetic diversity In addition, it is hoped that the monographs in the series will form a valuable reference source for all those scientists involved in conservation, research, improvement and promotion of these crops.

This series is the result of a joint project between the International Plant Genetic Resources Institute (IPGRI) and the Institute of Plant Genetics and Crop Plant Research (IPK). Financial support provided by the Federal Ministry of Economic Cooperation and Development (BMZ) of Germany through the German Agency for Technical Cooperation (GTZ) is duly acknowledged.

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We are most grateful to Miss Stella Ross-Craig for permission to reproduce the plate of *S. nigrum*, to the Director of the Adelaide Botanic Garden for permission to reproduce the figures of *S. chenopodioides*, *S. retroflexum* and *S. villosum*, to Professor van der Maesen for permission to reproduce the plate of *S. scabrum* and to Academic Press for permission to reproduce the figures of *S. physalifolium* var. *nitidibaccatum* and *S. sarrachoides* and Figure 1.

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1 General introduction

Traditional societies have always exploited edible wild plants to provide an adequate level of nutrition (Richards and Widdowson 1936; Beemer 1939; Quin 1959; Jelliffe *et al.* 1962; Keller *et al.* 1969; Lee 1969; Scudder 1971; Silberbauer 1972; Korte 1973; Newman 1975; Abe and Imbamba l977; Gomez 1981; Chweya 1997). Recent studies on agropastoral societies in Africa indicate that these, plant resources a play a significant role in nutrition; food security and income generation (Tallantire land Goode 1975; Grivetti 1976; Johnson and Johnson 1976; Fleuret 1979a, l979b). The nutritional composition of these food resources, although not well documented, could be comparable to or even sometimes superior to the introduced cultivars (Fox and Weintraub 1937; Platt 1965; Fox 1966; Wehmeyer 1966; Leung 1968; Schmidt 1971; Imbamba 1973; Calloway *et al.* 1974; Okigbo 1980; Martin 1984; Ruberté l984; FAO 1989; Chweya 1997). It is, therefore, worthwhile to note that the incorporation or maintenance of edible wild and noncultivated plant resources could be beneficial to nutritionally marginal populations or to certain vulnerable groups within populations, especially in developing countries.

Agricultural development and cultivation in developing countries are primarily based on subsistence crops and edible wild plant species, and only secondarily on the cultivation or utilization of .a wide diversity of food crops, whose total number of species is large (Leakey and Wills 1977; Tindall 1977; Martin 1984). However, dietary utilization of nondomesticated plants has received little attention and a dramatic narrowing of the food base in many traditional societies has occurred. For example, of the thousands of edible wild and domesticated plants documented globally (Tanaka 1976), as few as 150 enter world commerce. Out of these 150 species only 15 constitute main sources of human food energy (Wilkes 1977). The narrowing of domesticated species used as crops creates a vulnerable position in which the crops could be destroyed by drought, diseases and/or pests (Turton 1977). The domestication and cultivation of wild edible plants are, therefore, essential to increase the food base in developing countries. This will lead to diversification which will ensure dietary balance and the intake of essential micronutrients.

Edible wild leafy vegetables play an important role in African agricultural and nutritional systems (Keller *et al.* 1969). Okigbo (1980), for example, listed over 160 endemic vegetables used in one small area in West Africa while Chweya (1997) and Juma (1989) listed several leafy vegetables used in Kenya. Moreover, Ogle and Grivetti (1985) and Ogle *et al.* (1990) gave lists of traditional/indigenous leafy vegetables used in Swaziland and Zambia, respectively, while Tallantire and Goode (1975), Fleuret (1979a), Getahun (1974), Johnson and Johnson (1976) and Malaisse and Parent (1985) all indicated plant species used as leafy vegetables in Uganda, Tanzania, Ethiopia, Nigeria and the Zambezian Woodland Area, respectively. Owing to the lack of documentation of their total yields and sales, such traditional leafy vegetables have been regarded as minor crops and have been given low priority in most agronomic research and development programmes (Brown 1983; Ruberté 1984; Brush 1986; Altieri and Merrick 1987; Prescott-Allen and Prescott-Allen 1990). Little is known of the indigenous knowledge of utilization, cultivation techniques, extent: and structure of genetic variation and potential for crop improvement through domestication, selection, and/or breeding. Few systematic studies, have been conducted on the various species used in this way and virtually no systematic collections of their germplasm have been made (Tindall 1977; Martin 1984). Some. of these vegetables are treated as weeds in different parts of the world and as indigenous/traditional vegetables in others. Such is the case of the *Solanum* species related to the black nightshade – the subject of this monograph.

The black nightshades *(Solanum nigrum* L. and related species) are worldwide weeds of arable land, gardens, rubbish tips, soils rich in nitrogen, in moderately light and’ warm situations which occur from sea to montane levels. They are, however, also widely used as leafy herbs and vegetables, as a source of fruit and for various medicinal purposes. Therefore, human consumption of their leaves and fruits as food is widespread, particularly in Africa and SE Asia. Unfortunately, there is also widespread confusion over the precise identification of the taxa involved, especially in those areas in which the species are most commonly used as food sources. This monograph attempts to identify the species related to the black nightshade more accurately, by providing an identification key, descriptions of the taxa most widely reported to be of dietary and/or ethnobotanical use in various Asian, African and Indonesian countries, listing some of the many vernacular names used for the species, recording the precise uses of the various species and giving some information on their genetic resources.

2 Taxonomy

2.1 Introduction

Economic impotiance of Solanaceous plants

The Solanaceae, to which the genus *Solanum* L. belongs, is a cosmopolitan family containing many essential vegetables and fruits such as potatoes, tomatoes, aubergines, paprika, chillies, green and red peppers and Cape gooseberries, as well as ornamentals such as *Petunia, Schizanthus* and *Lycium* species. It also contains tobacco *(Nicotiana* spp.) — one of the most harmful yet economically important plants in the world — together with many other plants of both poisonous and medicinal value such as belladonna or deadly nightshade *(Atropa belladona* L.), stramonium *(Datura stramonium* L.) and black henbane *(Hyoscyamus niger* L.). Composed of approximately 90 genera and between 2000 and 3000 species, the family is widely distributed throughout tropical and temperate regions of the world, with centres of diversity occurring in Central and South America and Australia (Edmonds 1978a; D'Arcy 1991).

Within this family, *Solanum* constitutes the largest and most complex genus; it is composed of more than 1500 species, many of which are also economically important throughout their cosmopolitan distribution. Examples of food plants are the potato *(S. tuberosum* L.), the aubergine or egg plant *(S. melongena* L.) and the lulo or naranjilla *(S. quitoense* Lam.); horticulturally useful plants include the winter cherry *(S. pseudocapsicum* L.) and jasmine nightshade *(S. jasminoides* Paxt.); species cultivated for their drug use include bittersweet *(S. dulcamara* L.) and *S. viarum* Dun., both used as sources of corticosteroids. Though the species are distributed throughout the world, they occur in their greatest concentrations in tropical and warm temperate regions with centres of diversity occurring in the Southern Hemisphere, particularly in South America. Other centres of speciation occur in Australia and Africa, with relatively few and less diverse species being found in Europe and Asia (Symon 1981; D'Arcy 1991). The generic name *Solanum* is generally considered to be derived from the latin *solamen,* and to refer to the quieting or sedative effects associated with many of the species.

Solanum section *Solanum*

The section *Solanum,* centering around the species commonly known as the black, garden or common nightshade, *Solanum nigrum* L., is one of the largest and most variable species groups of. the genus. It is more usually referred to as the section *Morella (Maurella* (Dun.) Dumort.; *Morella* (Dun.) Bitt.), but since the generic type is *S. nigrum,* the correct name for this section is *Solanum* (Seithe 1962). Species belonging to this section are distributed from temperate to tropical regions, and from sea level to altitudes over 3500 metres.

Though this species group is often referred. to as the *Solanum nigrum* complex, the section is composed of a large number of morphogenetically distinct taxa, which show their greatest diversity and concentration in the New World tropics, particularly in South America. *Solanum nigrum* itself is a predominantly Eurasian species, which does not occur naturally in South America (Edmonds 1979a). In most parts of the world, particularly in Europe and North America, these species are considered to be troublesome weeds of agriculture, but in many developing countries they constitute a minor food crop, with the shoots and berries not only being used as vegetables and fruits, but also for various medicinal and local uses.

2.2 Taxonomic summary of *Solanum* L. section *Solanum*

Causes of taxonomic complexity inherent on the species

The taxonomic complexity of species associated with the section *Solanum* has long been accepted (Stebbins and Paddock 1949; Heiser 1963; Symon 1970; Venkateswarlu and Rao 1972; D'Arcy 1973, 1974). Various classical, experimental and numerical studies have demonstrated that the complexity is attributable to a number of causes (Edmonds 1972, 1977, 1979a). Among these are the following.

Historical

Species belonging to this section have been subjected to extensive taxonomic study since Dillenius first delimited four taxa with polynomials in 1732. Linnaeus subsequently modified Dillenius' work, describing, six varieties under the binomial *S. nigrum* in 1753. Since then, the species related to *S. nigrum* have been reclassified innumerable times. Characters used by later taxonomists to, separate, and describe additional taxa often differed very slightly from those given for species by earlier workers. Over 300 post-Linnean specific and infraspecific names have now been published, and synonymy is extensive within the section. (Edmonds 1977). However, no satisfactory revision of the whole section has yet been devised. The boundaries between many of the species are still ill-defined, with many of the 'new' taxa proving to be no more than slight morphological variants of those already described. The situation has been further complicated by, a number of authors who have persistently treated different members of the section as belonging to one highly variable species, namely *S. nigrum* (e.g. Tandon and Rao 1966a, 1966b, 1974; Rao and Tandon 1969; Rao *et al.* 1971, 1977; Venkateswarlu and Rao 1971, 1972). Fortunately, Ganapathi and Rao (1986) subsequently demonstrated that the Indian plants generally described as 'cytotypes' of *S. nigrum* were indeed conspecific with the distinct diploid tetraploid and hexaploid species recognized by western workers, so it is hoped that the correct taxonomic names will now be adopted for the taxa concerned.

Phenotypic plasticity

These *Solanum* species display varying amounts of phenotypic variation, particularly in their vegetative features such as plant habit, leaf size and form, and stem winging. In addition, senescence is often accompanied by smaller and fewer flowers and fruits than usual, while the gene for anthocyanin pigmentation in flowers seems to be dependent on light intensity and temperature for its expression, in some species. It is therefore often difficult to define the limits within which such features are genetically fixed (Baylis 1958; Henderson 1974; Edmonds 1977).

Genetic variation

In addition, many species exhibit considerable genetic variation, both florally and vegetatively. This variation may occur in different populations of the same species, or may characterize different infraspecific categories of a species. Sometimes, the character may be genetically controlled in one species, but phenotypically plastic in another. Thus leaf margins may vary from entire to sinuate-dentate in different populations of *S. americanum* Mill., *S. furcatum* Dun. and *S. nigrum,* while the different subspeciesof *S. nigrum* and S. *villosum* Mill. are characterized by different indumentum types. These two species also display a range of berry colours within each of their subspecies with that in *S. nigrum* varying from green through purple to black, and that in *S. villosum* from yellow through orange to red. Though flower colour is phenotypically plastic in some species, it is under genetic control in others, as in the purple striping on the petals of *S. retroflexum* Dun. for example (Henderson 1974).

Polyploidy

Species belonging to the section constitute a polyploid series, with diploid ($2n=2x=24$), tetraploid ($2n=4x=48$) and hexaploid ($2n=6x=72$) species occurring throughout most of the geographical range in which the section is found. Octoploid plants ($2n=8x=96$) also have been reported on two occasions (Heiser 1963; Edmonds 1977, 1979a). Edmonds has made somatic chromosome counts of over 200 accessions of known origin collected throughout the world, and subsequently used experimentally, though not all of these have been published (see Edmonds1972,1977,1982,1983,1984a,1986). Many other authors have reported counts for small species groups, but some of these are considered to be based on misidentified material.

The possibility of determining a rough estimate of ploidy level from herbarium material was discussed in Edmonds (1979a). Both pollen diameter and stomata1 length tend to increase with ploidy level, and though pollen sizes are not always directly proportional to chromosome number in these species (Heiser 1963; Edmonds 1979a), if used in association with stomatal length, a good estimate of ploidy level usually can be obtained (Fig. 1).

Natural hybridization

Species belonging to the section *Solanum* are predominantly self-pollinating, but out- and cross-breeding can occur, and natural inter- and infraspecific hybridizations, especially among the smaller-flowered diploids, have been reported by a number of workers (e.g. Stebbins and Paddock 1949; D’Arcy 1974; Henderson 1974). Natural hybrids also have been reported at higher ploidy levels, e.g. infraspecific hybrids of the hexaploid *S. nigrum* (Venkateswarlu and Rao 1972). In addition, spontaneous hybrids have been reported between taxa of different ploidy levels, as between the hexaploid *S. scabrum* and the diploid *S. americanum* (Henderson 1974) and between the hexaploid *S. nigrum* and the diploid now known as *S. physalifolium* Rusby var. *nitidibaccatum* (Bitt.) Edmonds (Leslie 1978; Edmonds 1981).

Natural hybridization is probably more widespread in this section than generally supposed. Though this is probably followed by subsequent genetic breakdown in F_1 or F_2 generations (see Edmonds 1977), it may also be followed by back-crossing to the parental species. This would result in morphogenetically complex population variation: the collection of specimens from such populations would explain some of the difficulties encountered in the morphological differentiation of these species in the herbarium (Edmonds 1979a).

Discordant variation

Jardine and Sibson (1971) defined discordant variation as “A pattern of variation in which the relative extents to which populations are differentiated do not coincide for different sets of attributes. The product of mosaic evolution.” A population study investigating the degree of discordance in 32 *Solanum* populations representing 20 species of four differing ploidy levels demonstrated that the taxa exhibit considerable inherent discordant variation, and that a large number of characters must be used for the differentiation of these species (Jardine and Edmonds 1974; Edmonds 1978b).

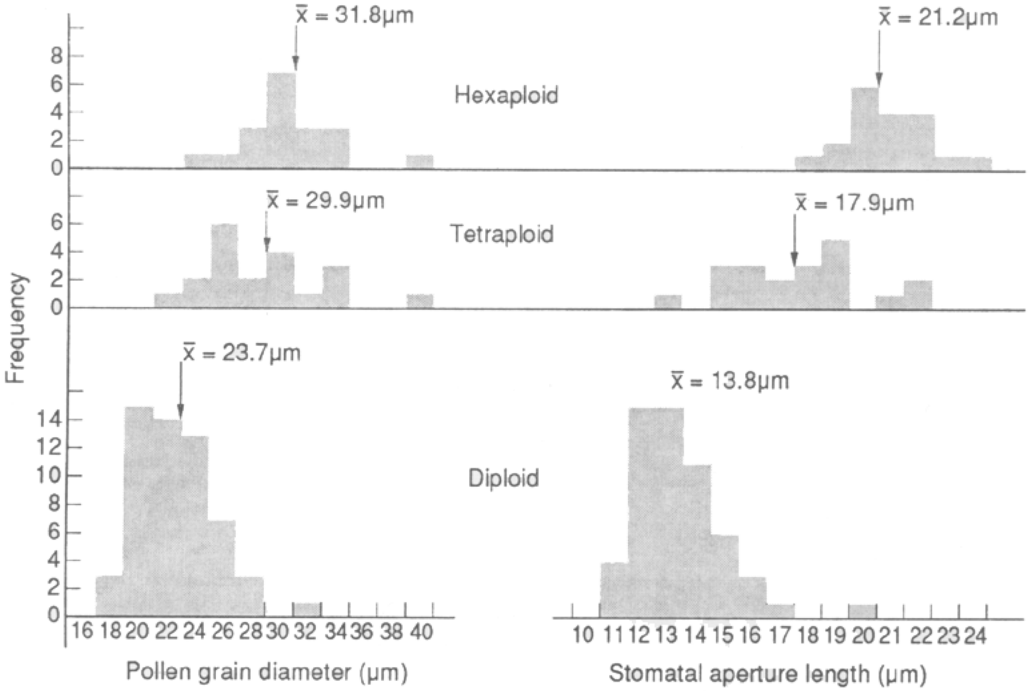

Fig. 1. Frequency histograms of pollen grain diameter and stomatal aperture lengths in various *Solanum* section *Solanum* accessions of known chromosome numbers. The frequency plotted represents the mean of ten measurements for each accession. (source: Edmonds 1979a)

This verified earlier work based on conventional herbarium methodology, when over 50 characters were used to differentiate the South American species belonging to this section (Edmonds 1972): these are summarized in Table 1.

Table 1. Characters used in morphological analysis of South American species of *Solanum* section *Solanum* (Edmonds 1972)

Character	Scoring method
Stem	
Stem ridging	Presence or absence
Ridge teeth	Presence or absence
Pubescence type	Pilose, tomentose, hirsute or villous
Degree of pubescence	Glabrous to dense (0-4 arbitrary scale)
Position of hairs	Appressed, erect or intermediate
Hair type	Glandular or eglandular
Leaf	
Shape	Rhomboidal, ovate, ovate-lanceolate, lanceolate or linear-lanceolate
Base	Cordate or cuneate
Apex	Obtuse, acute or acuminate
Margin	Entire, sinuate or sinuate-dentate
Number of lobes	Range per specimen
Depth of largest lobe	Ratio of lobe length to distance of lobe apex from midrib
Leaf length	mm
Leaf breadth	mm
Leaf length/breadth ratio	
Pubescence type	Pilose, tomentose, hirsute or villous
Degree of pubescence	Glabrous to dense (0-4 arbitrary scale)
Hair type	Glandular or eglandular
Petiole length	mm
Petiole/blade ratio	
Inflorescence	
Type	Cymose or cymose-umbellate
Peduncle position	Leaf-opposed or extra-axillary
Peduncle branching	Presence or absence
Pedicel number per inflorescence	Range per specimen
Peduncle length	mm
Pedicel length	mm
Pedicel reflexion	Presence or absence
Pubescence type	Pilose, tomentose, hirsute or villous
Degree of pubescence	Glabrous to dense (0-4 arbitrary scale)

Character	Scoring method
Flower	
Calyx length	mm
Sepal length (flowering)	mm
Sepal breadth (flowering)	mm
Sepal length (fruiting)	mm
Sepal breadth (fruiting)	mm
Mature calyx form and position	Reflexed, adherent or adherent-accrescent
Calyx pubescence type	Pilose, tomentose, hirsute or villous
Degree of calyx pubescence	Glabrous to dense (0-4 arbitrary scale)
Corolla shape	Stellate, semi-stellate, pentagonal or rotate
Petal length	mm
Petal breadth	mm
Corolla colour	white or purple
Corolla radius	mm
Anther length	mm
Pollen grain diameter	µm
Style length	mm
Style posture	Straight or geniculate
Stylar exsertion	Presence or absence (when present, measure in mm beyond anthers)
Berry	
Diameter	mm
Seed length	mm
Seed breadth	mm
Stone cells	Presence or absence

Species currently recognized

Various taxonomic treatments of species belonging to the section *Solanum* are fully discussed in Edmonds (1977, 1979a). Earlier workers were essentially ‘splitters’ basing large numbers of inter- and infraspecific taxa on characters now known to be insignificant in this variable species group. Most of the more recent authors, however, based their conclusions on material of fully documented, known wild origin and, in many cases, on considerable experimental work. As a result, the taxonomy of the species involved has been resolved for certain geographical areas, where the species relationships of the component taxa are now fairly well understood. The species currently recognized on the basis of such work are summarized in Table 2. The data are given in tabular form for each of the geographical areas concerned, together with the major reference sources. The cytological counts are all based on collections of known wild origin, verified by the authors cited.

Table 2. **Species belonging to *Solanum* section *Solanum* currently recognized in the major geographical areas**

Species	Chromosome no. (2*n*=)
AUSTRALIA (Henderson 1974,1988; Randell and Symon 1976; Symon 1981)	
Native:	
S. americanum Miller subsp. *nodiflorum* (Jacq.) R. Henderson	24
S. americanum Miller subsp. *nutans* (Henderson) R. Henderson	24
S. opacum A. Braun & Bouché	72
Introduced:	
S. chenopodioides Lam.	24
S. douglasii Dunal	24
S. furcatum Dunal	72
S. nigrum L. subsp. *nigrum*	72
S. nigrum L. subsp. *schultesii* (Opiz) Wess.	72
S. retroflexum Dunal	48
S. sarrachoides Sendtn.[†]	24
S. scabrum Miller	72
S. villosum Miller	48
EUROPE (Hawkes and Edmonds 1972; Edmonds 1979a, 1979b, 1981, 1984, 1986)	
Widespread:	
S. nigrum L. subsp. *nigrum*	72
S. nigrum L. subsp. *schultesii* (Opiz) Wess.	72
S. villosum Miller subsp. *villosum*	48
S. villosum Miller subsp. *miniatum* (Bernh. ex Willd.) Edmonds	48
Casual and sporadic:	
S. americanum Miller	24
S. chenopodioides Lam.	24
S. physalifolium Rusby var. *nitidibaccatum* Bitt.) Edmonds	24
S. sarrachoides Sendtn.	24
S. scabrum Miller	72
CENTRAL AMERICA (D'Arcy 1973; Nee 1993; Edmonds 1977)	
S. americanum Miller	24
S. nigrescens Mart. & Gal.	24
? S. macrotonum Bitter	72
INDIA and PAKISTAN (Schilling and Andersen 1990)	
S. americanum Miller	24
S. nigrum L.	72
S. villosum Miller	48
NEW GUINEA (Symon 1985)	
S. americanurn Miller	24
S. opacum A.Br. & Bouché	72

NORTH AMERICA (Schilling 1981)	
Native:	
S. americanum Miller	24
S. douglasii Dunal	24
S. interius Rydb.	24
S. pseudogracile Heiser	24
S. ptycanthum Dunal	24
Introduced:	
S. sarrachoides Sendtn.[†]	24
Infrequent:	
S. furcatum Dunal	72
S. nigrum L.	72
S. villosum Miller	48
Cultivated:	
S. retroflexum Dunal	48
S. scabrum Miller	72
SOUTH AMERICA (Heiser 1963; Edmonds 1972, 1977, 1978b, 1986)	
Glandular-haired taxa:	
S. excisirhombeum Bitter	48
S. fiebrigii Bitter	24
S. fragile Wedd.	48
S. glandulosipilosum Bitter	24
S. insulae-paschalis Bitter	24
S. physalifolium Rusby var. *nitidibaccatum* (Bitt.) Edmonds	24
S. sarrachoides Sendtn.	24
S. sinuatiexcisum Bitter	24
S. tweedianum Hooker	24
Eglandular-haired taxa:	
S. aloysiifolium Dunal	24
S. americanum Miller var. *americanum*	24
S. americanum Miller var. *patulum* (L.) Edmonds	24
S. arequipense Bitter	72
S. chenopodioides Lam.	24
S. cochabambense Bitter	24
S. furcatum Dunal	72
S. interandinum Bitter	48
S. itatiaiae Glaz. ex Edmonds	24
S. macrotonum Bitter *(Syn.: S. paredesii* Heis.)	72
S. nigrescens Mart. & Gal.	24
S. pentlandii Dunal	24
S. polytrichostylum Bitter	24
S. zahlbruckneri Bitter	24

[†] From the author's descriptions, this taxon is believed to be *S. physalifolium* var. *nitidibaccatum.*

The absence of species from Africa and Malesia (Melanesia, Malaysia, Indonesia) in Table 2 clearly demonstrates that these are the two major geographical areas for which taxonomic revisions of these Solanums are urgently required, especially since these are the two regions in which they are widely used as minor food crops. Georg Bitter had intended to monograph the African species, but died before completing the task, leaving a number of scattered publications in which he described various species and infraspecific variants (e.g. Bitter 1912, 1913, 1917, 1921). Working almost exclusively on dried material and basing most of his new taxa on one or at most very few specimens, Bitter thought of *Solanum* species as very narrow units displaying little infraspecific variability (Edmonds 1977). The taxonomic difficulties encountered in assessing the taxa described by Bitter have been enhanced by the destruction of a large number of his type specimens in Berlin-Dahlem during the Second World War.

The only recent taxonomic treatments of the *Solanum* species found in Africa are those of Jaeger (1985) who attempted a monographic revision of the entire genus in Africa, and of Bukenya and Hall (1988) and Bukenya and Carasco (1995) who revised the Ghanian and Ugandan species respectively. Emphasizing the complexity of the section *Solanum* in Africa, Jaeger did not attempt to resolve the problems inherent in this species group, but provisionally recognized 13 taxa, constructing a key to six of the most widely distributed. Most of the taxa that he recognized are included in the following sections. Similarly, the eight species belonging to the section *Solanum* which Bukenya and Carasco recorded as occurring in Uganda following discussions between Bukenya and Edmonds, are all included in the following account. These African species have not been included in Table 2, however, because the revisions by these authors were largely based on herbarium material and did not include any cytological data.

Provisional examination of the African representatives of the section *Solanum* revealed that the most common species were those also found in Europe and in Asia. An identification key was therefore formula ted to identify these taxa, some of which are native, and some of which are now common casuals in these areas. This key, however, has been formulated as a ‘working base’ on which a future comprehensive taxonomic revision of the African species belonging to the section *Solanum* can be based. It should not be considered as a definitive key to the taxa found in Africa. Future research based on living populations will undoubtedly show that additional good species, perhaps with comparatively limited distribution areas, must be recognized in this continent.

2.3 Morphological characteristics of *Solanum* L. section *Solanum* species

Species belonging to *Solanum* section *Solanum* are characterized as follows:

Habit: Unarmed herbs, sometimes suffrutescent, occasionally shrubs or epiphytes. **Stems:** terete or angled, the angles with smooth or dentate ridges; sparsely to densely pubescent with simple, uniseriate, multicellular, patent or appressed hairs with eglandular or glandular heads, interspersed with spherical four-celled glands.

Leaves: petiolate, simple, solitary and alternate or in unequal pairs or triplets, ovate to lanceolate, occasionally rhomboidal; apices acuminate, acute or obtuse; bases cuneate or cordate; margins entire to sinuatedentate; laminas sparsely to densely pubescent with hair types as on stems; **petioles** usually canaliculate and alate. **Inflorescences:** 2 to 36-flowered, cymose, pedunculate; **peduncles** simple or forked, erect or reflexed at maturity, glabrescent to pubescent with hairs as on stems; **pedicels** erect or reflexed at maturity, glabrescent to pubescent as stems; **cymes** umbellate to helicoid, compressed to lax. **Flowers** pedicellate, pentamerous; **calyx** campanulate-stellate, with broadly triangular to ovate-lanceolate sepal lobes, mature sepals persistent and reflexed or accrescent, pubescent externally with hairs as above; **corolla** <20 mm diameter, white to purple, often with a conspicuous basal star, stellate to rotate, the petals recurved, pubescent externally with hairs as above; **filaments** fused for approximately half their length, joined to the corolla tube, covered with uniseriate, muticellular patent hairs; **anthers** connivent, oblong, yellow to brown, dehiscing by oblong pores which often develop into longitudinal slits; **pollen** spheroidal to subprolate, tricolporate, with granular surface sculpturing, 17-40 µm diameter; **styles** straight or geniculate, often exserted, lower parts covered with short patent hairs; stigmas globular, usually capitate. **Fruits** succulent, 2-locular, many-seeded, globose to ovoid, black, brown, red, orange, yellow or green berries, 6-10 (-17) mm diameter. **Seeds** small, 0.75-2.5 mm long, compressed, obovate to obliquely ovate, with rough or reticulate testa, white, yellow or brown. **Sclerotic granules** present or absent.

Full details of the epidermal hair morphology characterizing these Solanums are given in Edmonds (1982), while their seed coat structure and development and their pollen morphology are described and discussed in Edmonds (1983 and 1984a, respectively). Variation in the berry colour and shape displayed by these species is illustrated in Figure 2.

Fig. 2. Berry colours and shapes exhibited by various species: a - *S. nigrum,* green-berried variant (T72); b - *S. nigrum,* purple-berried variant (Cl 13); c - *S. villosum,* yellow-berried variant (T95); d - *S. villosum,* orange-berried variant (T69); e - *S. americanum* (T198); f - *S. chenopudioides* (T355); g - *S. physalifolium* var. *nitidibaccatum* (T295); h - *S. scabrum* (T246). Provenance data for these accessions are given in Edmonds (1977).

2c

2d

2e

2f

2g

2h

2.4. Key to the species of *Solanum* L. section *Solanum* most commonly found in Africa and Eurasia

1a. Flowers rotate to pentagonal; fruiting calyces strongly accrescent, enclosing at least lower half of berries; berries with stone cells **2**

2a. Inflorescences umbellate cymes, 3 to 4(5)-flowered; corollas rotate to pentagonal with petals broader than long, white with yellow/translucent basal star; berries pale green, shiny becoming dull, opaque, usually completely enveloped by enlarged calyces; seeds pale yellow; 4-6 sclerotic granules usually present ....***S. sarrachoides***

2b. Inflorescences lax extended cymes, (3)4 to 8(10)-flowered; corollas rotate with petal lengths and breadths ± equal, white or purplish with distinct purple (or brown) and yellow basal star; berries dark green to green-brown, usually translucent and glossy, lower half of berries covered with enlarged calyces; seeds brown; 2 apical sclerotic granules usually present..........***S. physalifolium*** **var.** ***nitidibaccatum***

1b. Flowers stellate; fruiting calyces only slightly accrescent, deflexed or adhering to the base of berries; stone cells usually absent **3**

3a. Fruiting peduncles strongly deflexed from the base.................***S. chenopodioides***

3b. Fruiting peduncles erecto-patent, ascending or curved downwards **4**

4a. Flowers small, corollas about 4.5 mm diameter; anthers <l.5 mm long; fruiting pedicels usually erecto-patent; berries 6(8) mm diameter, spherical, black, and usually shiny when mature; seeds 1-1.5 mm long ....***S. americanum***

4b. Flowers medium, corollas >5 mm diameter; anthers 1.5-3.0 mm long; fruiting pedicels usually reflexed, occasionally erecto-patent; berries >7 mm diameter, usually ovoid, purple, red, orange, yellow or green and usually dull when mature; seeds >1.5 mm long **5**

5a. Leaf margins usually prominently sinuate-dentate; inflorescences condensed umbellate cymes, 3 to 5-flowered; peduncles short, usually 7 to 10(13) mm in fruit; berries spherical or longer than broad.. **6**

5b. Leaf margins entire, sinuate or sinuate-dentate with indistinct lobes; inflorescences lax cymes, 5 to 20-flowered; peduncles >15(30+) mm long in fruit; berries broader than long **8**

6a. Flowers white with distinct purple vein to outer surface of petals; berries usually spherical, purple with opaque cuticles..***S. retroflexum***

6b. Flowers white without purple veining on petals; berries usually longitudinally ovoid, red, orange or green with translucent cuticles..7

7a. Stems usually terete, with smooth ridges; plants villous, covered with glandular-headed and often patent multicellular hairs ....***S. villosum*** **subsp.** ***villosum***

7b. Stems usually angular with dentate ridges; plants glabrescent to pubescent with appressed eglandular-headed multicellular hairs ....***S. villosum*** **subsp.** ***miniatum***

8a. Plants glabrescent; stems prominently winged with dentate ridges; inflorescences lax cymes, 8 to 14+-flowered; anthers brown; berries purple, large, 15-17 mm diameter ....***S. scabrum***

8b. Plants pubescent; stem ridges inconspicuously dentate; inflorescences <10-flowered; anthers yellow; berries medium-sized, 6-10 mm diameter, purple, green or greenish-yellow.. **9**

9a. Plants subglabrous to pubescent usually with appressed, eglandular-headed multicellular hairs...***S. nigrum*** **subsp.** ***nigrum***

9b. Plants villous, usually with patent, glandular-headed multicellular hairs ....***S. nigrum*** **subsp.** ***schultesii***

2.5 Enumeration of the species

Only those species belonging to the section *Solanum* which are commonly found in Europe, Asia and Africa are included in this account, where they are dealt with in alphabetical order. Other taxa have been reported to occur in these areas, or have been encountered in various herbaria. However, the taxonomy of these — mainly African taxa — remains to be resolved, and they are not those species often referred to as being of use as crop plants. Those considered to be possible good species following examination of the Kew collection are summarized in Section **2.6.**

The following species descriptions have been compiled from data derived from herbarium specimens either examined in, or obtained on loan from, the major international herbaria, together with those taken from populations successively cultivated over many years in the Botanic Gardens of the Universities of Birmingham and Cambridge, and the Wytham Field Station of the University of Oxford. Herbarium collections used include those of A, B, BA, BERN, BIRM, BM, BR, BREM, BRLU, C, CAS, CGE, E, G, GH, GOET, H, HBG, HAJB, IND, K, KIEL, L, LD, LE, LINN, LP, LZ, M, MA, MICH, MO, MPU, NY, OXF, P, PR, RSA, S, SBBG, SI, U, UC, UPS, US, W, WIS, and Z (see Holmgren *et al.* 1990 for full names of herbaria). The information given on the distribution of these species in Africa, together with their vernacular names and the use made of them by local communities, were mostly taken from herbarium specimens, with the African data largely being derived from Kew (K) material. Similar data derived from the literature is given elsewhere. Full literature citations of the species considered to be synonyms of those taxa described here have not been given in the interests of brevity. Most are elaborated in chronological order of their publication in many of the papers cited in the following text.

***S. americanum* Miller,** The Gardeners Dictionary, Ed. 8, art. *Solanum* no. 5 (1768).
Type: Cult. Chelsea Physic Garden, origin Virginia, *Miller s.n.* (Holotype BM!)
Common synonyms:

S. adventitium Polgár
S. calvum Bitter
S. caribaeum Dunal
S. curtipes Bitter
S. gollmeri Bitter
S. inconspicuum Bitter
? *S. inops* Dunal
S. microtatanthum Bitter
S. minutibaccatum Bitter
S. minutibaccatum Bitter subsp. *curtipedunculatum* Bitter
S. nigrum L. var. *dillenii* A. Gray
S. nigrum L. *var. nodiflorum* A. Gray
S. nodiflorum Jacq.
S. nodiflorum Jacq. var. *acuminatum* Dunal
S. nodiflorum Jacq. var. *macrophyllum* Dunal *pro parte*
S. nodiflorum Jacq. var. *petiolastrum* Dunal
S. nodiflorum Jacq. var. *puberulum* Dunal
S. oleraceum Dunal
? *S. pachystylum* Polgár
S. photeinocarpum Nak. & Odash.
S. sciaphilum Bitter
S. tenellum Bitter

Plants glabrescent to moderately pilose with appressed eglandular hairs. **Stems** with edentate to inconspicuously dentate ridges. **Leaves** ovate-lanceolate to lanceolate, (2.2)3.0 to 6.2(11.0) cm long x 1.1-4.0(6.6) cm broad; lower surfaces glabrescent to moderately or densely pilose; margins entire to sinuate, rarely sinuate-dentate. **Inflorescences** simple, umbellate cymes, 3 to 6(10)-flowered; **peduncles** to 2.8 cm long fruiting; **pedicels** to 14 mm long fruiting, when usually erect and splayed, occasionally reflexed and nodding. **Calyces** 1.1 to 2.0(2.4) mm long; sepals reflexed away from mature berries. **Corollas** stellate, white, occasionally purple, with translucent to yellow-green basal star, 1.6 to 4.0(6.0) mm radius. **Anthers** yellow, 0.7 to 1.5(2.0) mm long. **Pollen** (12)15.0 to 21.7(24.8) µm diameter. **Styles** 1.2 to 3.5(4.5) mm long, usually exserted beyond anthers, up to **2.5** mm. **Berries** globose, black, rarely dark green, with shiny opaque cuticles, falling from calyces when ripe, 4 to 7(8) mm diameter. **Seeds** 0.8-l.5 mm long, 24 to 70(101) per berry. **Sclerotic granules** usually absent, occasionally present.

Cytology: $2n=2x=24$ (Baytis 1958; Edmonds 1972, 1977, 1982, 1983, 1984a and unpublished; Henderson 1974; Randett and Symon 1976; Symon 1981; Schilling and Andersen 1990; Bukenya 1996).

Illustrations: Figures 2e and 3.

Distribution (sea level to 2926 m): Africa: Aldabra Islands, Angola, Ascension Island, Assumption, Burundi, Cameroon, Central African Republic, Cape Verde Islands, Ethiopia, Gambia,, Ghana, Guinea, Côte d'Ivoire, Kenya, Liberia, Madagascar, Mauritius, Mozambique, Namibia, Nigeria, St. Helena, Seychelles (Aride, Bird, Denis, Frigate, Mahe and Silhouette Islands), Senegal, Sierra Leone, Socotra, Somalia, South Africa (Cape Province, Natal, Swaziland, Transvaal), Sudan, Tanzania, Togo, Tunisia, Uganda, Zaire, Zambia, Zanzibar; **Australia:** all States except South Australia, probably native to eastern Australia; **Caribbean Islands** including Cuba, Dominican Republic, Haiti, Jamaica; **Central America:** Costa Rica, Honduras, Guatemala, Mexico, Nicaragua to Panama; **China; Europe:** rare casual in parts of western, central and southern regions; **Hawaii** (Islands of Hawaii, Kauai, Lanai, Maui, Molokai, Niihau and Oahu); **Indonesia** (e.g. Borneo and Sumatra); **Irian Jaya; Jamaica; Japan; India; New Zealand:** North and South Islands; **North America:** southern Georgia to Florida and west to California; **Pacific Islands:** e.g. Society, Caroline and Marshall Islands; **Pakistan; Papua New Guinea; Philippines; Sri Lanka; South America** (? native): Argentina, Bolivia, Brazil, Chile, Colombia, Ecuador (incl. Galapagos Isl.), the Guianas, Peru, Paraguay, Uruguay and Venezuela; **Taiwan; Thailand; Tonga; Trinidad; Windward Isles**

Vernacular names: Argentina: Arachichu (Misiones); **Assumption:** Brede (West Isl.); **Australia:** Glossy nightshade; **Brazil:** Yerba morro, Eva amor; **Cameroon:** Wosangu-njika, wosangu (Bakweri), Huckleberry, legume verte (French); **Ghana:** Nsusúa (Twi), Ebibirba (Fante); **Guatemala:** Hierba more (Chimaltenango; Jutiapa), macuy (Alta Verapaz), quilete (Santa Rosa); **Kenya:** Ol'momoit (Masai), Isoyot (Kipsigis), Managu (Kikuyu), Ysudza; **Madagascar:** Brede; **Mauritius:** Brede martin, Brede (Mapau Isl.); **Mexico:** Yerba mora, Ekelite, quelite; **New Guinea:** Karakap; **New Zealand:** Small-flowered nightshade; Nigeria: òdú, o'dú, o'gunmo (Yoruba); **North America:** Hierba moura, small-flowered nightshade; **Panama:** Kaburgia; Seychelles: Brède martin (Aride Isl.); **Sierra Leone:** Kholekoleden-na (Yalunka), Efo-odu (Creole ex Yoruba), Sapota (Creole), "Eat-finish-and-broke-plate" (Creole); **South Africa:** Black nightshade (Swaziland); **Surinam:** Bietagomo, Bietawiwirie; **Tanzania:** Mnavu (Bondei, Shambaa), Msogo (Bende), Mhaki (Kibena); **Uganda:** Wsuggaenzirugavu; **West Indies:** Agouma, bitter gumma, black nightshade.

Recorded uses: Bolivia: locally cultivated, fruit edible; **Cameroon:** leaves pounded for sores, used in soup, leaves and young shoots eaten as pot-herb, leaf vegetable sold in markets by Bamileke tribe; **Ethiopia:** cultivated; **Ghana:** pot-herb, uncultivated herb; **Guatemala:** young plants eaten as a pot-herb, found in most markets, consumed in large quantities; **Kenya:** leaves eaten as vegetable, spinach

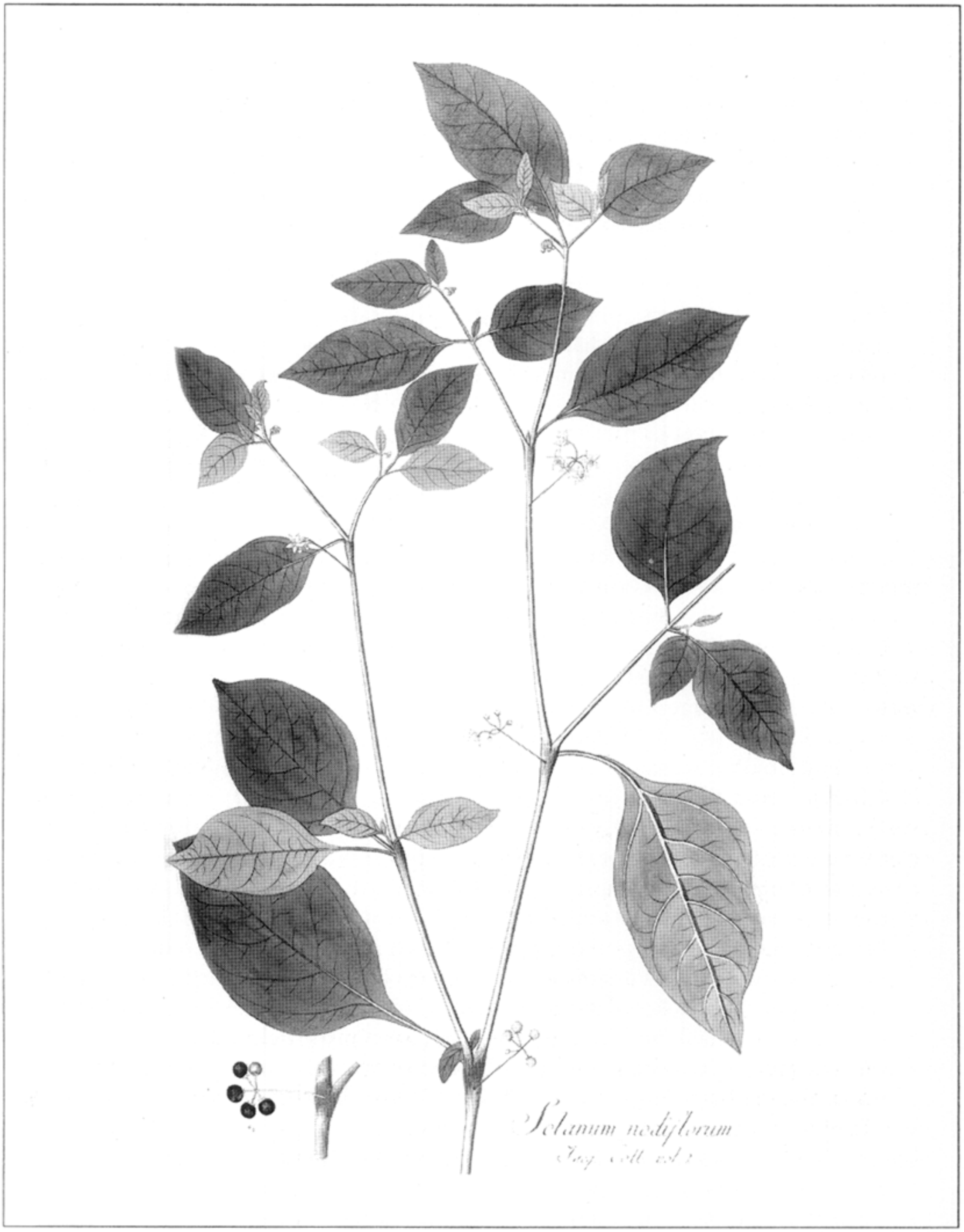

Fig. 3. *S. americanum* Mill. Flowering stem with immature and mature (inset) infructescences. Note the erect fruiting pedicels. (Jacquin; Ic. Pl. Rar. 2, t. 326 (1786))

made from leaves, Kipsigis children eat fruits, Masai make infusion from leaves to rub on body for pains (? rheumatism) (Narok Distr.); **Madagascar:** used as green vegetable for soup, on sale in Antananarivo market; **Mauritius:** commonly used locally as a pot-herb or in bouillons, cultivated (Mapou Isl.); **Hawaii:** leaves and tender stems cooked as substitute for poi, berries eaten raw, juice of leaves mixed with salt used as remedy for eye diseases, root chewed as cold cure; **Nigeria:** native pot-herb, cultivated; **Pacific Islands:** used as green vegetable; **Panama:** medicinal plants of the Bayano Cuna; **Papua New Guinea:** vegetable, cultivated for sale in local markets; **Peru:** edible fruit, locally cultivated; Seychelles: edible, cultivated around buildings (Bird Isl.), sometimes eaten as “spinat” (Aride Isl.); **Sierra Leone:** good medicine, leaf eaten raw for heart pains, leaves eaten in soup, juice from ripe berries used as ink by children, fruits very sweet leading to common name “eat-finish-and-broke-plate”; **South Africa:** leaves cooked and eaten (Natal); **Tanzania:** vegetable, boiled by Africans and used as vegetable, edible as spinach, used for inflamed eyes — fresh leaves pounded and juice sprayed into the eye — used with great effect on a case of severe conjunctivitis; **Uganda:** leaves eaten, used by natives as vegetable (near Butambuli).

This is probably the most widespread and morphologically variable species belonging to the section *Solanum*. It is found throughout the world, and a number of infraspecific variants have so far been formally recognized. These include the finely pubescent var. *americanum* largely found throughout the western parts of South America; the glabrescent var. *patulum* (L.) Edmonds common in the eastern parts of South America (Edmonds 1971, 1972, 1977); and the subsp. *nutans* (R. Henderson) R. Henderson and subsp. *nodiflorum* (Jacq.) R. Henderson (?= var. *patulum)* described from Australian specimens. Henderson considered the former, characterized by reflexed fruiting pedicels and sclerotic granules in the berries, to be native to Australia, with the latter, characterized by erect fruiting pedicels and an absence of sclerotic granules, to be introduced (Henderson 1974, 1988), However, hybrids occur where these subspecies are sympatric, and the subsp. *nutans* also has been recorded in other geographical areas. Baylis (1958) considered that the New Zealand forms represented three naturalized races differing in alleles controlling the distribution of anthocyanin colouration, white Healy (1974) later reiterated that both adventive and indigenous forms occur on the North and South Islands. Symon (1981) later discussed the variability displayed by this species in Australia, while Schilling (1981) reported that North American populations of this taxon formed four morphological groups with distinctive crossing behaviour which probably deserved format infraspecific recognition. It is the form with erect fruiting pedicels, treated in this account as *S. americanum sens. lat.* which is the most cosmopolitan species in the section *Solanum*. Henderson (1974) suggested that it is native to the western Indian Oceanic Islands, possibly the west coast of Africa, northern regions of South America, Central America and the southeastern United States. Schilling and Anderson (1990) later postulated that the species is native to South America and that a limited number of genotypes spread from there to colonize other areas of the world. It is generally considered to be an adventive in much of the Old World. A worldwide assessment of the variability exhibited by this diploid species together with crossability studies between the different variants recognizable both within and between different geographical areas is necessary before its taxonomy can adequately be resolved, and the formal recognition of infraspecific taxa clarified.

***S. chenopodioides* Lam.,** Tableau encyclopédique et méthodique des trois Règnes de la Nature. Botanique 2:18 (1794).

Type: *Herb. Lamarck* s.n. (Holotype P!).

Common synonyms:

S. chenopodifolium Dunal
S. gracile Dunal; *S. gracile* Link ex A. Gray; *S. gracile* Otto ex Cameron
S. gracile Dunal var. *microphyllum* Dunal
S. gracilius Herter
S. isabellii Dunal
S. ottonis Hylander
S. *pterocaulon* Dunal var. *aguaraquiya* Dunal
S. sublobatum Willd. ex Roem. & Schult.
S. subspatulatum Sendtn.
S. vile Bitter

Plants sprawling herbs to 1 m high, often greyish-green in colour, somewhat tomentose with soft appressed eglandular-headed multicellular hairs. **Stems** usually smooth with edentate ridges. **Leaves** elliptic to lanceolate, 2.7 to 5.4(10-0) cm long x (1.8)2.2 to 5.4 cm broad, margins entire to sinuate, apices obtuse to acute, distinct lobes usually absent; lower surface usually distinctly tomentose. **Inflorescences** simple, umbellate cymes, 4 to 6(8)-flowered; **peduncles** 1.0 to 2.5(5.0) cm long fruiting when distinctively deflexed and often subtended by small elliptic leaf; **pedicels** 8-12 mm long. **Calyces** 2.4-3.5 mm long in flower, sepals usually adherent to base of mature berry. Corollas stellate, white with greenish-yellow or brown and yellow basal star, 6.0-9.0 mm radius. **Anthers** yellow, 2.0-2.8 mm long. **Pollen** 18.0-24.8 µm diameter. Styles 4.0 to 5.5(6.5) mm long, exserted up to 2 mm beyond anthers. **Berries** globose to broadly ovoid, purple, with dull opaque cuticles, 6.3-8.5 mm diameter, deciduous when **ripe** and falling from calyces or with pedicels still attached. **Seeds** 1.0-1.8 mm long, 24 to 48(62) per berry. **Sclerotic granules** usually absent.

Distribution (sea level to 2438 m): Africa: South Africa (Cape Province, Lesotho, Natal, Transvaal); **Australia:** introduced and established as weed in temperate east coastal regions; **Europe:** locally naturalized especially in SW (France, Germany, Great Britain, Portugal, Spain, Sweden and Switzerland); New **Zealand:** naturalized especially in Westland (South Island); North **America:** mainly C and S States to Florida; **South America** (native): Uruguay, NE Argentina, S Brazil.

Fig. 4. *S. chenopodioides* Lam. Flowering stem with mature infructescences. Note deflexed fruiting peduncles and prominently stellate corollas (inset). (Symon 1981)

Cytology: $2n=2x=24$ (Edmonds 1972, 1977, 1982, 1983, 1984a and unpublished; Henderson 1974; Randell and Symon 1976).

Illustrations: Figures 2f and 4.

Vernacular names: Australia: Whitetip nightshade; **Brazil:** Liaghe; **New Zealand:** Velvety nightshade; **Uruguay:** Yerba mora.

Recorded uses: South Africa: used as spinach (Natal).

The complex nomenclatural problems surrounding this diploid species are discussed in Edmonds (1972, 1979b). Baylis (1968) considered the occurrence of this species in New Zealand, while Henderson (1974) and Symon (1981) discussed its occurrence in Australia. It is one of the most easily identifiable members of the section *Solanum.* However, *S. chenopodioides* does not seem to be utilized as a food source, with the only reference to its use as a 'spinach'-plant being Natal in South Africa — indeed the latter seems to be the only African country in which it is commonly found. The species is native to eastern parts of South America from where it has been introduced to other regions. Its occurrence around rail way stations and cuttings, docksides and mills, especially in Europe, is undoubtedly associated with the importation of grain, seeds and 'oil-fruits' from South America, especially from Argentina, together with the widespread practice of using wool waste or 'shoddy' as a manure. The latter has been extensively spread on light agricultural sandy soils, and has been a major source of South American adventives which have become established as weeds in Europe (Edmonds 1986). In a few cases it is known to have been introduced with the importation of a specific product, such as with Argentinian flax to Sweden.

***S. nigrum* L.,** Species Plantarum 186 (1753).

Type: *Herb. LINN 248.18* (Lectotype LINN!)

Plants subglabrous to villous annuals up to *70* cm high, covered with simple multicellular hairs with glandular or eglandular heads. **Stems** decumbent to erect. **Leaves** ovate, ovate-lanceolate, ovate-rhombic to lanceolate, 2.5-7.0cm long x 2.0 to 4.5(6.0) cm broad, margins entire to sinuate-dentate. **Inflorescences** simple, lax and often extended cymes, (3)5 to 10-flowered; **peduncles** (8)14 to 28 mm fruiting when usually erecto-patent; **pedicels** much shorter, recurved in fruit. **Calyces** 1.2-2.5 mm long, slightly accrescent, deflexed or adhering to base of mature berry, sepals usually ovate. **Corollas** stellate, white with translucent basal star, (4)5 to 7(9) mm radius, usually 1.5-3 times **as** long as calyx. **Anthers** yellow, 1.5 to 2.5(2.8) mm long. **Pollen** (26.6)29.5 to 33.9(35.7) µm diameter. Styles 2.8 to 3.5(4.5) mm long, not exserted beyond anthers. **Berries** usually broadly ovoid, dull purple to blackish or yellowish-green, 6-10 mm broad, remaining on plants or falling from calyces when ripe. **Seeds** 1.7-2.4 mm long, (15)26 to 60(96) per berry. **Sclerotic granules** absent.

Distribution (sea level to 3048 m): Africa: Angola, Botswana, Cameroon, Chad, Ethiopia, Ghana, Guinea, Kenya, Libya, Malawi, Morocco, Mozambique, Niger, Nigeria, Socotra, Somalia, South Africa (Cape Province, Lesotho, Natal,

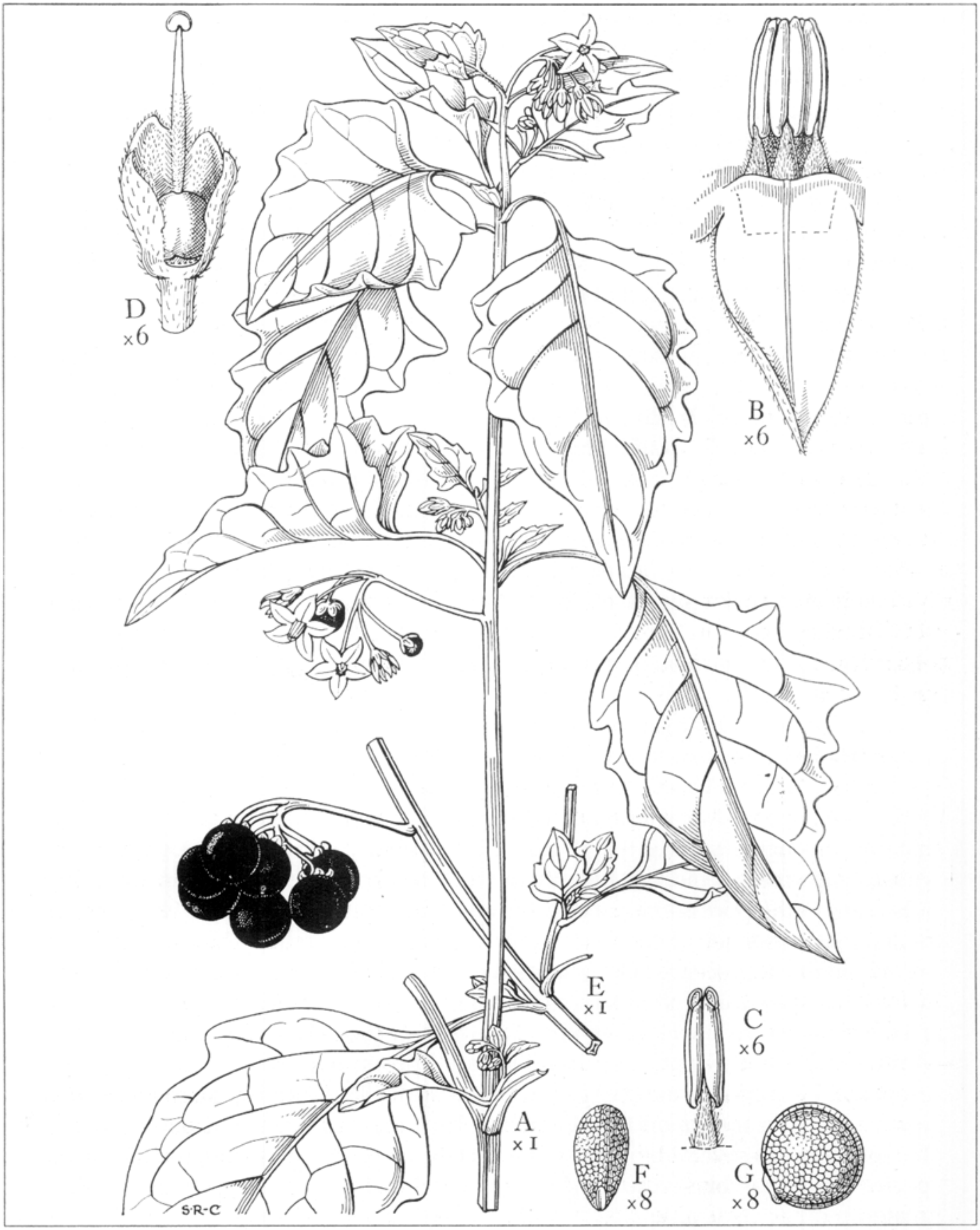

Fig. 5. *S. nigrum* L. A — upper part of flowering stem. B — part of corolla and androecium with length of corolla tube shown by dotted line. C — stamen. D — calyx and gynoecium. E — part of fruiting stem. F and G — seed in two views. (Stella Ross-Craig, Drawings of British Plants, Part 21, Plate 29 (1965))

Okavanga, Transvaal), Sudan, Tanzania, Tunisia, Uganda, Zambia, Zimbabwe; **Australia:** all States; **China; Europe:** widespread throughout (e.g. Austria, Balearic Islands, Belgium, Bosnia, Bulgaria, Corsica, Crete, Czech Republic, Denmark, Finland, France, Germany, Great Britain, Greece, Hungary, Italy, Jugoslavia, The Netherlands, Norway, Poland, Portugal, Romania, Russia, Sardinia, Sicily, Spain, Sweden, Switzerland and Turkey — doubtfully native in much of the north); **Egypt; India; Iraq; Israel; New Zealand:** widespread in North and South Islands, especially on cultivated and waste land; **North America:** widespread, especially in the northwest, locally abundant in irrigated fields in western States; **Saudi Arabia; Syria.**

Cytology: $2n=6x=72$ (Baylis 1958; Edmonds 1977, 1981, 1982, 1983, 1984a and unpublished; Henderson 1974; Randell and Symon 1976; Symon 1981; Bukenya 1996).

Illustrations: Figures 2a, 2b and 5

Vernacular names: Australia: Black or black berry nightshade; **Cameroon:** Kumbo (Banso), Ngah-nyi kob keh i lah bomnyah (Bali); **Ethiopia:** “Dime people eat”; **Europe:** Black nightshade, annual nightshade, common nightshade, garden nightshade, schwarzer Nachtschatten (German), morelle noire (French), solano nero, solatro (Italian), paslen cernyj (Russian); **New Zealand:** Black nightshade; **South Africa:** Nightshade (Cape Prov.); **Tanzania:** Mwha-ka (Kihehe), Suga (Swahili).

Recorded uses: Australia: used as vegetable by old cultures in NW; Chad: eaten by birds; **Ethiopia:** fruits and leaves edible, fruits edible when black or violet; **Nigeria:** leaves used as spinach; **Somalia:** used as a pot-herb; **Tanzania:** leaves boiled and eaten as a vegetable, green fruits edible, roots eaten raw for stomach ache (in Kigoma Distr.); **Uganda:** leaves eaten.

During the revision of *Solanum* section *Solanum* for Flora *Europaea* it became clear that two distinct entities of the hexaploid *S. nigrum* occurred in Europe. The most widespread form found throughout the region was glabrescent or only sparsely pubescent with appressed eglandular-headed multicellular hairs and was identical to Linnaeus’ specimen of this species in the Linnean Herbarium. The other exhibited a more villous pubescence of long spreading glandular-headed hairs, and was found in the drier and warmer parts of the specific range. These differences were recognized at subspecific rank in Hawkes and Edmonds (1972). However, other research workers, with the exception of Henderson (1974), have generally been unable to recognize these entities in other geographical areas. Thus Schilling (1981) found all North American specimens to fall within subsp. *nigrum;* Symon (1981), while being able to recognize several biotypes within this species in Australia, retained a broad species concept of this taxon, suggesting that the variability observed was probably greater in other areas of its distributional range. Indeed, Wessely (1960) described 12 infraspecific variants of this species in central Europe, differentiating most on variable leaf shapes together with berry colours. Most of these minor variants are considered to be synonyms of the two subspecies described here.

a. *S. nigrum* L. subsp. *nigrum*

Common synonyms:

S. dillenii Schultes
S. judaicum Besser
S. suffruticosum Schousboe ex Willd.
S. humile Bernh.
S. morella Desv. subsp. *nigrum*
S. moschatum Presl
S. nigrum L. subsp. *chlorocarpum* (Spenner) Arcangeli
S. nigrum L. subsp. *dillenii* (Schultes) Nyman
S. nigrum L.subsp. *humile* (Bernh.) Marzell
S. nigrum L.subsp. *luteovirescens* (C.C.Gmelin) Kirschleger

Plants subglabrous to moderately pubescent, with eglandular-headed multicellular hairs which are usually appressed.

Distribution: Throughout the range of the species.

b. *S. nigrum* L. subsp. *schultesii* (Opiz) Wessely, Feddes Repertorium, 63:311 (1960).

Basionym: *S. schultesii* Opiz in Bercht. & Opiz, Ökon.-Techn. Fl. Böhm. 3:24-25, No. 479 (1843).

Common synonyms:

S. decipiens Opiz
? *S. nigrum* L. subsp. *moschatum* (C. Presl) Arcangeli

Plants villous, with patent, occasionally appressed, glandular-headed multicellular hairs of varying lengths.

Distribution: Australia: SE of Adelaide; **Europe:** mostly in the drier parts of the species range in central, southern and eastern countries.

Solanum nigrum is the type species of both the section and the genus *Solanum*. Any taxon belonging to the section *Solanum* has invariably been identified as this species, especially in many of the older regional floras. This, together with the fact that many earlier workers failed to recognize the cytomorphological characteristics associated with this taxon, has led to much of the taxonomic confusion surrounding this species. References to this species in the literature must therefore be analyzed with great caution. Though its precise origin remains unknown, it is generally considered to be native to Eurasia; it is extremely well-adapted to the Mediterranean climate, and could have originated in the Middle East or even India. It is possibly also native in Africa where it is thought to be widely distributed, though little accurate taxonomic work has yet been carried out on populations from this vast area. The species has certainly been introduced into regions such as North America, New Zealand and Australia but has not, as far as is known, yet been found in either South or Central America, or on the Pacific Islands. It is a morphogenetically distinct hexaploid species, in which cytotypes do not occur (Edmonds 1984c), though variation in the berry colour from greenish-yellow to purple-black does occur in different populations. Hypotheses on the precise nature of the possible diploid taxa contributing genomes to the hexaploid ancestry of *S. nigrum sens. strict.* are dealt with in Section 4.

***S. physalifolium* Rusby var. *nitidibaccatum* (Bitt.) Edmonds** in Botanical Journal of the Linnean Society 92: 27 (1986).

S. physalifolium Rusby in Memoirs of the Torrey Botanical Club, 6: 88 (1896).

Type: Chile, *Poeppig 538* (B† destroyed), photographs (G!, WIS!); Chile, *Poeppig s.n.* (Lectotype W!)

Common synonyms:

S. atriplicifolium sensu Dunal *non* Gillies
S. chenopodioides sensu Dunal *non* Lam.
S. nitidibaccatum Bitt.
S. sarrachoides Sendtn. *pro parte (sensu* Sendtner quoad pl. Chilensi).

Plants usually small herbs, prostrate with many decumbent sprawling laterals arising from the base; moderately to densely pubescent with spreading glandular-headed hairs. **Stems** light green, terete, smooth with edentate or inconspicuously dentate ridges. **Leaves** ovate to ovate-lanceolate to trullate, 1.9-5.3 cm long x 1.3-3.5 cm broad; margins regularly sinuate-dentate with 2-6 antrorsely directed teeth on each margin, occasionally entire or sinuate; bases truncate or truncate-cordate. **Inflorescences** simple lax extended cymes, 4 to 8(10)-flowered; peduncles 6 to 16(23) mm long fruiting when usually deflexed; **pedicels** 4-10 mm long fruiting when splayed or reflexed. **Calyces** campanulate, (1.5)2.0 to 3.0(4.0) mm long in flower; sepals oblong-lanceolate flowering and broadly triangular and enlarged fruiting. **Corollas** rotate with petal lengths and widths ± equal, white or white tinged with purple, with distinct brown and yellow basal star, (3.5)4.0 to 6.0(7.0) mm radius; petals broadly triangular. **Anthers** yellow, 1.5 to 2.0(2.7) mm long. **Pollen** (20.3)22.6 to 29.4(33.4) µm diameter. Style 3-4 mm long, stylar exsertion usually absent. **Berries** usually broadly ovoid, dark green to purple- to brownish-green, usually with distinct reticulum of veins visible through cuticle, usually translucent, sometimes opaque, usually glossy occasionally becoming dull, falling with pedicels attached when ripe, 6 to 9(10) mm broad, lower half of mature fruit covered with appressed and enlarged calyces, whose sepals often reflex away from fully mature berries. **Seeds** 1.8-2.4 mm long, 5-34 per berry, brown, embedded in purple placenta. **Sclerotic granules** usually two situated apically, occasionally absent or up to five.

Cytology: $2n=2x=24$ (Henderson 1974; Edmonds 1977, 1981, 1982, 1983, 1984a, 1986; Randell and Symon 1976; Symon 1981).

Illustrations: Figures 2g and 6.

Distribution (sea level to 2300 m): Africa: Ethiopia, Uganda, Zaire; **Australia:** all States except the Northern Territories and Western Australia — introduced, persisting as weed of cultivation; **Europe:** Belgium, Czech Republic, Finland, France, Germany, Great Britain, Netherlands, Sweden, Switzerland; **Central**

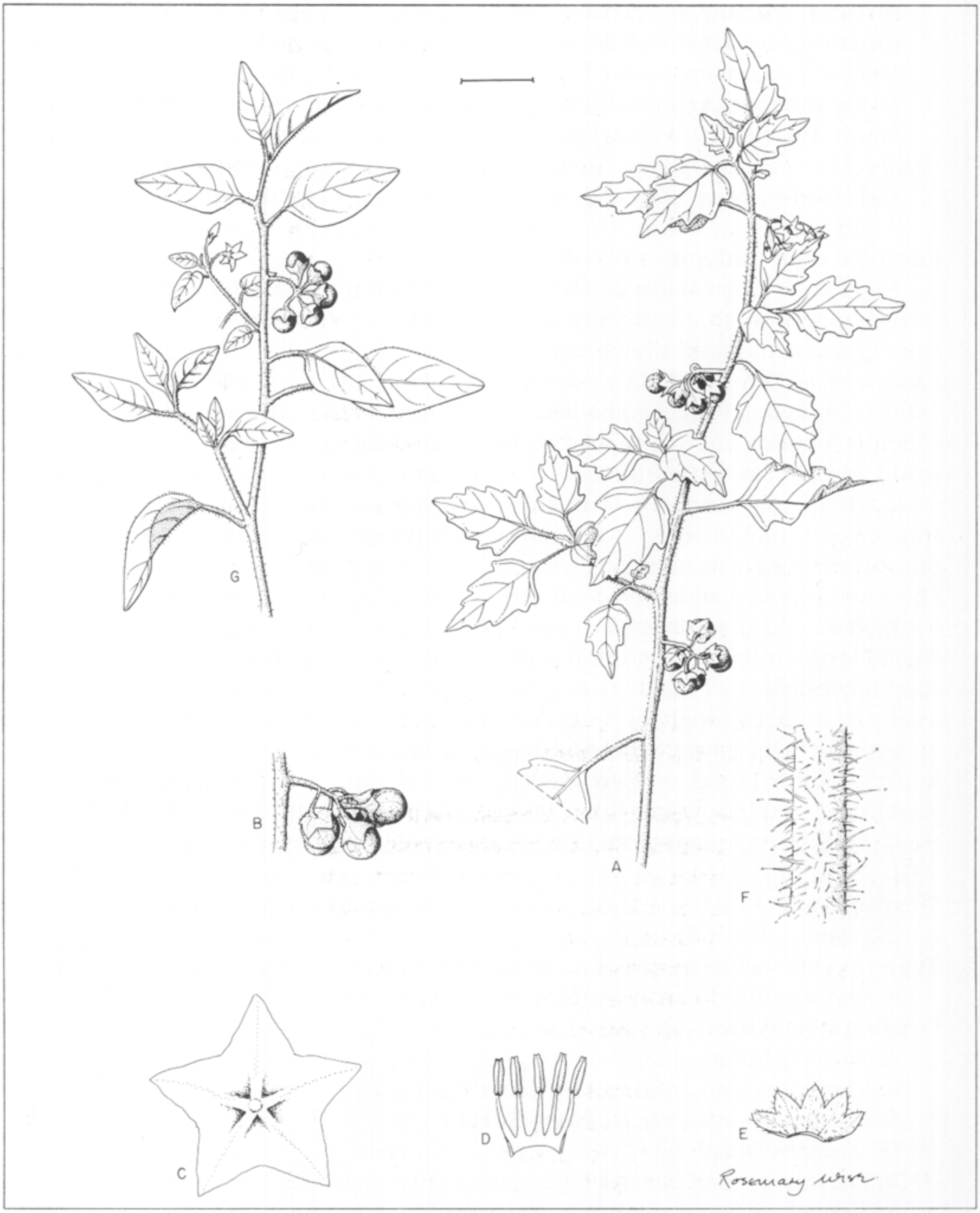

Fig. 6. *S. physalifolium* Rusby var. *nitidibaccatum* (Bitt.) Edmonds. A — apical part of stem; B — mature fruiting inflorescence; C. — corolla; D — dissected stamens; E — dissected flowering calyx; F — general appearance of stem indumentum; G — entire-leaved valiant. Scale bar = 20 mm in A and G; B-F not to scale. (Edmonds 1986)

America: sporadic, e.g. Panama; **New Zealand:** common on South Island; **North America:** occasional in fields and disturbed areas throughout the U.S.A., but especially common in the Plains and the Pacific States, and Canada; New **Zealand:** increasing on both Islands since its introduction *ca.* 1968 to South Island; **South America** (native): Argentina, Chile.

Vernacular names: Great Britain: Argentinian nightshade, Green-fruited nightshade; **New Zealand:** Hairy nightshade; **North America:** Hairy-nightshade.

Recorded uses: Ethiopia: fruits edible.

A full description of this diploid taxon, together with problems surrounding its correct identification, the reasons for its differentiation from another glandular-haired South American diploid species with which it is often confused, namely *S. sarrachoides* Sendtn., and its complex synonymy and lectotypification are dealt with in Edmonds (1986). It is another diploid species native to the southeastern parts of South America, and which has been introduced extensively to other parts of the world where it has become a prolific and successful weed of disturbed sites. Again, trade with South America — particularly the importation of grain, seeds and the spreading of wool ‘shoddy’ — has been largely responsible for its introduction into Europe, with one of its common European names being the Argentinian nightshade. The taxon is now a widespread adventive in Europe where it is rapidly becoming naturalized and often forms extensive populations. It has been introduced into Australia on a number of occasions, where it persists as a weed of cultivation and is sparingly established in all States (Henderson 1974; Symon 1981). The species is locally abundant throughout North America (Ogg *et al.* 1981) where it is particularly widespread in the Pacific States and the West (JME, pers. observ.). It was introduced into the South Island of New Zealand around 1968 where it rapidly became established, and is now also found in northern parts of North Island (Healy 1974). It also has been sparingly introduced into equatorial regions of Africa.

***S. retroflexum* Dunal in** A.P. de Candolle, Prodromus Systematis naturalis Regni vegetabilis, 13(1): 50 (1852).

Type: In promont. Bonae Spei, *Drège;* in Arabia circa Taifa (a Mus. Paris, mihi comm. n. 29) (Iso- or lecto-syntype MPU!).

Possible synonyms:

S. burbankii Bitter
S. retroflexum Dunal var. *angustifolium* Dunal
S. retroflexum Dunal var. *latifolium* Dunal
**S. sinaicum* Dunal

[*NB: The name *S. sinaicum* Boiss. was published in 1849 to describe a species found in Sinai; if conspecific with *S. retroflexum* this name must take precedence over the latter epithet. However, the latter is the name by which this taxon is commonly known in Africa, particularly in southern parts; it has therefore been used here, although future taxonomic investigation will probably demonstrate that the two are conspecific, with *S. retroflexum* then becoming a synonym of *S. sinaicum.*]

Plants spreading, erect, pubescent herbs to 70 cm tall, with eglandular-headed appressed hairs, which are villous, spreading and of different lengths in South Africa. **Stems** with smooth or inconspicuously dentate ridges. Leaves rhomboidal to ovate-lanceolate, 4.0-4.8 cm long x 3.0-4.2 cm broad, margins usually deeply lobed with 3 to 5(7) obliquely triangular lobes on each margin, bases truncate; **petioles** alate for at least 2/3 length. **Inflorescences** simple, ± umbellate erect cymes, 3 to 6(7)-flowered; **peduncles** 10 to 20 (50) mm long and erect fruiting; **pedicels** 6-12 mm long, reflexed in fruit. **Calyces 2-3** mm tong; **sepals** narrowly ovate, usually reflexed away from mature berries. **Corollas** stellate, white with yellow to green basal star, and usually with distinctive purple central stripe on outside of each petal, 4.5-6.0 mm radius. **Anthers** yellow, 1.5-2.0 mm long. **Pollen** about 23.6-26.6 µm diameter, Styles 2.0-4.5 mm tong, exerted up to 1 mm beyond anthers, **Berries** spherical, purple, dull with opaque cuticles, 7-9 mm diameter, falling from calyces when ripe. **Seeds** 1.5-2.3 mm tong, 14-27 per berry. **Sclerotic granules** recorded as present (in Australia) and absent (in South Africa).

Cytology: $2n=4x=48$ (Henderson 1974; Edmonds 1977, 1983 and unpublished; Randell and Symon 1976; Symon 1981).

Illustration: Figure 7.

Distribution (? sea level to 2340 m): Africa: Angola, Ethiopia, Malawi, Mauritania, Mozambique, Namibia, Nigeria, Sierra Leone, Somalia,. South Africa (Cape Province, Natal, Orange Free State, Transvaal), Sudan, Zambia, Zimbabwe; **Australia:** introduced and naturalized on the Eyre Peninsula; ? **Israel; North America:** occasionally cultivated.

Vernacular names: Namibia: Nastegaal (Rustenburg Distr.); **North America:** Sunberry, Wonderberry; **South Africa:** Nastergal (Cape — Veld name), Nastagal (? Natal), Mofhswe (Sesuto — OFS); **Zimbabwe:** m'sungula.

Recorded uses: Namibia: eaten (Winkenstein), seeds edible (Rustenburg Distr.), berries edible (Rustenburg Distr.); **Sierra Leone:** cultivated in gardens for palaver sauce; **South Africa:** edible berries (Cape Prov.), fruits eaten raw and leaves cooked and eaten (Orange Free State — Waterberg Distr.).

This tetraploid species is believed to be native to Africa, where it occurs throughout the continent; it has been sparingly introduced into parts of Australia and North America. There seems to be a great variation in the pubescence, with many specimens, particularly those from South Africa, exhibiting a strikingly villous indumentum in which the hairs are tong but have egtandular heads. Superficially they are virtually identical in the herbarium to specimens provisionally identified as *S. grossidentatum* A. Rich., which seem to differ largely through the presence of glandular-headed multicellular hairs. If later research proves these taxa to be conspecific, the tatter name will take precedence over *S. retroflexum.*

Fig. 7. *S. retroflexum* Dun. Flowering stem with mature infructescences. (Symon 1981)

Solanum retroflexum is believed to be the ‘Sunberry’ promoted by the plant breeder Luther Burbank as “a new food plant from a poisonous family” at the beginning of this century in North America (Whitson et al. 1914). Following its marketing, it was widely used, and widely acclaimed by some, for the preparation of pies, jams and sauces, with the dealer to which Burbank sold the plant rechristening it as the 'Wonderberry'. Burbank claimed to have derived his plant by hybridizing *‘S. guineense’* (= *S. scabrum* Mill.) — the garden huckleberry and *‘S. villosum’*. Since these two taxa are hexaploid and tetraploid respectively, the resultant progeny would have been pentaploid and almost certainly sterile — though Burbank claimed that his hybrid plants were prolific berry-producers which grew uniformly showing no signs of segregation in subsequent generations. Because of its obvious relationship to the black nightshade *S. nigrum* and the poisonous reputation then surrounding this species, at least in Europe and North America, controversy quickly ensued over the claims made for this new fruit. This controversy, which raged in the North American press, is fully dealt with by Heiser (1969), as are the abortive attempts to repeat the supposed hybridization in order to recreate the Sunberry and verify Burbanks' claims. Heiser had previously proved that the actual Sunberry was not the claimed hybrid derivative but a distinct tetraploid species native to South Africa, where it was known as “gsoba”, and from where it had been imported. Burbank may have inadvertently introduced it into his experimental garden and subsequently selected it as a plant “new to science” (Heiser 1969).

***S. sarrachoides* Sendtn.** in Martius, Flora brasiliensis, 10: 18 (1846) *pro parte* (pro planta Uruguayensi (Bitter 1912)).

Type: Southern Brazil, *Sellow* s.n. (Syntype B+ destroyed); Brazil, *Sellow s.n.* (Lectotype P!)

Common synonyms:

S. atriplicifolium Gill. var. *minus* Gill. ex Nees von Esenbeck
S. hirtulum E.H.L.Krause *non* Dunal
S. justi-schmidlii E.H.L. Krause
S. sarachidium Bitter
S. sarachoides Sendtn. *var. sarachidium* (Bitter) Morton
S. styleanum Dunal

Plants erect and bushy, up to 60 cm tall, moderately to densely pubescent with spreading viscid glandular-headed hairs of varying lengths. **Stems** pale green, terete, with edentate or inconspicuously dentate ridges. **Leaves** ovate-lanceolate to lanceolate, (3.2)3.9 to 7.6(11.2) cm long x (2.7)3.1 to 5.1(8.0) cm broad, margins sinuate-dentate with 3-9 obtuse to acute antrorsely directed teeth on each side, bases truncate or cordate. **Inflorescences** simple, umbellate cymes, 3 to 4(5)-flowered; **peduncles** 4 to 16(28) mm long fruiting when usually erect or ascending; **pedicels** 7-11 mm long fruiting when reflexed. **Calyces** campanulate, 3-6 mm long flowering; **sepals** oblong-lanceolate flowering, enlarged and narrowly triangular fruiting. **Corollas** semi-stellate to pentagonal with petals broader than long, white with yellow/translucent basal star, 5.0-7.5 mm radius; **petal** lobes broadly triangular. **Anthers** yellow/orange, (1.5)2.0 mm long. **Pollen** (17.9)20.3 to 28.0(30.0) µm diameter. **Styles** 3.0-3.5 mm long, stylar exsertion usually absent. **Berries** globose, pale green, glossy becoming dull, opaque, 6-9 mm diameter, falling with pedicels still attached when ripe, usually completely enveloped by enlarged calyces which, when fully mature dry and become 'papery' exposing the berries beneath. **Seeds** 1.3-l.5 mm long, (23)59 to 69(93) per berry, pale yellow, embedded in green placenta. **Sclerotic granules** 4-6.

Cytology: $2n=2x=24$ (Edmonds 1972, 1977, 1986; Bukenya 1996).

Illustration: Figure 8.

Distribution (sea level to 1433 m): Africa: South Africa (eastern Cape); **Europe:** Czech Republic, England, Finland, France, Germany, Hungary, Netherlands, Norway, Sweden, Switzerland; **North America:** sporadic especially in southern States; **South America** (native): Argentina, Bolivia, southern Brazil, Chile, Paraguay, Peru, Uruguay.

Vernacular names: None recorded for this species *sens. strict.*

Recorded uses: None.

The taxonomy of this glandular-haired species is fully dealt with in Edmonds (1986), where a full description is given, together with a discussion of the nomenclature and synonyms associated with it. Moreover, this paper tabulates the major features separating this species from *S. physalifolium* var. *nitidibaccatum* with which it was previously united, and also gives details of crossability studies justifying their recognition as distinct taxonomic entities. *Solanum sarrachoides* is another diploid native to South America where it is fairly widely distributed. Its introduction to Europe is again largely as a result of trade with South America and the importation of seeds and grain together with the practice of spreading wool waste ('shoddy') as a manure, and seems to have occurred since the beginning of this century This species is, however, relatively uncommon in both Europe and North America, with only one African collection, from the eastern Cape, having so far been identified by JME, though Phillipson (1990) recorded a second collection of this taxon from a locality in the Transkei. Most of the descriptions of *S. sarrachoides* in the literature, particularly those discussing this taxon in Australia, New Zealand and North America, apply to *S. physalifolium* var. *nitidibaccatum* (Healy 1974; Henderson 1974; Ogg *et al.* 1981; Schilling 1981; Symon 1981).

***S. scabrum* Miller,** The Gardeners Dictionary, Ed. 8, art. *Solanum* no. 6 (1768).

Type: Cult. Chelsea Physic Garden, origin North America, *Miller s.n.* (Lectotype BM!).

Common synonyms:

S. guineense (L.) Miller
S. intrusum Soria
S. melanocerasum All.
? S. memphiticum Mart.

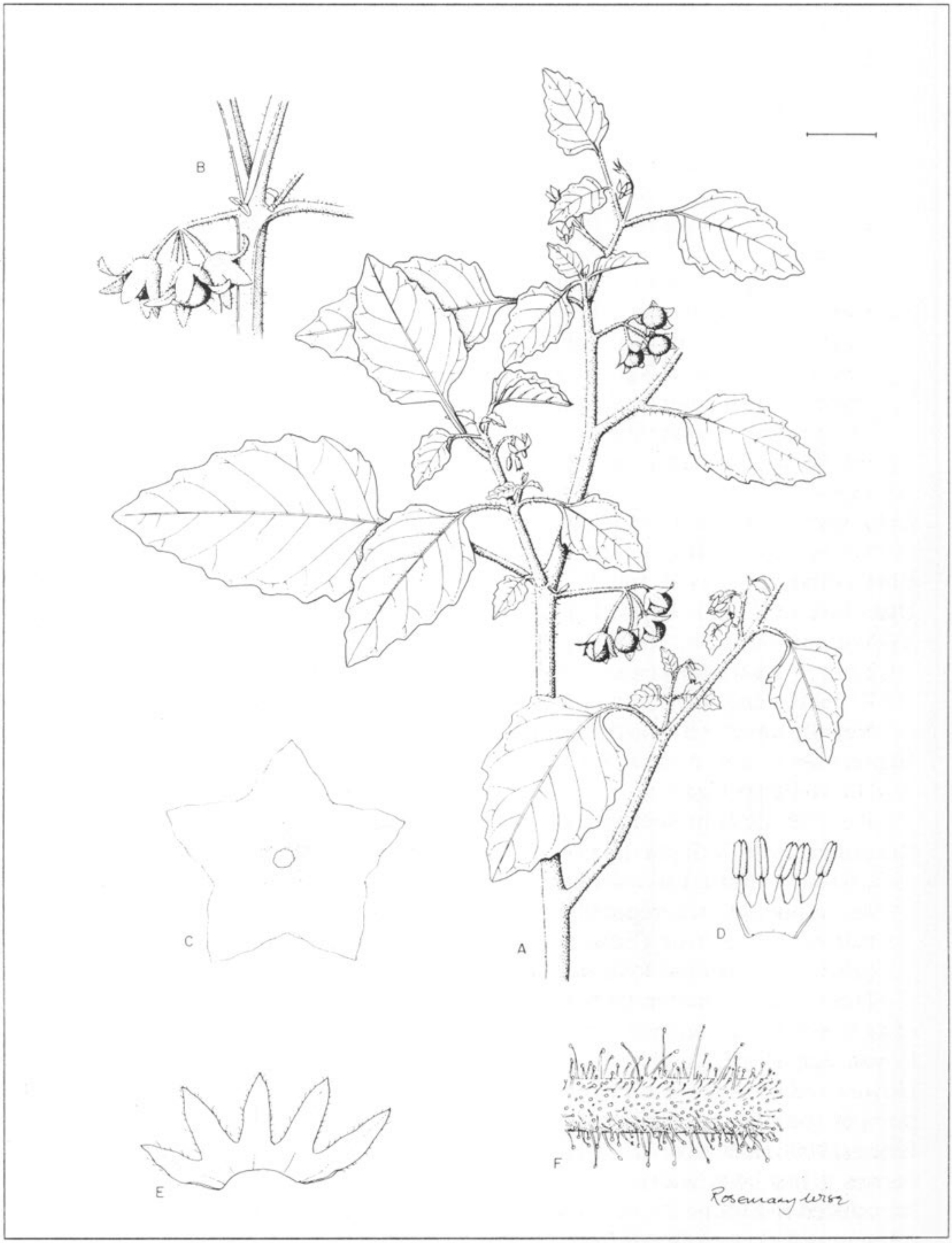

Fig. 8. *S. sarrachoides* Sendtn. A-F as in Figure 6. Scale bar = 20 mm in A; B-F not to scale. (Edmonds 1986)

S. nigrum L. var. *guineense* L.
S. nigrum L. subsp. *guineense* (L.) Pers.
S. tinctorium Welw.

Plants erect, glabrescent to subglabrous, with sparse eglandular-headed hairs; lateral branches sparse and usually spreading horizontally. **Stems** prominently and dentately winged. **Leaves** usually ovate, occasionally lanceolate, large, 10.0 to 12.0(16.0) cm long x 6.0 to 8.0(14.0) cm broad, margins entire to sinuate, lobes absent, apices acute to obtuse. **Inflorescences** simple or forked, lax and often extended cymes, 6 to 14(27)-flowered; **peduncles** 3.0-6.0 cm long fruiting when erect. **Calyces** 1.9 to 3.5(4.5) mm long; **sepals** usually reflexed away from mature berry. **Flowers** stellate, white, occasionally tinged purple, with yellow/green basal star, 7-9 mm radius. **Anthers** always brown or purplish/brown, 2.5-3.3 mm long. **Pollen** 25.5 to 32.1(37.7) µm diameter. Styles 2.9-4.5 mm long, not exserted beyond anthers. **Berries** broadly ovoid, deeply purple with opaque cuticles, 15-17 mm broad, remaining on plant and adhering to erect pedicels at maturity. **Seeds** 2.0-2.2 mm long, usually numerous, up to 144 per berry. Sclerotic granules absent.

Cytology: $2n=6x=72$ (Henderson 1974; Edmonds 1977, 1983 and unpublished; Symon 1981; Bukenya 1996).

Illustrations: Figures 2h and 9.

Distribution (? sea level to 2134 m — in Africa): Africa: Ghana, Ethiopia, Liberia, Nigeria, Reunion, Sierra Leone, South Africa (Transvaal), Sudan, Uganda, Zambia; **Australia:** known only in cultivation; **Europe:** casual in Belgium, Czech Republic, England, Germany and Sweden, where an escape from cultivation; **New Zealand:** cultivated; **North America:** cultivated.

Vernacular names: Australia: Huckleberry, Garden Huckleberry; **Europe:** Garden Huckleberry; **Uganda** — Nswiga ya Kizungu (Lukiga), Eshwiga (Kigezi Distr.); **West Africa:** Ogunmo, ogumon.

Recorded uses: Ethiopia: leaves used as greens when cooked (in Sidamo Prov.); **Ghana:** cultivated and semi-cultivated as a spinach plant, leaves edible, sold in Accra market as a vegetable; **Nigeria:** leaves used as spinach; **South Africa:** cultivated, nontoxic (Transvaal); **Uganda:** pot-herb, leaves eaten; **Zambia:** in cultivation, believed to be one of the native ink berries.

This species, commonly known as the garden huckleberry, has been the subject of a great deal of taxonomic attention. It is the plant which Linnaeus called *S. nigrum* L. var. *guineense* L., and which was generally considered to be native to Africa. However, there are few accurate data on its distribution and its origin remains a point of speculation. The synonymy of this species was successively dealt with by Heine (1960), Henderson (1974) and Edmonds (1979b). Because of its large and edible berries it has been widely cultivated throughout Africa as well as having been introduced to Europe, North America, Australia and New Zealand where it is also often recorded as an escape from cultivation.

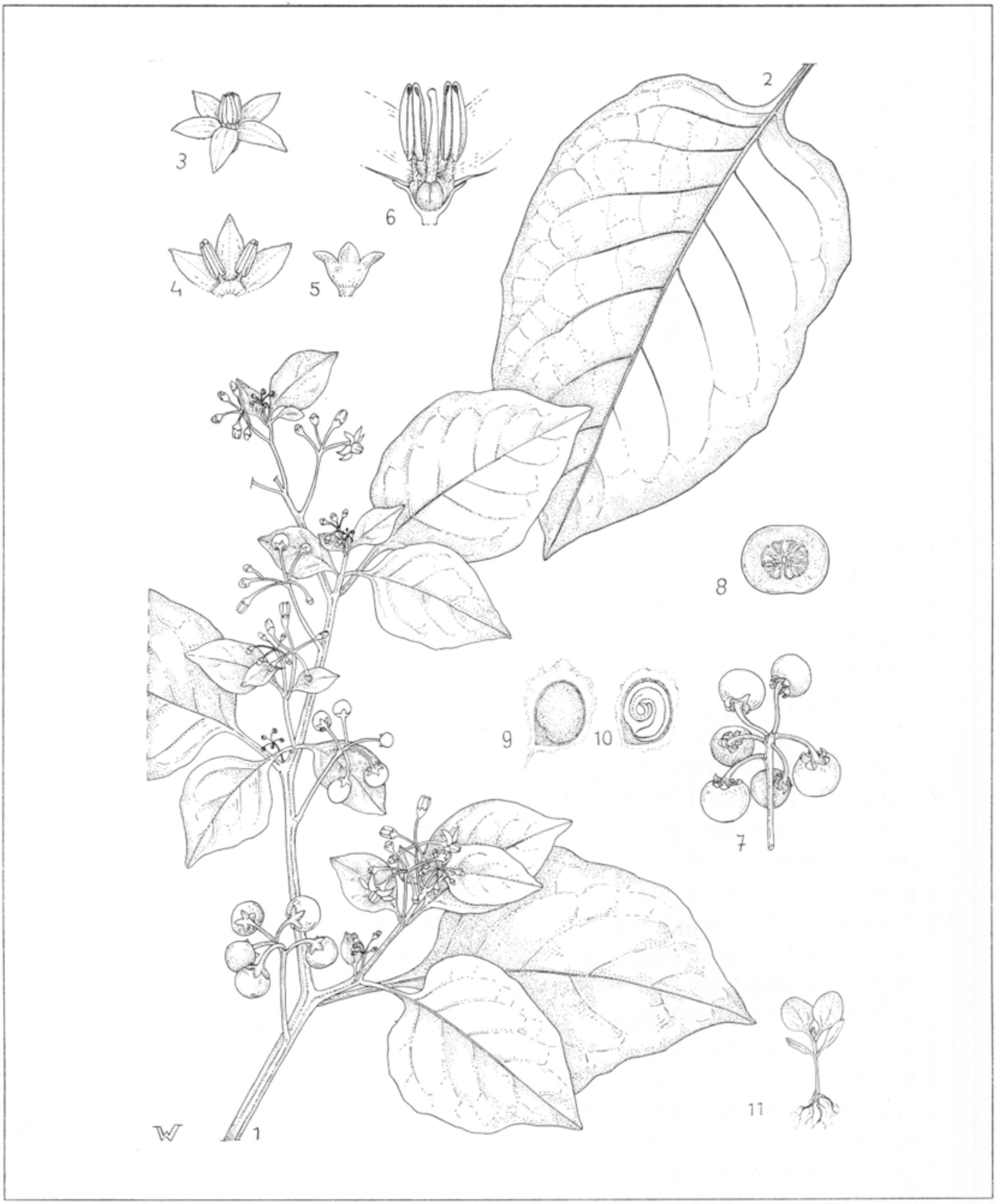

Fig. 9. *S. scabrum* Mill. 1. Flowering and fruiting stem (x 0.5). 2. Leaf (x 0.5). 3. Flower (x 1.3). 4. Part of corolla with two stamens (x 1.3). 5. Calyx (x 2.6). 6. Gynoecium with two stamens (x 2.6). 7. Peduncle with mature berries (x 0.5). 8. Transverse section through berry (x 0.6). 9 Seed (x 2.6). 10. Longitudinal section through seed, showing embryo (x 2.6). 11. Seedling (x 0.6). (Stevels, J.M.C., Wageningen Agric. Univ. Papers 90-1:223 (1990))

***S. villosum* Miller,** The Gardeners Dictionary, Ed. 8, art. *Solanum* no. 2 (1768).

Type: Cult. Chelsea Physic Garden, origin Barbados; *Miller s.n.* (Lectotype BM!).

Plants subglabrous to villous annuals, up to 50 cm high. **Leaves** rhombic to ovate-lanceolate, 2.0-7.0 cm long x 1.5-4.0 cm broad, margins en tire to sinuate-dentate. **Inflorescences** simple, umbellate to slightly lax solitary cymes, 3 to 5(7)-flowered, rarely 10 flowered (in the Middle East); **peduncles** erect, (4)7 to 13(19) mm fruiting; **pedicels** often longer, deflexed in fruit. **Calyces** 1.2-2.2 mm long, slightly accrescent, deflexed or adhering to base of mature berry; **sepal** lobes triangular. **Corollas** stellate, white with translucent to yellow basal star, 4 8 mm radius, 3-5 times as long as calyx. **Anthers** yellow, 1.5-2.5 mm long. **Pollen** (23.0)25.0 to 32.5(37.3) µm diameter. **Styles** 2.9 to 5.0(6.0) mm long, rarely exserted beyond dehiscing anthers. **Berries** usually longer than wide, occasionally globose, red, orange or yellow, 6-10 mm broad, falling from calyces when ripe. **Seeds** 1.6-2.2 mm long, usually visible through translucent cuticles; (18)30 to 45(56) per berry. **Sclerotic granules** absent.

Cytology: $2n=2x=48$ (Edmonds 1977, 1982, 1983, 1984a and unpublished; Henderson 1974; Randell and Symon 1976; Bukenya 1996).

Illustrations: Figures 2c, 2d and 10.

Distribution (sea level to 2438 m): Africa: Algeria, Angola, Burundi, Ethiopia, Kenya, Libya, Morocco, Nigeria, Somalia, ?South Africa (Lesotho), Sudan, Tanzania, Tunisia, Uganda, Zambia; **Australia:** sparingly naturalized in temperate areas; **Egypt; Europe:** widespread northwards to northern France and central Russia e.g. Albania, Austria, Azores, Balearic Isl., Bulgaria, Channel Isl., Corsica, Crete, Croatia, Cyprus, Czech Republic, France, Germany, Greece, Hungary, Italy, Jugoslavia, Macedonia, Malta, The Netherlands, Poland, Portugal, Romania, Russia, Sardinia, Sicily, Slovenia, Spain, Switzerland, Turkey, introduced further north, e.g. Belgium, Denmark, Finland, Great Britain, The Netherlands, ? Norway, and Sweden; **Iraq; Israel; North America:** occasional introduction; **New Zealand; Saudi Arabia; Syria.**

Vernacular names: Great Britain: Red-fruited nightshade; **Kenya:** Soiyot-Ap-Poinet (Kipsigis), Isoiyot (Kipsigis), Olmomoi (Masai), Ormomoi (Masai), Cheporusion (Pokot), Kusoyo (Pokot); **Tanzania:** Kisuhume soku (? Suhuma), en'songwe (Kisafwa); **Uganda:** Eswiga (Ankole), Ndolu (Kamba), Mayengo.

Recorded uses: Greece: eaten as boiled salad plant, sold in local markets in Crete; **Ethiopia:** fruit edible, orange berries edible, orange/red fruits edible; **Kenya:** vegetable, eaten by Africans as spinach, Kipsigis, Masai and Pokot use leaves as vegetable, Nandi women throw water away after boiling and replace with milk (in Eldoret), red berries edible (in Nairobi Distr.), pot-herb encouraged at edges of cultivation (in Kilifi), eaten by bush buck (Kipsigis), Masai children eat ripe red berries, berries eaten raw (in West Suk), browsed by goats (in Narok Distr.); **Sudan:** eaten by goats and sheep; **Tanzania:** leaves boiled as spinach (in E Kilmanjaro), whole plant used as vegetable (in Musoma), vegetable (in Mbulu Distr.), leaves cooked and eaten as vegetable but not cultivated (in Mbeya Distr.),

Fig. 10. *S. villosum* Mill. Flowering stem with mature infructescences. (Symon 1981)

orange berries used as fruit, red fruits eaten by Suhuma who also use fruits and leaves medicinally — by squeezing fruit juice into sore eyes and placing ground and soaked leaves on swellings; **Uganda:** leaves boiled and eaten as spinach.

The revision of the section *Solanum* for *Flora Europaea* demonstrated that two distinct but closely related entities occurred in Europe. Just as in the case of *S. nigrum,* one exhibited a predominantly glandular pubescence and smooth stems, and seemed to be confined to warmer and drier habitats; the other displayed a more glabrescent pubescence of eglandular hairs and dentate stems. The differences were again considered to merit subspecific ranking and resulted in the recognition of two subspecies of the red /orange/yellow-berried tetraploid species *S. villosum* (Hawkes and Edmonds 1972; Edmonds 1979a). The synonymy of these subspecies is fully dealt with in Edmonds (1979b, 1984b) where the problems associated with the nomenclature of the taxa are also discussed. In these two papers the synonyms are listed in chronological order of their publication, and all relevant type specimens are cited.

Only the more commonly cited taxa which are considered to be synonyms of this species are listed below. Recent taxonomic revisions including this species do not usually recognize the two subspecies described here, possibly because their differentiation is less conspicuous in habitats outside Europe (see Henderson (1974) and Symon (1981) for Australia, and Schilling and Andersen (1990) for India). All the synonyms cited below are therefore synonyms of *S. villosum sens. lat.* Both subspecies are tetraploid and fully compatible. The common names and economic uses recorded refer to the species in general, though it is likely that various African tribes are able to differentiate infraspecific variants of *S.villosum.*

a. subsp. *villosum*

S. nigrum L. var. *villosum* L., Species Plantarum: 186 (1753).

Type: *Herb. LINN 248.19* (Lectotype LINN!); *Solanum annuum hirsutius, baccis luteis.* Dillenius, Hortus Elthamensis, 2: 366, t. 274, f. 353 (1732). *Herb. Dillenius s.n.* (Lectotype OXF!).

Common synonyms:

S. flavum Kit. ex Schultes
S. kitabelii Schultes
S. luteum Miller
S. luteum Miller subsp. *villosum* Dostál
S. miniatum Bernh. var. *stenopetalum* Dunal
S. miniatum Bernh. var. *villosissimum* Dunal
S. minutiflorum Dunal
S. nigrum L. subsp. *luteum* (Miller) Kirschleger
S. nigrum L. subsp. *villosum* (L.) Ehrh.; *S. nigrum* L. subsp. *villosum* Harhnan
S. ochroleucum Bast. var. *flavum* sensu Dunal *pro parte (excludio lectotypus).*
S. villosum Lam.
S. villosum Lam. var. *miniatibaccatum* Blom

S. villosum Lam. subsp. *ochroleucum* (Bast.) Nyman
S. villosum Lam. var. *velutina* Lowe

Plants villous, the longer hairs usually patent and glandular-headed. **Stems** rounded with smooth ridges.

Distribution: Throughout the range of the species, but most frequent in warm, dry areas.

b. subsp. *miniatum* (Bernh. ex Willd.) Edmonds, in Botanical Journal of the Linnean Society, 89: 166 (1984).

Basionym: *S. miniatum* Bernh. ex Willdenow, Enumeratio Plantarum Horti regii botanici berolinensis, 1:236 (1809).

Type: *Herb. Willdenow 4366,* sheet 3 (Lectotype B!).

Common synonyms:

S. alatum Moench
? S. hildebrandtii A. Braun & Bouché
S. humile Bernh.
S. luteovirescens C.C.Gmelin
S. luteum (Döll) Posp. var. *humile* (Bernh.) Posp.
S. nigrum L. subsp. *alatum* (Moench) Celak.
S. nigrum L. var. *alatum* (Moench) Fiori
S. nigrum L. subsp. *luteovirescens* Kirschleger
S. nigrum L. var. *luteum* Döll
S. nigrum L. var. *miniatum* (Bernh.) Fries
S. nigrum L. subsp. *puniceum* Kirschleger
S. nilagiricum Schlechtendal
? *S. ochroleucrrm* Bast.
S. ochruleucum Bast. var. *flavum* Dunal
? S. paludosum Dunal
S. patens Lowe
? S. plebeium Rich. (also known as *S. plebejum* Rich.)
? S. pseuduvillosum Schur
S. puniceum C.C.Gmelin
? S. roxburghii Dunal
S. rubrum Miller
S. villosum Lam. var. *miniatum* (Bernh.) Kostel
S. villosum Lam. var. *laevigata* Lowe
S. villosum Miller subsp. *puniceum* (Kirschleger) Edmonds
S. vulgatum L. var. *miniatum* (Bernh.) Spenner
S. woronowii Pojark.
S. zelenetzkii Pojark.

Plants subglabrous to pubescent, the hairs usually appressed and eglandular-headed. **Stems** angled with dentate ridges.

Distribution: Throughout the range of the species.

Like *S. nigrum,* the origin of this tetraploid species remains unknown though it is thought to be native to Eurasia, perhaps again to the Mediterranean region. It has been sparingly introduced to Australia, New Zealand and North America, where it is still rather rare, and has probably also been introduced into Britain and parts of Northern Europe. The two subspecies recognized here seem to inhabit different ecogeographical regions. Schilling and Andersen (1990) reported that Indian and Pakistani specimens of this taxon are referable to the subsp. *miniatum,* while Karshon and Horowitz (1985) reported that the subsp. *villosum* is dominant in Israel. More detailed studies of collections of this taxon throughout its distributional range are therefore required to determine the precise ecogeographical limits of the infraspecific variants. The species appears to be common in northern parts of Africa, where it could well be native, but in the more southern countries, particularly in South Africa, the subsp. *villosum* is very difficult to differentiate from other glandular-haired taxa in the herbarium. Considerable further work involving living populations and cytogenetical analyses is therefore necessary before the problems associated with the taxonomy and ecogeographical limits of the infraspecific variants of *S. villosum* and indeed the differentiation of all the glandular-haired species found in Eurasia, Africa and Indonesia can be resolved.

2.6 African taxa in need of taxonomic revision

Although a large number of species belonging to the section *Solanum* have been described over the years, as yet no comprehensive taxonomic revision of these species on a world scale has been undertaken. The major geographical area for which a revision of the species and indeed the whole genus is urgently required is Africa. Jaeger's (1985) study represents the first such treatment in many years, but is as yet unpublished, with his account of species belonging to the section *Solanum* being only provisional. The species described in Section 2.5 are the most studied and hence the most understood members of this section found in Africa. They are also among those most commonly encountered in the herbarium. There are, however, a number of other taxa which may represent good species, but about which little is yet known. These are listed below with notes on their most important features, together with their distribution and native uses as noted from the African *Solanum* collection at Kew (K).

S. florulentum **Bitter** in Feddes Repertorium, 10: 544 (1912).

Type: Tanzania, Kwai cr.l600m, *Albers 189* (Holotype B†; no duplicate yet traced).

Plants glabrescent herbs to 1.5 m high; **stems** angled with ? dentate wings. **Inflorescences** forked extended cymes, 8 to 24-flowered; **peduncles** long, about 20 mm; **pedicels** reflexed fruiting. **Flowers** white with yellow basal star, small, about 3.5 mm radius. **Anthers** about 1.6 mm long. **Style** about 2 mm long. **Berries** purple to black, small, about 6 mm diameter.

Distribution (360-3048 m): Africa: Kenya, Namibia, Rwanda, Tanzania, Uganda, Zaire.

Vernacular names: Kenya: Usuga (Luo); **Uganda:** Enswiga, Eshwiga (Kigezi); **Zaire:** Mulunda.

Recorded uses: Kenya: leaves eaten as spinach (in Naivasha), much eaten by insects; **Uganda:** leaves eaten; **Zaire:** edible.

Representatives of this taxon so far examined exhibit a floral morphology which is very similar to that of *S. americanum sens. lat.* However, the inflorescences are forked and multiflowered. No living representatives have yet been seen, and neither has any type material yet been traced.

***S. grossidentatum* A. Richard,** Tentamen Fl. Abyss., 2: 101 (1851).

Type: Ethiopia, "Crescit in provincia Tchelikote", *A. Petit s.n.* (Lectotype P!; Isolectotypes G!, Z!).

Plants usually herbaceous annuals, to about 1.2 m tall, upright to decumbent, often succulent, usually conspicuously hirsute and covered with long spreading villous glandular-headed hairs interspersed with shorter appressed eglandular-headed hairs; stems terete and smooth. Leaves ovate-lanceolate, margins always sinuate-dentate with prominent lobes; petioles often equalling laminas in length, alate for almost entire length. **Inflorescences** simple umbellate cymes, 3 to 4-flowered; **pedicels** reflexed fruiting. **Flowers** white with greenish basal star, about 5 mm radius; **calyces** ± stellate fruiting, when sepals adherent to berries. **Anthers** 2.5 mm long. **Berries** blackish.

Distribution (792-3048 m): Africa: Cameroon, Ethiopia, Kenya, Somalia, South Africa (Cape Province, Lesotho, Natal, Orange Free State, Transvaal), Tanzania, Uganda.

Vernacular names: Kenya: Sujet (Kinandi), Isusa (Maragoli), Sucha (Kitosi), Ol'momoit (Masai), Soiyot (Kipsigis), Manago (Kikuyu); **Uganda:** Kyalakyente (Lukiga), Osiga (West Nile Distr.), Orushwiga.

Recorded uses: Kenya: sold as vegetable by women in markets, much grown in secondary cultivation of maize, leaves eaten as vegetable and made into spinach (in Nairobi and Machakos Distr.); **Uganda:** leaves used a vegetable, seeds eaten by children (in West Nile Distr. but ? not in Kigezi), edible fruits (in Kigezi), crop weed.

It is highly likely that this species is conspecific with *S. retroflexum.* They are superficially often identical with the exception of the indumentum. It is also possible, however, that eglandular-haired and glandular-haired variants occur just as in both *S. nigrum* and *S. villosum.* Though the berry colour is reported as being blackish on numerous herbarium specimens, there is as yet no cytological data available for this taxon. If it does prove to be tetraploid and conspecific with *S. retroflexum* then the latter name would become a synonym of *S. grossidentatum.* However, the earlier name *S. sinaicum* might prove to be the correct name for this tetraploid. Again further research on living material is necessary to clarify the taxonomy of these African species. Many of the specimens identified as *S. grossidentatum* in the herbarium are also very similar in overall morphology to the glandular-haired *S. villosum* subspecies *villosum.* Caution is therefore necessary when interpreting data reported for these taxa from herbarium material.

S. *hirsutum* Dunal, Hist. Nat. Solarium: 158 (1813).

Type: "In cultis hortisque Aegypti passim (Forsk.); in Arabia Yemen, *Dunal* 35 (Syntype ?P; Isosyntype MPU!)

Plants densely villous with spreading glandular-headed hairs. **Leaves** lanceolate, margins entire to sinuate. **Inflorescences** umbellate cymes, few-flowered. **Berries** cited as black.

Distribution (975-2835 m): Ethiopia; ? Tanzania.

This is a distinct glandular-haired taxon, which could, superficially, belong to the glandular-haired subspecies of either *S. nigrum* or *S. villosum* However, the berry colour is cited as black which might indicate that this taxon is a synonym of the former. A cytological assessment of living material is needed to resolve the correct taxonomic status of this species.

***S. hirtulum* Steudel ex A. Richard,** Tentamen Fl. Abyss., 2: 101 (1851).

Type: Ethiopia, Enschedcap, *Schimper 977* (Lectotype P!; Isolectotypes G-DC!, GOET!, K!, P!, S!).

Plants suffrutescent low herbs with tap root, branching from the base, branches procumbent, hirsute, hairs eglandular-headed. **Leaves** obovoid to lanceolate, small, margins entire. **Inflorescences** simple umbellate cymes, 2 to 4-flowered; **pedicels** spreading to deflexed fruiting. **Flowers?** white to purple, large, 6-l0 mm radius. **Fruits** unknown.

Distribution (2286-3000 m): Ethiopia.

This seems to be a distinctive taxon, possibly endemic to Ethiopia. However, no living material has so far been obtained, and there is no information on either its ploidy level or its mature berry colour.

***S. tarderemotum* Bitter,** in Feddes Repertorium, *10:* 547 (1912).

Type: Tanzania, Kilimanjaro, "oberhalb Marangu", cr. 1600 m, *Winkler 3856* (WRSL).

Plants spreading herbs to 1.2 m high, glabrescent to pubescent with appressed eglandular-headed hairs. **Leaves** ovate to lanceolate, margins entire to sinuate-dentate. **Inflorescences** simple lax extended cymes, 7-l2-flowered; **pedicels** reflexed fruiting. **Flowers** white to pale purple with yellow basal star, small. **Berries** green becoming purple, small, 4-6 mm diameter.

Distribution (76-2880 m): Africa: Burundi, Ethiopia, Kenya, Rwanda, Tanzania, Uganda, Zaire.

Vernacular names: Kenya: Isoiik (Kipsigis); **Tanzania:** Soko, Kibondei (in Tanga Prov.); **Uganda:** Eshwiga (Kigezi Distr.), Ensugga.

Recorded uses: Ethiopia: leaves eaten after cooking; **Kenya:** commonly used as a vegetable (in Nakuru Distr.), leaves used as vegetables, eaten by giraffe; **Uganda:** leaves eaten (in Kigezi Distr.), leaves eaten when cooked (near Kawanda), used as a vegetable, medicinal plant (in Karamoja Distr.).

This taxon is very similar to *S. americanum* but the inflorescences have an extended central axis and a larger number of flowers. Living material is again necessary to determine whether it is conspecific with this small-flowered diploid or a distinct species.

An annotated list of some of the species names encountered both in the literature and in the herbarium is given in Jaeger (1985). They have not been included here since they are not those by which any of the taxa commonly associated with Africa are known.

3 Common names

The black nightshades are known by various common names in different languages in different countries (Tallantire and Goode 1975; Kokwaro 1976; Hafliger and Brun-Hool 1975; Holm *et al.* 1977; Vernon 1983; FAO 1988; Willing *et al.* 1992; Sebit 1995; Chigumira 1997; Rubaihayo 1997; Swai 1997; Maundu *et al.*, unpublished[1]; Opole *et al.*, unpublished[2]). Some of these are summarized in Table 3. However, because of the difficulties of accurately identifying these *Solanum* species, and the habit of referring to them all as the 'black nightshade', many of the names listed in Table 3 could refer to any of the taxa. Indeed in Europe and North America all the species are generally collectively known as the "Black nightshades"; in South America they are similarly known as "Yerba mora" or "Erva moura", and in China as "Longkui" or "Dragon-wort". The paper by Schilling *et al.* (1992) is therefore particularly useful, since it not only lists the spelling of the common names applied to these plants in China, India and Pakistan, but also gives the Provinces or States relevant to each of the languages, as well as accurately identifying the nightshade species referred to. The Asian and Chinese data are summarized in Table 3. The identity of many of the names applied to the European and African species can be ascertained by referring to the lists of vernacular names given for each of the nightshade species in Sections **2.5** and **2.6** and compiled during the recent herbarium survey of these taxa. Table 3 is by no means a complete list of the many common names used for species belonging to the section *Solanum;* various others are listed in some of the papers cited in the bibliography, though the correct identity of the plants to which they refer is often questionable.

Table 3. Some common names reported in the literature for various nightshade species

Language	Common names
European:	
English	Black nightshade, annual nightshade, common nightshade, garden nightshade, Petit Morel, wonderberry, sunberry, garden huckleberry
Danish	Sort natskygge
Dutch	Zwarte nachtschade
French	Morelle noir, herbea calalou, creve-chien
German	Schwarzer Nachtschatten
Italian	Ballerina, erba morella, solano nero
Norwegian	Sort søtvider
Spanish	Tomatito de moro, tomatitos, Yerba mora
Swedish	Nattskatta
Turkish	Kopek uzumii

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[1] Maundu, P.M., C.H. Kabuye and G. Wambui. 1995. An illustrated guide to some indigenous food plants of Kenya (unpublished manuscript).

[2] Opole, M., J.A. Chweya and J.K. Imungi. 1995. Indigenous vegetables of Kenya: Indigenous knowledge, agronomy and nutritive value. Field and Laboratory Experience Report (unpublished manuscript).

Language	Common names
African:	
Swazi	Umsobo
Ethiopian	K'ey-awuti, t'ikur-awuti
Sudanese	Harsh
Kenyan	Mnavu, mnafu, olmomoit, olmomoi, imomo, kitulu, managu inagu, nagu, isoiyot, rinagu, namesaka, esufwa, litsusa, osuga, ormomai, ksoiyek, isoiyo, soyot, isoya, niolou, gengalat, lekuruu, ndunda, kisuchot, kisuchon, esuja, abune, lokitoemenyan, egwangira
West African	Ogumo, odu, bologi, efodu
Zambian	Ndulwe, nkwila, nthuma, black nightshade
Zimbabwean	Musungusungu, umsobo, mukundanyama
Tanzanian	Mnavu
Malawian	Mnadzi, mnesi, msaka, ausaka, inafu
Ugandan	Asuaka, ecugasa, ensugga, esnwiga, enzirugavu, enyorotin, enyoro, esiiga, eusufa, isufa, kakwa, lere, lugbara, ociga, ocokocok, ocugocuga, ocuga, okaku, oruswiga, osiga
Asian:	
Malaysian	Ranti
Thailand	Toem tok, ya-tomtok
Indian: Assamese	Latkochu (a)
Gujarati	Piludi (a)
Hindi	Makoi (a & n); Rasbhari (a); Kali makoy (n) - Black berry; Lal makoy (v) - Red berry
Kannada	Kari kachi hannu (a) - Black-berried fruit; Kempu hachi hannu (v) - Red berried fruit; Ganike hannu (v) - Red fruit
Malayalam	Puttari chunda (a) - Small-seeded berry
Tamil	Manathakali (v) - Home tomato
Urdu	Mako (n), Makoh
Brahvi	Tolangoor (n) - Jackal grapes
Pushtu	Kachmacho (n)
Punjabi	Peelak (n), Mamoli (n)
Pakistani	Kanper makoo
Chinese	Baihua cai - White-flowered greens: Denglong ca - Lantern grass; Di paozi - Ground bobble; Feitian long - Flying dragon; Hei qiezi - Black eggplant; Hei tiantiari - Black sweet-fruit; Jia denglong cao - False lantern grass; Kukui - Bitter wort; Shan lajiao - Mountain cayenne; Shi haijiao - Stone sea cayenne: Tianqie cai - Heaven eggplant greens; Tian qiezi - Heaven eggplant; Xiao guoguo - Little fruit; Xiao kucai - Little bitter greens; Yie haijiao - Wild sea cayenne; Yie lahu - Wild hot greens; Yie lajiao - Wild cayenne; Yie putao - Wild grape; Yie qieyang - Wild eggplant; Yie sanzi - Wild umbrella

NB: a = *S. americanum;* n = *S. nigrum;* v = *S. villosum* (Schilling *et al.* 1992).

4 Origin of the species and centres of diversity

As discussed in Section **2.2** the species belonging to the section *Solanum* form a polyploid series, with diploid, tetraploid and hexaploid taxa occurring on most continents. The centre of diversity of the diploid species, however, appears to be the New World, particularly in South America. Both Central and North America also appear to have morphogenetically distinct diploid species, while the morphologically variable taxon S. *americanum* occurs throughout the Old and New Worlds. Unfortunately little is yet known of the cytology of many of the variants of these species found in Africa and Malesia. It is interesting to note that in the Old World the tetraploids *S. villosum* and *S. retroflexum* and the hexaploid species *S. nigrum* and *S. scabrum* are native, and that the diploids found in these areas are introductions which have become naturalized. Conversely, in North America, the native species are diploid, with the polyploid species all being introductions. Good species of all three ploidy levels occur in South America, where the largest number of species belonging to this generic section are also found (Table 2). This, together with the morphological variability displayed by the species in this continent, suggests that South America is the centre of diversity of the section *Solanum,* and that many of the species evolved there (Edmonds 1979 and unpublished).

The black nightshade *S. nigrum,* however, does not occur in this continent; it is largely Eurasian in distribution, though it has been introduced into areas such as North America, Australia and New Zealand. The derivation of this hexaploid from the tetraploid *S. villosum* and the diploid *S. americanum,* or taxa considered to be conspecific with them, through the amphiploidy of a sterile triploid hybrid is now well established (Edmonds 1979a). Edmonds (1979a) confirmed the findings of a number of earlier Indian workers, demonstrating the relative ease with which the black nightshade could be synthesized artificially. The resultant seeds gave rise to vigorous hexaploid F_2 and F_3 generation plants, which flowered profusely and set seed spontaneously, and which were morphologically similar to naturally occurring accessions of this species. Moreover, they closely resembled the glandular-haired subsp. *schultesii,* which was not unexpected since the glandular-haired subsp. *villosum* had been used as the paternal parent. Reciprocal backcrossing of the F_3 generation plants to various accessions of *S. nigrum* resulted in a high percentage of fruit set with some seed numbers/berry approaching those of the natural parental accessions. Full fertility data of these crosses are given in Edmonds (1979a). However, in contrast to the findings of most Indian workers who reported that the initial crosses were only successful when the tetraploid was used maternally, this artificial synthesis resulted from the use of the diploid as the pistillate parent.

However, there is not yet any definitive evidence on the mode of origin of the tetraploid parent involved, namely *S. villosum.* The meiotic chromosomal behaviour of *S. nigrum* led several earlier workers to consider that it was either an autohexaploid or an autoallopolyploid containing two sets of identical genomes. Others, on similar evidence, favoured three sets of different genomes and allopolyploidy (bibliography in Edmonds 1979a). Since it has been established through cytological, hybridization and pigment analyses that *S. villosum* is not an autopolyploid form of *S. americanum,* the hexaploid *S. nigrum* cannot be an autohexaploid (Tandon and Rao 1966a, 1966b; Venkateswarlu and Rae 1972; Rao 1978). Depending on whether this hexaploid contains one or two sets of *S. americanum* genomes, one or two other diploid entities have been involved in its ancestry. Rao (1971), for example, considered that his crossability work demonstrated that *S. nigrum* is an autoallohexaploid containing two sets of largely homologous genomes from plants conspecific with *S. americanum.* Other Indian workers favoured allopolyploidy, with Tandon and Rao (1974) and Rao et al. (1977), citing the cytological behaviour of sterile triploid hybrids derived from Indian variants conspecific with *S. villosum* and *S. americanum* as evidence that three dissimilar genomes were involved and that the latter had not contributed to the origin of the former.

On the basis of hybridization work, seed protein electrophoresis (Edmonds and Glidewell 1977) and the known occurrence of natural tetraploid hybrids derived from *S. nigrum* and the glandular-haired diploid now known as *S. physalifolium* var. *nitidibaccatum* (Leslie 1978), together with various cytological reports by other workers, Edmonds (1979a, 1981) suggested that this diploid might have contributed a pair of genomes to *S. villosum.* Though native to South America, this diploid is commonly found as a casual introduction throughout Europe, as is another South American diploid - *S. chenopodioides.* Again on morphological and crossability evidence Edmonds (1979a) suggested that, if *S. nigrum* were of an allopolyploid origin, this might have been the third progenitor. However, later authors have questioned these suggestions. Schilling (1984) found that foliar flavonoid data almost certainly proved that plants conspecific with *S. physalifolium* subsp. *nitidibaccatum* could not have been involved in the ancestry of *S. villosum,* while Bhiravamurty and Rethy (1984) cited the absence of both *S. chenopodioides* and *S. physalifolium* var. *nitidibaccatum* from India as evidence that they could not have been-involved in the ancestry of the Indian *S. villosum.* Moreover, herbarium records suggest that the South American adventives are relatively recent introductions, at least into Europe, with the majority arriving during the last 100 years. *Solanum nigrum* is almost certainly a species of ancient origin. According to Salisbury (1961) this species is one of the weeds recorded from deposits of the Palaeolithic and Mesolithic Age in Britain, from which he suggested that these weeds might have been established members of the native flora before the agricultural activities of Neolithic Man. The species was mentioned by Pliny in the 1st century AD and by most of the great herbalists including Dioscorides in 1478; ancient Greek words for this plant are common in most of the 15th and 16th century Herbals. Indeed, Grieve (1931) mentioned that this plant was known by the name of “Petty Morel” in the 14th century when it was already used for medicinal purposes.

The precise mode of origin of *S. nigrum* is therefore far from being completely understood, though it almost certainly arose polytopically. The morphological variation in the species is extensive and identical to that exhibited by its proven progenitor *S. villosum.* The known diploid progenitor *S. americanum* is probably the most morphologically variable species in the section *Solanum.* The combination of such morphologically different biotypes during formation of triploid hybrids would account for the variability found in *S. nigrum* (Edmonds 1979a). Moreover, this diploid, though probably native to South America, is the most ubiquitous and widely distributed species found in the section; it is undoubtedly composed of several distinct infraspecific variants, as well as morphologically distinct ecogeographical biotypes. Depending on the source of these different biotypes contributing to the genome complement of *S. nigrum,* the latter could therefore have had several different modes of origin. Edmonds (1979a) suggested that if *S. nigrum* is an allopolyploid, then it is possible that the third progenitor may not be found in Europe, and that *S. nigrum* might have evolved in Africa or, more probably, in Asia where this hexaploid and its two known progenitors are particularly variable. There is also another glandular-haired species which is probably tetraploid, which seems to be confined to Africa. Superficially, this species — referred to in this monograph as *S. grossidentatum* — closely resembles *S. villosum,* but it has purple/black berries. This also might have contributed genomes to the ancestry of the black nightshade, and might account for the excessive variability found in the latter in the Middle East and Africa. It is also possible that *S. nigrum* might have had an autoalloploid origin, with *S. americanum* contributing two sets of genomes in the form of two infraspecific variants. Clearly more experimental work, especially involving the Afro-Asian taxa, is needed to resolve the precise mode of origin of this Old World hexaploid species.

As far as the other polyploid species found in the section *Solanum* are concerned, there is as yet little conclusive evidence on their modes of ancestry. At the tetraploid level, hybridization work and numerical analyses suggested that *S. chenopodioides, S. americanum* and *S. zahlbruckneri* Bitt. are the most likely diploid contributors to have been involved in the ancestry of the South American *S. interandinum* Bitt. (Edmonds 1979a); that the diploid *S. sarrachoides* or *S. physalifolium* var. *nitidibaccatum* could have contributed a set of genomes to the glandular-haired *S. excisirhombeum* Bitt., together with *S. americanum* (Edmonds 1979a); and that both the African tetraploid *S. retroflexum* and *S. villosum* might have originated from the same or common ancestors (Rao and Kumar 1981). If so the most likely contender is *S. americanum* (Edmonds, unpublished). As far as the hexaploid species are concerned, the tetraploid *S. interandinum* and the diploid *S. chenopodioides* might have been involved in the ancestry of the South American hexaploid *S. furcatum* Dun. (Edmonds 1979a). Another diploid possibly involved in the derivation of the latter is the New World species *S. douglasii* Dun. (Paddock 1941; Edmonds 1979a). Finally, Ganapathi and Rao (1987) suggested that the vigour of the sterile hybrids derived from crossing the hexaploid *S.* scabrum with *S. americanum* indicated that the latter was also a diploid ancestor of this species.

It is generally thought that the polyploid members of the section *Solanum* are mostly alloploids, since most species so far investigated cytologically show regular bivalent formation at meiosis. However, it is possible that some of these polyploids might have arisen through the functioning of unreduced gametes, as well as by somatic chromosome doubling. Edmonds (unpublished) recorded both such phenomena on several occasions when the hybridization of maternal diploids with paternal tetraploids resulted in tetraploid, instead of the expected triploid, progeny. It is also very likely that these polyploids have arisen from comparatively few diploid species contributing genomes in different combinations. The possession of common genetic material would explain the similar ranges of morphological variation found in species belonging to the section *Solanum* (Edmonds 1979a).

5 Properties and uses of the species

5.1 Beneficial properties

Species belonging to the section *Solanum* are often referred to in ethnobotanical studies. Unfortunately, because of the taxonomic confusion surrounding the component species, and the tendency to refer to all members as '*S. nigrum'* the information given has to be interpreted with caution. According to Schilling et al. (1992), the most important taxonomic distinction for ethnobotanists encountering members of the section *Solanum* is that between *S. nigrum* and *S. americanum*, because the former is most likely to have been misapplied while *S. americanum* is the most likely species to have been used ethnobotanically.

As is evident from the information extracted from herbarium material and summarized under each of the species dealt with in Sections **2.5** and **2.6**, species belonging to the section *Solanum* are widely used ethnobotanically, and have been since records began. However, they have mostly been harvested from spontaneous plants or populations, with relatively few records indicating that the various species are deliberately cultivated.

Among the enthobotanical uses reported for species associated with *S. nigrum*, either in the literature, or from herbarium material are the following.

Sources of food

Leaves and tender shoots are widely used as vegetables throughout the world and have provided a food source since early times, with *S. nigrum* being recorded as an ancient famine plant of the Chinese (Henderson 1974). The leaves and young shoots are boiled or stewed and used as a relish. They are also used in soups and sauces such as palaver. All the species are used as pot-herbs or leaf/stem vegetables more or less throughout their respective geographical ranges in Africa, Asia, Malesia and the Americas (see Section **2.5**). Indeed, Bailey (1881) reported that the herbage of forms of '*S. nigrum'* was considered to be a very valuable culinary vegetable in the Mauritius, and was imported to Australia by immigrants in the 1852 gold rush for use as a vegetable. Often the vegetable used is called 'spinach' and there are many ethnobotanical accounts of the water in which the vegetative parts have been boiled being discarded and replaced several times, or replaced with milk, to prevent the ingestion of toxins. In Malawi, Thomo and Kwapata (1984) reported that potash (which is a filtrate collected from ashes of dried amaranth or bean plants) or soda, groundnut paste and salt are added to boiled leaves. These additives add taste and flavor to the diets. The vegetable is used in both urban and rural areas, but since it is often bitter it is mixed with *Amaranthus* spp., *Corchorus* spp. or with other green leafy vegetables.

In Kenya, boiled leaves of these Solanums are apparently recommended for pregnant women, since their consumption is believed to result in the birth of children with dark eyes and smooth skin (Opole *et al.*, unpublished). Moreover, pregnant women who eat this vegetable are believed to recuperate well after delivery. It is also believed that children eating the vegetable do not get 'marasmus' or 'kwashiokor', especially if the vegetable is cooked with milk, groundnuts *(Arachis hypogaea* L.) or simsim *(Sesamum indicum* L.) (Opole *et al.,* unpublished).

Ripe berries from most of the species, but especially the orange or red forms from *S. villosum,* are frequently eaten raw as fruits, particularly in parts of Africa. They are also widely used in pies and preserves, and sometimes as a substitute for raisins in plum puddings, particularly in North America. They can also make a delightful jam, with the 'Wonderberry' making an excellent preserve for tea with bread and butter. Fisher (1977) reported that berries of the garden huckleberry grown in North America freeze well for winter pies after being washed and drained, while Simms (1997) reported that British-grown berries of this species are "admirably suited" for use in pies and preserves and that they are particularly suitable for mixing with less colourful fruits such as apples. Bromilow (1995) reported that the South African berries must be cooked, recording that green fruits are poisonous. Indeed, most of the berry uses recorded from herbarium material mentioned that they were edible "when ripe", "red", "yellow", or "turning purple", suggesting that the local communities eating these fruits know how to avoid potentially dangerous forms. In India, the berries are eagerly sought out and eaten by children (Schilling *et al.* 1992), and the berries of all species are eaten by a variety of bird species in all countries of their geographical ranges.

Nutritional value

Several studies have been conducted to investigate the nutritive value of the 'vegetable black nightshades'; these are summarized in Table 4. From this it is evident that these species constitute nutritious vegetables. The leaves can provide appreciable amounts of protein and amino acids, minerals including calcium, iron and phosphorus, vitamins A and C, fat and fibre, as well as appreciable amounts of methionine, an amino acid scarce in other vegetables (Fortuin and Omta 1980; FAO 1988). Moreover the berries can apparently yield high mounts of iron, calcium and vitamin B (Fortuin and Omta 1980), and appreciable amounts of vitamin C and carotene (Watt and Breyer-Brandwijk 1962). The seeds too contain vitamin C and carotene (Watt and Breyer-Brandwijk 1962). The nutrient values may, however, vary with soil fertility, plantage and type (i.e. variant or species) (Chweya 1997). Imbamba (1973), for example, found that the leaf protein content of *'S. nigrum'* was dependent on the age of the plant. Moreover, the application of nitrogen increases the amount of ascorbic acid and protein while decreasing the calcium content in the leaves (Chweya 1997). The values of available ascorbic acid depend on the method of cooking. Mathooko and Imungi (1994) observed that ascorbic acid content decreased with both an increase in the cooking time and in the volume of water used for cooking. This loss could reach as much as 75-89% when boiling the vegetable for as long as 20 minutes. However, leaves boiled with six volumes of water for 15 minutes resulted in the loss of approximately 70% of ascorbic acid. Similar reductions in the levels of vitamins A and C through excessive boiling have been reported for various other local vegetable plants. Drying reduces ascorbic acid content but does not affect crude protein and mineral nutrients. Similar nutritional data were recorded by Malaisse and Parent (1985) who analyzed the leaves of 'S. *nigrum'* used as a wild vegetable by the Kibemba in the Zambezian Woodland Area in southern Central Africa. They found that 22 g of dry weight yielded energy levels of 1232 kJ and 295 calories.

Table 4. Nutritive value of vegetable black nightshades

Nutrient per 100-g edible portion	Range of values	Reference
Water (%)	83-91	Oomen and Grubben 1978; Gomez 1981; Sreeramulu 1982; Onyango 1993; Chweya 1997; Opole *et al.* unpublished
Crude protein (g)	2.8-5.8	Oomen and Grubben 1978; Sreeramulu 1982; Sebit 1995; Chweya 1997; Opole *et al.* unpublished
Crude fibre (g)	0.6-1.4	Oomen and Grubben 1978; Tindall 1983; Sebit 1995; Chweya 1997
Fat (g)	0.8	Tindall 1983
Carbohydrate (g)	3.3-5.0	Sreeramulu 1982; Tindall 1983
Calories (kcal)	38	Tindall 1983
Etheral extract (g)	38-44	Oomen and Grubben 1978; Sreeramulu 1982; Sebit 1995
Total ash (g)	3.3-8.8	Sreeramulu 1982; Sebit 1995; Opole *et al.* unpublished
Iron (mg)	1.0-4.2	Oomen and Grubben 1978; Tindall 1983; Sebit 1995
Calcium (mg)	99-442	Oomen and Grubben 1978; Tindall 1983; Sebit 1995
Phosphorus (mg)	75	Tindall 1983
Beta-carotene (mg)	1.7-11.6	Oomen and Grubben 1978; Sebit 1995; Chweya 1997; Opole *et al.* unpublished;
Ascorbic acid (mg)	20-158	Oomen and Grubben 1978; Tindall 1983; Mathooko and Imungi 1994; Sebit 1995; Opole *et al.* unpublished
Oxalate (mg)	58.8-98.5	Sebit 1995; Chweya 1997
Nitrate-N (mg)	29-400	Chweya 1997; Opole *et al.* unpublished
Total phenolics (mg)	68.3-73.4	Mwafusi 1992; Chweya 1997

The species accumulate nitrates and contain oxalates and phenolics (Table 4.) These are antinutrients which therefore reduce the nutritive quality of the leaves.

Nitrates are harmful to humans when consumed and converted into nitrites which oxidize ferrous ions of the blood haemoglobin, resulting in reduced oxygen-carrying capacity of the blood (Lee 1970; Maynard *et al.* 1976; Mengel 1979). Oxalates indicate the presence of oxalic acid in plant material. When ingested by humans, the acid combines with calcium to form an insoluble salt which the body cannot absorb (Buck *et al.* 1966; Robinson 1973). This renders the calcium unavailable to the body. Phenolics bind proteins, hence interfering with the assimilation of proteins into the body (Haslam 1974; Singleton 1981).

Medicinal value

Various parts of many of the species belonging to the section *Solanum* are widely used medicinally throughout the world. Their use as such is recorded from the earliest times and various species, especially *Solanum nigrum*, are mentioned and often illustrated in all of the early Herbals, with Dioscorides being one of the first to record their medicinal properties. Since then this 'species' has continued to be widely acclaimed for its medicinal effects in every country in which the taxon is found.

Among the great British herbals, Gerard's Herbal of 1636 reported that the "Nightshade is used for those infirmities that need cooling and binding" and that it was "good against 'St. Anthonies fire', the shingles, panic of the head, heart burning or heat of the stomache". Later, in Culpeper's Herbal of 1649, the black nightshade was described as a "cold Saturnine plant", which was commonly used to cool hot inflammations either externally or taken internally. Among the soothing effects of the clarified juice of this plant he mentioned inflamed throats, eye inflammations, shingles, ringworm, running ulcers, testicular swelling, gout and ear pains. In Europe, '*S. nigrum*' has been used as a remedy for convulsions, and has been administered as a soporific in Germany — especially for children, with leaves being placed in babies' cradles to promote sleep in "Bohemia" (? Czech Republic) (Grieve 1931). The bruised fresh leaves used externally are reputed to ease pain and reduce inflammation; they are applied to burns and ulcers by the Arabs. Leaf juice has also been used for ringworm, gout and earache, while it is also reputed to be a good gargle and mouthwash when mixed with vinegar (Grieve 1931). In North America, the Houmas Indians use an infusion made from boiled roots of this 'species' to administer to babies with worms, and crushed green leaves mixed with a grease to make poultices for sores, while the Rappahannocks used a weak infusion to cure insomnia (Vogel 1990). There are relatively few reports of these species being used medicinally in South America, an exception being the moderate narcotic action attributed to flowers and leaves resulting in their use to calm fever and combat the effects of alcoholic excesses in southern Ecuador (Heiser 1963).

In India, the 'plant' is noted for its antiseptic and antidysenteric properties and is given internally for cardalgia and gripe. An infusion of the plant is used as an enema for infants with abdominal upsets. The plant is also a household treatment for anthrax pustules when it is applied locally It is further reported to have emollient, diuretic and laxative properties and its decoction is regarded as both antispasmodic and narcotic. Freshly prepared extracts of the plant are apparently effective in the treatment of cirrhosis of the liver and also serve as an antidote to opium poisoning. An alcoholic extract of leaves is active against *Staphylococcus aurens* and *Escherichia coli.* Infusions or decoctions of the plant, after transient stimulation, are reported to depress the central nervous system and the reflexes of the spinal cord. Small doses increase cardiac activity while large doses decrease it. Extracts also reduce blood pressure. Berries apparently possess tonic, diuretic and cathartic properties and are also useful in heart diseases and as a domestic treatment for fevers, diarrhoea, ulcers and eye troubles (Anon. 1965a, 1965b). The seeds are reportedly used to treat gonorrhoea and dysuria (Jain and Borthakur 1986). In Pakistan Akhtar and Muhammad (1989) showed that a powder from the aerial parts of the plant could be "antiulcerogenic".

In China leaves are used as a febrifugal or detoxicant drug. Medicinally used preparations consist of dried aerial parts of plants which are used as a diuretic, antihypertensive and anticancer agent for infections of the urinary system, hypertension and cancer of the digestive system Schilling *et al.* 1992). Fresh leaves are also used to treat wounds.

In Japan Saijo *et al.* (1982) observed that immature fruits of *'S. nigrum'* contain steroidal glycosides which show considerable anticancer activity. These glycosides could be solasonine, solamargine, diosgenin and solasodine.

In Hawaii plants conspecific with *S. americanum* are used in disorders of the respiratory tract, skin eruptions, cuts, wounds and trachoma, while in the Mauritius, a poultice of the plant is used to relieve abdominal pain and inflammation of the urinary bladder (Watt and Breyer-Brandtwijk 1962).

In the Orient Tandon and Rao (1974) reported that the fruits and juices of *'S. nigrum'* are used to cure stomach ailments, fevers and blood impurities and young shoots to cure skin diseases. In the Philippines, leaf extracts are apparently used to restore body skin pigment.

In East Africa the raw fruit is chewed and swallowed for treatment of stomach ulcers or for general abdominal upsets which lead to continued stomach-ache. Infusions of leaves and seeds are rubbed onto the gums of children who have developed crooked teeth. Pounded leaves are soaked in water, fermented and used for the treatment of boils, ulcers and swollen glands. Unripe berries are used to treat ring worms. Various parts of the plant are also believed to cure malaria, black fever, dysentery and urinary infection (Kokwaro 1976). The Zulus use an infusion as an enema for abdominal upsets in children; the southern Sotho rub burnt and powdered root in to scarifications on the back for the relief of lumbago; a paste made from unripe berries is used among African tribes as an application for ringworm; the Xhosa also use the plant for disinfecting anthrax-infected meat; in Zimbabwe the plant is used as a remedy for malaria, blackwater fever and dysenteries, while the juice or decoctions of the herb were formerly made into an ointment for foul ulcers (Watt and Breyer-Brandwijk 1962).

In Kenya unripe fruits are applied to aching teeth and squeezed onto babies' gums to ease pain during teething. Leaves and fruits are pounded and the infusion used against tonsillitis. Roots are boiled in milk and given to children as a tonic (Maundu *et al.*, unpublished). Indigenous information reported by Opole et al. (unpublished) indicates that leaves boiled with milk are used to relieve sudden stomach ache, boost the health of expectant mothers and/or relax the uterus of both pregnant and lactating mothers. The same mixture prevents muscular pains among old people or those suffering painful joints, especially those associated with arthritis or with malarial fever. Furthermore, the same mixture is believed to increase the strength of weak people and prevent skin eruptions. Notes taken from herbarium specimens confirmed that these nightshade species are widely used medicinally in Africa. Thus *S. americanum* was found to be used for the treatment of sores (using pounded leaves) in the Cameroon, for rheumatic pains (leaf infusions) in Kenya; as a cold cure (chewed roots) and an eye-disease remedy (leaf juice mixed with salt) in Hawaii; for heart pains (raw leaves) in Sierra Leone; and for inflamed eyes, especially for conjunctivitis (fresh leaves pounded and juice sprayed into infected eyes) in Tanzania. Raw roots of *S. nigrum* were also found to be eaten for stomach-ache in Tanzania, where ground and soaked leaves of *S. villosum* were reportedly placed on swellings and fruit juice squeezed into sore eyes. The report of a case of conjunctivitis in Tanzania which had failed to respond to conventional treatment administered over a week is particularly interesting; the pain was instantly relieved and all inflammation disappeared within 4 days when treated with a leaf juice extract from *S. americanum.*

Recent reports attribute antitumour and anticancer effects to herbal extracts of the Chinese '*S. nigrum*'. Boik (1996) reported such extracts to have inhibited SA, WA ascites cancer and cervical cancer in mice, as well as suppressing the growth of meningeal tumour cells, inhibiting Hela cells and ascitic SA in mice. Of more importance, these extracts were also reported to reduce the signs and symptoms of carcinomas of the cervix, oesophagus, breast, lung, liver and ovary chorioepithelioma, hepatoma and sarcoma in humans. Though the accuracy of this information is uncertain, in view of the crudeness of the herbal preparations used and the results observed, such potential value clearly deserves further investigation.

Sources of fodder and browse

The species are apparently used as fodder and browse by various animals, especially in Africa. Herbarium records showed that plants tentatively identified as *S. villosum* are eaten by sheep and goats in the Sudan, and by bush-buck and browsed by goats in Kenya, with the taxon '*S. tarderemotum*' being eaten by giraffe in Kenya. The use of the 'black nightshades' as fodder for cattle and goats in Kenya also has been reported by Maundu *et al.* (unpublished).

Commercial value

Both the leaves and berries are used as a source of dyes. Leaves are macerated to extract a dye used to colour sisal baskets (Nzioka 1994), while the purple/black berries of both *S. scabrum* and *S. americanum* are reportedly used as a source of ink.

The anthocyanin pigments of *S. scabrum,* moreover, are used as a colourant for fruit juices and apple sauce (Francis and Harborne 1966). These authors consider that this species is a particularly useful source of colourants, because the pigment is present in high concentration, and the plants are vigorous and easy to grow. Molluscidal activity indicates that extracts from these plants might also be of use in mollusc control (Shoeb *et al. 1990).*

Rural and urban economic value

These *Solanum* species are found on sale as a vegetable in both rural and urban markets in Africa, especially in Cameroon, Ghana, Kenya, Madagascar and Nigeria, as well as in Guatemala, New Guinea and the Mediterranean (e.g. Crete). Fortuin and Omta (1980) further report that the 'black nightshade' is also sold in the markets of Hawaii, Trinidad, Suriname, India, Indonesia, China and the Philippines. The plants therefore provide a source of income for rural farmers, who are mostly women. In some districts of South Africa Zulu women often take baskets of berries to sell in nearby villages or townships. Both the vegetative shoots and the fruits are probably harvested casually as weeds of other crops. There are very few reports of controlled cultivation for any of these species, apart from those noted on herbarium sheets for the Seychelles and Zambia, or those reporting that the plants are encouraged at the edges of cultivation in parts of Kenya. Economic returns from the use of these Solanums as a vegetable have not yet been quantified, though Fortuin and Omta (1980) reported that the 'black nightshade' has a low market price and a low economic' value in those countries in which it is sold as a market crop.

5.2 Deleterious properties

Weeds of agriculture and horticulture

Species related to the black nightshade are notorious and often troublesome weeds of agriculture and horticulture in most parts of the world. They are recorded as occurring in at least 73 countries where they are associated with 37 major crops (Rogers and Ogg 1981). Including it among the world's worst weeds, Holm *et al.* (1977) describe *'S. nigrum'* as being a serious weed of crops as diverse as banana, barley, cereals, coffee, corn, cotton, field bean, garlic, lima bean, melon, onion, orchards, pea, pepper, pineapple, potato, sorghum, soybean, sugar beet, sugarcane, sunflower, tobacco, tea, tomato, vineyards, wheat and vegetables, and in countries as widespread as Asia, Australia, Europe, the Middle East, New Zealand, North and South America and the Pacific Islands.

Not only do these Solanums compete with the crops for moisture, light and nutrients, but they can also contaminate a commercial crop such as field bean, lima bean, soyabean and navy bean through staining from the juice released by the berries rupturing during harvesting; this greatly reduces both the quality and economic return to growers (Burgert *et al.* 1973; Ogg *et al.* 1981). They can even stain wool when sheep graze infested land after crop harvesting (Healy 1974).

So-called *S. nigrum* or related species are included in most accounts of weeds or troublesome plants throughout the world. Interestingly, however, Africa, India, Malesia and South America are all excluded from the distribution map given of areas in which this so-called species is a common, serious or principal weed (Holm *et al.* 1977). It is principally in these areas that species related to *S. nigrum* have been recorded as being used a minor crop. It is highly possible that their use as such, which must result in their being hand-weeded out of the crops concerned, simultaneously results in the prevention of these species becoming troublesome or contaminating the actual commercial crops being grown. Moreover, Schilling and Andersen (1990) reported that none of these *Solanum* species found in India and Pakistan were weeds of significant agronomic importance, except under irrigation and then only in localized areas. Nevertheless, these species do feature in various African, Asian and Malesian accounts of weeds; examples include Henty and Pritchard (1973) for New Guinea, Vernon (1983) for Zambia, Grabandt (1985) for Southern Africa, Sauerborn and Sauberborn (1988) for West Asia, Akobundu and Akyakwa (1987) for West Africa, Ivens (1989) for East Africa and Bromilow (1995) for South Africa.

Methods of control

Methods of control of these species as weeds are widely documented, A comprehensive review of herbicidal control is given in Weller and Phipps (1978/79), who concluded that effective control can usually be achieved in most agricultural and horticultural crops. Many authors report that some of these species are relatively easy to eradicate if attacked during the seedling stage. The actual herbicides most effective in their control, together with the application rates and control times, are all tabulated by these authors, who also include a complete bibliography. Most of the other authors cited above also report that the Solanums involved are controllable either by appropriate herbicides or by cultivation methods. Further details on the herbicidal control of '*S. nigrum*' can be obtained by referring to the bibliographies in each of these papers.

Alternative hosts to destructive diseases of crops

Species related to the black nightshade are frequently associated with a broad spectrum of potentially destructive nematodes and microorganisms, serving as alternative hosts and potential disease vectors (Karschon and Horowitz 1985). Rogers and Ogg (1981), reviewing the diseases associated with these species in North America, listed 13 nematode, three bacterial, 15 fungal and 31 viral pathogens, which affect crops as diverse as chillies, cucumber, potato, sugarbeet, tobacco and tomato. The nematode pathogens found in association with weeds of the *S. nigrum* complex included burrowing nematode *(Rotylenchus similis, Radopholus similis),* foliar nematode *(Aphelenchoides ritzembozi),* golden nematode of potato and root knot nematode *(Heterodera marioni, Meloidogyne* spp.), lesion nematode *(Pratylenchus neglectus),* northern root knot nematode *(Meloidogyne hapla),* potato rot nematode and stem nematode *(Ditylenchus destructor)*, reniform nematode *(Rotylenchus reniformis)*, silver-leaf nightshade nematode *(Ditylenchus phyllobis, Nothangirina phyllobia)*, southern root knot nematode *(Meloidogyne incognita)*, stunt nematode *(Tylenchorhynchus claytoni)*, and sugar beet nematode *(Heterodera schachtii)*. Bacterial pathogens included bacterial spot *(Xanthomonas vesicatoria)*, bacterial wilt *(Pseudomonas solanacearum)* and wildfire *(Pseudomonas tabaci)*. Fungal pathogens included anthracnose *(Colletotrichum atramentarium)*, *Cercospora nigrescens*, *Diporotheca rhizophila*, early blight *(Alternaria solani)*, late blight *(Phytopthora infestans)*, leaf spot *(Macrophoma subconica)*, powdery mildew *(Erysiphe cichoracearum)*, root rot *(Rhizoctonia solani)*, rust *(Puccinia subtriata)*, *Septoria solanina*, southern blight *(Sclerotium rolfsii)*, verticillium wilt *(Verticillium albo-atrum)*, violet root rot *(Rhizoctonia crocorum)* and white smut *(Entyloma australe)*. The viral pathogens were listed as arabis mosaic, aster yellows, atropa belladona mosaic, chili pepper mosaic, cucumber green mottle mosaic, cucumber mosaic, curly top, leaf roll, lucerne mosaic, petunia mosaic, potato acuba mosaic, potato leaf roll, potato paracrinkle, potato stunt, potato viruses A, M, X and Y, red currant ring spot, tobacco etch, tobacco leaf curl, tobacco mosaic, tobacco necrosis, tobacco ring spot and ring spot No. 2, tobacco streak, tobacco yellow dwarf, tomato bunch top, tomato spotted wilt, vaccinium false blossom and western aster yellows. Rogers and Ogg (1981) also mentioned that numerous destructive insects such as the Colorado potato beetle are frequently found in association with these species. However, while these plants may be alternative hosts for these pests and diseases and therefore serve as potential vectors, these authors also pointed out that these *Solanum* species could also be of use as control agents for some of the organisms. Indeed, Henderson (1974) reported that plants of both *S. americanum* and *S. nigrum* persisting as weeds of cultivation in Australia were known to be alternative hosts for insects attacking crops such as tobacco, for plant viruses transmitted by insects, and for pathogenic bacteria attacking commercial strains of ginger.

Toxicity

Most species associated with *Solanum* section *Solanum* are reputedly poisonous to both humans and livestock; many of the reports of their toxic effects are reported in the older literature. Indeed, nearly every manual on poisonous plants in every geographical region of the world includes *S. nigrum*. The widely reported toxicity of *S. nigrum* has been attributed to the alkaloid solanine causing varying degrees of poisoning in humans, cattle, pigs, goats, ducks and chickens, with death resulting in some cases. The effects of solanine poisoning in humans are reported to be nausea, vomiting, diarrhoea, colic, headache, dizziness, loss of speech, fever, sweating and tachycardia, reduced heartbeat, pupil dilation, blindness, mental confusion, convulsions, coma and death (Watt and Breyer-Brandwijk 1962; Cooper and Johnson 1984). Such effects normally appear around eight hours after ingestion. In animals, such ingestion can cause rapid pulse and respiration, dark-coloured diarrhoea followed by constipation, lack of rumination, somnolence and dry muzzle in cattle, pale mucous membranes, widely dilated pupils, low body temperature, oedema, incoordination, tremors and staggering movements (Wetter and Phipps 1978/79; Cooper and Johnson 1984). However, the level of solanine, the toxin responsible for these effects, is apparently reduced if animal forage contaminated with *S. nigrum* is ensiled; the resultant fermentation process probably converts the sotanine to the less toxic sotanidine by acid hydrolysis (Weller and Phipps 1978/79).

These plants also contain high levels of nitrate nitrogen (NO_3-N) and are included in the group of plants which can cause $N0_3$-N toxicity in livestock (Wetter and Phipps 1978/79). The levels of NO_3-N apparently reach a peak as the plants come into flower and then decline. Acute nitrate toxicity can lead to death, with chronic toxicity resulting in a decrease in milk yield, abortion, impaired vitamin A and iodine nutrition, muscle tremors, staggering gait, rapid pulse, frequent urination, laboured breathing, followed by collapse and coma, with or without convulsions (Welter and Phipps 1978/79). However, the level at which this nitrate toxicity can cause detrimental effects in animal health and production is uncertain, while the actual effects noted following ingestion of black nightshade plants could be due to either solanine or $N0_3$-N or both (Weller and Phipps 1978/79).

Nevertheless, the comparable number of accounts reporting that these species are harmless as a food and fodder sources suggest that this toxicity is variable. Indeed a chemical survey of various members of the section *Solanum* reported the presence of potentially toxic alkaloids only in unripe fruits, with ripe berries and vegetative parts tacking these compounds. Schilling *et al.* (1992) therefore concluded that the plants are probably only poisonous to indiscriminate feeders such as livestock who might consume the whole plant. However, these plants are browsed and used as fodder for animals without any detrimental effect in some areas, and Rogers and Ogg (1981) suggested that the development of toxic levels of these alkaloids is dependent on their growth under certain conditions or in certain localities, and even on the age of the plants concerned. Other reports suggest that the amounts of poisonous ‘principles’ vary greatly with climate, season and soil type (Cooper and Johnson 1984). It is highly probable that boiling destroys any toxicity inherent in these species; most ethnobotanical reports of their use as vegetables refer to cooking, boiling and even repeated boiling with the liquid being discarded; similar reports of the use of berries also refer to their being poisonous when uncooked or unripe. Drying, however, does not destroy the toxicity of the solanine-type alkaloids (Everist 1974). It is these glycosidal alkaloids which are responsible for the bitter taste often associated with these Solanums.

5.3 Chemicals identified in the species

The occurrence of the steroidal alkaloid solasodine and of solasodine-like alkaloids in most species belonging to the genus *Solanum* has resulted in a number of phytochemical surveys of various taxa from different geographical regions throughout the world. The toxicity and/or medicinal effects of these plants are generally attributed to these glycoalkaloids. Those so far identified in the black nightshade include solanine, solasonine, solamargine and chaconine (Everist 1974; Wetter and Phipps 1978/79; Cooper and Johnson 1984). Solanine is found in all parts of the plants, with the level increasing as the plant matures, though it is apparently modified by soil type and climate (Wetter and Phipps 1978/79). The most comprehensive study dealing with species belonging to the section *Solanum* was carried out by Carle (1981) who analyzed plant material from 55 strains representing 32 so-called species for both steroidal alkaloids and the biogenetically closely related steroidal sapogenins. He demonstrated that the characteristic steroidal alkaloid solasodine was absent from plant material of all these samples, though it was present in their unripe fruits. However, the steroidal sapogenins, identified as diosgenin and tigogenin, were universally present though not always together, in both the vegetative parts and the unripe berries. The importance of these substances ties in their potential use as raw materials for the industrial production of hormonal steroids. Of particular interest is the identification of diosgenin which is highly sought after as an alternative to that derived from *Dioscorea* (Bradley et al. 1978). Pushpa Khanna and Rathore (1977) had earlier reported significant amounts of diosgenin (1.2%) and solasodine (0.65%) in green berries of the Indian diploid *'S. nigrum'* (=*S. americanum)* with lesser amounts of both chemicals in the Indian tetraploid (=*S. villosum)* and hexaploid (=*S. nigrum)* species. Máthé *et al.* (1980) had also found solasodine in all parts of *S. americanum,* but advocated that since the highest concentration occurred in the green berries, these might be a suitable source of solasodine for steroid hormone synthesis. All authors reported that these compounds are present in the greatest concentrations in green (i.e. unripe) berries, and that the actual concentration can be very variable and can vary according to the stage of plant development, as well as being affected by genetic, seasonal, edaphic and environmental factors.

So far, few attempts have been made to isolate and identify the various chemicals responsible for the medicinal effects observed in species belonging to *Solanum* section *Solanum.* The little work done on glycoalkoloids, which are said to be responsible for anticancer activity, indicated that solasonine and solamargine, from leaves and unripe fruits, are the two most important. The ripe fruit of *S. americanum* is said to contain 0.3-0.45% of solasonine (Watt and Breyer-Brandwijk 1962). Solasonine concentrations are reported highest during fruiting white solamargine is highest during flowering (Aslanov and Novruzov 1978).

Various other chemicals have been identified in species associated with the section *Solanum.* Fresh leaves of S. *nigrum* are said to contain 1 mg/100 g of ascorbic acid (Watt and Breyer-Brandwijk 1962). The flavonols have been widely analyzed for their use as indicators of phylogenetic relationships in the Solanaceae, both within and between various generic sections. Schilling (1984) isolated 10 flavonoids from leaf extracts of 11 species belonging to the section *Solanum;* they were all flavols with the predominant glycosidic moiety being glucose. Other chemicals identified include coumarins (such as scopoletin), flavonols and anthocyanidins for *S. scabrum* in Nigeria (Gbile and Adesina 1984) and the anthocyanin pigments found in

European samples of this species (Francis and Harborne 1966). The tatter authors found that the major pigment (93%) in the berries of this species was petanin (petunidin-3-(p-coumaroyl rutinoside)-5-glucoside) with minor pigments constituting the remainder. There are also various reports of the anthocyanins responsible for the purple/black berry colouration and the carotenoids responsible for the red/orange/yellow berry colouration, but these are mostly concerned with the inheritance of these characters rather than their biochemical analyses. Rao (1978), however, identified the anthocyanin pigment present in the Indian forms of both *S. nigrum* and *S. americanum* as "petunidin3-(p-coumoryl) rhamnosyl glucoside".

6 Genetic resources

6.1 Genetic variation

Species belonging to the section *Solanum*, display considerable genetic variation both florally and vegetatively. Thus, as reported in **Causes of taxonomic complexity inherent in the species,** infraspecific variation can and does occur in the sectional species. Among the more common features affected are the following characters: stems (and leaves) from green to purple; stem winging from smooth to dentate; pubescence from sparse to dense and with glandular- or eglandular-headed trichomes; leaf margins from entire to sinuate-dentate; flowers from white to purple; fruiting pedicels from erect to reflexed; berries from greenish-yellow to purple, or from yellow to orange or red. Features such as plant height and spread, the vegetative vigour, the number of berries per plant, and the number of seeds per berry, however, seem to be phenotypically plastic and dependent on the prevalent growing conditions. This is clearly illustrated by Figure 11 where the contrast between the

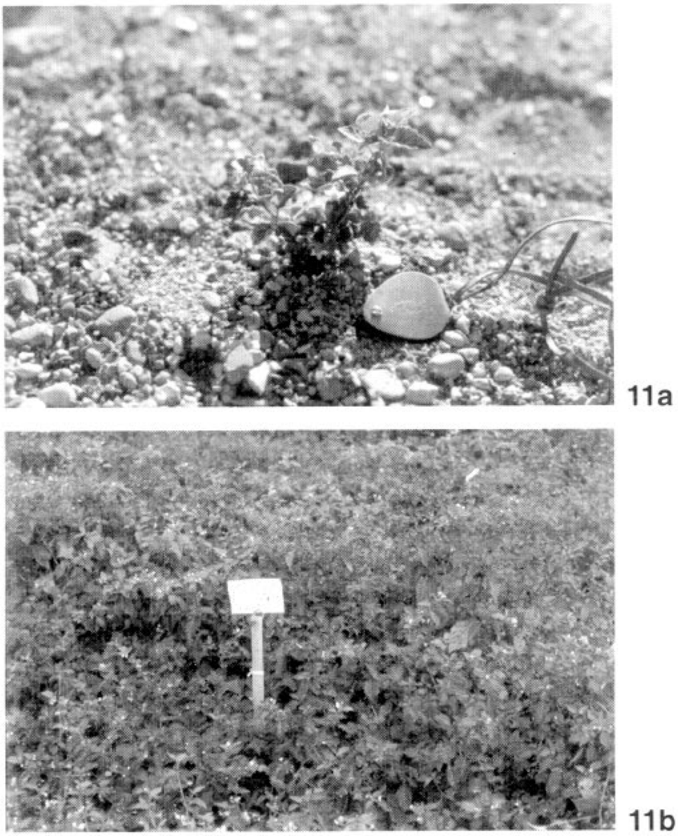

Fig. 11. Variation in stature, vigour and berry set exhibited by *S. nigrum* subsp. *nigrum.* a — original plant, growing in Dassia, Corfu, Greece *(Edmonds 45);* b — plant derived from original seed later grown in Cambridge University Botanic Garden (C126)

stature and potential berry set of a plant of *S. nigrum* collected in Corfu, Greece, with that of the plants subsequently grown from the original seeds in cultivation in England is clearly evident. This difference in stature and fertility between the original collections and those subsequently grown on experimental field plots was continually encountered, regardless of the species concerned.

6.2 Sources of germplasm

As far as is known, no collecting expeditions have been organized yet, largely because the black nightshades used as vegetables are regarded as weeds or volunteer crops and have not been completely domesticated. The species, therefore, only occur as wild and/or semidomesticated plants. In Africa, some local collections are being made but no records are available on the number of accessions so far involved. The information on germplasm conserved in genebanks has been summarized in Table 5. However, since many of these accessions have almost certainly been incorrectly identified, their usefulness as germplasm collections is virtually negligible.

Table 5. Status of collections and conservation of *solanum nigrum sens. lat.* germplasm in the world

Country/Station[†]	No. of accessions and storage conditions
France	*S. nigrum* (1), *S. scabrum* (2) Medium-term seed storage at 3°C, 30% RH
Germany	*S. nigrum* (17), *S. americanum* (11) Long-term seed storage at -15°C, 5-6% moisture content, passport data computerized, germplasm available
Ghana	*S. scabrum* (7) Short-term seed storage, passport data and germplasm available
Kenya	*S. nigrum sens. lat.* (43) Short-term seed storage at 12-15°C and 40% RH
India	*S. nigrum* (1) Short-term seed storage, passport data available
Mauritius	*S. nigrum* (2) Long-term seed storage
The Netherlands, CGN	*S. nigrum* (2), '*S. nigrum* var. *americanum*' Long-term seed storage at -20°C, 3-7% moisture content, computerized passport and characterization data
University of Nijmegen	*S. nigrum* (12), *S. scabrum* (4), *S. americanum* (7) Medium-term seed storage, passport data available, germplasm available free

Source: Frison and Serwinski 1995.

† For full addresses, see Appendix II.

Probably the most useful and genetically diverse source of 'black nightshade' germplasm currently available is that held by the Botanic Garden of the University of Nijmegen in the Netherlands. Their current catalogue of the Solanaceae Germplasm Collection lists over 120 accessions belonging to the section *Solanum,* many of which are correctly identified (Barendse and van der Weerden 1996). Moreover, this germplasm collection is to be expanded for both documentation and research, especially because species of wild origin from Africa and South America are currently considered to be under-represented. The Nijmegen Solanaceae Germplasm Catalogue represents a working list of Solanaceous accessions acquired from different sources, which are propagated for identification. Following accurate identification, the accessions are maintained through propagation and the resultant seeds stored dry in a seedbank at 2°C. The verification data, source data, place of origin, data on conservation and literature references are all stored in a computer database. Seeds, or occasionally plant material, are available on an exchange basis to interested research workers.

In Africa, the Genebank of Kenya has accumulated approximately 43 accessions of vegetable black nightshades *(S. nigrum sens. lat.)* collected between 650 and 2200 m asl and from diverse habitats including undulating landscapes, plains, hillsides and floodplains. The samples have been described as wild (9), weedy (13) or as landraces (12); 9 accessions are without any such data. No accessions have been received from any other countries. The Kenyan collections are currently being multiplied and evaluated. Seeds are being maintained at temperatures of 12-15°C and at a relative humidity of about 40%. In Zimbabwe several samples of vegetable 'black nightshades' have been collected and are being multiplied (Chigumira 1997). In Tanzania an unspecified number of accessions are maintained by HORTI Tengeru as seeds, stored in small plastic bottles in a cold room environment (Swai 1997). However, at the National Plant Genetic Resources Center (NPGRC) of Tanzania germplasm is kept in sealed aluminium foil packets in cabinet freezers at a temperature of -18°C and moisture content below 7%. Seed is being multiplied at Tengeru and Dakawa. Evaluation for potential yield and other agronomic attributes has apparently been done but the results have not been released yet. Documentation of the various accessions involved is available from NPGRC. However, the usefulness of all these accessions is dependent on their accurate identification.

Since the vegetable 'black nightshades' are still regarded as wild, weedy or semicultivated plants, most of the relevant germplasm is undoubtedly being conserved by the users *in situ,* especially where the plants are used for medicinal and/or culinary purposes. The species also may be conserved in communal lands and in shrines which are safeguarded by strong taboos prohibiting interference with the relevant plants.

6.3 Gaps in collections and constraints in conservation

There have been no specific expeditions to collect germplasm of the black nightshade species used as vegetables from the major geographical areas in which they are consumed, and where their diversity is greatest. Furthermore, very few, if any, accurately identified accessions representing morphogenetically different species have been collected. This is probably due to the reputation of these species as troublesome weeds, and the failure to recognize them as potentially valuable sources of food and therefore as a minor crop. There is probably a need to organize deliberate expeditions to collect the different species from those areas in which they are important as food and folk medicines. If this is not done, pockets of valuable germplasm might disappear, especially where any relevant habitats are currently threatened by development.

The main constraints in the conservation of these species are largely due to the failure of relevant institutions to recognize their potential as minor crop plants. Consequently no financial aid has been available to promote the plants as such; no well-defined programmes designed to promote and improve these species as crop plants have been implemented, and no personnel directly responsible for the evaluation and conservation of valuable sources of germplasm both *in situ* and *ex situ* have been appointed.

6.4 Potential utilization of germplasm

There has been very little utilization of germplasm derived from species belonging to the section *Solanum* in research, breeding studies and crop improvement work. Some investigations have been made on their nutritive value (Chweya 1997), but very few studies have been conducted on the genetic enhancement of the species, and no breeding or crop improvement work has been initiated yet.

However, it is evident from the literature that species related to the black nightshade might be of considerable value in certain crop-improvement experiments. Among the areas showing the most promise are:

- The possibility that '*S. nigrum*' may be a source of atrazine-resistant cytoplasm (Guri *et al*. 1988), through which herbicide tolerance could be conferred to tobacco (Jain *et al.* 1981; Donato *et al.* 1990).
- The use of '*S. nigrum*' in plastic gel fusion and DNA synthesis inhibitors studies (Ye and Sayre 1990).
- The possibility of this 'species' exhibiting tobacco mosaic virus (TMV) resistance, since extracts have been found to inhibit lesion production from TMV infection (Roychoudhury 1980).
- The possibility of both *S. nigrum* and *S. villosum* being valuable sources of resistance to potato late blight caused by *Phytophthora infestans* (Mont.) de Bary. Colon *et al.* (1993) reported that al though the black nightshade was present as a very common weed in late blight field trials, no trace of infection was ever found on these plants despite heavy infection of potato plants in the same fields. Both of these species are considered to be completely resistant to *P. infestans*, in view of the absence of spreading lesions or sporulation in a number of experiments. Indeed, *S. nigrum* is apparently often considered to be a non-host to this pathogen. The transfer of such resistance from these *Solanum* species to S. *tuberosum* has

recently become possible through the use of ‘embryo rescue’, thereby providing a possible method of breeding germplasm to late potato blight.

- The possibility of this ‘species’ being a source of resistance to *Phomopsis* fruit rot caused by *Phomopsis vexans* (Sacc. & Syd.) Harter (Datar and Ashtaputre 1983).
- Both *S. americanum* and *S. nigrum* are known to be alternative hosts for plant viruses transmitted by insects, for pathogenic bacteria attacking commercial strains of ginger and for insects attacking tobacco crops in Australia (Henderson 1974). These species may therefore be exploitable as alternative hosts for these crops. Similarly, various species related to the black nightshade are known to be associated with a wide range of potentially destructive nematodes and microorganisms which affect a wide range of crop plants (Rogers and Ogg 1981). Their possible commercial exploitation as alternative hosts or control agents for some of these organisms therefore needs further investigation.
- The possibility of using the high concentrations of the glycoalkaloid solasodine and the steroidal sapogenins diosgenin and tigogenin found in the green berries of species such as S. *americanum* in commercial steroid hormone synthesis (Máthé *et al.* 1980).

7 Breeding system

7.1 Pollination

The species belonging to the section *Solanum* are predominantly self-pollinating or autogamous though natural out- and cross-breeding can and does occur (Edmonds 1979a). Most species will set fruit when grown in insect-proofed glasshouses, and emasculation of the flowers while still in bud is usually necessary to prevent self-pollination if the plants are required for artificial hybridization studies. Schilling considered the pollen/ovule ratios and the amount of fruit set in the absence of pollinators to be indicative that the North American diploid species *S. americanum, S. ptycanthum* Dun. and *'S. sarrachoides' (=S. physalifolium* var. *nitidibaccatum)* were facultatively autogamous (Rogers and Ogg 1981). The autogamous nature of the breeding system in these *Solanum* species favours the rapid increase in a population from a few individuals, and confers an evolutionary advantage on these taxa in environments in which populations are frequently destroyed. It therefore partially explains the phenomenal success of the members of this section of *Solanum* as weeds of disturbed habitats, especially in agricultural areas (Rogers and Ogg 1981). This autogamy also explains the high degree of homozygosity and concurrent genetic uniformity of plants both within a population and from generation to generation that is often encountered within these species. Thus, within each species a series of populations can be found within which the plants are highly homogeneous but which are distinctly different ecomorphologically from other populations (Rogers and Ogg 1981). Such variability is particularly apparent in the taxon *S. americanum* where the recognition of a number of infraspecific categories or 'microspecies' will probably become necessary once the species has been studied on a worldwide scale.

Nevertheless, some species of the section *Solanum* are highly adapted to cross-pollination, particularly by bees and Syrphid flies. These are "buzz" or vibratile pollinators which alight on the anther cone, resulting in the inversion of the flowers. The pollen is propelled out of the apical introrse slits of the anthers in a cloud by the vibration resulting from the shivering of the indirect flight muscles of these bees while their wings are held closed over the thorax. The resultant buzzes are audible several metres from the plants (Symon 1976; Buchmann *et al.* 1977). The manipulation of the effectively poricidal anthers associated with these Solanums (since the anthers — though dehiscing by introrse longitudinal slits — remain in a cone) by bees and Syrphids has been extensively studied and recorded. Such pollination of the European Black Nightshade by two common Syrphids was recorded as early as 1883 (Symon 1976).

Buchmann *et al.* (1977) demonstrated that the anthers of the North American diploid *S. douglasii* Dun. are morphologically adapted to such a method of pollination by having septa attached to the central columellae and uneven thickenings (sclereids) in the endothecial walls near the anther apices. The flowers of this species, though visually white to pale purple, apparently have a hidden ultraviolet (UV) pattern which changes with the age of the flower; the bees are therefore visually sensitive to the flowers in both visual light and in the UV region of the spectrum. Though pollen is released only during the first 2 days following anthesis, which occurs at sunrise, the flowers remain on the plants for 10 days acting as a visual ‘flag’ to the pollinators (Buchmann *et al.* 1977). In addition, these authors detected a floral odour in the flowers of this species, which probably functions as a nearby orientation marker for smaller bees. The wide variety of native North American polylectic bees observed visiting *S. douglasii* flowers is fully recorded in Buchmann *et al.* (1977). In addition to these bees Buchmann *et al.* also noted black Syrphid flies collecting pollen from this species. They suggested that these flies buzz a number of flowers, then fly to a *Brassica* plant where the pollen is probably mixed with nectar and ingested. Moreover, the anther cone of *'S. nigrum'* collected as a ruderal weed in Japan was found to show strong ultraviolet absorbency. Utech and Kawano (1975) considered that these cones therefore present a central ‘visual target to a visiting bee for its vibratory activities.

Symon (1976), reviewing the role of pollen-collecting insects in the genus *Solanum,* pointed out that the morphological constancy of the flowers with purple-blue stellate corollas and prominent yellow anther cones contrasts with the morphological divergency of all other parts of the plants. He considered this simple floral structure to be closely related to a narrow range of pollinating insects and indicative of a specialized mechanism. The flowers of a number of South American species belonging to the section *Solanum* are consistently purple, while those of others can range from white to pale purple on the same plant..

Some species within the section *Solanum* are therefore morphologically and physiologically adapted to insect pollination. Bees and bumble bees have been observed on flowers of various species both in open glasshouses and on experimental field plots in Britain (Edmonds, unpublished) and elsewhere, and it is likely that these and other insects effect cross-pollination throughout the geographical ranges of these taxa. Little is known of the balance between self- and cross-pollination in these species, or indeed if certain species are exclusively self- or cross-pollinated. However; the occurrence of cross-pollination is another factor responsible for the wide morphogenetical variation encountered in these species.

7.2 Hybridization

Most taxa belonging to the section *Solanum* can be successfully hybridized artificially, at least initially, though genetic breakdown in the F_1 or F_2 generation usually follows interspecific hybridization. Crosses between infraspecific variants are usually highly successful. Edmonds (1977) found that for both *S. nigrum* and *S. villosum*, crosses within and also between the two subspecies recognized in each taxon resulted in morphologically intermediate, extremely vigorous and fertile F_1 progeny (Edmonds 1977, 1979a). Segregation of various characters subsequently ensued in the F_2 generations which usually remained highly fertile. Similar successes were recorded for various accessions, now known to be conspecific with each of the species *S. chenopodioides*, *S. physalifolium* var. *nitidibaccatum* and *S. sarrachoides* (Edmonds

1977, 1986). Those involving different variants of the two diploids *S. americanum* and *S. douglasii* are not always so successful. Infraspecific variants of *S. americanum* exhibit variable crossing behaviour; Baylis (1958) reported fully fertile F_2 progeny from crossing New Zealand and Australian plants of this species while Edmonds (1977) recorded a significantly reduced fertility in the F_1 generation of progeny derived from hybridizing the two varieties recognized in South America, and Schilling (1981) found that distinctive crossing behaviour accompanied the four morphological groups of this species distinguishable in North America. Similarly, some hybridizations involving accessions of *S. douglasii* from different geographical areas were unsuccessful (Edmonds 1977), while Schilling and Heiser (1979) found that infraspecific hybrids of this species exhibited a wide range of pollen fertilities and sometimes yielded only abortive, inviable seeds. Schilling (1981) further noted that the colonization of many diverse habitats within its natural range seems to have led to the establishment of a number of genetically distinct populations of *S. douglasii.*

Interspecific hybridizations are considerably more successful when species of the same floral sizes are involved. Crosses using the smaller-flowered species paternally and the large-flowered species maternally were generally unsuccessful, presumably due to the inability of the pollen tubes from the small flowers to traverse the long styles of the female parent. Reciprocally, when the larger-flowered species were used as the paternal parent, such a barrier would not exist, and hybrid seed was often obtained (Edmonds 1977). Nevertheless, morphological divergence is generally accompanied by genetical isolation in these *Solanum* species with the crosses failing pre- or post-zygotically. Although hybridization attempts often appeared successful, the resultant 'hybrid' berries were often found to be empty or to contain inviable seeds, while any resultant hybrid seed often gave rise to sterile F_1 plants or to F_2 generation plants exhibiting genetic breakdown (Edmonds 1977, 1979a). The possible causes of the genetic breakdown encountered are reviewed by Edmonds (1977) and range from genome disharmony to genic or chromosomal sterility

The genetical isolation of the diploid species belonging to the section *Solanum* is apparently maintained by a variety of different mechanisms, with the number of mechanisms observed reflecting the relative ease with which they are distinguishable morphologically Some of the smaller to medium-flowered diploids, including *S. americanum* and *S. douglasii*, which are often difficult to identify in the herbarium, are generally considered to be 'species in the making' which have not yet developed complete isolatory barriers to hybridization (Stebbins and Paddock 1949). Contrasting with the diploids, the tetraploid and hexaploid species of this section seem to be more genetically isolated from one another, with genetic breakdown occurring at various stages from pollination to the maturation of the F_2 progeny (Edmonds 1977). However, the occurrence of polyploidy in the section is probably the most efficient barrier to natural hybridization between these species. Successful crosses are more difficult between taxa of differing ploidy levels than they are between taxa of the same chromosome number, with interploidy crosses leading to the development of morphologic intermediate but sterile progeny. In contrast with some reports (Rae *et al.* 1971; Tandon and Rao 1974), Edmonds (1977) found that such interploidy crosses were not dependent on the use of the higher ploidy level as the maternal parent. Nevertheless, species of differing chromosome levels can be induced to cross, and the chromosome number of the resultant progeny can often be doubled experimentally, to restore the fertility of such amphiploid plants (Edmonds 1979a).

Many authors have attempted to hybridize various species belonging to the section *Solanum.* Among the most comprehensively reported are those of Baylis (1958) who studied the crossability behaviour of the taxa found in New Zealand; Henderson, (1974) who hybridized most of these *Solanum* species that occur in Australia; Edmonds (1977, 1979a, 1986) who attempted to hybridize accessions belonging to 25 different species from Europe, North, Central and South America and which represented all four polyploid levels found in the section; Stebbins and Paddock (1949), Heiser *et al.* (1965) and Schilling and Heiser (1979) who studied the crossing relationships among the species found in North America; and many Indian workers who looked at the genome relationships of the small species groups found in Asia. Natural infra- and interspecific hybridization, especially among the smaller-flowered diploids, has been reported by a number of workers (Stebbins and Paddock 1949; D'Arcy l974; Henderson 1974). Natural hybrids also have been reported within the higher ploidy levels (Venkateswarlu and Rao 1972) as well as between diploid and hexaploid taxa (Henderson 1974; Leslie 1978; Edmonds 1981). In view of the specialized floral adaptations to insect pollination now observed in some species belonging to the section *Solanum*, natural hybridization is probably much more widespread than previously supposed, and would explain the complex morphological and genetical variation associated with many of these species.

7.3 Breeding methods

No cultivars have yet been developed through conventional plant breeding techniques, but local variants or landraces may have been selected in some of the regions in which these plants are utilized as food and/or medicinal plants. Such selection of plants exhibiting desirable culinary or medicinal characteristics is probably the method by which these *Solanum* species will be developed as a crop plant.

Superior-yielding variants could be raised through conventional breeding methods. Plants selected as the maternal parents should be raised in insect-proof glasshouses, and the young buds emasculated l-3 days before pollination to allow full development and reflexion of the petals. The stigmas remain receptive for 3.5 days after the opening of the flower buds, and are thus unaffected by such early emasculation. Bagging of artificially pollinated flowers is thought to reduce fruit set by inducing slightly unfavourable temperature and humidity conditions; such a reduction of berry set was recorded by Edmonds (1977) when Kristal Glassine bags were placed over lateral branches bearing unopened buds in self-pollinated parental controls. Artificial pollination is effected by tapping pollen from the dehiscing anther cone of the appropriate paternal parent onto a thumb nail, and wiping the latter across the stigma to be pollinated. Each flower should be labelled with a small jewellers' tag showing the appropriate cross details before pollination. Sterilization of the thumb nail with 70% alcohol between each pollination is necessary to prevent cross-contamination. Maturation of the berries occurs within 6-8 weeks following pollination. The ripe berries should be harvested together with the identificatory tags attached to the subtending pedicels, and stored in Kristal Glassine bags at about 4°C until required for seed extraction.

Such artificial hybridization programmes should probably be confined to infraspecific variants, especially those associated with the species *S. americanum, S. nigrum, S. villosum* and *S. scabrum.* It is possible that hybridization work using these species might result in higher vegetative-yielding plants of all four species, and of higher berry-yielding variants of *S. scabrum.* There is also the possibility that natural races of these species selected for particularly useful attributes could be regenerated *in vitro* on a large scale, following the successful regeneration of plantlets from *'S. nigrum'* by Wang and Xia (1983). Any such hybridization or regeneration work would, however, need to be conducted on a local scale, with the characters of the plants selected- for crossing or regeneration reflecting the particular culinary, medicinal or ethnobotanical requirements of the appropriate users and local communities.

8 Ecology and agronomy

8.1 Natural distribution

The species related to the black nightshade are widely distributed in various habitats throughout the world, from tropical to temperate regions and from sea level to. altitudes exceeding 3500 m. Their wide tolerance of habitat types, their ability to flower while still young and their prolific seed production all contribute to the success of these species as widespread weeds (Henderson 1974). They are generally found in disturbed habitats, such as roadsides, often on arable land especially the edges of cultivated fields and plantations, in hedgerows, on railway cuttings, quaysides and rubbish tips, in areas around buildings and houses, under trees, on forest and grassland margins, as garden weeds, on shingle beaches, riverbanks and in gullies.

The species mainly colonize moist environments, only occurring in areas of low rainfall when the land is subject to irrigation. Indeed the intensification of agriculture, particularly when associated with the extension of irrigation systems has been largely responsible for the rapid spread of species such as *S. nigrum* and *S. villosum* as weeds of cultivated crops in countries such as Israel (Karschon and Horowitz 1985). The taxon now known as *S. physalifolium* var. *nitidibaccatum,* however, is tolerant of dry soils and high summer temperatures in New Zealand (Healy 1974).

The plants grow well in fertile soils, especially those high in nitrogen or phosphorus (Helm *et al.* 1977). The Saxon name "Mixplenton" — meaning the plant of mixen or dung heap, used for *S. nigrum*— is indicative of the partiality of this species to nitrogen-rich soils (Salisbury 1961).

Most species belonging to the section *Solanum* are frost susceptible, dying with the onset of the first frosts in temperate regions. The major exception to this is the glandular-haired South American species *S. sarrachoides* which is frost resistant and though potentially annual, will perennate (Edmonds 1986). All other species grown in Britain generally flower and fruit profusely throughout the summer and autumn in the field, until they are killed by the first frosts. In contrast, in some species, plants reared in the glasshouse exhibit one major flowering period and die following fruit maturation, while others can be induced to perennate (Edmonds, unpublished).

8.2 Natural seed dispersal

In most species belonging to the section *Solanum* the berries fall from the plants when mature; occasionally they remain on the plants. Often the seeds germinate *in situ* when the prevailing environment conditions are optimal. The ripe berries are extremely succulent, often brightly coloured and/or aromatic, and are attractive to a variety of birds and animals. They are therefore effectively dispersed by birds all over the world, as well as by various animals such as rodents, lizards, rabbits, cattle and man. There is evidence that the seeds pass through the digestive tracts of both birds and animals undamaged (Burgert *et al.* 1973; Weller and Phipps 1978/79). The seeds can also be dispersed by water (Burgert *et al.* 1973) and by contaminating harvested seed crops such as sugar beet (Weller and Phipps 1978/79). Cultivation of these species will therefore inevitably result in their dispersal and spread outside the cultivation areas. Indeed, Simms (1997) warned of such a hazard, noting that the ease of cultivation of the garden huckleberry meant that once introduced, volunteer plants were likely to spring up everywhere the following season,

8.3 Cultivation

These species are only semicultivated in a few countries in Africa and Indonesia, and are largely utilized as a vegetable and fruit source through harvesting from plants growing spontaneously as weeds in cultivated fields, or in weedy plant communities, under trees, along fences and roads, in shaded areas, near buildings and on waste land. They therefore constitute a volunteer crop. Some communities semicultivate the vegetable in home gardens or on fertile land portions near homesteads. There are a few reports of the cultivation of the garden huckleberry for its fruits in North America; Fisher (1977), for example, considered that this species (i.e. *S. scabrum)* was an excellent fruit crop for growing on small areas of land or in 12-inch (about 30-cm) pots filled with “good rich soil”.

8.4 Propagation and planting

Propagation is mainly by seed; seedling development is epigeal. Shoot cuttings may be used as propagules though plants propagated in this way branch, spread and yield less than those propagated by seed (Mwafusi 1992). Plantlets have also been regenerated from *'S. nigrum'* mesophyll chloroplasts (Wang and Xia 1983).

Seed extraction

In the tropics, seeds are usually extracted from the berries by squeezing out the seeds and pulp, thoroughly washing the seeds with water and drying the seeds in the shade for a day. Exposure to full sun must be avoided, as this can cause overheating, killing the embryos, especially in humid climates. Seeds may be also extracted by a fermentation process, when they are extracted with the pulp and left to ferment for 3 days. They are then washed in water and dried in the shade for 24 hours. For immediate use, seeds can be extracted using concentrated hydrochloric acid. Edmonds (unpublished) extracted seeds by macerating the harvested berries in water in a liquidizing blender; the seeds were then washed with several rinses of water, and left to dry on absorbent paper at room temperature. The harvested seeds were subsequently stored in Kristal Glassine bags, either at room temperature or at 4°C in plastic boxes. In the humid-tropics, dry silica gel must be placed either in or between these bags during seed storage.

Seed viability

These *Solanum* seeds can remain viable for several years, depending on the storage conditions and the seed moisture content. They are known to retain their viability for long periods of time in the soil, with their subsequent germination causing problems in succeeding seasons of crop growth for many years. There are records of buried seed of *S. nigrum* remaining dormant for at least 39 years in Britain, and then resulting in germination percentages of 83 when moved into a suitable environment (Salisbury 1961). A viability study of seed stored at room temperature between one and nine years gave germination percentages of 99, 100, 96, 98, 91, 73, 27, 2 and 0 (Weller and Phipps 1978/79). This clearly demonstrates that the seeds are orthodox (Hong *et al.* 1996). Formanowiczowa and Kozlawski (1980) reported 80% germination in seeds which had been stored for 5 years in paper bags in unheated conditions. Edmonds (unpublished) has recorded good viability from seeds stored for over 20 years, although pretreatment with 2000 ppm gibberellic acid was always used to overcome any dormancy requirement. A short review of seed survival in *S. nigrum* is given in Roberts and Lockett (1978).

Optimal conditions for germination

Temperature

The optimum germination temperature for these species lies between 15 and 30°C, though temperatures fluctuating between these values are apparently required to break their dormancy. Constant temperatures have generally been found to inhibit or even prevent germination (Roberts and Lockett 1978; Rogers and Ogg 1981). The requirement of a fluctuating temperature above 15°C before germination occurs would explain why the black nightshade appears later in spring and early summer than many other weeds, at least in Britain. (Weller and Phipps 1978/79). Similar germination temperature requirements are reported in North America, where the plants can germinate between early spring and midsummer, because of this wide tolerance in germination temperature (Burgert *et al.* 1973).

Wakhloo (1964) reported that the optimal conditions for the germination of *'S. nigrum'* in his Indian trials were an alternating temperature of 15-20°C for 16 hours and. 25°C for 8 hours. Moist storage of the seeds at cool temperatures and winter storage outdoors; at least in temperate climates, has also been found to enhance the germination of these species (Rogers and Ogg 1981).

In addition to these temperature requirements, some of these species exhibit a dormancy requirement in certain geographical regions. In Britain, for example, a change in the physiological state of the seeds of *S. nigrum* occurs to prevent or greatly restrict seedling emergence during late summer and early autumn, regardless of the prevailing temperatures (Roberts and Lockett 1978). In contrast, Israeli populations of this species apparently display. no such dormancy requirement after harvest; the seeds germinate once temperatures reach 17-20°C (Karschon and Horowitz 1985).

Light

Reports on the effects of light on the germination of these seeds vary from low light intensities favouring germination to intermittent light enhancing germination at less favourable temperatures (Rogers and Ogg 1981). Wakhloo (1964) found that complete darkness or low diffuse light for a period of 8 hours contributed to the optimal germination conditions of *'S. nigrum'* in India. Singh (1970) reported that light modifies the ‘effect of temperature on germination with Indian plants conspecific with *S. nigrum* and *S. villosum* failing to germinate under continuous light when subjected to alternating temperatures of 15 and 30°C. Under diffuse lighting conditions, however, the same alternating temperature values resulted in good germination of both variants.

Moisture

Wakhloo (1964) reported a seed moisture content of 35-40% to be a necessary contributary factor for optimal germination in India. Such conditions prevail in the winter season in the tropics, from November to February in areas of irrigation, and from spring to autumn in temperate regions. Seeds sown in pots in glasshouses must be kept moist.

Planting for cultivation

In West Africa, seed is sown in boxes or seedbeds and seedlings transplanted 3 to 4 weeks after emergence into well-prepared beds. In Britain, seeds have been sown in seed-pans in temperate glasshouses, pricked out into larger pots at regular intervals until large enough to be transplanted into experimental field plots, after any ‘danger of frost occurring (Edmonds, unpublished). Under glasshouse conditions, Edmonds (unpublished) found that seeds of various species germinated between3 and 30 days after sowing. Wakhloo (1964), however, recorded germination in *S. nigrum* to occur 10-15 days after sowing under favourable conditions in the glasshouse in India.

Seed can also be broadcast or directly drilled into well prepared seed beds. Although few studies have been conducted on the optimal depth of planting, in North America the best germination occurred from seeds planted 0.25 cm deep. Seeds sown at deeper levels did not germinate so well, though seedlings did emerge from seeds planted up to 5 cm deep (Burgert *et al.* 1973; Roger and Ogg 1981).

A spacing of at least 15 to 50 cm should be left between plants to encourage leaf production (FAO 1988). Between-row spacing should be 30-60 cm. For seed production, a spacing of 75-120 cm between plants should be used (Epenhuijsen 1974). Fisher (1977) reported a spacing of 3 feet (about 1 m) between both plants and rows to provide optimal growth conditions for plants conspecific with *S. scabrum* in North America. Moreover, those plants growing in full sun produced twice as many berries as those receiving afternoon shade. Edmonds (unpublished) used spacings of 2 m between plants with the rows also being 2 m apart.

8.5 Nutrient requirements

Plants respond positively to increased soil fertility. Seedbed preparation requires good manuring; where manure is unavailable, a generous application of a complete fertilizer before planting or sowing may be necessary. Top-dressing of the plants with a nitrogenous fertilizer may be required up to the flowering stage. Good soil fertility encourages vigorous growth and increased leaf production (FAO 1988).

8.6 Weeding

Seedbeds should be kept weed-free, preferably by hand-hoeing. Plants can branch profusely which can make weeding difficult, though by this stage, many weeds are themselves shaded out by the spreading *Solanum* plants.

8.7 Optimal growth requirements

Species related to the black nightshade are generally intolerant to water stress, and thus thrive in irrigated areas (Burgert *et al.* 1973); they are generally unable to survive drought conditions. They thrive during the rainy seasons in the tropics, though an annual rainfall of 500-1200 mm is adequate for their growth. Frequent watering is required during dry periods in temperate areas, while glasshouse-grown plants generally require watering twice daily.

Optimal temperatures for’ the growth of these plants lie between 20 and 30°C, but most species will grow within the range of 15-35°C.

The plants are best adapted to soils of high ertility, especially those high in nitrogen and phosphorus (Helm *et al.* 1977). Sandy loam to friable clay soils with a pH range of 6.0-6.5 are particularly suitable for these plants (Helm *et al.* 1977; Fawusi 1983). In Britain, however, Simms (1997) reported that providing the soil is well drained, the actual soil type appeared almost irrelevant to good growth of the garden huckleberry.

Most authors report a photoperiod requirement of approximately 16 hours for optimal growth; natural. daylight is usually supplemented by artificial light to achieve this total in glasshouse-grown plants. Shade causes a decline in the total plant weight and changes the distribution of the biomass. Fortuin and Omta (1980) found that in West Java, fruit production was strongly affected by shade, but that the production of edible leaves was unaffected by light shade and only moderately affected. by heavy shade in *'S. nigrum'.* Moreover, the leaves harvested from the shade-grown plants were more palatable, being less bitter’ than those harvested from plants grown in full sun. Fawusi *et-al*. (1983) later found that plants of *‘S. nigrum’* would tolerate up to 60% shading, but that full sun was beneficial to growth. Earlier shade experiments by Singh (1971), however, demonstrated that full sun was necessary for floral initiation, but that partial shade resulted in a better growth performance in Indian plants conspecific with *S. nigrum* and *S. villosum.* Moreover, she obtained significantly higher growth and biomass values when these plants were grown in open conditions during the Indian winter and in shade during the summer. Such observations were undoubtedly associated with accompanying temperature and soil moisture values, but were considered to explain the restriction of these plants to shady moist localities during summer months, and their occurrence in more open habitats during the winter in India.

8.8 Pests and diseases

Black aphids *(Aphis fabae* Scop.) may cause a considerable reduction in harvest. Large numbers of the aphids can infest the underside of the leaves causing leaf curl, while the young apices of similarly infested plants can fail to develop (Epenhuijsen 1974). In North America, aphid infections of plants of the garden huckleberry cultivated for their berries are reportedly easily controlled with a dusting of rotenone (Fisher 1977). In Britain, blackfly, one of the few pests found to "bother" plants of the garden huckleberry, is apparently easily controlled with pirimicarb or by natural predators such as ladybirds (Simms *1997).* Flea beetles *(Epilachna hirta)* can also attack these plants, causing appreciable damage (Epenhuijsen 1974). Root knot nematodes have been found to affect experimental plants of *'S. nigrum'* grown in West Java (Fortuin and Omta 1980). Heavy damage to ripe fruits can be caused by the variegated grasshopper *(Zonocerus variegatus* (L.)), but regular sprays with appropriate insecticides may control the damage from such pests (Epenhuijsen 1974).

During the rainy season in West Africa a viral disease — yellow vein clearing — may attack these plants The virus is transmitted by white flies *(Bemisia tabaci* (Genn.)), and affected leaves become yellowish green with a dark green colouration developing near the veins. Regular spraying will prevent these virus vectors from visiting the plant (Epenhuijsen 1974).

Fungal diseases do not seem to be a serious problem in these species. However, plants can become infected with *Cladospurium oxysporum* Berk. & M.A. Curtis. Affected leaves then show a light-green or yellowish coloration on the upper side, while a greenish-grey 'mould' develops on the undersides. The leaves subsequently dry out and die. This pathogen can be controlled by regular spraying with an appropriate fungicide (Epenhuijsen 1974). A bacterial wilt was found to attack approximately 1% of the experimental plants grown by Fortuin and Omta (1980) in West Java.

8.9 Harvesting

In Africa, the harvesting period occurs during the rainy season. Young shoots are harvested when the plants reach a height of approximately 15 cm. This is usually 4-6 weeks after seedling emergence and before flowering begins. At the first harvest, plants are topped to a height of not less than 5 cm after which regrowth of young shoots occurs. Regular harvesting of the young shoots and debudding encourages the production of lateral growth (side shoots) and thus extends the harvesting period. A total of five to eight harvests, at weekly intervals over a 6-8 week growing period, is usually possible (FAO 1988). In Britain, the berries of all species ripen throughout the summer, with most plants bearing green unripe and coloured ripe fruits simultaneously (Simms 1997).

8.10 Yields

Cumulative edible leaf yields of 12-20 t/ha per season are possible. Mnzava (pers. comm.) reported that a total yield of 5 t/ha per season was obtained after six sequential harvests when plants were transplanted at a spacing of 60 x 10 cm. Depending upon the agro-ecological zone in which the plants are grown, more than one crop per year could be obtained, with two crops per year possible in areas of bimodal rainfall, for example. Fortuin and Omta (1980) recorded a harvest of 28 g of leaves/plant, yielding 0.8 t/ha when growing *'S. nigrum'* for a period of 2 months in West Java. In addition, these authors reported fruit production figures of 1070 g/plant (30.5 t/ha) 113 days after planting this species, which was comparable to that obtained from high-yield tomato varieties tested at the same experimental station. They further calculated that a leaf yield of at least 15-20 t/ha could be expected if the plants were spaced at 30 x 30 cm intervals and the whole plant uprooted after 1 months' growth. The protein content of these leaves was calculated to provide 15-59 g/kg of edible portion (Fortuin and Omta 1980). FAO (1988) reported a yield of 5.6 kg leaves from a plot of 4 m^2 containing 40 plants of *S. americanum,* while Fisher (1977) reported an average yield of 1.5 quarts of "plump berries" from each plant of the garden huckleberry cultivated in West Virginia, North America for use in pies, jams and "cobblers".

8.11 Seed production

Likely values of seed production have not yet been established for these species as potential crop plants, although there are many reports of their potential seed production with regard to their economic importance as weeds. Among these, Salisbury (1961) reported that although the average production of each plant of *S. nigrum* is around 240 berries in Britain, large individuals have been found to produce over 3600. Since each of these contains around 40 seeds, such plants could produce nearly 130,000 seeds apiece. With over 90% of these germinating the following season, the potential nuisance of this species as a weed is clearly apparent. Similar data are recorded by other-authors, e.g. Holm *et al.* (1977) who reported a seed production of 178 000 per plant. Edmonds recorded berry size and seed number/berry data for most species belonging to the section *Solanum* collected over many years from both glasshouse and field-grown accessions These data include the range and the mean values for each accession; the mean seed numbers recorded for many of the species are given in Edmonds (1977).

In Zambia, Mnzava (pers. comm.) observed that a seed yield of 132 kg/ha could be obtained after plant defoliation. He also recorded 62 seeds per fruit from which he calculated that ripe fruit. weighing 500 g may produce 44 g clean dry seed containing 2486 seeds (Mnzava, unpublished).

8.12 Storage

The quality of the leaves deteriorates within 4 days of harvest if stored at ambient temperatures. Occasionally harvested leaves and young shoots are sun-dried and stored for use during periods of scarcity (dry seasons). In Africa, the leaves are dried for winter use (Watt and Breyer-Brandwijk 1962). Seeds harvested from mature berries and dried using the methods described above should be stored under long-term storage conditions. IPGRI recommends the following conditions for long-term seed conservation: -18°C or less in airtight containers at a seed moisture content of 5 ± 1% (Hong *et al. 1996).*

There are reports that the berries of *S. americanum* can be dried (FAO 1988), and that the berries of plants conspecific with *S. scabrum* freeze well (Fisher 1977). Harvested berries should be stored at temperatures of about 4°C until required, for either seed or pigment extraction.

9 Production areas

Vegetable black nightshades are still regarded as wild, weedy, ‘volunteer’ crop or semidomesticated plants. Only two species are reportedly cultivated or semicultivated ‘locally’. The ubiquitous diploid *S. americanum* appears to be the most widely utilized species which is apparently 'cultivated' in Bolivia, Ethiopia, Mauritius (Mapou Island), Nigeria, Papua New Guinea, Peru and the Seychelles (Bird Island). Reports of the ‘cultivation’ of the hexaploid *S. scabrum* or garden huckleberry are confined to Ghana, Togo and Zambia. Various species are reportedly semicultivated in home gardens in eastern, western and southern Africa, Hawaii, Guatemala, Trinidad, Suriname, India, Indonesia, the Philippines and China. The plants are widely sold in some rural and urban markets, especially in the African countries of Cameroon, Ghana, Kenya, Madagascar, Nigeria and South Africa, as well as in Guatemala, New Guinea and some Mediterranean regions. However, most of the plants sold in these markets are unlikely to have been specifically cultivated. These species have not yet entered the international market as a minor vegetable plant, and are unlikely to do so at least in areas in which arable crops are economically important, especially in temperate regions.

10 Potential value as crop plants

Despite their reputed deleterious qualities, it is clear from the various documented uses of the vegetable 'black nightshades' that the species do exhibit many potentially valuable characteristics which deserve conservation and utilization. Their 'more important features include:

- both the leaves and fruits are edible;
- the vegetative parts are highly nutritious and contain proteins, fibre, minerals and vitamins;
- the berries contain calcium, iron, carotene and vitamins B and C, while the seeds also contain vitamin C and carotene;
- the plants can be grown on a small piece of land or simply in pots to provide a good harvest of berries for use in pies, jams and preserves or as a raw fruit;
- the species can be used as fodder for cattle and goats and browse for wild animals;
- the berries can be used as a dye and a food colourant;
- the plants can provide a source of income for rural farmers;
- the plants can be harvested over a period of time; which could be beneficial in soil conservation when used in intercropping systems; studies in Java (Fortuin and Omita 1980) have shown that 35-60% shade does not affect the edible yield of the species;
- the species exhibit various medicinal properties which are used throughout the world to treat a variety of illnesses; many of these could have great potential in medical research, especially those suggesting that certain species might have anticarcinogenic properties;
- the species are sources of several traits which might be useful in improving various economically important crops; these include
  - atrazine resistance
  - resistance to tobacco mosaic virus
  - resistance to potato late blight
  - resistance to *Phomopsis* fruit rot;
- the species show potential molluscicidal activity;
- the species serve as alternative hosts for a variety of pests, bacterial and fungal pathogens of a number of commercial crops; they might therefore be of use as potential control agents.

11 Limitations of their use as crop plants

The species have not yet been commercialized or promoted as crop plants. This is largely due to the attitude of farmers and research workers who generally discourage the use. of such a notorious weed as a crop plant. Indeed, the success of species belonging to the section *Solanum* as weeds in areas in which vegetable, cereal and root crops are economically important is probably the major reason responsible for their lack of promotion as minor crop plants. The problems caused by these species as weeds, range from economic losses due to competition with the crop being grown, to contamination of the actual crop through berry juice or seeds, to costs incurred for herbicidal and insecticidal control of the plants. The actual type and number of crops affected by these weed species is now vast (see Deleterious properties, Section 5.2). In Nebraska alone, the damage done to field beans contaminated with juice from ruptured berries of the 'black nightshade' has been estimated at US$1.5 million a year which represents approximately 12% of the total income from the production of this crop in this one American state (Burgert *et al*. 1973). Similar reports for other crops from various countries therefore suggest that it is unlikely that these species could be promoted as crop plants in the United States and Canada, New Zealand, Britain or Israel, for. example.

Moreover, the young people in those countries in which these species are consumed regard the black nightshades as low-status vegetables, which are usually associated with poor people. In addition, the plants are generally low-yielding and have bitter-tasting substances which enhance their unpopularity, especially amongst the young. Their leaves are known to accumulate nitrates and contain oxalic acid, phenolic compounds and alkaloids. Controversial accounts on the poisonous properties reported for most of the species have discouraged their adoption as a potential minor crop. Most national research systems have therefore failed to allocate either personnel or resources for research on the taxa associated with the section *Solanum*, which are generally considered to be low-priority species.

12 Current research requirements

No relevant research is currently being conducted on the black nightshades used as vegetable plants, though various species groups have been thoroughly revised taxonomically for certain geographical regions (see Section 2). It is therefore suggested -that the following research activities need pursuing in order to exploit the potential inherent in these species as minor crop plants:

- Thorough taxonomic revisions by research workers familiar with the taxonomy of the section *Solanum* in areas in which the species are important as food and medicinal plants. This is especially necessary in Africa, South East Asia and Indonesia. Such taxonomic treatments will provide further information on the centres of diversity and distribution of the relevant species.
- Collection of information on the precise ecogeographic distribution of the various species, followed by efforts to collect and conserve the germplasm of accessions collected from diverse habitats and countries.
- Characterization and evaluation of the diversity exhibited by each of the nightshade taxa for their agronomic and nutritive value.
- Accurate cytological assessment and identification of both existing conserved accessions and all new material collected for both conservation and research by recognized international experts on the species, together with an assessment of any inherent beneficial traits.
- Accurate and illustrated botanical descriptions of the local 'cultivars' of the various species used as vegetables for distribution to rural farmers and interested growers in each of the relevant ecogeographical regions.
- Agronomic studies to determine the optimal growth and harvesting conditions and to disseminate the resultant information together with that on the beneficial properties of these species to interested rural farmers.
- Genetic enhancement of the species for increased yield and nutritive quality. This could be done through simple selection, plant breeding (perhaps including hybridization) and the adoption of optimal cultivation practices.
- Seed production programmes to provide bulk samples of those taxa required for specific ethnobotanical uses.
- Scientific evaluation of any indigenous knowledge existing on the use of these species in the various countries in which they are currently utilized.
- Socioeconomic studies on the production and use of the various species.
- Clarification of the potential toxicity reported for many of the species.
- Extensive screening for the chemicals responsible for the medicinal and toxic effects associated with all the species, so that any of potentially useful commercial or medical value can be identified and exploited.
- Establishment of a ‘Black Nightshade Database’ into which all the above information could be incorporated, and subsequently disseminated to relevant interested growers and research workers. Such a database could, perhaps, be established and coordinated by IPGRI.

- Initiation of localized crop improvement programmes using the data accumulated from the above studies.

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Mrs G.N. Thitai National Council of Science and Technology POB 30623 Nairobi Tel: 254-2-748281/749747	Ethnobotany utilization, diversity
Mr E.N. Seme Mr J.K. Kemei National Genebank of Kenya POB 781 Kikuyu Tel: +254154-32880/l/2 Fax: +254-154-32587	Collecting, characterization, evaluation, conservation
Mrs D. Mwamba Mr Obiero Mrs M. Onyango Kenya Agricultural Research Institute POB 57811 Nairobi	Agronomy

Madagascar

Mr Manitra Rakatoarisoa Dept. of Agronomic Research POB 1444 Antananarivo	Surveys, utilization

Malawi

Dr M.B. Kwapata Dept. of Crop Science University of Malawi POB 219 Lilongwe	Germplasm collecting, improvement and production
Mr Moses Maliro University of Malawi Bunda College of Agriculture POB 219 Lilongwe	Agronomy, conservation, utilization

Mauritius

Dr C. Ricaud Mauritius Sugar Industry Research Institute The Mauritius Herbarium Reduit Tel: +230-4541061 Fax: +230-4541971	Ethnobotany, taxonomy
Prof I. Fagoonee Dept. of Chemistry University of Mauritius Reduit Tel: +230-4541041 Fax: +230-4549642	Botany, taxonomy, phytogeography

Namibia

Ms Gillian Maggs National Botanic Research Institute Private Bag 13184 Windhoek Tel: +264-61-2022196 Fax: +264-61-233459	Conservation, utilization, agronomy

The Netherlands

Dr G.W.D. Barendse (Director) G.M. van der Weerden (Curator) Botanical Garden University of Nijmegen Toernooiveld 6525 ED Nijmegen Tel: +31-243652751/3652883 Fax: +31-24.3553450 E-mail: gerardb@sci.kun.nl gerardw@sci.kun.nl	Solanaceae germplasm collection - largest *ex situ* collection of non-tuberous Solanaceae species in the world, including a large number of accessions belonging to *Solanum* section *Solanum*

Nigeria

Dr C.O. Ajakaye Dept. of Biological Sciences Ahmadu Bello University Zaria, Kaduna State Tel: +234-62-50581 x 108	Germplasm storage
Dr Y.Y. Karatela Dept. of Biological Sciences Bayero University PMB 3011 Kano Tel: +234-61660036	Surveys, ethnobotany
Dr B.M. B. Ladu Dept. of Biological Sciences Federal University of Technology PMB 2076 Yola, Adamawa State Tel: +234-34-200090	Medicinal properties
Mr O.A. Bakare Ecology Division Forestry Research Institute of Nigeria PMB 5054 Ibadan Tel: +234-22-410771 Fax: +234-22-417715	Taxonomy, herbarium collections, ethnobotany

Prof. A.E. Akingbohungbe Dept. of Natural History Obafemi Awolowo University Ile-ife, Oyo State Tel: +234-36-230290/l 1-9x2651	Inventories
Dr J.O. Okafor FAME Agricultural Centre POB 3856 Enugu Tel: +234-42-335060	Medicinal properties, utilization
Prof. A. Sofowora Dept. of Pharmacognosy Ile-Ife, Oyo State Tel: +234-36-230290 Fax: +234-36-36231733	Ethnobotanical surveys
Prof. A.I. Ahianzu Dept. of Food Science and Technology Rivers State University of Science and Technology PMB 5080 Port Harcourt, Rivers State Tel: +234-84-300368	Production techniques, nutritional evaluation
Prof. A. Egunyoni Dept. of Botany University of Ibadan Ibadan, Oyo State Tel:+234-22-400550x 1403	Ethnobotanical surveys
Dr O.A. Denton National Horticultural Research Institute PMB 5432 Ibadan, Oyo State Tel: +234-22-412490/412296 Fax: +23422-2413121 Email: c/o D.Ladipo@cgnet.com	Utilization

Rwanda

Dept. of Vegetables National University of Rwanda Tel: +250-30716	Extracts against pests and diseases

Senegal

Dr Meissa Diouf Centre pour le Developpement de 1’Horticulture Institut Senegalaise de Recherches Agricoles BP 219 Dakar Tel: +221-352506 Fax: +221-322127/350610	Utilization
Dr Abdoulay Seck TROPICASEN BP 999 Dakar Tel: +221-320505 Fax: +221-320536	Surveys, utilization

South Africa

Dr R.D. Heinsohn ACER (Africa) POB 276 Mtunzunil, 3867 Tel: +273-53-401799/402715 Fax: +273-53-402232	Indigenous plant cultivation
Mrs Erika van den Heever Vegetable and Ornamental Plant Institute Agriculture Research Council Private Bag X293 Pretoria 001 Tel: +27-l2-8419611 Fax: +27-12-8080844	Utilization, diversity
Dr D.B. Arkcoll Dept. of Crop Production Elsenburg Agricultural Development Institute Private Bag Elsenburg 7607 Tel: +27-2231-94620 Fax: +27-2231-94226	Identification of new crops

Mr T. Arnold
Dept. of Data Management
National Botanical Institute
Private Bag Xl01
Pretoria, 0001
Tel: +27-128043200
Fax: +27-12-8043211

Database of indigenous
South African plants

Prof. M.A.T. Poswal
Dept. of Agronomy
University of Fort Hare
Private Bag Xl314
Alice 5700
Tel: +27-404-22232
Fax: +27-404-31740

Sources of natural
or botanical pesticides

Sudan

Dr El Tair I. Mohamed
Sudan Natural Centre for Plant Genetic Resources
POB 126
Wad Medan

Cultivation utilization,
conservation

Tanzania

Mr R.E.A. Swai
Ministry of Agriculture
Tengeru Horticulture Research & Training Institute
POB 1253
Arusha
Tel: Deluti 94
Fax: +255-57-8254

Conservation, utilization,
agronomy, seed production

Network Vegetable Production Africa
PO Box 8182
Arusha

Dr. N.A. Mnzava
Consulting Horticulturist
POB 1371
Arusha

Agronomy, seed production,
nutritive value

Uganda

Mrs J. Ochola
Botanical Gardens c/o NARO
POB 295
Entebbe

Utilization

Ms E.K.Z. Kakudidi
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Makerere University
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Kampala
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Ethnobotany

Mrs. E. Rubaihayo
Dept. of Horticulture
Kawanda Agricultural Research Station
POB 7065
Kampala
Tel: +256-41-567648
Fax: +256-12-21070

Germplasm collecting and conservation, seed multiplication and distribution

United Kingdom

Dr J.M. Edmonds
Dept. of Biology
University of Leeds
Leeds, LS2 9JT
Tel: +44-113-2332814
Fax: +44-113-2332882

Taxonomy, ethnobotany herbarium collection data, species relationships

Zambia

Mr G.P. Mwila
National Plant Genetic Resources Centre
Mt. Makulu Research Station
P/B7
Chilanga
Tel: +260-l-278263

Inventory and collecting

Dr D.S. Mingochi
Dept. of Agriculture
National Irrigation Research Station
PB S-3
Mazabuka
Fax: +260-32-248028

Agronomy, utilization, conservation

Dr Godwin Mkamanga SADC Plant Genetic Resources Centre Private Bag CH6 153 02, Lusaka Tel: +260-l-230511 Fax: +260-l-241927/290440	Germplasm conservation

Zimbabwe

Dr J.E. Jackson Dept. of Research and Specialist Services Horticultural Research Institute Private Bag 3748 Marondera Tel: +263-7924122	Development of indigenous leafy vegetables
Mr Fabeon Chigumira Horticultural Research Centre P/B 3748 Marondera Tel: +263-7924122 Fax: +263-4-791223	Utilization
Mr Andrew Mushita Community Technology Development Association POB 7232 Harare Tel: +263-4-732360	Conservation and cultivation

Appendix II. Genebanks maintaining collections

Country/Station	Accessions (number)
France	
Station d'Amélioration des Plantes Maraîchères Centre de Recherches d'Avignon Institut National de la Recherche Agronomique Domaine Saint-Maurice - BP 94 F - 84143 Montfavet Cedex Tel: +33-90316000 Fax: +33-90316398	*S. nigrum* (1), *S. scabrum* (2)
Germany	
Genebank Institute for Plant Genetics and Crop Plant Research Corrensstr. 3 06466 Gatersleben Tel: +49-39482-5280 Fax: +49-39482-5155	*S. nigrum* (17), *S. americanum* (11)
Ghana	
Crop Research Institute Plant Genetic Resources Unit PO Box 7 Bunso	*S. scabrum* (7)
Kenya	
National Genebank of Kenya POB 781 Kikuyu Tel: +254-154-32880/l/2 Fax: +254-154-32587	*S. nigrum sens. lat.* (43)
India	
Krishna Chandra Mishra Research Institute of Wild Vegetable Crops PO Bandanwar Godda, Bihar 814 147	*S. nigrum* (1)

Mauritius	
Barkly Experiment Station Barkly Beau Bassin	*S. nigrum* (2)
The Netherlands	
Centre for Genetic Resources, the Netherlands (CGN) Droevendaalsesteg 1 PO Box 16 6700 AA Wageningen Tel: +31-8370-77045/77001 Fax: +31-8370-18094 E-mail: cgn@pro.agro.nl	*S. nigrum sens. lat.*(3), *S. nigrum* var. *americanum* (1)
Botanical Garden University of Nijmegen Toernooiveld 6525 ED Nijmegen Tel: +31-24-3652751/3652883 Fax: +31-24-3553450	*S. nigrum* (12), *S. scabrum* (4) *S. americanum* (7)

Source: Frison and Serwinski 1995.

Related IPGRI publications

Promoting the consecration and use of underutilized and neglected crops.

1. Physic nut. *Jatropha curcas* L.	1996
2. Yam bean. *Pachyrhizus* DC.	1996
3. Coriander. *Coriandrum sativum* L.	1996
4. Hulled wheats	1996
5. Niger. *Guizotia abyssinica* (L. f.) Cass.	1996
6. Pili nut. *Canarium ovatum* Engl.	1996
7. Safflower. *Carthamus tinctorius L.*	
8. Chayote. *Sechium edule* (Jacq.) Sw.	1996
9. Bambara groundnut. *Vigna subterranea* (L.) Verdc.	1997
10. Breadfruit. *Artocarpus altilis* (Parkinson) Fosberg	1997
11. Cat's whiskers. *Cleome gynandra* L.	1997
12. Tef. *Eragrostis tef* (Zucc.) Trotter	1997
13. Sago palm. *Metroxylon sagu* Rottb.	1997
14. Oregano	1997

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